

Visual fields and eye morphology support color vision in a color-changing crab-spider

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ABSTRACT

Vision plays a major role in many spiders, being involved in prey hunting, orientation or substrate choice, among others. In *Misumena vatia*, which experiences morphological color changes, vision has been reported to be involved in substrate color matching. Electrophysiological evidence reveals that at least two types of photoreceptors are present in this species, but these data are not backed up by morphological evidence. This work analyzes the functional structure of the eyes of this spider and relates it to its color-changing abilities. A broad superposition of the visual field of the different eyes was observed, even between binocular regions of principal and secondary eyes. The frontal space is simultaneously analyzed by four eyes. This superposition supports the integration of the visual information provided by the different eye types. The mobile retina of the principal eyes of this spider is organized in three layers of three different types of rhabdoms. The third and deepest layer is composed by just one large rhabdom surrounded by dark screening pigments that limit the light entry. The three pairs of secondary eyes have all a single layer of rhabdoms. Our findings provide strong support for an involvement of the visual system in color matching in this spider.

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1. Introduction

Vision plays a main role in different aspects of spiders' biology, including spatial orientation, prey capture, predator detection, courtship, substrate choice and probably morphological color changes, as in *Misumena vatia* (Homann, 1934; Weigel, 1941; Land, 1969a,b; Land, 1971; Hill, 1979; Foelix, 1996; Oxford and Gillespie, 1998; Dacke et al., 1999, 2001; Defrize et al., 2010).

M. vatia has attracted the interest of scientists and naturalists for more than a century (Heckel, 1891; Rabaud, 1918, 1919; Morse, 2007). This species hunts on a wide range of flower species and has the ability to reversibly change its coloration from white to yellow over several days (Weigel, 1941; Théry, 2007). It has been generally assumed that vision plays a major role in the color change of *M. vatia*. Several studies have revealed not only that reflected light from the substrate influences color change (Gabritchevsky, 1927; Théry, 2007; Théry et al., 2010), but also that white spiders fail to change their color when they are placed on a yellow background if their eyes are black-painted (Weigel, 1941). Recent

conflicting evidence, however, casts doubt on those earlier results. Indeed, Defrize et al. (2010) showed that the color matching in the field was indistinguishable from a random assortment, while Brechbühl et al. (2010) observed no difference in prey capture according to the degree of color matching. The question of the ability of *M. vatia* to see colors and the possible use of this capacity in color change is therefore as open as it was a century ago. Electrophysiological evidence revealed that at least two types of photoreceptors are present in this species (Defrize et al., 2011), but data are not backed up by morphological evidence. The aim of this study was therefore to investigate by means of optical, histological and ultrastructural methods the functional morphology of the visual system of this spider to relate these aspects of its visual system to its remarkable color-changing abilities.

2. Materials and methods

Adult females of crab-spiders *M. vatia* (Araneae: Thomisidae) (Clerck 1757) were collected on flowers in the surroundings of Tours, France, during the spring and summer. Upon capture, they were maintained in clear plastic vials (7 cm high, 5 cm diameter) containing pieces of damp cotton, and were fed on houseflies (about one a week). We removed discarded prey items and cleaned the vials weekly.

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2.1. Optics

We used the reflectance properties of the tapetum of *M. vatia* to map out the visual fields of the anterior lateral (AL), posterior median (PM) and posterior lateral (PL) eyes using an apparatus first described by Homann (1928). The reflecting crystal layers of this type of tapetum reflect out light almost exactly along its original direction of incidence (Land, 1985). Each eye was rotated around a telescope and one coaxial light was targeted into the eye, allowing us to measure the angular extent of the retina. Thus, by using the Homann's method (Homann, 1934), the co-ordinates of the field of view of each eye were obtained at various latitudes and longitudes and plotted onto a sphere. The lack of tapetum in the anterior median eyes (AM) of *M. vatia* did not allow us to assess their visual fields by this technique. The visual field of the AM eyes was measured by means of serial histological sections in the three planes (horizontal, transverse and sagittal) ($n = 3$) following the method used by Nørgaard et al.

(2008). The histological procedure was the same as for the morphological analysis.

2.2. Morphological analysis

For the morphological analysis, light and transmission electron microscopy were performed on the spiders ($n = 5$) following the same technique described by Insausti and Casas (2008, 2009). Briefly, the prosoma region containing the eyes was dissected rapidly under fixative (2.5% glutaraldehyde and 2.0% paraformaldehyde in phosphate buffer, at pH 7.3, with 2.2% glucose and 0.9 ml 1% CaCl₂/100 ml added) and stored in the same solution for about 3 h. Subsequently, the pieces were postfixed with buffered 1% osmium tetroxide for 1–2 h. After dehydration, they were embedded via propylene oxide in Durcupan ACM (Electron Microscopy Sciences no. 14040). Blocks were serially sectioned at 1.5–5 μm using glass knives mounted in a microtome. The sections were stained on a hot plate with Toluidine Blue-Basic Fuchsin and

