Identification of Photoreceptor Locations in the Compound Eye of *Coccinella septempunctata* Linnaeus (Coleoptera, Coccinellidae)

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Three spectral types of photoreceptor with sensitivity maxima in the 360 nm (u.v. light), 420 nm (blue light) and 520 nm (green light) were characterized in the compound eye of *Coccinella septempunctata* Linnaeus by intracellular electro-physiological recording. All three different spectral types of photoreceptor were found to respond to polarized light with an average polarization sensitivity (PS) value around 4.0. Referring the longitudinal direction (*Y*-axis) of the compound eye as 0°, the e-vector of polarized light giving maximal sensitivity were 45° for the u.v. receptor, 75° for the blue receptor, 45 and 135° for the green receptor. These values were compared to the angles between the *Y*-axis of the compound eye and the microvillar directions in the rhabdomeres of eight retinula cells. It was concluded that all six peripheral retinula cells (Nos 1–6) were green receptors and that the two central retinula cells (Nos 7 and 8) were u.v. and blue receptors, respectively.

Coccinella septempunctata   Compound eye   Photoreceptor   Spectral sensitivity   Polarization sensitivity

INTRODUCTION

Coccinella septempunctata, commonly known as the seven-spotted ladybeetle, is distributed worldwide. In both larval and adult stages, *C. septempunctata* is a natural predator on several species of aphids and thus considered to be one of the most important biological control agents against aphids. Ecologists have long recognized the importance of its role. There are many reports regarding ecological and morphological studies on *C. septempunctata* (Home, 1975; Nakamuta, 1984; Schaeffer *et al.*, 1987; Lin *et al.*, 1992). But investigations on visual physiology are so far limited to electroretinogram studies of spectral sensitivity of compound eyes (Agee *et al.*, 1990; Lin and Wu, 1992), which indicated that *C. septempunctata* is capable of recognizing u.v. and green light. However, our previous study with electroretinogram adaptation method suggested the existence of an additional blue receptor (Lin and Wu, 1992).

In a behavioral study, Nakamuta (1984) found that adult beetles prey on aphids only in bright sunlight and hide in the absence of sunlight. Under normal indoor illumination, a hungry beetle can only see and catch aphids within 7 mm. Without illumination, no predation of aphids beyond 2 mm was observed. This study suggested that there is a close relationship between vision and the predatory behavior of *C. septempunctata*. The

structural anatomy of compound eyes reveals that *C. septempunctata* has an apposition, partially fused rhabdom eye and each ommatidium is composed of eight retinula cells, with both peripheral and central types of rhabdom (Lin *et al.*, 1992). What then, is the functional difference between these two types of rhabdom? Do three spectral types of photoreceptor really exist in *C. septempunctata* eye? If these eight retinula cells can recognize three different spectral types of light, which retinula cell is responsible for the recognition of u.v., blue and green light? To explore these questions, the intreacellular recording method was used to determine spectral sensitivity for each photoreceptor. Polarized light at the wavelength exhibiting maximal sensitivity was illuminated on the cell. The angles which gave maximal polarization sensitivity was then compared to the angles between the microvillar directions in rhabdomeres and the *Y*-axis of compound eye in order to determine the relative location of the eight photoreceptors within the ommatidium.

MATERIALS AND METHODS

Insects

Adult males of *C. septempunctata* Linnaeus collected in the field were kept at $22 \pm 2°C$ in a 12 h light–12 h dark photoperiodic regime and fed with either live aphids or drone honeybee powder.

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Electron microscopy

The right eye was dissected and prefixed in 2.5% glutaraldehyde buffer with 0.1 M cacodylate (pH 7.3) at 4°C. Samples were then dehydrated, fixed, embedded and observed by methods described by Wu *et al.* (1985).

