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Source: Zoological Science, 31(10) : 653-659

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zs140094

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ZOOLOGICAL SCIENCE **31**: 653–659 (2014)
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[REVIEW]

Functional Properties of Opsins and Their Contribution to Light-Sensing Physiology

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Many animals have developed systems for sensing environmental conditions during evolution. In sensory cells, receptor molecules are responsible for their sensing abilities. In light sensing, most animals capture light information via rhodopsin-like photoreceptive proteins known as opsin-based pigments. A body of evidence from comparisons of amino acid sequences and in vitro experiments demonstrates that opsins have phylogenetically and functionally diversified during evolution and suggests that the phylogenetic diversity in opsins correlates with the variety of molecular properties of opsin-based pigments. In this review, we discuss the various molecular properties of opsin-based pigments and their contribution to light-sensing ability by providing two examples: i) contribution of photoregeneration ability and chromophore retinal binding property of an Opn3 homolog to non-visual photoreception, and ii) contribution of an absorption characteristic of a visual pigment to depth perception in jumping spiders.

Key words: opsin, visual pigment, Opn3, non-visual photoreception, depth perception

INTRODUCTION

Most animals capture light information with rhodopsin and related photosensitive proteins and utilize this for vision and non-visual functions, such as light-dependent regulation of the circadian rhythm. The photosensitive proteins are composed of a protein moiety opsin and a chromophore retinal, which is a vitamin A derivative. Thus, we refer to the photosensitive pigments as opsin-based pigments in this review.

Historically, by the 1950s, rhodopsins of vertebrates and cephalopods were extracted from their eyes and spectroscopically and biochemically studied. The late professor G. Wald and his colleagues discovered that rhodopsins have 11-*cis* retinal as the chromophore and its photoisomerization to the all-*trans* form is an essential reaction for the functional expression of rhodopsins (Wald, 1968). In 1965, the late professor T. Hara and Dr. R. Hara discovered a new pigment protein named retinochrome in the squid retina (Hara and Hara, 1965). Retinochrome has quite different molecular properties from those of rhodopsin; i.e., retinochrome binds to all-*trans* retinal as the chromophore in the dark state, and more interestingly, light irradiation causes photoisomerization of the retinal to the 11-*cis* form, indicating a retinal photoisomerase activity of retinochrome for generating the 11-*cis* configuration (Hara and Hara, 1968). These unique molecular properties have led to the suggestion that retinochrome generates 11-*cis* retinal with light energy and supplies it to opsins to form opsin-based pigments in the squid retina (Terakita et al., 1989). In 1990s, the amino acid sequence of retinochrome was determined, which demonstrated that the retinochrome, as well as rhodopsins, is a member of the opsin family (Hara-Nishimura et al., 1990; Terakita, 2005). A homolog of retinochrome, retinal G protein coupled receptor (RGR), was also found in the mammalian retina in 1993 (Jiang et al., 1993). These observations highlight not only the structural diversity but also the functional diversity of the opsin family (Terakita, 2005).

Furthermore, in 1997, we discovered a novel opsin in scallops, which couples with Go type G protein and forms a group distinct from well-known G protein-coupled rhodopsins such as vertebrate visual opsins coupled to transducin (Gt) and invertebrate opsins coupled to Gq (Kojima et al., 1997). This report was subsequently followed by the identification of other novel opsins along with the whole genome sequences of several animals and their functional analyses, and the diversity of opsin-based pigments was gradually revealed.

Diversity of opsins

Several thousand opsins have been identified from both deuterostomes and protostomes and are divided into eight classes, vertebrate visual and non-visual opsin, Opn3 (encephalopsin) and TMT opsin, invertebrate visual opsin/Opn4 (melanopsin), Opn5 (neuropsin), invertebrate Go-coupled opsin, cnidarian Gs-coupled opsin, peropsin, and photoisomerase (RGR/retinochrome) groups (Fig. 1). Most