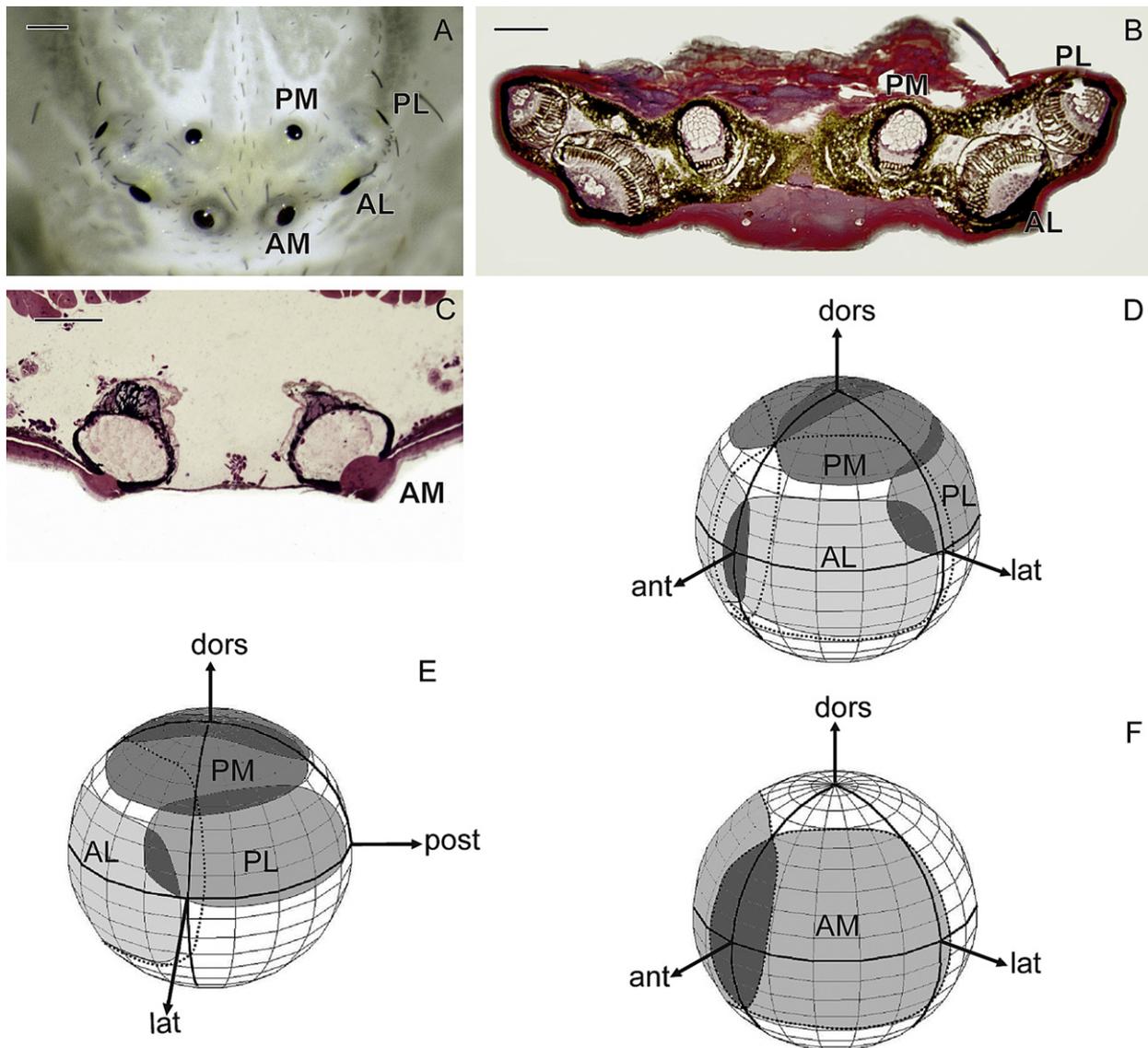


Fig. 1. A: Micrograph of the ocular region of *Misumena vatia* showing the external disposition of the eyes. B, C: Horizontal sections from the spider prosoma showing the arrangement of the eyes. D–F: Fields of view for *M. vatia*. The fields are plotted onto a globe with the spider at the center. The visual fields of the primary eyes are based on histological measurements. The dashed lines mark the visual field of the AM eyes. The equator defines the horizontal plane. D, antero-lateral view. E, lateral view. F, antero-lateral view for AM eyes. AM, antero-median eye; AL, antero-lateral eye; PL, postero-lateral eye; PM, postero-median eye. Scale bar: A–C: 100 μm.

Table 1
Comparison of the visual fields of the different eyes of *M. vatia*.

Eye type	Horizontal	Vertical	Binocular area
AM	102°	98°	35° horizontal 90° vertical
AL	94°	72°	20° horizontal 45°
PL	96°	52°	–
PM	95°	55°	80° anteroposterior 20° lateral

mounted on a slide with DPX (Electron Microscopy Sciences no. 13510). For electron microscopy, ultrathin sections were cut with an ultramicrotome using a diamond knife. The sections were doubly stained by uranyl acetate and lead citrate and observed using a JEOL 1010 transmission electron microscope. All the preparations were made during the morning hours, with the eyes light adapted.

The morphology of the whole eye was reconstructed by means of the photographic montage of longitudinal and cross sections covering the total retinal area. Photomicrographs were adjusted for brightness and contrast by using Adobe Photoshop CS2.

3. Results

3.1. External organization

The crab-spider *M. vatia* has eight eyes arranged in two rows in the anterior region of the prosoma (Fig. 1A, B, C). There are differences in sizes of the four different pairs of eyes. The antero-lateral (AL) and postero-lateral (PL) eyes are larger (75 and 65 μm diameter, respectively) than the antero-medial (AM) and postero-medial (PM) eyes (59 and 55 μm diameter, respectively). On gross inspection, the AL, PL and PM eyes appear dark, whereas the AM eyes are clearer. The AM eyes constitute the *principal eyes* of spiders and the others, the so called *secondary eyes*.

3.2. Visual field

The AL and PL eyes, visual fields have a similar shape, with a frontal and lateral field of view respectively, extending to the back for PL eyes. The PM eyes look upwards (Fig. 1D, E). We observed

