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A test for basic animal consciousness through distraction by inward-directed attention, and a case study with black widow spiders

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Abstract
At the most basic level, an individual has consciousness when it has subjective experience. And subjective experience is generated by the individual constructing a mental model of its environment and its position in it, and perceiving and navigating the world through that internal, brain-generated model. Here we use this rationale to derive a prediction and behavioural assays to test for basic consciousness in animals. Animals that perceive the world through their internal mental model will sometimes be distracted from the current state of their environment due to attention to an object in their mind. We tested this prediction with black widow spiders, and found evidence that they have basic consciousness. Some of the spiders were distracted from cues of a prey item on their web — not by a competing cue on the web — but by inward directed attention, and only eventually switched their attention to the prey. We were unable to manipulate whether the spiders would become distracted by inward directed attention, but we rule out potential confounds due to our experimental manipulations. We discuss how the prediction and assays we showcase may be useful to test for basic consciousness in a broad range of animals.

Keywords
Araneae, invertebrate, sentience, subjective experience, Theridiidae.

1. Introduction

This paper is about the scientific study of animal consciousness. Some think this is not possible. But we regard consciousness as a cognitive phenotype —

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a real trait that is expressed in brains as the product of neural processing (cf. Mendelson et al., 2016). Consider mate preferences. They are mental representations of the relative attractiveness of potential mates, and they are expressed in animal brains as a function of the features of the individuals encountered in mate searching (Ritchie, 1996; Jennions & Petrie, 1997; Andersson & Simmons, 2006; Rodríguez et al., 2013b; Mendelson et al., 2016; Kilmer et al., 2017). We cannot give questionnaires to animals as to humans in psychology research. But we can present them with suites of stimuli, note their behavioural or neurophysiological responses, and describe their subjectively expressed preferences (Rodríguez et al., 2013b; Kilmer et al., 2017). Attention to behaviour and creative experiment design make mate preferences accessible to scientific study, and their subjective and ephemeral nature takes nothing away from their power as causes of evolution (Rodríguez et al., 2013a). So with other cognitive phenotypes (Mendelson et al., 2016), including consciousness.

At the most basic level, an organism has consciousness when it has subjective experience (Harris, 2014; Webb & Graziano, 2015; Barron & Klein, 2016). And subjective experience is generated by an organism constructing a mental model of its environment and its position therein, which it uses (attends to) for navigating and decision-making (Hawkins & Blakeslee, 2004; Webb & Graziano, 2015; Barron & Klein, 2016; Feinberg & Mallatt, 2016). This attention to mental model, this perceiving the world through that internal model, is what generates subjective experience — the basic philosophers' notion of consciousness that there be "something it is like to be" an organism (Nagel, 1974; Hawkins & Blakeslee, 2004; Harris, 2014; Barron & Klein, 2016). In these terms, it is obvious that consciousness cannot be restricted to humans. But how widespread is it among other animals?

There is some agreement that hierarchical bottom-up/top-down feedbacks in neural processing are necessary to generate consciousness in the sense of attention to mental model (Barron & Klein, 2016; Feinberg & Mallatt, 2016; Hawkins, 2021). The extent and form of the hierarchical processing required is not clear, however. Perhaps only the kind of feedbacks that occur between the mammalian cortex and thalamus, and between the avian pallium and thalamus, can generate consciousness (Butler et al., 2005; Edelman et al., 2005; Butler, 2008; Cabanac et al., 2009). If so, consciousness may be restricted to mammals and birds. But there is evidence that a broader range of vertebrates and even invertebrates like arthropods and cephalopods have complex hierarchical feedbacks (Strausfeld, 2011; Barron & Klein, 2016; Feinberg & Mallatt, 2016; Haberkern & Jayaraman, 2016; Chittka & Wilson, 2018; Gazzaniga, 2018). Comparative neuroanatomy suggests that insects and spiders, if not all arthropods, have brain structures that form representations of the animal within its environment, thereby functioning like the structures that create subjective experience in vertebrate brains (Barron & Klein, 2016; Feinberg & Mallatt, 2016; Gazzaniga, 2018). Simulation of human cortical neurons shows that surprisingly few neurons (1000s–10 000s) suffice to create models of objects and make predictions about them (Hawkins & Ahmad, 2016; Hawkins et al., 2017). These numbers are easily met in insect and spider brains, which range from ca. 5000 to nearly a million neurons except in very small species (Babu, 1975; Miklos, 1998; Eberhard & Wcislo, 2012; Menzel, 2012; Quesada-Hidalgo et al., 2021). And there is evidence that arthropods like bees and jumping spiders create internal models of their environment in relation to their bodies that span multiple sensory modalities (e.g., Cross & Jackson, 2017; Solvi et al., 2020; Chittka, 2022; Gibbons et al., 2022).

