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Review

Polarized-light vision in spiders

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ABSTRACT

This paper reviews the anatomical, physiological, and behavioral studies carried out on polarized-light vision in spiders. This invertebrate group has a variable number of simple eyes, according to the family. The eyes are designated as principal eyes or anterior median eyes (AMEs), and the other pairs, called secondary eyes, are the anterior lateral eyes (ALEs), the posterior median eyes (PMEs) and posterior lateral eyes (PLEs). The retinas of these eyes have rhabdomeric photoreceptors. This paper summarizes the arrangement of the two-channel system that could allow some spiders to detect the polarized skylight patterns either in their AMEs or their PMEs. The physiological studies carried out on some species, which reveal the presence of UV and green receptors in the AME retinas are also described. Finally, the behavioral studies that show that in all species of spiders, except in the family Gnaphosidae, the AMEs are functionally related to polarized-light vision, are reviewed. In the case of Gnaphosidae, the polarized-light perception is through the PMEs. Spiders, in comparison with the other prominent group of terrestrial arthropods, the insects, need more research into their anatomy, physiology and behavior related to polarized light.

KEYWORDS: spiders, vision, orientation, retina, polarized light

INTRODUCTION

Some terrestrial animals such as insects and spiders can use the celestial polarized-light patterns as a compass during path integration to guide them back to their home.

The linearly polarized light (also called plane-polarized light, [1]), due to Rayleigh scattering in the sky, has been shown to be used by several terrestrial animals for navigation and object detection. Linearly polarized light is characterized by the e-vector or direction of polarization and the degree of polarization [2-5]. The celestial e-vectors are arranged forming regular patterns around the sun, with the solar meridian being a symmetry plane (Fig. 1). The region of the sky that exhibits maximal polarization is placed at an angle of 90º from the sun in such a way that the pattern changes in accordance with the elevation of the sun (Fig. 1); for example, when the sun is rising the maximal polarization is placed above the observer.

Waterman and Horch [6], working on the receptor potentials of crab eyes, proposed that for a polarized-light compass there must be a two-channel intraretinal system.

This two-channel system has been described in several insects and consists of rhabdoms orthogonally arranged to each other in ommatidia located in a special region of the compound eye called the dorsal rim area (DRA) [7, 1, 8].

Polarization sensitivity has been determined in Crustacea and insects by means of behavioral or electrophysiological analyses (Crustacea: see review in [9]; insects: see review in [10]). The first study that revealed the use of polarized light for navigation was the behavioral study carried out by Karl von Frisch [11] on bees performing recruitment dances in the hive. He found that if he opened a small window over the hive,

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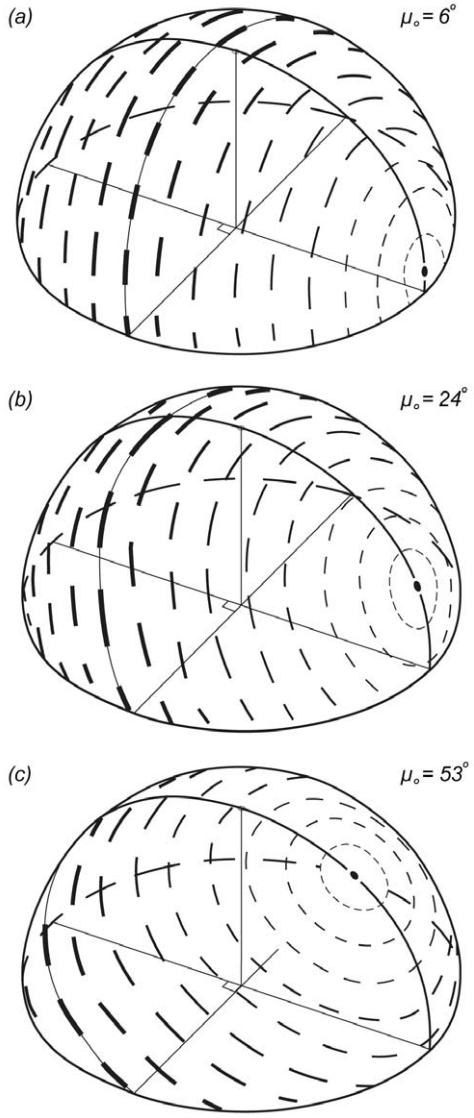

Fig. 1. Polarized skylight patterns for three different elevations of the sun (6º, 24º, and 53º). The directions of the black bars represent the directions of polarization while the width of the black bars represent the degree of polarization (Courtesy of Dr. Rüdiger Wehner, Brain Research Institute, University of Zürich; published in Wehner (1983)).

providing a small patch of cloudless sky, there were no changes in the direction of the dances. However, if he placed a Polaroid sheet over the window and rotated it, the bees changed the direction of their dance as he rotated it. With the availability of these Polaroid sheets, many scientists began to try to demonstrate the presence of sensitivity to polarized light on different species, including spiders [12, 13]; see the historical review in [14] and a review of the research on ants and bees in [10].

