

## RESEARCH ARTICLE

# Anterior lateral eyes of *Lycosa tarantula* (Araneae: Lycosidae) are used during orientation to detect changes in the visual structure of the substratum

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Accepted 23 April 2011

## SUMMARY

Previous studies in the wolf spider *Lycosa tarantula* (Linnaeus 1758) have shown that homing is carried out by path integration and that, in the absence of information relative to the sun's position or any pattern of polarized light, *L. tarantula* obtains information as to the angle it must turn to home through the anterior lateral eyes (ALEs). In the present study, spiders were trained to walk over a black-and-white grating and afterwards tested either over a white substratum, the same substratum used for training or the same substratum rotated 90deg (two groups: ALEs covered and only ALEs uncovered; they were tested first without their eyes covered and then with their eyes covered). The directional bearing was measured both in training and test conditions. Under the white or the same substratum in test conditions, the directional bearing had the same mean direction and a distribution similar to that of the training sessions. When the substratum was rotated 90deg, the directional bearing had the same mean direction but the distribution was significantly different from that of the training sessions. Moreover, if ALEs were covered, spiders behaved as if the substratum had not been rotated and the directional bearing distribution was similar to that of the training sessions. But, if ALEs were the only eyes uncovered, spiders behaved as if no eyes were covered and directional bearing distribution was similar to that of the test condition. It is suggested that, when homing, *L. tarantula* uses both idiothetic information and visual information gathered through ALEs. These findings present the first evidence that spiders can use the visual structure of the substratum to return home.

Key words: spider, *Lycosa tarantula*, anterior lateral eye, homing, home direction estimation.

## INTRODUCTION

Homing in animals is the ability to return to the place where the animal lives and has its shelter, den or nest after an active displacement (e.g. to capture prey or looking for potential mates, for example) or a passive displacement (due to atmospheric conditions, such as wind, or displaced by an experimenter). Path integration is a route-based homing (Papi, 1992) that allows the animal a direct return path after a more-or-less winding outward trip.

Path integration has been demonstrated in several species of spiders. In the dancing white lady spider, *Leucorchestris arenicola* (Araneae: Sparassidae), males wander through the sands of the Namib Desert searching for females during moonless nights (Henschel, 2002; Nørgaard et al., 2006; Nørgaard, 2008). It seems that the anterior median eyes and both pairs of lateral eyes are necessary for long-distance navigation in *L. arenicola*, although the details of how vision is used during this behavior remain unresolved (Nørgaard et al., 2008). The nocturnal spider *Cupiennius salei* uses path integration based on idiothetic cues to return with a high degree of precision to a previous place from which it has been chased away (Seyfarth et al., 1982). When lyriform organs (a kind of proprioceptor organ in the legs) were destroyed, the rate of success and the starting angle differed significantly from those of control spiders. *Agelena labyrinthica* has been the subject of a detailed study on the cues used for homing by means of path integration; it has been shown that this species relies on idiothetic and visual cues (e.g. polarized light or the position of a light spot in relation to the burrow) (Görner, 1958; Schröer, 1976; Görner and Claas, 1985).

Within the Lycosidae family, several species of the *Arctosa* genus have been studied in relation to their homing system [*A. cinerea* (Papi and Syrjämäki, 1963); *A. perita* (Papi, 1955; Papi et al., 1957); and *A. variana* (Magni, 1966; Magni et al., 1964)], as have some members of the *Lycosa* genus [e.g. *L. fluviatilis* (Papi and Syrjämäki, 1963) and *L. tarantula* (Ortega-Escobar and Muñoz-Cuevas, 1999; Ortega-Escobar, 2002; Ortega-Escobar, 2006)]. Both genera use astronomic orientation (sun compass and polarized-light compass). Under natural conditions, *L. tarantula* homes by means of path integration in which the information relative to changes of direction is provided by the anterior median eyes (Ortega-Escobar and Muñoz-Cuevas, 1999). These eyes have visual fields that encompass the celestial zenith and also have specialized photoreceptors in the ventral part of the retina. Further, the retinal cup can be moved up and down through the use of two muscles attached to it (Kovoor et al., 1993). In a previous study (Ortega-Escobar, 2006), I demonstrated that functioning anterior lateral eyes (ALEs) were necessary for path integration after an L-like outward trip. When ALEs were uncovered and the rest of the eyes were covered, the turning angle for homing was not different from that observed in the control situation (all eyes uncovered). When ALEs were covered and the rest of the eyes were uncovered, the turning angle for homing was randomly oriented in all but one of the animals. I suggested that ALEs could supply information as to the direction of turning and the angle turned.

In this study, the role of ALEs in homing was analyzed by training the spiders in half of a circular arena with a substratum which

consisted of a black-and-white grating ( $\lambda=6$  mm). For testing, the spiders were placed on a white substratum, the control grating or the control grating rotated 90 deg. Spiders tested with a 90 deg-rotated grating had either their ALEs or the remaining eyes subsequently covered. Results are discussed in the context of a conflict between proprioceptive and visual information used by the spider to home.