For animals to create mental models of their environment is not sufficient for consciousness. Animals could store a model in memory and use it to guide behaviour without directing attention internally to it. This would not generate inner subjective experience. It is the inward direction of attention to the model that is both necessary and sufficient to create subjective experience (Hawkins & Blakeslee, 2004; Webb & Graziano, 2015; Barron & Klein, 2016; Feinberg & Mallatt, 2016).

The requirement of inward attention might seem to add difficulty to testing for animal consciousness, but it actually provides the basis for a powerful test. In conscious experience, what is perceived is an internal, mental model, not direct sensory information (Hawkins & Blakeslee, 2004; Edelman et al., 2005; Webb & Graziano, 2015; Hawkins, 2021). Such mental models are often not up to date, and fill in many details from memory and processing heuristics (Hawkins & Blakeslee, 2004; Harris, 2014). Thus, an animal that perceives its brain-generated model may fail to notice obvious sensory cues. Consider being lost in thought — perhaps mulling how to phrase a difficult sentence — and failing to notice a friend call your name. That is distraction due to inward attention. To be distracted by an object in the mind one must attend to that object and experience the attention subjectively (Webb

& Graziano, 2015). Processing without subjective experience could involve distraction by external stimuli. Only subjective experience can produce distraction by inward attention.

The hypothesis of basic consciousness therefore predicts distraction from the current state of the environment due to inward directed attention to (out of date) mental models. This prediction comes with a qualifier of "at least sometimes" that follows from human experience. Although we all navigate by mental model, not all our models are out of date all the time. But most of us have out of date models some of the time. Thus, the prediction is that some individuals in a conscious species should be distracted by attention to an object in their mind some of the time.

The beauty of this prediction is that the content of the model does not matter, as consciousness can arise from inward attention to relatively simple models. The prediction can therefore be applied to a broad range of animals with different natural histories and cognitive abilities. What is required is assays of distraction due to inward directed attention.

We suggest two broadly applicable assays to test for basic consciousness: (i) Animals that are conscious should often fail to detect highly salient cues present in their current environment. This is along the lines of an assay of the subjective experience of pain, whereby animals are distracted by an irritant from noticing salient cues such as of predators (Balcombe, 2016). But note that we predict distraction by attending — not to an external cue — but to an object in the mind. That would reveal the subjective experience of inward attention. (ii) Such animals should eventually update their model with a noticeable outward switch in attention to model the current environment, as we might turn our head and open our eyes wide when we finally notice our name being called.

Here we showcase this test with *Latrodectus hesperus* black widow spiders (Araneae: Theridiidae). In prior work, we showed that these spiders form mental models of the contents of their web and their position in it (Sergi et al., 2021, 2022). The hypothesis that they subjectively experience attention to those models makes the following predictions: (i) (Some) spiders should be distracted (by inward attention) from a salient proximate cue from the web, with no other competing stimulus on the web. (ii) The spiders should eventually switch their attention outward to the salient cue. We also attempted to manipulate the likelihood of such distraction occurring, and tested for potential confounds from the disturbance caused by our experimental manipulations or variation in satiety.

2. Methods

We collected sub-adult and adult female *L. hesperus* black widows from urban areas in Medford, OR, USA in June of 2017 and 2018. We housed spiders individually in plastic deli cups and fed them 1.5-cm-long crickets. We fed each spider 2 crickets on her first day in the lab, then a cricket every 2 weeks. Prior to testing, we fed each spider a cricket 10 days and 3 days before her trial, to standardize satiety. We tested each spider only once. All spiders were adults when we tested them.

