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Identification and localization of visual pigments in the retina of the moth, *Antheraea polyphemus* (Insecta, Saturniidae)

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Summary. In the compound eye of the moth *Antheraea polyphemus*, three types of visual pigments were found in extracts from the retina and by microspectrophotometry in situ. The absorption maxima of the receptor pigment P and the metarhodopsin M are at (1) P 520–530 nm, M 480–490 nm; (2) P 460–480 nm, M 530–540 nm; (3) P 330–340 nm, M 460–470 nm. Their localization was investigated by electron microscopy on eyes illuminated with different monochromatic lights. Within the tiered rhabdom, constituted of the rhabdomeres of nine visual cells, the basal cell contains a blue- and the six medial cells have a green-absorbing pigment. The two distal cells of most ommatidia also have the blue pigment; only in the dorsal region of the eye, these cells contain a UV-absorbing pigment, which constitutes a portion of only ~5% of the visual pigment content within the entire retina. The functional significance of this distribution is discussed.

Key words: Compound eye – Photoreceptor cells – Microvillar structure – Visual pigments – Silk moth, *Antheraea polyphemus*

The superposition eyes of moths are very suitable objects for the investigation of visual pigments in insects. A substantial part of their retina consists of densely packed rhabdomeric microvilli, which form tiered rhabdoms. A sphingid moth, *Deilephila elpenor*, was the first insect in which a trichromatic system of visual pigments could be characterized by microspectrophotometry and by spectrometric measurements on extracts (Höglund et al. 1973; Schwemer and Paulsen 1973). Its components are very similar to those expected in the worker honey-bee, in which the spectral sensitivity curves of single receptor cells, obtained from intracellular electrophysiological measurements, were already known at that time (Autrum and v. Zwehl 1964). Approximately the same system as in *Deilephila* has been found in another sphingid species, *Manduca sexta* (Schwemer and Brown, cited in Schwemer and Langer 1982; White et al. 1983), but in the noctuid moth, *Spodoptera exempta*, there is a tetrachromatic system consisting of almost the same three components as in *Deilephila* and in addition a yellow-red-sensitive pigment (Langer et al. 1979); a similar type of pigment occurs also in several species of butterflies (Bernard 1979). By electron-microscopic investigations, the distribution of the visual pigments among the different morphological types of receptor cells within an ommatidium could be found, using eyes after illumination with different monochromatic lights (Welsch 1977; Meinecke and Langer 1984).

Until now, species belonging to only two families of moths have been investigated which differ with respect to their colour-vision systems. Therefore, a species from another large family, the Saturniidae, was investigated. As example, the silk-moth *Antheraea polyphemus* was used, which is – in contrast to *Deilephila* – an exclusively night-active species.

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Materials and methods

Imagoes of *Antheraea polyphemus* Cramer were used for the present experiments. Pupae were obtained from the Max-Planck-Institut für Verhaltensphysiologie at Seewiesen and kept at 23 to 25° C until emergence. Moths of 8 to 10 days of imaginal age were dark-adapted for 2 h before the experiments. Retinae were prepared after removing cornea and pigment cell layer including crystalline cones by cutting with a razor blade under red dim light. This preparation was also carried out on heads that were deep frozen (at −80° C) for several weeks.

Spectrophotometry on extracts. Prepared retinae were collected in 1 ml ice-cold Sörensen phosphate buffer (pH 6.5) and washed several times on a centrifuge at this pH or at pH 8.2. After replacing the buffer by 3% digitonin solution (pH 6.5), 2.5 µl per retina, they were extracted at room temperature for 2 h. In some cases hydroxylamine was added to the extract to give a final concentration of 0.1 M. The spectral absorbance of the extract was measured by a recording two-wavelength double-beam spectrophotometer (Hitachi 356). An additional light source (Xenon arc lamp XBO, 150 W, Zeiss), equipped with Schott IL interference filters, allowed monochromatic illumination of the extract within the cuvette while staying in measuring position. Measurements were performed at room temperature or at 5° C by cooling the cuvette chamber.

Microspectrophotometry. Slices of a retina from a freshly removed head were cut with a razor blade after freezing the eye over dry ice. Slices, in insect Ringer solution (Ephrussi and Beadle 1936), were placed between two quartz coverglasses. The coverglasses were mounted in an object

holder made of metal, which could be continuously cooled on the microscope table by using Peltier elements. The measurements were made by the microspectrophotometric apparatus described by Schlecht et al. (1978). Rhabdoms were usually measured by a small light beam in orthodromic direction; in some cases – especially for the distal part of the rhabdom – the measuring beam was oriented perpendicular to the optical axis of the ommatidium. Measuring fields of 10 to 30 μm in diameter were used.

Difference spectra were used for identification of visual pigments. They were obtained from two succeeding measurements of a given area before and after illumination with monochromatic light from the monochromator of the microspectrophotometer for 1 to 5 min. A suitable wavelength as adaptation light shifted the rhodopsin-metarhodopsin-system to a new equilibrium. The difference spectra are free from absorbance of photostable pigments and influences of stray-light within the preparation. The following pairs of wavelengths were used for adaptation: 450/560 nm, 550/450 nm, 450/350 nm. From the difference spectra obtained, λ_{max} values of the pair of rhodopsin and metarhodopsin present in the measuring area and the relative heights of their absorbances (in the present maxima) were calculated by a computer procedure (Langer et al. 1982). This procedure compares the directly measured difference spectrum with computed differences between various spectra of rhodopsin and metarhodopsin in order to obtain the best fit. These latter spectra were derived from the nomogram of Ebrey and Honig (1977).

The light-induced changes in absorbance are reversible. Therefore, difference spectra can be obtained repeatedly by alternating illuminations with two adequate wavelengths. The difference spectra given in the figures of this paper are means of several (mostly 8 or 10) curves measured at the same site in the preparation. Within the slice preparation from a retina, usually 2 or 3 sites were measured, each covering up to three rhabdoms. Successful measurements were obtained from 57 sites in about 40 retina preparations.

