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Devoted to the 80th anniversary of the birthday of academician A.Yu. Rozanov

Rhodopsin: Evolution and Comparative Physiology

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Abstract—A review of physicochemical properties, photochemistry, functions, and evolution of retinal-containing proteins (microbial and of metazoan rhodopsins, mostly visual rhodopsins) is provided. Comparative physiology of visual rhodopsins is considered in detail, mainly the molecular mechanisms of their spectral tuning.

Keywords: vision, photoreception, rhodopsins, rhodopsin of metazoans, microbial rhodopsin, spectral tuning, retinal photoisomerization, G-protein-coupled receptor, physiology of vision

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FAMILY OF RETINAL-CONTAINING PROTEINS: RHODOPSINS METAZOANS AND MICROBIAL RHODOPSINS

The term *rhodopsin* descends from the Greek ῥόδεος (pink) and ὄψις (vision, show). The rhodopsin as a photosensitive visual protein was discovered by F. Boll in 1876 and named *Sehestoff,* visual substance. Up to the end the 1950s and beginnings of the 1960s, rhodopsin was referred to as "visual purple" because of its color. At present, the term *rhodopsin* is extended onto the entire family of retinal-containing proteins and metazoan rhodopsins, including visual rhodopsins (G-protein-coupled receptors), and microbial rhodopsins (channel and pump proteins). All retinal-containing proteins are similar, first, in the structure of the apo-protein opsin, with its seven transmembrane alpha-helix "bars" and, second, in the cofactor (chromophore) retinal absorbing a photon quantum of light. In a molecule of retinal-containing proteins, the retinal is covalently bonded to lysine residue of opsin in the seventh alpha-helix bar. The most conservative domain of retinal-containing proteins is the chromophore center. The essential importance of the protein surroundings of retinal in the chromophore center is beyond doubt with reference to spectral tuning of these proteins and realization of their ultrafast photochemical reaction of isomerization (one of the rapidest photochemical reactions in nature) and realization of their photoenergetic or photoinformation physiological functions (Ostrovsky and Feldman, 2012; Wand et al., 2013; Smitienko et al., 2014; Luk et al., 2015). The protein environment of retinal is what determines the unique spectral and photochemical properties of retinal-containing proteins. In the case of the visual pigment rhodopsin, the quantum yield of photoisomerization of 11-*cis*-retinal is 0.67; this is the time of an elementary act of isomerization which is about 80–100 fs (Polli et al., 2010; Nadtochenko et al., 2012). The reaction is accomplished at 200 fs with the formation of a photoproduct, the so-called photorhodopsin (Schoenlein et al., 1991).

Note that parameters of photoisomerization reaction of the chromophore group in retinal-containing proteins are comparable to the theoretically estimated rate of isomerization of retinal in the gas phase (Martinez, 2010). This means that the rate and efficiency of photoisomerization of retinal in the tight protein environment of the chromophore center, the volume of which is only 660 A^3 (Li et al., 2004), are comparable to the rate of its isomerization in free volume. In other words, the chromophore center of retinal-containing proteins has an ideal structure and interaction of retinal with its nearest protein environment is highly efficient. Such a perfect chromophore center was already formed at the earliest stages of biosphere evolution.

Rhodopsins have been revealed in all three domains (kingdoms), i.e., archeans, eubacteria, and eukaryotes (Terakita, 2005). According to the primary structure, rhodopsins are divided into two types, the first is microbial rhodopsins and the second already appears in eukaryotic unicellular organisms (Spudich et al., 2000). Microbial rhodopsins comprise proteorhodopsin (bacterial version of rhodopsin observed in Dinoflagellata), sensory rhodopsins, channel rhodop-

sins of unicellular algae, halorhodopsin, and bacteriorhodopsin of halophilic archaeobacteria (Spudich et al., 2000; Sineshchekov et al., 2002; Terakita, 2005; Waschuk et al., 2005; Fuhrman et al., 2008; Consani et al., 2011; Grote and O'Malley, 2011). The functions of microbial rhodopsins are an evolutionarily ancient variant of photosynthesis (bacteriorhodopsin) and photokinesis (sensory rhodopsins), which are provided by light-induced transportation of a proton, cations, or anions (chloride). During the last decade, channel rhodopsins of unicellular green (Sineshchekov et al., 2002) and cryptophytic (Govorunova et al., 2015) (in near future) algae have attracted great attention. Channel rhodopsins became one of the main tools of a new, extensively developing field, optogenetics (for a review, see Deisseroth, 2015). The methods of optogenetics have provided a breakthrough in neurobiology. They are also rather promising for application in medicine, particularly for prosthetics of a degenerative (blind) retina (for review, see Kirpichnikov and Ostrovsky, 2015; Ostrovsky and Kirpichnikov; 2015). At present, works in this field are actively performed in the United States, Germany, France, Japan, and Russia (e.g., Dolgikh et al., 2015).

