

**ANTERIOR MEDIAN EYES OF *LYCOSA TARENTULA*
(ARANEAE, LYCOSIDAE) DETECT POLARIZED LIGHT:
BEHAVIORAL EXPERIMENTS AND
ELECTRORETINOGRAPHIC ANALYSIS**

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ABSTRACT. We studied solar light cues that may be used by *Lycosa tarentula* (Linnaeus 1758) (Araneae, Lycosidae) for homing. Experiments performed under clear skies, under overcast skies, and under clear skies as seen through a plastic sheet (which changed the polarization from linear to elliptical), allowed us to discover which attributes of daylight were used by the spiders during orientation and homing. We found that patterns of linearly polarized light in the natural sky were sufficient to allow accurate homing by the spiders. The homing behavior of individuals having the anterior median eyes (AME) or all other eyes blinded allowed us to determine that AME were responsible for the reception of polarized light. Electroretinography of all eyes confirmed that only the anterior median eyes were differentially sensitive to the orientation of polarization in linearly polarized light.

Arthropods are known to detect linearly polarized light by means of structural specializations of their eyes, whether compound or single ocellar. An orthogonal arrangement of rhabdoms in certain parts of the retina is the anatomical basis of polarized light perception (for review see Wehner 1989). This has been demonstrated in the compound eyes of some insects. A retinal specialization, called “POL area” (Wehner & Strasser 1985), is located in the marginal dorsal part of the compound eyes and oriented towards the zenith when the animal is walking. In other insects, for example in the water bug *Notonecta glauca*, the POL area occurs in the ventral rather than dorsal part of the eye; and this insect uses polarized light reflected from the water surface to detect the ponds into which it dives (Schwind 1984). It has been experimentally shown that the polarization-sensitive POL area plays a role in celestial navigation in *Cataglyphis* spp. (Wehner 1982) and *Apis mellifera* (Wehner & Rosset 1985; Wehner & Strasser 1985). These Hymenoptera were unable to orient themselves correctly when the POL area was masked.

For spiders, Wehner (1992) reviews the processes and mechanisms by which they can return home: they can use idiothetic, tacticochemical or visual information for homing.

Linearly-polarized light is among the visual cues used by some spiders. In this group, an orthogonal disposition of rhabdoms in the ventral part of the retina of the anterior median eyes (AME) has been found in the agelenid *Agelena gracilens* C.L. Koch 1841 (see Schröer 1976) and the lycosid *Lycosa tarentula* (Linnaeus 1758) (see Kovoor et al. 1993), and in the peripheral part of the retina of *L. erythronatha* Lucas 1836 and *L. thorelli* (Keyserling 1876) (see Melamed & Trujillo-Cenoz 1966), while Baccetti & Bedini (1964) could not find a similar arrangement in the lycosid *Arctosa variana* C.L. Koch 1847. In *A. variana*, Magni et al. (1965) analyzed the electroretinographic responses of the different eyes to polarized light. They found that both AME and PME (posterior median eyes) are capable of analyzing the plane of polarized light.

Behavioral studies on orientation by polarized light in spiders were initiated by Papi (1955a, b) in lycosids and by Görner (1958) in agelenids. Both investigators found that the only eyes involved in polarized-light detection were the AME (Görner & Claas 1985; Magni et al. 1964). Papi & Syrjämäki (1963) studied the orientation of an Arctic population of *Lycosa fluviatilis* (= *Pardosa agricola* (Thorell

1856)), which exhibited a correct solar orientation throughout the day.

In the present study, the ability of *Lycosa tarentula* to use celestial cues, mainly the polarized light pattern of the sky, for homing was examined experimentally. The role of the anterior median eyes in the expression of this behavior was determined through eye-painting experiments, and polarization sensitivity was studied by electroretinography of all the eyes.

METHODS

Subjects.—*Lycosa tarentula* is a ground-living lycosid which constructs a burrow nearly 15 cm in depth and 3 cm in diameter. As do the other members of the family, it has eight eyes arranged in three rows. The front row is composed of the anterior lateral eyes (ALE) and anterior median eyes (AME). The middle row comprises the posterior median eyes (PME); and the posterior one, the posterior lateral eyes (PLE). This spider is active during the day and at night.