Electron microscopy. Intact, dark-adapted imagoes were anaesthetized with chloroform, placed on a closely fitting perspex holder, and secured by placing adhesive tape across the wings. The head of the animal was illuminated from ventral through a hole in the holder using collimated light from a 30 W tungsten microscope lamp, which passed through one of the following interference line filters (type IL, Schott, Mainz). 114 animals, treated in this way, and 65 unilluminated controls were examined in this experiment. The respective illumination and energy were as follows:

Table 1

Transmission maximum	Quanta $\frac{}{cm^2 \cdot s}$	W $\frac{}{m^2}$
678 nm	$8.5 \cdot 10^{15}$	24.9
648 nm	$6.54 \cdot 10^{15}$	20.0
604 nm	$5.81 \cdot 10^{15}$	19.1
543 nm	$5.36 \cdot 10^{15}$	19.6
500 nm	$3.12 \cdot 10^{15}$	12.4
447 nm	$1.17 \cdot 10^{15}$	5.2
415 nm	$4.12 \cdot 10^{14}$	1.97
352 nm	$4.43 \cdot 10^{13}$	0.25

After a period of illumination between 15 min and 1 h, the animals were decapitated and the eyes excised in the initial fixative solution. The specimens were prefixed for 6 to 8 h at 4° C in a solution of 2% paraformaldehyde and 2.5% glutaraldehyde buffered to pH 7.3 with cacodylate. Tissues were briefly washed with the same buffer and postfixed for 3 h in 2% osmium tetroxide buffered with cacodylate. Then the specimens were dehydrated in a graded series of ethanol and – using acetone as the intermediate – embedded in ERL 4206 low viscosity epoxy resin (Spurr 1969). Sections were cut on a Reichert Om U2 ultramicrotome, stained with lead citrate (Venable and Coggeshall 1965) and observed in a Siemens Elmiskop 101 electron microscope.

Results

1. Spectrophotometry of extracts

Partial bleaching. A digitonin extract from about 40 retinae, containing hydroxylamine, was illuminated by monochromatic lights at room temperature for successive bleaching of different receptor pigments. A difference spectrum with maximal absorbance change (ΔE) was obtained after 20 min illumination with 590 nm. It demonstrates a decrease of absorbance between 630 nm and 415 nm and an increase between 415 nm and 330 nm (Fig. 1a); its minimum is at 515 nm and its maximum at 370 nm. This points to a "green" visual pigment.

A second difference spectrum was obtained after illumination with 472 nm for 10 min. It has a maximum between 360 nm and 370 nm and a minimum between 460 nm and 470 nm (Fig. 1b). This is the difference between a "blue" visual pigment and its retinal oxim.

A third illumination by 354 nm caused a decrease between 310 nm and 365 nm and an increase between 365 nm and 545 nm (Fig. 1c). This difference spectrum is due to a "UV" visual pigment.

Evidently, the green receptor pigment is most prominent in the extract. From the absorbance changes in several extracts, this pigment can be estimated to make up three quarters of the entire visual pigment content of the retina. The blue pigment may be about 20% and the UV pigment only 5%.

Demonstration of metarhodopsins. Measurements of spectral absorbance in extracts without hydroxylamine were made at +5° C to detect metarhodopsins. By illumination with 590 nm for 15 s a difference spectrum was obtained with a maximum at about 470 nm and a minimum at about 550 nm; its isosbestic point was at about 520 nm. The computer analysis of this spectrum indicates a rhodopsin with λ_{max} at 512 nm and its metarhodopsin with λ_{max} at 492 nm (Fig. 2a). The ratio between the absorbance of metarhodopsin and rhodopsin in their respective maxima was F = 1.21. This green-absorbing visual pigment was totally bleached by 590 nm illumination for 40 min to free retinal and opsin. Afterwards, the extract was illuminated with 472 nm light for 30 s and a second difference spectrum was obtained. It had a maximum at about 540 nm and a minimum at about 450 nm. This indicates a rhodopsin with

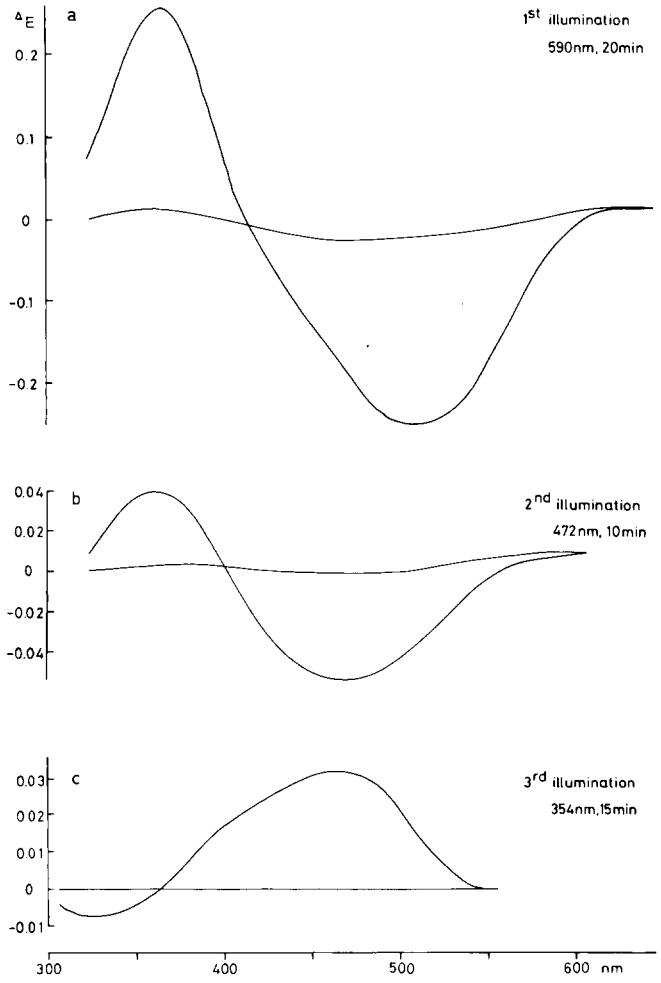

Fig. 1. Three visual pigments identified by selective bleaching in solution. 40 retinae were extracted in 0.1 ml digitonin solution with hydroxylamine and successively bleached by monochromatic lights of three different wavelengths. A new base-line was taken before changing the wavelength of illumination. Note the significantly different concentrations of the three pigments

λ_{max} at 480 nm and its metarhodopsin with λ_{max} at 532 nm; F = 1.41 (Fig. 2b). After bleaching of this second visual pigment with 472 nm, a third one could be demonstrated by means of its difference spectrum, obtained from alternating illuminations with 354 and 472 nm, respectively: These wavelengths caused a large change in absorbance around 460 nm and a small change around 330 nm. The difference curve indicates a rhodopsin with λ_{max} at 331 nm and its metarhodopsin with λ_{max} at 461 nm; F = 2.28 (Fig. 2c). The metarhodopsin of this UV-absorbing visual pigment is thermostable also at room temperature and can be completely reconverted to its rhodopsin by blue light.

