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ABSTRACT

Adequate homing is essential for the survival of any animal when it leaves its home to find prey or a mate. There are several strategies by which homing can be carried out: a) Retrace the outbound path; b) Use a ‘cognitive map’; or c) Use path integration (PI). Here, I review the state of the art of research on spiders (Araneae) and whip spiders (Amblypygi) homing behaviour. The main strategy described in the literature as being used by these arachnids is PI. Behavioural and neural substrates of PI are described in a small group of spider families (Agelenidae, Lycosidae, Gnaphosidae, Ctenidae and Theraphosidae) and a whip spider family (Phrynidae). In spiders, the cues used to detect the position of the animal relative to its home are the position of the sun, polarized light patterns, web elasticity, and landmarks. In whip spiders, the cues used are olfactory, tactile and, with a more minor role, visual. The use of a magnetic field in whip spiders has been rejected both with field and laboratory studies. Concerning the distance walked in PI, the possibility of using optic flow and idiothetic information in spiders is considered. The studies about outbound and inbound paths in whip spiders seem to suggest they do not follow the PI rules.

As a conclusion, these arachnids’ navigation relies on multimodal cues. We have detailed knowledge about the sensory origin (visual, olfactory, mechanosensory receptors) of neural information but we are far from knowing the central neural structures where sensory information is integrated.

1. Introduction

Homing is the behaviour by which an animal can go from its present place to a new one, and then return to the first place. The first place is normally its nest or the place where it lives. The goal is attractive because prey or mates can be found there. To return

from the goal to its nest or living place the animal can use three strategies: a) Retrace the outbound path, b) Use a ‘cognitive map’, representing geometric information of relevant landmarks in the environment of the animal (Wehner and Menzel 1990), or c) Use path integration (PI) (Mittelstaedt 1983). To carry out PI, the animal must be kept informed about the translational and rotational components of its movement and integrate them in a home vector that carries it back to its departure point (Cheung et al. 2012, Heinze et al. 2018, Wehner and Srinivasan 2003). This home vector is stored in its memory and could be used for the next foraging trip by a simple reversal of it. The procedure commonly used to investigate whether an animal homes by PI (also called ‘vector navigation’, Wehner 1983) and not a) or b) is by picking it up when it is returning home after an outward journey, and displacing it to a distant location where the familiar visual landmarks are absent (Wehner and Wehner 1986). In the final part of the inbound journey, the animal can use landmark information (desert ant, Collett et al., 1992) or olfactory information (desert ant, Steck et al., 2009), to locate the nest given that PI is prone to cumulative errors (Collett 1996). Landmarks surrounding the goal can also be learned and used for the inbound journey without active displacement, that is when the animal PI system has been reset to zero (Wehner et al. 1996). The distance travelled is measured by an odometer and the direction to the goal is measured using some kind of compass. When the sole input for obtaining the direction in which the animal will take is self-motion this is referred to as idiothetic path integration, but when the input comes from an external source, which is sensed by the animal, this is referred to as allothetic path integration (reviewed in Heinze et al. 2018). The information coming from self-motion, which is called an idiothetic cue, can be obtained from kinaesthetic cues, inertial cues from the vestibular system, efference copies of the motor commands, and optic flow. External cues

can be celestial cues (i.e. the sun, moon, stars, polarized light patterns), as well as web structure (in the case of web spiders), the geomagnetic field and landmarks.

Pioneering studies showed that some arthropods, in particular desert ants, use the position of a light source, or the sun, to select and maintain a direction of movement. In his laboratory experiment, Lubbock (1881) used a rotatable disk illuminated by a distant candle. Field experiments have also been carried out by Santschi (1911) who investigated the use of the position of the sun in his mirror experiments

In insects, two parameters have been proposed to be involved in odometry: optic flow and stride integration. The use of optic flow to measure the distance walked has been described in ants mainly during social carrying behaviour (desert ants of the genus *Cataglyphis*, Duelli 1976; Fourcassie et al. 2000; Pfeffer and Wittlinger 2016) and in flying insects (e.g. honeybees *Apis mellifera*, Esch and Burns 1995; Srinivasan et al. 1996, 1997; Esch et al. 2001; Tautz et al. 2004; for a review see Srinivasan 2014 and Wolf 2011). The use of stride integration has been shown in desert ants (Wittlinger et al. 2006, 2007) by manipulating the leg length, making them either longer or shorter. The explanation for this is that the number and length of the strides taken during a journey reflect the distance walked. However, recently Wolf et al. (2018) carried out experiments from which they proposed that there are two memories for the odometer, one related to stride integration, and the other to the optic flow, and these interact with each other.

In insects, different kinds of compasses have been described: the sun compass (fruit flies: Giraldo et al. 2018; domestic flies: Philipsborn and Labhart 1990; dung beetles: Byrne et al. 2003; Dacke et al. 2014; monarch butterflies: Mouritsen and Frost 2002; bees: Lindauer 1960; von Frisch 1949; desert ants: Santschi 1911; Wehner and Müller 2006); a polarization compass (see Wehner 2014 for a historical review of the

study of polarization vision; fruit flies: Warren et al. 2019; dung beetles: el Jundi et al. 2014; locust: Mappes and Homberg 2004; honey bees: Rossel and Wehner 1984a; von Frisch 1949; crickets: Brunner and Labhart 1987; desert ants: Wehner 1997); the celestial intensity gradient (dung beetles: el Jundi et al. 2014); the celestial spectral gradient (dung beetles: el Jundi et al 2015; honey bees: Rossel and Wehner 1984b; desert ants: Wehner 1997); the star compass (dung beetle: Dacke et al. 2013; Foster et al. 2017); the geomagnetic field (Fleischmann et al., 2018) and piloting using familiar landmarks (honey bees: Cartwright and Collett 1983; Chittka and Kunze 1995; ants: Collett et al. 2001; Collett et al. 2007; Wehner and Müller 2010).

The objectives of this review are: a) To describe the behaviour by which arachnids of the Araneae (spiders) and Amblypygi (whip spiders) orders are able to move from their home to a new place and return to the first one (homing behaviour); b) To describe the cues of external or internal origin that are used in these movements; c) To describe the neural mechanisms that pick up these cues and allow homing behaviour. I have reviewed only these two Arachnid orders because they are the more intensively studied morphologically, physiologically and behaviourally. However, there are some recent homing studies for other orders such as Opiliones (dos Santos Silva et al. 2018) and Scorpiones (Gaffin and Curry 2020; Prévost and Stemme 2020).

2. Homing in spiders (Araneae)

Arachnids are a large group of arthropods for which more than 46,000 species of spiders (Arachnida, Order Araneae) have been described to date (Platnick 2017). They include, among others, the following orders: Spiders (Araneae), scorpions (Scorpiones), harvestmen (Opiliones), pseudoscorpions (Pseudoscorpiones), wind scorpions (Solifugae), mites and ticks (Acari), and tailless whip spiders (Amblypygi).

Gaffin and Curry (2020) have conducted a review of studies on homing in spiders, scorpions and amblypygi. Unlike the review by the mentioned authors, who provide a case-by-case description of the existing studies on each of these species as model animals, the present review is focused on the path integration mechanisms (allothetic and idiothetic homing processes; landmark orientation) that allow these animals to gauge changes of direction during their trajectory and the distance covered by means of proprioceptive and visual information. An outstanding feature of the present review is a description of the retinal structure that enables spiders to detect polarised light patterns to be used as a compass.

In the following text, I will describe the main results obtained about homing in spiders and whip spiders, the main orders of arachnids in which homing studies have been carried out.

Although there were some homing studies carried out by German researchers in the 1920s (Baltzer 1930; Bartels 1929; Bartels and Baltzer 1928; Holzapfel 1934; Peters 1932) the in-depth studies about spider homing started in 1955 with the investigation of homing in the spider *Arctosa perita* by Papi (1955) using the sun and polarized light as external cues.

Another milestone in spider homing was the publication in 1958 by Görner, who demonstrated that the spider *Agelena labyrinthica* homed through path integration using either external cues such as the sun, polarized light patterns, gravity, elasticity pattern of the web, or internal cues such as afferent signals from the proprioceptors on their legs (Görner 1958, 1962; reviewed in Görner and Claas 1985).

Thus, studies about spider homing followed almost immediately the honeybee study by von Frisch (1949). Research on the homing behaviour of arachnids has

progressed far less rapidly than research on other arthropods. The general lack of knowledge about the physiology of the spider's central nervous system is due to the difficulty of unicellular recordings given the nature of their internal body fluids, but the first records were made by Menda et al (2014). Another explanation for the relative absence of homing studies in spiders is the progressive reduction in the number of research groups working on this order.

