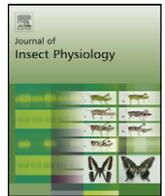




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Spectral sensitivity of a colour changing spider

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ABSTRACT

Vision plays a paramount role in some spider families such as the Salticidae, Lycosidae and Thomisidae, as it is involved in prey hunting, orientation or choice of substrate. In the thomisid *Misumena vatia*, for which the substrate colour affects the body colour, vision seems to mediate morphological colour changes. However, nothing is known about which component of visual signals from the substrate might be perceived, nor whether *M. vatia* possesses the physiological basis for colour vision. The aim of this study is thus to investigate the vision of this spider species by measuring the spectral sensitivities of the different pairs of eyes using electrophysiological methods. Extra- and intracellular electrophysiological recordings combined with selective adaptation revealed the presence of two classes of photoreceptor cells, one sensitive in the UV region of the spectrum (around 340 nm) and one sensitive in the green (around 520 nm) regions in the four pairs of eyes. We conclude that *M. vatia* possesses the physiological potential to perceive both chromatic and achromatic components of the environment.

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1. Introduction

In some spider families such as the Salticidae, Lycosidae and Thomisidae, the sense of vision plays a major role in different aspects of their biology (Foelix, 1996). Visual signals can be used for the recognition of male and female conspecifics, triggering either courtship or threat behaviors, as in the Salticidae (Land, 1969). Some Lycosid spiders use polarized light for spatial orientation (Dacke et al., 2003), while motion detection plays a role in prey detection and capture in the Salticidae and probably also in the Thomisidae (Homann, 1934; Land, 1971). In some thomisid species, experimental evidence strongly suggests that vision may be involved in both the choice of foraging sites and in morphological colour change (Weigel, 1941; Heiling et al., 2005; Théry, 2007).

Several crab spider species are sit-and-wait predators hunting on flowers and ambushing pollinator prey, such as honeybees and hoverflies (Morse, 2007). In such species, the choice of the flower species is crucial, as this strongly affects the foraging success (Morse, 2007). Studies have shown that crab spiders can use, in addition to the flower shape, other properties of the substrate for foraging decisions, such as its spectral composition. Bhaskara et al. (2009) observed that the white UV reflecting Australian crab spider *Thomisus spectabilis* prefers to sit on UV absorbing flowers to attract

prey. Moreover, Heiling et al. (2005) showed that yellow *T. spectabilis* exhibits a preference for yellow flowers, although it is not clear if this choice is based on chromatic or achromatic cues. Once on a flower, some of these species have furthermore the ability to change colour according to the flower colour. Among those, *Misumena vatia* has attracted interest from scientists and naturalists for more than a century (Heckel, 1891; Rabaud, 1923).

M. vatia species hunts on a wide range of flower species and has the ability to reversibly change its colouration from white to yellow over several days (Weigel, 1941; Théry, 2007). The morphological colour change is often assumed to allow *M. vatia* to be cryptic against the substrate to avoid being seen by predators and/or prey (see review in Oxford and Gillespie, 1998 and Théry and Casas, 2009 for alternative hypotheses). It has thus been generally assumed that vision plays a role in the colour change of *M. vatia*. Indeed, several studies have not only revealed that reflected light from the substrate influences colour change (Gabritschewsky, 1927; Théry, 2007), but also that white spiders with black-painted eyes do not change their colour even when placed on a yellow background (Weigel, 1941). However, it has been observed that a white spider on a yellow substrate does not systematically change its colour (Théry and Casas, 2009; Defrize, personal observation), indicating that other factors may also drive the morphological colour change. Nothing is known about which of the substrate's spectral or achromatic cues mediate the colour change for those white spiders that do change colour on a yellow substrate.

Colour properties of flowers may thus be quite important for the choice of foraging site and the colour change process in *M. vatia*, but the evidence is not fully conclusive. Indeed, Brechbühl

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et al. (2010) did not find any difference in capture rates as function of the degree of crypticity and Defrize et al. (2010) observed in the field an assortment of spiders and flowers colours which was not different from random. To understand the ecological interactions between spiders and flowers, it is thus necessary to have a better knowledge of the sensory abilities of the spiders. The question arises then whether the visual system of *M. vatia* possesses the physiological capacities necessary to analyse the chromatic and/or achromatic properties of flowers. The aim of this study was therefore to investigate, by means of electrophysiological methods, the spectral sensitivities of this colour-changing spider.