Electrophysiological analyses have been carried out in insects by intracellular recordings of different cell types, for example, the descending neurons that connect the locust brain and thoracic ganglia [15], the neurons of the cricket's central complex [16], and the photoreceptors of the dorsal rim area [17]; for a review of polarized-light processing in the insect brain, see [18].

What is the spectral sensitivity of the DRA photoreceptors in insects?

DRA ommatidia contain homochromatic photoreceptors whose spectral sensitivity varies according to the species. In the locust *Schistocerca gregaria*, all the DRA cells peak in the blue region of the spectrum [19]. In the cricket *Gryllus bimaculatus*, the DRA contains a receptor with a blue- and an ultraviolet (UV)-opsin [20]. In the desert ant *Cataglyphis fortis*, [21] and the honeybee *Apis mellifera*, [22] the DRA contains ultraviolet (UV) receptors.

This paper describes the arrangement of the rhabdoms in the anterior median eyes (AMEs) of several species of spiders and the use of a special arrangement of the tapetum in the posterior median eyes (PMEs) of a different species. In addition, the electrophysiological data that have been obtained from some species, and the behavioral data relating to spider orientation in the presence of polarized light, are also described. The anatomical and electrophysiological data pertaining to insects are used to compare the arrangement of spider rhabdoms and spectral sensitivity. The most recent reviews on this subject were carried out in 2001 [23] and 2004 [24] and besides the time lapsed, some interesting aspects were not covered in these studies.

Spider eyes

Spiders have camera-type eyes with rhabdomeric photoreceptors [25-27]. From an anatomical point of view, eyes are classified as either principal eyes or secondary eyes. This terminology was introduced by Bertkau [28] who called the anterior median eyes 'Hauptaugen' (principal eyes) and the other eyes 'Nebenaugen'

(secondary eyes). The rhabdomeres of the photoreceptor cells in the principal eyes are located behind the vitreous body and the receptor somas are located behind the rhabdomeres. However, in the secondary eyes the photoreceptor somas are located behind the vitreous body and the rhabdomeres are located behind the photoreceptor somas. The other differences between the principal and the secondary eyes are: a) the presence of a variable number of muscles attached to the retina of the anterior median eyes that allow movement; and b) the absence of a reflecting tapetum of guanine. The principal eyes are always the anterior median eyes (AMEs) while the secondary eyes are the posterior median eyes (PMEs), posterior lateral eyes (PLEs), and anterior lateral eyes (ALEs). The photoreceptor cells can have rhabdomeres all around the cell membrane while in other cases the rhabdomeres are present only in the two opposite sides of the cell. When in contact with each other the rhabdomeres of two adjacent cells form a rhabdom [25, 27].

Spider species and polarized-light vision

Polarized-light vision has been studied in a small group of spider species in which anatomical, physiological or behavioral analyses have been carried out to different extents. Some of the studied species are: the agelenid spiders *Agelena labyrinthica* Clerck [12, 29, 30] and *Agelena gracilens* C. L. Koch [31, 32]; the lycosids *Arctosa variana* C. L. Koch [13, 33, 34] and *Lycosa tarantula* Linnaeus [35, 36]; the gnaphosid spider *Drassodes cupreus* Blackwall [23, 37, 38] and several lynx spiders (*Peucetia cauca* Lourenço, *P. gerhardi* Van Niekerk & Dippenaar-Schoeman, *P. graminea* Pocock and *Oxyopes lineatus* Latreille) [39].

The anatomical basis of polarized-light vision, as well as the physiological and behavioral data will be described in this review.

Structural basis of polarized-light vision in spiders

The studies on agelenid spiders have been carried out on two species: *Agelena labyrinthica* which was used in behavioral and structural studies and *Agelena gracilens*, for structural studies.

The visual cells of the ventral part of the AMEs of *A. gracilens* [31, 32] and *A. labyrinthica* [30] have rhabdomeres located in two parallel sides, while the central and dorsal cells have rhabdomeres in three or four sides of the cell. Therefore, the ventral part of the AMEs has the anatomical characteristics of a two-channel analyzer and is the most probable structure to detect polarized light (Fig. 2a). The most recent and in-depth study on agelenids has been carried out in *A. labyrinthica* [30]. In this species, the AMEs are tilted by 45º with respect to the horizon, looking towards the zenith. In the central retina, Schröer [30] has described an “irregular twisting” of the rhabdomere along its length. This twisting has never been found in the rhabdomeres of the ventral retina. This twist was first described in insects (bees: [40]; ants and crickets: [41]) and it would degrade or eliminate the polarization sensitivity of the photoreceptors.