Path integration has been described in spiders with laboratory studies (*Lycosa tarentula*, Ortega-Escobar 2006; *Cupiennius salei*, Seyfarth et al. 1982), in outdoor experiments (*Lycosa tarentula*, Ortega-Escobar and Muñoz-Cuevas 1999), and natural conditions (*Leucorchestris arenicola*, Nørgaard 2005). In all of them, the spiders did not retrace the outbound path; on the contrary, they took the more direct inbound path.

2.1. Allothetic path orientation in spiders (Araneae)

2.1.1. Web elasticity

Cues from the web (i.e. its elasticity) have been described as relevant for orientation in the spider *Agelena labyrinthica* (Baltzer 1930; Görner 1988; Görner and Claas 1985; Holzapfel 1934). For example, in studies by Baltzer (1930) where the web was attached to a flexible square frame, the spider was lured out of the retreat, and when the animal was going to run back, the frame was re-shaped to form a rhombus. In this study, it was observed that the spider ran back in the direction along the line of highest tension. Studies of web elasticity have shown that there is a gradient in the web whereby elasticity decreases with increasing distance enabling the spider to find the retreat using this gradient (Holzapfel 1934). However, the elasticity pattern information is not used if the spider is lifted from the web in darkness. In this case, the spider has neither self-motion cues nor visual cues. When the spider is put back onto the web, it runs in a random

direction. It has been proposed by Görner and Claas (1985) that the spider must run a certain distance before using the web elasticity pattern.

2.1.2. Sun compass

Before describing orientation related to celestial cues from the sun and polarized light patterns, I am going to characterize the spiders' eyes.

Most spiders have eight eyes arranged in two or three rows on the frontal carapace (Foelix 2011). All the eyes are simple or camera-type. The disposition over the prosoma changes from one family to another and has been used in the systematic characterization of spiders (Homann 1971; Ramírez 2014). According to the arrangement on the carapace, they are referred to as Anterior Median Eyes (AMEs), Anterior Lateral Eyes (ALEs), Posterior Median Eyes (PMEs) and Posterior Lateral Eyes (PLEs) (Figure 1, left). The AMEs are also referred to as principal eyes, and the remaining are referred to as secondary eyes (Land 1985). AMEs have photoreceptors with rhabdoms placed behind the vitreous body (so-called everted eyes) (Figure 1, right), they lack a tapetum and the retina is movable by the contraction of between one and six muscles according to species. Secondary eyes have photoreceptors with rhabdoms placed after the receptor nucleus (so-called inverted eyes), they have a tapetum, and their retina is static (Foelix 2011; Land 1985).

-----Insert Figure 1 here-----

The studies of a sun compass in lycosids began in the 1950s. Papi (1955) studied homing behaviour in *Arctosa perita* (Araneae, Lycosidae), a medium-sized spider living in coastal dunes and sandy riverbanks. Under natural conditions, either with a clear sky or an overcast sky, the spiders were taken from one shore of the river and they were

thrown into the water; the spiders returned to their shore displaying the so-called ‘zonal orientation’ or ‘orientation to Y-axis’. The Y-axis was the one perpendicular to the separation between two zones (i.e. the river and the shore) (Papi 1992). Each population had its theoretical escape direction, which corresponded to the azimuth of the bank it inhabited. Following the method of changing the position of the sun by 180° using a mirror, it was possible to observe a change in the zonal orientation near to 180° (Papi 1955). Although the experiment was carried out using only six spiders which exhibited some individual variability, the difference between the direction taken when a mirror was used, and that obtained by summing 180° to the natural zonal orientation, was in the range of 11°-45°. The spiders also exhibited zonal orientation when they were placed in a cylinder under a clear sky and with the sun shaded. The orientation remained constant throughout the day, independent of the position of the sun, as if the spiders had used an internal clock (Papi 1955; Papi et al. 1957). Under an overcast sky, the spiders became disoriented (Papi, 1955). From the experiment under a clear sky and with the sun shaded, and the experiment under an overcast sky, Papi (1955) supposed that, as in the honeybee and the sand hopper *Talitrus saltator*, the orienting cue could be the polarized light pattern.

In addition to the study of sun orientation in the spider *A. perita*, Papi (1959) made a comparative study of other species of the genus, in particular *A. variana* and *A. cinerea*, and obtained similar results.

Magni et al. (1964) observed the homing orientation of the wolf spider *Arctosa variana* in outdoor experiments. The spiders were studied either in the sun or the shade. Through selective eye covering, they demonstrated that the wolf spider’s AMEs were responsible for correct orientation, both in sun and shade.

Several studies have involved changes in the position of light sources under laboratory conditions (*Agelena labyrinthica*, Görner 1958; Görner and Claas 1985). The basic procedure was to attract the spider to capture a fly on its horizontal web, running for example for 20 cm, while a lateral light was on; then when the animal started to return to the retreat, the original light was switched off and another, placed at an angular distance of 90°, was turned on. The spider deviated following a direction between the new light and the retreat, based on visual cues received from the light and idiothetic cues gained from the outbound journey. In other laboratory experiments, spiders could home by a lateral light source using either their principal or secondary eyes. The only difference observed was that homing using only their principal eyes needed a higher light intensity (Görner and Claas 1985).

2.1.3. Polarized light pattern compass

In the following paragraphs, I will describe first the homing behaviour of the different species and later (Section 2.1.4) the particular retinal anatomy that enables them to perceive polarized light.

Studies carried out by Görner (1958, 1962) and resumed by Görner and Claas (1985) have demonstrated that the spider *A. labyrinthica* (Araneae, Agelenidae) orientates over the web using polarized light patterns. The rotation of a polarization filter placed above the web caused the spider to walk back either to the right or the left of its retreat with considerable scatter. Another experiment that showed the influence of the natural polarization pattern was carried out outdoors by rotating the web frame by 180°; in this case, the spiders again deviated from their course to the retreat. A complementary experiment consisted of covering the web with a polarization filter. When the direction of maximal transmission of the filter coincided with the e-vector of the polarization

pattern at the zenith, the spider came back straight to their retreat. When the polarization filter was rotated by 90°, the spiders often deviated from the straight return. The spider *A. labyrinthica* could not navigate using the sky polarization pattern when their principal eyes were covered; however, covering their secondary eyes did not affect this ability.

In addition to the experiments described in Section 2.1.2, Papi (1955) carried out an experiment in which a Polaroid sheet was placed over a cylinder in which the spider *A. perita* (Araneae, Lycosidae) tried to escape following their zonal orientation. Changing the Polaroid sheet from the direction of maximal transmission to null, or a turn of 45° to the right or left showed that spiders can perceive polarized light and use it for homing.

There is behavioural evidence that the spider *L. tarantula* (Araneae, Lycosidae) uses polarized light for homing. Ortega-Escobar and Muñoz-Cuevas (1999) performed outdoor experiments under the following conditions: a) a clear sky and all eyes functional, b) an overcast sky and all eyes functional, c) a clear sky filtered through a sheet that changed linearly-polarized light into elliptically-polarized light, d) a clear sky and AMEs covered, e) a clear sky and only AMEs functional. In all these conditions, the sun was not in the spider's visual range. The procedure was as follows: Spiders living in a rectangular terrarium were forced to walk along an L-shaped path and were then placed, in a random direction, in a nearby circular arena. The spiders did not retrace the outward trip but instead took the shortcut that would carry them to the burrow (Figure 2).

-----Insert Figure 2 here-----

Under condition (a), the spiders were capable of orienting correctly when they were displaced; under condition (b), their orientation was random and many of them began the return by a systematic search (Turner's loops) such as that shown by ants

(Turner 1907); under condition (c), the spiders showed a homing behaviour similar to condition (b); and under conditions (d) and (e), the covering of eyes showed that only the AMEs supplied information for homing under the clear sky condition. The spiders could use either the intensity gradient of the sky or the polarization pattern; however, the sheet did not significantly modify the intensity gradient and therefore the cue used by the spiders must have been the polarization patterns perceived through the AMEs.

Dacke et al. (2001) described an optomotor response to the rotation of polarized light in the spider *Pardosa tristis* (Araneae, Lycosidae). Over a lightweight ball, the spiders exhibited two locomotor modes: ‘progress’ and ‘rotation’. If a polarizer filter was rotated over the dorsal field of view, the spider quickly rotated; if a neutral density filter was rotated, the spider continued in the ‘progress’ locomotor mode.

In the spider *Drassodes cupreus* (Araneae, Gnaphosidae), another way of analysing polarized light was found (Dacke et al. 1999). *D. cupreus*, which lives in a silk nest spun under small rocks, was studied behaviourally, electrophysiologically and morphologically. Behavioural tests were carried out in the laboratory in a circular arena where the polarized light and PME functioning were manipulated. The spiders found their shelter more easily when they could use polarized light and their PMEs were uncovered. If these eyes were covered, or the light was not polarized, the percentage of spiders finding their shelters did not differ from a random search.