2. *Microspectrophotometry*

In slice preparations obtained by tangential sections through the retina, circumscribed areas were used for microspectrophotometric measurements indicating their rhabdom structure by refraction and the absence of screening

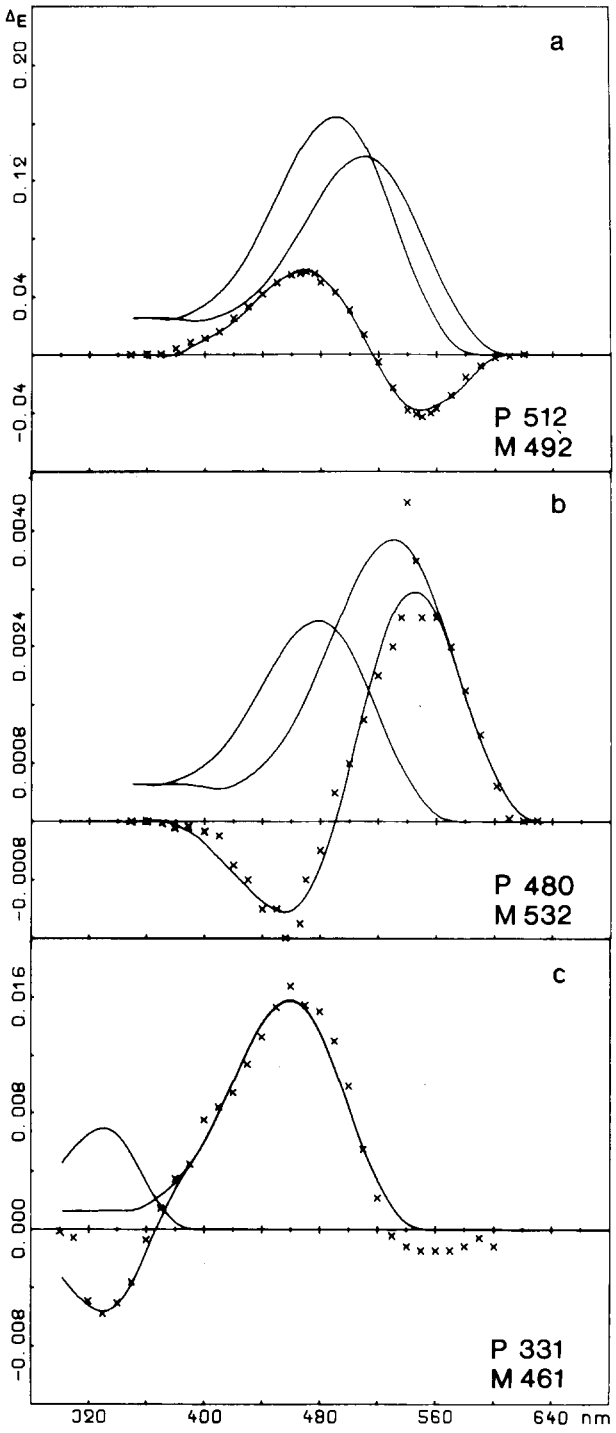

Fig. 2a–c. Evidence for the presence of stable metarhodopsins in visual pigment extract at low temperature. 40 retinae were extracted in 0.1 ml digitonin solution without hydroxylamine and successively illuminated at +5° C. Illuminations: **a** with 569 nm for 15 s; **b** with 472 nm for 30 s; **c** with 354 nm and 472 nm alternating for 5 min each. Before illuminations **b** and **c** the preceding pigment was completely destroyed by saturating illumination. Difference curves are given as measuring points (*crosses*) in **a**, **b** and **c**. They were analyzed by comparison with two standard spectra of visual pigments according to the Ebrey-Honig-nomogram. The optimal pair of visual pigment (*P*) and metarhodopsin (*M*) and the calculated difference spectrum are shown as *solid lines*