In lycosids, some old light-microscopy studies showed a ventral arrangement of photoreceptor cells [42] in the anterior median eyes of different species (v.g.: *Trochosa ruricola* De Geer), which is very similar to that observed more recently by Kovoor *et al.* [35] and Dacke *et al*. [23]. Scheuring [42] showed a longitudinal section of the AME in which it is possible to distinguish two populations of rhabdoms: one ventral and another median and dorsal (Fig. 2b); the rhabdomeres of the ventral population were located in two tiers. The arrangement described by Scheuring in 1914 has not been acknowledged by recent authors working on lycosids, except in the paper by Kovoor *et al.* [35].

The first modern microscopic study of lycosid spider eyes was carried out by Baccetti and Bedini [43] on *Arctosa variana* Koch. In their fig. 1 they showed a longitudinal section of an anterior median eye (AME) and they showed the rhabdoms were arranged in a regular way without any regional differentiation. They also studied the dorsal and ventral populations of cells in the transverse sections of this eye (their fig. 4). They showed a dorsal population of cells with a pentagonal transverse section and rhabdomeres in all the membranes, and a ventral population of cells with a rectangular transverse section. However, it is difficult to discern if there were

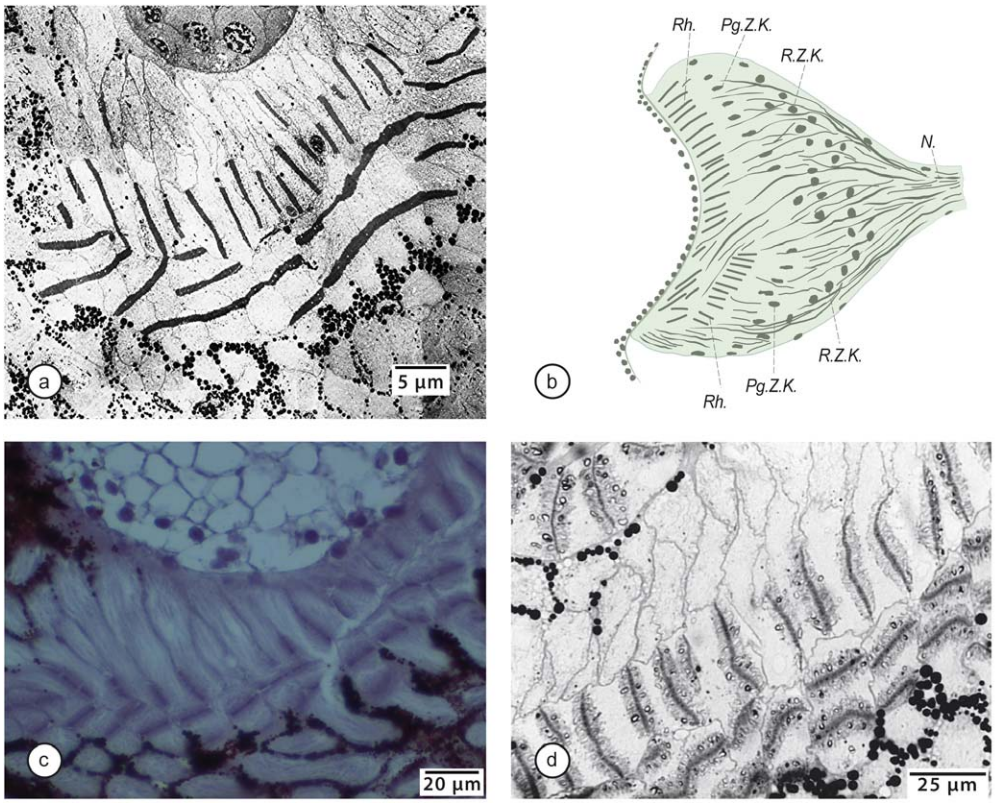

Fig. 2. Arrangement of the two-channel system of rhabdoms in the ventral part of the AMEs of different species of spiders. **a.** Electronic micrograph of a frontal section of the AME of *Agelena gracilens* (courtesy of Dr. Wolgang Schröer, unpublished). **b.** Schema based on a drawing of a sagittal section of the AME of *Trochosa ruricola* (based on Scheuring, 1914) Abbreviations: Rh, rhabdoms; Pg.Z.K., nucleus of the pigment cell; R.Z.K., nucleus of retinal cell; N, nerve. **c.** Light micrograph of a frontal section of the AME of *Lycosa tarantula*. **d.** Electronic micrograph of a frontal section of a lycosid wolf species (species A) (courtesy of Dr. David C. O'Carroll, published in Dacke *et al*., 2001).

rhabdomeres in all of the membranes or not and they do not make any reference in the text to the pattern of rhabdom distribution. Furthermore, in the discussion of their study they state "We are therefore unable to find, so far, any feature in the anatomy of the eye that can be correlated with a differential sensitivity to polarized light" [43, p. 120]. Magni [44] indicated that although Baccetti and Bedini [43] had found a different pattern of rhabdom organization, they had not found any anatomical feature which could be related to the differential sensitivity to polarized light that these spiders exhibited. Eakin and Brandenburger [45] also made reference to the work of Baccetti and Bedini [43] but they considered that the latter's fig. 1, as described earlier, was semi-diagrammatic and it did not reveal the differences in the rhabdomere orientation-planes.

