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[RAPID COMMUNICATION]

Spectral Sensitivity of Single Photoreceptor Cells in the Eyes of the Ctenid Spider *Cupiennius salei* Keys

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ABSTRACT—Intracellular recordings from photoreceptor cells of all eyes of the spider *Cupiennius salei* Keys reveal 3 groups of cells with spectral sensitivity maxima in the blue (480 nm), green (520 nm), and UV (340 nm), respectively. The blue and green cells show secondary peaks in the UV at 340-380 nm. In the posterior median, posterior lateral and anterior median eyes, the majority of photoreceptor cells are the blue and green cells in roughly equal numbers. In the anterior lateral eye, however, the green cells dominate. UV cells were only found in the secondary eyes and only once in each of them.

INTRODUCTION

The ctenid spider *Cupiennius salei* is a nocturnal hunting spider living on plants (Barth and Seyfarth, 1979; Barth *et al.,* 1988). Mechanosensation such as the detection of air- and substrate borne vibrations is of particular importance for the guidance of this spider's behavior(Barth, 1985; Barth, 1993; Barth *et al.,* 1993). Recently, however, a high quality of image formation and rather good spatial resolution were described for all four pairs of eyes (Land and Barth, 1992). According to the preceding ERG-analysis, the spectrum of wavelengths seen by the eyes of *C. salei* is between 300 and 680 nm with maximum sensitivity at 520 nm, a small shoulder at 480 nm and a secondary sensitivity peak at 340-360 nm (Barth *et al.,* 1993). Besides all this the neuroanatomy of the visual centers behind both the principal and secondary eyes favor the assumption of a highly developed visual system in *C. salei* (Strausfeld and Barth, 1993; Strausfeld *et al.,* 1993).

Our previous ERG recordings had not only shown the main sensitivity of the eyes to be in the green (Barth *et al.,* 1993), but consistently also demonstrated a secondary peak in the UV and a small shoulder in the blue. The existence of more than one receptor cell type therefore seemed to be a possibility. In the present study, we report on the intracellular measurements of the spectral sensitivity of single photoreceptor cells of both principal and secondary eyes of *C. salei.*

MATERIAL AND METHODS

Female adults of *Cupiennius salei* Keys (Ctenidae) raised in Vienna were taken to Yokohama City University, Japan, where all electrophysiological experiments were carried out. In Japan, the spiders were exposed to the normal day- and night cycle of Yokohama. After 1 month of acclimation, the spiders were used during a period of 7 months. The methods are the same as those described in our previous paper (Barth *et al.,* 1993) except the intracellular recordings.

Glass microelectrodes filled with 3M KCl (resistance 30-80 M Ohm) were used as recording electrodes, and silver wires as indifferent electrodes which were inserted into the opisthosoma.

The spiders were dark adapted for about 3-4 min before each of the experiments.

The light of a Xenon arc lamp (500W Ushio UXL 500D-O) was used for stimulation. To measure spectral responses from 290 nm to 700 nm, 22 interference color filters in 20 nm steps were used. All monochromatic lights were adjusted to contain an equal number of photons (3×10^{10} photons $cm^{-2}sec^{-1}$) with a quartz neutral density filter (optical wedge). The light was guided through a quartz-glass fiber and the direction of the light beam was adjusted by a goniometer device so as to elicit the biggest ERG response. For the spectral sensitivity measurements, stimulus duration was 15 msec and the interval between stimuli 1 sec. The obtained spectral response curves (in mV) were transformed into spectral sensitivity curves (in %). These represent the reciprocals of the relative intensities (highest sensitivity = 100 %) of each monochromatic light necessary to evoke a constant amplitude of responses (Autrum and von Zwehl, 1964).

RESULTS AND DISCUSSION

Posterior median eye

The great majority of photoreceptor cells responded maximally either in the blue (480 nm) or in the green (520 nm) in roughly the same numbers. All cells had small secondary peaks in the UV (340-380 nm). Out of a total of 129 intracellular recordings only one cell (UV cell) responded maximally in the UV at 340 nm. The spectral responses of 16 blue cells with λmax at 480 nm, 15 green cells with λmax at 520 nm and 1 UV cell with λmax at 340 nm could be transformed into spectral sensitivities (Fig.1). Thin solid lines in the figure are the theoretical absorption