Experiments were performed on adult females of *L. tarentula* collected at Canto Blanco, 25 km from Madrid. They were captured as immature individuals and maintained in the laboratory under an artificial light/dark cycle of 12:12 h (light on at 0800 h local time) and at 25 ± 2 °C. They were fed with mealflies (*Calliphora vomitoria*) and crickets (*Acheta domestica*). Spiders were used for experiments at least 5 days after their last molt. Voucher specimens of the adults have been deposited in the Muséum National d'Histoire Naturelle (Paris, France).

Behavioral experiments.—Adult females were transferred from their individual containers to a terrarium measuring $60 \times 30 \times 35$ cm placed on the roof of the Faculty building. This terrarium had a 15 cm deep substratum of soil; in the middle of one long side of the terrarium, an artificial burrow was built, similar to that which the spider digs in the field.

Experimental procedure: After 5 days of habituation to the terrarium, experiments began. Spiders were gently pushed forward in one of two paths running, right or left from the burrow, along half-the-length and the full width of the terrarium (Fig. 1). The orientation of the shortest return path was 30° NE for one direction and 300° NW for the other and a distance of 35 cm. When the spider arrived at the end of the path, it was placed into a trans-

parent open glass container and transferred to the center of an open field 90 cm in diameter, and left in the center of it, and in a different direction from that of the burrow. The walls of the open field were 60 cm high and completely white. The periphery was divided into 10° sectors to identify the direction followed by the spider. The position of the spider was recorded when it was at 40 cm from the center.

Experiments were carried out under five conditions, in all cases with the sun obscured by an opaque screen (Table 1). Eyes were made non-functional by covering them with three coats of black paint (Pelikan Hobby Tempera #11).

It was further ensured that the acrylic plastic (a Plexiglas[®] sheet with a polyethylene film) changed linearly-polarized light to elliptically-polarized light with maximum efficiency at a specific angle between the electric field of the light and the orientation of the sheet. This arrangement was accomplished by using a He/Ne laser ($\lambda = 632.8$ nm) and introducing the Plexiglas sheet or the polyethylene film between crossed polarizers, together with a Soleil-Babinet compensator. We were able to compensate for the phase change introduced by the sheet and produce zero light at the detector. The transmission characteristics of this sheet, measured with a spectrophotometer (Hitachi U-2000), are shown in Fig. 2.

Statistical analysis: The directions followed by the animals are shown as circular distributions, which were analyzed using circular statistics (Batschelet 1981), calculating the mean resultant vector for every distribution. Appendix I shows how we calculated the mean angle of the sample and the angular deviation and it describes the Rayleigh and Mardia-Watson-Wheeler tests. The statistical evidence of directness was tested following the Rayleigh test. If directness was evident, the confidence interval for the mean angle was calculated to test whether the mean direction of the sample deviated significantly from the direction of the burrow. For each condition (e.g., overcast sky, blue sky, etc.) the Mardia-Watson-Wheeler test was used to test whether the two samples (animals that should orient towards 30° NE versus animals that should orient towards 300° NW) differed significantly from each other.