Another species whose ability to orientate to polarized light has been demonstrated, is the tarantula *Aphonopelma californica* (Theraphosidae) (Henton and Crawford 1966). The tarantulas were studied in a T-shaped maze in which they had to learn to turn towards one of the arms. Henton and Crawford (1966) used three groups of spiders: a control group in which the stem and the arms of the maze were uniformly

illuminated; a second group where the light intensity of both arms differed, although the light intensity in one of the arms was the same as that in the stem; and a third group in which the positive arm had a 90° or 180° polarization angle concerning the maze stem. After the acquisition period, three successive response shifts were given. The best performance, as measured by the least number of errors and the shortest running time, was that of the polarization group compared with the control group. The authors concluded that the tarantula *Aphonopelma californica* was able to use the polarized light to establish its position, but to date it is not known if their retinae have specialized regions to detect polarized light.

2.1.4. The structural retinal basis to detect polarized light

In arthropods, the polarized light will be maximally absorbed when the skylight e-vector is parallel to the microvilli axis –given that the visual pigment molecules are aligned within the microvilli membrane (Labhart and Meyer, 2002). To facilitate this, the receptor must not show a twist of the rhabdomere along it because this would reduce the polarization signal [for example Wehner et al. (1975) described a regular twisting of the rhabdomeres in the dorsal part of the bee compound eye]. Another characteristic of these receptors is that their visual field must include the zenith of the sky (in insects, they are placed in the Dorsal Rim Area (DRA)) (dung beetle: Dacke et al. 2003; ants, bees and wasps: reviewed in Zeil et al. 2014; desert locust, field cricket and monarch butterfly reviewed in Heinze 2014). Finally, the photoreceptors must be arranged as two orthogonal sets (Labhart and Meyer 1999; Mathejczyk and Wernet 2017; Wehner and Strasser 1985).

Baccetti and Bedini (1964) tried to find the structural basis for polarized light detection by the AMEs of the spider *A. variana* employing light and electron microscopy. They did not observe any particular positioning of the rhabdomeres in the receptor cells;

rhabdomeres were placed on all sides of the distal part of the receptor cell. However, in their transverse sections to the optic axis in AME (compare their figure 4 in Baccetti and Bedini 1964) two patterns of rhabdom positioning are visible: a ventral part of the retina in which it appeared that the rhabdoms were placed on parallel sides of the receptor cell and a dorsal part of the retina in which the rhabdoms occupied all the sides of the receptor cell. Therefore, the authors were very close to the correct description of the two-channel rhabdom positioning for the polarized light perception.

In an electron microscopy study of the AME's retina of the spider *Lycosa erythrognatha*, Melamed and Trujillo-Cenoz (1966) described the distribution of rhabdoms, which followed two patterns. At the periphery of the retina, they were placed on two opposite sides of a prismatic receptor cell with four sides, and the rhabdoms were oriented either parallel or perpendicular to the retinal radii. In the centre of the retina, the cells were also prismatic but with five sides, three of which carried rhabdomeres; the rhabdoms did not show a preferential orientation. Melamed and Trujillo-Cenoz (1966) provided a schematic drawing of a quarter of the retina that illustrated these two patterns of rhabdom distribution. However, if the whole retina followed this pattern, adding the radial and tangential inputs of the peripheral retina, would cancel out e-vector discrimination (Waterman 1981).

A light microscopy study carried out at the beginning of the 20th century by Scheuring (1914) (Figure 3b) (see Ortega-Escobar 2017 for a more detailed explanation) described a ventral arrangement of receptor cells in the AMEs of different lycosid species (e.g., *Trochosa ruricola*) which were different from those placed in the central and superior part of the retina. This arrangement is similar to that described by using light microscopy by Kovoov et al. (1993) who investigated the AMEs of the spider *Lycosa tarantula* (Figure 3c). The AMEs are oriented 20° upwards, towards the sky zenith; the

AME retinas are movable by the action of two muscles. In the median and dorsal parts of the retina, receptor cells had a polygonal transverse section and carried rhabdomeres in all of them. However, in the inferior part of the retina, the receptor cells had transverse sections with four sides and they carried rhabdomeres on two parallel sides; in the ventral retina, there were two rows of rhabdoms oriented at right angles. This disposition was similar to that described by Melamed and Trujillo-Cenoz (1966) but without the possibility of a generalization to other parts of the retina. The AME optic nerve was composed of two kinds of fibres according to their diameter that terminated in two different parts of the first optic centre. This disposition of the two rhabdom rows in the ventral retina was already present in juveniles that were leaving the egg case. The rhabdoms of the ventral zone would constitute a two-channel system analogous to the polarization area or DRA of an insect compound eye. The analysis of the e-vector of polarized light through retinal ventral receptors could be assisted by the retinal movement elicited by the two muscles attached to the retina, as had been previously proposed by Schröder (1974, 1976). Kovoov et al. (1993) described two kinds of fibres in the AME optic nerve according to their diameter, which terminated in separate regions of the first and second neuropils. The authors suggested that although they were unable to visualize the connection, the information about polarized light would be treated in the mushroom body while information proceeding from the central receptors would be analysed in the arcuate body.

-----Insert Figure 3 here-----

Dacke et al. (2001) studied the AME retina of the spider *Geolycosa godeffroyi*, and an undescribed *Geolycosa* species using light microscopy. The ventral part possessed receptors with square profiles and two parallel rhabdomeres on opposite sides of the photoreceptor; there were two populations of receptors with rhabdoms orthogonally

arranged (Figure 3d); the rest of the retina had receptors with rhabdomeres on all their sides.

Histological studies have also been carried out on the web spider *Agelena labyrinthica* (Agelenidae). In the 1970s, Schröder (1974, 1976) carried out an electron microscopy analysis of the AMEs of *A. labyrinthica* and more extensive studies have subsequently been published (Schröder 2017). The optic axis of the AME is not parallel to the substratum but is raised by about 45° in such a way that they can see the sky. There are several differences between the sensory cells in the central part of the retina and those of the ventral part. In the central part of the retina, the sensory cells have rhabdomeres on two to four sides, whereas the sensory cells on the ventral part of the retina have two rhabdomeres on opposite sides (Figure 3a). Also, more ventral sensory cells have their rhabdomeres arranged to form tangential rows whereas those cells arranged towards the centre have their rhabdomeres forming rows in a radial direction. There is an irregular rhabdomeric twist in the sensory cells of the central retina that could degrade or eliminate the polarization sensitivity of these cells. In the ventral part of the AME retinas, two channels can analyse the polarized light by vibrating in two orthogonal directions. The retina displacement carried out by the muscle attached to the retina could also help to form the image of different sky parts on the retina.

Do the PMEs of the spider *Drassodes cupreus* (Gnaphosidae) have a particular structure? Yes, there are several characteristics in these eyes that make them different (Dacke et al. 1999). Both PMEs point dorsally and are arranged with their longitudinal axes at roughly 90° and the tapetum polarizes the light along the long axis of the eye. It has about 60 receptors ('main receptors') whose rhabdomeres are aligned along the long axis of the eye and therefore have intrinsic polarization sensitivity when incident polarized light is parallel to the long axis. The comparison of signals from cells with

different polarization sensitivity is carried out by the main receptors of both PME (it is as if the two populations I have described in the AMEs of Lycosidae and Agelenidae were in different eyes, orthogonal among them). Therefore, in this case, the eye working to detect polarized light is the PME.

In summary, all studied species possess a two-channel system consisting of two sets of photoreceptors with rhabdoms aligned orthogonally to each other. This system is placed in the ventral part of AME retinas in the families Lycosidae and Agelenidae. In the family Gnaphosidae, the retinas of the PMEs, which are aligned orthogonally, constitute the two-channel system.

2.1.5. Landmark orientation

Ortega-Escobar (2006) studied PI in *Lycosa tarentula* under laboratory conditions in the absence of information relative to the sun's position or any pattern of polarized light. The question analysed was if visual information coming from the substrate and perceived through the ALEs would be important for PI. After observing animals with all eyes unmasked, two experimental groups were made: one group with only ALEs covered and another group with all eyes except ALEs covered. Only the group with ALEs uncovered was capable of turning adequately in the burrow direction. It was proposed that ALEs would perceive substrate structure and use it for homing.

The possibility of using substrate orientation as a visual landmark was studied in *L. tarantula* (Ortega-Escobar 2011). The spiders were studied in the laboratory in a circular arena 90 cm in diameter. The substratum of the arena was a black-and-white grating ($\lambda=6$ mm). The spiders were trained by pushing them gently with a small stick along a path perpendicular to the grating longitudinal axis, and the return angle was compared with burrow direction was measured. For the test, the spiders were displaced

in the same way and moved to another substrate that could be either white, or the same grating turned by 90°. Test spiders formed four groups: Group A in which the substrate of the test was white; Group B (control) in which the substrate of the test was that of the training (black-and-white grating); Group C with the same substrate as in B, rotated by 90° and, after making the test displacements their ALEs were masked; and finally Group D, with the same substrate as in C (B substrate rotated by 90°) and, after making the test displacements all their eyes were masked with the exception of ALEs. The comparison of the control and test trials of groups C and D before covering any eyes showed that there were not any differences between the homeward mean angles. However, in both experiments, there was a high bearing dispersion suggesting that the rotation of the substrate had a role in the homeward paths. Could this bearing dispersion be related to the functioning of the ALEs? If this was the case, the bearings of the spiders in groups C and D would be different. And this is what was found. These experiments also showed that the inbound trajectories were the result of taking into consideration both proprioceptive and visual information.