Electrophysiology

After anesthetizing at low temperature, a beetle was immobilized by waxing the body onto a stand. The head was fixed rigidly by placing staples over the neck. The position of the stand was adjusted until the longitudinal axis (*Y*-axis) of beetle's eye was perpendicular to the table surface. A tiny piece of cornea on the dorsal area of the right eye was cut away with a sharp razor blade to form a triangular opening. The hole was immediately sealed with a drop of liquid vaseline to prevent moisture loss. Intracellular recordings were made possible by 3.0 M-KCl filled glass microelectrode with a resistance of 70–120 MΩ. The electrode facilitated by a three-dimensional micromanipulator was inserted vertically into the retinula cell through the hole in the cornea to a depth of 200 μm. A reference electrode of tungsten wire was placed in the thorax. The light source was a 150 W Xenon Arc lamp (Ushio UXL-150) mounted inside an monochromator. The monochromatic light was then focused onto one end of a 1 mm dia quartz light guide. The other end of the light guide was mounted onto an apparatus allowing adjustment of the position of the light stimuli around the target cell. The light intensities were measured by a radiometer (Sanso U-3580). The light beam was attenuated by quartz neutral density filters and spectral cut-off filters, so that the log 0 of stimuli intensity at the corneal surface was 4.03×10^{14} quantra/cm^2/s. A shutter, driven by a stimulator, controlled the duration of flashes delivered to the right eye as 300 ms at 6 s intervals. The depolarization response of retinula cells stimulated by the flash was amplified by a preamplifier (MEZ-8201, Nihon-Kohden), displayed on a digital recording oscilloscope (Gould 1604), and recorded simultaneously on a chart recorder (San-Ei 8K21) and a magnetic tape of a video-cassette recorder (Toshiba DX-900).

Spectral sensitivity

Spectral sensitivity recordings of receptor cells were obtained by focusing the light stimuli on the tested cell where the microelectrode was inserted, and stepping through the wavelength series from 300 to 700 nm then 700 to 300 nm twice in 10 nm steps. The responses of retinula cells (*V*) to various light intensities expressed in log units (log *I*) were plotted. The responses of tested receptors to various light wavelengths (at the same intensity) were normalized to the maximal response and plotted as the spectral sensitivity curve.

Polarization sensitivity

To generate polarized light, light with wavelength giving the maximal spectral sensitivity of tested receptor was used as a light stimulus, and u.v.-transparent polar-

izer (Polaroid HNP'B) was added between the light beam and the object. Polarization sensitivity curves for retinula cells were obtained by using the *Y*-axis of the compound eye as reference (0°) and rotating the polarizer from 0 to 180° then from 180 to 0°, twice, in 5° steps. The polarized light was delivered to the eye every 6 s at a duration of 300 ms, and the responses from retinula cell were recorded. *V*–log *I* curve and polarization sensitivity curve were then plotted according to the methods described above. The angles of polarized light which gave maximal polarization sensitivity and the polarization sensitivity (PS) values (defined as the ratio of maximal and minimal sensitivity as the e-vector is rotated) were determined from the curves.

RESULTS

Anatomy

Adult males of *C. septempunctata* have one pair of compound eyes with no ocelli. Every compound eye consists of approx. 1000 ommatidia which are packed in a highly ordered hexagonal orientation. Thus the location of each ommatidium on the surface of compound eye can be easily determined by *X*, *Y* and *Z* axes. By using the apparatus and adjusting the beetle's head positions, the spectral responses of the target photoreceptor in identified ommatidium to various light wavelengths can be recorded through the microelectrode.

The arrangement of the eight photoreceptors and the semifused rhabdoms in a single ommatidium of *C. septempunctata* have been described and published (Lin *et al.*, 1992). Here, Fig. 1 shows the microvillar orientations of rhobdomere in the identified ommatidium in which spectral and polarization sensitivities of photoreceptors were recorded. The hexagon-shaped peripheral rhabdoms are composed of the rhabdomeres of the six peripheral retinula cells (Nos 1–6) and their microvillar axes are arranged in two directions. In other words, the microvillar orientations of cells Nos 1, 3, 4 and 6 are approximately perpendicular to those of cells Nos 2 and 5. These rhabdoms have a length of only 10 μm, measured from below the base of the crystalline cone. The central rhabdom runs along the ommatidial axis through the entire receptor layer. This rhabdom is divided into three parts, of which two belong to the central cell No. 8, and one belongs to the central cell No. 7. The microvillar direction of cell No. 7 is parallel to those of peripheral cells Nos 1, 3, 4 and 6, whereas the two microvillar directions of cell No. 8 are oriented 45° to those of peripheral cells Nos 1, 3, 4 and 6.