Electroretinographic analysis.—*Lycosa*

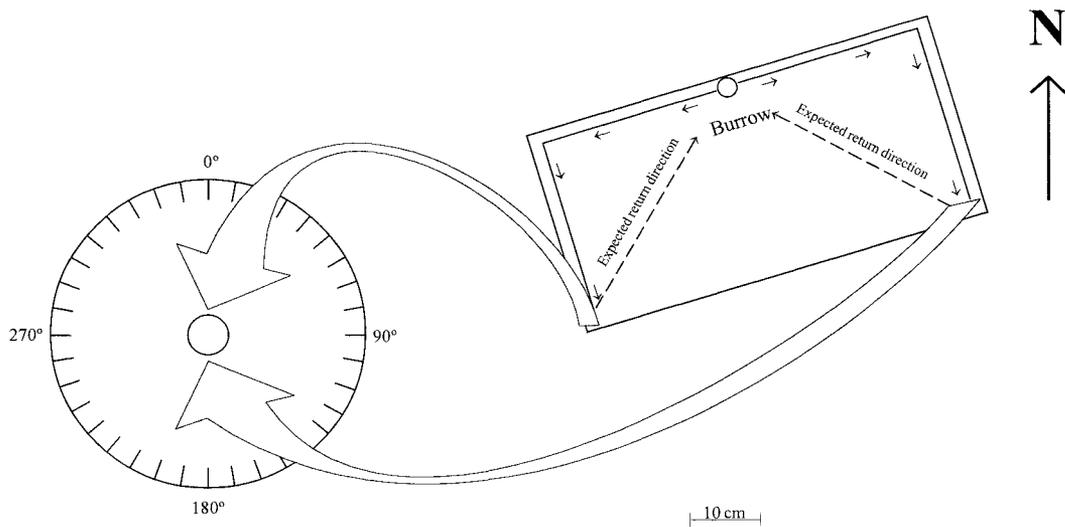


Figure 1.—Apparatus used to study homing in *L. tarentula*. Right, top view of terrarium in which the animal lived during the study; arrows indicate the possible outward paths. Left, dorsal view of the open field in which the animal was left after being taken from one of the corners opposite to the burrow. 0° was always oriented towards the north. The big arrow indicates the translation of the animal to the center of the open field (shown at half of its actual size in relation to the terrarium).

tarentula females from Canto Blanco (Madrid, Spain) were maintained in the laboratory, in Paris, at 20 °C and under natural light-dark cycles (LD: 10/14). Animal weight was about 2 g. Diurnal electroretinograms were obtained as described in Carricaburu et al. (1990). For the recording of ERGs, the animals were placed on a metallic plate used as the indifferent electrode. The different elec-

trode was a thin wire, positioned on the cornea by means of a Prior micromanipulator. The electrodes were connected to a high input impedance solid state amplifier. The animal, the micromanipulator and the amplifier were enclosed in a Faraday cage. The output of the amplifier was connected to a cathode ray oscillator (CRO), the ERGs were displayed on the screen and photographed. The light stimuli

Table 1.—Experimental conditions that were used in this study and cues available to the spiders in each one.

Experimental conditions	Cues available to the spider
Releases under a clear sky All eyes functional	Linearly polarized light pattern Light intensity gradient Unintended landmarks
Releases under an overcast sky All eyes functional	Unintended landmarks
Releases under a clear sky filtered through plastic All eyes functional	Elliptically polarized light pattern Light intensity gradient Unintended landmarks
Releases under a clear sky Only anterior median eyes not functional	Linearly polarized light pattern Light intensity gradient Unintended landmarks
Releases under a clear sky Only anterior median eyes functional	Linearly polarized light pattern Light intensity gradient Unintended landmarks

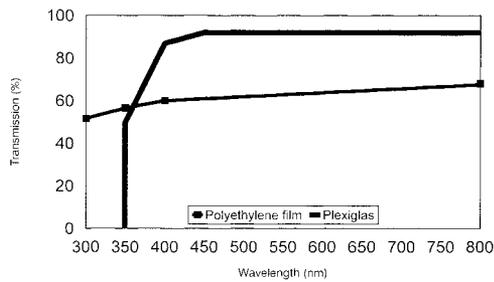


Figure 2.—Transmission (%) characteristics of the components of the plastic sheet.

were given by an electronic flash and were conveyed to the eyes by an optic fiber. A small device was placed between the tip of the fiber and the eyes making it possible to insert one of two polarizing sheets (Polaroid) and consequently to stimulate the eye by linearly polarized light, the plane of polarization being either vertical or horizontal. A light flash was delivered to adapt the eye to light and after a variable lapse of time named duration of dark adaptation, a second flash elicited the recorded ERG. The durations of dark adaptation were 1 s, 2 s, 5 s, 10 s, 20 s, 60 s, and 300 s. In arachnids, the full ERG is composed of two negative waves, β and γ , and a positive wave, δ (Fig. 3), in contrast to insects, in which there is a first positive wave, α , prior to β , γ , and δ (Fouchard & Carricaburu 1972). For each ERG, the amplitude (between the isoelectric line and the top of the β wave) and the latency (between the stimulus and the top of the β wave) were measured: both were found to be highly dependent on dark-adaptation and the hour of recording.

Experiments were carried out on three animals for 24 hours. Only one spider provided a complete electroretinographic record series, without any trouble. Results shown in Fig. 6 relate to this animal.

