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ORIGINAL ARTICLE

Black widow spiders use path integration on their webs

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Abstract

Many animals store information about their external environment in memory and use this information to facilitate movement and decision-making. The information used to navigate has been described for numerous animals and is dependent on the ecology of the animal. Spider webs make up nearly all of a spider's physical and sensory environment. Here, we first asked whether black widow spiders form memories of their web and then asked whether the contents of these memories include a path integration vector. Black widows made navigational errors when we rotated their web in their absence and searched about the web upon realizing they made an error. Black widows were able to move on their web without retracing their steps, often taking shortcuts to a goal location without sensory cues to guide navigation. Black widows also began moving back to their retreat on a path parallel to their path out from the retreat, even after being moved on the web, and searched about the web for the retreat after not finding it initially. These results show that black widows use path integration when navigating. These results suggest that using internal representations of an animal's position within its environment, such as by using path integration, is widespread among animals with varied brain types and sensory ecologies, representing perhaps a convergent solution to common navigational problems.

Significance statement

The ability of animals to store information in memory that is then used in decision-making has evolved multiple times, in vertebrates and invertebrate lineages. The information and cognitive mechanism used for representing an animal's location within its environment vary in complexity, but the methods that have been described rely on vision for at least some of the sensory information used to form representations. Using behavioral assays, we have shown that black widow spiders represent their position relative to their home as a path integration vector. Black widows have poor vision and rely primarily on vibrations transmitted through the web to sense their environment. Our results indicate that internal representations are a general solution to brains' problem of integrating sensory information, and do not need acute vision to evolve.

Keywords Memory · Navigation · Mental Model · Invertebrate · Path integration

Introduction

Many animals store information about their environment and the relation of their bodies to their environment in memory and use this information to guide their behavior as they move about their surroundings (Shettleworth 2010). The information content of these memories varies widely, from the cumulative distance and direction from a reference location used in path integration, to representations of the spatial relationship between multiple landmarks (Shettleworth 2010; Webb 2019; Toledo et al. 2020). Explaining this variation in information content, and how the information is used in navigation, requires taking into account differences in sensory biology, ecology, and brain architecture across animals (Healy and Braithwaite 2000; Shettleworth 2010).

A wide variety of ambulatory invertebrates have been shown to navigate using information from memory, rather than by following immediately available sensory cues. The use of path integration is widespread, occurring for example in ants, bees, dung beetles, and spiders (Seyfarth et al. 1982; Moller and Goerner 1994; Müller and Wehner 1988; Collett and Collett 2000; Ortega-Escobar 2002; Cheng 2006; Wehner 2009; Ortega-Escobar and Ruiz 2010; Webb 2019; Cross et al.

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2020; Dacke et al. 2020; Ortega-Escobar 2020). Some invertebrates use more sophisticated forms of navigation. Honeybees, for instance, learn the location of food using information communicated by the waggle dance of another bee and use this information to guide their navigation to food patches they have not visited before (Menzel et al. 2006). *Portia* jumping spiders perform feats of navigation in complex environments by planning indirect prey-attack routes that put the prey out of sight of the spider for prolonged intervals (Tarsitano and Jackson 1997; Cross and Jackson 2016; Cross et al. 2020).

Navigation using information stored in memory has for the most part been previously documented in ambulatory animals that possess acute vision, and rely at least partially on visual input for navigation (although *Cupiennius salei* wandering spiders do not seem to need vision when navigating, even though they possess acute vision; Seyfarth et al. 1982; Land and Barth 1992; Webb 2019). However, there is evidence that suggests that even invertebrates that navigate only in a small and well-defined area may also do so using information stored in memory. Web spiders, for example, are sit-and-wait predators with poor vision that locate prey through cues provided by web vibrations caused by the prey (Landolfa and Barth 1996; Clemente et al. 2005; Foelix 2011; Eberhard 2020). These spiders might therefore be expected to primarily follow web cues and require little in the way of information stored in memory to navigate. Nevertheless, there is evidence that web spiders form memories of the position or direction of their retreat on the web (LeGuelte 1969); of distances between web components (Eberhard 1988; Eberhard & Hesselberg 2012); and of the content of their webs (e.g., captured prey and egg sacs) (Rodríguez et al. 2015). Whether and how web spiders navigate using information stored in memory remains to be explored.

Here, we ask whether a web spider navigates its web using information stored in memory, and whether it does so by representing its location relative to its retreat as a path integration vector. We worked with western black widow spiders (*Latrodectus hesperus*). These spiders make webs with distinct components that serve prey-capture, structural, and defensive functions: a tangle of lines and a sheet from which descend a forest of gum-footed lines anchored to the substrate, and a retreat (Blackledge and Zevenbergen 2007) (Fig. 1). Here, we focus on how the spiders navigate on the sheet plane. Specifically, we analyze how they return to their retreat when they are out on the sheet.