2.1. Assay of distraction due to inward directed attention

This test requires distinguishing the predicted distraction from merely “not sensing”. To make this distinction, we took advantage of the fact that web spiders, including black widows, form memories of the layout and content of their web (Eberhard, 1988, 2020; Eberhard & Hesselberg, 2012; Rodríguez et al., 2015; Sergi et al., 2021, 2022). Web spiders also sometimes encounter a mismatch between their memory of the web and the actual web; e.g., if they lose prey they have captured. In such cases, spiders engage in distinctive and prolonged non-directional searching: they walk about the web turning repeatedly in circles or half-circles, tugging on the web to obtain vibrational feedback (LeGuelte, 1969; Rodríguez et al., 2015; Sergi et al., 2021). Video 1 at 10.6084/m9.figshare.28497263 provides an example of this non-directional searching in black widows. Note that this searching is not prompted by any cue on the web (e.g., when a spider is searching for prey it has lost, the prey is no longer on the web; LeGuelte, 1969; Rodríguez et al., 2015; Sergi et al., 2021). Instead, this non-directional searching is prompted by spiders noticing a difference between their memory (of the web) and the web. This is the key for our assay: Should searching spiders in this situation not attack a prey item present on the web, it would not be because they could not sense it, but because they failed to notice it while attending to their memory as they sought sensory feedback from the web. Thus, this prolonged, non-directional searching provides a natural assay of spiders attending to their internal model of the web.

2.2. Assay of switching attention outward

The natural behaviour of web spiders in general, and black widows in particular, also provides a clear assay for an outward switch in attention. When trying to locate prey snared by their web, web spiders turn in the direction of the prey and position their legs to sense prey-generated web vibrations (Nakata, 2010, 2013; Briceño et al., 2011; Foelix, 2011). When black widows direct their attention towards web vibrations they adopt a distinctive "listening posture" with their first pair of legs extended wide (Video 1 at 10.6084/m9.figshare.28497263). This posture provides a natural and highly noticeable assay of switching attention outward to current stimuli on the web.

2.3. Attempting to manipulate distraction due to inward attention

Besides testing for distraction due to inward directed attention, we also attempted to manipulate the likelihood of such distraction occurring. We aimed to create mismatches between the spiders' models of their web and the web they currently occupied.

We placed each spider in a cardboard frame (28 cm long × 14 cm wide × 10 cm high) with a retreat (a 5 × 5 × 5 cm-prism) on the top centre of one of the short sides. We cut a hole in the frame behind the prism retreat, to allow us to remove the spider from the frame without damaging or altering the sheet of her web (see below). The frames were open on top and bottom to allow us unobstructed viewing of the spiders on their web (Fig. 1A; see also Videos 1 and 2 at 10.6084/m9.figshare.28497263). We allowed each spider to build a web in a frame over a week, then moved her to another frame to build another web over another week. To move each spider between her webs, we used the hole behind her retreat: we coaxed the spider to the end of the retreat and scooped her up with a plastic specimen vial.

Half the frames had an open interior, the other half had a 10 × 10 cm cardboard wall that partly divided the frame halfway between the retreat and the far end of the frame (Fig. 1A). We assigned each spider at random to one of four frame sequence combinations: no-wall frames on both weeks; frames with a wall on both weeks; a no-wall frame on week 1 and a frame with a wall on week 2; or a frame with a wall on week 1 and a no-wall frame on week 2.

The spiders built typical black widow cobwebs that spanned the interior of the frames, with a horizontal sheet at the top and vertical sticky gum lines projected downward (Benjamin & Zschokke, 2003; Foelix, 2011; Thompson et al., 2020). In no-wall frames, the space available to spiders to build webs was rectangular viewed from above, while in frames with a wall the space available was roughly "C"-shaped when viewed from above (Fig. 1A).

After a week of building web 2, we implemented the last stage of the "web change" treatments by moving each spider from her web 2 to her web