Responses of photoreceptors

After the microelectrode was introduced to the retinula cell, the resting membrane potentials detected were between −35 to −40 mV, occasionally −50 mV. The maximal depolarization response of a retinula cell can be obtained under the illumination of "white light" (containing all wavelengths). The inset in Fig. 2 shows a typical potential response of an arthropod photo-
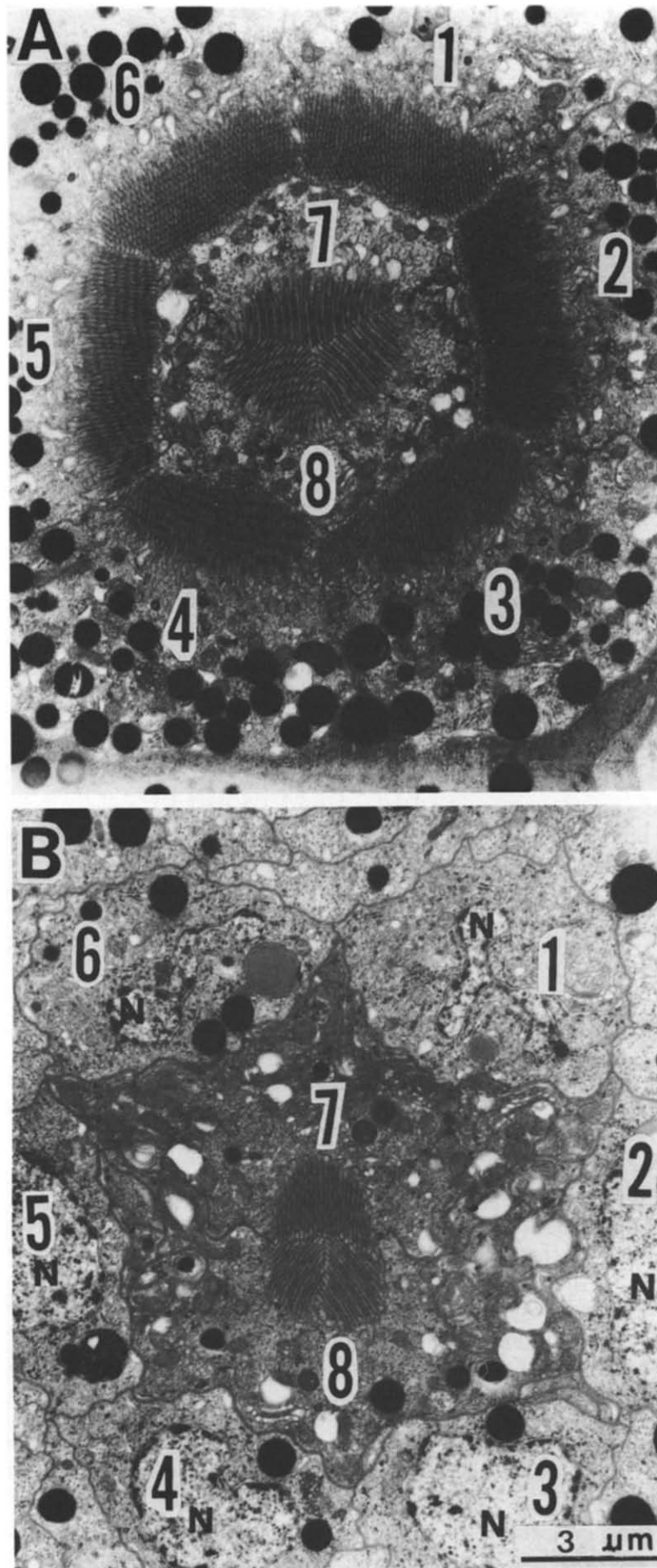
FIGURE 1. Cross sections through the distal (A) and proximal (B) layer of the identified ommatidium in the right compound eye. The peripheral rhabdom comprises the rhabdomeres of six peripheral retiula cells (Nos 1–6), whereas the central rhabdom consists of the two central retinula cells (Nos 7 and 8). The microvilli of each rhabdomere are well aligned. They are arranged in two directions in the peripheral rhabdom, and three in the central rhabdom. N, Nucleus.