2. Materials and methods

The crab spider *M. vatia* possesses eight simple eyes arranged in two rows (Fig. 1). The anterior lateral (AL) and posterior lateral (PL) eyes are larger (75 and 65 μm diameter respectively) than the anterior (AM) and posterior median (PM) eyes (59 and 55 μm diameter respectively). The AM eyes constitute the *principal eyes* of spiders and the other eyes, the so called *secondary eyes*.

2.1. Animals

Adult females of *M. vatia* (Clerck, 1757) (Araneae: Thomisidae) were collected during spring and summer 2007 on several flower species in the surroundings of Tours, France (47°20'18"N, 00°42'52"E) and maintained individually in clear plastic vials containing pieces of damp cotton. Spiders were fed with flies (*Lucilia* sp.) weekly. Vials were cleaned and discarded prey were removed weekly.

For the electro-retinograms (ERG) experiments, spiders were anesthetized with CO₂ for five minutes and placed on double-coated adhesive tape. We fixed the sternum and the four pairs of legs. Using a microscope, lateral parts of the prosoma as well as the chelicerae and palps were glued to the support with wax to prevent movements (Barth et al., 1993). All spiders survived the experiments.

2.2. Stimulation

A monochromator (Polychrome IV, Till-photonics), containing a Xenon lamp (150 W) as a light source, was used to provide monochromatic light flashes. In the monochromator, the white light of the xenon lamp is deflected onto a grating fixed to a galvanometric scanner. By turning the scanner, a specific spectral fraction of the light is projected onto the exit slit. A quartz light guide led the light to the preparation. The end of the light guide (diameter 5 mm) was positioned 40 mm away from the eye surface. The spider and the light guide were positioned so that light

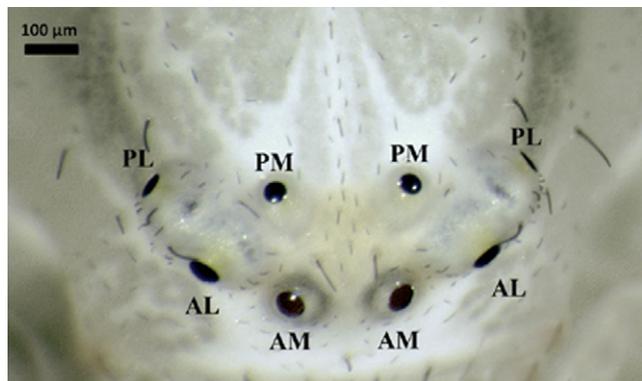


Fig. 1. Organisation of the four pairs of eyes of *Misumena vatia*. AM = anterior median, PM = posterior median, AL = anterior lateral and PL = posterior lateral.

reached the eye in the middle of its visual field. The intensity of each monochromatic light was calibrated by means of neutral density filters (Melles-Griot fused silica filters; 03 FNQ 089: 39.8% transmittance; 03 FNQ 057: 10% transmittance; 03 FNQ 049: 19.9% transmittance; Schott, Mainz, Germany: NG 4) to create flashes containing equal numbers of photons. For each monochromatic light, the light intensity reaching an eye was measured with a radiometer equipped with a flat response detector (IL 1400A radiometer International Light, Newburyport, USA). Intensities were converted into photon flux according to wavelength. In our experiments, the photons flux was 4.7×10^{14} photons/cm²/s¹ for each tested wavelength. We transformed the amplitude signal to equivalent intensities ($\log I$) through a $V\text{-}\log I$ (response-intensity) curve established for each run. We then used the following equation to convert each recorded bioelectrical signal into sensitivity value (S_n):

$$\text{Sensitivity } (S_n) = 100 \times 10^{-[\log I_{\text{max}} - \log I_n]} \%$$

where $\log I_{\text{max}}$ represents the equivalent intensity of the largest voltage response and $\log I_n$ the equivalent intensity of each voltage response. Finally, each individual record was normalized, using its maximal value, before pooling over spiders.

The flash duration was 200 ms and the interval between flashes was 20 s. Recordings were made from 340 nm to 680 nm or from 680 nm to 340 nm, in steps of 10 nm. Individuals were randomly allocated to either stimulation direction, and any dependence on the direction of stimulation was noted.