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doi:10.2108/zs140094

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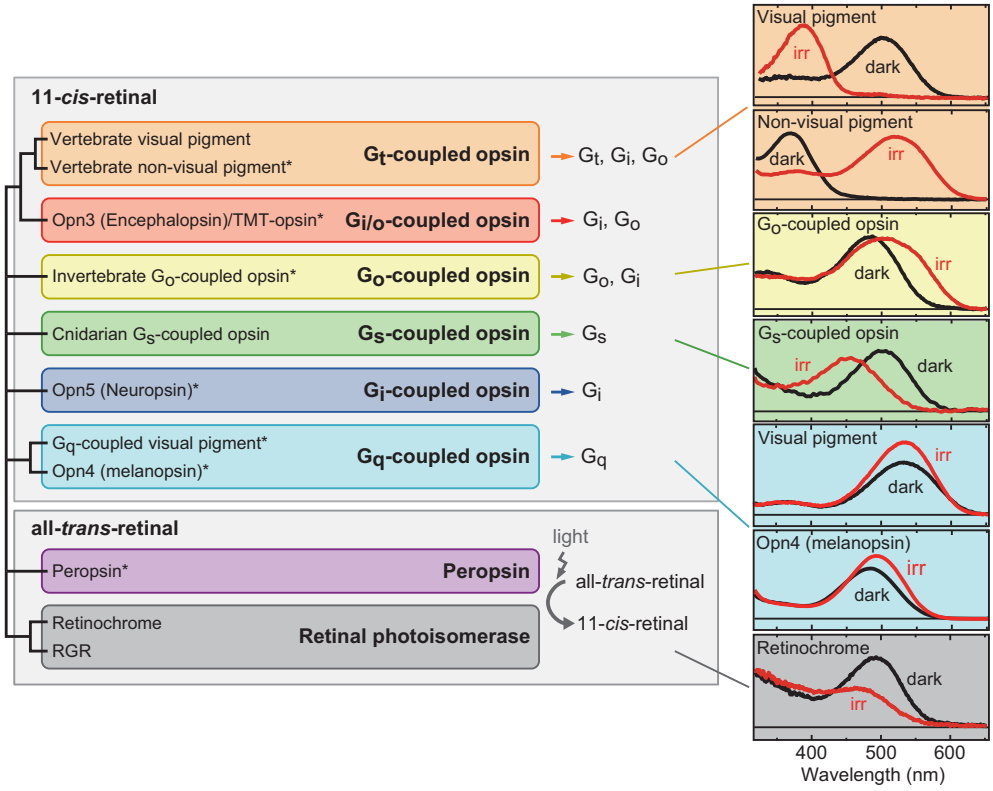


Fig. 1. Schematic diagram of phylogenetic relation of opsins and basic molecular properties of opsin–based pigments. Opsins are generally divided into eight classes, and the classification basically corresponds to the differences in the molecular functions, coupling in a light-dependent manner to different G protein-mediated signal transduction cascades and photoisomerase activity. The right panels schematically indicate the spectra of opsin-based pigments whose in vivo typical molecular functions have been characterized in the dark (black lines) and after light irradiation (red lines). Most G protein-coupled opsin-based pigments other than vertebrate visual opsin-based pigments are bistable, as shown in Fig. 2A. Asterisks indicate subclasses including opsins that form bistable pigments.

animals have multiple opsin genes; for example, humans have nine opsin genes from five classes out of eight; namely, four visual opsins, Opn3, Opn4, Opn5, peropsin, and RGR.

We have comparatively studied the molecular properties of diversified opsin-based pigments, e.g., absorption maximum, chromophore selectivity, photoreaction, and G protein coupling, to understand the differences in molecular and functional properties of pigments. Our group succeeded in functional reconstitution of one or more opsin-based pigments in each opsin class by using chromophore retinoids and recombinant opsins, most of which were expressed in mammalian cultured cells. An accumulated body of evidence from in vivo and in vitro experiments suggested that the classification roughly corresponds to similarities in molecular functions, namely which type of G protein-mediated signal cascades opsin-based pigments drive. Our previous findings, together with observations on Opn5 by other groups (Yamashita et al., 2010; Kojima et al., 2011), are summarized in Fig. 1. Opsin-based pigments belonging to the following six classes, vertebrate visual and non-visual opsin (Gt-coupled), invertebrate visual opsin/Opn4 (Gq-coupled), invertebrate Go-coupled opsin, Opn3 and TMT opsin (Gi/Go-coupled), Opn5 (Gi-coupled), and cnidarian opsin (Gs-coupled), function as light sensing G protein-coupled receptors. Members of the other two groups, retinochrome and peropsin, are considered to be retinal photoisomerases that produce 11-*cis* retinal. Opsins of different classes generally drive different G protein-mediated phototransduction cascades, although it is still unclear why animals utilize different signal transduction cascades to generate electrophysiological responses.

We recently hypothesized that animal phototransduction cascades can be evolutionary and biochemically divided into two groups, phosphoinositol signaling in rhabdomeric-type photoreceptor cells and cyclic nucleotide signaling in ciliary-type photoreceptor cells (Koyanagi et al., 2008); the phosphoinositol signaling is driven by Gq-coupled opsin-based pigments such as invertebrate visual opsins and Opn4 and the cyclic nucleotide signaling is driven by Gs-coupled, Gt-coupled, and Go-coupled opsin-based pigments such as jellyfish opsin-based pigments, vertebrate visual opsins, and scallop Go-rhodopsin.