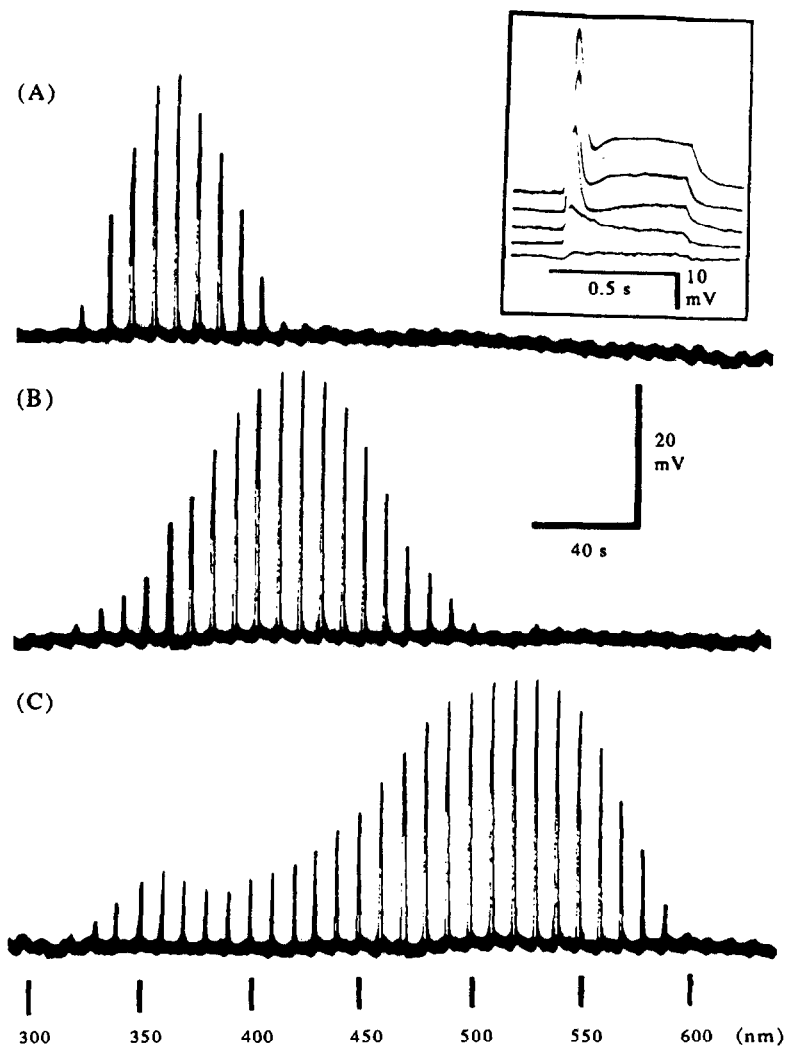
FIGURE 2. Intracellular recording of spectral responses of three different photoreceptors found in the dorsal area of the compound eye. (A) u.v. receptor (B) blue receptor (C) green receptor. Ordinate: the electrical responses (mV) of photoreceptors to flashes at different wavelengths of the same intensity. Abscissa: wavelengths of the flashes. All responses were recorded with slow spectral scanning from 300 to 700 nm, then from 700 to 300 nm (not shown), at 10 nm interval. Inset: the high-speed recording of electrical responses of a retinula cell to flashes of five different intensities at 520 nm. From top to bottom the light intensity is given in log unit with decreasing order: 0, −1, −1.5, −2.5, −3.5.