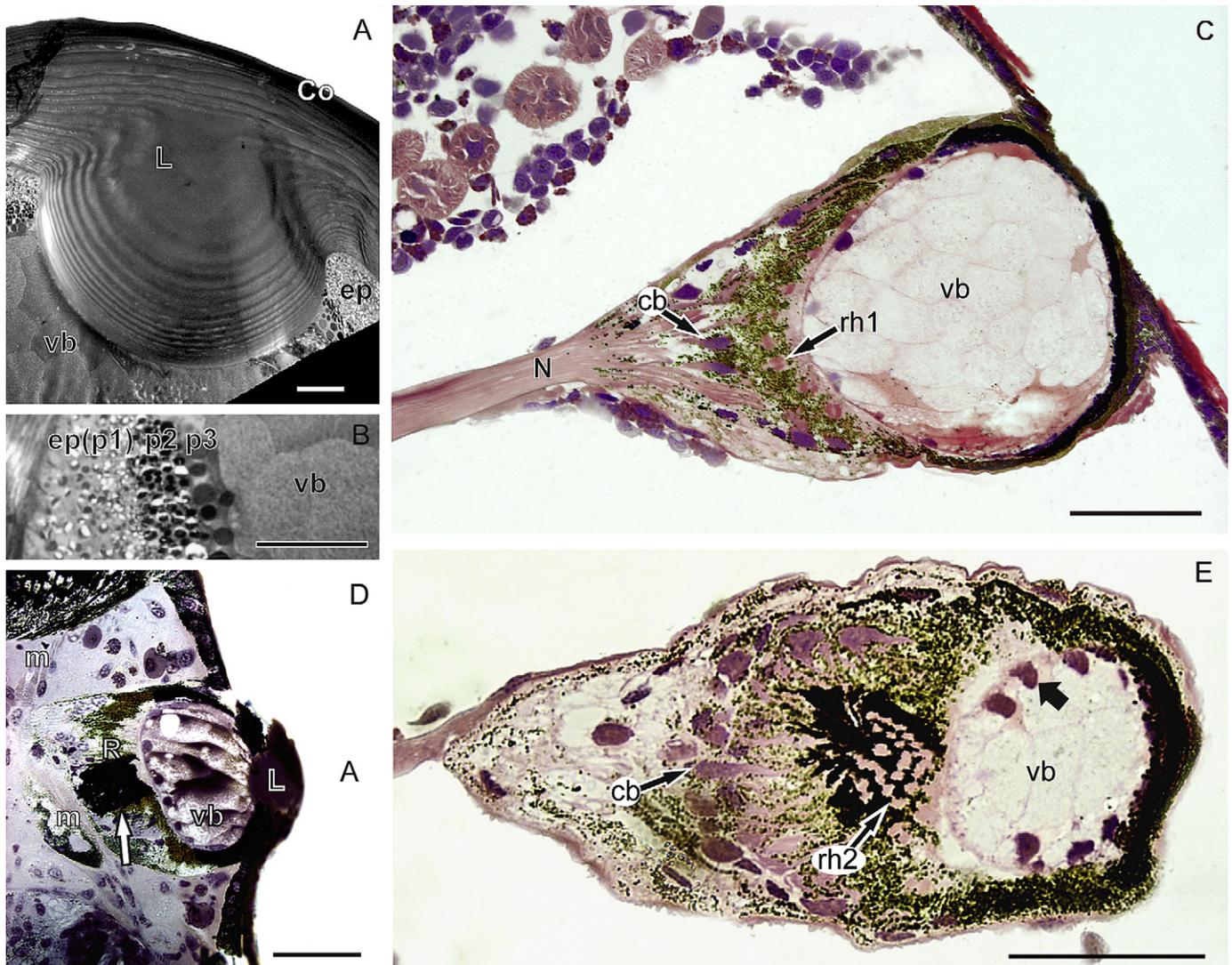


Fig. 2. A, B: Transmission electron micrograph of the dioptric apparatus. In B a detail of the three layers of pigment granules which isolates the eye. Co, cornea; L, lens; ep(p1), epidermis with pigments granules and microcristals; p2, intermediate layer of pigment granules; p3, internal layer of big pigment granules; vb, vitreous body. C–E: Photomicrographs of longitudinal sections of the AM eye showing the organization of the retina with the different types of rhabdom. A, anterior; cb, cell bodies; L, lens; m, ocular muscle; N, nerve; R, retina; rh1, rhabdom type 1; rh2, rhabdom type 2; vb, vitreous body; short arrow in E, nuclei of the vitreous body cells; arrow in D, dark pigmented pocket. Scale bars: A, B: 10 μm ; C–E: 50 μm .

