Paper

Photon Reception and Seeing Light in Squid Eye

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Synopsis: A review on retinal conformation change is given by the present paper. The retinal conformation change occurs by absorption of light. The wavelength of the absorbed light depends upon the structure of retinal. This problem is not so simple because the structures of various retinals are different to each other. Our data depends upon rhodopsin types, but the PDB data is limited. We do not yet have every type of rhodopsin in the PDB data for every condition. As the next step, we review previous literature on rhodopsin-based photoreceptor cells. There are many studies of the cells. Unfortunately the available papers are not in all the areas required. But we can nevertheless understand photreceptor cell function by the steps from absorbing the light to cell potential changes. Our ultimate goal is to find the reason why squids are easily caught only using a lamp. The image is simple: that is the squid can recognize the light at its eye. But we would like to understand the mechanism of light perception of squids. All facts regarding light perception of squids have not yet been resolved. There stands our contribution to understanding squid vision.

1. Introduction

There exist many studies about squid eyes and photon reception [1–35]. Photon reception has at its base the conformation change of retinal [1–35]. We have been studying the conformational change of retinal [61–69]. The molecule referred to as retinal exists in the rhodopsin protein found in the outer segment of rod cells of vertebrate photoreceptors and the rhabdomeres of most invertebrates including squids [35]. Many such cells are found in retinas of squids [35]. For convenience we will refer to all rhodopsin bearing photoreceptors as *rods*. A good review of the structure and function of squid eye can be seen the book ''Squid as Experimental Animals''. H. R. Saibil provided a chapter [19] for this book [35]. The cuttlefish is a class of squid [35–60]. We know that squid is the general name for a class of sea creatures [1–35]. The fishing of squid is usually at night using light provided by a lamp. Many squid are got in this manner. Interestingly the cuttlefish is caught by different manner.

Since almost all quid can detect light catching squid is the good fishing for boat crews. Squid can recognize the brightness of light, and lamp-light is better used for catching the squid at night. Then we can understand the development of Japanese squid fishing well. The mechanisms of light detection by squids have many studies [1–60]. The first step of light recognition is the conformation change of retinal. For this reason, we have been studying retinal, not only the conformation change of cis-trans structure, but also other things about retinal, using Protein Data Bank (PDB) data [61–68]. Retinal attaches to the amino acids of the rhodopsin protein [62–64]. The rhodopsin molecule is a transmembrane protein, and rhodopsin helices form a transmembrane ion channel [19]. The photo-activated rhodopsin binds and activates a G-protein. Thus we know that rhodopsin is the initiating protein of the photo-transduction cascade.

The retinal acts like a gate to conformation changes to rhodopsin. The molecular level func-

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tion of retinal and rhodopsin structure are well-understood via many studies of squid [1–35]. Our work should now step up to the much higher level of squid light recognition. For this purpose, a chapter given by Saibil [19] is better roundup to read. The retina of the squid eye contains many rod cells. The rod cells produce electrical potentials that ultimately governs squid brain function. The brain function decides the squid behavior as the response to light input.

We review photon absorption concentrating upon conformational changes of the retinal molecule. Section 2 summarizes this evidence and other related material. Section 3 summarizes light recognition by squids, with role of rod cells are summarized in Section 3. In Section 4, we summarize all the material and then we conclude that the squid behavior at the night to the lamp-light of a boat is to the squid just like solar brightness.

2. Retinal conformation and Rhodopsin function

We have been studied the structure of squid retinal. The structure of retinal has the alternative form of trans-configuration and 11-cis configuration as shown by quantum orbital distributions [61]. Fine structural changes are caused by the structure of the cis-trans conformation of retinal driven by light absorption [61]. We also quantified that change in terms of the distance between nearest pairs of atoms of retinal calculated from PDB data [62]. We confirmed that the retinal ring part faces the amino acid with the ring part of Phenylalanine and tryptophan [63]. In the Mem KU paper [64], we explored vector analysis of carbons ^{10}C–^{12}C of squid retinal. In a second round of vector analysis of squid retina, we presented each line between carbons of retinal as three dimension vectors and applied vector analysis [65]. The energy of wavelength for visible light was estimated as the squid absorbs in-coming lamp-light [66]. The wavelengths of Lamps have a continuous distribution across intensity. The exact distribution depends upon the lamp. We understand light in terms of energy [66]. The structure change of retinal by absorbing of the light was also considered [67]. It is difficult to estimate what intensity distribution should be taken for actual squid eyes so that we estimate the energy for visible light over the range from blue to red [67]. We further examined the PDB data using the RasMol software representation for viewing [68]. We published pictures of PDB data on RasMol views [68]. This concludes our studies on retinal structures.