receptor. It can be divided into three phases: rapid depolarization, plateau and repolarization. The peak height of the rapid depolarization phase varies, depending on the intensity of the flash. It also depends on whether the flash was focused on the target receptor or not. Results showed that when the light stimuli was exactly aligned with the tested receptor's visual axis, the maximal amplitude of receptor potential (V_{max}) was between 25–30 mV. Therefore, in the subsequent experiments, only cells with V_{max} greater than the 25 mV were accepted.

Spectral receptor types

The spectral sensitivities of the retinula cells recorded between 300 and 700 nm indicated that there are three different spectral types of photoreceptor: u.v., blue and green light. The u.v. receptor absorbs light between 320–410 nm. The blue receptor, with a broader spectral range, absorbs light from 320 to 500 nm. The green receptor, with the broadest spectral range, covers 320–590 nm, and some spectral responses were also detected in the shorter wavelength region. However, from successful recordings, scanned back and forth twice, no response was detected in the spectrum shorter than 310 nm or longer than 600 nm.

Spectral sensitivity curves

In this experiment, although there were 121 successfully recorded cells, only 39 had complete recordings (that is two consecutive scannings from 300 to 700 nm then from 700 to 300 nm). Among these 39 cells, 25 were recorded as green receptors, six as u.v. receptors, and eight as blue receptors (Fig. 3). The mean spectral sensitivity curves in Fig. 3 show that the u.v. receptor has a sensitivity maximum at 360 nm, the blue receptor at 420 nm and the green receptor at 520 nm. The band-

width of the curve is narrower for the u.v. receptor and wider for the blue receptor than the absorption spectra of respective ideal visual pigments from Dartnall's nomogram (Dartnall, 1953). As for the green receptor, an additional absorption was detected in the shorter wavelength region.

Polarization sensitivity and polarization angles

Because the diameter of retinula cells in *C. septempunctata* is relatively small (Fig. 1), the retaining time for an electrode to record in the cell stably rarely exceeded 6 min. Therefore, the cells which had been measured for complete spectral sensitivity curve could not be used for polarization sensitivity and polarization angle experiments. The above results showed that the three types of photoreceptor have different spectral sensitivities. Therefore, when the depolarization potential of recorded cell was over 25 mV with "white light" illumination, a 520 nm light source was delivered. If there is any response over 25 mV, the target cell was concluded to be a green receptor. Otherwise, 420 and 360 nm light sources were used to determine if it was a blue receptor or a u.v. receptor. After confirming the wavelength at which the tested cell exhibited maximal sensitivity, a light source at that wavelength in conjunction with a polarizer was applied to measure the polarization sensitivity of photoreceptor. As shown in Fig. 4, all three spectral types of photoreceptor detected in *C. septempunctata* showed appreciable sensitivity to the polarized light with a PS value of 3.16 ± 0.29 (average from three cells) for u.v. receptor, 4.94 ± 0.9 (five cells) for a blue

receptor and 4.42 ± 1.94 (24 cells) for a green receptor. Referring to the Y-axis of the compound eye as 0°, the angles which gave the maximal polarization sensitivity were 45° for 360 nm, 75° for 420 nm, and 45 and 135° for 520 nm, the latter two angles being perpendicular to each other (Figs 4 and 5).

DISCUSSION

The results of this study using intracellular electrophysiological techniques directly proved the suggestion of the previous report (Lin and Wu, 1992): *C. septempunctata* is like most insects in that it is sensitive to three types of light: u.v., blue and green (Menzel, 1979). Although the spectral response was found to be more sensitive in female beetles, as well as in the one-month-old group (Agee *et al.*, 1990), no discrepancy was found in terms of wavelength discrimination. For the sake of convenience and species preservation, only male adults were used regardless of the age group—which should not have affected the conclusions of this experiment.