A study by Nørgaard et al. (2008) suggested the possible use of landmark orientation by the Namib desert spider, *Leucorchestris arenicola*. The visual fields of each pair of eyes, the inter-receptor angle, and the homing success of spiders with selected groups of eyes covered were analysed. As *L. arenicola* does not walk constantly along its path but often stays motionless, Nørgaard et al. (2008) correlated the duration of these motionless phases, which they called ‘stops’, with the ambient light intensity to ascertain whether this spider could use temporal summation to obtain enough photons to be able to see. The behavioural experiments showed that males with all their eyes covered were unable to return to their burrow. Therefore, vision is necessary for homing. But, which of the four pairs of eyes is the most important for this

task? The group of spiders with only their AMEs, which are the biggest eyes in this species, with an inter-receptor angle of 2.5° , uncovered could home without any difference to the control group composed of untreated and sham-operated spiders; the group with only their PME uncovered exhibited drastically diminished homing abilities; the group with only their ALEs uncovered did not differ from the control group in their homing abilities; the group with only their PLEs uncovered had a homing success lower than the AME and ALE groups, and higher than the PME group. They found a weak but significant negative correlation between ambient light intensity and the duration of the motionless phases of their trips. The authors considered that *L. arenicola* could employ temporal summation for improving night vision and that the spatial resolution of the secondary eyes would be sufficient to detect a few landmarks in their habitat such as grass hummocks; on the other hand, the AMEs, PLEs and the ALEs would be sufficient to obtain skyline snapshots. In any case, Nørgaard et al. (2008) concluded: “Hence, at this juncture, idiothetic path integration complemented by the use of visual landmarks cues is the spider’s most likely mode of navigation” (p. 822).

L. arenicola is the only spider in which the development of departure walks has been studied in ‘naïve’ individuals (the term ‘naïve’ is used here as shorthand for those adult individuals that were induced to build another burrow in a different place) (Nørgaard et al. 2012). Their departure walks were sinusoidal in form and, in this respect were different from the ‘learning walks’ of insects (Collett and Zeil 2018; Fleischmann et al. 2016; Müller and Wehner 2010; Zeil and Fleischmann 2019). The sinuosity of the departure walks disappeared on consecutive departures. Another difference with the insects’ learning walks is the absence of full rotations on a spot during which insects look frontwards towards their nests. In *L. arenicola*, the departure walks of the spider maintain its burrow in the visual fields of its ALEs and PLEs.

Although these eyes are not very sensitive, it has been suggested that they could use temporal summation to obtain enough light to identify landmarks during their night displacements (Nørgaard et al. 2008). However, these ‘stops’ during walking have not been described in the departure walks of ‘naïve’ spiders.

2.2. Idiothetic path orientation in spiders (Araneae)

Leucorchestris arenicola (Sparassidae) is a nocturnal spider that inhabits the Namib desert building sand burrows. Both females and males move during the night to prey and to mate (Henschel 1990, Nørgaard et al. 2006). The males of *L. arenicola* travel long distances in the night over seemingly featureless dune surfaces searching for females to mate with. The registered paths of this spider species are the longest distances recorded for any spider, amounting to approximately 810 m (Figure 4) (Nørgaard 2005).

-----Insert Figure 4 here-----

However, although it has been studied in-depth, the cues that this spider uses to return to its burrow remain unknown. Several external cues have been excluded as necessary to return to the burrow. The sun, the moon, and polarized light patterns cannot play a significant role (Nørgaard et al. 2006) given that this spider is more active during the period between the beginning and the end of the astronomical twilight period. The slope of the substrate has also been excluded as a cue for homeward trips (Nørgaard et al. 2003). Together with the experiments described in Section 2.1.5, this research group suggested that during the inbound journey they could obtain information from both idiothetic cues and visual cues.

Cupiennius salei (Ctenidae) is a nocturnal spider (Seyfarth 1980) whose homing capacities have been studied in the laboratory, with a focus on the role of the lyriform slit sense organs. These are strain detectors placed on the walking legs, pedipalps, spinnerets

and chelicerae (Barth 2002). In general, in these studies other non-idiothetic orientation cues were prevented: the visual cues, by covering all the eyes with black paint; gravitational orientation, by the horizontal levelling of the arena floor; any vibrations were also reduced experimentally. Barth and Seyfarth (1971) carried out an initial study into the role of lyriform slit sense organs on idiothetic orientation. They observed spiders returning to a place where they had caught prey and from which they were chased away ca. 25 cm. This control situation showed that spiders returned to the prey-capture site as close as 5 cm and only 2° from it, indicating that the spiders did not orientate at random. Afterwards, the lyriform slit sense organs of some spiders were destroyed on the tibiae of all legs (all tibiae destroyed group), and in another group these sensory organs were destroyed in the femora of all legs (all femora destroyed group). In both experimental groups, there was great dispersion in the return direction that was higher in the first group.

2.3. Odometry in spiders (Araneae)

In spiders, there are two possible mechanisms for the measurement of the distance walked: the information obtained from proprioceptors placed on the legs and the optic flow of the surroundings as the spider moves.

The use of the first mechanism has been described in the spider *Cupiennius salei* (Barth and Seyfarth 1971; Seyfarth and Barth 1972; Seyfarth et al 1982) by destroying the lyriform slit sense organs. Seyfarth et al. (1982) carried out experiments in which the spider *C. salei* was chased away from a previously captured prey in a rectilinear or curvilinear path. As in the experiment by Barth and Seyfarth (1971), the spiders were rendered blind using black paint. When the spiders were chased away following a rectilinear path, six returning distances were used: 20, 25, 30, 35, 40 and >40 cm. In the intact spiders, the success rate diminished as a function of the increase in the return

distance, while in femora destroyed spiders, the success rate was smaller, with two-thirds or more of the return paths not achieving the criterion of approaching 5 cm to the goal. The return paths after being chased away from the prey through a semi-circular corridor showed that the intact spiders were capable of PI returning more or less directly to the goal, whereas the experimental spiders showed a success rate lower than 50%. The authors suggested that the lyriform slit sense organs could be related to the repeated choice of correct directions in each segment of the return path.

The other species in which odometry has been studied is the spider *Lycosa tarantula* (Reyes-Alcubilla et al. 2009; Ortega-Escobar and Ruiz 2014, 2017). Do *L. tarantula* females need active locomotion information to return home, or are they able to return with the visual information gathered during passive displacement? This question was analysed by Reyes-Alcubilla et al. (2009). The spiders were submitted to active or passive displacements, all preceded by a training phase; the training was carried out in the same channel that the spider lived in, and the test was carried out in a parallel channel. During the training, the burrow position was delineated by a black-and-white grating ($\lambda=2$ cm) placed lateral to it. During the test, the grating was placed at a distance of 10 cm from the virtual burrow. The most important results were: a) after a passive displacement, the homeward distance walked by the spiders was shorter than half the distance they had to walk; b) after an active displacement, the spiders walked longer distances than needed to find the burrow; c) the presence of the visual landmark (i.e. the black-and-white grating) did not give any information about the burrow position; d) the number of tactile searches of the burrow was higher under passive displacements. Therefore, under passive displacement the spiders behaved as if they had not been displaced and the tactile search was the final pattern in the search for the burrow (Reyes-Alcubilla et al. 2009). This

behaviour is similar to that described for ants when they are displaced passively (Turner 1907; Wehner 2016; Wehner and Srinivasan 1981).

According to studies carried out with black-and-white gratings placed on the substrate or the walls of experimental channels in walking (desert ant: Ronacher et al. 2000; Ronacher and Wehner 1995) or flying insects (honeybee: Srinivasan et al. 1997; Srinivasan et al. 1996), several studies have analysed the effect of changing the stripe period of a black-and-white grating on the odometry of the spider *Lycosa tarantula* (Ortega-Escobar and Ruiz 2014, 2017). The first question asked about *L. tarantula* odometry was: Is this spider able to go back to its burrow when it is displaced with all its eyes covered both on the outbound and inbound paths? Or, put another way: Is the spider capable of homing using only proprioceptive information? The spiders were trained to walk a distance of 30 cm out of their burrow and after completion of 10 trials all their eyes were covered. In the control condition, where all the eyes were uncovered, the spiders walked a mean distance of 26.5 cm before searching for the burrow; in the test condition, where all their eyes were covered, the spiders walked a mean distance of 18.4 cm, and with a greater variation. More importantly, in 25% of the trials carried out on spiders that had no vision at all, these spiders walked in the opposite direction to the burrow. Therefore, proprioceptive information alone does not allow this species to find its burrow.