Rhodopsin function is tightly dependent on the structure of the included retinal. Following Hargrave's lecture [69], the rhodopsin is the protein that interacts with other molecules—substrates, inhibitors, ions, nucleic acids, carbohydrates, lipids, and other proteins—to provide the ways in which they carry out their various functions. The rhodopsin molecules show many functions so we cannot summarize them briefly. The photon absorbing molecule is the retinal in the rhodopsin. The retinal cis-trans conformation change [61–68] effects the structure change of rhodopsin [69].

We show a schematic picture of rhodopsin in figure 1. There are many helices to form the rhodopsin protein. In figure 1, every helix is a coiled one. We denoted a line to connect the helix and that structure is determined by the amino acid residues. Rhodopsin is a transmembrane molecule containing n-pieces of rhodopsin in the outer segment of each rod cell. The rhodopsins exist on the disk membrane of outer segment of rod cell of vertebrates and in the tubular microvilli of invertebrate rhadomeres as in the squid. The structure of a vertebrate rod cell is schematically shown at

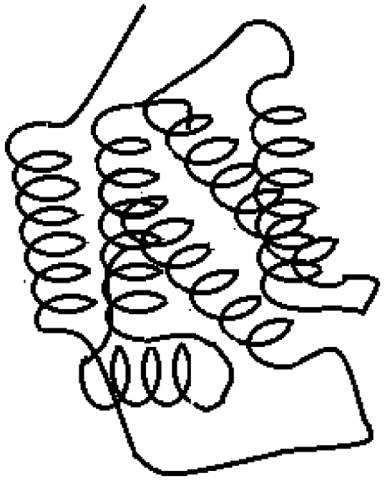

Fig. 1 schematic picture of rhodopsin
The coiled parts are helices with connected lines that consist of amino acids.

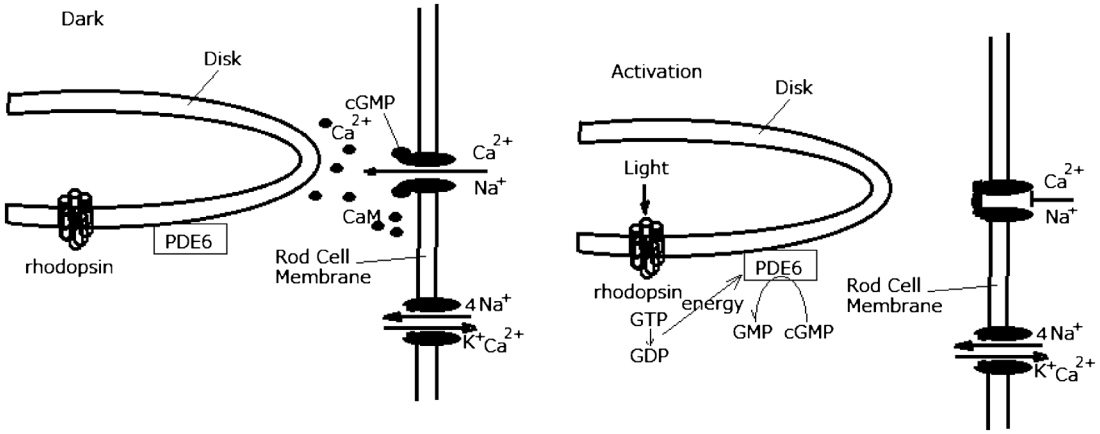

Fig. 2 Scheme for light activation of rhodopsin

figure 2.