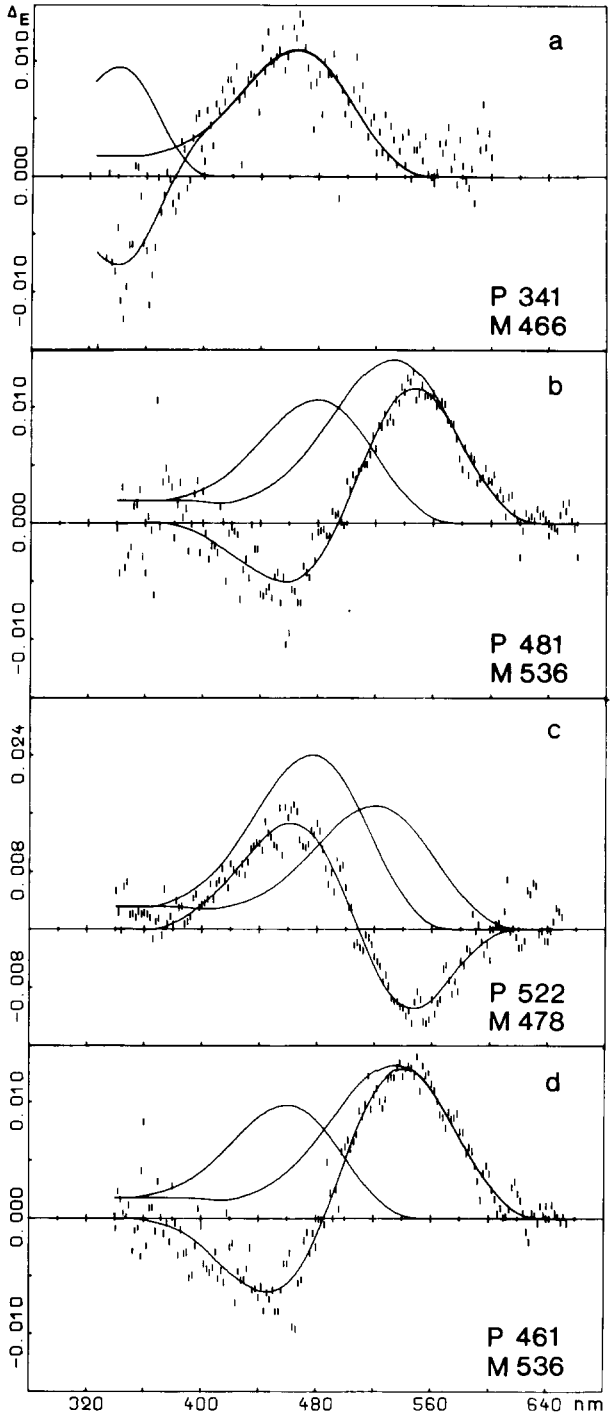

Fig. 3a–d. Typical microspectrometric measurements of visual pigments in slices from different layers of the retina (see "Materials and methods"). The difference spectra (indicated by *points*) were computed as in the case of Fig. 2 to obtain the best fitting pair of rhodopsin and metarhodopsin spectra. **a** Distal layer of the retina from the dorsal region of the eye. Illumination with 350 nm and 450 nm: UV receptor pigment. **b** Distal layer of the retina from the central region of the eye. Illumination with 450 nm and 550 nm: blue receptor pigment. This pigment is also found distally in the retina of the ventral region of the eye. **c** Medial layer of the retina. Illumination with 560 nm and 450 nm: green receptor pigment. **d** Proximal layer of the retina. Illumination with 450 nm and 550 nm: blue receptor pigment. Difference spectra as shown in **c** and **d** are found in all regions of the eye

pigments. In such sites, alternating adaptations to lights of wavelengths 560 nm and 450 nm, respectively, produced difference spectra as shown in Fig. 3c. A maximal decrease in absorbance is seen at 540 nm and a maximal increase at 460 nm. Computer analysis of a series of ~10 of these difference spectra, taken at the same site, gave the mean λ_{max} values of this rhodopsin at 522 nm and of the associated metarhodopsin at 478 nm (Fig. 3c). The maximal extinction of this metarhodopsin is higher than that for rhodopsin by a factor F = 1.4. This green visual pigment is present in every region of the eye.

In slices from the proximal parts of the ommatidia, another difference spectrum was obtained after adaptations to 450 nm and 550 nm, respectively. It shows a minimum at 440 nm, a maximum at 530 nm and an isosbestic point at 490 nm (Fig. 3d). The computer analysis revealed a rhodopsin with $\lambda_{max} = 461$ nm and a corresponding metarhodopsin with $\lambda_{max} = 536$ nm, with a factor F = 1.4.

The same type of visual pigment was also found in slices of the distal parts of the ommatidia taken from the central or ventral region of the eye (Fig. 3b). However, in slices of the distal parts of the ommatidia, taken from the dorsal eye region, a difference spectrum was additionally found after alternating adaptations to 350 nm and 450 nm lights, respectively. This demonstrates a rhodopsin with λ_{max} at 341 nm and a metarhodopsin with λ_{max} at 466 nm, F = 1.16 (Fig. 3a). This limitation to the most dorsal region of the eye may be the reason for the surprisingly low overall concentration of this UV visual pigment within extracts from the whole retinae (Fig. 1c).

To check these results, separate extracts by use of digitonin were made from retinae divided in dorsal and ventral halves. Spectrophotometry after partial bleaching in the presence of hydroxylamine demonstrated the presence of the UV visual pigment only in the dorsal half of the eye, while in the ventral half no visual pigment with λ_{max} in the UV part of the spectrum could be found.

Attempts were made to demonstrate a "red"-absorbing visual pigment using microspectrophotometry on slices as well as spectrophotometry on extracts, which were illuminated with long wavelengths ($\lambda \geqq 600$ nm). In contrast to other moths and to butterflies, in which such a visual pigment has been found to occur, no evidence for such a rhodopsin could be obtained in *Antheraea polyphemus*.

There were no differences found between males and females with respect to the types of rhodopsins, their relative amounts in extracts and their distribution within the retina, as revealed by microspectrophotometry.

3. Electron microscopy

By illumination of intact animals with monochromatic lights of different wavelengths, structural changes were induced in the rhabdomeres of their visual cells. Depending on the light intensity and the duration of exposure, the microvilli gradually lost their regular structure, first showing slight bending, then irregular deformations, which appeared to be caused by swelling of microvilli, and finally exhibiting a complete destruction of the rhabdomere (Welsch 1977; Meinecke and Langer 1984; Anton-Erxleben and Langer, in preparation). Such changes of microvillar structure have not been found in any of the 17 eyes of dark-adapted animals prepared under infrared light.