Rhodopsins of the second type have mainly a photoreceptor (visual) function. However, this is optionally, since to date several subgroups of nonvisual opsins have been revealed. They include *melanopsin* found in ganglion cells of the retina responsible for circadian rhythms and iris contraction reflex; *neuropsin* (Opn5) recognized in nerve cells; *encephalopsin* recognized in cells of the brain and visceral organs; *photoisomerase* expressing in cells of the retinal pigment epithelium and glial Muller cells of the retina; *peropsin* observed in cells of the retinal pigment epithelium (for review, see Lamb et al., 2007; Mackin et al., 2014). Although the overwhelming majority of metazoan opsins function as G-protein-coupled receptors, there are also rare exceptions. In particular, a function of *photoisomerase* as a nonvisual rhodopsin is photoisomerization of completely *trans*-retinal into 11-*cis* isomer, providing a mechanism for regeneration of visual pigment and, hence, dark adaptation of a photoreceptor cell.

WHETHER OR NOT RHODOPSINS OF THE FIRST AND SECOND TYPES ARE EVOLUTIONARILY CONNECTED

First of all, it should be emphasized that microbial rhodopsins are one of the most ancient proteins in the biosphere. Rhodopsins of metazoans, including visual ones are among the earliest proteins of the animal kingdom.

Figure 1 shows an evolutionary scheme of retinal-containing proteins. Bacteriorhodopsin is the first discovered microbial rhodopsin responsible for photosynthesis (photoenergetic process), which was formed in prokaryotic cells about 3.5 Ga. Metazoan rhodopsin (prototype of G-protein-coupled receptors), including visual rhodopsin responsible for photoreception (photoinformation process), which was formed in eukaryotic cells about 2.0 Ga (for review, see Lamb et al., 2007; Rozanov, 2009).

The chromophore center (chromophore-binding domain) of bacteriorhodopsin contains as a chromophore group a completely *trans*-isomer of retinal and, in the case of visual rhodopsin, 11-*cis*-retinal (and none of other 16 retinal isomers occur in nature as a chromophore group of visual rhodopsins).

It should be taken into account that, in essence, the evolutionary relationships of microbial and metazoan rhodopsins remain an open question. At the level of the aminoacid sequence, such relationships have not been established. At the same time, while in biochemistry, the study of the evolution of proteins is usually based on the analysis of their aminoacid sequence, in paleontology, it is based on comparisons of their structure, which seems rather fruitful, discussing relationships between rhodopsins of the first and second types.

Certainly, they are undoubtedly similar, since retinal is a chromophore group making a covalent bond of the Schiff base always with a lysine residue in the seventh alpha-helix bar of opsin and, in the topography of apo-protein (opsin), there are always seven alpha-helixes crossing membrane and hydrophilic loops on its sides. However, this may result from convergent evolution (Mackin et al., 2014).

On the other hand, as discussed in the literature, their similarity may result from the existence of a common lost predecessor. In particular, Shen et al. (2013), based on the structure of the transmembrane domain and using the statistical method of Fitch (1970) for distinguishing between homologous and nonhomologous proteins, came to the conclusion that microbial rhodopsins of the first type and metazoan rhodopsins of the second type are homologous proteins and that rhodopsins of the first type are predecessors of rhodopsins of the second type. At the same time, the assumption of the homology of rhodopsins of the two types undoubtedly requires confirmation.

Along with the question of evolutionary relationships between microbial and metazoan rhodopsins, the question of the evolution of the entire class of G-protein-coupled receptors and visual rhodopsin as their predecessor are hotly debated.

It is known that G-protein-coupled receptors form in human genome the most numerous family of membrane receptors (Pierce et al., 2002; GPCRDB, http://www.cmbi.kin.nl/7tm/). They are responsible for perception by the organism of various external and internal signals, the carriers of which are light, peptides, low-molecular organic molecules, and calcium ions. About 90% of all G-protein-coupled receptors belong to the family of rhodopsin-like receptors. To date, 24 G-protein-coupled receptors, 20 of which are