Working with the lycosid spiders *Lycosa erythrognata* Lucas and *L. thorelli* Keyserling, Melamed and Trujillo-Cenoz [46] found two patterns in the arrangement of the rhabdoms in the retinae of AMEs. In the peripheral parts of the retina, the rhabdoms were oriented either parallel or perpendicular to the retinal radii, while in the central region they were oriented forming a pentagon. Although the authors presented a photographic montage of a cross section of the whole AME retina, the pattern of distribution that they presented occupied only a quarter of the retina and their results led Waterman [3] to reject the possibility of a two-channel system for polarized-light perception because "adding all the radial or tangential inputs would cancel out e-vector discrimination, at least optically, if the system is radially symmetrical" (p. 423).

The first modern study that associated the microanatomy of the AME of a lycosid spider and the perception of polarized light was carried out by Kovoor *et al*. [35] in the AMEs of *Lycosa tarantula* Linnaeus (Araneae, Lycosidae). In the *L. tarantula* AMEs, the authors described two kinds of photoreceptors: one placed dorsally and medially, polygonal in cross-section, which bore rhabdomeres on all their faces; the other placed ventrally in the retina, that bore rhabdomeres on two parallel faces, and there were two populations of rhabdoms oriented orthogonally to each other (Fig. 2c). This disposition had already been observed in the second instar juveniles [35]. The information coming from these two groups of photoreceptor cells end in two different regions of the first, second, and third synaptic zones [47]. A frontal section of the AME of *L. tarantula* clearly showed the presence of the two specialized populations in the ventral region of the retina, while the central region had cells with rhabdomeres on all their faces (Fig. 2c).

The AME retina can be moved by two antagonist muscles attached obliquely to its lateral external surface. The alternating contraction of these two muscles can give place to the up and down movements of the retinal cup (ophthalmoscopical unpublished observations by the author). So, *L. tarantula* could analyze the celestial polarization pattern by a successive process [35]. This hypothesis was first proposed in spiders by Schröer [31] for *Agelena gracilens* and recently [30] for *A. labyrinthica*.

Dacke *et al*. [23] carried out a light-microscopy study of the AME retina of five lycosid spiders, *Pardosa prativaga*, *Alopecosa pulverulenta*, *Geolycosa godeffroyi*, *Geolycosa* sp. and an unknown species which they called species A. They also described two populations of rhabdoms which were similar to those previously described in other lycosids (Fig. 2d).

The two orthogonal populations of photoreceptors described in the ventral part of the retinas of different lycosids could enhance the polarization sensitivity by the antagonistic interaction between them.

Several other histological studies on lycosid eyes have been published, for example, on *Pardosa astrigera* [48] and *Lycosa leuckartii* [49]. Jeong and Moon [48] studied the histological structure of AMEs; however they did not make any reference to the two ventral layers described by Kovoor *et al*. [35] and Dacke *et al*. [23]. Jeong and Moon [48] showed a series of sections from the lens to the intermediate segments of the receptor cells; although, the poor quality of the photographs makes it very difficult to discern the presence of the two populations of photoreceptor cells described by Kovoor *et al*. [35] and Dacke *et al*. [23]. Also, the study on *L. leuckartii* does not supply any data about the structure of the AME photoreceptor.

Uehara *et al*. [50] studied the fine structure of the AMEs in the family Argiopidae, using the species *Argiope amoena* L. Koch. They described the AMEs as having an optic axis that looks towards the zenith. Microvilli are oriented in various directions and they discussed this arrangement in comparison with that described in Lycosidae, Salticidae and Agelenidae. *A. amoena* being a highly evolved web-building spider, they considered that it would preferentially use receptors that could detect web vibrations.

In the gnaphosid spider *Drassodes cupreus*, the polarization-detecting organ is located in the posterior median eyes (PMEs) which look towards the zenith and have their longitudinal axes roughly orthogonal to each other [37]. In this species, the canoe-type tapetum acts as a polarizing reflector and the polarization signal must be obtained by comparing the activity of about 60 main receptors found in each eye, which have orthogonal orientations among them. The rhabdomeres of the main receptors are aligned along the long axis of the eye and there are two cells, called ‘shallow receptors’ by Dacke *et al*. [37], and ‘central receptors’ by Mueller and Labhart [38], whose rhabdomeres are aligned along the short axis of the eye. Mueller and Labhart [38] determined by histochemistry that the crystals of the tapetum of *D. cupreus* consist of guanine, as had been previously proposed by Land [51, 52] and Schwab *et al*. [53]. In this case, there is an antagonistic interaction that enhances the polarization sensitivity, by the comparison of the outputs from both PMEs [38].

