

THE EXECUTION OF PLANNED DETOURS BY SPIDER-EATING PREDATORS

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Many spiders from the salticid subfamily Spartaecinae specialize at preying on other spiders and they adopt complex strategies when targeting these dangerous prey. We tested 15 of these spider-eating spartaecine species for the capacity to plan detours ahead of time. Each trial began with the test subject on top of a tower from which it could view two boxes: one containing prey and the other not containing prey. The distance between the tower and the boxes was too far to reach by leaping and the tower sat on a platform surrounded by water. As the species studied are known to avoid water, the only way they could reach the prey without getting wet was by taking one of two circuitous walkways from the platform: one leading to the prey ('correct') and one not leading to the prey ('incorrect'). After leaving the tower, the test subject could not see the prey and sometimes it had to walk past the incorrect walkway before reaching the correct walkway. Yet all 15 species chose the correct walkway significantly more often than the incorrect walkway. We propose that these findings exemplify genuine cognition based on representation.

*Key words:* cognition, planning, representation, detouring, jumping spiders, Spartaecinae

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Sometimes, we have to wonder what Descartes, the philosopher who was famous for characterizing nonhuman animals as being mindless automatons (Descartes, 1637/1994), would have thought about twenty-first century science (see Wasserman, 2009). Of course, Descartes lived long ago; however, we have seen remarkable shifts in attitude even in our own lifetimes whereby research on animal cognition, including research on spider cognition, has become scientifically respectable. Not so long ago, simply hinting that a spider might be cognitive had a way of sounding ludicrous but we now often feel disconcerted by how blasé scientists can be when they hear and talk about spider cognition. We like the thought that the lowly spider has earned more respect but what we are now seeing is probably more attributable to the way the word 'cognition' has evolved to include more than what had been the case in the past, sometimes seeming to include anything related to information processing.

Yet, in casual language, 'cognition' still seems to mean 'thinking'. Although 'thinking' might be ill defined, we can usually count on the general public and scientists alike being exceptionally interested whenever nonhuman animals show capacities that resemble prevailing intuitions about the meaning of 'thinking'. This includes a wide interest in research on animals making plans (Shettleworth, 2010) and yet we realize that much of this research

goes beyond anything we would ascribe to a spider.

For example, our research is not concerned with spiders planning for a future time when their motivational state will be different from their present motivational state (Bourjade, Thierry, Call & Dufour, 2012; Raby, Alexis, Dickinson & Clayton, 2007). We are not proposing that spiders “plan for breakfast” (Janmaat, Polansky, Ban & Boesch, 2014; Shettleworth, 2007; Sulikowski & Burke, 2015). Nor are we proposing that spiders, like people and perhaps some other animals, engage in elaborate “time travel” based on having episodic projections into the future, along with having a sense of self situated in the past and in the future (Osman, 2014; Raby & Clayton, 2009; Suddendorf & Corballis, 2010). Nonetheless, spiders sometimes behave in a way that makes at least a rudimentary capacity for planning difficult to deny.

Geffner (2013) proposed that there are three basic ways by which an individual might make plans, with these ways being aligned with Dennett’s (1995, 1996) distinctions between Darwinian, Skinnerian, and Popperian animals (also see Raby & Clayton, 2009). A Darwinian animal relies on what Geffner called a “hard-wired approach”, with the animal’s “innate” or “instinctive” (Lorenz, 1965) plan being derived by natural selection, a trial-and-error process acting over evolutionary time (e.g., see Catania, 2010). By practicing trial-and-error in its own lifetime, a Skinnerian animal is more plastic in the adjustments it can make to its environment (Domjan, 2010; Jakob, Skow & Long, 2011). However, Popperian animals are distinctly different because, instead of solving problems by physically acting in the environment in real time, they derive solutions to problems ahead of time by formulating plans and then by acting on them (Dennett, 1996). As Geffner put it, the Popperian animal is “thinking before acting” (p. 341), with “thinking” referring to a model-based approach to choosing actions.