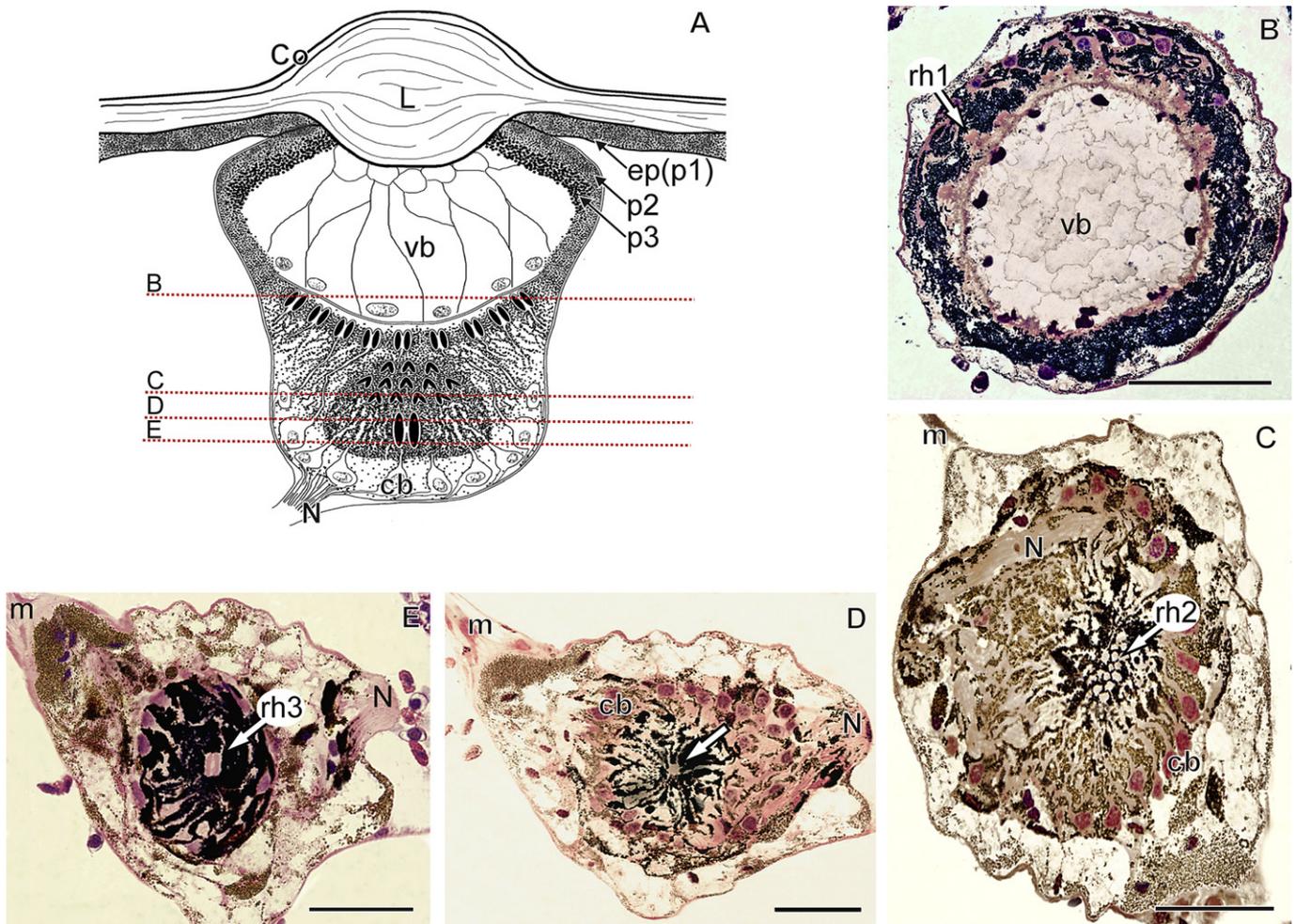


Fig. 3. A: Diagram of the principal eye, reconstructed from frontal and longitudinal sections (light and electron microscopic observations). B–E: Photomicrographs of frontal sections of the principal eye at the different levels indicated in the diagram (A) showing the organization of the retina. In B the rhabdom of type I is shown. C: Section at level of the layer of the type II rhabdom. In D, the arrow shows the small aperture in the middle of the dark pigmented area through which the light reaches the rhabdom type III. E: Section at level of the single rhabdom of type III (arrow) located right in the center of the dark pigmented pocket. cb, cell bodies; Co, cornea; ep(p1), epidermis with pigments granules and microcrystals; L, lens; m, ocular muscle; N, nerve; p2, intermediate layer of pigment granules; p3, internal layer of big pigment; rs, receptive segment; rh, rhabdom; vb, vitreous body. Scale bars: A–E: 50 μ m.

a slight overlap of fields of view between AL and PL eyes (Fig. 1D) and between PL and PM eyes, whereas PM and AL eyes have contiguous fields of view (Fig. 1D). A region of binocularity was observed for AL eyes (Fig. 1D, Table 1). The AM eye (Fig. 1C) exhibits a wide field of view, nearly circular, overlapped partially with that of the PL and PM (Fig. 1D, E), and with the whole AL (Fig. 1F). A medial binocular area could also be determined for AM eyes (Table 1). Thus, the horizontally elongated visual fields of AL, PM and PL eyes cover almost the whole upper hemisphere of the globe, indicating that the spider eye organization might provide visual information about almost its entire upper environment, whereas the inferior hemisphere is covered in the frontal region by the AL and AM eyes (Fig. 1D, E, F).

3.3. Internal organization

3.3.1. General characteristics

The eyes consist of a dioptric apparatus, formed by a cuticular cornea and a lens, a cellular vitreous body and a retina. The dioptric apparatus of the four pairs of eyes is essentially similar in structure (Figs. 1C, 2A, 4A). The lens is separated from the retina by the columnar cells of the vitreous body. The nuclei of these cells lie at

their base, adjacent to the retina (Figs. 2C, E (short arrow), 3B, 4A, B). The basal part of the vitreous body is separated from the retina by a basal membrane. The vitreous body is surrounded by three layers of different pigment cells. The most external layer consists of the epidermis full of electron-dense granules and electron-lucent inclusions of micro-crystals. The medial layer is made of dark homogeneous pigment granules. The internal one is a layer of glial cells filled with dark pigment granules bigger than the granules of the median layer (Figs. 2B, C, 4A, B). These three layers completely isolate the eyes, in such a way that the light coming through the adjacent transparent cuticle does not reach the retina. The retina is composed of photoreceptor cells as well as pigmented and non pigmented supporting cells. The principal eyes and the secondary eyes differ in two main aspects. First, the retina of the secondary eyes contains monopolar receptor cells whereas the retina of AM eye contains bipolar receptor cells (as described for spiders by Blest, 1985). Second, a well-developed tapetum crosses the retinal area of the secondary eyes. No reflecting tapetum is present in the AM eye.

A summary diagram of a principal eye and a secondary eye of *M. vatia* is given in Figs. 3A and 5F. Table 2 presents a comparison of the main characteristics of the four pairs of eyes of this spider.

Table 2Overview of the morphological characteristics of the different eyes of *M. vatia*.

	AM	AL	PL	PM
Lens	- depth: 70 μm - width: 70 μm	- depth: 60 μm - width: 70 μm	- depth: 65 μm - width: 80 μm	- depth: 60 μm - width: 65 μm
Retina (diameter)	100 μm	200 μm	140 μm	135 μm
Rhabdom (length)	type 1: 5 μm type 2: 4–5 μm type 3: 10–12 μm	25–30 μm	20–25 μm	12–15 μm
Number of photoreceptors	type 1: 100–110 type 2: 20–30 type 3: 1	about 600	about 400	about 400

3.3.2. The principal eyes

The AM eye in longitudinal section is pyriform (Fig. 2C, E), while it is almost circular in transverse section (Fig. 3B–E). The lens is biconvex and almost spherical, of approximately 70 μm in diameter (Fig. 2A). Beneath the lens, the cells of the vitreous body are arranged to form a flattened spheroid of approximately 135 μm in diameter and 90 μm depth (Figs. 1C, 2C and 3B).

The entire retina is hemispherical (approximately 100 μm in diameter \times 70 μm in depth) and formed by two well differentiated areas, a central dark pigmented pocket-shaped area surrounded by a peripheral brown pigmented area (Fig. 2E, D). The bodies of the photoreceptor cells are located in the peripheral region of the retina (Figs. 2C, E, 3C, D). The cells are bipolar, with a short receptive segment bearing the rhabdomeres on two opposite faces of the cell, and a long axonal segment which makes part of the optic nerve (Figs. 2C, 3B, C, E, 4). The retinal axons converge at the bottom of the retinal cup forming the slightly eccentric optic nerve. We counted about 130 retinal cell axons with similar diameter in a transversal section of the optic nerve. The eye is attached at its base by two oblique muscles, one dorsal and one ventral, fastened to the more anterior region of the prosoma (Figs. 2D, 3D).