With respect to molecular properties of photoproducts, we have found that upon photon absorption, most opsin-based pigments, except for vertebrate visual opsins, convert into photoproducts, which then revert to the original dark state by subsequent absorption of another photon (Koyanagi et al., 2004; Koyanagi et al., 2005; Tsukamoto et al., 2005; Nagata et al., 2010; Koyanagi et al., 2013) (Fig. 2A). Such a photoregenerative nature is referred to as a bistable or bleach-resistant nature. In contrast, vertebrate visual opsin-

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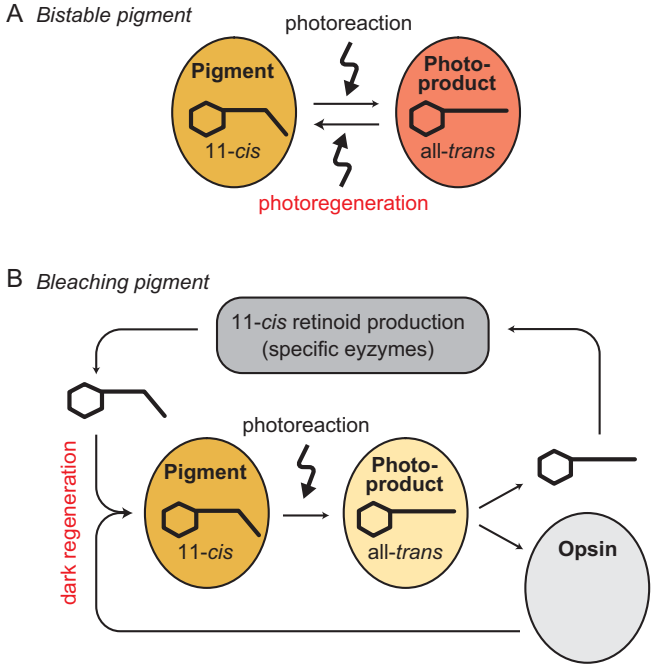


Fig. 2. Schematic diagram of the photoreaction and regeneration of opsin-based pigments. **(A)** Bistable pigments have two stable states, dark state and light activated state (photoproduct). Upon light absorption, the pigment converts to the photoproduct with 11-*cis* to all-*trans* retinal isomerization, and the photoproduct reverts to the original dark state by subsequent light absorption. Most opsin-based pigments other than vertebrate visual opsin-based pigments exhibit bistable nature (see Fig. 1). **(B)** The photoproduct of the bleaching pigments is thermally unstable, releases the chromophore, and bleaches. The resulting opsin requires 11-*cis* retinal, which is produced by specific enzymes in photoreceptor organs, to revert to the dark state. Vertebrate visual opsin-based pigments and some vertebrate non-visual opsin-based pigments exhibit bleaching nature.