## MATERIALS AND METHODS

### Animals

*Lycosa tarantula* (Linnaeus 1758) adult virgin females were used for the study. These animals had been captured from a wild population in Madrid (central Spain; 40°32'N, 3°42'W) and went through the final two to three molts in the laboratory; all were close to the same age and all trials were conducted after maturation. They were maintained in individual containers measuring 17×13×8 cm with sufficient substratum (earth) in which to move around and dig burrows. They were fed blow flies (*Calliphora vomitoria*) and given water twice a week.

### Experimental procedure

Spiders were placed in a circular arena 90 cm in diameter with opaque walls (wall height, 48 cm; visual angle, 47 deg) with an artificial burrow in the central part. The arena was divided into two semicircles by an opaque screen in such a way that the spider could move about only in one half of the arena (control zone). The substratum of this half was a black-and-white grating ( $\lambda=6$  mm) with bands parallel to the screen position. The substratum of the other half (test zone) could be the same grating, a white substratum or the same grating rotated 90 deg (Fig. 1).

The arena was in a room without natural lighting. The room was lit in the daytime (08:00–20:00 h) with white light by two SYLVANIA™ Standard F36W fluorescent tubes producing 200 lux at the floor level of the arena. The arena was not surrounded by any curtains, so the spiders could see all the cues above it; however, in a previous study (Ortega-Escobar, 2002) it was shown that *L. tarantula* females did not use distant visual landmarks in the room housing the arena.

The image of the arena was captured by an Ikegami ICD-42B B/W CCD video camera (Ikegami Electronics, Neuss, Germany), displayed on a Sony Trinitron colour video monitor and registered by an AG-6124 Panasonic time lapse video cassette recorder.

For the control trials, spiders were displaced in the control zone by pushing them gently with a small stick along a path perpendicular to the separating partition between the test and control zones to a point 30 cm away from the burrow, where they entered a glass cup, which was lifted by the experimenter and then gently placed on the substratum. To avoid changes in body orientation while they were being pushed, an opaque screen was placed between the burrow and the point of release; in general, spiders were displaced in contact with this screen and parallel to it. Displacements not parallel to the screen were not used in the analysis. For the test trials, spiders were displaced in a similar way in the control zone and, after entering the glass cup, were transferred to a point on the opposite side (i.e. the test zone) and placed with the anterior region of the spider in a direction opposite to the burrow. In experiment A, the substratum of the test zone was white. In experiment B, the substratum of test zone was the same as that of the control (black and white grating,  $\lambda=6$  mm). In experiments C and D, the substratum of the test zone was the same as that of the control but rotated 90 deg (Fig. 1).

Thirty-six females were studied. In each experiment, nine different females were used. In experiments A and B, each animal was tested

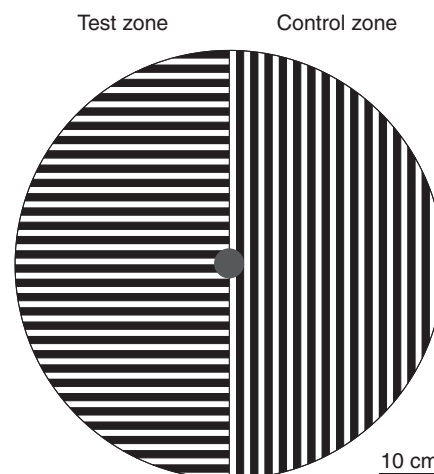


Fig. 1. Experimental setup (top view; grating not to scale); central circle: burrow. Each spider was placed in the arena 4 d before the beginning of the experiment. For control trials (in the control zone), the spider was displaced following a linear path perpendicular to the longitudinal axis of the grating. For test trials, the spider was transferred, after the outward trip in the control zone, in a glass cup to a point (in the test zone) placed at approximately 180 deg and released there with the same body orientation as when it was taken.

first in the control zone (control condition) and afterwards in the test zone (test condition). In Experiment C, spiders were tested first in the control zone (control condition), then in the test zone (test condition) and finally in the test zone with ALEs covered (test/ALEs covered condition). In Experiment D, spiders were submitted to the same sequence of trials (control and test conditions) but the latter trials were with all eyes covered except ALEs (test/ALEs uncovered condition). The directional bearing of the spider was recorded when it reached a point 20 cm (linear) from the point of release. If the spider had not moved during 20 min it was returned to the burrow. The floor of the arena was thoroughly cleaned with ethanol before each test. All the trials were run between 11:00 and 18:00 h with the lights on. The eye-covering procedure is described in a previous paper (Ortega-Escobar, 2006). After the experiments, the eye cover was removed and checked for its integrity by using a magnifying glass.

All experiments complied with the current laws of the country (Spain) where they were performed.

### Data analysis

The directional bearing was taken when the spider was 20 cm from the point of release. Each spider was tested 10 times in each condition (except in experiment A, where each spider was tested eight times in each condition) and the eight or 10 bearings were added together to produce a mean vector for each spider. Circular statistics and associated tests were used (Batschelet, 1981). First, the mean vectors of each animal were calculated. In order to determine whether the mean angles of the animals of the same group were oriented at random, the non-parametrical Moore test was used. If there was no difference, second-order mean vectors were then calculated. These were tested for significant directional preference to the burrow by using the *V*-test. The mean vectors of two samples were compared by using the Watson–Williams test and differences in distribution were compared by use of the Mardia–Watson–Wheeler test. To run the different tests, the circular statistics program Oriana (Kovach, 2004) was used.