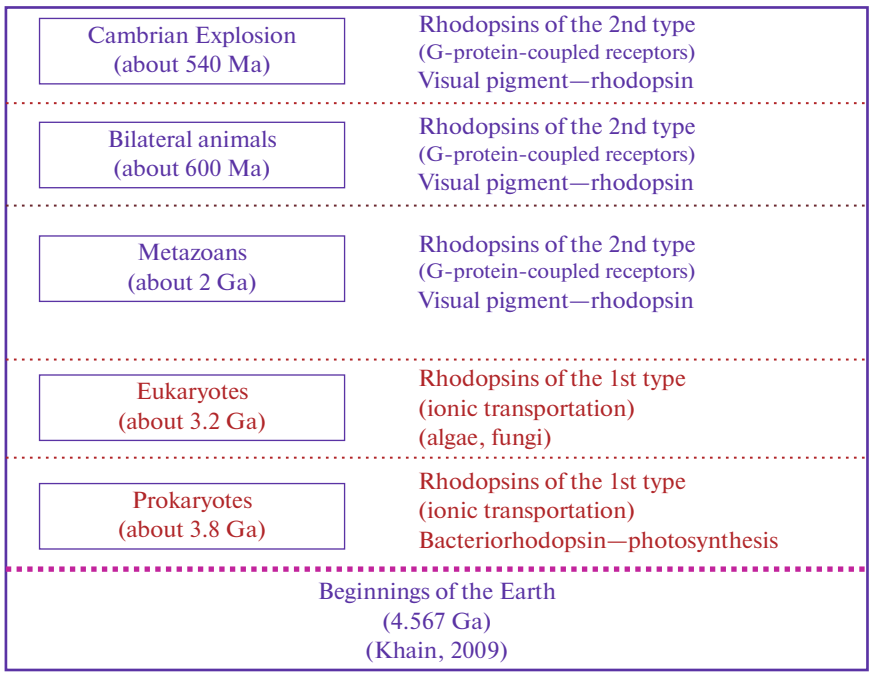

Fig. 1. Scheme of the evolution of retinal-containing proteins (dating after Rozanov, 2009).

rhodopsin-like, have been crystallized (for review, see Wolf and Grünewald, 2015). X-ray analysis of all 24 G-protein-coupled receptors allowed the revelation of their structures with a high spatial resolution. Based on comparative phylogenetic analysis of these structures, Wolf and Grünewald (2015) concluded that, in the course of evolution, apo-protein (opsin) of visual rhodopsin became the predecessor of peptide-binding receptors. The presence of relationships between the primary rhodopsin-like G-protein-coupled receptor and peptide receptors are supported by other authors (Pele et al., 2011). Peptide receptors are in turn regarded as predecessors of the receptors connecting low-molecular molecules, the neuromediators. In this case, apo-protein of visual rhodopsin can be considered as a predecessor of both hormone receptors and neuromediator G-protein-coupled receptors of the central nervous system. A probable candidate for the predecessor could have been melanopsin recorded in ganglionic cells of the retina and responsible for a number of light-dependent nonvisual functions of organism, including the iris contraction reflex and circadian rhythms (Hankins et al., 2008). At the same time, the opportunity for G-protein-coupled receptors, including visual rhodopsin, to evolve from the cyclic AMP-binding receptor (Krishnan et al., 2012).

Interestingly, metarhodopsin II (light-activated state of visual rhodopsin capable of interaction with G-protein transducine) appears similar in structure to the olfactory receptor, although olfactory G-protein-coupled receptors do not belong to the family of rhodopsin-like ones (Gelis et al., 2012; Park et al., 2013). Perhaps, chemoreceptors could have been predecessors of photoreceptor receptors. In any event, visual pigment rhodopsin serves is presently the most probable model for the study of the structures and mechanisms of activation of the entire class of G-protein-coupled receptors.

EVOLUTION OF VISUAL RHODOPSINS AND PHOTORECEPTOR CELLS

Visual pigments and genes encoding their protein part (opsins) are one of the most convenient and adequate systems for the study of molecular bases of evolutionary changes caused by environments and developing be means of natural selection. Visual pigments, i.e., photosensitive G-protein-coupled receptors, appeared in Metazoa about 2.0 Ga. Subsequently, metazoans were divided into two groups; one has a radially symmetrical body, the other is bilaterally symmetrical. In turn, bilateral forms gave rise to the majority of presently existing invertebrates and vertebrates (Fig. 2).

The species emerging during the Cambrian Explosion (545–535 Ma) and showing excessively wide diversity had a huge diversity of visual organs, which are grouped in two main types. The first is the complex eye of the majority of invertebrates (e.g., arthropods), which consists of a set of small eyes (ommatidia) with photoreceptor cells (rhabdoms); the second is the chamber eye of vertebrates. Although modern higher cephalopods, like vertebrates, have a chamber eye,