We first tested the broad hypothesis that black widows navigate using information stored in memory. We tested two predictions of this hypothesis. First, the spiders should make navigational errors when returning to the retreat after the web has been rotated in their absence so that there is a mismatch between their memory of their position on the web relative to the retreat and their actual position relative to the retreat. The second prediction arises from a detail of the behavior of web spiders. When their memory-based expectation about a feature of the web does not match the actual web (e.g., when its contents are removed in their absence), they engage in prolonged searching behavior, moving around the web, plucking, or tugging on its lines in an attempt to reacquire the lost item or re-orient themselves on the web (LeGuelte 1969; Rodríguez and Gamboa 2000; Rodríguez and Gloudeman 2011; Rodríguez et al. 2013; Rodríguez et al. 2015; Kilmer et al. 2018). This first hypothesis therefore makes the prediction that spiders that have made navigational errors should evince having an expectation of finding the retreat where they went to by engaging in sustained localized searching at or near the site where they would expect the retreat to be but do not find it (as opposed to immediate exploration to seek cues indicating the position of the retreat, which would of course occur eventually when spiders have become lost).

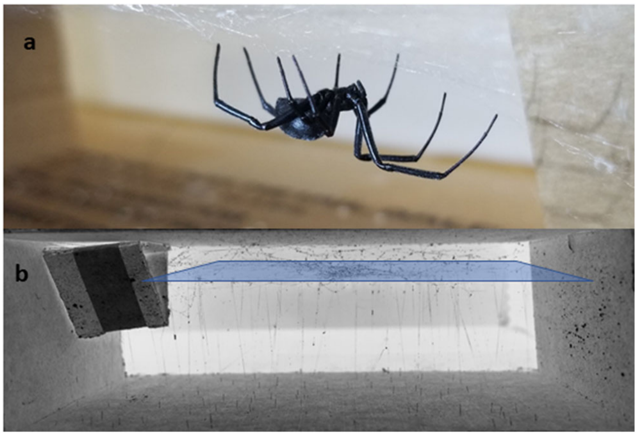

Fig. 1 Black widow spider and representative web with a sheet and vertical gum-footed lines. Black widow spiders construct space-filling cobwebs (Benjamin and Zschokke 2003). **a** A female black widow spider in a typical posture on the sheet of her web. **b** Negative image of a black widow web constructed in a cardboard frame. The spiders use the triangular prism we provide (left) as a retreat. The sheet extends from the retreat to the far side of the frame. The bottom of the sheet forms a two-dimensional plane (blue rectangle inset in **b**). Spiders do most of their navigation along this plane, and all of the navigation we describe in our experiments occurred on the plane formed by the web sheet. The gum-footed lines are the primary prey-capture structures of black widow webs

Having found support for this hypothesis (see below), we then tested the hypothesis that the information that black widow spiders store in memory takes the form of a path integration vector (path integration hypothesis). We tested three predictions of this hypothesis. First, spiders should be able to navigate their web without retracing their steps (e.g., they should be able to take shortcuts). Second, spiders lured away from the retreat and then prompted to return should be able to head broadly in the direction of the retreat predicted by a path integration vector created on their path out from the retreat without first searching, and search upon reaching the expected location of the retreat without finding it. We did not expect spiders to head exactly in the direction of the retreat as predicted by a path integration vector, because path integration is prone to error accumulation (Collett 1996; Pavel and Cronin 2020). We expected spiders to search in a sustained localized manner upon reaching the area they expect to find the retreat (Wehner and Srinivasan 1981; Durier and Rivault 1999; Pavel and Cronin 2020). Third, spiders lured away from the retreat and then displaced to a new location on the web before being prompted to return to the retreat should follow a path that approximates a path integration vector extending from the location they were lured to the retreat. Thus, after being lured to an initial location and then moved to a new location, spiders should follow a path that is parallel to the path integration vector, but displaced by the distance between the initial and new locations.

Methods

We collected sub-adult and adult female *L. hesperus* from urban areas of Medford, Oregon in June 2017 and June 2018 and shipped them to our lab at UWM. Once the spiders were in the laboratory, we housed them individually in plastic cups and provided them with two 1.5-cm-long crickets. During periods of normal husbandry, we provided each spider with one cricket every 2 weeks. When spiders were going to be used in an experiment, we fed them 10 and 3 days before experiments began to standardize satiety. We preserved voucher specimens in 95% ethanol.

In all experiments, we attempted to reduce the potential for spiders to use external cues when navigating by forcing spiders to build webs in plain cardboard frames or plastic boxes in which their sheet formed a flat plane and to build retreats within triangular prisms that we affixed to the rigid wall of the frame or box (Fig. 1). This removed the possibility of spiders using up/down cues to find their retreat and reduced the possibility that the cardboard of the retreat would contrast against the wall of the enclosure enough to be visible given web-building spiders' poor eyesight (Clemente et al. 2005).

Do black widow spiders make navigational errors when their web has been rotated in their absence? If so, do spiders engage in sustained localized searching in the area where they expect to find their retreat?