Next, Ortega-Escobar and Ruiz (2014) analysed whether the lateral optic flow was necessary to gauge the distance walked. They trained the spiders using a horizontal black-and-white grating ($\lambda=2$ cm) and tested them with the same grating placed vertically to the spider's walking direction. This resulted in a decrease of the mean walking distance before searching behaviour from 34 cm to 24.9 cm. When the experiment was carried out with the same procedure but with the grating placed on the substrate, the mean distance

changed from 33.1 cm to 29.4 cm. Therefore, the optic flow experienced both in the lateral and ventral field of views was important to measure the distance travelled, although it seemed that the most important factor was the experience in the lateral field of view.

The third question analysed was if an increase in the grating period (from $\lambda=2$ cm to $\lambda=1$ cm) either on the walls or on the substrate of the channel, would be perceived by the spiders, and as a consequence, would they walk a shorter distance. This change in the grating period caused the spiders to look for the burrow at a smaller distance although the effect was greater when the change was made on the channel walls.

Ortega-Escobar and Ruiz (2017) analysed the question of what pair of eyes (PMEs, PLEs, AMEs, ALEs) perceived the black-and-white grating ($\lambda=1$ cm) placed either on the walls or on the substrate of the channel while the spiders walked searching for their burrow. When the grating was placed on the walls of the channel there was a reduction in the distance walked due to the PLEs masking. When the grating was placed on the substrate of the channel, there was a reduction in the distance walked due to the ALEs masking, and to a lesser degree to the PMEs masking. Therefore, in the spider *L. tarantula* there is an interaction between the PLEs and ALEs to measure the distance walked using optic flow. There is anatomical data to support this interaction. A light microscopy study of the visual centres of *L. tarantula* (Kovoor et al. 2005) described the existence of fibres running from the first order neuropil of the ALEs to the second-order neuropil of the PLEs, and also the ventral face of the mushroom body receives fibres linked to the PLE and ALE second neuropil. This connectivity is similar to that found in another spider, the salticid *Marpissa muscosa*, whose behaviour was also mainly based on visual stimuli (Steinhoff et al. 2020). On the contrary, the connectivity in the well-studied spider *Cupiennius salei*, that appeared to home without any visual information,

did not show a convergence of first order neuropils of ALEs and PLEs on the second-order neuropil (Strausfeld and Barth 1993; Steinhoff et al. 2020).

3. Homing in whip spiders (Amblypygi)

Amblypygids or whip spiders are a small order of arachnids that like spiders have bodies divided into a prosoma and an opisthosoma; however, contrary to spiders they do not possess spinnerets or venom glands (Santer and Hebets, 2011). They have four pairs of legs, but the first pair does not have a walking function but one of mechano- and chemosensation. This first pair is very long and the name ‘whip’ comes from the frontal and lateral movement of these legs, also called ‘antenniform legs’.

Most of the species of whip spiders live in the dense rain forests of tropical and subtropical regions. They are strictly nocturnal, spending the day in burrows or tree crevices in forests. At night, they leave their hiding place and during locomotion, they constantly move their antenniform legs to scan the environment (Santer and Hebets 2011). The antenniform legs have several kinds of sensilla placed mainly on the tarsus, some of which have a candidate morphology of olfactory receptors such as the porous sensilla. In addition to the morphological studies on the sensilla of the distal tarsus of the antenniform legs, Hebets and Chapman (2000) confirmed the olfactory sensitivity of these sensilla electrophysiologically. The olfactory sensilla responded to chemicals that were common in the environment of the whip spiders, mostly produced by plants, and some by animals.

Whip spiders have eight small eyes, two placed centrally on a cuticular protuberance called median eyes, and six distributed in two groups placed laterally called lateral eyes. The receptor cells of median eyes are everted while the receptor cells of the lateral eyes are inverted (Santer and Hebets 2011).

A description of the homing behaviour of some neotropical whip spiders, *Paraphrynus laevifrons*, *Phrynus pseudoparvulus* and *P. marginemaculatus*, has recently been carried out (Hebets et al. 2014a, b; Graving et al. 2017; Wiegmann et al. 2016), together with research into the possible sensory mechanisms through which these arachnids could get information about the location of their hiding place (Bingman et al. 2017; Hebets et al. 2014a; Wiegmann et al. 2019).

3.1 Cues used for homing

Amblypygid navigation has been studied in the field by manipulating both olfactory and visual inputs (Hebets et al. 2014a; Bingman et al. 2017). To manipulate olfactory input, the distal tarsi of the antenniform legs were clipped with scissors (Hebets et al. 2014a), or the tarsi were covered with nail polish (Hebets et al. 2014a; Bingman et al. 2017). To exclude any visual input, all the eyes were covered with either dental resin (Hebets et al. 2014a) or nail polish (Bingman et al. 2017).

In the study by Hebets et al. (2014a), the researchers measured the return rates to the place from where the whip spiders had been taken, and the time taken to return. After the experimental sensory manipulation, whereby the olfactory input was excluded by clipping the tarsi, the whip spiders could be placed either on the opposite side of the home tree or at a distance of 8 m from it. The results of both experiments suggest that olfactory information facilitated returning to the home refuge in the amblypygid *P. pseudoparvulus* with visual information only playing a minor role. The whip spiders that were re-sighted were found at their home refuge.

In the study by Bingman et al. (2017), who carried out their research on *P. laevifrons*, the whip spiders were experimentally displaced 10 m from their home refuge. The control and vision-deprived whip spiders were well oriented towards their

home refuge after their first displacement. On the contrary, the olfaction-deprived whip spiders were randomly oriented after their first displacement.

However, the past navigational experience and potential knowledge of the surroundings of the tested whip spiders were unknown (Hebets et al. 2014a). The authors stated that PI could not be used by their experimental individuals due to the passive displacement carried out in their experiments, although it could have been used by the whip spiders in their initial walks as young. This means that, at their first walks as young, they might show walks similar to the ‘learning walks’ (Collet and Zeil 2018; Fleischmann et al. 2016; Müller and Wehner 2010; Zeil and Fleischmann 2019) previously also termed ‘exploration runs’ of desert ants (Wehner et al. 2004). These learning walks, controlled by a path integrator, would enable the amblypygids to associate their hiding place with surroundings that could be associated with odours or visual landmarks such as trees. However, in subsequent documents (Hebets et al. 2014b, Wiegmann et al. 2016, Graving et al. 2017; Wiegmann et al. 2019) the same research team wrote that PI is not used by amblypygids, although they made no reference to their previous considerations about learning walks. Even though they associate the desert ant *Cataglyphis fortis* as the paradigm of PI, they did not consider that this ant can return home without actively walking (Wehner et al. 1996) due to the learning of visual features characterizing its route. Given the absence of studies about homing development, or detailed studies about the nocturnal visual abilities of amblypygids and the results obtained with near-distance olfactory localization (Bingman et al. 2017; Casto et al. 2019; Wiegmann et al. 2019), it is not possible at present to state if these arachnids start their learning walks using PI, that could provide a scaffold for odour learning.

In addition to olfactory information, amblypygids can also use tactile information for the near-distance location of a home refuge as has been shown by Santer and Hebets (2009) where these animals learned to link texture cues with a home refuge. This tactile information is detected by mechanosensory sensilla (Santer and Hebets 2011) positioned at the antenniform leg tip and is received by giant neurons in the distal segments of the antenniform legs.

Wiegmann et al. (2020) have conducted two studies to determine if the homing behaviour in the whip spider *P. laevifrons* is guided by the local magnetic field. One of the studies was carried out in the field and the other in a laboratory. In the field study, the experimental whip spiders were fitted with a solenoid neodymium magnet while the control whip spiders were fitted with a similar-sized brass disk. In the laboratory study, the whip spiders were trained and tested daily to associate a magnetic anomaly, whose mean horizontal polarity was North-South, to access a shelter near which the magnetic field intensity was higher. In the field study, the magnet-fitted whip spiders were significantly oriented to their home refuge whereas the control subjects exhibited random orientation. Therefore, the local disruption of the local magnetic field did not affect the direction they took to search for their home refuge. In the laboratory study, the whip spiders failed to associate a magnetic landmark with access to a shelter. On the other hand, it is unknown either whether whip spiders have magnetic receptors, or where those receptors might be located in their body.