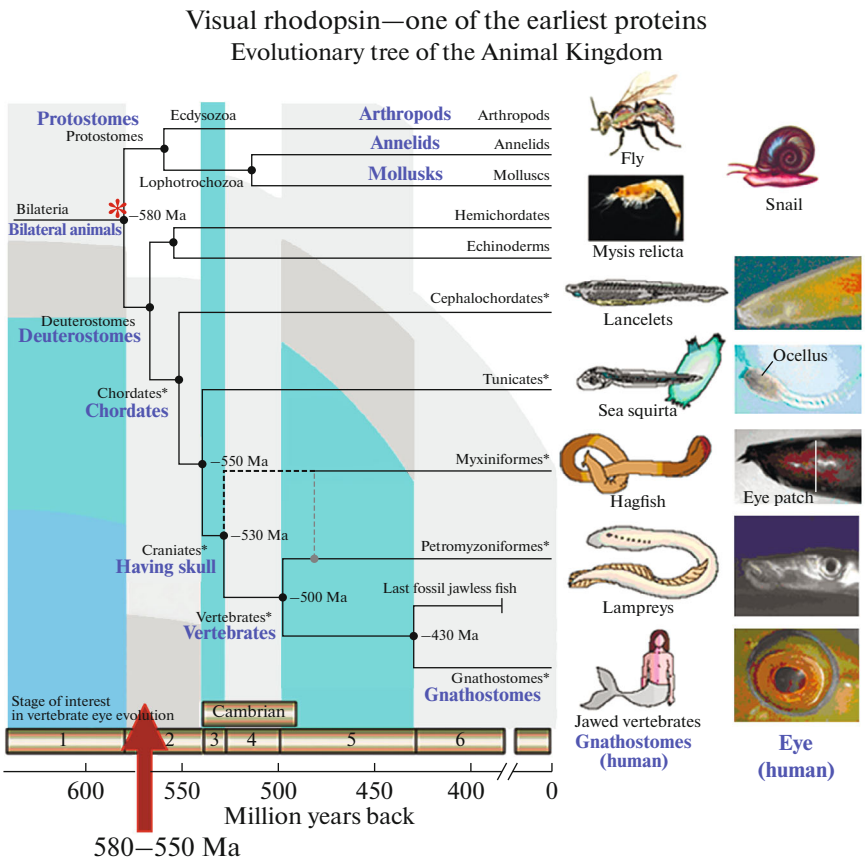

Fig. 2. Evolutionary tree of the animal kingdom: visual rhodopsin, one of the earliest proteins.

their photoreceptor cells are rhabdomeres, as in arthropods. In the majority of vertebrates, including primates, the retina of the chamber eye contains photoreceptor cells of two types, rods and cones. Rods are responsible for high-sensitive twilight vision; they respond to light slowly and are sated at moderate daytime illumination. Cones are responsible for daytime and color vision. They are one-thousandth as sensitive as rods, but their reaction to light is an order of magnitude rapider. In addition, they are not sated even at the maximal illumination intensity occurring in nature. Recently, the data were obtained enabling in a new insight into the evolution of photoreceptor cells of vertebrates. Initially, it seemed obvious that rods are evolutionarily primary. Actually, the black-and-white pictures provided by night vision are undoubtedly more primitive than color daytime vision. Therefore, cone color vision with a rapid response and high spatial resolution appeared much perfecter and, hence, evolutionarily later. This point of view was long considered classical, as stated in the book by Walls (1942). However, it was later replaced by the opposite opinion. Actually, rods are more specialized and perfecter photoreceptors capable of "counting" individual photon light quanta. On the contrary, cones function at high illumination and, in this respect, their function is much simpler. Therefore, it has become generally accepted that cones are evolutionarily more ancient photoreceptor cells than rods and that rods evolved from cones (Rodieck, 1998). A comparison of features of the phototransduction process in cones and rods has shown that modern rods and cones were apparently formed as a result of long specialization of the initial (ancestral) photoreceptor cell following two directions essentially different and important for the physiology of vision. The first direction is achievement of extreme light sensitivity; these are rods. They display physiological reaction in response to a single absorbed quantum of light; furthermore, the level of the dark noise in a rod is extremely low. The molecular mechanisms providing such a low level of noise are presently intensely investigated. The second direction is achievement of as perfect as possible work of the visual system at daytime illumination. Modern cones provide this completely; their relatively high dark noise in comparison to that of rods, particularly in red-sensitive cones, is not a disturber for daytime vision (Govardovsky and Astakhov, 2015). In this case, an almost centenary-long discussion about the evolutionary primacy of modern cones or rods of vertebrates becomes senseless.