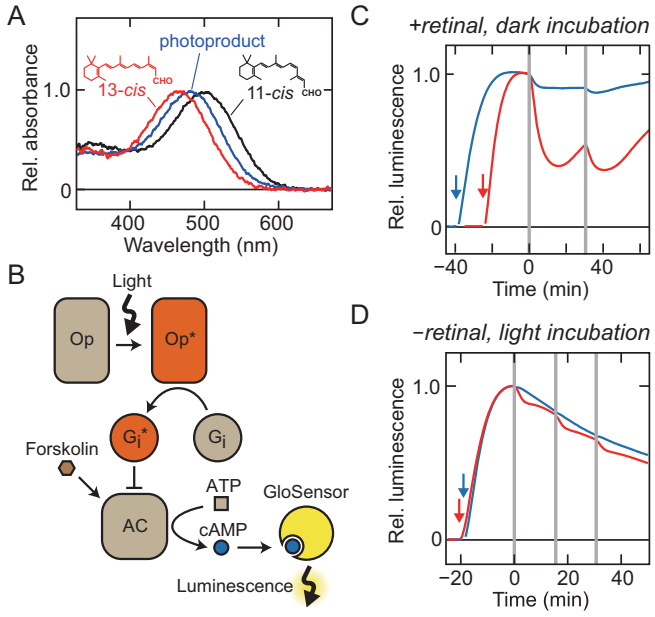


Fig. 3. 13-*cis* retinal binding ability of a mosquito homolog of Opn3 and its functionality in the cultured cells. **(A)** Spectra of 13-*cis* retinal-bearing, 11-*cis* retinal-bearing Mosquito Opn3 homologs (MosOpn3) and their photoproduct. The generation of MosOpn3-based pigments was analyzed after incubation with all-*trans* or 11-*cis* retinal. MosOpn3 selectively binds to 13-*cis* retinal rather than the all-*trans* form when incubated with all-*trans* retinal, although it binds to 11-*cis* retinal when incubated with 11-*cis* retinal. Both 13-*cis* and 11-*cis* retinal-bearing MosOpn3-based pigments convert to spectroscopically identical photoproducts. **(B)** Schematic presentation for measuring cAMP level in cultured cells expressing opsin-based pigments. Changes in cAMP levels, which are initiated by light absorption of opsin-based pigment via activation of a Gi-mediated cascade, were measured with GloSensor, a cAMP-sensitive luciferase. **(C)** Light-induced decrease in cellular cAMP levels in the cultured cells expressing MosOpn3 (red line) and Bovine rhodopsin (blue line) after addition of 11-*cis* retinal and dark adaptation. **(D)** Light-induced decrease in cellular cAMP level in the cultured cells expressing MosOpn3 (red line) and bovine rhodopsin (blue line) without adding 11-cis retinal and after light adaptation. Grey bars and arrows in **(C)** and **(D)** respectively indicate light irradiation and additions of forskolin, which elevates cellular cAMP level.

based pigments release the chromophore and bleach (become colorless) after light absorption (Fig. 2B). The photoregeneration ability of non-visual opsin-based pigments could contribute to retaining their photosensitivity in non-photoreceptor cells, which generally lack retinal-isomerase-like enzymes or enough available 11-*cis* retinoids.

Further, we discuss two examples of the contribution of the molecular properties of opsin-based pigments to biological functions.

Contribution of 13-cis retinal binding ability of an opsin to non-visual function

Most G protein-coupled opsins bind to 11-*cis* retinal, and its photoisomerization to the all-*trans* form initiates their conformational change, leading to functional expression. Therefore, for opsins, including the non-visual opsins expressed in extraocular tissues, the presence of chromophore retinal is essential to its function as a light-sensor protein. However, tissues outside of the photoreceptor organs, namely eyes and pineal organs, contain significantly less 11-*cis* retinal because such tissues do not express enzymes generating 11-*cis* retinoids, such as photoisomerases (RGR/retinochrome), and RPE65, which are specifically expressed in photoreceptor organs (Fig. 2B). Recently, we found that a mosquito homolog of Opn3 (MosOpn3), a non-visual opsin whose mRNA is found in various kinds of non-photoreceptive tissues including brain, has an ability to bind to 13-*cis* retinal (Koyanagi et al., 2013), which is ubiquitously present along with the all-*trans* form in animals.

Experimentally, MosOpn3 formed a 13-*cis* retinal-bearing pigment with an absorption maximum at 465 nm after incubation with all-*trans* retinal (Koyanagi et al., 2013) (Fig. 3A). MosOpn3 selectively bound to 13-*cis* retinal, which was produced slightly in thermal equilibrium with the all-*trans* form (Groenendijk et al., 1980). 13-*cis* retinal-bearing MosOpn3 is spectroscopically distinct from 11-*cis* retinal-bearing MosOpn3 (Fig. 3A), which was generated after incubation with 11-*cis* retinal. Both of these pigments convert to the stable photoproduct (Fig. 3A), which reverts to 11-*cis* retinal-bearing MosOpn3 by subsequent light absorption, thus

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showing the bistable nature (Fig. 2A). The photoproduct activated Gi and Go, indicating that both 11-cis and 13-*cis* retinal-bearing MosOpn3s can serve as light-sensor proteins. 13-*cis* retinal might serve as a partial agonist or partial inverse agonist for MosOpn3 (Koyanagi et al., 2013).