3.2 Odometry in whip spiders (Amblypygi)

In a laboratory study, Graving et al. (2017) studied the use of space by the whip spider *Phrynus marginemaculatus* in a square-shaped arena. The arena had two shelters, one provided darkness during daylight hours in contrast to the alternative shelter which

did not. They registered the outbound and inbound paths of the nocturnal walks. In most of the inbound paths, the test animals walked in contact with the walls. It is interesting to highlight that the sinuosity was higher for inbound than for outbound paths. And, as Graving et al. (2017) stated, this is contrary to the result found if the animal walks using PI, although the authors proposed that it is likely PI in amblypygids does not follow the general rules observed in other animals, like other arthropods or mammals.

4. Conclusions

Homing behaviour in spiders and whip spiders has been less studied in comparison to insects. Part of this situation is due to the comparatively fragmented knowledge of their nervous system, for example, the cellular components of the retina, and the visual neuropils, and their physiology. Another key to the few spider homing studies is the modest number of research teams working on this arthropod group. This situation can be a consequence of some insects, such as honeybees and desert ants, having proved to be the best models due to their clear behaviour in searching food items, homing and re-visiting the foraging place.

As a generalization to the studies presented above we can say that PI in spiders and whip spiders has a multisensory basis because a) Web-spiders (Agelenidae) can use web structure, sun or light position, polarized light pattern and idiothetic input as cues; b) Cursorial spiders (Lycosidae, Gnaphosidae, Sparassidae, Theraphosidae) can use the position of the sun, polarized light patterns, landmarks and idiothetic input; and c) Whip spiders (Amblypygi) can use olfactory information and, perhaps, visual information.

In all the spiders in which polarized light navigation has been studied, the neural mechanism observed is similar. It consists of two sets of receptors arranged orthogonally to each other. In species of the families Agelenidae and Lycosidae the

receptors are arranged in the ventral part of the AME retinas that receives light from the zenith of the sky. In species of the family Gnaphosidae the receptors are on the orthogonally arranged PME retina. In Lycosidae we know that these receptors are connected to a different region of the first and second neuropils and, probably to the mushroom bodies.

In the studies on nocturnal species, like *Leucorchestris arenicola* and *Cupiennius salei*, there is contradictory information about the possibility of using vision for homing. However, it is necessary to bear in mind that, in the first species, there have been behavioural nocturnal studies covering different eyes but in the second species all the studies have been carried out without precluding visual information. In *C. salei* there are anatomical data [lenses of all eyes supply very bright images of a quality that the retinal mosaic can exploit (Land and Barth 1992); length and diameter of the rhabdoms and the absence of pigment isolation between the photoreceptors (Grusch et al. 1997)] and physiological data [the electroretinography study by Barth et al. (1993) suggesting that vision is possible under moonlight although not under starlight; the electrophysiological study of PME and AME receptors (Pirhofer-Walzl et al., 2007) showing that they are adapted to vision in dim light] that indicate that some eyes can function in dim light. Thus, it would be interesting in the future to analyse the homing behaviour of *C. salei* under ambient light intensities, with different eyes covered.

As observed in other arthropods, studies on Arachnida have combined behavioural, physiological and morphological studies relative to homing behaviour, as well as to laboratory and field analyses, but we are still far away from the in-depth knowledge that has been acquired for insect models such as the honey bee and desert ant.

Compliance with ethical standards

Conflict of interest The author declares that he has no conflict of interest.

Ethics approval This article does not contain any studies with animals performed by the author.

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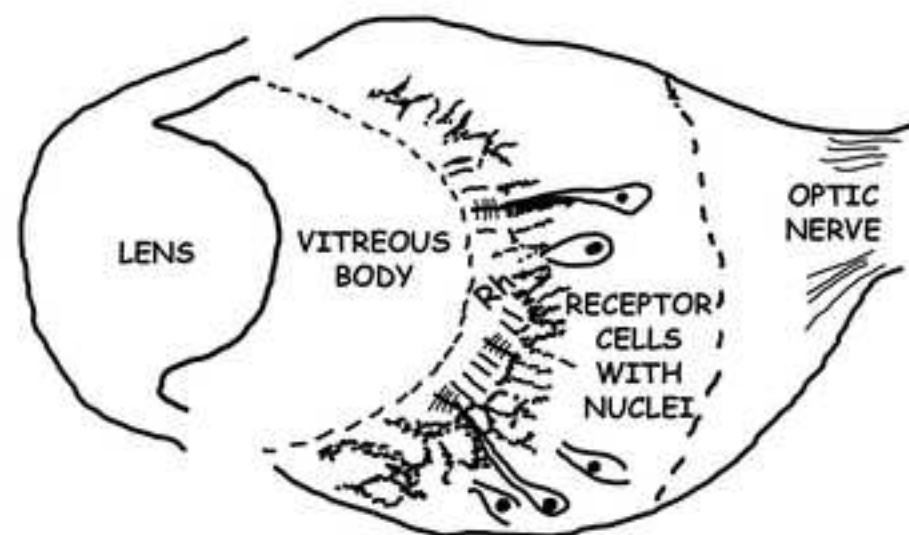
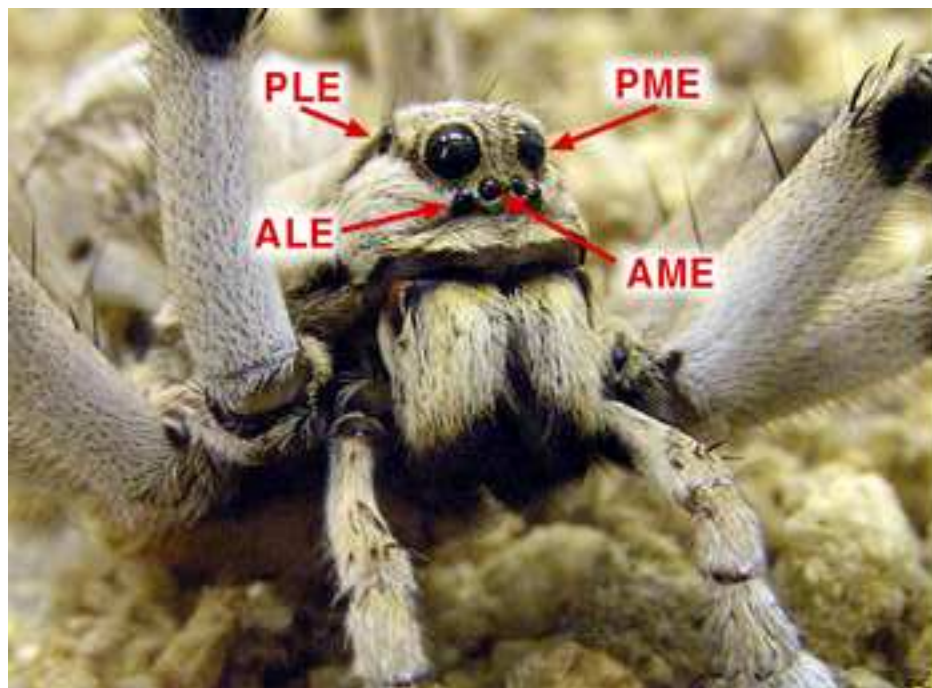
Figure captions

Fig. 1 Left: Layout of the four pairs of eyes in *Lycosa tarantula* (Photo by J. Ortega-Escobar). Right: Sagittal schema of an Anterior Medial Eye (AME) of *L. tarantula*; at left of the schema we found the external part of the eye, the lens; this is followed by the vitreous body; following it, we found the receptor cells with their rhabdoms (Rh) oriented towards the light and the nuclei set after them; finally, the optic nerve is composed of receptor cell axons