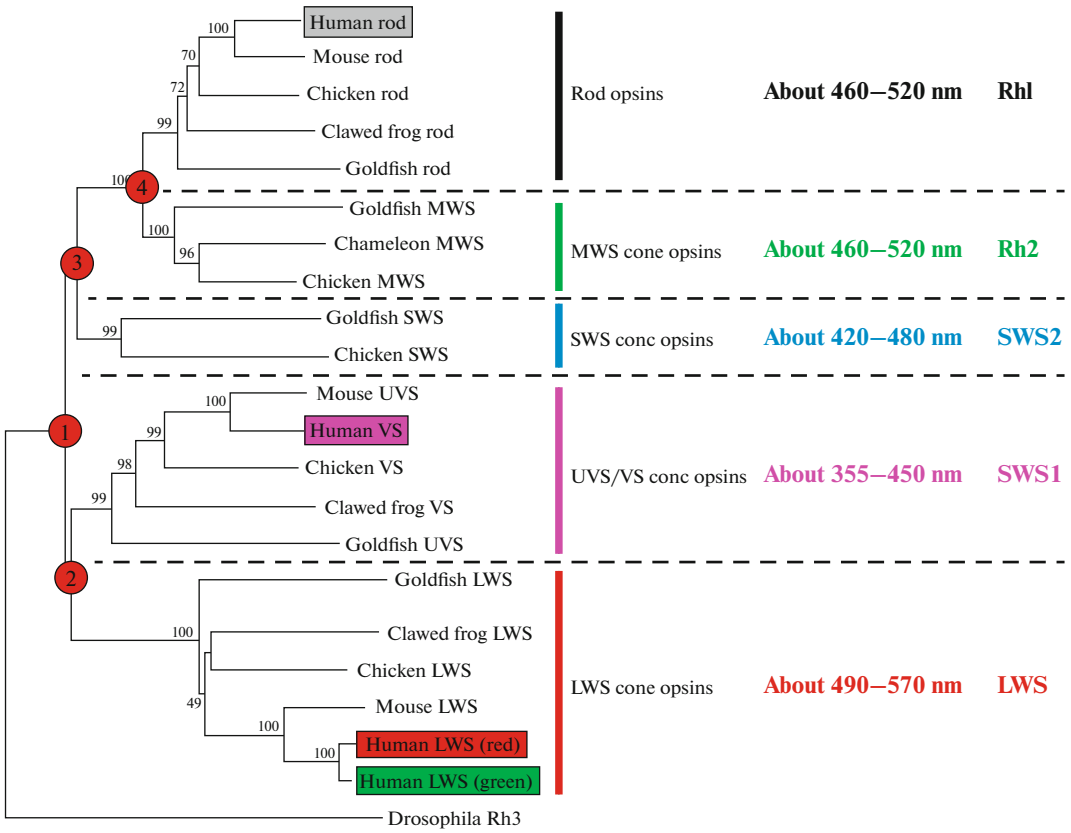

Fig. 3. Scheme of the evolution of visual rhodopsins (after Bowmaker and Hunt, 2006).

However, it is essentially important that, in all various types of visual organs, in all types of photoreceptor cells from photosensitive cells of the most primitive metazoans to photoreceptor cells of the rhabdomere or ciliate (rods and cones) types of highly organized invertebrates and vertebrates, the photosensitive molecule is G-protein-coupled visual pigment rhodopsin with 11-*cis* isomer of retinal as the chromophore group.

It is interesting that Ch. Darwin (1859) in his classical work *The Origin of Species* ... noticed that he is unable to explain by natural selection the origin of the eye as "an organ of the highest perfection." Only recently, based on extensive data accumulated to the present time, it has become evident that the Darwinian theory of natural selection is rightful in relation to the evolution of visual organs and their photoreceptor apparatus (Lamb et al, 2007; Lamb, 2009, 2011).

As for the diversity of visual pigments in photoreceptor cells and their evolution, it seems plausible that the picture shown in Fig. 3 is presently generally accepted (Bowmaker and Hunt, 2006). All of five opsin classes, i.e., four conelike and one rodlike, appeared in the course of evolution of vertebrates at very early stages of Cambrian Explosion, more than 500 Ma, perhaps, even earlier. The question in what are relations between the appearance of the five opsins and evolutionary tree of vertebrates? Even primitive agnathans, such the lamprey *Geotria australis,* have one longwave, two shortwave cone opsins and one rhodopsin-like. Possessing such a set of opsins, early agnathans potentially could have had color vision.

As for the visual pigment rhodopsin, it appeared relatively late in evolution. Since the rhodopsin-type gene has two forms, after divergence of agnathan and gnathostome vertebrates, these forms probably differentiated into two rhodopsin groups (Collin et al., 2003). In lamprey, rhodopsin-like gene could diverge into cone RhA and RhB, although the RhA group is apparently closer to rodlike one. Duplication of the Rh rhodopsin-like gene into Rh1/Rh2 of gnathostomes was probably independent.

Since conelike, spectrally distinguished visual pigments appeared at the earliest stages of vertebrate evolution, color tetrachromatic daytime vision could have appeared in them very early. Four classes of cone opsins—longwave-sensitive, 490–570 nm (LWS); rhodopsin-like green-sensitive, 460–520 nm (Rh2, rhodopsin-like-2); shortwave cyan-sensitive, 420–480 nm (SWS2, shortwave-sensitive-2); and shortwave ultraviolet–violet-sensitive, 355–450 nm (SWS1, shortwave-sensitive-1)—appeared as a result of gene duplication. According to the modern concept, the cone rhodopsin gene (Rh1) was the last to appear in evolution as a

result of duplication of the green-sensitive cone opsin Rh2 gene.

All four classes of cone pigments are retained in extant bony fishes, amphibians, reptiles, and birds. As for mammals, they have lost perfect four-component color vision of reptile predecessors. Emerging about 200 Ma, mammals passed a long way of nocturnal mode of life, retaining only minimal requirements for color sense, namely, two classes of cone pigments, providing only imperfect dichromatic vision. In other words, mammals do not distinguish green and red colors, preserving only spectrally extreme classes of cones, longwave red-sensitive (LWS) and shortwave ultraviolet/violet/blue-sensitive (SWS1). Quite satisfactory trichromatic color vision appeared again only in primates, including humans. This question is discussed in many works, the essence of which is considered below. For primates, it was extremely important to distinguish between red and green in a search for food; they required recognition of yellow mature fruit and green unripe ones. In heterozygous female monkeys of the New World, trichromatic vision appeared due to polymorphism of the red-sensitive opsin gene (LWS). Males remained dichromatic. Monkeys of the Old World (and humans) about 35 Ma due to duplication of the inherited red-sensitive opsin gene (LWS) reacquired quite good trichromatic vision. It is interesting that, recently, using the methods of gene therapy in cones of the retina of dichromatic New World monkeys, it appeared possible to express the red-sensitive opsin gene. As a result, they had become trichromates, like monkeys of the Old World and humans. Due to surprising plasticity, the brain of these monkeys rapidly and efficiently adapted to the new for it "human" color vision (Mancuso et al., 2009).