A variety of experimental techniques have been developed to identify the localization of photoreceptors in insect compound eyes. With microscopic dissecting methods to observe the compound eyes of *Periplaneta americana*, Butler (1971) identified the locations of u.v. receptors and green receptors in the ommatidium by measuring the arrangement of retinula pigments after a long period exposure to certain wavelengths. Meinecke and Langer (1984) located four different photoreceptors in the compound eye of the noctuid moth *Spodoptera exempta* by applying high intensity monochromatic
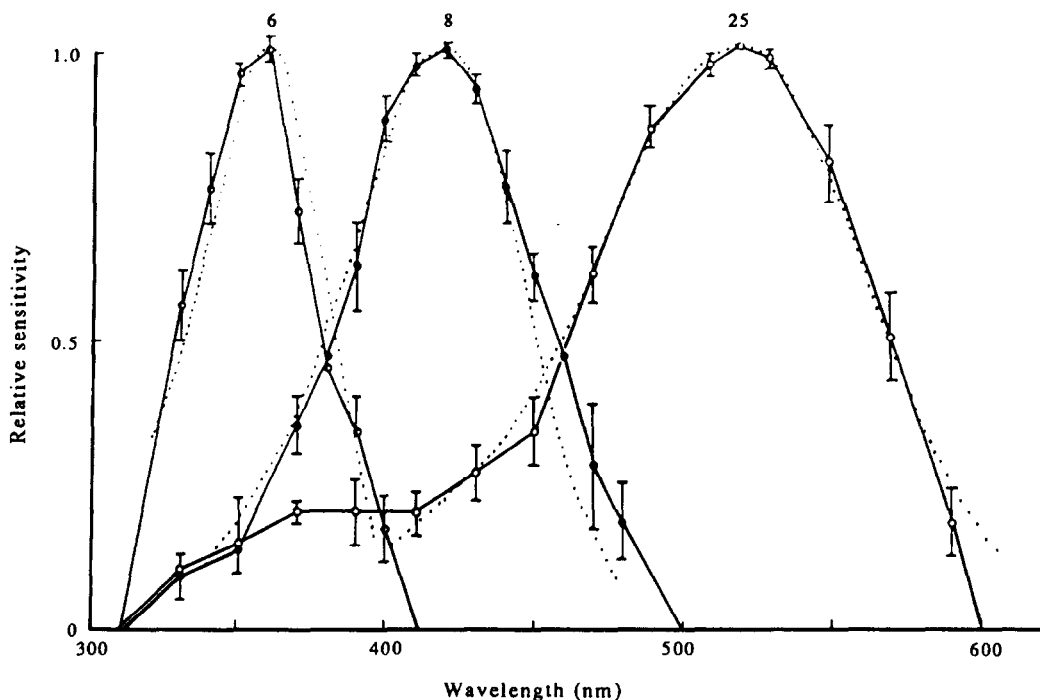

FIGURE 3. Spectral sensitivity curves of three photoreceptors detected in the dark-adapted compound eye. The dashed curves are Dartnall's nomogram of ideal visual pigments. The vertical bars are standard deviations. The number of recorded cells is shown on top of each curve.
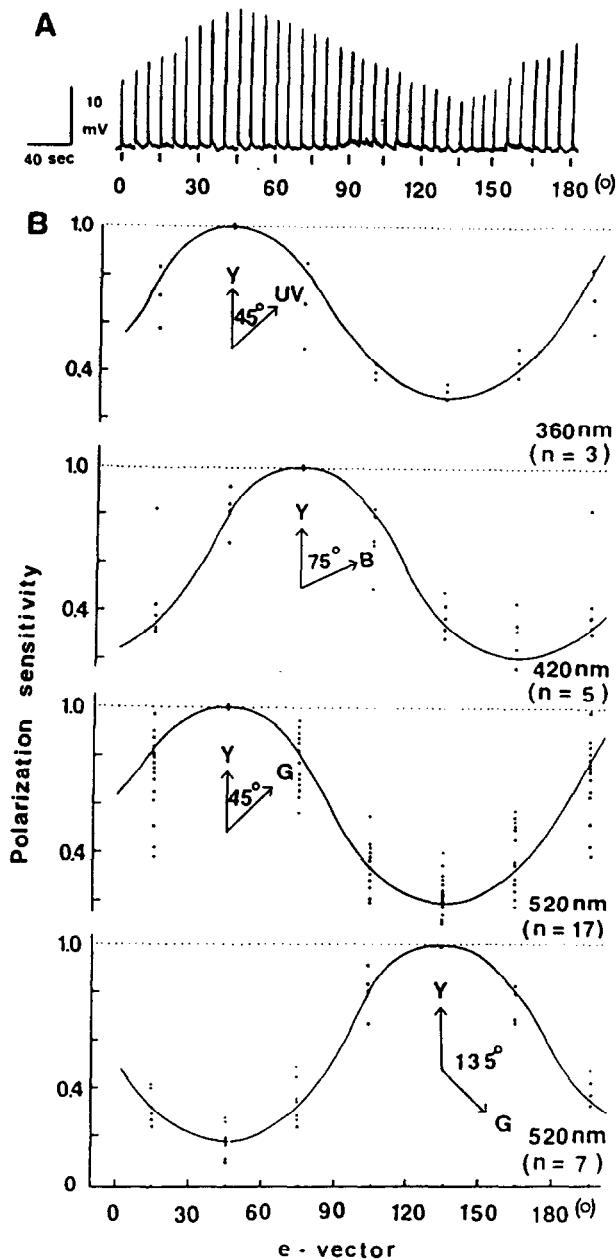
A