mRNAs of Opn3 homologs are found in various kinds of extraocular tissues of varied animals (Blackshaw and Snyder, 1999; Moutsaki et al., 2003; Arendt et al., 2004; Velarde et al., 2005). The molecular properties of MosOpn3, i.e., the binding ability of 13-*cis* retinal, which is ubiquitously present in the body, and its bistable nature, suggest that Opn3 could serve as a light-sensor protein, even in extraocular tissues that do not contain 11-*cis* retinal. We therefore further examined whether MosOpn3 actually functions as a photosensitive pigment in "non-photoreceptor cells" by using HEK293 cultured cells without addition of 11-*cis* retinal. MosOpn3 activates Gi-mediated signal transduction cascade, which generally leads to the inhibition of adenylyl cyclase activity. We monitored changes in the intracellular cAMP level of MosOpn3-expressing HEK293 cells upon light irradiation by the GloSensor cAMP assay, which is based on a cAMP-dependent luciferase (Fig. 3B). When the MosOpn3-expressing cells were incubated in the serum-containing culture medium with 11-*cis* retinal in the dark, the luminescence intensity increased with forskolin treatment, which decreased markedly with light irradiation (Fig. 3C). In contrast, bovine rhodopsin-expressing cells incubated with 11-*cis* retinal showed small decreases. The MosOpn3-expressing cells that were maintained without the addition of 11-*cis* retinal in the room light also exhibited light-dependent decreases in the levels of cAMP (Fig. 3D), showing a reusable pigment formation with retinal endogenously contained in the culture medium. Bovine rhodopsin-expressing cells showed no cAMP decrease in this condition. These results suggest that MosOpn3 was bound to the retinal that was present in the serum-containing culture medium and retained their functionality even after the continuous light exposure, possibly because of their bistable nature and 13-*cis* binding ability.

Contribution of absorption maximum of opsin-based pigment to depth perception in jumping spider

Many invertebrates and vertebrates have more than two visual opsin-based pigments with different absorption characteristics in retinas to achieve color vision. In such animals, absorption maximum wavelengths of visual pigments are generally discussed from the viewpoint of color vision. Here we show an example of the absorption characteristics of the opsin-based pigment that contributes to depth perception in the jumping spider.

Jumping spiders, as well as most species of spiders, have four pairs of eyes (ocelli), i.e., principal eyes (anterior median eyes), anterior lateral eyes, posterior lateral eyes, and posterior median eyes (Fig. 4). These eyes, particularly in jumping spiders, have several different morphological characteristics and have been suggested to play different

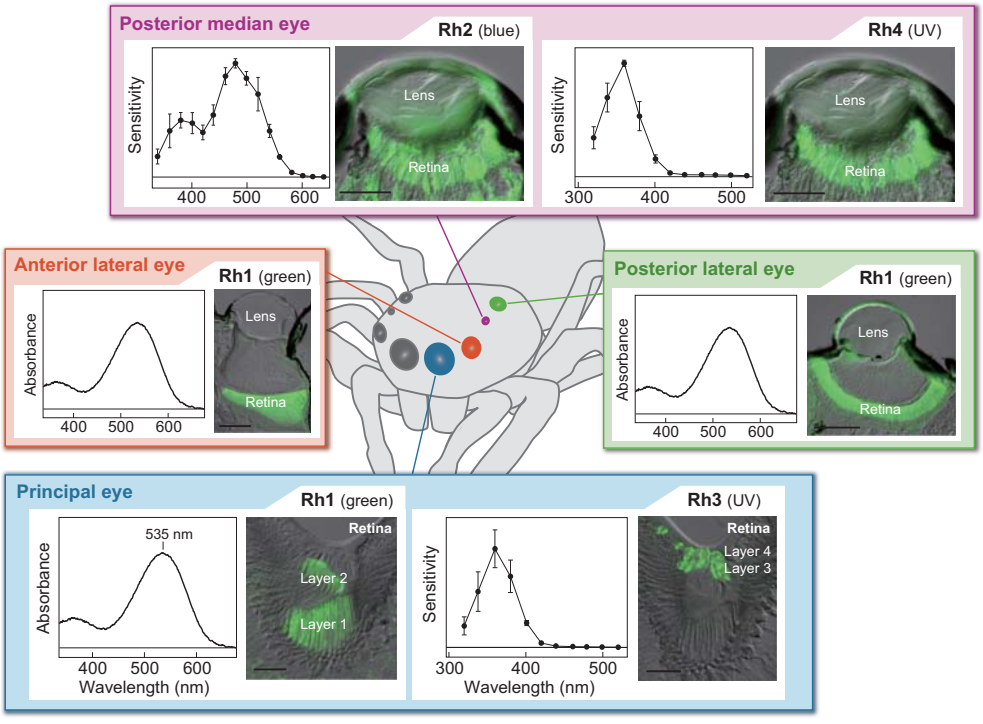


Fig. 4. Schematic diagram of the absorption characteristics and expression of visual pigments in the four pairs of jumping spider eyes. The absorption spectrum of Rh1 was spectroscopically determined in vitro. Absorption characteristics of the other pigments were electrophysiologically determined using transgenic flies that expressed each of Rh2-4 in the photoreceptors of the compound eyes (Nagata et al., 2012), because we did not succeed in the functional reconstitution of these pigments in vitro. The photographs show expression and localization of each visual pigment, which was immunohistochemically examined with specific antibodies. Scales indicate 20 μm (principal eyes and posterior median eyes) or 100 μm (anterior and posterior lateral eyes).