RESULTS

Behavioral experiments.—*Releases under a clear sky:* As a control, prior to the release of spiders in the open field, the homing behavior of each individual was observed in the terrarium in order to see if it could return home and was well-adapted to the burrow. Only those spiders well-adapted to the burrow (i.e., those immediately entering it upon contact with the first pair of legs) were used in the open-field experiments. Upon release,

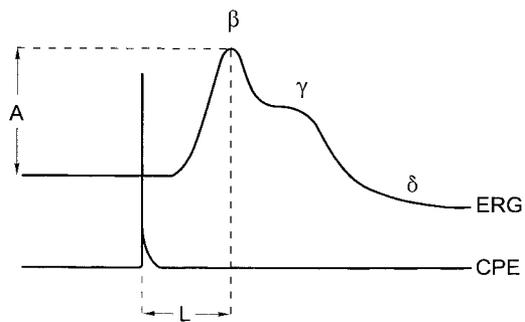


Figure 3.—Electroretinogram of an arachnid. *Abbreviations:* ERG = electroretinogram; CPE = photoelectric cell response; A = Amplitude; L = Latency.

each spider remained motionless for several minutes and then began to walk following a linear path, sometimes after a turn to re-orient itself. When each spider had run 40 cm or more, it began to make nest-searching movements: legs I and II flexed towards the spider body. These movements have also been observed in the terrarium when the spider was returning to the burrow (the entrance of which had been blocked by soil) and do not occur in other situations. These movements, when seen in the open field, indicated that the spider was in search of its burrow entrance. Figure 4A shows the distribution of movement directions by spiders after open-field releases under a clear sky. The spiders show a correct orientation towards the burrow direction (mean value for 30° NE burrow direction sample: $34^\circ \pm 5^\circ$, $r = 0.98$, $n = 5$, Rayleigh test: $P < 0.001$; mean value for the 300° NW burrow direction sample: $290^\circ \pm 18^\circ$, $r = 0.83$, $n = 21$, Rayleigh test: $P < 0.001$), although a bimodal distribution was observed, with some spiders searching for the nest 180° away from it. There was a significant difference between the NE group and the NW group (Mardia-Watson-Wheeler test, $P < 0.01$).

Releases under an overcast sky: Some spiders began by making a systematic search in the open field. This behavior consisted of circular movements by the animals beginning at the release point and increasing in radius with time. From time to time the spider returned to the release point. Such spiders were not included in the analysis. Figure 4B shows that the orientation of the rest of the spiders under an overcast sky was random (mean value for

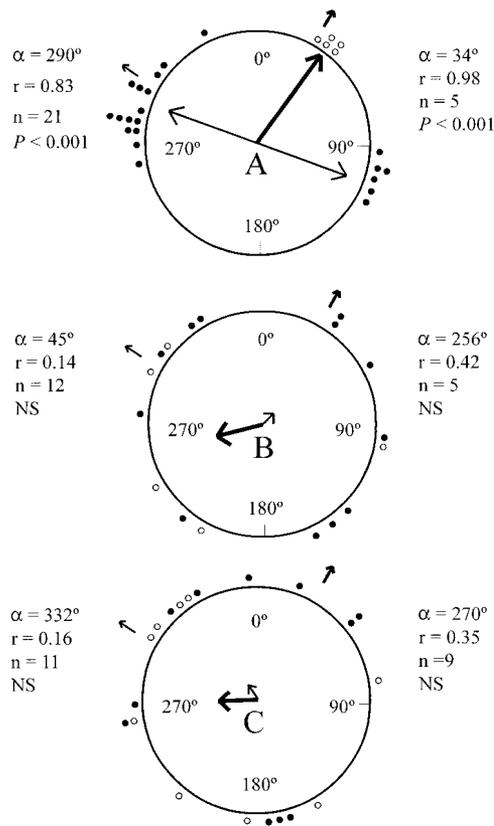


Figure 4.—Directions followed by individual spiders in the open field under different conditions. A = Releases under a clear sky; B = Releases under an overcast sky; C = Releases under the plastic sheet. Arrows outside of the circles point toward the two possible directions for returning to the nest, according to the outbound paths: 30° (thick arrow) and 300° (thin arrow). Filled circles correspond to home directions of animals that should orient to 300°, while open circles correspond to home directions of animals that should orient to 30°. The thick arrow inside the circle is the mean vector direction for the sample of animals that should return to 30°; the thin arrow inside the circle is the mean vector direction for the sample of animals that should return to 300°. *Abbreviations:* α = mean vector direction; r = length of the mean vector; n = sample size.