Considering the evolution of visual pigments, it should be kept in mind that the chromophore group of both all cone and rod visual pigments was and retained the same chromophore group, i.e., 11-*cis* isomer of retinal, while amino acid substitutions occurred in the protein part of the molecule, mostly the chromophore center of opsin.

Aminoacid substitutions near the chromophore group, 11-*cis*-retinal or 11-*cis*-dehydroretinal, provide spectral tuning of visual pigments. Fundamentally, spectral tuning is possible in two time scales, i.e., long evolutionary and relatively short-term adaptive physiological (adaptive tuning is considered below).

Intramolecular mechanisms of evolutionary spectral tuning of visual pigments of vertebrates are sufficiently well understood. For example, the shift of the absorption spectrum of shortwave ultraviolet pigment to the violet–dark blue region of visible light requires only one aminoacid substitution in the chromophore center of opsin (Hunt et al., 2007). At the same time, spectral tuning of longwave pigments in "red" cones of reptiles, birds, and mammals requires several aminoacid substitutions, involving anion (chlorine)-binding centers in the chromophore center. Removal of chlorine ions displaces not only the maximum of the absorption spectrum of red-sensitive cones to the shortwave (green) region by approximately 30 nm (Slobodyanskaya et al., 1980; Novitsky et al., 1989); but also, as we have shown using an isolated retina of goldfish as an example, suppresses their functional activity (Zak et al., 2001). A decrease in concentration or complete removal of chlorine ions from Ringer's solution washing the retina resulted in a decrease or even disappearance of their electric response (late receptor potential) to red light flash (Zak et al., 2001). As for spectral tuning of rod visual pigment (rhodopsin), it is almost absent; in almost all terrestrial vertebrates, the absorption spectrum maximum of rhodopsin is in the region of 500 nm.

In addition to slow evolutionary spectral tuning of visual pigments, there is also rapid adaptive tuning, the mechanisms of which are rather diverse. It provides adaptation of vision to varying conditions, primarily light environments.

COMPARATIVE PHYSIOLOGY OF VISUAL RHODOPSINS: ADAPTIVE SPECTRAL TUNING

Comparative physiology of vision and visual pigments in particular is an independent and extremely fascinating field of biology of vision (see, e.g., Feuda et al., 2012; Nilson, 2013). When discussing adaptive spectral tuning of visual pigments (seasonal or dependent on illumination), it is usually considered substitution of the 11-*cis*-retinal chromophore group (retinal$_1$—aldehyde of vitamin A$_1$), which absorbs light in relatively shortwave region of the spectrum, by 11-*cis*-dehydroretinal (retinal$_2$—aldehyde of vitamin A$_2$), which absorbs light in a more longwave region due to additional double bond in the beta-ionic ring of retinal molecule. However, this generally accepted mechanism not always works, at least in relation to invertebrates (Belikov et al., 2014).

We, along with Finnish colleagues, performed an extensive comparative physiological study of the mechanisms of changes, depending on environments, spectral sensitivity of the eye, and spectral tuning of visual pigment of rhodopsin of the shrimp genus *Mysis* (Donner et al., 2016). For such studies, mysids are rather advantageous. Many species of the genus form the isolated populations inhabiting various water environments, including Arctic and northern marine coastal waters, northern freshwater lakes, and even coastal waters of the continental Caspian Sea. They repeatedly changed light habitats, salinity, and certain other factors. They changed environments at both interspecific and intraspecific levels. These changes occurred during different periods of time from million to several thousand years and depended even on the season of year. Therefore, this crustacean genus can be

regarded as a very convenient model for the study of their epigenetic and rapid physiological adaptive response to the change in conditions the light surroundings and other ecological factors. We examined the mechanisms responsible for the shift of spectral sensitivity of the eye and absorption spectra of visual pigment. The shift into the longwave region in a lake population of *Mysis relicta* compared with a sea population of this species was examined particularly thoroughly. These populations were separated relatively recently, at the end of the Pleistocene, about 10 ka.