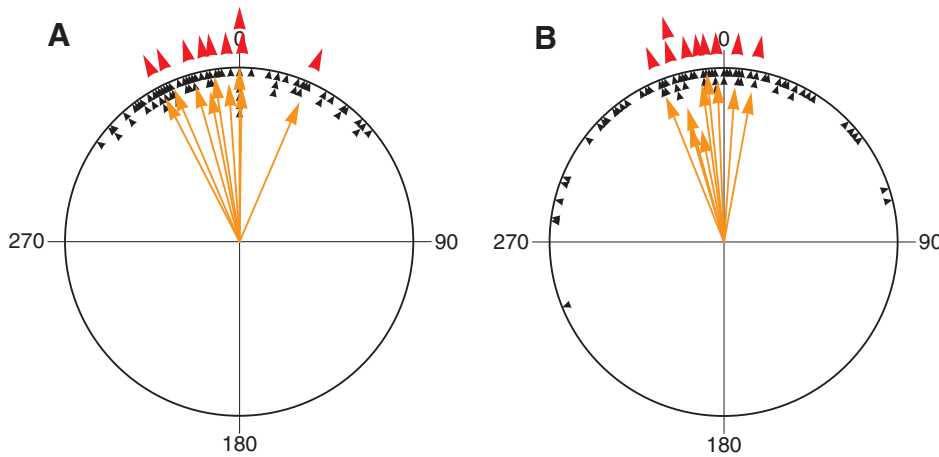


Fig. 2. Directional bearings of Experiment A. (A) Control trials walking over a black-and-white grating. (B) Test trials walking over a white substratum. Black triangles represent directional bearings of all spiders used in this experiment. Red arrowheads and yellow arrows represent the mean vector of each spider and its length, respectively. To return to the burrow, the spider should walk towards 0 deg.

In addition, in experiments B, C and D, the trajectories of three spiders for control and test displacements were digitized in order to determine the linearity of trajectories. To accomplish this, a translucent paper sheet was placed over the video monitor and all the changes of direction or stops were registered.

## RESULTS

### Experiment A: control trials with grating substratum and test trials with a white substratum

Fig. 2 shows the individual spider's vectors under the control and test conditions. In both conditions, there were no differences among the mean vectors of spiders (Moore test: control,  $D=1.6363$ ,  $P<0.001$ ; test,  $D=1.6458$ ,  $P<0.0001$ ) and spiders were well oriented towards the burrow position with little error ( $V$ -test: control,  $u=10.651$ ,  $P<0.001$ ; test,  $u=9.978$ ,  $P<0.001$ ). There were no differences in the mean angles of the spiders in the control and test conditions (Watson-Williams test:  $F_{1,142}=0.018$ ,  $P=0.893$ ) or in the distribution (Mardia-Watson-Wheeler test:  $W=3.329$ ,  $P=0.189$ ).

This would suggest that spiders do not need the control visual substratum to orientate towards the burrow after displacement.

### Experiment B: control trials and test trials with the same grating substratum

Trajectories of both control and test trials were quite similar, being almost linear and directed towards burrow neighborhoods (Fig. 3A,B).

Fig. 3C,D shows the individual vectors under the control and test conditions. In both conditions, the spiders were well oriented towards the burrow position, returning directly towards it with little error ( $V$ -test: control,  $u=12.714$ ,  $P<0.001$ ; test,  $u=12.369$ ,  $P<0.001$ ). There were no differences in the mean headings among spiders (Moore test: control,  $D=1.6533$ ,  $P<0.001$ ; test,  $D=1.6363$ ,  $P<0.001$ ). There were no differences in the mean angles of the spiders in the control and test conditions (Watson-Williams test:  $F_{1,178}=0.876$ ,  $P=0.351$ ) or in the distribution (Mardia-Watson-Wheeler test:  $W=1.929$ ,  $P=0.381$ ), which suggests that transport to the test zone