30° NE burrow direction sample: 256°, $r = 0.42$, $n = 5$, Rayleigh test: $P = 0.440$; mean value for 300° NW burrow direction sample: 45°, $r = 0.14$, $n = 12$, Rayleigh test: $P = 0.797$). There was no significant difference between the samples (Mardia-Watson-Wheeler test, NS).

Releases under a plastic sheet: As indicated in the Methods section, when sun light passes through the plastic sheet, its polarization changes from linear, which is its predominant characteristic (Waterman 1981), to elliptical, with a small modification of intensity. Spiders released in the open field in these conditions either exhibited the behavior of systematic search or headed in a random direction, as they did under an overcast sky. Only the latter individuals were considered in the analysis. Fig. 4C shows that (mean value for 30° NE burrow direction sample: 270°, $r = 0.35$, $n = 9$, Rayleigh test: $P = 0.342$; mean value for 300° NW burrow direction sample: 332°, $r = 0.16$, $n = 11$, Rayleigh test: $P = 0.710$). There was no significant difference between the NE group and the NW group (Mardia-Watson-Wheeler test, $P > 0.368$).

Releases with AMEs blinded: When the AMEs were blinded by black opaque paint, a non-directed distribution was observed (Fig. 5A). In this case, spiders did not show the systematic search behavior described in Experiments B and C. The behavior of these animals was completely normal except that their orientation was not to the burrow (mean value for 30° NE burrow direction sample: 45°, $r = 0.04$, $n = 6$, Rayleigh test: $P > 0.900$; mean value for 300° NW burrow direction sample: 144°, $r = 0.22$, $n = 10$, Rayleigh test: $P = 0.574$). There was no significant difference between the NE group and the NW group samples (Mardia-Watson-Wheeler test, NS).

Releases with PMEs, PLEs, and ALEs blinded: When all eyes, except the AMEs, were blinded (Fig. 5B), a clear orientation of the spiders to the burrow direction was observed (mean value for 30° NE burrow direction sample: $31^\circ \pm 5^\circ$, $r = 0.97$, $n = 5$, Rayleigh test: $P < 0.001$; mean value for 300° NW burrow direction sample: $298^\circ \pm 20^\circ$, $r = 0.90$, $n = 10$, Rayleigh test: $P < 0.001$). There was a significant difference between the NE group and the NW group (Mardia-Watson-Wheeler test, $P < 0.01$).

Electroretinographic analysis.—The electroretinographic responses of the AMEs were very different, depending on the plane of light polarization. During the photophase, vertical polarization resulted in a much higher ERG amplitude than did a horizontal one (Fig. 6 shows the change of amplitude with dark adaptation). A maximum was reached at 20 s of

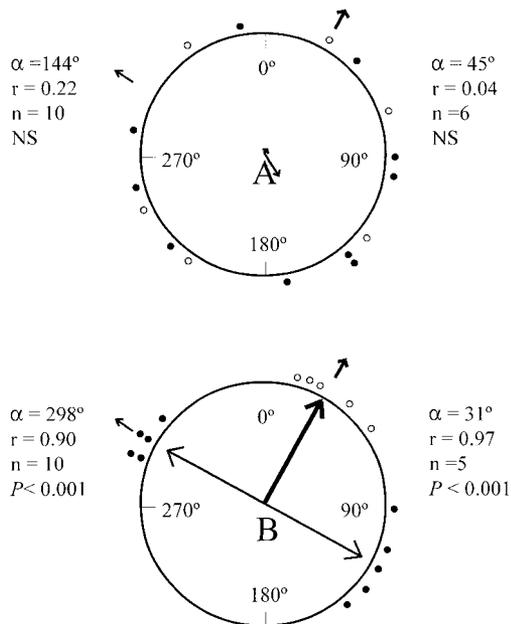


Figure 5.—Directions followed by individual spiders in the open field with different eyes blinded. A = Releases of animals with AMEs blinded. B = Releases of animals with PMEs, PLEs and ALEs blinded. Symbols as in Fig. 4.

dark adaptation, and the amplitude did not change for adaptation up to 5 minutes. Latencies of ERG responses obtained for vertically (5 mn in daytime) or horizontally polarized light were similar, about 30 ms. ERGs of other eyes (ALE, PME and PLE) were not significantly different, whether light was polarized or not.