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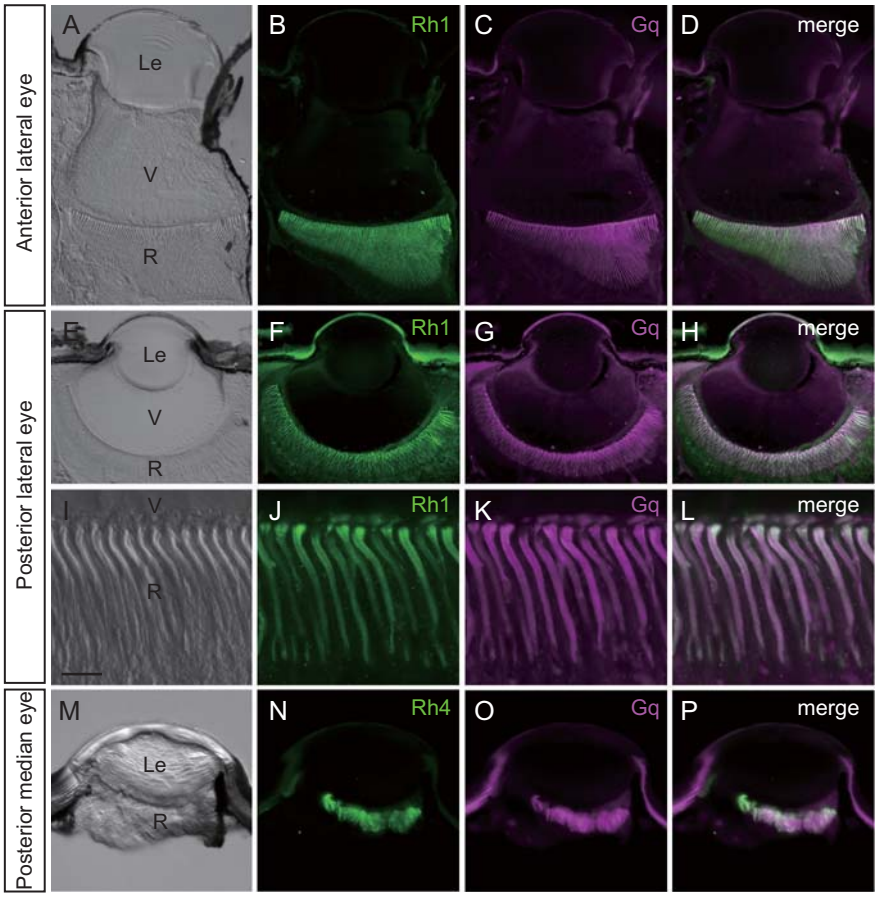


Fig. 5. Co-localization of visual pigments with Gq in secondary eyes. Visual pigments and Gq in the anterior **(A–D)** and posterior **(E–L)** lateral eye and posterior median eye **(M–P)** were labeled with antibodies against Rh1 **(B, F, J)**, Rh4 **(N)** and Gq **(C, G, K, O)**. Scale bar indicates 50 μm **(A, E)** or 10 μm **(I, M)**. Le, Lens; V, vitreous body; R, retina.

roles in visual behaviors (Land and Nilsson, 2002). The eyes also have different expression pattern of the visual pigments, Rh1-4, in a jumping spider, *Hasarius adansoni* (Nagata et al., 2012) (Fig. 4). Visual pigments are colocalized with a common G protein, Gq, in the principal eye (Nagata et al., 2012) and in the other eyes (Fig. 5), suggesting that the Gq signaling cascade underlies phototransduction in all the eyes.

In the anterior and posterior lateral eyes, which mainly function in detection of moving objects (Land, 1971; Zurek and Nelson, 2012), almost all the photoreceptors express green-sensitive Rh1 (Fig. 4, orange and green panels), indicating that these eyes monochromatically detect moving objects. *Drosophila* also have monochromatic motion vision based on a single visual pigment (Yamaguchi et al., 2008). These facts imply that monochromaticity might be important for highly sensitive motion vision. Rh1 is predominantly expressed in all the eyes except for the posterior median eyes, suggesting that green light might be the most efficient source for visual information in natural habitats of *H. adansoni*.