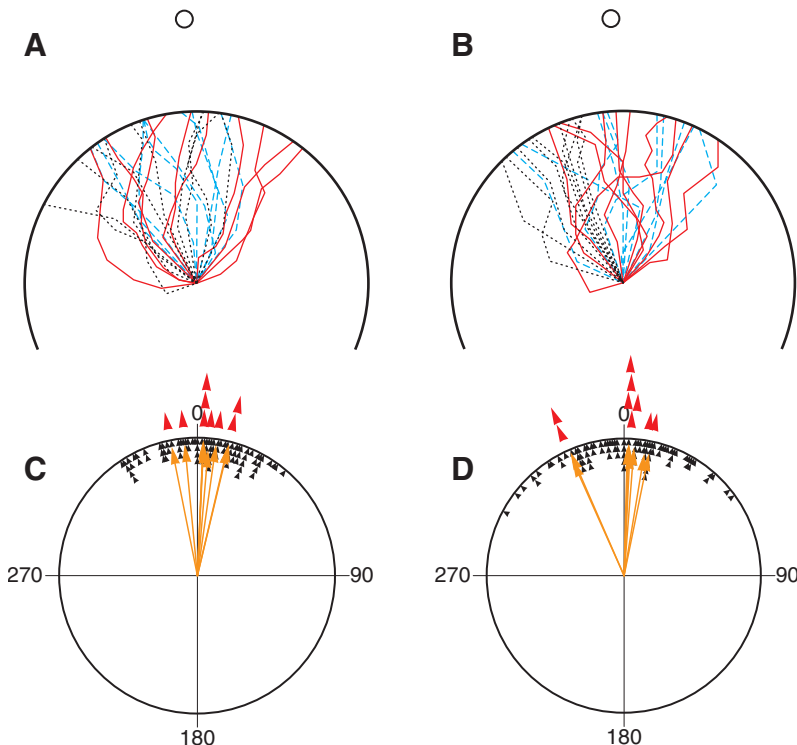


Fig. 3. Experiment B. (A,B) Trajectories of three spiders under the (A) control and (B) test conditions. The radius of the semicircle is 20 cm; the small open circle is the burrow. (C,D) Directional bearings of spiders under the (C) control and (D) test conditions. Symbols and other graphical conventions are the same as those described in Fig. 2.

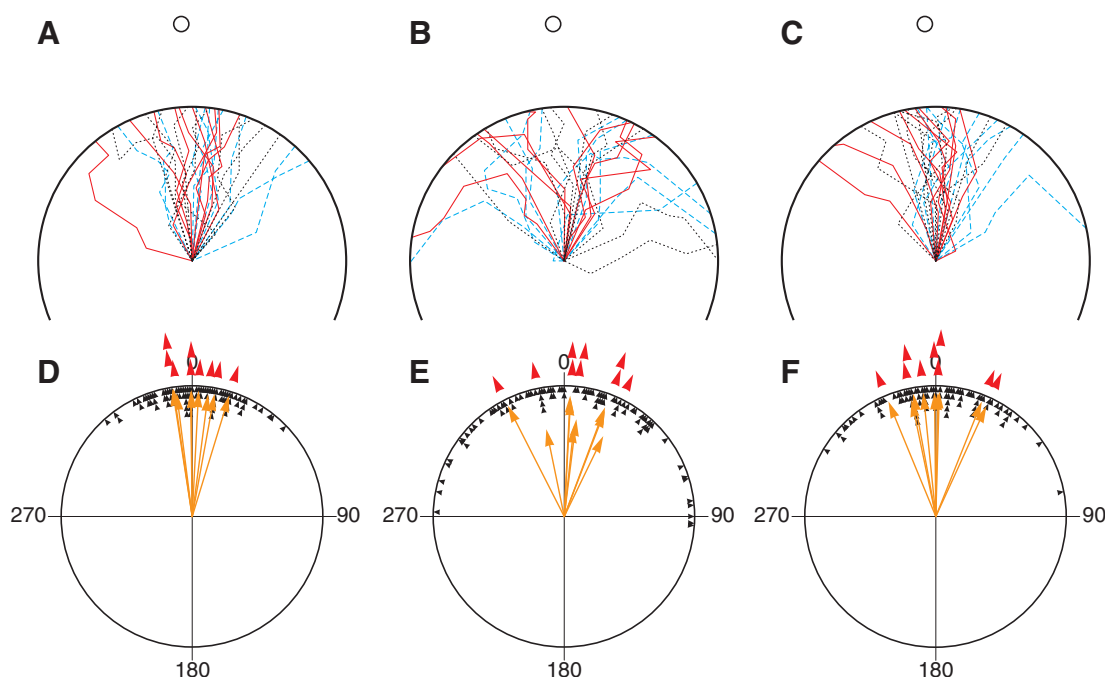


Fig. 4. Experiment C. (A–C) Trajectories of three spiders under the (A) control, (B) test and (C) test/ALEs covered conditions. The radius of the semicircle is 20 cm; the small open circle is the burrow. (D–F) Directional bearings of spiders under the (D) control, (E) test and (F) test/ALEs covered conditions. Symbols and other graphical conventions are the same as those described in Fig. 2.

does not affect orientation behavior and also excludes the possible use of tactile, slope or olfactory cues in homing.

#### Experiment C: control trials with visual texture and test trials with the same texture rotated 90 deg; ALEs covered

The trajectories of the control condition (Fig. 4A) were rather similar to those of animals in Experiment B, whereas the trajectories of the test condition were less linear (Fig. 4B). Some of the latter went first in the direction of the burrow and afterwards changed direction abruptly, whereas others went in a direction nearly 90 deg to the right or left of the burrow. In the test/ALEs covered condition, most of the trajectories became linear again and were directed towards the burrow (Fig. 4C).