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curves for visual pigments with λmax at 480 nm and 520 nm respectively (Dartnall, 1953). Both blue cells and green cells showed secondary peaks in the UV region at 340-380 nm. They may have to be attributed to the β-peak of the visual pigment. In addition to the the secondary peaks in the UV, all blue and green cells have small shoulders closer to the wavelengths of their sensitivity peaks. The small shoulders of the blue cells in the green at 520 nm which is the λmax of the green cells, and the shoulders of the green cells in the blue at 480 nm which is the λmax of the blue cells (Fig. 1) might be explained by electric coupling. In addition, some differences between the theoretical absorption curves of visual pigments at λmax of the blue and green cells and the recorded spectral sensitivity curves should be noted. The spectral sensitivity curve of the green cells is shifted by about 10 nm towards shorter wavelengths in the range of wavelengths longer than its λmax, and the corresponding curve of the blue cells by about 15-30 nm towards longer wavelengths. Although all these modifications of the spectral sensitivity curves may be due to electric coupling between

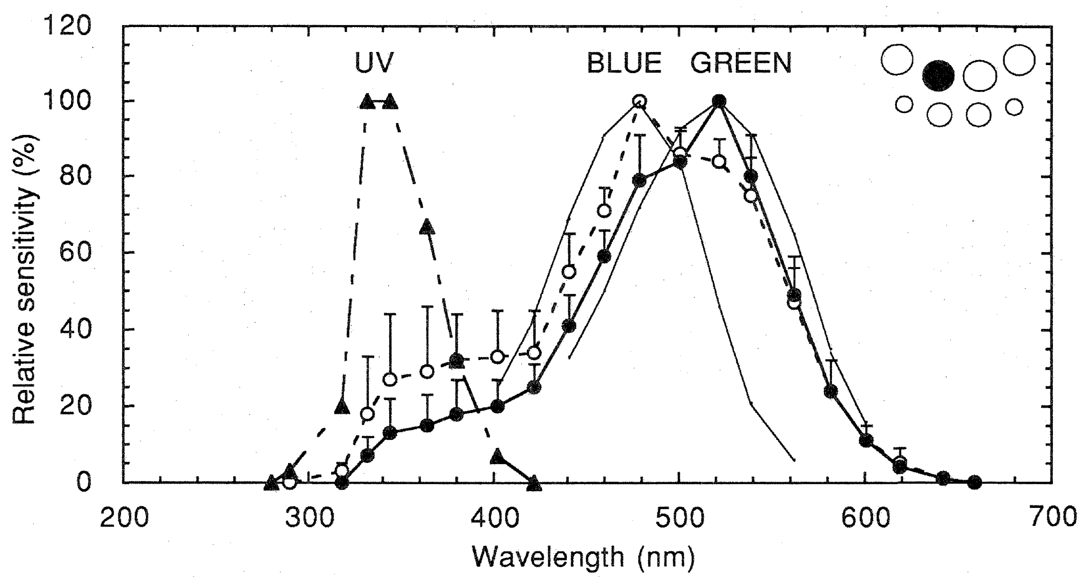

Fig.1. Posterior median eye, mean spectral sensitivities of single photoreceptor cells. 1 UV cell (λmax at 340 nm), 16 blue cells (λmax at 480 nm) and 15 green cells (λmax at 520 nm). Solid lines without marks are theoretical absorption curves for 480 and 520 nm (Dartnall nomogram). Bars indicate SD; inset shows arrangement of eyes in *C. salei* and the eye recorded from (filled circle).