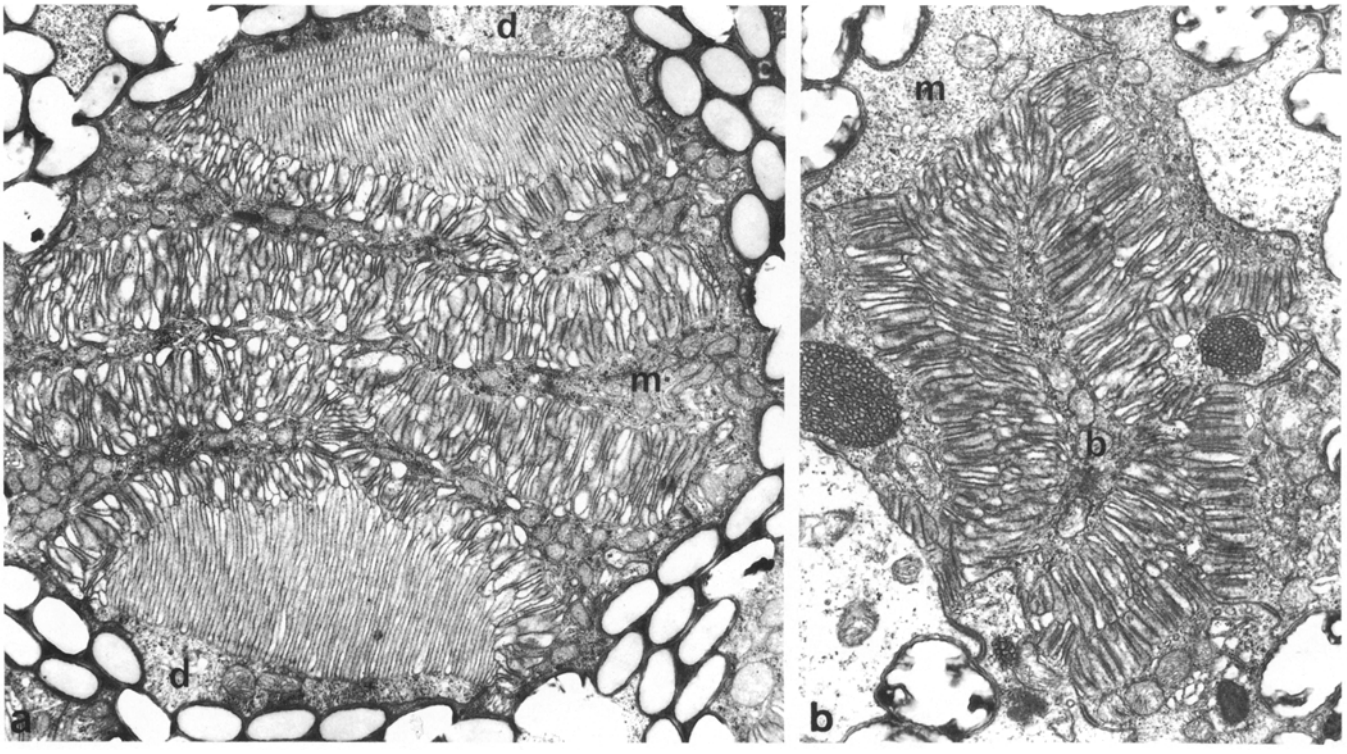

Fig. 4. a, b Cross sections through ommatidia in the dorsal region of the eye after illumination with 543 nm for 40 min. **a** Medial part of an ommatidium: Two distal cells (*d*) with unaffected rhabdomeres (UV receptors) and six medial cells (*m*) with affected rhabdomeres (green receptors). **b** Proximal part of an ommatidium: Basal cell (*b*) displaying circularly arranged microvilli in the center (blue receptor) surrounded by six medial cells (*m*) (green receptors); all seven rhabdomeres affected. **a** × 8000; **b** × 10000

At a given illumination[1], the degree of structural changes was found to depend on the wavelength of incident light. From their reactions, it was possible to estimate the spectral sensitivities of different morphological types of retinula cells.

Green illumination. By illumination with light of 543 nm, the microvilli of the medial cells (Fig. 4a) and of the basal cell (Fig. 4b) undergo typical changes, whereas the microvilli of the distal cells remain unaffected. By increasing the illumination, the distal cells of the central and ventral regions are also affected, but give weaker reactions. Also lights of longer wavelengths (up to 648 nm) are still effective, but to a lesser degree.

Blue illumination. By illumination with light of 447 nm, the microvilli of the basal cell (Fig. 5b) and of the two distal cells (Fig. 5a) react strongly. In the medial cells, the same illumination causes responses which are considerably weaker. These effects were found only in the ommatidia of the central and ventral regions of the eye, whereas in the dorsal region the two distal cells of the ommatidia show no response. Within a small field between the central and the dorsal region of the eye, occasionally only one distal cell of an ommatidium is affected by blue light.

Ultraviolet illumination. Since UV light is absorbed by all visual pigments, the microvilli of all receptor cells should be affected by high UV intensities. Therefore, it was of special interest, whether the two distal cells in the dorsal region of the eye are much more sensitive than all other cells. By illumination with 352 nm these cells indeed show a much stronger reaction than the others (Fig. 6a). Such cells are totally unaffected by illuminations with light of longer wavelengths. Towards the central region of the eye, occasionally only one distal cell of the ommatidium (see above) is affected (Fig. 6b).

"Hypersensitive" cells. In general, exposure to red light is ineffective. However, after illumination with light of 648 nm, single medial cells exhibit a very strongly altered microvillar structure (Fig. 7a). Such a reaction was also found in single medial cells after illumination with green, blue, or UV light (Fig. 7b). Their reaction was still stronger than that of adequately illuminated cells. The same effect was seen even in eyes of dark-adapted animals, which had been prepared under dim red light (interference filter 678 nm), but never after preparation under infrared light. Obviously, these cells exhibit an unusual high sensitivity not only to their adequate, but also to illumination with long-wavelength light. Therefore, these cells are characterized as "hypersensitive" cells.

Distribution of spectral sensitivity types. The rhodopsin of the two distal cells is most sensitive to light of short wavelengths. About 20% of the distal cells – restricted to the

1 The term "illumination", as it is used here, includes the duration of the light influence, the intensity of the light source and the geometry of the incident light. This last part of the definition is variable with the position of the ommatidium within the eye, causing a considerable difference between effective quantum fluxes into rhabdoms of ommatidia belonging to different parts of the eye. For this reason, the real effectivity of a certain light intensity cannot be estimated, and only comparisons between the effects on the rhabdomeres of the different visual cells within one and the same rhabdom are made