Fig. 4D,E shows the individual vectors under the control and test conditions. In the control condition, all spiders were well oriented towards the burrow position with little dispersion ( $V$ -test:  $u=12.819$ ,  $P<0.001$ ). In the test condition, although the mean vector was oriented towards the burrow position ( $V$ -test:  $u=10.491$ ,  $P<0.001$ ), there was a great dispersion of bearings with some homeward displacements having an error angle nearing 90 deg. There were no differences in the mean headings among spiders (Moore test: control,  $D=1.6470$ ,  $P<0.001$ ; test,  $D=1.5951$ ,  $P<0.001$ ). There were no differences among the mean vectors of the control and test conditions (Watson–Williams test:  $F_{1,178}=0.722$ ,  $P=0.397$ ); however, there were differences in distribution between both conditions (Mardia–Watson–Wheeler test:  $W=32.2$ ,  $P<0.001$ ).

In the test/ALEs covered condition, the length of the mean vector of each spider increased and the mean direction was towards the burrow position (Fig. 4F) ( $V$ -test:  $u=12.294$ ,  $P<0.001$ ). There were no differences in the mean headings among spiders (Moore test: test/ALEs covered,  $D=1.6273$ ,  $P<0.001$ ), and there were no differences in the mean direction between the spiders in the control and the test/ALEs covered conditions (Watson–Williams test:  $F_{1,178}=0.194$ ,  $P=0.66$ ) nor between the test and test/ALEs covered conditions (Watson–Williams test:  $F_{1,178}=1.144$ ,  $P=0.286$ ). There were differences in the distribution between the test condition and the test/ALEs covered condition (Mardia–Watson–Wheeler test:  $W=15.856$ ,  $P<0.001$ ), but there were no differences in distribution

between the control and test/ALEs covered conditions (Mardia–Watson–Wheeler test:  $W=3.325$ ,  $P=0.19$ ).

#### Experiment D: control trials with visual texture and test trials with the same texture rotated 90 deg; ALEs uncovered

The control trajectories were rather linear and directed towards the burrow neighborhoods (Fig. 5A). When placed over the same substratum rotated 90 deg (Fig. 5B), the trajectories were less linear and there were some that were directed initially towards the burrow and afterwards showed a change of direction of nearly 90 deg. Other trajectories showed an orientation of nearly 90 deg in relation to the burrow from the beginning. After covering all the eyes except the ALEs, the result was rather similar to that observed in the test condition.

Fig. 5D,E shows the individual vectors under the control and test conditions. In the control condition, all of the spiders were well oriented towards the burrow position ( $V$ -test:  $u=12.582$ ,  $P<0.0001$ ). In the test condition, the mean vector was also oriented towards the burrow position ( $V$ -test:  $u=9.563$ ,  $P<0.0001$ ). There were no differences in the mean headings among spiders (Moore test: control condition,  $D=1.6447$ ,  $P<0.001$ ; test condition,  $D=1.5994$ ,  $P<0.001$ ) and there were no differences between the mean vectors of the control and test conditions (Watson–Williams test:  $F_{1,178}=0.932$ ,  $P=0.336$ ). However, there were differences in distribution between both conditions (Mardia–Watson–Wheeler test:  $W=14.587$ ,  $P<0.001$ ).

In the test/ALEs uncovered condition, there were no differences in the mean headings among spiders (Moore test:  $D=1.5297$ ,  $P<0.001$ ). Spiders were well oriented towards the burrow ( $V$ -test:  $u=9.503$ ,  $P<0.0001$ ). There were no differences between the mean vectors of the test and test/ALEs uncovered conditions (Watson–Williams test:  $F_{1,178}=0.859$ ,  $P=0.355$ ) nor were there differences between the control and test/ALEs uncovered conditions (Watson–Williams test:  $F_{1,178}=0.079$ ,  $P=0.779$ ). There were differences in distribution between the control and test/ALE, uncovered conditions (Mardia–Watson–Wheeler test:  $W=44.832$ ,  $P<0.001$ ). There were no differences in distribution between the test and test/ALEs uncovered conditions (Mardia–Watson–Wheeler test:  $W=3.486$ ,  $P=0.175$ ).