We used an assay similar to that used by LeGuelte (1969): we briefly removed spiders from their webs and rotated the frame that housed the web while the spiders were removed, so that in our treatment group (below), the location of the retreat relative to the spider had changed by 180° (i.e., if the spiders were removed with the retreat to their left, the retreat would be to their right when placed back on the web). We constructed cardboard frames modeled after those used by Blackledge and Zevenbergen (2007) (Fig. 1b). These frames measured 25 cm long × 7.5 cm tall × 15 cm wide and were open on the two long sides. The frames contained a 5 × 5 × 5 cm triangular prism that we attached with tape to the top center of one short side in which spiders constructed their retreat, and ensured that the retreats of all spiders were in the same relative location within the frame and on the same horizontal plane as the web sheet. Over 2 weeks, spiders constructed webs that spanned the entirety of each frame (Fig. 1b).

To begin a trial, we lured each spider to the edge of the sheet, halfway between the retreat and the far side of the frame, by vibrating a forceps on the sheet to imitate trapped prey. When spiders approached the forceps and turned around (facing the middle of the web) to begin flicking silk, we briefly removed the spider off the web using a plastic vial and severed the spider's dragline so the spider was no longer attached to the web. We alternated which edge we lured spiders to so we had equal numbers of spiders that we lured to the edge to the right and to the left of their retreat. In the experimental treatment, we then rotated the frame 180° and then replaced the spider on the edge of its web sheet facing the middle of the web (as much as possible, we matched the direction spiders were facing relative to the sheet when we removed and replaced them), so the retreat was on the opposite side of the frame relative to where the spider had been removed from (n = 28). In two control groups, we removed the spider as above but then either did not rotate the frame (n = 11) or rotated it 360° (n = 9).

Immediately after replacing each spider on the web, we administered a puff of air by squeezing the bulb of an aspirator to prompt them to return to the retreat. In the 0° and 360° rotation treatments, we were able to place the spiders approximately on the same spot from which we had removed them. In the 180° rotation treatment, we were not able to do this, as removing and replacing spiders from the edge of the sheet meant that in the 180° rotation, we replaced spiders on the opposite edge of the sheet from where we removed them. The gum-footed lines of each web prevented us from removing/replacing spiders at the center of the sheet (perhaps the ideal) without damaging the web and introducing potential sensory cues. We placed these spiders at approximately the same distance as the retreat from which we removed them. This difference in the site of replacement of the spiders on the web may have introduced a confound into this experiment, whereby spiders in the 0° and 360° controls may have been more likely to be placed near their (now severed) draglines than spiders in the 180° treatment. However, the spiders in the 0° and 360° controls would have needed to search briefly to locate those draglines (or other cues); we therefore checked whether they did so or started moving to the retreat right away.

After replacing the spiders on the web and puffing them with the aspirator, we noted the direction in which the spider moved. We also noted whether spiders searched before initiating their return and after reaching either the retreat or another end of the cardboard frame where there was no retreat. In this experiment, our view of the spiders was from the side and allowed for us to record whether a spider moved toward or away from the retreat when attempting to return to it. All spiders that moved when puffed moved toward or away from the retreat (i.e., no spiders moved directly across the web to the opposite edge of the sheet). Thus, all data for this experiment are binary measurements taken from real-time observations of spider behavior.

We excluded spiders that did not move when puffed (*n* = 4); these spiders did not move from the area where we replaced them on the web and instead adopted a "crouch" posture in which all legs were drawn close to the body and the body pressed tightly against the web sheet.

We used logistic regression to test for differences in the likelihood of moving toward or away from the retreat between the 0°, 360°, and 180° rotation treatments. We also used logistic regression to test for differences in likelihood of searching between spiders that moved toward the expected or toward the actual retreat location in the 180° rotation treatment.

Do black widow spiders use path integration?

To test the first prediction of the path integration hypothesis (that black widows can use shortcuts to return to the retreat), we placed spiders in plastic boxes that were 40 cm long by 33 cm wide by 17 cm tall. The boxes contained a 2.5 × 2.5 × 2.5-cm hollow cardboard triangular "prism" approximately 5 cm from the top of the box in the center of the long side, which the spiders used as a retreat. We gave the spiders 2 weeks to construct a web.

To begin a trial, we lured spiders from their retreat using rubber-tipped forceps that we vibrated on the web at the edge of the sheet furthest from the retreat to simulate prey. We attempted to lure the spiders out from their retreat in a circuitous path. Once spiders were within approximately 2.5 cm of the forceps and edge of the sheet, we removed the forceps from the web and administered a puff of air by forcefully squeezing the bulb of an aspirator to make spiders move back to their retreat.

We filmed each trial and converted each video into a series of jpeg images captured every 10th frame with DVDVideoSoft (Digital Wave Ltd., UK). We then used ImageJ to stack and focus each image to produce a single image with a visible trace of each spider's movement during each trial (Fig. 2). We used the stacked images to compare the route spiders took from the retreat to the forceps and the return route after being puffed with air.

Although we attempted to lure spiders out from their retreat in a circuitous path, we only succeeded in some cases (*n* = 15); other spiders took straight paths out (*n* = 8) (Fig. 2). We report all results, but the focus of our test was on the spiders that took circuitous routes out from the retreat (spiders that took straight paths out could have been using path integration to return to the retreat, but their return paths would be the same if they followed cues left behind on their path out, making these spiders uninformative regarding path integration).