We have identified three different morphological types of rhabdom in the retina of the AM eye. The first type is located immediately beneath of the vitreous body, covering the totality of the retinal surface. Each rhabdom is isolated from its neighbor by pigment and glial cells. The rhabdom covers approximately 5 μm of the end of the receptive cell segment (Figs. 2C, 3B and 4A). The second type is located in the central dark pigmented area, beneath the layer of the type I rhabdom. It covers the distal region of this area and is distributed in three strata (Figs. 2E, 3C, 4B). The rhabdom covers about 4–5 μm of the end of the receptive segment. The third type is the process of a unique single cell which bears a rhabdom located right in the center of the dark pigmented pocket, deeply hidden beneath the layer of type II rhabdom. This rhabdom is bigger than the others, covering approximately 10–12 μm of the cellular process and is surrounded by glial cells and dark pigment (Figs. 2D, 3E and 4C). The light reaches this rhabdom through a small aperture of about 9 μm width \times 40 μm depth, located in the middle of the dark pigmented area (Fig. 3D). This rhabdom has then an acceptance angle of about 12°.

3.3.3. The secondary eyes

The AL, PL and PM eyes display a similar organization, but differ in number of photoreceptors and size (see Table 2). As pointed out above, the photoreceptors of the secondary eyes are monopolar cells. The layer of body cells is located underneath the vitreous body, in the distal area of the retina. Three regions of a receptor cell can be distinguished: a pear shaped soma containing a large nucleus, a receptive segment bearing the rhabdomeres on two opposite faces of the cell, followed by a segment from which the axon arises (Fig. 5A–D). There are no pigment granules in the region of the receptive segment between the body cell and the rhabdom. The rhabdom of every receptor cell is separated from