The retinal is attached at the pore area of rhodopsin, but it is not shown in figure 1. Figure 1 is only a schematic illustration of a rhodopsin. The rhodopsin forms an ion channel path with gating proteins to realize the rhodopsin functions. Rhodopsin function is schematically understood by figure 2. Inward current of Ca^{2+} and Na^{+} is blocked by closed channel in brightness of light. Rhodopsin catalyzes GTP and releases energy by the chemical reaction (GTP->GDP + Pi + energy). The energy comes from the third phosphate of GTP is catalyzed by rhodopsin protein. The energy transport thus occurs via absorption of light by the retinal molecule. The absorption drives the cis-trans conformation change of retinal. We know rhodopsin function from figure 2. We have no idea why rhodopsin exist on disks or microvilli. Invertebrate opsins are elongated and the microvilli thus constrain the rotation of the opsin causing the retinals to be somewhat aligned

making the microvilli dichroic. Orthogonal sets of microvilli allow squids and other animals to see linear polarization, which probably substitutes for color vision. Potential change is observed at rod cell as the voltage difference between inner and outer membrane of rod cell.

Rhodopsin is activated by light. Activated rhodopsin catalyze GTP to GDP so that this catalysis produce the decomposition energy from chemical reaction (GTP- > GDP + Pi + energy). PDE 6 get this energy and opens on the cGMP to GMP. transition When rhodopsin is activated by light, inward current of Ca2+ and Na+ is stopped by the closed channel.

3. Rod cell and Light

Usually getting squid at night employs fish-boats and lights. Squid can recognize the incoming light by their eyes. The rod cells in the squid eye catches the light. Lights have an uneven distribution between wavelength and energy. The absorption of light is caused by the conformation change of retinal. The conformation change means structure change between trans-form and cis-form. Retinal binds to rhodopsin molecule at the inside of pore formed by rhodopsin on the disk mem-

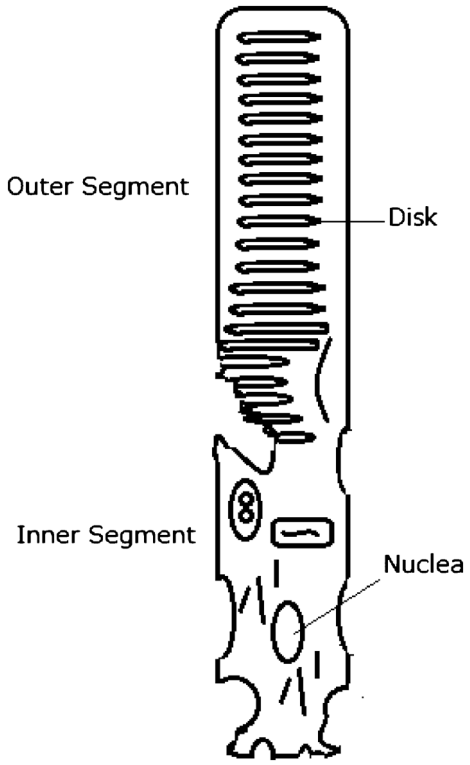

Fig. 3 Schematic Picture of Rod cell
The outer segment of a vertebrate rod cell, is occupied by many disks. Rhodopsin molecules exist in the membrane of disk of outer segment. In most invertebrate eyes the membranes are rolled into tubular microvilli. An exception are the day-time photoreceptors of scallops in which the photoreceptive membranes are rolled like paper towels where the axis about which the membranes are rolled pointing at the light. The scallop's night photoreceptors have microvilli like those of squid retinas.

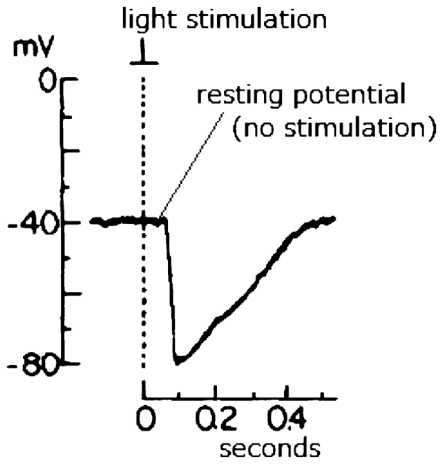

Fig. 4 Time course of potential change of rod cell after brief light stimulation
As seen the figure, a negative potential change appeared after light stimulation to the rod cell. from Dr. Janet Fizakerley homepage Copy right 2015 University of Minnesota Medical School Duluth, and we add a bit letters in the original figure.

brane. As seen from figure 3, rhodopsin exists on the outer segment of rod cell. The outer segment has a shell membrane and rhodopsin locate on the shell membrane from outside and inside of disk membrane with gating units. [35].