“Model-based” thinking suggests that the Popperian animal relies on *representations* when deriving and acting on plans for solving specific problems. At its most basic, a representation can be thought of as something that stands for something else (Webb, 2012) or, more accurately, something that is used to stand in for something else (Grush, 1997).

Gallistel (1990) emphasized a functional equivalence between internal representations and relevant entities or events in the outside world, with representations serving as theoretical constructs that have a role in cognitive science analogous to the way isomorphism works in mathematics. Both Grush and Gallistel emphasize how, by using representations as a step toward interfacing with the outside world, an individual can predict events as well as anticipate actions that are likely to be beneficial. Relying on representations in this way is implied by saying an animal is Popperian, and we take the stance that Popperian animals cross an unambiguous threshold into the realm of genuine cognition (see Grush, 1997).

Our interest in Popperian animals has come especially from research on *Portia* (Jackson & Cross, 2011), a genus of jumping spiders (Salticidae). Salticids have unique, complex eyes and an exceptional ability for seeing detail in visual objects (Harland, Li & Jackson, 2012; Land & Nilsson, 2012). More than 5,800 salticid species have been described (Maddison, 2015), most of which probably prey primarily on insects captured without the use of webs (Foelix, 2011; Jackson & Pollard, 1996). However, *Portia* has a preference for other spiders as prey (Jackson & Wilcox, 1998); evidence of planning by *Portia* has mainly been in the context of invading other spiders’ webs, where the resident spider is targeted as prey (Jackson & Cross, 2013; Jackson, Pollard, Li & Fijn, 2002; Tarsitano, 2006; Tarsitano & Andrew, 1999; Tarsitano & Jackson, 1992, 1994).

One study in particular has been designed specifically for determining whether *Portia* plans ahead before taking a detour path to prey. In this study (Tarsitano & Jackson, 1997), the test spiders were *P. fimbriata* from north Queensland in Australia. Each individual began a trial on top of a tower from which it could view two paths made from ramps and poles. One of these paths led to a dish that held a lure made from a prey spider, whereas the other path led to an empty dish. The beginning of each path was a pole that could be reached only by leaving the tower and by walking across a platform, with the design of the apparatus precluding the test spider having any way of reaching the prey other than by going to the pole for the correct path.

In the field, different detour paths tend to be unique to the particular time and place of each encounter with prey (Jackson & Wilcox, 1993). The situation in the laboratory experiments (Tarsitano & Jackson, 1997) was similar because the paths were configured in different ways. Any direct role of associative learning was also ruled out because no individual was ever tested more than once and no individual had any prior experience with the apparatus or with the testing procedure. The design of the experiments also precluded test spiders responding to seeing the prey while executing detours because there were rims on the dishes that prevented the test spider seeing the prey after leaving the tower. Moreover, *P. fimbriata* sometimes had to walk past the wrong pole before reaching the correct pole, and sometimes it had to walk directly away from the prey before it could arrive at the correct pole. Yet, with each different path configuration, *P. fimbriata* chose the correct pole significantly more often than the incorrect one.

It has been proposed that the complexity of *Portia*'s predatory strategy, including expertise at taking planned detours, is related to targeting potential predators as preferred prey (Harland & Jackson, 2004). The impetus for our present research is appreciating that, for testing this hypothesis, it would be better to have evidence from more than one experimental design. Moreover, *Portia* is from the subfamily Spartaeinae and most spartaeines that we know about (Su, Meier, Jackson, Harland & Li, 2007) are araneophagic (i.e., they specialize at preying on spiders), and yet we currently have no understanding of how widespread the capacity to plan detours might be among araneophagic spartaeine salticids.

We endeavoured to investigate the detouring abilities of as many of the known araneophagic spartaeines as would be feasible, but we found that other species were not as cooperative as *P. fimbriata* had been when we used the earlier methods (Tarsitano & Jackson, 1997). However, all of the spartaeines that we used here are known to avoid contacting water (Cross & Jackson, 2015), so we designed new methods that exploited this aversion to water. At the same time, our doing so gave us an opportunity to determine whether the earlier findings for *P. fimbriata* could be replicated by using the new experimental design.