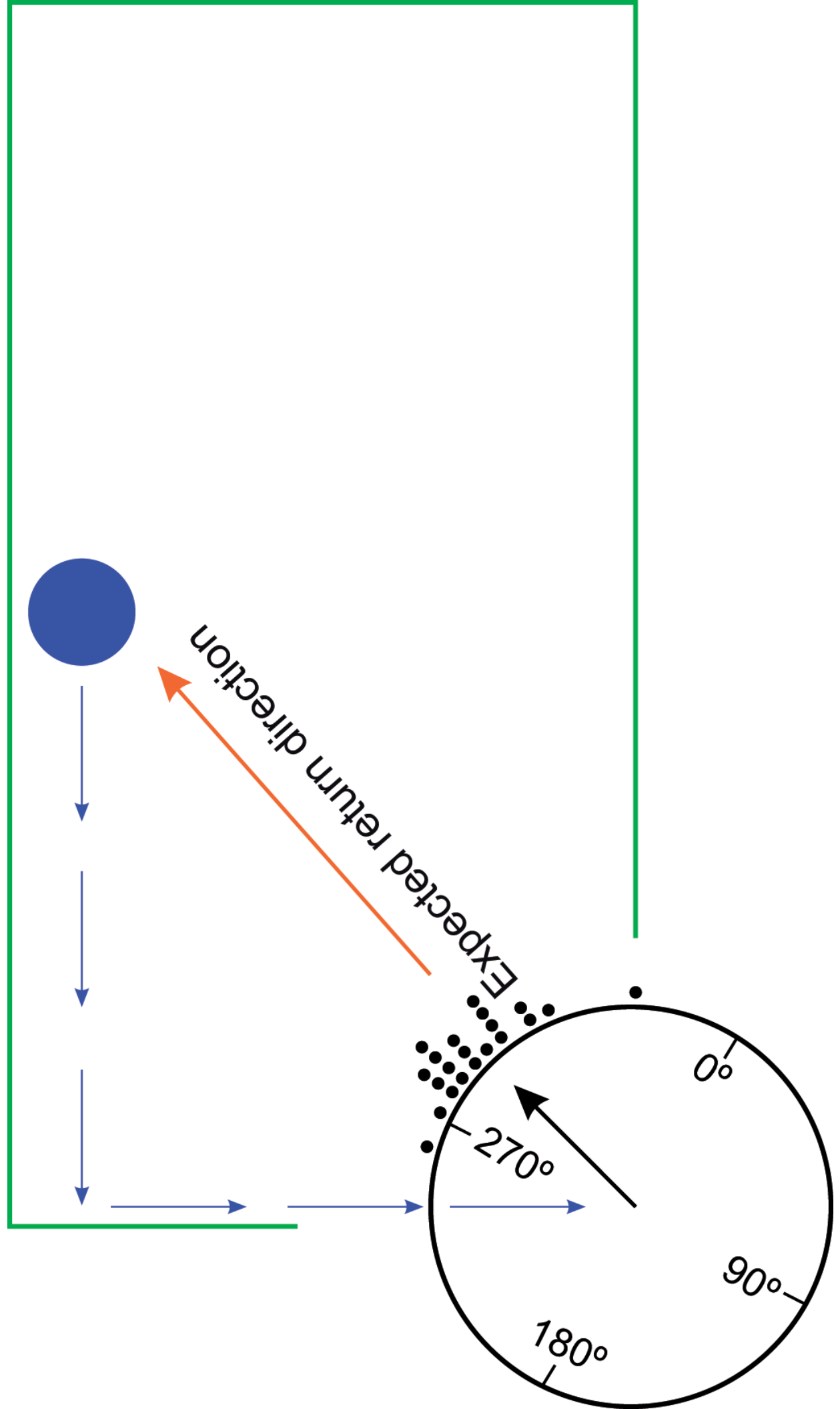
Fig. 2 An experiment in which *Lycosa tarantula* living in a burrow (blue circle) was forced to walk following a two-leg trajectory (blue arrows). Dots represent the inbound direction taken by different spiders (n=21). The direction spiders should take was 300 °. The rectangular terrarium measured 60x30x35 cm; the open field was 90 cm in diameter and 60 cm in height; the L-path was approximately 50 cm. Modified from Ortega-Escobar and Muñoz-Cuevas (1999)

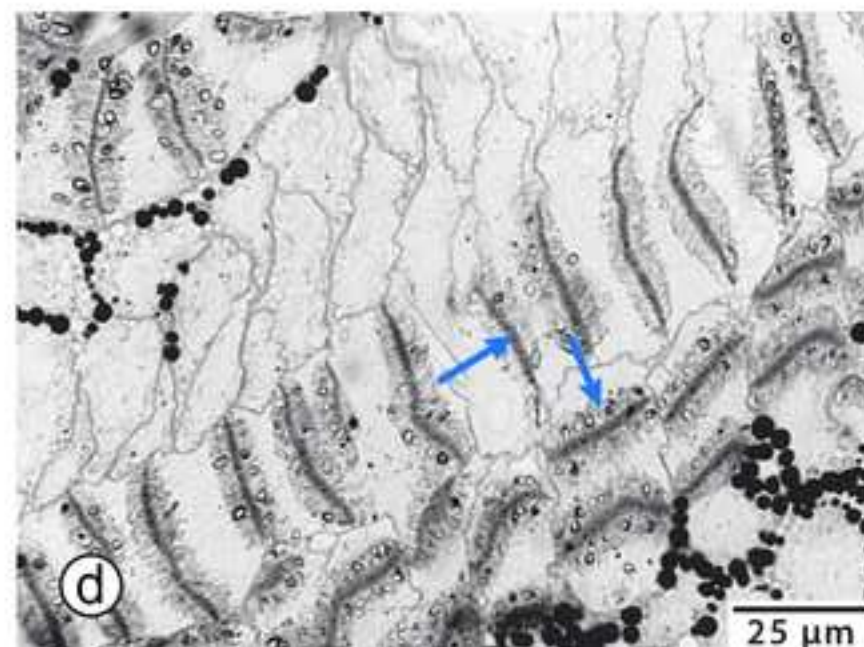
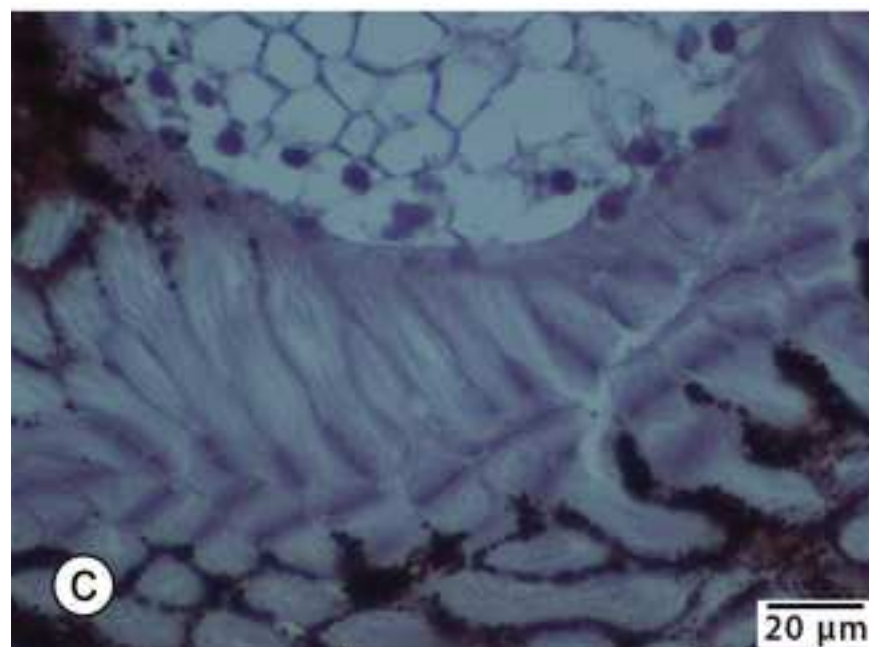
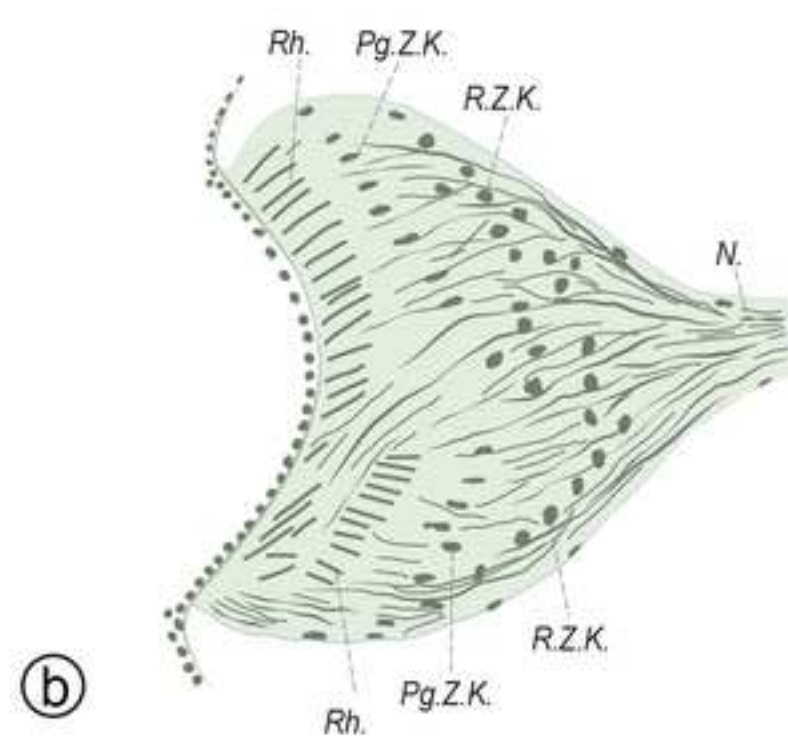
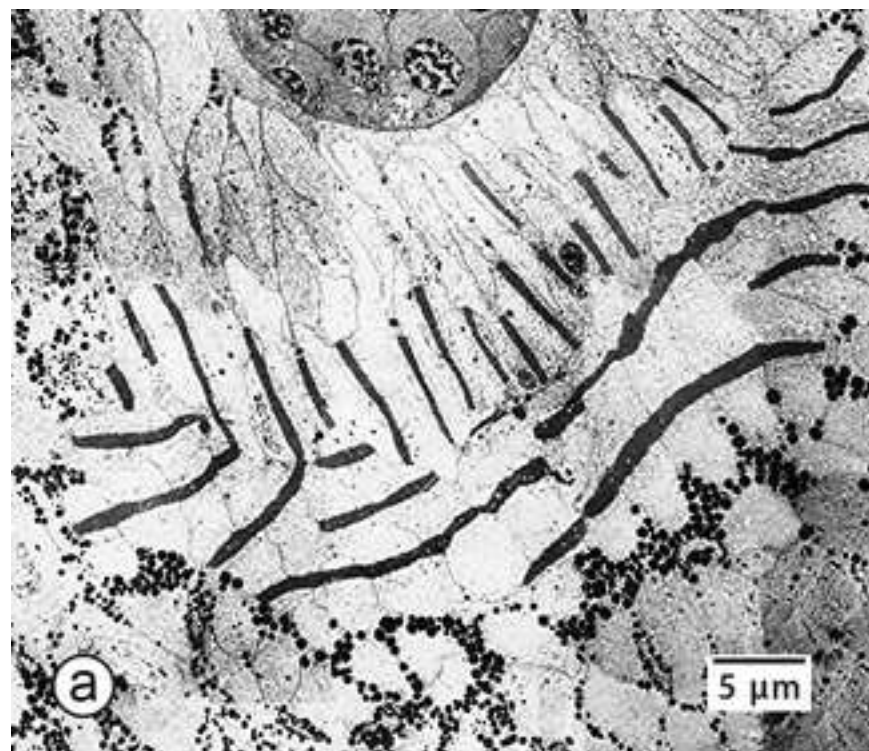
Fig. 3 Disposition of the two-channel system in the AMEs of different spider species (Although it is present in the four species, we have shown it only in the electron micrograph image **d**). **a.** Electron micrograph of a frontal section of the AME retina of *Agelena gracilens* (courtesy of Dr Wolfgang Schröer, unpublished). **b.** Schema published by Scheuring (1914) of a sagittal section of the *Trochosa ruricola* AME retina. Abbreviations: Rh, rhabdoms; Pg. Z. K., the nucleus of the pigment cell; R. Z. K., the nucleus of the retinal cell; N., nerve. **c.** Light micrograph of a frontal section of the AME retina of *Lycosa tarantula*. **d.** Electron micrograph of a frontal section of a lycosid spider. Blue arrows point to the orthogonal disposition of two different sets of rhabdoms (courtesy of Dr David C. O'Carroll, published in Dacke et al., 2001). Reproduced with permission from Joaquin Ortega-Escobar (2017). Polarized-light vision in spiders. Trends in Entomology, Vol. 13, 25 – 34