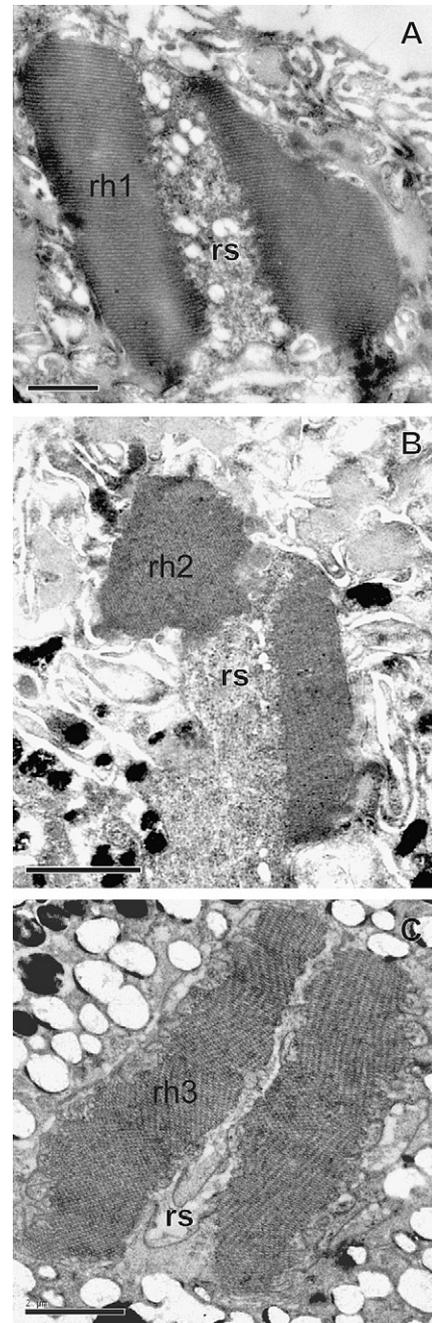
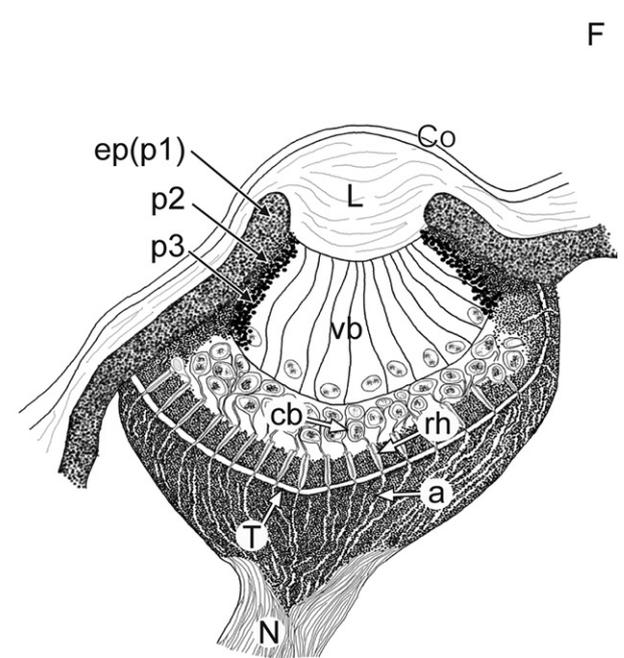
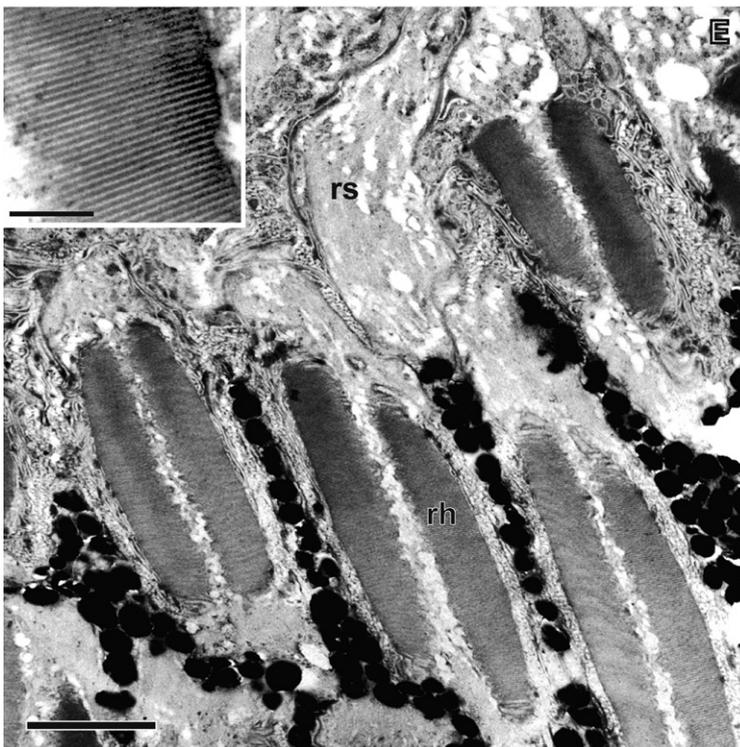
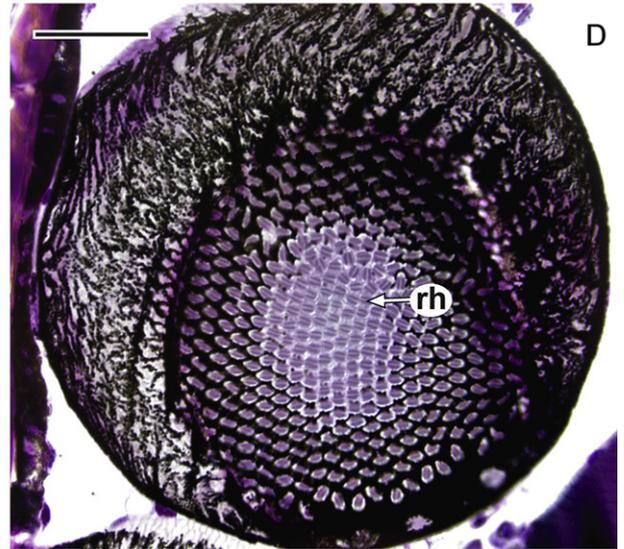
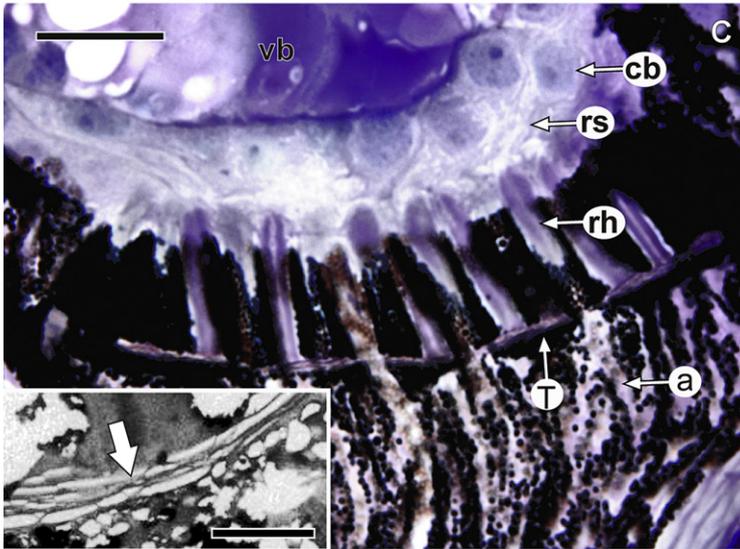
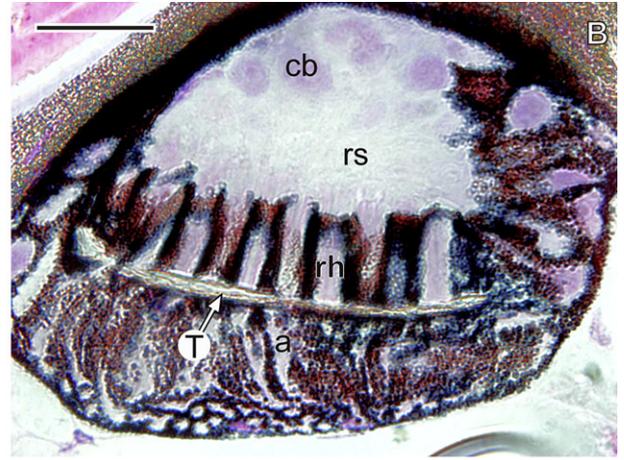
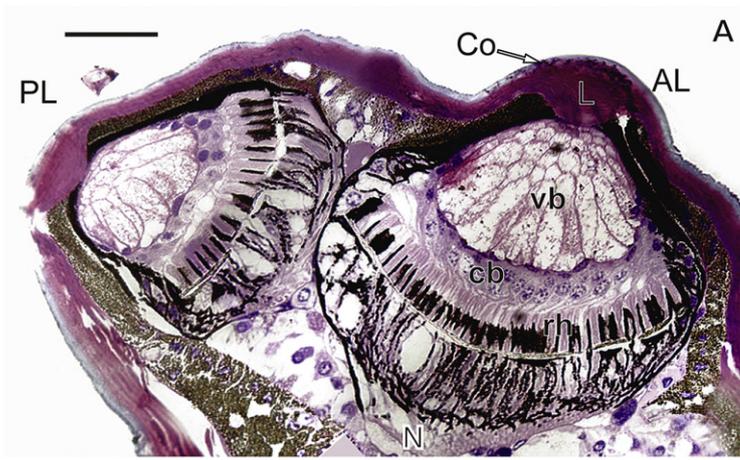


Fig. 4. Transmission electron micrographs showing the appearance of the different types of rhabdoms identified in the AM eyes. A: rhabdom type I (cross section). B: rhabdom type II (longitudinal section). C: rhabdom type III (cross section). rh, rhabdom; rs, receptive segment. Scale bars: A: 1 μm , B, C: 2 μm .



each other by pigmented cells (Fig. 5C, E). The rhabdoms are organized in a simple layer, resting on the tapetum (Fig. 5A–C). The tapetum is a discontinuous layer of crystals ($0.5 \times 3 \mu\text{m}$), about $2 \mu\text{m}$ thick, organized in 3–4 strata (inset in Fig. 5C). The cellular segment following the rhabdomeres crosses the tapetum to form the nerve at the base of the eye (Fig. 5A). Adjacent axonal processes in the retina are separated from one another by pigmented and not pigmented glial cells. The secondary eyes have no ocular muscles.