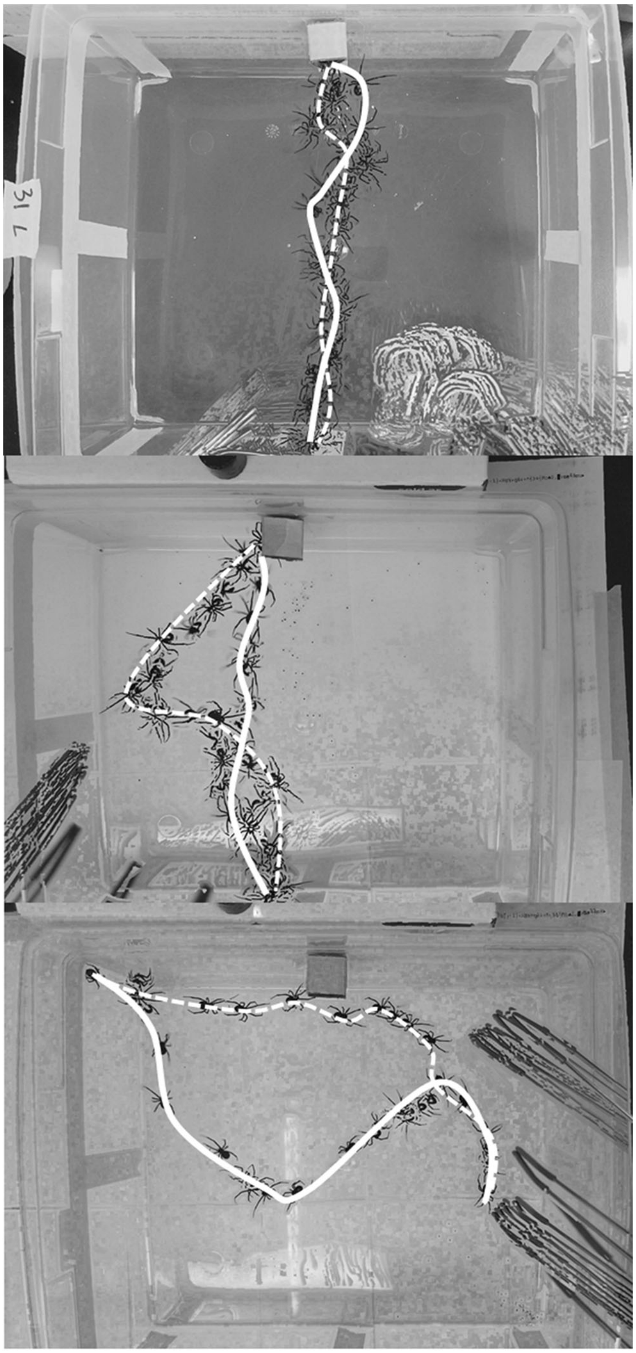

Fig. 2 Examples of paths followed by black widow spiders from and back to the retreat. Paths out from retreat (dashed lines) and back into the retreat (solid lines) of spiders in the first experiment testing the path integration hypothesis. Some spiders retraced their paths when returning to the retreat (top image); some spiders took more direct, shorter paths back into the retreat (middle image); and some spiders took different, but not direct, paths back into the retreat (bottom image)

We used logistic regression to test whether spiders that took circuitous paths out from the retreat were more likely to take a path back to the retreat that did not overlap the path out than spiders that took a straight path out from the retreat. We also used a binomial test to investigate whether spiders that took a circuitous route out from the retreat and did not retrace their paths on the return route were more likely to take a shorter route on the way back to the retreat. We also used a paired t-test to investigate whether the paths back to the retreat of spiders that took circuitous paths away from the retreat were shorter than the paths out.

To test the second prediction of the path integration hypothesis (that black widows should be able to head in the direction of the retreat predicted by a path integration vector created on their path out from the retreat without first searching, and search upon reaching the expected location of the retreat without finding it), we used 40 × 33 × 17-cm plastic boxes as in the experiment above, except we partially coated the interior of the boxes with petroleum jelly so that the spiders could not attach silk to part of the box. This resulted in spiders constructing webs that had sheets that extended approximately two-thirds of the way across the box from the retreat and left the third of the box furthest from the retreat open, allowing us room to conduct the experimental manipulation (below). Spiders constructed full webs in these frames within 1 week.