2.3. Recording

2.3.1. Extracellular electroretinograms

To register ERG responses, the tip of a glass microelectrode filled with a Ringer solution was placed close to the eye's surface so that the electrolyte bridged the small gap between the electrode and the lens through an electrical contact (Barth et al., 1993). A silver wire was used as an indifferent electrode. It was slightly inserted into the posterior dorsal part of the prosoma. Recordings were made from all eyes of the four pairs (AM: anterior median, PM: posterior median, AL: anterior lateral, PL: posterior lateral). A Syntech ID AC-02 signal interface box was used to amplify and digitize signals. All recordings took place at 20 °C.

2.3.2. Selective adaptation

ERG recordings were conducted on eyes having undergone either dark-adaptation eyes, i.e. spiders were maintained 30 min in darkness before beginning a recording; or adaptation to monochromatic lights. In this case, the eyes were adapted to a specific wavelength for 30 min before recording. The rationale behind this procedure is that selective adaptation to a wavelength decreases the sensitivity of a photoreceptor whose peak is near the chosen wavelength (Jacobs, 1993; Kirchner et al., 2005). This decrease may reveal other peaks due to the presence of other visual pigments. After 30 min of adaptation, the monochromatic adaptation light continued to be applied, except during each 200 ms flash, for the duration of the experiment.

2.3.3. Intracellular recordings

Intracellular recordings were performed in posterior median and both anterior and posterior lateral eyes. Spiders were first anesthetized with CO₂. They were then glued ventrally with wax, immersed in spider Ringer solution (Rathmeyer, 1965), and the pedicel cut off to avoid the possible influence of heart movement (Yamashita and Tateda, 1978). We removed a specific part of the prosoma and inserted a microelectrode (40–60 M Ω) filled with

3 M KCl into the retina under microscope control. Intracellular recordings were done on dark-adapted eyes, i.e. spiders were maintained 30 min in darkness before beginning a recording. Intracellular recordings were not possible in AM eyes as it was difficult to position an electrode in a stable fashion.

3. Results

The ERG electrical responses obtained in the different eyes were negative-going waves similar to those found for *Cupiennius salei* and many other arthropods (Autrum, 1958; Barth et al., 1993) (Fig. 2). The highest ERG amplitude was 15 mV.

3.1. Principal eyes

ERGs of the dark-adapted AM eyes (Fig. 3A) revealed a maximal peak around 340 nm (1.0 ± 0.0) in the ultraviolet A region of the spectrum. Moreover, a second peak around 530 nm reached a relative sensitivity of 0.89 ± 0.06 . Selective adaptation to monochromatic light of 340 nm (Fig. 3B) modified the shape of the dark-adapted spectral sensitivity curve, leaving a peak around 520 nm (0.91 ± 0.07). A visual pigment template with peak absorption at 525 nm (Stavenga et al., 1993) fitted the spectral sensitivity curve for wavelengths between 450 nm and 680 nm well, suggesting the presence in this region of a single green visual pigment type (Fig. 3B). Next, selective adaptation to monochromatic light of 480 nm was tested to answer the question whether the spectral sensitivity curve between 400 and 680 nm is due to a single class of visual pigment or due to the presence of two different pigment classes. Indeed, if two visual pigments have their sensitivity peaks between 490 nm and 530 nm, this adaptation will favour a putative receptor around 500 nm quite strongly but will leave a receptor around 530 nm

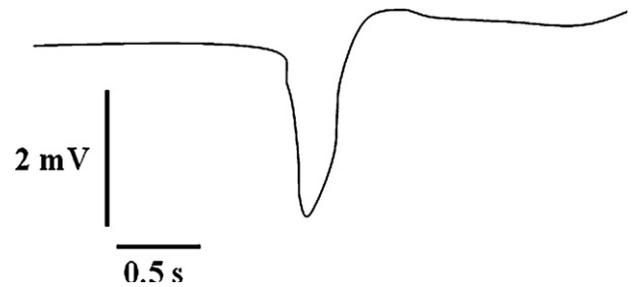


Fig. 2. A typical ERG recording from *Misumena vatia* at 520 nm stimulus.

unaffected. We observed no change in the overall shape of the spectral sensitivity curve in the green region (Fig. 3C) in the 480 nm-adapted AM eyes, especially in the 500/540 nm ratio, compared to dark-adapted eyes (0.85 and 0.91 for dark-adapted eyes and 480 nm-adapted eyes respectively). This confirmed the presence in the AM eyes of a single type of visual pigment in the green region, in addition to the UV one.