In the posterior median eyes, two visual pigments, blue-sensitive Rh2 and UV-sensitive Rh4, are specifically

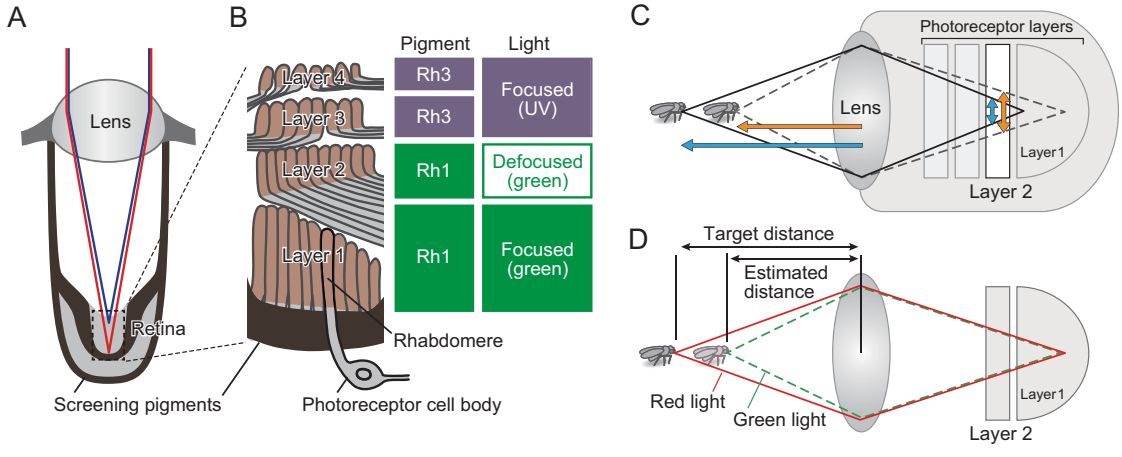


Fig. 6. Tiered retinal structure of the principal eye involved in depth perception from defocus. **(A)** Schematic drawing of the principal eye. Chromatic aberration of the lens results in a longer focal length of long wavelength (red line) than short wavelength light (blue line). **(B)** Schematic representation of a horizontal section of the principal eye retina. Rhabdomeres (light brown) of photoreceptor cells form four tiered layers. The cell body of a photoreceptor cell is shown as an example. **(C)** Schematic drawing of the light from two targets (solid and broken lines) received by Layers 1 and 2. The amount of defocus at Layer 2 (double-headed arrows) depends on the distance between the lens and the objects (arrows). **(D)** Depth perception mechanism based on the amount of defocus account for the shortening of distances estimated by spiders under red light. The same amount of defocus at Layer 2 is generated by red light from the target (red solid line) and green light from a closer point (green broken line).

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expressed (Nagata et al., 2012) (Fig. 4, purple panel). It has been suggested that the posterior median eye might be a vestigial organ because it cannot receive focused images (Blest, 1985). However, the visual pigment repertoire was completely different from the image-forming eyes, or the principal and lateral eyes, which implies that the posterior median eye is rather specialized in an unknown non-image-forming visual function than degenerated. Insect non-image-forming eyes, ocelli, also have photoreceptors expressing UV- or violet-sensitive pigment (Feiler et al., 1988; Pollock and Benzer, 1988; Velarde et al., 2005) and are located at the dorsal side of the head in many insects, similar to that of the jumping spider posterior median eyes. These similarities might suggest that the posterior median eyes could function similarly to insect ocelli, which play some roles by receiving light from the sky (Mizunami, 1995).

The principal eyes have the largest lenses that are located at the front and center of the cephalothorax. It has been suggested that jumping spiders mainly use the principal eyes for visual tasks such as discriminating preys and mates and judging distances. The green-sensitive and UV-sensitive visual pigments, Rh1 and Rh3, are expressed in the principal eye (Nagata et al., 2012) (Fig. 4, blue panel and Fig. 6B), indicating that the principal eye may be involved in color discrimination. In fact, behavioral studies show that the choice of the mate is influenced by the presence or absence of UV light (Lim and Li, 2006; Lim et al., 2007), although there is no direct evidence of color vision.

In the principal eyes, absorption characteristics of the pigments are directly involved in visual functions other than color vision. The principal eye has a unique retina, where rhabdomeres, a photoreceptive portion of photoreceptors, form four tiered layers (Land, 1969b) (Fig. 6A). It was hypothesized that visual pigments in each layer would be different in absorption spectra because light of different wavelengths is focused on each layer due to the chromatic aberration of the lens (Land, 1969b; Blest et al., 1981). In fact, Layer 1, the layer on which green light focused, contains the green-sensitive pigment, whereas in Layers 3 and 4, the layers on which UV light focused, contain the UV-sensitive pigment (Nagata et al., 2012) (Fig. 6B). This indicates that the relationship between the layered structure of retina and the absorption characteristics of the pigments compensates chromatic aberration and allows spiders to receive in-focus images.