In each trial in this experiment, we lured spiders to one of the corners of the edge of the sheet furthest from the retreat, then subjected them to one of two treatments or a control before disturbing them by puffing them with air at a rate of approximately one puff per second until they either found the retreat or adopted a crouching posture somewhere on the web. We attempted to puff air at an angle perpendicular to the edge of the sheet. (We tested for correlation between the angle of the first puff and the angle spiders moved immediately after the first puff and found no overall correlation; $r = -0.12$, $p = 0.67$. However, we also checked for individuals that moved perpendicularly to the angle of puffed air; see below.) In the two treatments, we briefly lifted each spider from the web, severed its dragline, and replaced the spider on the edge of the sheet of the web either at the same ($n = 4$) or a different location ($n = 4$) from where we removed it (the latter being directly in front of the retreat and approximately 15 cm from the location we removed spiders from) before puffing them. The sample size in these treatments is small because this manipulation was difficult and we only succeeded in these few cases. In the control group ($n = 18$) where we did not lift the spiders from the web at all, we began to puff them with air as soon as they reached the corner of the web we lured them to. Thus, the data from all individuals in this experiment, whether in a treatment or control group, served to test that the spiders should be able to head in the direction of the retreat predicted by a path integration vector created on their path out from the retreat without first searching, and search upon reaching the expected location of the retreat without finding it (follow a path approximately the same direction and length as the solid arrows in Fig. 3). Furthermore, the spiders in the displacement treatment test whether they follow a path approximately parallel to the one that would bring them to the retreat had they not been displaced.

We video-recorded all trials and converted each video into a series of stacked jpegs captured every 10th frame to allow us to observe the paths spiders took away from and back to the retreat. From these images, we obtained the following data: whether spiders searched before fleeing to the retreat when puffed with air; whether they moved in the direction of the retreat predicted by a path integration vector; whether they searched after arriving at the expected position of the retreat; whether they found the retreat; and whether they ceased searching after finding the retreat. We used two criteria for whether spiders moved in the predicted direction of the retreat. First, we used ImageJ to measure the angles spiders moved on their return path toward the retreat relative to the edge of the sheet, and the angle of the most direct path back to the retreat from where we lured the spiders to, i.e., the angle of the path integration vector, (also relative to the edge of the sheet). We tested for a correlation between these angles. Second, considering that one would not necessarily require the spider to follow *exactly* the same angle back, we also used a more relaxed criterion: whether spiders initially moved in a direction that was within 30° on either side of the direction of the retreat predicted by a path integration vector (i.e., within 30° of solid arrows in Fig. 3) (the actual range of angle differences for these spiders was 1.9 to 23.8°, with an average difference in angle of 11.7°).

Because we were only able to obtain small sample sizes in crucial treatments for this experiment ($n = 4$ spiders lifted from the web and replaced at the same location on the sheet; another $n = 4$ lifted from the web and replaced at a different location), we focused our analysis on qualitative descriptions of the behavior and the correlation between predicted and observed path angles of spiders returning to their retreats.

Data availability

All data generated or analyzed during this study are included in this published article and its supplementary information files.

Results

Black widow spiders make navigational errors when their web has been rotated in their absence (and search locally when they have made such errors)

We briefly removed spiders from their web, rotated their web by 0°, 180°, or 360° around the vertical axis, replaced the