3.2. Secondary eyes

A common feature of the spectral sensitivity curves of dark-adapted secondary eyes was a high sensitivity in the green region, between 500 and 540 nm (0.97 ± 0.03 , 0.89 ± 0.14 , 0.95 ± 0.04 at 510 nm for the PM, PL and AL eyes respectively) (Fig. 4A, C, and E). A visual pigment template with a sensitivity peak at 525 nm fits our data at wavelengths between 450 nm and 680 nm well, indicating that a green visual pigment with this peak absorption might be present (dotted line; Fig. 4A, C, and E). To make sure that no further visual pigment was present in this region of the spectrum, we

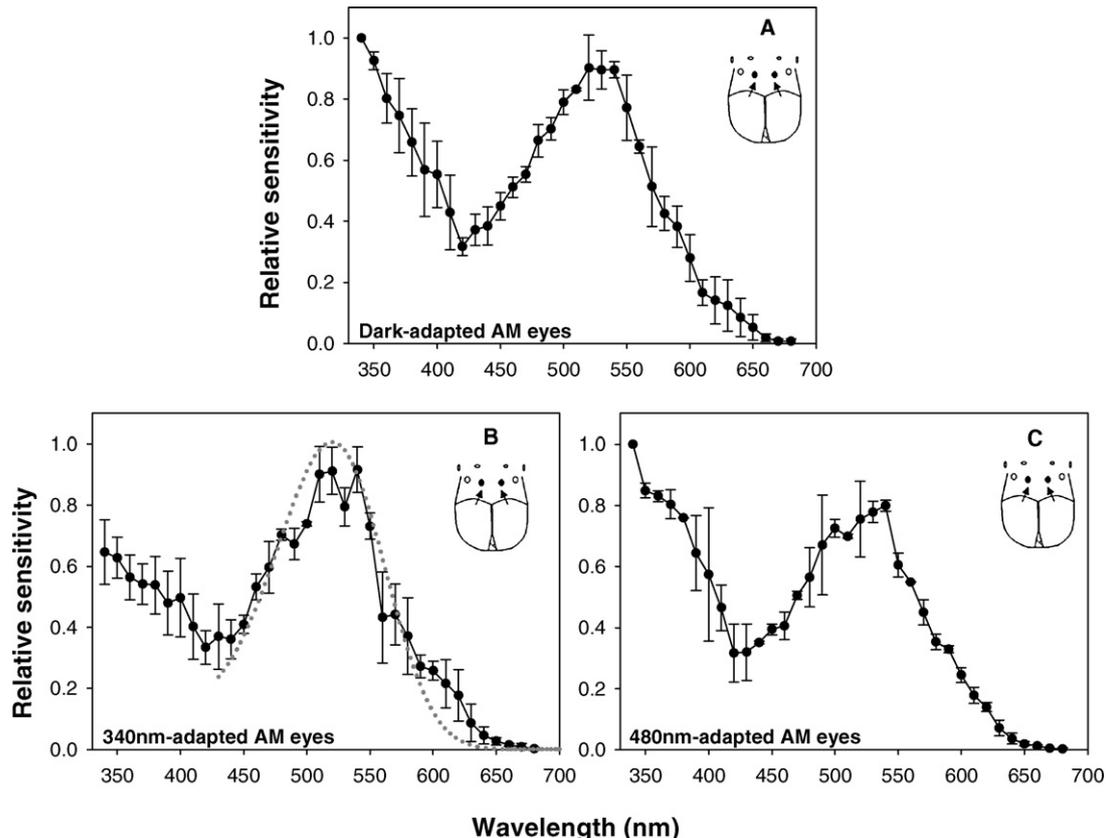


Fig. 3. ERG recordings. Spectral sensitivity curves for the anterior median eyes (AM eyes) in the dark-adapted state (A), after adaptation for 30 min to 340 nm monochromatic light (B) and after adaptation for 30 min to 480 nm monochromatic light (C). The dashed line represents the predicted absorption curve of a visual pigment with a sensitivity peak at 525 nm (C). Values are means \pm S.D. $N = 3$ for each graph.