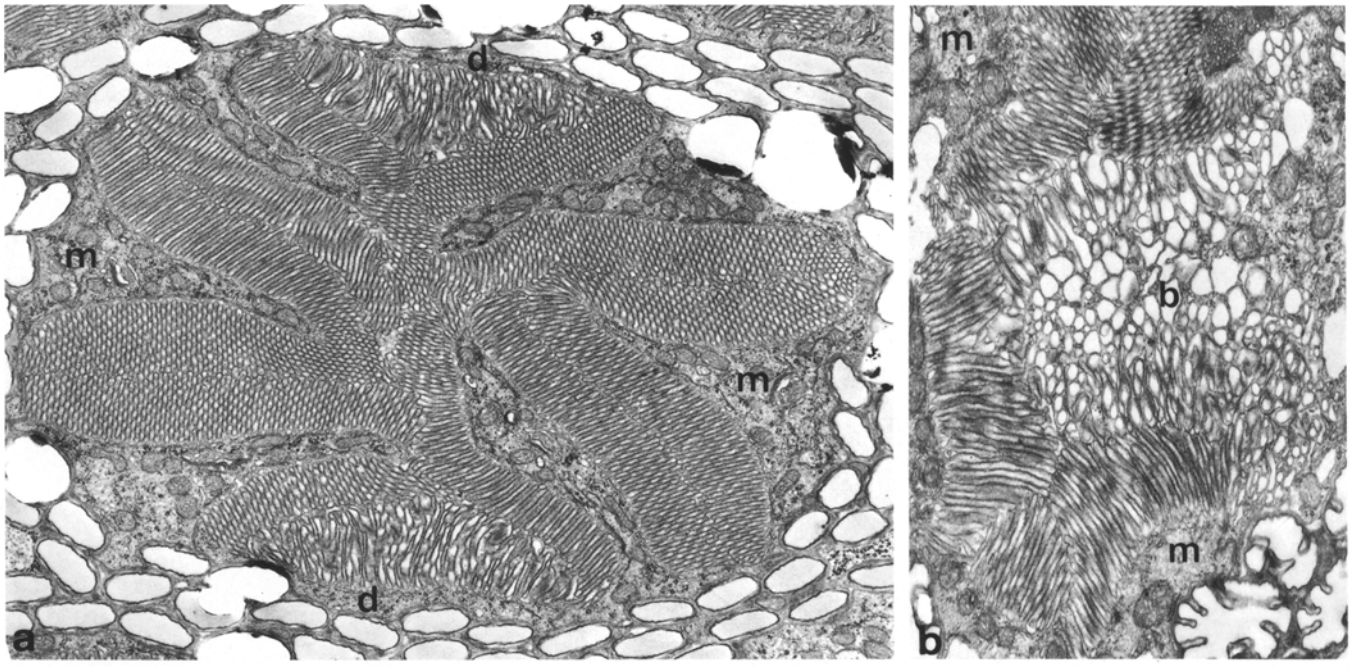

Fig. 5. a, b Cross sections through ommatidia in the ventral region of the eye after illumination with 447 nm for 60 min. **a** Medial part of an ommatidium: Two distal cells (*d*) with affected rhabdomeres (blue receptors) and six medial cells (*m*) with unaffected rhabdomeres (green receptors). **b** Proximal part of an ommatidium: Basal cell (*b*) with strongly affected rhabdomere (blue receptor) in the center, surrounded by six medial cells (*m*) (green receptors). **a** ×9000; **b** ×12000