In the marine environment, at a certain depth, illumination is very poor and restricted to a rather narrow shortwave spectral region. In contrast to light blue ocean water, in fresh waters containing various suspended substances, the shortwave region of the spectrum is filtered and, even at a rather small depth, illumination is poor and shifted to the longwave region from yellowish green to reddish brown. Therefore, the absorption spectra of rhodopsins, which provide twilight vision in fresh and weakly transparent waters, are usually shifted to the longwave region of the spectrum in comparison with marine water. This spectral shift occurs at almost all phylogenetic levels. Such spectral tuning of visual pigment, corresponding to this rule has been revealed in marine and lake populations of *M. relicta*. It turned out that the maximum absorption of rhodopsin in marine shrimps is about 530 nm, while lake shrimps dwelling at a considerable depth, it is about 560 nm (Jokela-Maatta et al., 2005). Spectral sensitivity of the eye in lake population is also displaced by approximately 30 nm to the red region of the spectrum in comparison with sea population (Lindstrom, 2000). In other words, in both populations of *M. relicta,* spectral sensitivity of the eye is shifted considerably to the longwave region in relation to the absorption spectra of their visual pigments. Actually, the maximum absorption of rhodopsin in marine shrimps is about 530 nm, while spectral sensitivity of their eye has its maximum about 570 nm; and in lake populations, the maximum absorption of rhodopsin is about 560 nm; the maximum spectral sensitivity of the eye is about 600 nm. It is known that, in the longwave shift of spectral sensitivity of the eye, yellow, partially filtering dark blue light screening pigments, xanthomatines included in ommochrome granules and carotinoids (Frank et al., 2009). We have shown that just xanthomatine in ommochrome granules can be regarded as the intraocular light filters forming the longwave shift of spectral sensitivity of the eye in both shrimp populations (Abu Khamidakh et al., 2010). In other words, ommochromes, partially cutting off dark blue region of the spectrum potentially dangerous for eye structures, perform not only antioxidant photoprotective function (see below), but also filters light. Since depths that are inhabited by lake shrimps are only attained by a minor portion of light within the range of 680 nm and 99% of the light shorter than 550 nm is completely lost, such longwave spectral tuning of both visual pigment and spectral sensitivity of the eye are essentially important for adaptation of their vision to light environments. A similar longwave spectral shift (by 20–30 nm) in lake populations compared with sea ones has been recorded in three northern mysid species, which underwent more than two-million-year-long period of evolution and divergence of the opsin gene (Audzijonyte et al., 2012).

Thus, a comparative physiological study of spectral sensitivity of the eye and absorption spectra of visual pigments in several mysid species inhabiting fresh and sea waters has shown that the spectral maxima of visual pigments of the first and second are about 530 and 560 nm, respectively.

This raises the question, what are the mechanisms of spectral tuning of the visual pigment? It was natural to propose that visual pigments of these populations contain different forms of 11-*cis*-retinal, i.e., 11-*cis*-retinal-1 (A_1 or aldehyde of vitamin A_1) in sea population and 11-*cis*-retinal-2 (A_2 or aldehyde of vitamin A_2) in lake population. It is well-known that replacement of chromophore A_1 by A_2 in the same opsin results in the longwave shift of the absorption spectrum maximum by approximately 30 nm (Dartnall and Lythgoe, 1965; Harosi, 1994). The replacement $A_1 \leftrightarrow A_2$ (rhodopsin $\leftrightarrow$ porphyropsin) provides rapid, for example, seasonal, tuning of spectral sensitivity of the eye in fishes and amphibians (Schwanzara, 1967; Ostrovsky, 1971; Bridges, 1972; Temple et al., 2006; Enright et al., 2015) and at least in one crustacean species, the crayfish *Procambarus clarkia* (Suzuki et al., 1984). The balance between the two chromophore forms depends on the factors of environment, primarily, the light and temperature (Suzuki et al., 1985, 1993). However, contrary to expectation, we have shown with certainty that distinctions in the absorption spectra of visual pigments in rhabdoms of lake and sea populations of *Mysis relicta* are not connected with the use by them of different chromophore forms; both have the same 11-*cis* isomer of retinal-1 (A_1) as the chromophore, while chromophore A_2 in visual pigments of these populations is absent (Belikov et al., 2014). Possibly, visual pigments of other mysid species contain only chromophore A_1. At the same time, freshwater crustaceans, which have the $A_1 \leftrightarrow A_2$ system, essentially differ from mysids, which are primarily marine crustacean. Therefore, they lack the $A_1 \leftrightarrow A_2$ system, as marine crustaceans. Although mysids subsequently repeatedly moved from marine to freshwater environments, the biochemical system of $A_1 \leftrightarrow A_2$ exchange has not developed in them. In other words, as initially marine crustaceans, mysids did not use $A_1 \leftrightarrow A_2$ exchange for the change in spectral sensitivity of the eye.

Let us consider the protein part of the rhodopsin molecule, aminoacid substitutions in which, mostly in the chromophore center, determine evolutionary spectral tuning of visual pigments. The essence of

presently available experimental data is that differences in the opsin gene encoding the aminoacid sequence of rhodopsin in rhabdoms of lake and sea populations of *Mysis relicta* have not been recognized (Audzijonyte et al., 2012). At the same time, a comparison of three mysid species, *M. relicta, M. salemaai,* and *M. segerstralei,* has revealed that they differ in the aminoacid sequence of the opsin genes (Audzijonyte et al., 2012). It remains uncertain why DNA analysis of the opsin genes in two populations has not revealed distinctions between them, although their rhabdoms undoubtedly contain two visual pigments with different absorption spectra (see below) and both pigments have A_1 as chromophore group (see above). Possible explanations of this phenomenon were considered by Donner et al. (2016). In any event, this question requires further, more thorough investigation.