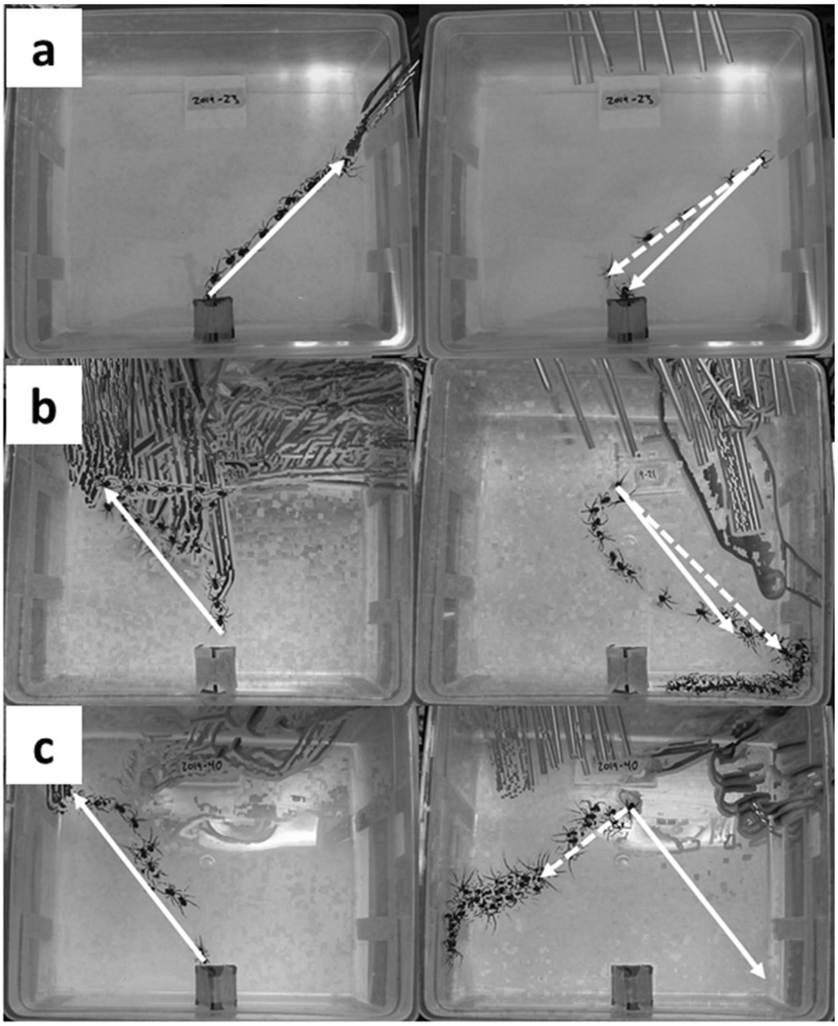

Fig. 3 Examples of predicted and observed paths of black widow spiders in our test of the path integration hypothesis. Paths taken by spiders on their path from the retreat to the lure (left images) and back to the retreat (right images). Solid arrows in left images show the direct path from the retreat to the location spiders were lured. Solid arrows in right images show the predicted path of each spider if they navigated using path integration. The solid arrows in right images are the same length and opposite direction as the solid arrows in left images and are therefore equivalent to a path integration vector for each spider. The dashed arrows in right images show the actual path spiders took from the start of their return path (beginning of arrows) until the location they began to search (head of arrows). **a** An unmoved control spider that followed a path that closely matched the predicted path to return to the retreat. **b** A moved spider that followed a path that closely matched the predicted path to return to the retreat. **c** A moved spider that followed a path that did not closely match the predicted path to return to the retreat

spiders on their web, and prompted them to return to the retreat by puffing them with an aspirator. None of the 48 spiders in this experiment searched before starting to attempt to return to the retreat. Spiders in the 180° rotation treatment were significantly more likely to move toward the original location of the retreat (away from its current location) than spiders in the 0° or 360° rotation treatments ($\chi^2_2 = 11.86$, $p = 0.0027$) (Fig. 4a). Interestingly, no spider moved in any other direction (e.g., orthogonal to the retreat-opposite wall line as would be expected if spiders were merely fleeing directly away from the puffed air). Furthermore, in the 180° rotation treatment, spiders that moved away from the current location of the retreat were significantly more likely to search upon reaching the end of the cardboard frame (where the mental model would have

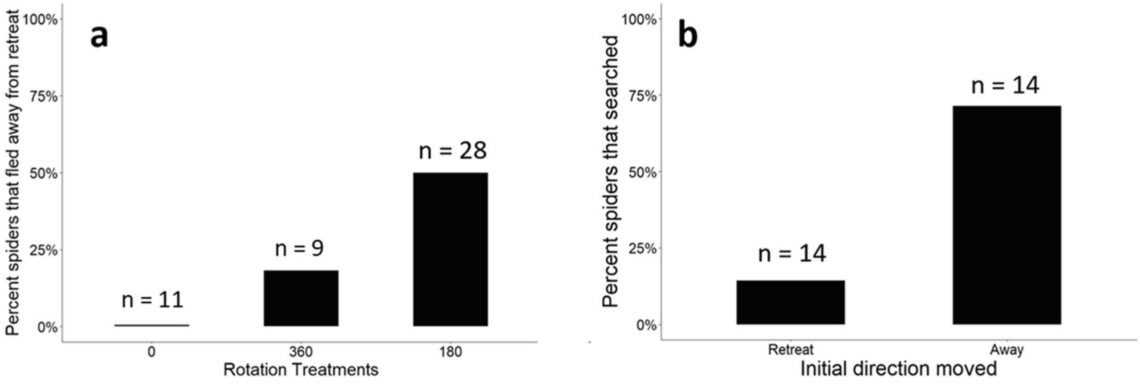

Fig. 4 Test of the ability of black widow spiders to form memories of their web. **a** Percent spiders that fled away from the retreat across box rotation treatments. **b** Percent spiders that searched after fleeing away from or to the retreat (180° rotation treatment)

generated an expectation for the position of the retreat) (χ^2_2 = 10.01, p = 0.0016) (Fig. 4b). No spider~~s~~ searched before reaching the end of the cardboard frame. Spiders that searched after fleeing in the wrong direction initially searched in a localized manner, near where the retreat would have been had they fled the correct direction. These spiders eventually expanded their search area until they found the actual location of the retreat. The few spiders that searched after fleeing in the actual direction of the retreat searched near the retreat before entering the retreat and remaining there.

Black widow spiders take shortcuts

We attempted to lure black widows out from their retreat in a circuitous path by simulating a prey item on their web with a forceps, and then disturbed them with a puff of air from an aspirator to induce them to return to the retreat. We were able to get 15 spiders to take circuitous routes out from the retreat, but 8 spiders took straight routes out (Fig. 2).

Thirteen of 15 spiders that took circuitous routes out took a different path back to the retreat (Fig. 5a, gray lines); the other 2 spiders retraced their steps (Fig. 5a, blue lines). By contrast, only 1 of 8 spiders that took straight routes out took a different (circuitous) path back (Fig. 5b, blue line), all others retracing their steps (Fig. 5b, gray lines) (χ^2_1 = 12.98; p = 0.0003). Spiders that took circuitous routes out from the retreat were significantly more likely to take more direct (shorter) paths back to the retreat (two-tailed binomial test, p-value = 0.035; Fig. 5a). Those return paths were on average 22% shorter than the paths out (paired t-test: t_{14} = 2.26; p = 0.04; Fig. 5a).