B

e - vector

FIGURE 4. Polarization sensitivities of the three spectral types of photoreceptors in the eye of *C. septempunctata*. (A) Intracellular recording of the responses of green photoreceptor (λ = 520 nm) to various polarized lights. Ordinate: the potential response (mV) of tested photoreceptor to e-vector of polarized light. Abscissa: e-vector of polarized light, a linear polarizer was rotated from 0 to 180°, then from 180 to 0° (not shown), recorded every 5°. (B) Polarization sensitivity curves of three spectral types of photoreceptor. Referring to the *Y*-axis of compound eye as 0°, the e-vector that gave maximal polarization sensitivity for u.v. receptor (λ = 360 nm) and blue receptor (λ = 420 nm) are 45 and 75°, respectively. Both 45 and 135° were found to give maximal polarization sensitivity for the green receptor. Ordinate: relative polarization sensitivity. *n*, Recorded cells.

light, followed by electron-microscopic examination of the induced selective deformation of the rhabdomeres in each type of retinula cell. The similar method was used to identify the photoreceptors of the moth, *Antheraea polyphemus* (Langer *et al.*, 1986). Recently the locations

of photoreceptors in the ommatidium of the butterfly *Papillo xuthus* have been determined by polarization sensitivity (Bandai *et al.*, 1992). In the present study, the intracellular recording technique was used to determine the polarization sensitivity of the three different types of photoreceptor and to locate these receptors in the ommatidium of the compound eye of *C. septempunctata*.

Sensitivity to polarized light in invertebrate photoreceptors is based on the dichroic properties of microvilli, resulting from the alignment of photopigment molecules. These visual pigment molecules are strictly aligned within the microvilli. When the e-vector of polarized light is parallel to the axis of the microvilli, polarized light is maximally absorbed by the pigment and the sensitivity is highest. On the other hand, if the two are perpendicular, the sensitivity is the lowest (Kirschfeld, 1969; Snyder and Laughlin, 1975; Israelachvili and Wilson, 1976; Goldsmith and Wehner, 1977; Hardie, 1984, 1985). Hence, the polarization sensitivity of the tested receptor can be ascertained by its microvillar direction in the rhabdomere (Bandai *et al.*, 1992).

The identification of the photoreceptor locations in ommatidia by polarization method is based on the relationship between the polarization angles of photoreceptors and the microvillar directions in the rhabdomeres. Therefore, during the measurement of polarization sensitivity, it is important to immobilize the compound eye and to record the retinula cells of an identified ommatidium. It is also important that the rhabdomeres are strictly aligned and not twisted around one another. It was not difficult to orient the position of each ommatidium in this study because the surface of the *C. septempunctata* compound eyes is relatively flat, the number of ommatidia is limited (approx. 1000), and all the ommatidia are almost arranged on the same surface. It is also known that the microvilli in *C. septempunctata* rhabdom are well aligned and are not twisted (Lin *et al.*, 1992), which makes them a good model with which to identify the location of photoreceptors in ommatidia through the use of polarized light.