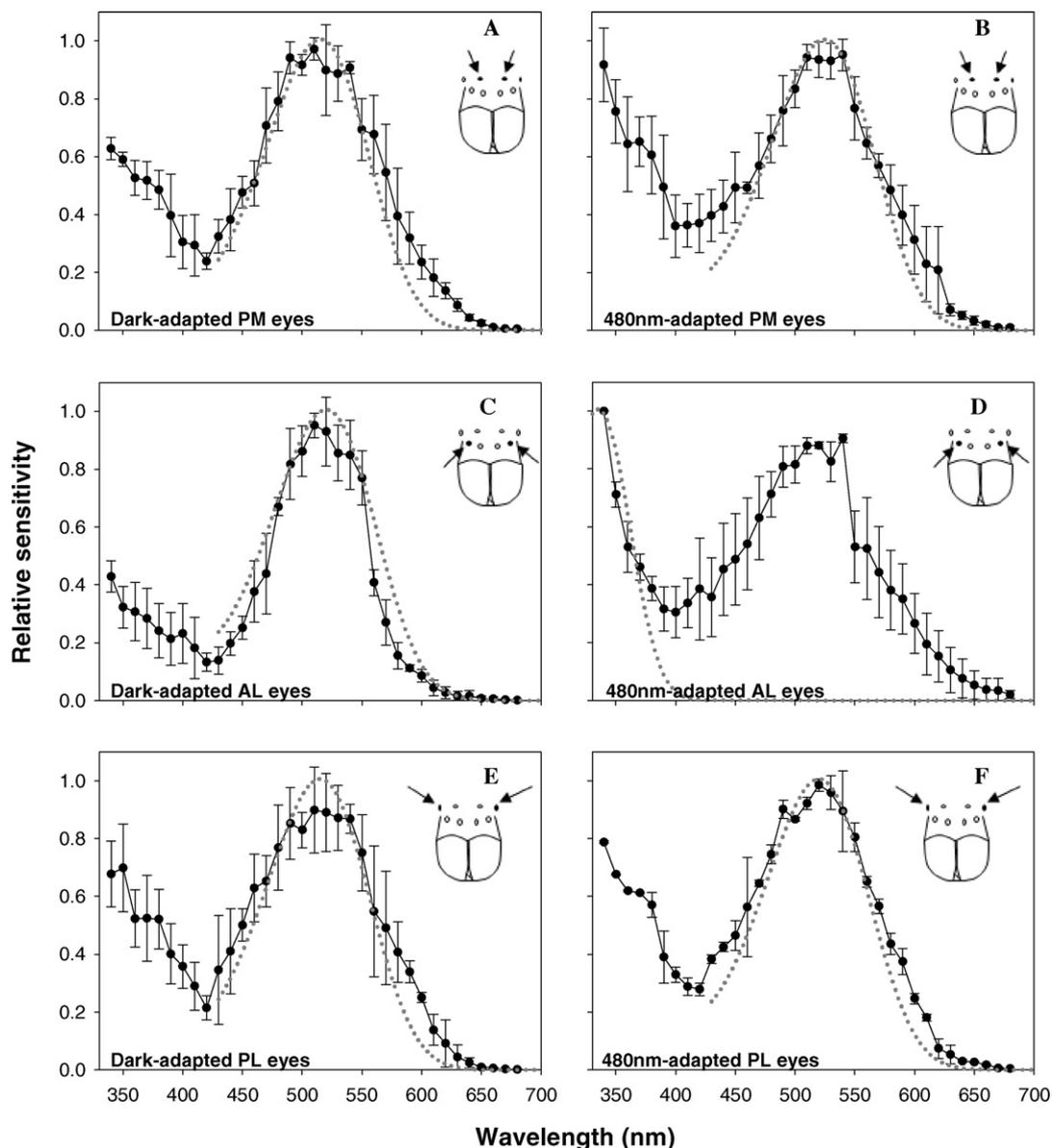


Fig. 4. ERG recordings. Spectral sensitivity curves for the posterior median eyes (A, B), the anterior lateral (C, D) and the posterior lateral (E, F) eyes in the dark-adapted state and after adaptation for 30 min to 480 nm monochromatic light. The dotted lines represent the predicted absorption curve of a visual pigment with a sensitivity peak at 525 nm or at 335 nm. Values are means \pm S.D. $N = 3$ for each graph.

adapted the secondary eyes with 480 nm monochromatic light. This did not alter the shape of the green region of the spectral sensitivity curves and so did not reveal other peaks (Fig. 4B, D, and F). Selective adaptation to 560 nm also yielded similar results (data not shown).