The salticid spider retina has been the most intensively studied both by light and electron microscopy [42, 45, 54-57]. Although Scheuring [42] and Homann [56] assumed that there was a single layer of photoreceptors in the AME retina, Land [57] described four separate layers along the optic axis. These layers were designated I, II, III, and IV, with layer I being the deepest. As a result of the optical studies carried out, Land [57] suggested that "the receptors in layer IV are ultraviolet-sensitive, or else that this layer performs some other task for which a well-resolved image is not required" (p. 462). Later in his discussion, Land [57] proposed that this other task could be the detection of the plane of polarization, to assist the animal in its navigation to its retreat after hunting.

Electron microscopy of the salticid AME retina was carried out by Eakin & Brandenburger [45], Blest and Price [58] and Blest and Sigmund [59].

Eakin & Brandenburger [45] confirmed Land's findings and they described photoreceptors with two rhabdomeres in layer IV, that could be either dorsal and ventral, or medial and lateral, arranged in such a way that they are at right angles to each other. They proposed that the rhabdomere arrangement in layer IV of the AME "satisfies the anatomical requirement for an analyzer of the e-vector of plane polarized light" (p. 652).

Blest & Sigmund [59] accepted the proposal of Land [57] and Eakin & Brandenburger [45] that the photoreceptors in layer IV could act as polarization analyzers in UV light. These analyzers could be used to navigate their return to the silken retreats where they spend the night.

Blest [60], discussing the development of the AME retina in "primitive" or "advanced" salticids, writes that all salticids possess the same arrangement of layer IV rhabdomeres, and that, given that several salticid species have been observed hunting a substantial distance from their nest, it is most likely that they use the sky polarization pattern than other mechanisms such as landmark-based navigation or dead-reckoning.

The final proposal concerning layer IV receptors as a polarization compass in Salticidae was made by Harland *et al*. [61] although they do not provide any new data to compare with the studies previously cited.

Physiological studies related to polarized-light vision

There is no physiological data about polarization vision in the family Agelenidae.

In Lycosids, DeVoe [62] carried out the only study which used intracellular recordings of the AMEs of wolf-spiders. He performed intracellular recordings of the anterior median eyes of *Lycosa baltimoriana*, *L. miami* and *L. lenta* and showed that the cells in the AMEs responded maximally in the visible range (510 nm) and in the UV range (360-370 nm or less). But he reported that "The unexpected finding of this paper is the great variability of the spectral sensitivities of cells in anterior median eyes." (p. 263). He also proposed that wolf-spider AME cells have a pigment which absorbs visible light, and a UV-absorbing pigment.

Yamashita and Tateda [63] studied the spectral sensitivities of the AMEs of orb-web spiders *Argiope bruennichii* and *A. amoena* (Argiopidae). They found three types of photoreceptors, with maximum sensitivities at 360 nm, 480-500 nm and 540 nm. They discussed these results in the context of the duplicity theory of vision.

In *A. argentata*, Tiedemann *et al*. [64] found only one receptor type, with a maximum sensitivity of 525 nm, in the AMEs.

Dacke *et al*. [37] made intracellular recordings of the two main cells in Gnaphosids. They found that their polarization sensitivity (PS) was higher than that measured in the polarization area of insects such as the desert ant *Cataglyphis* and the honeybee *Apis*. The spectral sensitivity of the cell with the highest PS peaked in the UV range (350 nm). This is the only study on polarization vision in spiders, in which the polarization sensitivity has been investigated. The study by Mueller and Labhart [38] carried out wavelength-dependent measurements of the polarizing properties of the tapetum of the PMEs and they found that the degree of polarization was weakest for UV light (370 nm) and higher for green light (580 nm).

In Salticids, DeVoe [65] found three types of cells in the AMEs: UV cells with a peak sensitivity at 370 nm, green cells with peak sensitivity at 532 nm, and UV-green cells with dual peaks of

sensitivity at 370 and 535 nm. He could not identify the layers in which the registered cells were placed.

Yamashita and Tateda [66] found four types of receptors, UV, blue, green and yellow; but as in the study of DeVoe [65], they could not identify the cells they had recorded from.

However, unlike previous studies, Blest *et al*. [67] were able to identify the receptors cells and, afterwards, they were marked with the dye Lucifer yellow. They found two classes of spectral receptors: UV, with a peak sensitivity at 360 nm and green, with a peak sensitivity at 520-530 nm. The green cells were located in layers I and II, and the UV cells were located in layer IV.