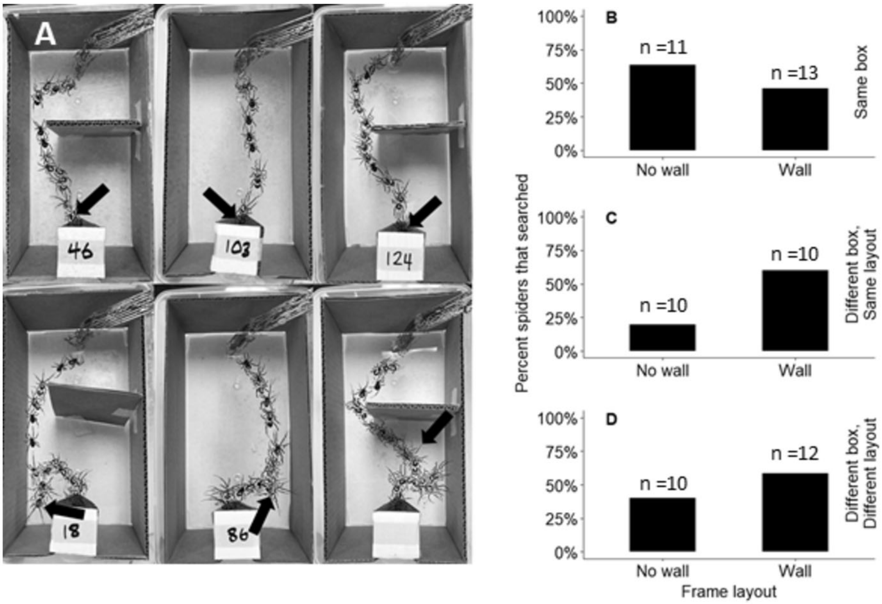

Figure 1. Behaviour of black widow spiders offered a cricket in webs that we expected matched/did not match their mental model of their web. (A) Examples of the non-directional searching/prey-approach behaviour of the spiders. Top row: some spiders immediately attended to and moved to attack the cricket. Bottom row: other spiders first searched before switching their attention to the cricket. Each image shows stacked images of spiders navigating in experiment three. Arrows indicate the individual image in the stack in which the spiders adopted the listening posture, after which all spiders moved toward the cricket. (B–D) Percentage of spiders that searched before approaching the cricket across levels of expected mismatch between their mental model of the web and the actual web. The levels of mismatch were as follows: (B) Spiders tested with no mismatch that were removed and replaced in the same frame, with or without a wall present. (C) Spiders tested with relatively low mismatch that were removed and replaced in a different box with an identical layout. (D) Spiders tested with high mismatch that were removed and replaced in a different box with a different layout.

1, using the hole behind their retreat as above. We aimed to create different levels of perceived mismatch between the web spiders had occupied immediately before testing (their web 2) and the web on which we tested them (their web 1): (i) large difference: different wall/no-wall layouts; (ii) small difference: same layout but different web details due to variation between each spider's webs 1 and 2 (Enders, 1975; Benjamin & Zschokke, 2003; Thompson et al., 2020); (iii) no difference: spiders removed from their retreat and replaced right away in the same retreat, so we tested them in their web 2. Black widows move about and explore their environment as they build webs

(Benjamin & Zschokke, 2003), so their memories of their webs likely allow them the opportunity to notice at least the large differences and perhaps the small ones too. Note that all spiders were moved only between webs that they themselves built. Thus, chemical cue differences, if any, were likely minimal.

Right after placing each spider in the testing web, we vibrated a cricket on the sheet of the web at the far end of the frame, opposite the retreat (the furthest location from the spider) (Videos 1 and 2 at 10.6084/m9.figshare.28497263). We allowed spiders 2 min to leave the retreat. For spiders that left the retreat within the 2 min, we continued to vibrate the cricket until they approached it and began to flick silk at it ($n = 66$ out of 87 trials). We excluded spiders that exited the retreat and either escaped from the box or ceased all behaviour without approaching the cricket (21 out of the 87 trials).

As an unmanipulated control we conducted undisturbed feeding trials of spiders in frames as above, matching hunger levels to experimental groups ($n = 14$). We offered these spiders a cricket by vibrating it on the sheet of their web as above, and noted whether the spiders searched before approaching the cricket.

2.4. Testing whether disturbance alone elicits searching

To assess the effect of the disturbance of our manipulations, we conducted a separate experiment in which we allowed spiders 2 weeks to build webs in no-wall frames. We randomly assigned spiders to one of two disturbance treatments administered by puffing them with an aspirator (we did not contact the web with the aspirator). In the low disturbance treatment ($n = 9$), we started puffing each spider wherever she was on the web, and continued at ca. 1 puff/s until she adopted a “crouch posture” for 3 consecutive puffs. In black widows, the crouch limits sensory input from the web (Mhatre et al., 2018). The spiders adopt it as a response to strong and sustained disturbance, as in this experiment (pers. obs.) At that point, we offered the spider a cricket opposite on the web from where she crouched, and continued to vibrate the cricket on the web until she approached and flicked silk at it or had remained inactive for 2 min. In the high disturbance treatment ($n = 8$), we started as above, but removed the cricket as soon as the spider began to flick silk at it, puffed her again until she adopted the crouch posture for 3 consecutive puffs, then offered her another cricket.