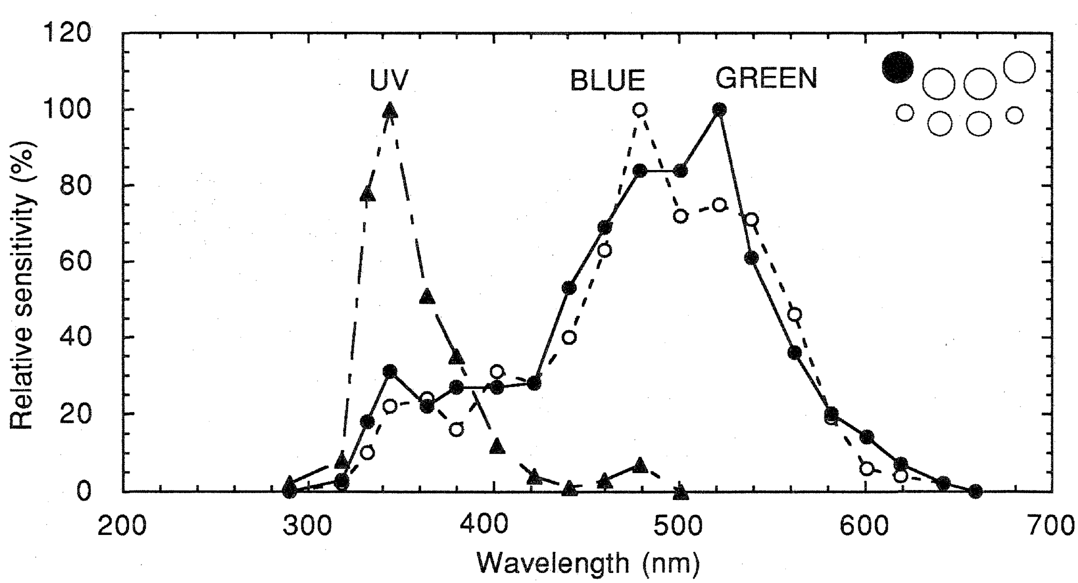

Fig.2. Posterior lateral eye, spectral sensitivity curves of 1 UV cell (λmax at 340 nm), mean of 2 blue cells (λmax at 480 nm) and 1 green cell (λmax at 520 nm); inset see Fig.1.

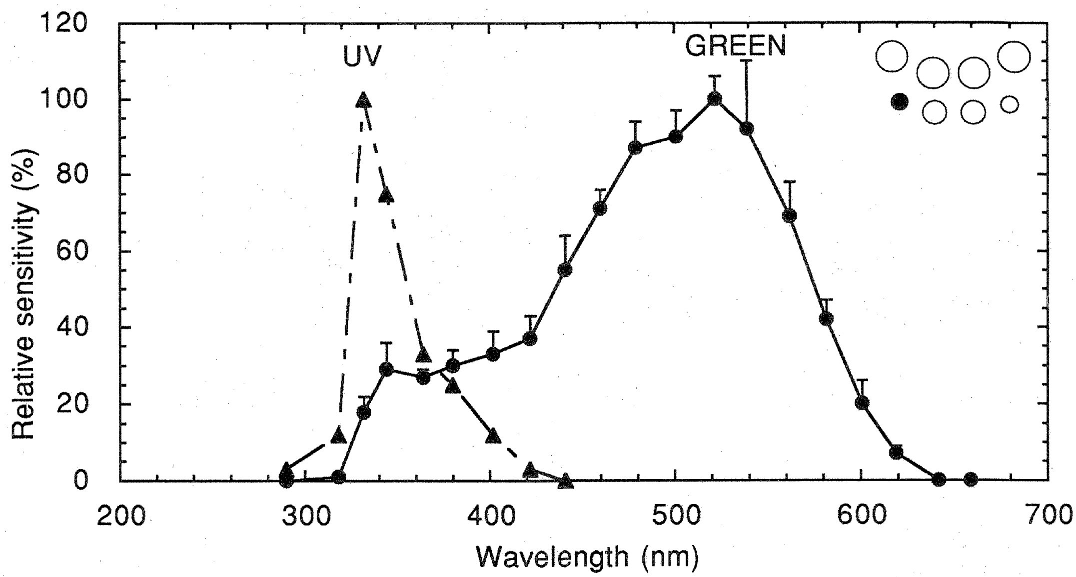

Fig.3. Anterior lateral eye, spectral sensitivity curves of 1 UV cell (λmax at 335 nm), mean of 5 green cells (λmax at 520 nm; small secondary peak at 340-360 nm). Bars indicate SD; inset see Fig.1.