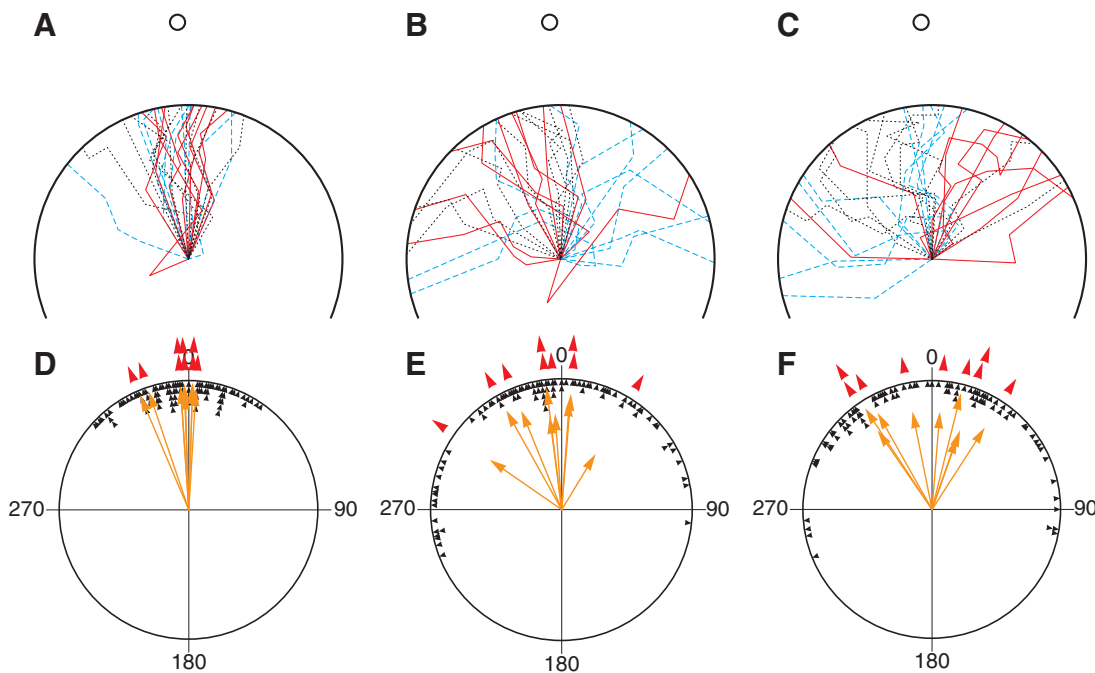


Fig. 5. Experiment D. (A–C) Trajectories of three spiders under the (A) control, (B) test and (C) test/ALEs uncovered conditions. The radius of the semicircle is 20 cm; the small open circle is the burrow. (D–F) Directional bearings of spiders under the (D) control, (E) test and (F) test/ALEs uncovered conditions. Symbols and other graphical conventions are the same as those described in Fig. 2.

#### Comparison of experiments B, C and D

There were no significant differences in distribution among the control conditions of the three experiments (Mardia–Watson–Wheeler test: B versus C,  $W=3.282$ ,  $P=0.194$ ; B versus D,  $W=5.58$ ,  $P=0.061$ ; C versus D,  $W=2.717$ ,  $P=0.257$ ).

There was no significant difference in bearing distribution between test conditions of experiments in which the substratum was rotated 90deg in relation to the training trials (Mardia–Watson–Wheeler test:  $W=2.997$ ,  $P=0.223$ ).

Although the substratum was the same, there was significant difference in bearing distribution between test conditions with eyes covered in experiments C and D (Mardia–Watson–Wheeler test:  $W=34.013$ ,  $P<0.001$ ).

#### DISCUSSION

The results of this study suggest that homing in *L. tarantula* is a process in which idiothetic and visual information are used together. These results also suggest that, under the experimental conditions in the present study, there is not a role for olfactory information or information associated with silk threads because spiders could not leave this kind of signal in the test zone.

In all experiments, the control displacements showed that *L. tarantula* homed by turning at an angle of approximately 180deg and walking towards the burrow after some stops or changes of direction, as has been observed previously in this species (Ortega-Escobar, 2002; Ortega-Escobar, 2006) and in other spiders [e.g. *Cupiennius salei* (Seyfarth et al., 1982)]. Once the spider was at the point where it considered the burrow should be placed, a systematic search began by turning abruptly and beginning a series of loops of increasing diameter until finding the burrow or contacting and following the separation between the control and test zones and finding the burrow.

As shown by the results of experiment A, *Lycosa tarantula* can home only with proprioceptive information obtained during the outward path if there is no change in the direction of its body axis when transported to the test zone (see also Ortega-Escobar, 2002).

When the visual textures of the control and test zones were the same (Experiment B), directional bearing dispersions were very

similar (Fig. 3C,D); therefore, it could be deduced that homing was exclusively idiothetic. Although we have not controlled for the slopes of the control and test zones and spiders have sensory receptors to detect the slope (Barth, 2002), my results do not suggest an effect of slope on homing in *L. tarantula*. However, the dancing white lady spider *L. arenicola* could use this kind of sensory information to navigate. The possibility of information coming from the slope substrate for navigation has been studied by Nørgaard et al. (Nørgaard et al., 2003) in *L. arenicola*, and they concluded that their data do not support the possibility that a substrate slope is used as a compass in the spider's navigation.

When the visual texture of the test zone was rotated 90deg in relation to the control zone, there were no differences between the homeward mean angles of the control and test conditions. However, there was an important change in the bearing dispersion in relation to the burrow position. In both experiments C and D, there was a significant dispersion of the directional bearing, suggesting that the rotated visual structure of the test zone substratum had also been used as a cue to return to the burrow. In the test zone, spiders would experience a conflict between proprioceptive and visual information. In this case, there has been a dissociation of idiothetic and visual information not previously observed, because both sensory cues worked in the same direction. The effect of visual substratum would probably be higher if both the length of the homeward path and the intervals of the grating were also higher. In spiders, this kind of change affecting the visual texture of the substratum has not been studied, although there have been studies of homing after manipulation of the web structure (e.g. Görner and Claas, 1985). Analogous studies to the ones carried out on *L. tarantula* have been carried out on insects, notably on ants and bees, but using channels whose floors consisted of some kind of texture [bees (Dacke and Srinivasan, 2007; Esch et al., 2001; Si et al., 2003; Srinivasan et al., 1997; Srinivasan and Zhang, 2004); ants (Ronacher and Wehner, 1995)].