Nevertheless, selective adaptation at 480 nm and 560 nm revealed a UVA peak around 340 nm in AL and PM eyes, whereas the UVA sensitivity level for the PL eyes remained unaltered. Indeed, in the AL and PM eyes, the change in the 340/540 ratio between dark-adapted and 480 or 560 nm-adapted eyes strongly suggests the presence of a UVA visual pigment with an absorption peak around 340 nm. A visual pigment template (Stavenga et al., 1993) with a sensitivity peak at 335 nm fits our data well between 335 nm and 380 nm in AL eyes (Fig. 4D), suggesting the presence of a UV visual pigment. Thus, we can conclude that the AL and PM eyes, like the AM eyes, possess two types of visual pigments, one sensitive in the UVA region and the other in the green region. In contrast, the PL eyes may only possess a single green-sensitive visual pigment.

Intracellular recordings were stable enough to carry out a complete spectral scan in only 6 dark-adapted preparations in PL and AL eyes. Despite numerous intracellular attempts, we did not find any UV or Green cells in PM eyes. In both anterior and posterior lateral eyes, we recorded cells which responded maximally in the green region of the spectrum, at around 520–530 nm (Fig. 5A and B). Visual pigment templates, with a sensitivity peak at 525 nm for the anterior lateral eyes and 530 nm for the posterior lateral eyes, match the physiological data between 430 and 680 nm quite well. This is consistent with the green-sensitive photoreceptor class detected using ERGs.

4. Discussion

The aim of this work was to investigate whether *M. vatia* possesses the physiological basis to see colours, as this ability may be used in different contexts, in particular for the morphological colour change process. Our results, which we discuss below, offer a positive reply.

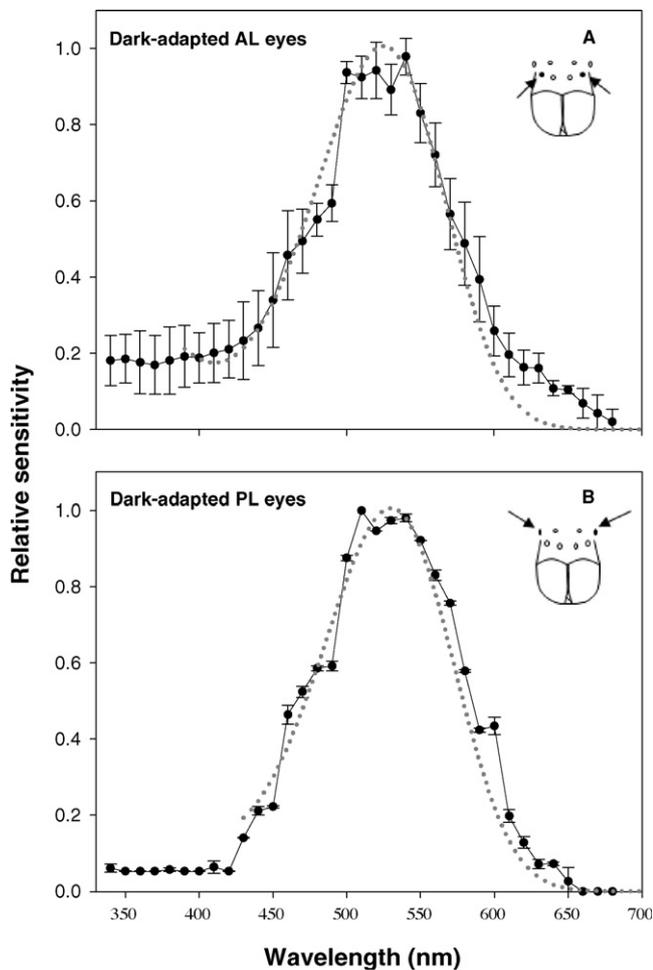


Fig. 5. Intracellular recordings. Mean (\pm S.D.) dark-adapted spectral sensitivities of single photoreceptors in (A) anterior lateral and (B) posterior lateral eyes (solid lines). Dotted lines are theoretical absorption curves with a sensitivity peak at 525 nm (A) and 530 nm (B) (Dartnall nomogram). $N = 4$ and 2 for anterior lateral and posterior lateral eyes respectively.