Fig. 4 The trajectory of a path of a *Leucorchestris arenicola* male. Total path length was 810 m. Black arrows indicate the direction of walking. Taken from Nørgaard (2005)

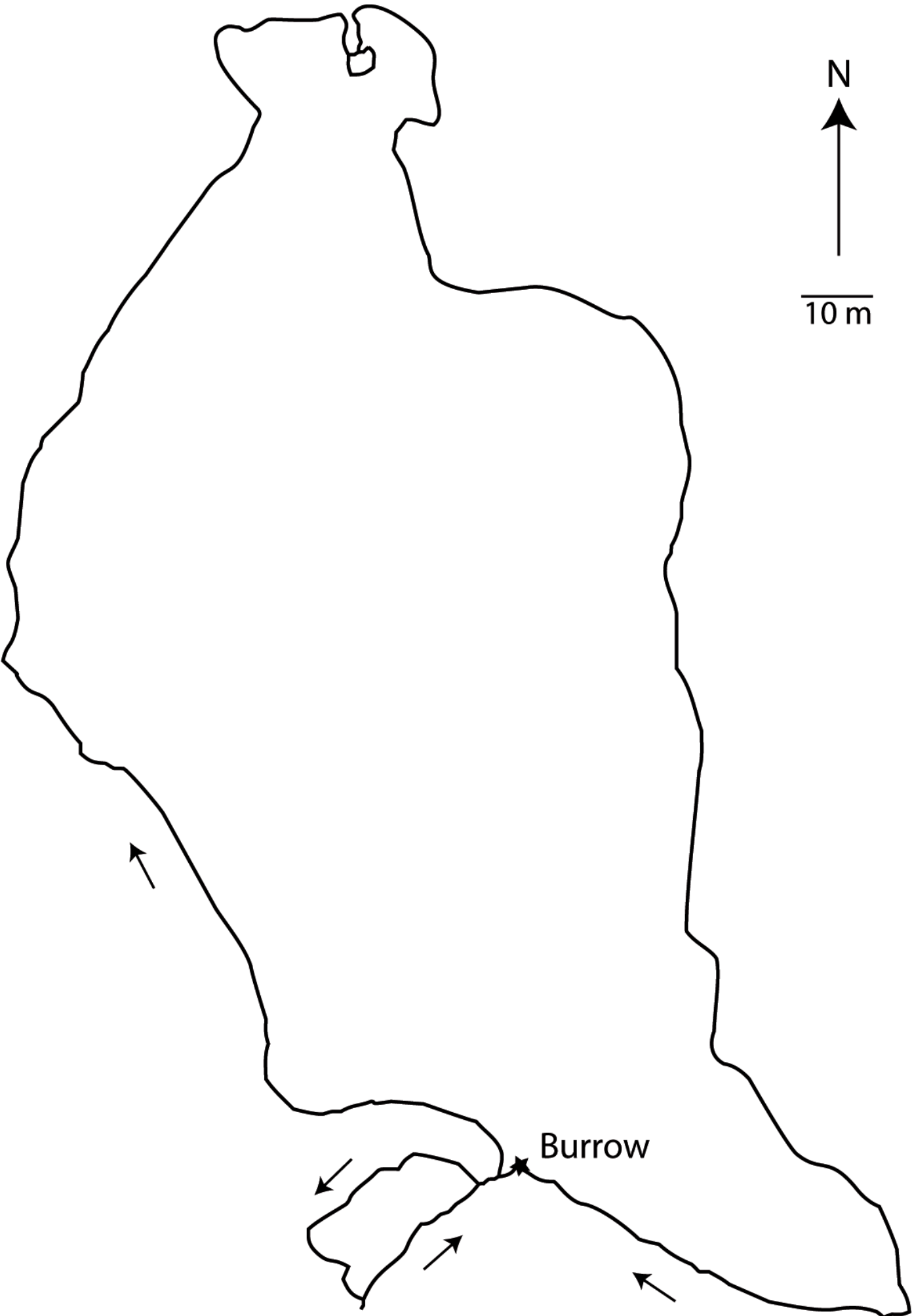


Figure





Figure



Title: Homing in the arachnid taxa Araneae and Amblypygi**Running title: Homing in Arachnids****Joaquín Ortega-Escobar****School of Psychology, University Autónoma of Madrid, 28049-Madrid, Spain****E-mail for correspondence: joaquin.ortega@uam.es****ORCID: 0000-0001-9929-5686****Conflict of interest** The author declares that he has no conflict of interest.**ABSTRACT**

Adequate homing is essential for the survival of any animal when it leaves its home to find prey or a mate. There are several strategies by which homing can be carried out: a) Retrace the outbound path; b) Use a ‘cognitive map’; or c) Use path integration (PI). Here, I review the state of the art of research on spiders (Araneae) and whip spiders (Amblypygi) homing behaviour. The main strategy described in the literature as being used by these arachnids is PI. Behavioural and neural substrates of PI are described in a small group of spider families (Agelenidae, Lycosidae, Gnaphosidae, Ctenidae and Theraphosidae) and a whip spider family (Phrynidae). In spiders, the cues used to detect the position of the animal relative to its home are the position of the sun, polarized light patterns, web elasticity, and landmarks. In whip spiders, the cues used are olfactory, tactile and, with a more minor role, visual. The use of a magnetic field in whip spiders has been rejected both with field and laboratory studies. Concerning the distance walked in PI, the possibility of using optic flow and idiothetic information in spiders is considered. The studies about outbound and inbound paths in whip spiders seem to suggest they do not follow the PI rules.

As a conclusion, these arachnids' navigation relies on multimodal cues. We have detailed knowledge about the sensory origin (visual, olfactory, mechanosensory receptors) of neural information but we are far from knowing the central neural structures where sensory information is integrated.

Key words: Homing, spiders, amblypygids, optic flow, polarized-light navigation, idiothetic orientation, olfaction, web elasticity, landmarks.

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Authors' contribution: J. Ortega-Escobar conceived the study, collected the data, and guided the interpretation of findings and the development of manuscript, both in drafting and in review.