With a rotated substratum in the test zone, covering of eyes had a very different effect on directional bearing dispersion. When ALEs were covered, all spiders tested showed a tendency to return towards the burrow position, whereas when anterior median eyes (AMEs), posterior median eyes (PMEs) and posterior lateral eyes (PLEs) were

covered (i.e. ALEs were uncovered), the directional bearing dispersion persisted. These results suggest that only ALEs, whose visual fields are directed towards the substratum (Land, 1985), are capable of perceiving the change in the visual substratum between the outward path and the homeward path. If this hypothesis is correct, when ALEs were uncovered and the visual substratum had not changed, the directional bearing dispersion would be small, because the spider would use only proprioceptive information. In contrast, when ALEs were uncovered and the substratum was rotated, the directional bearing dispersion would be higher due to cue conflict.

According to Land, there is a downwards extension of the field of view of PME's and they could have usurped the function of the ALEs (Land, 1985). Our results clearly show that this is not the case and that, although ALE resolution is poor (3.4deg) (Reyes-Alcubilla et al., 2009), it is enough to distinguish the black and white grating used in our experiments. The function of ALEs is related to the visual structure of the substratum the spider traverses and this function has not been usurped by the PME's, because when these eyes are functioning (ALEs covered group) there is not an effect of the visual substratum on homing.

The functions of spider ALEs are relatively unknown. There have been few studies specific to them. In *Rabidosia rabida* (Araneae: Lycosidae), Rovner studied the role of different pairs of eyes in detecting visual stimuli coming from video images of conspecifics (Rovner, 1993). The behaviors studied in females and males were orientation and long-range approach (a displacement of up to 10 cm). When ALEs were covered, the behavior was similar to spiders with the other eyes covered. However, when ALEs were the only functional eyes, there were no spiders showing the long-range approach and very few showing orientation. In *Cupiennius salei* (Araneae: Ctenidae), Schmid studied target discrimination by masking several combinations of AMEs and PME's; however, ALEs were not studied (Schmid, 1998). Recently, Zurek et al. studied the role of the anterior lateral eyes in the hunting behaviour of *Servaea vestita*, a jumping spider (Zurek et al., 2010). When only visual information from ALEs was available, spiders showed orientation behaviour towards low-contrast dot stimuli either moving to slower or faster speeds.

More closely related to this study is the work on navigation in *L. arenicola*, in which homing success was studied when spiders could see through all eyes or when particular groups of eyes were functional (Nørgaard et al., 2008). There was no difference in homing ability between spiders with only ALEs functional and the spiders with all eyes functional. However, given that the visual fields of ALEs are horizontally elongated and would provide information relative to the horizon (Nørgaard et al., 2008), the mechanism of navigation by using ALEs in these two species is probably different. *Leucorchestris arenicola* probably uses information coming from the nocturnal horizon skyline whereas *L. tarantula* uses information coming from the visual texture of the substratum.

Therefore, our results, with those by Nørgaard et al. (Nørgaard et al., 2008), show that the role of ALEs has been underestimated in the literature and that they have an important function in orientation in spiders. There is a possibility that ALEs are also used by *L. tarantula*, together with idiothetic information, to measure the distance travelled when it goes out from its burrow, as Reyes-Alcubilla et al. (Reyes-Alcubilla et al., 2009) have already demonstrated. This hypothesis is already under study.