In contrast, Layer 2, the layer on which blue, not green, light is focused (Blest et al., 1981), has the green-sensitive pigment, suggesting that this layer could not receive focused images under natural light conditions. If Layer 2 had the blue-sensitive pigment, Rh2, spiders could receive focused images of the blue light with Layer 2. Therefore, the presence of the green-sensitive pigment, not the blue-sensitive one, in Layer 2 indicates that spiders may positively use defocused images for some type of visual information.

Measuring distances or absolutely perceiving depth leads directly to a matter of life or death for jumping spiders because they have to accurately jump onto their preys to catch them. Although the principal eyes were known to be responsible for depth perception in catching preys (Forster, 1979), the mechanism for depth perception was unknown. Because the amount of defocus in Layer 2 reflects the distance to objects, we hypothesized that jumping spiders measure distances based on the amount of defocus in Layer 2 (Fig. 6C). This hypothesis was supported by the observation that the jumping spider can measure distances with only one principal eye; spiders made accurate jumps when all the front-facing eyes, i.e., pairs of anterior lateral eyes and principal eyes, were occluded except for one principal eye (Nagata et al., 2012), demonstrating that spiders have a monocular depth perception mechanism. Presently, the only known mechanisms for absolute monocular depth perception in animals are accommodation (i.e., focal adjustment) and motion parallax (i.e., image motion on the retina). These mechanisms, however, could not account for the accurate jumps with one eye since the principal eyes have no focal adjustment mechanism (Land, 1969a) and spiders showed no behavior that generated significant motion parallax cues before jumps.

We examined the depth perception of jumping spiders by a further behavioral study with green and red lights, which are not discriminated as different “colors” because green and red lights are captured by the same visual cells (Nagata et al., 2012). First, it was confirmed that the spiders could make accurate jumps to target flies under an illumination of green light, which is most effectively received by the visual pigment Rh1 in Layer 2. Furthermore, under a brighter illumination of monochromatic red light, which was as bright as the green illumination to spiders, jump distances were significantly shorter than the target distances. The shortening of jump distances indicates that spiders underestimate the target distances under the red light. Our hypothesis may account for this wavelength effect on depth perception; because chromatic aberration of the lens results in a larger amount of defocus under red light than under green light, distances estimated from the amount of defocus become shorter than actual target distances (Fig. 6D). Furthermore, we experimentally determined optical parameters of the lens and calculated theoretical values of distances estimated from the amount of defocus (Nagata et al., 2012). This theoretical prediction well matched the behavioral data of jump distances both under green and red light, thus strongly supporting our hypothesis.

In the layered retina of jumping spiders’ principal eyes, absorption characteristics of visual pigments, together with the retinal structure, are crucial for visual functions. As mentioned above, if Layer 2 had a blue-sensitive pigment, it would have received focused images and spiders could not have perceived depths. On the other hand, a green-sensitive pigment is needed in Layer 1 so that spiders can finely discriminate visual objects. These provide excellent examples of how absorption characteristics of opsin-based pigments can support not only color vision but also other visual functions in animals.

CONCLUSION

Until now, thousands of opsins have been identified from a wide range of invertebrates and vertebrates and are divided into eight classes. More than one member in each class has been characterized in terms of their molecular properties regarding chromophore binding, absorption spectrum, photoreaction, and G protein activation. We introduced two interesting molecular properties contributing to biologi-

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cal functions. The mosquito homolog of Opn3 can bind 13-*cis* retinal, which is ubiquitously present in animal bodies, and the 13-*cis* retinal-binding ability could be involved in non-visual function in non-visual organs, including the brain. In the principal eyes of the jumping spider, the absorption spectrum of a green-sensitive opsin-based pigment underlies detection of the amount of defocus, and contributes to depth perception from image defocus. However, it remains difficult to explain why different class-opsins drive different G-protein-mediated cascades, i.e., Gs, Gi, Go, Gt, and Gq-mediated ones. Further studies are required to comprehensively understand the functional diversity of opsins.

ACKNOWLEDGMENTS

We thank Dr. Koyanagi (Osaka City University) for his kind discussion. This work was supported in part by grants-in-aid for Scientific Research from the Japanese Ministry of Education, Science, Sports and Culture.

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(Received April 28, 2014 / Accepted June 18, 2014)

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