Behavioral studies of polarized-light vision

Behavioral orientation by means of polarized light was studied in Agelenids by Görner [12, 29] either under laboratory conditions by rotating a polarizing filter above the web, or in an outdoor experiment in which a polarizing filter was arranged either with the direction of maximal transmission being coincident with the e-vector of the zenith, or perpendicular to the e-vector of the zenith. Under indoor conditions, the rotation of the polarizing filter produced a higher scatter in the directions the spiders took to return to the funnel. In the outdoor experiment, the spiders returned directly to the retreat only when the direction of maximal transmission of the polarizing filter was coincident with the e-vector of the zenith [29]. By means of occlusion experiments, Görner [12] also determined that it was the principal eyes and not the secondary eyes that were responsible for polarization navigation.

In Lycosids, a behavioral study carried out by Ortega-Escobar and Muñoz-Cuevas [36] showed that *L. tarantula* females used linearly-polarized sunlight and that this polarized light was perceived only through their AMEs. To demonstrate this, two groups of spiders in which the principal (AMEs) or the secondary eyes (PMEs, PLEs and ALEs) were masked, were used. Only those spiders with masked AMEs, orientated randomly when homing.

Dacke *et al*. [23] studied the behavior of the lycosid spider *Pardosa tristis* by analysing its optomotor response to the rotation of polarized light. In response to the rotation of a linear polarizer, the spiders, which were placed on a ball, rotated in unison with the rotation imposed by the polarizer. When a neutral filter was placed over the spiders, there was no change in their trajectory. However, Dacke *et al*. [23] did not carry out any experimental manipulation, e.g. masking the different eyes in order to determine which ones perceived the polarized light.

There are no studies in Argiopids relating to polarized-light orientation.

In Gnaphosids, behavioral studies also were carried out on *Drassodes cupreus* by Dacke *et al*. [37] who used a circular arena with four symmetrically placed shelters. Three conditions were studied: a) with a polarization sheet under the illumination lamp; b) with the sheet removed; c) with all the secondary eyes covered with opaque paint and the principal eyes uncovered. They measured the rate of return to the home shelter and found that polarized light was necessary, and that painting the PMEs and the other secondary eyes significantly affected the rate of their return to the shelter.

Regarding the behavioral studies which have investigated the use of polarized light in Salticidae, Hill [68] studied the mechanisms of orientation of *Phidippus* spiders during the pursuit of prey. He designed outdoor experiments in order to demonstrate the ability of these spiders to orient to a path of clear blue sky, without directly seeing the sun. After having been oriented towards a lure, the spiders climbed up the central stem of an artificial plant which had 4 branches at different levels. After the initial sighting of the "prey" (the lure), the artificial plant was rotated by 90º in either direction. If the spider was using the sky polarization pattern, it should ascend in the same direction without reorientation; however, 82.2% of the displacements were reoriented according to the plant's rotation. Hill [69] studied the mechanisms of orientation of two salticid species: *Phidippus pulcherrimus* Keyserling and *P. princeps* Peckham & Peckham. In his study he described outdoor and indoor experiments using a polarizing filter placed between the spider and a patch of blue sky, or under a lamp. In both cases, he did not observe any change in the

direction of the spider following a change in the direction of the filter.

CONCLUSION

The spider families whose AME retinas have been studied possess a two-channel system of rhabdoms similar to that found in insects. This system must be orientated towards the zenith in order to get information from the sky polarization-pattern. In the compound eyes of insects the two-channel system is located in the dorsal region of the eye called the DRA. However, because spiders have camera-type eyes, the polarized-light-detection mechanism should be in the ventral part of one retina in order to receive light from the zenith when the animal moves. This arrangement has been found in the AME retinae of all the species of spiders (Agelenidae, Lycosidae) studied to date, either by light or electron microscopy. In another family, the Gnaphosidae, the two-channel system is not located in the AME retina but in the canoe-type tapetum of the PMEs. There are two other spider families (Argiopidae, Salticidae) whose AME retinae have been studied. In the Argiopidae, the two-channel system has not been found, although in the Salticidae, rhabdoms have been found arranged orthogonally in the so-called layer IV.

Electrophysiological recordings of the AME retina have been carried out in Lycosidae, Argiopidae, Gnaphosidae, and Salticidae. In all the species studied, cells that respond to UV light have been found and, as in the case of insects, they could be the basis for the detection of polarized light.

Behavioral analysis of polarized-light orientation has been carried out in indoor (Agelenidae, Gnaphosidae, Salticidae) and outdoor experiments (Agelenidae, Lycosidae, Salticidae) either by rotating a polarizing filter and/or masking the AMEs or the secondary eyes. Polarized-light navigation has been demonstrated in Agelenidae, Lycosidae, and Gnaphosidae.

By comparison with the other large group of terrestrial arthropods, the insects, polarized-light orientation in spiders has not been extensively studied and much more anatomical, physiological and behavioral research is needed.

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CONFLICT OF INTEREST STATEMENT

The author declares that he has no conflict of interest.