Anatomical studies reveal that there are two types of rhabdoms in *C. septempunctata* eye: the central rhabdom with a length around 170 μm and the peripheral rhabdom with a length only 10 μm (Lin *et al.*, 1992). The peripheral rhabdom comprises the microvilli of six peripheral cells (Nos 1–6). These microvilli are well aligned and are perpendicular to each other as shown in Figs 1 and 5. The results of this study show that there are two angles, differing by 90°, where the green receptor has maximal polarization sensitivity. Furthermore, the green receptor cell was the most frequently recorded type both in spectral sensitivity and in polarization sensitivity experiments, which implies that the microelectrode was more easily inserted into the green receptor cells than into the others. These results prompted the conjecture that the six peripheral cells are probably all green receptors. On the other hand, the central rhabdom comprises the microvilli of two central cells. These
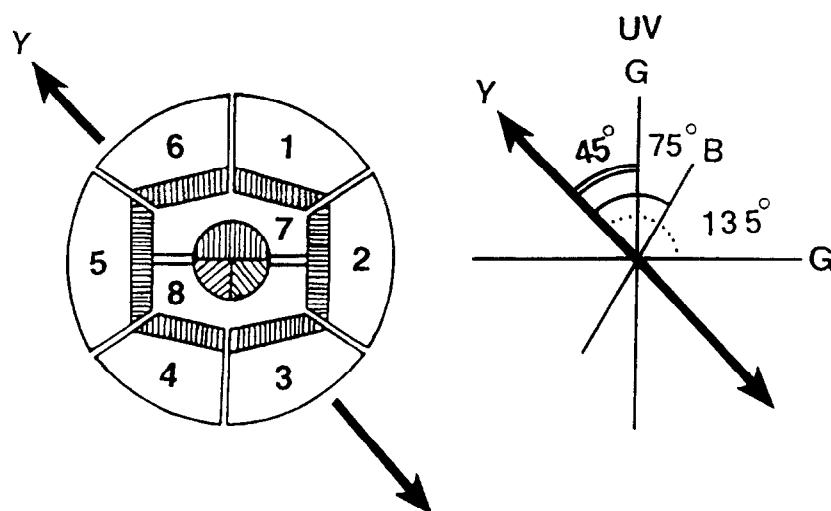
FIGURE 5. Schematic presentation of the location of photoreceptors within an ommatidium of adult *C. septempunctata*. Comparing the microvillar direction in each rhabdomere (left) and the angle of maximal sensitivity between the e-vector of polarized light and the Y-axis of compound eye, it is suggested that all peripheral retinula cells (Nos 1–6) are green receptor, while the two central retinula cells (Nos 7 and 8) are u.v. and blue receptors, respectively.

microvilli are also well aligned but run in three directions. The only microvillar direction found of No. 7 cell is parallel to those of peripheral cells Nos 1, 3, 4 and 6, while the other two microvillar directions of cell No. 8 are oriented 45° to those of cells Nos 1, 3, 4 and 6. These findings suggested that the two central retinula cells (cells Nos 7 and 8) are u.v. and blue receptors, respectively. This study also suggested that the functions of the two rhabdoms are indeed different: the long central rhabdom is responsible for short wavelength absorption, while the short peripheral rhabdom is specialized in long wavelength (green light) absorption.

Electrophysiological and morphological studies have demonstrated that insect photoreceptors that have well-aligned microvilli are expected to be polarization sensitive with high PS values (Wehner *et al.*, 1975; Labhart, 1980, 1986; Hardie, 1985; Nilsson *et al.*, 1987). Among the Coleoptera, those with the ommatidia of unlobed rhabdoms have high PS values, such as the cockchafer, *Melolontha melolontha*, PS = 3.0–10.0 (Labhart *et al.*, 1992), while those with ommatidia of flower-shaped rhabdoms and misaligned microvilli show comparatively low PS values, such as *Anoplognathus pallidicollis*, PS = 1.5 (Meyer-Rochow and Horridge, 1975), and *Onitus alexis* PS = 1.3 (Warrant and McIntyre, 1990).

The electrophysical and behavioral studies indicated that most insects use u.v. receptor to detect polarized light such as *Apis* (von Helversen and Edrich, 1974; Labhart, 1980), *Cataglyphis* (Duelli and Wehner, 1973; Labhart, 1986) and *Musca* (Hardie, 1984; von Philipsborn and Labhart, 1990), while some insects like *Gryllus* (Brunner and Labhart, 1987; Herzmann and Labhart, 1989; Zufall *et al.*, 1989) use blue receptors and few such as *Melolontha* (Labhart *et al.*, 1992) use green receptors. This result indicated that all three spectral types of photoreceptor found in *C. septempunctata* are sensitive

to polarized light and their PS values, with an average of about 4.0, are higher than those reported in other insects. However, no significant difference was found among the PS values of the three spectral types of photoreceptor. This may be due to recording the spectral responses only from a small area of the compound eye.

In conclusion, eyes of a ladybeetle *C. septempunctata*, like most insects, have three spectral types of photoreceptor: u.v., blue and green receptors. Each ommatidium contains eight photoreceptors and their well aligned microvilli forms a non-twisted rhabdom and therefore, all the eight photoreceptors are sensitive to polarized light. The microvillar orientation examined by electron microscopy and the spectral and polarization sensitivity from a single photoreceptor recorded by electrophysiology, suggest that all the six peripheral retinula cells are green receptors and the two central cells are u.v. and blue receptors, respectively.

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