2.5. Testing whether satiety influences the likelihood of searching

We estimated each spider's satiety by the relative size of her abdomen. Spider abdomens are flexible and expand as spiders consume more prey, and abdomen size is correlated with nutritional state (Gunnarsson, 1988). By contrast, spider sternums are inflexible parts of the cephalothorax. We used abdomen width/sternum width ratios to estimate relative satiety. We measured sternum and abdomen width from video stills (Fig. 1A) in ImageJ. For this analysis, we included only spiders for which we could obtain stills that were clear enough to distinguish the edges of the sternum and abdomen and in which the spider was oriented so that her sternum was horizontal ($n = 26$ spiders that searched and 25 that did not search).

2.6. Video analysis

We filmed trials with a Samsung Galaxy 6 camera, and conducted video analyses blind to treatments. We noted whether and how long it took each spider to leave her retreat, whether and how long she searched before approaching the cricket, and whether she showed a switch in attention (adopting the "listening posture") before approaching the cricket.

We used the program ImageJ (National Institute of Health, Bethesda, MD, USA) to stack and focus each image to produce a single image with a visible trace of each spider's movement during each trial. We imported videos to ImageJ as a series of stills and used the Stack Focuser plugin to create a single stacked and focused image that traced each spider's movements along a trial (Fig. 1A shows examples of stacked and focused images). We used the stacked images to describe each spider's movements on the web. To create stacked images, we converted each video to a series of jpeg images captured every 10 frames with the program DVDVideoSoft (Digital Wave, London, UK). We isolated frames from the image series that showed clear views of the spiders on their webs, and used ImageJ to measure the widths of sternums and abdomens. We used the 5 cm × 5 cm retreat visible in each image to set the scale, but note that the accuracy of this scale was unimportant, as our interest was in the ratio abdomen/sternum ratios.

2.7. Statistical analysis

Our main interest was on the qualitative predictions that spiders should be distracted from attending to a cricket on the web; and that they should eventually evidence a switch in attention to the cricket by adopting the listening posture. The more spiders initially distracted that then adopt the listening posture before attacking the cricket, the stronger the support for the hypothesis.

We also assessed our attempt to manipulate the likelihood of inward distraction in the "web mismatch" experiment. We used models with the following explanatory variables: layout change (whether we moved spiders to same/different wall/no-wall layout frames); presence of a wall in the frame; and their interaction. The models and dependent variables were as follows: (i) To test for an effect on the likelihood of searching, we used a logistic regression model with whether spiders searched as the dependent variable (binomial error distribution). In the below tests, we included only spiders that searched: (ii) To test for an effect on the number of times spiders changed direction while searching, we used a logistic regression model with the number of turns as the dependent variable (Poisson error distribution). (iii) To test for an effect on the time spiders searched before switching their attention to the cricket, we used a standard least squares model with searching time (log transformed) as the dependent variable (Gaussian error distribution). (iv) To test for an effect on the distance the spiders moved while searching, we used a standard least squares model with distance moved (log transformed) as the dependent variable (Gaussian error distribution).

To ask whether disturbance alone may prompt searching, we used the data from the "puffing" experiment. We compared the time it took spiders to attack the cricket between treatments with an ANOVA. To ask whether satiety may influence searching, we compared abdomen/sternum ratios between spiders that did and did not search in the "web change" experiment with a Welch ANOVA.

We conducted all statistical analyses using JMP v. 15.2.1. (SAS Institute, Cary, NC, USA) and used the ggplot2 package (Wickham, 2016) in R (R Core Team, 2020) to create figures. We assessed the normality of each response variable in our statistical models below using Shapiro-Wilks tests, and assessed heterogeneity of variance using Levene's tests. We log transformed response variables when appropriate, and if that did not achieve homogeneity of variance we used Welch ANOVAs that allow for heterogeneity of variance.