REFERENCES

1. Labhart, T. 2016, J. Exp. Biol., 219, 3844-3856.
2. Homberg, U. and el Jundi, B. 2014, Polarization visión in arthropods, J. S. Werner and L. M. Chalupa (Eds.), The New Visual Neurosciences. Massachusetts Institute of Technology, Cambridge MA, pp. 1207-1217.
3. Waterman, T. H. 1981, Polarization sensitivity, H. Autrum (Ed.), Handbook of Sensory Physiology, Vol. VII/6B Comparative Physiology and Evolution of Vision in Invertebrates. Springer-Verlag, Berlin, pp. 283-469.
4. Waterman, T. H. 1984, Natural polarized light and vision. M. A. Ali (Ed.), Photoreception and Vision in Invertebrates. Springer-Verlag, Berlin, pp. 63-114.
5. Wehner, R. 1983, The perception of polarized light. D. J. Cosens and D. Vince-Price (Eds.), The Biology of Photoreception. Cambridge University Press, Cambridge, pp. 331-369.
6. Waterman, T. H. and Horch, K. W. 1966, Science, 154, 467-475.
7. Bernard, G. D. and Wehner, R. 1977, Vision Res., 17, 1019-1028.
8. Labhart, T. and Meyer, E. P. 1999, Microsc. Res. Techniq., 47, 368-379.
9. Marshall, J. and Cronin, T. 2014, Polarization Vision of Crustaceans. G. Horváth (Ed.), Polarized Light and Polarization Vision in Animal Sciences. Springer-Verlag, Berlin, pp. 171-216.
10. Zeil, J., Ribi, W. A. and Narendra, A. 2014, Polarization Vision in Ants, Bees and Wasps. G. Horvath (Ed.), Polarized Light

and Polarization Vision in Animal Sciences. Springer-Verlag, Berlin, pp. 41-60.
11. von Frisch, K. 1949, Experientia, 5, 142-148.
12. Görner, P. 1958, Z. Vergl. Physiol., 41, 111-153.
13. Papi, F. 1955, Pubbl. Staz. Zool. Napoli, 27, 76-103.
14. Wehner, R. 2014, Polarization Vision: A Discovery Story. G. Horvath (Ed.), Polarized Light and Polarization Vision in Animal Sciences. Springer-Verlag, Berlin, pp. 3-26.
15. Traeger, U. and Homberg, U. 2011, J. Neurosci., 31, 2238-2247.
16. Sakura, M., Lambrinos, D. and Labhart, T. 2008, J. Neurophysiol., 99, 667-682.
17. Greiner, B., Cronin, T. W., Ribi, W. A., Wcislo, W. T. and Warrant, E. J. 2007, J. Comp. Physiol. A, 193, 591-600.
18. Heinze, S. 2014, Polarized – light processing in insect brains: recent insights from the desert locust, the monarch butterfly, the cricket, and the fruit fly. G. Horvath (Ed.), Polarized Light and Polarization Vision in Animal Sciences. Springer-Verlag, Berlin, pp. 61-112.
19. Schmeling, F., Wakakuwa, M., Tegtmeier, J., Kinoshita, M., Bockhorst, T., Arikawa, K. and Homberg, U. 2014, J. Exp. Biol., 217, 3557-3568.
20. Henze, M. J., Dannerhauer, K., Kohler, M., Labhart, M. and Gesemann, M. 2012, BMC Evol. Biol., 12, 163.
21. Labhart, T. 1986, J. Comp. Physiol. A, 158, 1-7.
22. Labhart, T. 1980, J. Comp. Physiol., 141, 19-30.
23. Dacke, M., Doan, T. A. and O'Carroll, D. C. 2001, J. Exp. Biol., 204, 2481-2490.
24. Horváth, G. and Varjú, D. 2004, Polarized Light in Animal Vision. Polarization Patterns in Nature. Springer-Verlag, Berlin.
25. Blest, A. D. 1985, The fine structure of spider photoreceptors in relation to function. F. G. Barth (Ed.) Neurobiology of Arachnids. Springer-Verlag, Berlin, pp. 79-102.
26. Eakin, R. M. 1968, Evolution of photoreceptors. T. Dobzhansky, M. K. Hecht and W. C. Steere (Eds.), Evolutionary Biology, Vol. 2. Appleton-Century-Crofts, New York, pp. 194-242.
27. Homann, H. 1971, Z. Morph. Tiere, 69, 201-272.
28. Bertkau, Ph. 1886, Arch. Mikr. Anat., 27, 589-664.
29. Görner, P. and Claas, B. 1985, Homing behavior and orientation in the funnel-web spider, *Agelena labyrinthica* Clerck. F. G. Barth (Ed.), Neurobiology of Arachnids. Springer-Verlag, Berlin, pp. 275-297.
30. Schröer, W.-D. 2017, Arthropod Struct. Dev., 46, 196-214.
31. Schröer, W.-D. 1974, Z. Morphol. Tiere, 79, 215-231.
32. Schröer, W.-D. 1976, Ent. Germ., 3(1/2), 88-92.
33. Magni, F., Papi, F., Savely, H. E. and Tongiorgi, P. 1964, Arch. Ital. Biol., 102, 123-136.
34. Magni, F., Papi, F., Savely, H. E. and Tongiorgi, P. 1965, Arch. Ital. Biol., 103, 146-158.
35. Kovoor, J., Muñoz-Cuevas, A. and Ortega-Escobar, J. 1993, Boll. Zool., 60, 367-375.
36. Ortega-Escobar, J. and Muñoz-Cuevas, A. 1999, J. Arachnol., 27, 663-671.
37. Dacke, M., Nilsson, D. E., Warrant, E. J., Blest, A. D., Land, M. F. and O'Carroll, D. C. 1999, Nature, 401, 470-473.
38. Mueller, K. P. and Labhart, T. 2010, J. Comp. Physiol. A, 196, 335-348.
39. Kovoor, J. and Muñoz-Cuevas, A. 1996/97, Zool. Anz., 235, 133-145.
40. Wehner, R., Bernard, G. D. and Geiger, E. 1975, J. Comp. Physiol. A, 104, 225-245.
41. Nilsson, D.-E., Labhart, T. and Meyer, E. 1987, J. Comp. Physiol. A, 161, 645-658.
42. Scheuring, L. 1914, Zool. Jahrb. Anat., 37, 369-464.
43. Baccetti, B. and Bedini, C. 1964, Arch. Ital. Biol., 102, 97-122.
44. Magni, F. 1966, Analysis of polarized light in wolf-spiders. C. G. Bernhard (Ed.), The Functional Organization of the Compound Eye. Pergamon Press, New York, pp. 171-186.
45. Eakin, R. M. and Brandenburger, J. L. 1971, J. Ultrastruct. Res., 37, 618-663.
46. Melamed, J. and Trujillo-Cenoz, O. 1966, Z. Zellforsch., 74, 12-31.