We also wanted to address the question of whether the spiders' behavior in these experiments represents at least rudimentary evidence of genuine cognition. To be more precise, we will follow Grush (1997) by referring to 'genuine cognition' as 'relying on representation'. The alternative would be reliance solely on presentation, which would mean behavior that can be fully explained by stimulus-response chains.

## Method

### General

Our test spiders were second through fourth generation individuals from laboratory cultures started from specimens collected at field sites in Australia, Kenya, the Philippines, Portugal, Sri Lanka, and Uganda (Table 1). As we adopted the standard rearing, maintenance, and basic testing procedures normally used in our laboratory (Jackson & Cross, 2015), only essential details are provided here.

Starting when they dispersed from their egg sacs, all spiders were housed one per cage and kept isolated from other salticids. Each test spider was either an adult female or a juvenile. Our rationale for not using adult males was a prevalent trend in salticids of adult males being less responsive to prey than juveniles and adult females (Jackson & Pollard, 1996). Each adult-female test spider reached maturity 5 to 10 days before being used in an experiment and none of these females had mated. Each juvenile test spider had last moulted at least 5 days beforehand and did not moult again during the 5 days following use in an experiment. The size of all test spiders was standardized (body length 4 to 5 mm, accurate to the nearest 0.5 mm).

The prey we used in experiments were juveniles (body length 2 to 3 mm, accurate to the nearest 0.5 mm) of *Oecobius amboseli*, a spider species found in Africa. However, there are *Oecobius* species in the environments of all the spartaeines that we used. All of these spartaeines readily accept *Oecobius* as prey and all *Oecobius* species are similar in size and general appearance. For our experiments, we presented test spiders with clusters of four prey, as *O. amboseli* in the field are often found in aggregations (Glatz, 1967; Jackson, Pollard & Salm, 2008).

Table 1

Spartaeine-salticid species that were used in detouring experiments. Locality: site from which spiders used for culturing in the laboratory originated (see References for details)

Test spider species	Locality	Reference
<i>Brettus adonis</i>	Sri Lanka (Kandy)	Jackson & Hallas (1986b)
<i>Brettus albolimbatus*</i>	Sri Lanka (Kandy)	Jackson & Hallas (1986b)
<i>Cocalus gibbosus</i>	Australia (Cairns, Queensland)	Jackson (1990a)
<i>Cyrba algerina</i>	Portugal (Sintra)	Jackson (1990c)
<i>Cyrba ocellata</i>	Kenya (Mbita Point)	Jackson (1990c)
<i>Cyrba simoni</i>	Kenya (Kisumu)	Jackson (1990c)
<i>Gelotia lanka</i>	Sri Lanka (Galle)	Jackson (1990b)
<i>Meleon solitaria</i>	Uganda (Entebbe)	Unpubl.
<i>Neobrettus nangalisagus</i>	Philippines (Luzon)	Su et al. (2007)
<i>Portia africana</i>	Kenya (Mbita Point)	Jackson & Hallas (1986a)
<i>Portia albimana</i>	Sri Lanka (Kandy)	Jackson & Hallas (1986a)
<i>Portia fimbriata</i>	Australia (Queensland)	Jackson & Hallas (1986a)
<i>Portia labiata</i>	Sri Lanka (Kandy)	Jackson & Hallas (1986a)
<i>Portia cf. occidentalis**</i>	Philippines (Luzon)	Li, Jackson & Barrion (1997)
<i>Portia schultzi</i>	Kenya (Malindi)	Jackson & Hallas (1986a)