At the same time, as we have shown, rhabdoms of each population contain two types of visual pigments with the absorption maxima in the medium wavelength (green, ~525–530 nm) and long wavelength (red, ~565–570 nm) regions of the spectrum, and they express in different cells and in different proportion (Zak et al., 2013). Moreover, rhabdoms containing these pigments differ in the polarizing sensitivity. Possibly, the appearance and proportions in the eye of each population of *M. relicta* of long and medium wavelength photoreceptor cells, rhabdoms, is determined in the course of development by certain, other than light signals from environments. For sea and lake populations, these signals are apparently different.

Another important physiological distinction of sea and lake populations is different sensitivity to the damaging effect of light; lake population is much more sensitive than sea one (Lindstrom and Nilsson, 1988). We investigated in detail the mechanisms underlying the damaging effect of light and protection against it in both populations (Dontsov et al., 1999; Feldman et al., 2010). It has been shown that the biochemical system of antioxidant protection is similar in essence. The only clear distinction that we revealed is the content in the eye structures of screening pigments ommochromes and also carotinoids, which have both light-absorbing and well-pronounced antioxidant properties. Eyes of sea population contain much more ommochromes and carotinoids than in lake population. This fact possibly explains the much greater stability of the eye to the damaging effect of light in sea population of the shrimp *M. relicta* than in lake one (Lindstrom and Nilsson, 1988).

CONCLUSIONS

As for the evolution of retinal-containing proteins, continuity and relationships between microbial and metazoan rhodopsins remain an urgent and unsolved question. If these are homologous proteins, we should admit that, in the course of evolution, there existed and was lost an intermediate form of the opsin gene within the way from the microbial rhodopsin gene to the gene encoding G-protein-coupled photoreceptor (photoinformation) opsin. The idea that these proteins are homologous is very tempting, since it is difficult to imagine that the seven-alpha-helix transmembranous structure and chromophore center perfect with reference to unique photochemical reaction were formed completely independently. Actually, except for microbial rhodopsin, a different seven-alpha-helix membrane protein, which is comparable in age with the biosphere of the Earth, does not exist.

However, an alternative idea, that is, the hypothesis of convergent evolution, according to which the gene encoding photoreceptor G-protein-coupled opsin appeared independently after the appearance of microbial rhodopsin, is impossible to exclude (see, e.g., Mackin et al., 2014). If this is the case, it is possible to discuss the question as to whether the photoreceptor rhodopsin opsin was the predecessor of other G-protein-coupled receptor proteins (Feuda et al., 2012; Shen et al., 2013) or, on the contrary, the chemoreceptor G-protein-coupled receptor was the predecessor of visual opsin (rhodopsin), since seven-alpha-helix transmembranous domain is intrinsic to all of them. In any case, it is highly probable that all G-protein-coupled receptors have common origin irrespective of the fact whether photo- or chemoreceptor opsin was initial (see, e.g., Nordstreom et al., 2011; Katritch et al., 2012).

Regarding visual pigments themselves, evolutionary tree has rather reliably been reconstructed (see above). Due to capability for spectral tuning and unique photochemical properties, visual pigments determine fundamental properties of the physiology of vision, such as spectral and absolute sensitivity of the eye, color vision. Further studies of the visual rhodopsin molecule are connected, first, with features of interaction 11-*cis*-retinal as the chromophore group and its nearest protein environment in the chromophore center, which provides ultrafast and efficient reaction of photoisomerization, and, second, with features of the change in conformation of this protein environment at the initial stages of rhodopsin phototransformation. In this connection, a comparison with microbial rhodopsin is of great interest. The modern methods for fine structural and physicochemical studies enable this to be implemented. Our comparison of the kinetics of the quantum yield of ultrafast direct and reverse photochemical reactions of visual (bull) rhodopsin and bacteriorhodopsin indicates that, in the course of evolution of retinal-containing proteins, interaction of chromophore with the nearest protein environment in the visual molecule rhodopsin became more perfect and specific than in bacteriorhodopsin (Feldman, in press). Therefore, triggering by rhodopsin in visual cells of the mechanism of phototransduction as a photoinformation process is apparently more efficient and more reliable than initiation by

bacteriorhodopsin in halobacteria of the mechanism of photosynthesis as a photoenergetic process.

Another actual field of physiology of vision is further investigation of features of the process of phototransduction in both rhabdoms of the eye in invertebrates and rods in the retina of vertebrates responsible for twilight (scotopic) vision and in cones responsible for daytime (photopic) vision. These features have a direct effect on the ability of the visual system to function perfectly at night or daytime illuminations and also adapt efficiently for the shifts in illumination. In addition to photosensitive visual pigments, in complex multicomponent adaptation of the visual system for light environments, an important role is played by intraocular nonphotosensitive screening pigments and, certainly, neurophysiological mechanisms of processing visual information in the retina and visual regions of the brain. Therefore, a complex comparative physiological study of the adaptation mechanisms of vision in invertebrates and vertebrates to varying conditions of light environment and the role in these mechanisms of visual pigments remains a particularly interesting problem of the physiology of vision.

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