Black widow spiders flee in the expected direction of the retreat

We lured spiders away from the retreat, lifted some to a different area of the web, and then puffed them with air. We noted whether the black widows searched immediately after being puffed before attempting to return to the retreat, whether they initially moved in the direction of the retreat predicted by use of a path integration vector, and whether they searched after getting near the predicted location of the retreat (see Fig. 3a–c for examples of spiders that initially did or did not move in the predicted direction of the retreat after we puffed them with air).

None of the 26 spiders in this experiment searched before beginning their return to the retreat. Seventeen of the 18 control spiders initially moved in the direction of the retreat (one-tailed binomial test, p < 0.0001). Nine of those 17 spiders found the retreat immediately without searching; the remaining 8 began to search after reaching the expected location of the retreat and not finding it.

All four spiders that we lifted from the web and replaced in the same spot initially moved in the predicted direction (i.e., within 30° on either side of the direction predicted by a path integration vector). One of those four spiders found the retreat immediately; the remaining three found it after searching. Three of the 4 spiders that we moved to a different location initially moved in the predicted direction. All three of these spiders began to search after reaching the expected location of the retreat. Only 1 of those 3 spiders found the retreat after searching; the other two adopted a crouching posture in the corner of the web. The one spider that was displaced and did not initially move in the predicted direction took a path that was approximately perpendicular (still not toward the retreat)

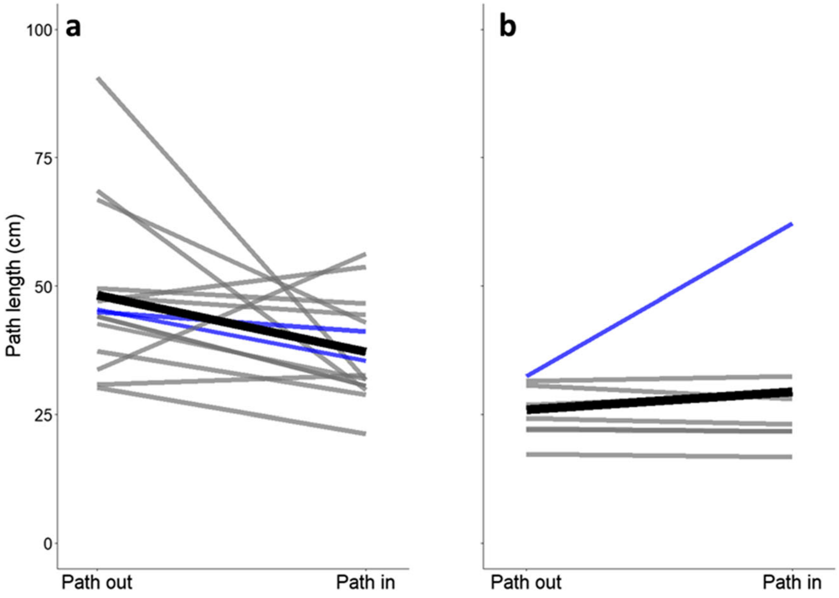

Fig. 5 Test of the ability of black widow spiders to take short cuts. Path lengths of spiders that took circuitous (**a**) or straight (**b**) paths out from the retreat. **a** The paths of spiders that took different paths are shown in gray and the paths that overlapped are shown in blue. **b** The paths of spiders that retraced their paths are shown in gray and the spider that took a longer path back is shown in blue. The black lines show the average path length of spiders in each panel

to the predicted path and adopted a crouching posture in the corner of the web after reaching the edge of the box. Thus, across all treatments, 14 out of 14 spiders that got to the expected position of the retreat without finding it there searched. By contrast, none of the ten spiders that immediately found the retreat searched. The spiders that searched initially did so near the expected location of the retreat (search times ranged from 1 to 89 s, average 19 s) and expanded their search location until they found the retreat (except for the two spiders that did not find the retreat after being displaced, which adopted a crouching posture after expanding their search area).

Across all spiders, the angle of the paths out from the retreat was significantly correlated with the angle of the paths back to the retreat, with a medium effect size ($r = 0.45$, $p = 0.022$, $n = 26$) (Fig. 6). However, two spiders did not seem to be using path integration nor sensory cues to find the retreat. One spider moved perpendicularly to the puffed air (suggesting this may have been due to the angle of puffing); the other moved in a direction orthogonal to the predicted direction of the retreat (suggesting overcompensation for the displacement) (Fig. 6, black and blue asterisks, respectively).

Discussion

We provide evidence that black widow spiders, an invertebrate with a non-ambulatory lifestyle that senses the world mainly through substrate vibrations, use path integration to navigate their webs. The spiders made navigational errors when the contents of their memory did not match the web; searched in a localized way when their expectation of arriving at the retreat was violated; were able to return to the retreat with short cuts, without searching about for cues nor retracing their steps; and when experimentally displaced tended to move in a direction consistent with following a path integration vector, and searched in a localized manner upon reaching the predicted location of the retreat and not finding it.