\* Previously *Brettus cingulatus*

\*\* Previously *Portia labiata*

We standardized the prey stimulus by using lures (dead spiders mounted in lifelike posture) instead of using living prey (see Jackson & Cross, 2015). Test spiders had no prior experience with the apparatus we used in our experiments nor did they have any prior contact with living or dead *Oecobius* individuals or any other spiders from the family Oecobiidae. The maintenance diet we used for test spiders were juveniles of *Argyrodes* (Theridiidae), *Leucauge* (Tetragnathidae), *Nephilengys* (Nephilidae), and *Pardosa* (Lycosidae), these being spiders that do not, to human observers, bear especially close resemblance to *Oecobius*. *Oecobius*'s abdomen is roughly circular in shape, its body is dorso-ventrally flattened, and its legs extend crab-like out from its body; its forelegs curve backward and there is a long, distinctive anal tubercle at the posterior end of its abdomen (Millot, 1931). However, maintenance-diet spiders had abdomens that were conspicuously longer than wide, their bodies were more elevated in the vertical plane, their legs were held in closer to the body, their forelegs did not curve backward, and they had no anal tubercles.

## Apparatus

We use upper case for the component parts of the apparatus and, except where stated otherwise, all of the components were made from

2-mm thick glass that was opaque and nonreflective (see Cross & Jackson, 2015). The apparatus (Fig. 1) included a Pan filled with distilled water to a depth of 18 mm, a Platform glued to the floor of the Pan, two Boxes used for displaying Scenes on Holders, a Tower and two Walkways that began from different positions on the Platform.

A trial began with a test spider on top of the Tower, where it could view the Scene inside each Box and the Walkway that led to each Box. The beginnings of the Walkways were positioned such that, to reach them, the test spider first had to walk down from the Tower and then move across the Platform almost directly away from the Boxes. After reaching the beginning of one of the Walkways, the test spider could then start walking toward a Box. The spartaeines we used avoided going into the Pan because they were averse to getting wet (Cross & Jackson, 2015), and the only way they could reach the prey without getting wet was by using a Walkway instead of going into the water-filled Pan.

There was a Window in each Box. At the beginning of each trial, prey lures were visible on a Holder in one Box's Window and control stimuli (dead leaves) were visible on the Holder in the other Box's Window. However, after leaving the Tower, the test spider could no longer see the prey lures or control stimuli because we removed them from the apparatus.