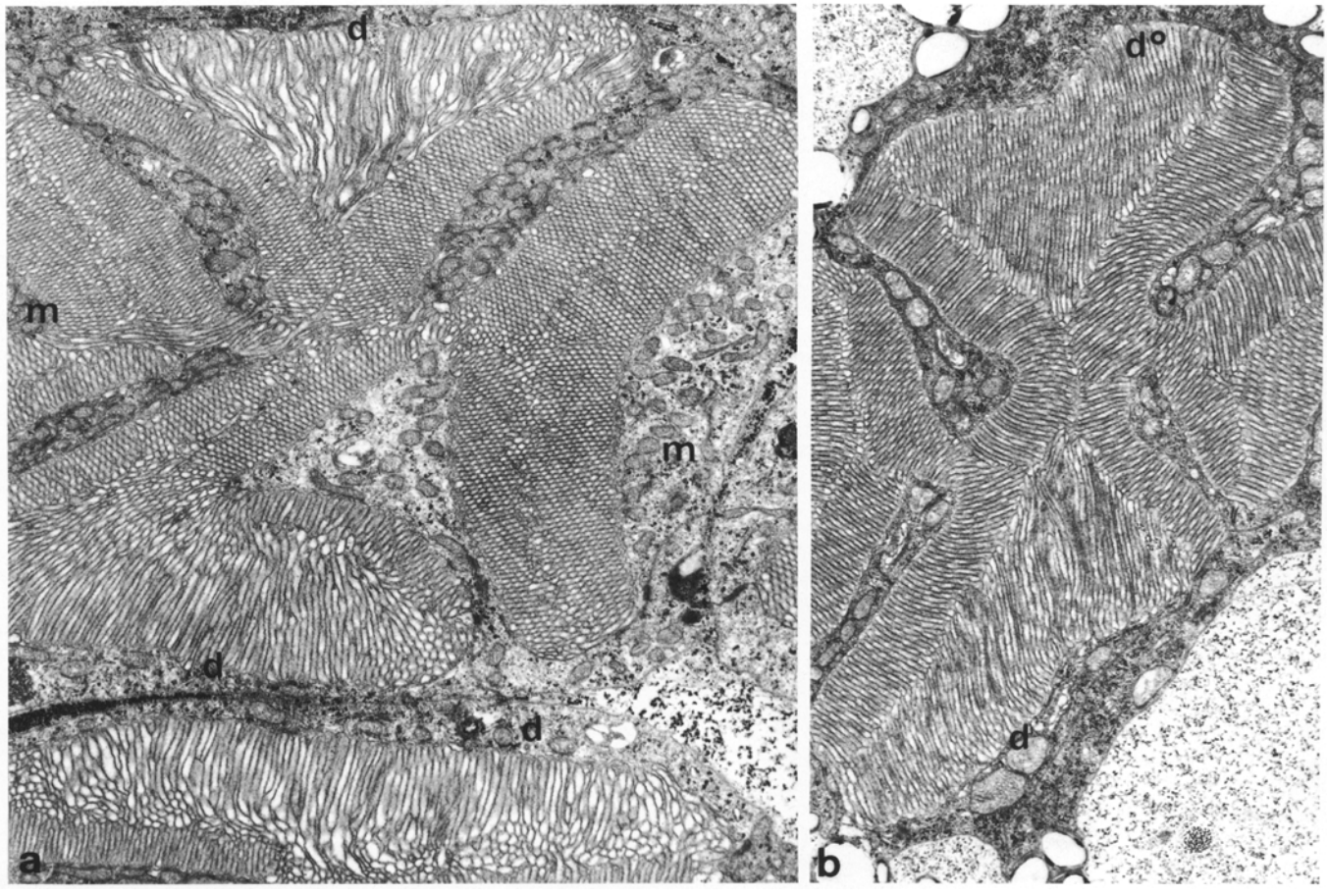

Fig. 6. a, b Cross sections through most distal parts of ommatidia of eyes after illumination with 352 nm for 60 min. **a** Ommatidia in the most dorsal region of the eye: Three rhabdomeres of distal cells (*d*), all affected (UV receptors), and unaffected rhabdomeres of medial cells (*m*) (green receptors). **b** Ommatidium in the dorsal region bordering the central region of the eye: Two distal cells, only one of which shows light-dependent changes in its rhabdomere (*d*) (UV receptor), the other one exhibits an unaffected rhabdomere (*d*°) (blue receptor). **a** ×8000; **b** ×10000

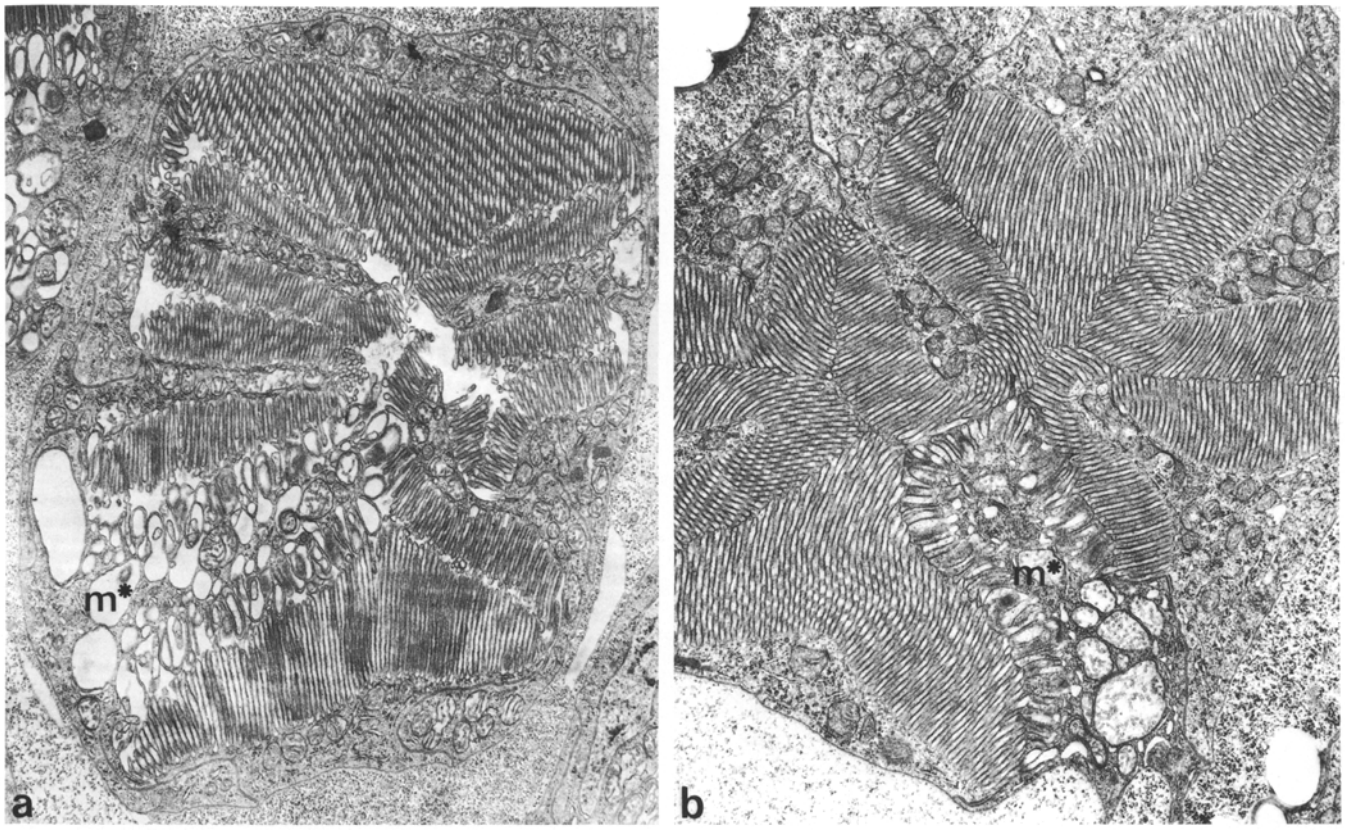

Fig. 7. "Hypersensitive" cells. **a** Cross section through the most distal part of an ommatidium in the central region of the eye after illumination with 648 nm for 10 min. In one medial cell (*m**) this generally little effective illumination has led to a complete destruction of the rhabdomere. **b** Cross section through the distal part of an ommatidium in the central region of the eye after illumination with 352 nm for 45 min. In one medial cell (*m**) this usually uneffective illumination caused a strong reaction in the rhabdomere. Two distal cells with unaffected rhabdomeres (blue receptors). **a**, **b** ×9000

dorsal, marginal region of the eye – are strongly sensitive to UV illumination, whereas the remaining 80% of the distal cells situated in the other regions of the eye are mainly sensitive to blue light. Between these regions, ommatidia are occasionally found, which contain one UV and one blue sensitive distal cell. All over the eye, the six medial cells exhibit maximal sensitivity to green light, while the basal cell is mainly blue sensitive. In comparison to the blue sensitive distal cells, its sensitivity range appears to be more extended into the longer wavelength range.

The arrangement of the rhabdomeres of the nine receptor cells within a rhabdom and the distribution of visual pigments thereon are schematically shown in Fig. 8.