## ACKNOWLEDGEMENTS

E. Ortega-Escobar is gratefully acknowledged for his preparation of the figures.

## REFERENCES

- Barth, F. G. (2002). *A Spider's World. Senses and Behavior*. Berlin: Springer-Verlag.
- Batschelet, E. (1981). *Circular Statistics in Biology*. London: Academic Press.
- Dacke, M. and Srinivasan, M. V. (2007). Honeybee navigation: distance estimation in the third dimension. *J. Exp. Biol.* **210**, 845-853.
- Esch, H. E., Zhang, S., Srinivasan, M. V. and Tautz, J. (2001). Honeybees dances communicate distances measured by optic flow. *Nature* **411**, 581-583.
- Görner, P. (1958). Die optische und kinästhetische Orientierung der Trichterspinnne *Agelena labyrinthica*. *Z. Vgl. Physiol.* **51**, 111-153.
- Görner, P. and Claas, B. (1985). Homing behavior and orientation in the funnel-web spider, *Agelena labyrinthica* Clerck. In *Neurobiology of Arachnids* (ed. F. G. Barth), pp. 275-297. Berlin: Springer-Verlag.
- Henschel, J. R. (2002). Long-distance wandering and mating by the Dancing White Lady spider (*Leucorchestris arenicola*) (Araneae, Sparassidae) across Namib dunes. *J. Arachnol.* **30**, 321-330.
- Kovach, W. (2004). *Oriana v. 2. 02a*. Anglesey, Wales: Kovach Computing Service.
- Kovoor, J., Muñoz-Cuevas, A. and Ortega-Escobar, J. (1993). Microanatomy of the anterior median eyes and its possible relation to polarized-light reception in *Lycosa tarantula* (Araneae, Lycosidae). *Boll. Zool.* **60**, 367-375.
- Land, M. F. (1985). The morphology and optics of spider eyes. In *Neurobiology of Arachnids* (ed. F. G. Barth), pp. 53-78. Berlin: Springer-Verlag.
- Magni, F. (1966). Analysis of polarized light in wolf-spiders. In *The Functional Organization of the Compound Eye* (ed. C. G. Bernhard), pp. 171-186. Oxford: Pergamon Press.
- Magni, F., Papi, F., Savely, H. E. and Tongiorgi, P. (1964). Research on the structure and physiology of the eyes of a lycosid spider. II. The role of different pairs of eyes in astronomical orientation. *Arch. Ital. Biol.* **102**, 123-136.
- Nørgaard, T. (2008). Nocturnal spider navigators in the Namib desert. *Newsletter Br. Arachnol. Soc.* **112**, 10-12.
- Nørgaard, T., Henschel, J. R. and Wehner, R. (2003). Long-distance navigation in the wandering desert spider *Leucorchestris arenicola*: can the slope of the dune surface provide a compass cue? *J. Comp. Physiol. A* **189**, 801-809.
- Nørgaard, T., Henschel, J. R. and Wehner, R. (2006). The night-time temporal window of locomotor activity in the Namib Desert long-distance wandering spider, *Leucorchestris arenicola*. *J. Comp. Physiol. A* **192**, 365-372.
- Nørgaard, T., Nilsson, D.-E., Henschel, J. R., Garm, A. and Wehner, R. (2008). Vision in the nocturnal wandering spider *Leucorchestris arenicola* (Araneae: Sparassidae). *J. Exp. Biol.* **211**, 816-823.
- Ortega-Escobar, J. (2002). Evidence that the wolf-spider *Lycosa tarantula* (Araneae, Lycosidae) needs visual input for path integration. *J. Arachnol.* **30**, 481-486.
- Ortega-Escobar, J. (2006). Role of the anterior lateral eyes of the wolf spider *Lycosa tarantula* (Araneae, Lycosidae) during path integration. *J. Arachnol.* **34**, 51-61.
- Ortega-Escobar, J. and Muñoz-Cuevas, A. (1999). Anterior median eyes of *Lycosa tarantula* (Araneae, Lycosidae) detect polarized light: behavioral experiments and electro-retinographic analysis. *J. Arachnol.* **27**, 663-671.
- Papi, F. (1955). Ricerche sull'orientamento astronomico di *Arctosa perita* (Latr.) (Araneae, Lycosidae). *Pubbl. Staz. Zool. Napoli* **27**, 76-103.
- Papi, F. (1992). General aspects. In *Animal Homing* (ed. F. Papi), pp. 1-18. London: Chapman & Hall.
- Papi, F. and Syrjämäki, J. (1963). The sun-orientation rhythm of wolf spiders at different latitudes. *Arch. Ital. Biol.* **101**, 59-77.
- Papi, F., Serretti, L. and Parrini, S. (1957). Nuove ricerche sull'orientamento e il senso del tempo di *Arctosa perita* (Latr.) (Araneae, Lycosidae). *Z. Vgl. Physiol.* **39**, 531-561.
- Reyes-Alcubilla, C., Ruiz, M. A. and Ortega-Escobar, J. (2009). Homing in the wolf spider *Lycosa tarantula* (Araneae: Lycosidae): the role of active locomotion and visual landmarks. *Naturwissenschaften* **96**, 485-494.
- Ronacher, B. and Wehner, R. (1995). Desert ants *Cataglyphis fortis* use self-induced optic flow to measure distances travelled. *J. Comp. Physiol. A* **177**, 21-27.
- Rovner, J. S. (1993). Visually mediated responses in the lycosid spider *Rabidosia rabida*: the roles of different pairs of eyes. *Mem. Queensland Mus.* **33**, 635-638.
- Schmid, A. (1998). Different functions of different eye types in the spider *Cupiennius salei*. *J. Exp. Biol.* **201**, 221-225.
- Schröder, W.-D. (1976). Polarization sensitivity of rhabdomeric systems in the principal eyes of the funnel spider *Agelena gracilis* (Arachnida: Araneae: Agelenidae). *Ent. Germ.* **3**, 88-92.
- Seyfarth, E.-A., Hergenröder, R., Ebbes, H. and Barth, F. G. (1982). Idiothetic orientation of a wandering spider: compensation of detours and estimates of goal distance. *Behav. Ecol. Sociobiol.* **11**, 139-148.
- Si, A., Srinivasan, M. V. and Zhang, S. (2003). Honeybee navigation: properties of the visually driven "odometer". *J. Exp. Biol.* **206**, 1265-1273.
- Srinivasan, M. V. and Zhang, S. W. (2004). Visual motor computations in insects. *Annu. Rev. Neurosci.* **27**, 679-696.
- Srinivasan, M. V., Zhang, S. W. and Bidwell, N. J. (1997). Visually mediated odometry in honeybees. *J. Exp. Biol.* **200**, 2513-2522.
- Zurek, D. B., Taylor, A. J., Evans, C. S. and Nelson, X. J. (2010). The role of the anterior lateral eyes in the vision-based behaviour of jumping spiders. *J. Exp. Biol.* **213**, 2372-2378.