47. Kovoor, J., Muñoz-Cuevas, A. and Ortega-Escobar, J. 2005, Ital. J. Zool., 72, 205-216.
48. Jeong, M. J. and Moon, M. J. 1993, Korean J. Electron Microsc., 23, 84-93.
49. Clemente, C. J., McMaster, K. A., Fox, L., Meldrum, L., Stewart, T. and Main, B. Y. 2010, J. Arachnol., 38, 398-406.
50. Uehara, A., Toth, Y. and Tateda, H. 1977, Cell Tissue Res., 182, 81-91.
51. Land, M. F. 1985, The Morphology and Optics of Spider Eyes. F. G. Barth (Ed.), Neurobiology of Arachnids. Springer-Verlag, Berlin, pp. 53-78.
52. Land, M. F. 2000, J. Opt. A: Pure Appl. Op., 2, R44-R50.
53. Schwab, I. R., Yuen, C. K., Buyukmihci, N. C., Blankenship, T. N. and Fitzgerald, P. G. 2002, Trans. Am. Ophthalmol. Soc., 100, 187-200.
54. Blest, A. D. 1983, Zoomorphology, 102, 125-141.
55. Blest, A. D. 1987, Comparative aspects of the retinal mosaics of jumping spiders. A. P. Gupta (Ed.), Arthropod Brain. Its Evolution, Development, Structure, and Functions. John Wiley & Sons, New York, pp. 203-229.
56. Homann, H. 1928, Z. Vergl. Physiol., 7, 201-269.
57. Land, M. F. 1969, J. Exp. Biol., 51, 443-470.
58. Blest, A. D. and Price, G. D. 1984, Protoplasma, 120, 172-184.
59. Blest, A. D. and Sigmund, C. 1984, Proc. R. Soc. Lond. B, 221, 111-125.
60. Blest, A. D. 1988, Phil. Trans. R. Soc. Lond. B, 320, 489-504.
61. Harland, D. P., Li, D. and Jackson, R. R. 2012, How jumping spiders see the world. O. F. Lazareva, T. Shimizu and E. A. Wasserman (Eds.), How Animals See the World. Oxford University Press, Oxford, pp. 133-163.
62. DeVoe, R. D. 1972, J. Gen. Physiol., 59, 247-269.
63. Yamashita, S. and Tateda, H. 1978, J. Exp. Biol., 74, 47-57.
64. Tiedemann, K. B., Ventura, D. F. and Ades, C. 1986, J. Arachnol., 14, 71-78.
65. DeVoe, R. D. 1975, J. Gen. Physiol., 66, 193-207.
66. Yamashita, S. and Tateda, H. 1976, J. Comp. Physiol., 105, 1-8.
67. Blest, A. D., Hardie, R. C., McIntyre, P. and Williams, D. S. 1981, J. Comp. Physiol., 145, 227-239.
68. Hill, D. E. 1979, Behav. Ecol. Sociobiol., 5, 301-322.
69. Hill, D. E. 2010, Peckhamia, 83, 1-103.