4. Discussion

The aim of this work was to provide the morphological basis of the organization of the visual system of *M. vatia* necessary for functional studies. In particular, we were interested in the optical and structural characteristics necessary for matching its own color to that of the substrate, as this ability has been suggested to be associated with the spider's vision (Weigel, 1941). This can be expressed in two main questions: 1) does the visual field allow spiders to look at their own body and the substrate at the same time? 2) is the organization of the retina compatible with color vision? In other words, does the information potentially gathered by the visual system allow for color matching?

4.1. The fields of view

All pairs of eyes have wide visual fields, covering almost the whole dorsal hemisphere and partially the ventral one (Fig. 1D–F). The principal eyes (AM eyes) present the most extended field of view, covering the antero-lateral region above and below the eye equator. They completely cover the visual field of AL eyes and overlap with the visual field of the other pairs. Despite a high variability in the eye pattern across spider species, a nearly full view of the upper visual environment has been highlighted in a majority of species for which visual fields has been assessed (Land, 1985; Foelix, 1996; Nørgaard et al., 2008). In *M. vatia*, a binocular zone is present as a vertical frontal band. Interestingly, the binocular zones of AL and AM eyes overlap frontally, determining an area of visual “tetraocularity” looking forwards. AM eyes also cover regions of the visual fields of PM and PL eyes, but unilaterally. So, almost any point of the entire dorsal hemisphere and of the meridional region of the ventral hemisphere is looked at by at least two different eyes. In particular, PL eyes look towards the opisthosoma and AL/AM eyes simultaneously to legs and substrate. Thus the extension and superposition of the visual fields could allow for simultaneous analysis of the color of both substrate and body.

The extended binocular areas of AL and AM eyes, in particular their superposition in the frontal area, seems to represent an adaptation to prey capture. Instead of relying in just a pair of highly performant frontal eyes as in Salticidae, each point in front of the spider is simultaneously looked by photoreceptors located within four different eyes in *M. vatia*. It is interesting to note that this feature is not frequent in other spider families (Land, 1985; Nørgaard et al., 2008). This could increase the ability of the spider to precisely estimate the distance of the prey at the moment of the attack. It should be also noted that the AM eyes possess a mobile retina. Its muscles are less developed than in Salticidae (Kaps and Schmid, 1996) and the retina is not elongated as in jumping

spiders, but the visual field of each eye changes dynamically as in Salticidae, making it wider. Hence the areas of superposition with other eyes are probably larger than those measured here.

The space over the equator is well covered by the different eyes and the PM eyes look directly upwards. *M. vatia* are predated upon birds and these eyes could be related to their detection. So, the binocular dorsal area could provide some information related to the distance and approaching speed of prey and predators, allowing the spider to display adaptive movements (e.g. evasion or attack).

4.2. Eye muscles

In many spiders, the retinae of the AM eyes have muscle attachments to control the direction of vision (Foelix, 1996). The retinae of the six secondary eyes cannot be moved. Most of the web-building spiders possess only one dorsal muscle, whereas hunting spiders have at least two (Widmann, 2008). The AM retinae of the jumping spiders (Salticidae) seem to be the most complex since they were moved by six muscles, with three degrees of freedom: vertical, horizontal and rotational, performing four types of movements (Land, 1969a). The movements of the AM eyes, which can be complex, are probably a critical factor in how salticids process visual information, especially shape and form (Land, 1969a; Land and Furneaux, 1997). *Cupiennius salei*, a nocturnal hunting spider, is able to move the retinae of the AM eyes by two muscles performing two types of movements (Kaps and Schmid, 1996). The arrangement of the muscles presents in the retina of *M. vatia* is similar to those of the *C. salei*, with two muscles, a ventral and a dorsal one; as a result, the movements produced by these muscles include a medial component. Land (1969a) suggested that the function of the AM eyes of salticids is to examine stationary objects, whereas the unmovable secondary eyes serve to detect motion. Kaps and Schmid (1996) concluded that the motility of the AM eyes of *C. salei* might be used to detect immobile targets of interest, such as stationary prey or the plants in which these spiders live, and also to shift the ‘gaze’ of the spider towards the direction of any mechanical stimulation.

4.3. Retinal layout

The structure of the retina of crab-spiders was first described by Homann (1934, 1975), who analyzed the eyes of several species belonging to eight genera. This author provided a general description of the retina of principal and secondary eyes.

The structure of the hemispherical retina of secondary eyes of *M. vatia* evinces a single photoreceptor layer. In contrast, the retina of principal eyes (AM) is much more complex and organized in strata. This retina possesses a hemispherical area in the periphery composed of a monolayer of one type of rhabdomeres (type I) and a U-shaped dark pigmented area in the central region. This region harbors two types of rhabdoms: a type II distributed in three strata and a type III, the process of a unique single cell in the center of the dark pigmented pocket. A similarly complex retinal layout has been observed in other thomisids. Indeed, the U-shaped structure of the Australian crab-spider *Hedana* sp. contains four morphologically distinct types of photoreceptive segments (type 1, 2, 3, 4), each having a specific spatial arrangement (Blest and O'Carroll, 1990).

Fig. 5. Photomicrographs of the secondary eyes. Horizontal sections from the spider prosoma. A: Arrangement of the PL and AL eyes. B: PM eye. C: detail of the cell bodies and rhabdomeric layer of the PL eye. The inset in C shows a transmission electron micrograph of the tapetum layer organized in strata of crystals (arrow). D: Frontal section from the rhabdomeric region of the AL eye showing the arrangement of the rhabdoms in the retina. E: transmission electron micrograph showing a detail of the rhabdoms of the secondary eyes. The inset shows a detail of the PM rhabdom. F: Diagram of a secondary eye, reconstructed from frontal and longitudinal sections (light and electron microscopic observations). a, axon; cb, cell bodies; Co, cornea; ep(p1), epidermis with pigments granules and microcrystals; L, lens; N, nerve; p2, intermediate layer of pigment granules; p3, internal layer of big pigment granules; rh, rhabdom; rs, receptive segment; T, tapetum; vb, vitreous body. Scale bars: A, B, D: $50 \mu\text{m}$; C: $20 \mu\text{m}$ (inset: $5 \mu\text{m}$); E: $5 \mu\text{m}$ (inset: $0.5 \mu\text{m}$).