4.1. Spectral sensitivity

Electrophysiological recordings on spider photoreceptor cells are notoriously difficult and explain the paucity of the results obtained in the literature. Electroretinograms combined with chromatic adaptation revealed a green-sensitive visual pigment which, once fitted with a known template, peaked at about 525 nm in each of the four pairs of eyes. Furthermore, we identified a UV visual pigment in the anterior median, the anterior lateral and the posterior median eyes. Moreover, in the anterior lateral eyes, between 340 nm and 380 nm, the spectral sensitivity of this pigment is well fitted by a template with a peak at 335 nm (Fig. 4B). The enhanced relative ultraviolet sensitivity revealed for the anterior median eyes of *M. vatia* is similar to the one observed for the anterior median eyes of wolf spiders and jumping spiders (DeVoe et al., 1969; DeVoe, 1975).

The presence of a UV visual pigment in the posterior lateral eyes cannot be ascertained with the same degree of confidence. One hypothesis to explain why the UV peak cannot be revealed in this eye is that the number of UV-sensitive cells might not be high enough to be detected by chromatic adaptation. Alternatively, the UV peak might lie outside the measured region, as our device did not enable us to stimulate eyes with wavelengths shorter than 340 nm. Indeed, the lowest UV peak found so far in spiders lies at 335 nm, in the anterior lateral eyes of *C. salei* (Walla et al., 1996)

and recently, between 280 nm and 315 nm in females of the jumping spider *Phintella vittata* are sensitive to a UVB light (which is reflected from the dorsal scales of males, Li et al., 2008).

Whether the eyes possess two spectral classes of photoreceptor cells, or whether a single photoreceptor cells contain a mixture of green and UV visual pigments is our next question.

Visual pigments in single or mixed composition have already been found in spiders. Anterior lateral eyes with pure UV and green photoreceptor classes have been observed in the ctenid spider *C. salei* (Walla et al., 1996). In contrast, the presence of multiple visual pigments in a single visual cell has been suggested in wolf spiders. Indeed, DeVoe (1972) recorded a UV and a green peak from single cells of the anterior median eyes of the wolf spiders *Lycosa baltimoriana*, *Lycosa miami* and *Lycosa carolinensis*. The presence of UV and green photoreceptor cells is also observed in the principal eyes of Salticidae and Argioidae (DeVoe, 1975; Yamashita and Tateda, 1976; Blest et al., 1981), and in secondary eyes of the Salticidae and Ctenidae (Yamashita, 1985; Walla et al., 1996). In *M. vatia*, the few intracellular recordings of green photoreceptor cells in anterior median and anterior lateral eyes strongly suggest that their retina are composed of photoreceptor cells containing only one type of visual pigment. Thus, we conclude that *M. vatia* has at least two classes of photoreceptor cells, one UV and one green. It would not be surprising if the AM eyes turn out to have more than two types of photoreceptor cells. This idea is supported by the presence of four morphologically distinct types of photoreceptor cells in the principal eyes of the crab-spider *Hedana* sp. (Blest and O'Carroll, 1990).

4.2. Structural retinal organisation

Apart from spectral sensitivities, the ERGs also gave clues about the retinal organisation of the principal eyes. Our results indeed suggest that the two types of photoreceptor cells in the AM eyes are arranged in layers, as shown by the suppression of sensitivity to UV and not to green when we adapted the eye to 340 nm. Because only the UV part of spectrum revealed adaptation, this means that a UV receptor probably absorbed most of the UV light before it reached the green receptor, i.e. the UV receptor was distal to the green. Such an organisation of photoreceptors in layers has been reported in the AM eyes of salticids and the thomisid *Hedana* sp. (Land, 1969; Blest and O'Carroll, 1990). If the order had been the opposite (i.e. green overlying the UV), then the UV adapting light would have adapted the green receptor as well as the UV receptor since the UV light would have stimulated the UV beta-peak of the green pigment.

4.3. Does *M. vatia* see colours?

The AM, AL and PM eyes of *M. vatia* seem to be at least dichromatic. Since one of the prerequisites for colour vision is the presence of at least two types of photoreceptor cells (Kelber et al., 2003), we can conclude that *M. vatia* has the retinal basis to discriminate wavelength. Colour vision has yet to be behaviorally proven, although the prospects for colour vision are good, given that dichromatic colour vision has already been shown in both vertebrates and invertebrates (Jacobs et al., 1998; Hemmi, 1999; Roth et al., 2007).

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