3. Results

3.1. *Distraction due to inward directed attention, and outward attention switching*

Of the 66 spiders in the web change experiment, 32 searched for 7–161 s (mean = 36 s) before approaching the cricket (Fig. 1A; also see Video 1 at 10.6084/m9.figshare.28497263). The other 34 spiders approached the cricket directly (Fig. 1; also see Video 2 at 10.6084/m9.figshare.28497263). Thus, ca. 50% of spiders delayed attending to the salient cue of a cricket on their web, for up to almost 3 min. Searching spiders moved around the web, waving their first pair of legs in circular movements, and using those legs to tug on the web's lines (Video 1 at 10.6084/m9.figshare.28497263). As they searched, spiders turned repeatedly (1–11 times; mean = 3 turns). These turns seemed to be in random directions, with as much or more movement laterally along the web as toward the cricket. Searching spiders thus repeatedly turned away from the direction of the cricket.

All 32 spiders that searched eventually adopted the listening posture and began to attend to the cricket. This listening posture was distinct from any movement spiders made during searching (Video 1 at 10.6084/m9.figshare.28497263). Spiders then promptly approached and reached the cricket within 1–21 s of adopting the listening posture. Of the 32 spiders, 23 reached the cricket without further searching — with no further turns, except as necessary when a wall was present in the web frame — and started flicking silk at it. The other 9 spiders turned and adopted the listening posture once more before reaching the cricket and flicking silk at it.

In the feeding trials with undisturbed spiders ($n = 14$), no spider searched before attacking the cricket. Thus, black widows did not need to search in order to locate prey we vibrated on the web as in the experimental trials.

3.2. *No manipulation of distraction*

Even though there was variation in whether spiders searched before attending to the cricket, we were unable to manipulate the likelihood of this occurring. The web change experiment did not influence the likelihood of spiders searching before attending to the cricket (Table 1; Fig. 1B–D). Among the spiders that searched, the experiment also did not influence the number of times spiders turned while searching, nor search time or distance covered while searching (Table 1). Not only were these terms not significant, they

Table 1.
Analysis of variation in the searching behaviour of *L. hesperus* black widow spiders in the "web change" experiment that attempted to manipulate their distraction due to inward directed attention.

Model term	Likelihood of searching	Searching behaviour		
		No. of turns	Searching time	Distance covered
Layout change	$\chi_1^2 = 1.14$, $p = 0.56$	$\chi_1^2 = 1.84$, $p = 0.40$	$F_{2,26} = 0.34$, $p = 0.72$	$F_{2,26} = 0.98$, $p = 0.39$
Wall/no wall in frame	$\chi_1^2 = 0.74$, $p = 0.39$	$\chi_1^2 = 1.06$, $p = 0.30$	$F_{1,26} = 3.89$, $p = 0.06$	$F_{1,26} = 0.70$, $p = 0.41$
Interaction	$\chi_1^2 = 3.98$, $p = 0.14$	$\chi_1^2 = 2.26$, $p = 0.32$	$F_{2,26} = 2.80$, $p = 0.08$	$F_{2,26} = 0.55$, $p = 0.58$

were also of small size and unlikely to be biologically meaningful. For example, the mean difference in the likelihood of searching between spiders tested in frames with/without a wall was only 12% (Fig. 1B–D); and the mean difference in their search times was only 6 s.

3.3. Disturbance per se did not prompt searching, nor did satiety influence it

A concern with the web change experiment is that searching might be prompted by the disturbance of moving spiders between webs, rather than indicate distraction by inward directed attention. We tested this in a separate experiment in which we manipulated disturbance with puffing/prey theft treatments. None of the 17 spiders searched. Fifteen approached the cricket directly (7 of 9 in the low disturbance group; all 8 in the high disturbance group). Spiders started to approach the cricket within 0–90 s (mean = 9 s) after it touched the web, and reached it within 3–107 s (mean = 19 s). The 2 spiders that did not approach the cricket adopted a crouch for the duration of the trial. The time from being puffed to getting to the cricket did not differ between treatments ($F_{1,15} = 0.003$; $p = 0.95$). Thus, disturbance per se did not prompt searching. Relative abdomen size did not differ between spiders that searched ($n = 26$) or not ($n = 25$) (Welch ANOVA: $F_{1,24} = 0.71$; $p = 0.40$).

4. Discussion

Animals with basic consciousness construct a mental model of their environment and their position in it, and what they perceive of the world is that internal, brain-generated model, not direct sensory information (Hawkins & Blakeslee, 2004; Harris, 2014; Webb & Graziano, 2015; Barron & Klein, 2016; Feinberg & Mallatt, 2016). Such animals should sometimes be distracted from the current state of their environment due to their internally directed attention. It is therefore possible to test for consciousness in animals by testing for evidence of: distraction from highly salient cues in the current environment due to inward directed attention; and eventual outward direction of attention to update the model of the current environment.