Furthermore, the same authors also noted that rhabdomeres of segment types 2 and 4 are organized in layers in the U-shaped region, with type 2 lying distally to the type 4. Particularly intriguing is the unique “giant” rhabdom located in the central retina of AM eyes of Thomisidae. Blest and O’Carroll (1990) indicated its presence in *Hedana* sp., but the layering of the retina is quite different to that observed in *M. vatia*. These authors speculated that this giant rhabdom could be derived from rhabdomeres contributed by several receptors. In the case of *M. vatia*, it is located in the lowermost retinal layer and its double structure is formed by a single cell (Fig. 3). This cell is thus stimulated by light coming only along its optic axis, which looks at different directions with retinal movements. Thus, instead of an X-shaped mobile retina as present in Salticidae, *M. vatia* could compose images by integrating the information gathered by a single point, like Copepods do (Land, 1988). The relatively big size of this rhabdom suggests that this photoreceptor should be particularly sensitive to low light intensities.

4.4. Functional implications of a tiered retina

Tiered retinæ were first described in the Salticidae by Land (1969b). *Phidippus johnsoni* (Peckham) and *Metaphidippus aeneolus* (Curtis) possess a retina with four layers of morphologically distinct photoreceptor classes (Land, 1969b). It is widely assumed that several layers in Salticidae display a specific spectral sensitivity and that the UV layer is distal to the green one (Blest et al., 1981). Salticidae and *M. vatia* thus share structural and physiological retinal features. However, some differences also arise, especially the number and density of photoreceptors in each layer, which is higher in Salticidae (Land, 1969b; Blest et al., 1981; Blest and Sigmund, 1984). The functional significance of this organization in Salticidae is assumed to be in reducing chromatic aberration and facilitating accommodation (Blest et al., 1981). The specific tiered structure of the retina plays a critical role in color vision (Land, 1969b; Harland and Jackson, 2004).

Electrophysiological evidence (Defrize et al., 2011) confirmed the presence of green and UV receptors in the retina of *M. vatia*. Other photopigments are most likely also present, for instance in the giant rhabdom (type III) or in other types of photoreceptors. The peculiar retinal organization of *M. vatia*, in particular the presence of three different rhabdom types, strongly suggests that the anterior median eyes have more than two visual pigments. Thus, the visual system of *M. vatia* has all the necessary conditions to see colors. Electrophysiology also provided indications that the layering of different types of photoreceptors found in jumping spiders also occurs in *M. vatia*, since the adaptation of the eye to light of 340 nm suppressed the UV sensitivity, with sensitivity to the green remained unchanged. It implies that the UV sensitive distal layer filters out UV light, avoiding the stimulation of the beta-peak of green receptors (Defrize et al., 2011). This would imply that the UV receptor is lying distally to the green.

4.5. The function of principal and secondary eyes in *M. vatia*

In Salticidae, the functional distinction between both types of eyes is related to spatial acuity, movement perception and color vision. Their principal eyes exhibit a high spatial acuity, a narrow field of view and a tiered retina which, together with photoreceptors having different spectral sensitivity, allow color vision. Secondary eyes are characterized by wide fields of view, high sensitivity to the movement of objects and monochromacy. Jumping spiders bring the principal eyes to bear by orienting towards moving stimuli that are detected by secondary eyes (Land, 1971). In this way, the visual system is modeled to prey capture and

recognition of the color of conspecifics (Land, 1969b; Harland and Jackson, 2004).

The eyes of *M. vatia* exhibit characteristics that differ from Salticidae. The AM eyes have wider view fields and less complex retinal movements, as judged by the limited number of muscles. They share with Salticidae a tiered retina and probably also color vision (Defrize et al., 2011). Secondary eyes show at least two different photoreceptor populations, differing in spectral sensitivity (i.e., dichromacy; Defrize et al., 2011) and a different coverage of the visual space. Whereas the PM eyes cover large lateral areas in Salticidae, aiding to the detection of prey on the surrounding substrate, they look upwards in *M. vatia*, with an important binocular area which should facilitate the detection of flying prey and flowers above the level of the animal. There are no data concerning the response of crab-spiders to peripheral object movement but if secondary eyes are implicated, their dichromacy (Defrize et al., 2011) indicates that this would not be their only function. Dichromacy makes the discrimination of light wavelengths possible. As explained above, *M. vatia* adapts its body color to that of the substrate on which it hunts. It is not fully clear how color change is triggered (Insausti and Casas, 2008, 2009), but independently of the exact process (i.e., active body color adjustment, choice of flower color, etc.), it needs to be at least able to analyze the color of actual or potential substrates, if not that of the body. In this respect, it is interesting that another crab-spider species opted for increasing its contrast with the substrate, albeit in the UV-range (Heiling et al., 2003). This is another strategy, which requires also some form of color assessment.

The recent study by Defrize et al. (2011) provides electrophysiological evidence for the occurrence of different receptor populations in principal and secondary eyes of *M. vatia*, with the exception of the PL eyes, in which sensitivity to UV and green light could not be split apart. Electrophysiological measurements revealed in the rest of the eyes a spectral sensitivity ranging from UV to orange and at least two types of photoreceptors exhibiting maximal sensitivity to wavelengths of 520 nm and 340 nm (Defrize et al., 2011). This study did not exclude, however, the probable occurrence of other sensitivities. Thus, the physiological evidence is indicative of color vision. Our work provides strong support for an involvement of the visual system in color matching in this spider: the visual field enables it to see both, its own body and the substrate at the same time and the retina organization shows multiple types of photoreceptors. These observations provide additional support to the hypothesis of color vision.

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