Following the homepage of Janet Fitazakerly at the University of Minnesota, the potential change occurs by light activation. Potential change against the time is illustrated by figure 4. If there is no light, the potential is a flat with small fluctuations (noise, mainly from failed intermittent stages in the catalytic cascade). The potential size depends somewhat upon the species, although are governed principally by the Nernst and Goldman equations for particular ion species. Figure 4 is seen when we chose one of retrieval results.

In the rod cell, conformation change of retinal by absorbing light is the first step of light activation. The retinal conformation change leads to structure change of rhodopsin. The retinal received the light energy and then that energy gates chemical energy stored in chemical bonds. This chemical energy induces the decomposition of GTP. The chemical reaction is written GTP->GDP +Pi+energy. The released energy makes the structure change: cGMP to GMP. This structure change is catalyzed by the enzyme phosphodiesterase (PDE6). This enzyme utilizes the released energy of GTP decomposition. The enzyme actively works in the brilliant conditions brought by lamp-light. The potential of rod cells is temporally changed to a more negative value as shown as figure 4. We only show potential change by light stimulation in the figure. Figure 4 says about a 40 mV change is seen against time development. This is the response of rod cell by light stimulation.

The rod cell function for absorbing the light has been summarized here. The details of the photochemical reaction were also reviewed in this section. Rod cells are found in the retina, and potential changes of the rod cells by light stimulation causes communication across retina. The potential change of the rod cells is transformed by other retinal cells and then reaches squid brain via action potentials, and the brain is controlled by those potential changes to produce a perception of the squid brain. The response of squid brain generates the behavior of the squid. The night behavior of

squid around the boats causes the squid fishing of the boats. The rod cell action by light is summarized in this section.

4. Summary and Discussion

The behavior of squid to see lights in the night is brought by a pathway, namely, retinal conformation change->rhodopsin function change->rod cell function->impulse movement of nerve cell->light recognition in the squid brain->response action of squid. This pathway of the squid runs within a very short time when the squid sees the light on the boat. Fishers know the squid behavior for the light and they get many squids. The behavior of squid is induced by rod cells in retina when the squid is seeing the light. The squid brain perceives brilliance or darkness, and squids come to brilliant light. Thus fisher gets the many squids using lamp-light. The behavior is different for squid or cuttlefish. The squid swims like a rocket with high speed, whereas the movement of cuttlefish is not high, namely it is not a rocket. Squids are fished at night using lamps and boats. Cuttlefishes are an alternative fishing target. In Japan, squids are used as the dried shredded ones. These dried squids are edible as foods. We know that Japanese people like the dried squid, so that owners of fish boats fishes the squids in Hokkaido prefecture because of easier fishing of squids compare than other areas.

One of the authors (Masashi Kito) has an interest squids, therefore he suggested that we write papers about squids. As stated above, we studied the retinal molecule in detail. But our overall goal is to understand what a squid is. The squid can perceive light, namely it understand dark and bright. Hence we should know the mechanism of understanding light in a squid. The pathway for understanding light is to know the root from light absorption through to the response behavior of squid. In the present paper, we consider rod cell functions. Since rod cell has the function of absorbing light and to mediate chemical reactions. As mentioned this paper, the required chemical energy is obtained by the decomposition of GTP (GuanineTriPhosphate). The required energy arises from the chemical bonding of the third phosphate. This may be written down as the chemical reaction GTP->GDP + Pi (phosphate) + energy. The chemical reaction needs water (chemical symbol is H_2O). When we write the present paper, we know that a group of guaninephospate (GTP, GDP, GMP, cGMP) plays an important role to realize photon absorption to the potential change of rod cells. The function of rod cell is much the same for any species in as much as eyes have rod cells in retina. The rod cell potential change occurs by closing the channel to stop the inward current of Na^+ and Ca^{2+}.

We should consider the further steps of the neurons connected with the rod cell, and ultimately the function of brain. The behavior of the squid to recognize the light appears to occur automatically. Fishers in boats can get many squids at the same time only using lamps and a fishing net. Extensive works about rod cells have been carried out so it is difficult to find new evidence. The PDB data of rhodopsin exist, and each PDB data contains retinal molecule data. The crystallized condition can be controlled so we know what configurations retinal molecules may undergo. We have therefore infered information about retinal from the PDB data. We reviewed rod cell function and what things happen there. We may consider further visual processing steps work in the future.

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