DISCUSSION

Path integration is a route-based homing which allows the animals a straight return after a more or less winding outward trip (Papi 1992). It is a process that allows an animal to deduce its position, in relation to a point of departure, from its own movement. To achieve this the animal has to measure two components of its outward journey: the direction and the distance. The first component can be measured using external references to calculate the directions followed or using internal references such as centrally stored recordings of their own movements. Following Etienne et al. (1998), "The ability to "home" irrespective of familiar references from the environment remains the hallmark and safest opera-

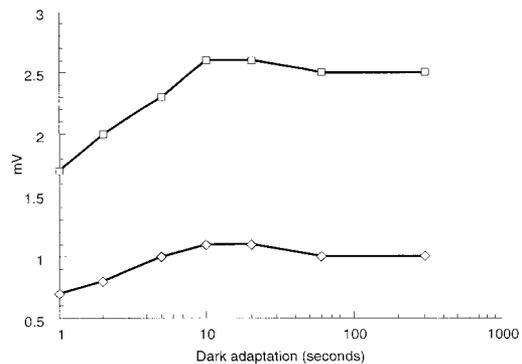


Figure 6.—Electroretinograms (ERG) under polarized light. Diurnal amplitudes (mV) of AME ERGs, recorded for different times of dark adaptation. The \diamond = the horizontal plane of polarization; the \bullet = the vertical plane of polarization.

tional criterion for dead reckoning [path integration]" (p. 56). Our results show that *L. tarentula* is capable of homing by means of a mechanism which does not use familiar references and it is based on visual information as external reference to calculate home direction. In experiments with *Arctosa* (Magni et al. 1964; Papi 1955a, b), the animals were typically placed in the center of a cylinder and their escape directions were registered. They display so-called zonal orientation that generally is not considered as homing (Papi 1992). In contrast, we have used a paradigm that has been used to test homing through path integration in arthropods and mammals (Etienne et al. 1998). In this paradigm, the subjects followed an L-shaped detour and they returned directly to the point of departure. In our study, *L. tarentula* also shows the ability to shortcut the outward path when returning. Generally, our spiders did not retrace the outward path. As with other spiders (Görner & Claas 1985; Seyfarth et al. 1982), *L. tarentula* could use tacto-chemical information, visual, or idiothetic information to return home. Tacto-chemical information is used by lycosid males to find females (reviewed by Tietjen & Rovner 1982), and virgin females of *L. tarentula* leave silk threads placed several millimeters over the substratum (unpubl. data) that can be used by males to recognize females' sexual status and to find them. However, in our study, this information was not available to the animal because the spider was placed in an open field that did not contain

this source of information. Idiothetic information was not used by *L. tarentula* in homing because the spiders did not follow any particular direction under an overcast sky. If *L. tarentula* used idiothetic information, we should have observed successful homing behavior under an overcast sky, as in the idiothetic orientation of blind *Cupiennius salei* (Keyserling 1877) (see Seyfarth et al. 1982) towards a prey from which it has been chased. In this latter ctenid spider it has been argued that homing orientation could be based on non-visual cues, given its nocturnal habits. On the other hand in *L. tarentula*, a diurnal as well as nocturnal spider, visual and non-visual cues can be used for orientation.

Which celestial cues are used by *L. tarentula* to return home? The sun's position is excluded by the experimental conditions of our study. Other cues could be the skylight patterns of linearly-polarized light and the intensity gradient. *L. tarentula* may use these cues since it has a good orientation towards the burrow under a blue sky, while it becomes disoriented under an overcast sky. Under this condition, the spider lacks information about the sun's position and the skylight polarization pattern. We obtained similar results when we used the plastic sheet, which did not significantly modify the intensity gradient but did cancel out the skylight pattern of linearly polarized light. So, we think that the relevant cue for homing is the skylight polarization pattern. In *Arctosa perita* (Latreille 1799) Papi (1955b) also found that this cue was more important for orientation than the light intensity gradient.