Discussion

The retina in the compound eye of the saturniid moth *Antheraea polyphemus* contains three different visual pigments, located in different receptor cells. The absorbance maxima of the visual pigments (P) and their corresponding metarhodopsins (M) are the following:

(1) green pigment: P 520–530 nm/M 480–490 nm;
(2) blue pigment: P 460–480 nm/M 530–540 nm;
(3) UV pigment: P 330–340 nm/M 460–470 nm.

These figures are near those measured in sphingid moths such as *Deilephila elpenor* (Höglund et al. 1973), *Manduca sexta* (Schwemer and Brown, cited in Schwemer and Langer 1982; White et al. 1983), *Proserpinus proserpina* (Wiltrud Wasserthal, unpublished). Three similar pigments are expected in the pyralid moth *Amyelois transitella* (Bernard et al. 1984). In a noctuid moth, *Spodoptera exempta*, a tetrachromatic system has been found in which three of the pigments are nearly the same as in other moths, and, in addition, a red receptor occurs in this species (Langer et al. 1979; Meinecke and Langer 1984).

Colour-vision systems with three or four visual pigments are also known from butterflies (*Heliconius numata*, Struwe 1972; *Papilio aegeus*, Matič 1983) and from some species of other insect orders, especially Hymenoptera (*Apis mellifica*, Autrum and v. Zwehl 1964; *Cataglyphis bicolor*, Kretz 1979), Heteroptera (*Gerris lacustris*, Hamann and Langer 1980; *Notonecta glauca*, Schwind et al. 1984) and Odonata (*Sympetrum rubicundulum*, Meinertzhagen et al. 1983).

The blue receptor pigment has its absorption maximum at a longer wavelength than in *Deilephila elpenor* and *Manduca sexta* but near to that which is found in *Spodoptera exempta* and also in the water-strider *Gerris lacustris* (Hamann and Langer 1980). This type of receptor pigment seems to be the same as was found in very few visual cells of worker honey-bees by intracellular electrophysiological measurements (Autrum and v. Zwehl 1964).

From measurements of extracts an estimate could be made about the relative amounts of the three receptor pigments within the entire retina: The green receptor pigment, which is present in six of the nine visual cells of an ommatidium, is by far the most prominent within the retina: it

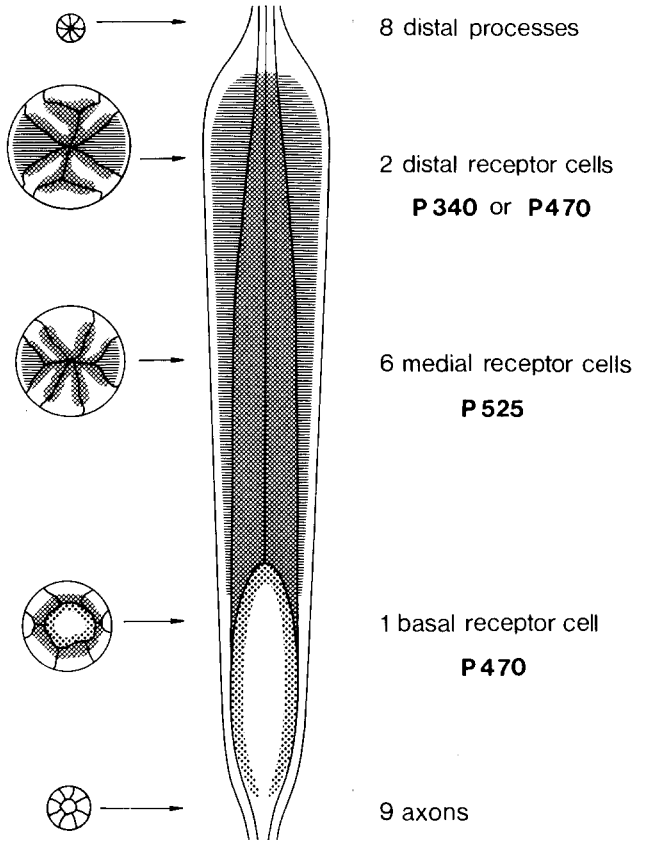

Fig. 8. Schematic representation of a longitudinal section through a rhabdom and of cross sections at different levels. To the names of cell types and their numbers in an ommatidium, the types of visual pigments (*P*) found within their rhabdomeres are added

constitutes about 75% of all the visual pigments. In contrast, the UV pigment, which is found in the two distal cells of an ommatidium, amounts to only 5%. Given an equal amount of visual pigment in each of the nine cells of an ommatidium, there would be a discrepancy of at least a factor of four, if all the ommatidia contained receptor cells with this visual pigment. But microspectrophotometric and morphological investigations of different regions of the eyes have shown that only about 20% of the ommatidia, located most dorsally in the eyes, have these receptor cells especially sensitive to UV light. Only these ommatidia are really trichromatic. Within the larger part of the eye, containing about 80% of the ommatidia, the latter are equipped with blue receptor cells in the distal and also in the proximal part of the rhabdom and may therefore be only dichromatic. Electron microscopy indicates that the basal blue receptor may possess a sensitivity that extends further into the longer wavelength spectrum and reacts to lower intensities of light than the distal blue receptor cells. However, as revealed by microspectrophotometry, the visual pigment in both distal and proximal receptor cells has about the same spectral absorption properties. Therefore, the difference in their sensitivities to long wavelength light is not yet clarified. The location of the UV visual pigment in the distal receptor cells of the ommatidia in the small part of the dorsal marginal region of the eye guarantees the most direct access of UV light from the sky especially at its low intensity during the night.

In a tiered rhabdom, the serial arrangement of the different rhodopsins and of their metarhodopsins is of physiological interest because of the optical consequences for the visual processing. The larger part of the rhabdomeres of the pair of UV and blue receptors, respectively, is located at the distal end of the rhabdom, where the full intensity of light is available. Calculations from *Deilephila elpenor* have shown that an UV receptor in a proximal position would receive only half of the light (Schlecht 1979). On the other hand, light reaching the rhabdomere of the basal cell has been filtered by all the microvilli of the distal and the medial cells. If the UV and the green pigments act as colour filters, the absorption probability within the rhabdomere of the basal receptor is depressed for these spectral ranges. Therefore, the effective spectral sensitivity of this cell is changed and its function for colour discrimination may be improved.

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