Researchers interested in our assays will need to fit them to the natural history of their study species. Our black widow spiders offer distinctive behaviours that helped implement the assays. When they notice a difference between their mental model of the web and the web, they engage in a unique form of searching — not quick and directed toward prey, but prolonged and non-directional (Sergi et al., 2021). This searching behaviour allowed us to test for distraction from a highly salient cue on the current web (prey, for hungry spiders) due to inward attention. Black widows also provide a clear assay of an outward switch in attention, adopting a distinctive "listening posture".

Using these assays, we find evidence of basic consciousness in black widow spiders: Distracted not by a competing cue on the web, but by inward attention, almost half of the spiders we tested ignored a salient real-time cue of a prey, and instead searched about the web, only eventually switching their attention to the prey. In this context, only distraction by attention to an object in the mind could lead an otherwise highly motivated spider to ignore an obvious prey cue. A key feature of our assay is the combination of behavioural evidence of distraction to an internal model (non-directional searching, rather than targeted searching and approaching the prey) with behavioural evidence of an eventual switch in attention to the external real-time stimulus not noticed initially (adopting the "listening posture"). This combination is key in ruling out alternative possibilities, such as that the spiders were not initially distracted but instead decided to give priority to exploring an unfamiliar web (in which case they would not have needed the switch to the listening posture).

In our hubris, we also attempted to manipulate how likely spiders were to become distracted by inward directed attention. In this we failed. Varying the likely mismatch between internal model of the web and the current web had no effect on whether or how the spiders searched before attacking the prey. But we were able to confirm that searching was not prompted by disturbance (as it also was not in prior work; Sergi et al., 2021). We were also able to establish that variation in whether and how spiders searched was not related to satiety.

In short, we have evidence of subjectively-experienced attention to internal models of spiders' webs, but we do not understand variation in whether spiders are distracted from real-time cues by such inward directed attention. Note, however, that we would also not expect all humans to always be distracted from real-time cues either.

These findings suggest that a broad range of invertebrates may possess basic consciousness, in the sense of forming and subjectively attending to mental models of their body in relation to their surroundings. Some consider that consciousness evolved as a solution to the challenge of processing the vast amounts of input that arise when vision evolves (Feinberg & Mallatt, 2013, 2016). However, web spiders have poor vision, likely since the emergence of their lineage in the Cambrian (Clemente et al., 2005; Strausfeld et al., 2006). Instead, we suggest that consciousness may evolve to solve perceptual and decision-making problems, regardless of sensory modality. Even for animals that do not sense primarily through vision, their umwelts are astonishingly complex, and may select for consciousness.

The last common ancestor of arthropods and vertebrates had a simple neural system that likely did not form models of its body and environment (Feinberg & Mallatt, 2016). Thus, consciousness in these groups likely represents convergence, as may even be the case for mammals and birds (Edelman et al, 2005; Damasio, 2018). Consciousness may thus arise in animals as a common solution to the challenges of adaptive perception and decision-making, making its phylogenetic distribution likely to be more widespread than currently anticipated (Wallace & Wallace, 2009; Barron & Klein, 2016; Feinberg & Mallatt, 2016; Chittka & Wilson, 2019) (but see Strausfeld & Hirth, 2013 for evidence of common descent).

The prediction and assays we showcase here make no assumptions about the content or sophistication of animal mental models. This is advantageous, because the nature and content of conscious experience may vary widely among animals (Birch et al., 2020). We suggest that seeking predictions and assays that can be applied to animals with varying natural histories and cognitive abilities will help broaden the empirical base of behavioural evidence to delineate the distribution of basic consciousness among animals. This will in turn lead to progress in understanding the variety of brain architectures that can generate consciousness (cf. Frégnac, 2017; Krakauer et al., 2017), and the range of life histories that select for it.

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Supplementary material

Video 1. In this clip, the spider emerges from her retreat and searches for several seconds before adopting the listening posture twice, then heading towards the cricket. This clip can be accessed at 10.6084/m9.figshare.28497263.

Video 2. In this clip, the spider emerges from her retreat and immediately heads towards the cricket. This clip can be accessed at 10.6084/m9.figshare.28497263.

Table A1. *Latrodectus hesperus* inward attention data sheets. This table can be accessed at 10.6084/m9.figshare.28497263.