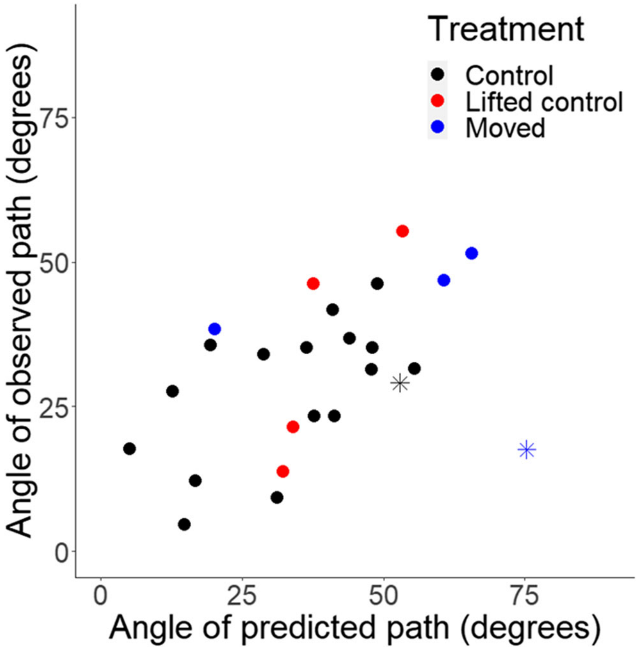

Fig. 6 Correlation between angles of predicted black widow spider paths to the retreat and observed paths to the retreat. Treatment shown by point color

These findings are interesting given the umwelt of black widows (Landolfa and Barth 1996; Clemente et al. 2005; Foelix 2011). It is highly unlikely that black widows use visual information when creating their path integration vectors or navigating to their retreats, because web-building spiders lack acute vision, black widows are active primarily at night, and spiders in our experiments searched in close proximity to the retreat (where tactile searching would be least necessary if the spiders were using visual input to locate the retreat). This offers an interesting contrast with other invertebrates that navigate with path integration, because even among animals that use proprioceptive information (such as the number of steps walked or the direction of the wind) to determine the distance or direction of a goal to navigate toward, visual input is also important for orienting during the trip (Ortega-Escobar 2002; Müller and Wehner 2007; Wehner 2009; Ortega-Escobar and Ruiz 2010).

It is also interesting that black widows use path integration to navigate, because webs likely provide enough structural cues to guide navigation as to make the use of path integration unnecessary (Benjamin and Zschokke 2003). In each of our experiments, we forced spiders to create webs in which the retreat and plane of the sheet were at the same height and the sheet began immediately at the entrance of the retreat. In natural *Latrodectus* webs, spiders construct retreats at a location peripheral to the sheet of the web, and often at a different height than the sheet (Benjamin and Zschokke 2003). The entrances to retreats are small relative to the rest of the web, so this peripheral location results in a funnel-shaped area of web leading from the sheet to the retreat (Benjamin and Zschokke 2003). This web structure could provide black widows with information about whether their location on the web is above or below the entrance to the retreat, as well as a web structure that could guide navigation to the retreat by following the narrowing web to the retreat entrance.

Although spiders navigated using path integration, it is also clear that the spiders used external cues present on the web (as is broadly the case in web spiders; Foelix 2011; Eberhard 2020). In each of our experiments, a number of the spiders initially navigated using only path integration and made the predicted errors in finding their retreat after we had displaced them on the web. However, these spiders eventually began searching the web for the retreat, which suggests that there are sensory cues in the web the spiders are able to follow. This searching behavior after moving to the expected location of the retreat is also a classic feature of navigating by path integration, as path integration is error-prone and animals often must search for a goal location after using path integration to move near the goal (Wehner and Srinivasan 1981; Durier and Rivault 1999; Pavel and Cronin 2020). It is also possible that black widows can choose whether to navigate using path integration or by following cues present on the web, and this could explain the even split in our first experiment of spiders that initially fled toward or away from the retreat.

In our present study, we provide evidence of the use of path integration by black widow spiders. Further investigation of the specific information web spiders use for path integration and how they supplement path integration with direct sensory cues from the web would be fruitful. It is obvious why some invertebrates would need path integration for successful navigation, such as desert ants that navigate between food sources and their nest in environments that may not provide direct sensory cues to guide navigation (Müller and Wehner 1988; Wehner 2009). It is not obvious why web spiders should need path integration, given the availability of direct cues on the web. Thus, our findings indicate that animals differing widely in brain architecture, sensorium, and umwelt share the ability to create and use representations of their position relative to their surroundings in memory. These shared capabilities across vertebrates and invertebrates likely represent convergence, as the last common ancestor of all these groups likely had a simple neural system (Feinberg and Mallatt 2016). These capabilities are therefore likely to be a relatively basic feature that many brain types can express that they evolved as a common solution to the problems presented by navigating a complex world.

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Availability of data All data used to support the conclusions in this article are available as supplemental files associated with this article.

Code availability We used R or JMP for all analyses. We wrote no custom code for this study.

Declarations

Ethics approval This work did not require any ethics approval.

Consent to participate No human subjects were used in this study.

Consent for publication No data from human subjects are used in this study.

Competing interests The authors declare no competing interests.

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