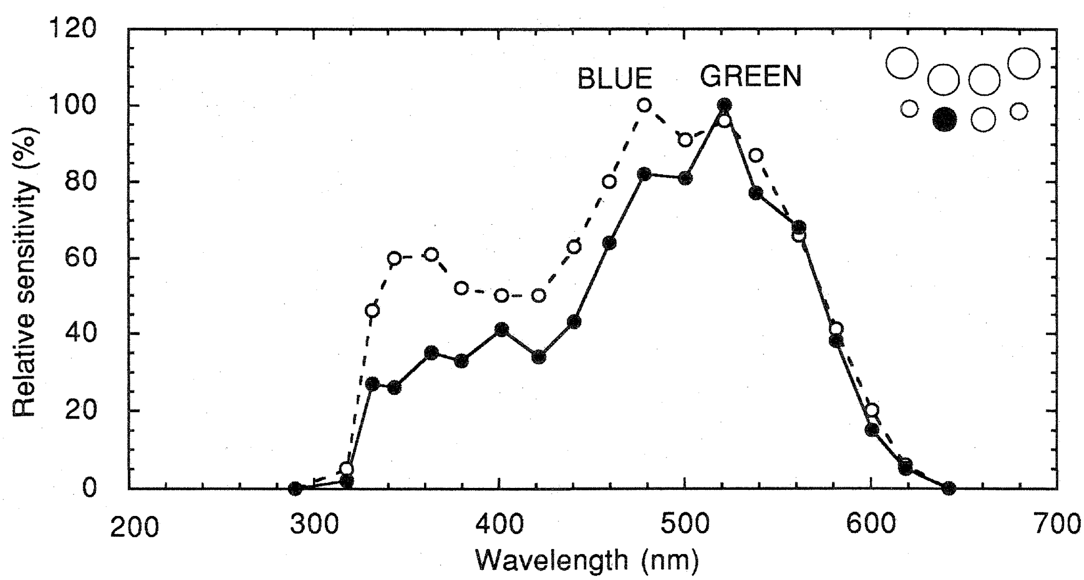

Fig.4. Anterior median eye, mean spectral sensitivity curves of 2 blue cells (λmax at 480 nm), and of 2 green cells (λmax at 520 nm) with small secondary peaks in the UV (360-400 nm); inset see Fig.1.

blue and green cells, there is at least one alternative explanation: The receptor cells may contain two types of visual pigments at different ratios as shown for grapsid crabs (Sakamoto *et al.,* 1996).

Posterior lateral eye

Three types of color receptor cells were recorded from the posterior lateral eye as well. Among the 10 spectral response curves recorded, only one was from a UV cell (λmax at 340 nm) with a small secondary peak at 480 nm. The others were from 4 blue (λmax at 480 nm) and 5 green (λmax at 520 nm) cells which all had a small secondary peak in the UV (340-380 nm). Examples of typical spectral sensitivity curves are shown in Figure 2. The general features of the spectral sensitivity curve of each color receptor cell are basically the same as those found for the photoreceptor cells of the posterior median eye.

Anterior lateral eye

Again, there was a only one UV cell (λmax at 335 nm) among the 10 cells reliably recorded from. The other 9 cells were all green cells (λmax at 520 nm) with small secondary peaks in the UV region (340-360 nm). Figure 3 shows spectral sensitivity curves of a UV and green cells. No blue cell could be recorded. Though this does not necessarily exclude the existence of blue cells in the anterior lateral eye, the dominance of green cells seems to be characteristic for this eye.

Anterior median eye

Amongst the 4 pairs of eyes of *C. salei,* only the retinae of the anterior median eyes can be moved by the activity of the eye muscles. Because of the retina movements, it was difficult to keep an electrode in a single cell long enough to record its spectral responses. Only 2 blue (λmax at 480 nm) and 3 green cells (λmax at 520 nm) could be successfully studied (Fig. 4). Both had small secondary peaks in the UV (360-400 nm). No UV cell was found.

The present intracellular study indeed reveals 3 groups of cells (UV, blue and green) with their spectral sensitivity maxima in the wavelength ranges also eliciting the largest ERG responses (Barth *et al.,* 1993). Our results set *C. salei,* which is nocturnal, apart from diurnal lycosids like *Lycosa baltimoriana*, which exhibit similar ERGs but have only one type of photoreceptor cell (DeVoe, 1972; DeVoe *et al.,* 1969).

Although the Lycosidae and the Ctenidae are considered closely related taxonomically (Lachmuth *et al.,* 1985), *C. salei* is more similar to argiopid web spiders regarding the spectral sensitivity of its photoreceptor cells. The posterior lateral and the anterior median eyes of *Argiope bruennichii* and *Argiope amoena* have blue, green and UV cells, too. The large posterior median eyes of *Dinopis subrufus* contain only green cells with λmax at 517 nm (Yamashita, 1985), whereas salticids like *Menemerus confusus* have no less than 4 types of photoreceptor cells maximally sensitive in the UV, blue, green, and yellow (Yamashita and Tateda, 1976).

It is puzzling to have found only a single photoreceptor cell with maximum sensitivity in the UV in each of the secondary eyes of *C. salei*. Different from the anterior median eyes of jumping spiders (Salticidae) whose retinae are composed of 4 layers of photoreceptor cells (Land, 1969), the retinae of all eyes in *C. salei* are composed of a single layer of photoreceptor cells. We assume that either the number of UV cells is very low or that they are located in particular restricted areas where our electrodes hardly reached.

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