How could one explain the presence of a bimodal distribution under a blue sky and with the PMEs, PLEs, and ALEs blinded? We suggest that the time of day at which observations resulting in orientation opposite to the burrow direction were made is the determining factor. These observations were carried out at the first hours of daylight (near sunrise) or when the sun was at its noon location. Under either of these conditions, a symmetrical distribution of the e-vector patterns occurs around the solar-antisolar meridian. So, the spiders tested at these hours could be confused by the symmetry of the e-vector pattern. This would also be the reason for the absence of a bimodal distribution for the animals that should go towards 30° NE under a blue sky and with the

PMEs, PLEs, and ALEs blinded. Although in both samples we are at the low limit of sample size, we think that the results are not invalidated because we have an equal sample size for the animals that should orient towards 30° NE under an overcast sky or with the PMEs, PLEs, and ALEs blinded, and in the latter case the distribution is at random. This bimodal distribution has also been observed in the celestial orientation of sandhoppers (Ugolini et al. 1993) in the morning and at sunset.

The skylight polarization pattern is detected by the anterior median eyes of *L. tarentula*. In *Arctosa variana*, a wandering ripicolous lycosid species, Magni et al. (1964) have shown that polarized light detection is carried out by the AMEs and PMEs. The indirect eyes (PMEs, PLEs and ALEs) have no role in linearly-polarized light detection by *L. tarentula*, since a completely random distribution is observed when the AMEs are blinded. This is in accordance with a morphological analysis of the AME retina (Kovoor et al. 1993) which has shown that, in ventral photoreceptors, successive lines of rhabdoms are oriented orthogonally to each other; such an arrangement was not observed in any other eye type of *L. tarentula*.

From the analysis of the ERGs, it can be concluded that the anterior median eyes of *L. tarentula* perceive polarized light well, which is unlikely for the other eyes. This correlates perfectly with the results of behavioral experiments. The change in the direction of the polarization plane produces a large change in the response (amplitude) of the ERG of the AMEs. During the photophase, *Lycosa tarentula* being inside the burrow in an almost vertical position or outside the burrow with its body axis parallel to the ground, both vertical and horizontal planes of polarization will play a role in homing. Ongoing experiments will determine if a change in the direction of the polarization plane induces a change in the homing direction taken by the spiders as it has been shown for other spiders like *Agelena labyrinthica* (Görner & Claas 1985).

APPENDIX I

Suppose that $\phi_1, \phi_2, \dots, \phi_n$ are the directions taken by n animals to return home, then to calculate the mean angle and the angular deviation of the sample we proceed as follows:

$$\bar{x} = \frac{1}{n}(\cos \Phi_1 + \cos \Phi_2 + \dots + \cos \Phi_n)$$

$$\bar{y} = \frac{1}{n}(\sin \Phi_1 + \sin \Phi_2 + \dots + \sin \Phi_n)$$

and the mean angle of the sample will be

$$\bar{\Phi} = \arctan \frac{\bar{y}}{\bar{x}} \quad \text{if } \bar{x} > 0$$

$$\bar{\Phi} = 180^\circ + \arctan \frac{\bar{y}}{\bar{x}} \quad \text{if } \bar{x} < 0.$$

To calculate the angular deviation we use

$$s = \frac{180^\circ}{\pi} \sqrt{2(1 - r)}.$$

The length of the mean vector, r , is a measure of the dispersion of the data and it is calculated with the following formula

$$r = \frac{1}{n} \left(\sum \cos \Phi_i^2 + \sum \sin \Phi_i^2 \right).$$

With n , sample size, and r , length of mean vector, the Rayleigh test gives us the critical level, P , that the parent population is randomly distributed.

Mardia-Watson-Wheeler test: The purpose of this test is to discover whether two independent samples of n_1 and n_2 observations differ significantly from each other. This test is also known as a uniform-score test because it uses only the order in which the observations of both samples are arranged. We pooled both samples and we ranked the elements of one sample, for example the smallest one. We calculate $\delta = [360^\circ/(n_1 + n_2)]$ where n_1 and n_2 are the sizes of both samples and we multiply each rank by δ , transforming each initial value to β_i . The resultant vector of the first sample has the following components

$$C_1 = \sum \cos \beta_i, \quad S_1 = \sum \sin \beta_i$$

and the length of the resultant vector is $R_1 = \sqrt{C_1^2 + S_1^2}$ and as a test statistic we use $B = R_1^2$.

If $n > 17$, we use the quantity

$$\chi^2 = 2(n - 1) \frac{R_1^2}{n_1 n_2}$$

which is approximately distributed as chi-squared with two degrees of freedom.

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