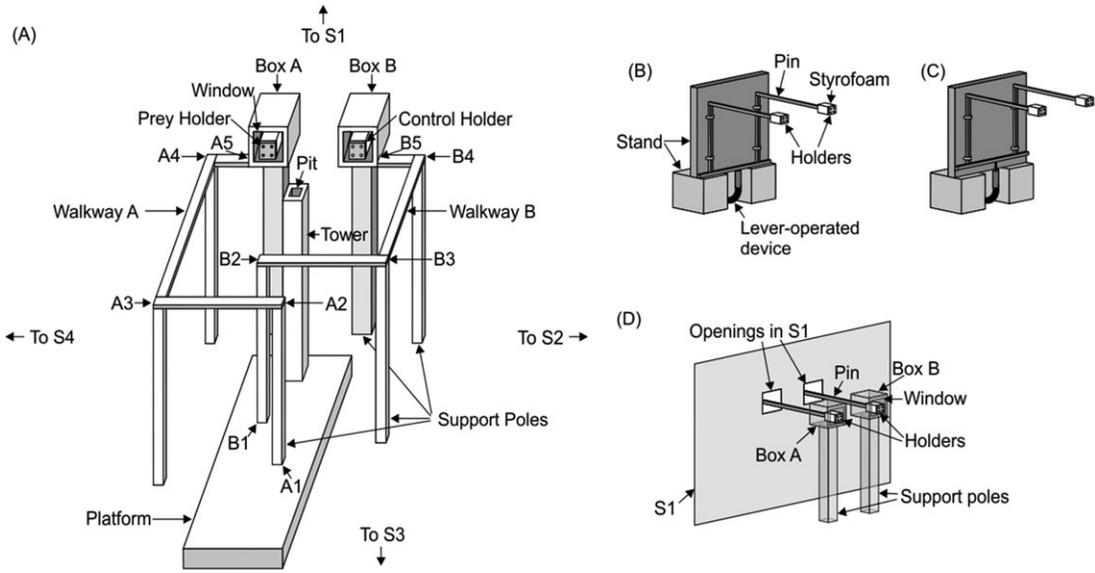


Fig. 1. Apparatus used in detour-choice experiments. Not drawn to scale. (A) Pan (filled with water) and Walls (S1, S2, S3, S4) not shown. Beginning of trial: Lid (not shown) covering Pit was removed and test spider walked out of Pit and on to top of Tower. Two Boxes (Box A and Box B) positioned on Support Poles above water. Prey Holder (with four lures made from *Oecobius amboseli*) in one Box and Control Holder (with four green-leaf pieces) in other Box. Box with Prey Holder determined at random. After test spider leaves top of Tower, Holders moved out of Boxes and hidden behind S1. To complete successful trial, test spider chooses A1 or B1 after leaving Tower and walking across Platform. To reach Box A or Box B, test spider walks along Walkway A or Walkway B until reaching Intersection A5 or Intersection B5, respectively. Walkways held above water by Support Poles. Test spider could opt out of taking detour by walking across Platform to reach S3. (B) and (C) Stand for supporting Pins and Holders positioned behind S1. Button (not shown) pressed on lever-operated device to move Holders up (7 mm) and down (7 mm) in unison while test spider is on Tower. (B) Pins and Holders in lowered position. (C) Pins and Holders in raised position. (D) Holders positioned inside Box A and Box B (Boxes shown are transparent for view of positioning of Holders). Boxes were open at back. Pins in Styrofoam keep Holders in place. Pins go through openings of S1 to Stand out of view behind S1.

It was important that the prey, in particular, were no longer visible because this eliminated any opportunity for the test spider to respond to the prey while off the Tower, on the Platform, or on a Walkway (i.e., we had the objective of determining whether test spiders would choose the Walkway that provided access to the Box in which the no-longer-visible prey lures had previously been seen).

The Pan was rectangular, with the four side Walls being referenced as S1 to S4 (lengths of Walls: S1 & S3, 420 mm; S2 & S4, 410 mm). The two Boxes were positioned between S1 and the Platform, and each Box was held above the water by a Support Pole that was 20 mm × 20 mm in cross section and 180 mm high (measured from the floor of the Pan). The top of the Support Pole was centered on the bottom of each Box. The Platform was rectangular (230 mm × 100 mm) and it, along

with S3 (the Pan Wall opposite S1), was 20 mm high (2 mm above water level). One of the narrow sides of the Platform was flush with S3. The Pan's other three Walls (S1, S2, and S4) were 300 mm high, and there was a wide expanse of water between the Platform and each of these Walls (180 mm for S1, 160 mm for S2, and 160 mm for S4). The only way a test spider could leave the Platform without entering the water and without taking a Walkway was by going to the end of the Platform that was flush with S3.

The Tower (20 mm × 20 mm in cross section) was centered on the side of the Platform closest to S1, its front edge being 10 mm from the edge of the Platform. The top of the Tower was 180 mm above the Platform, which meant it was 200 mm above the Pan floor. A Pit (10 mm × 10 mm; depth, 10 mm) was centered in the top of the Tower, leaving a

5-mm wide rim. Covering the Pit, there was a removable Lid (a Petri dish, diameter 25 mm). The Lid was removed at the beginning of each trial.

Each Box was a cube (40 mm × 40 mm × 40 mm), with the front and back being parallel to S1. The front edge of each Box was positioned 40 mm from the nearest side of the Platform (i.e., about 50 mm from the nearest side of the Tower). The back of each Box was open and there was a Window (30 × 30 mm) centered in the front wall of each Box, leaving a 5-mm wide rim (the Windowsill). There were two matching openings (each 40 mm × 40 mm) in S1. One was directly behind and aligned with the open back of Box A and the other was directly behind and aligned with the open back of Box B. Owing to the height of the Box Support Pole (180 mm), the centre of the Window in each Box was the same height as the top of the Tower.

When viewed from the Tower, Box A was on the left and Box B was on the right. The distance between the closest sides of the two Boxes was 50 mm. Walkway A connected the Platform to Box A and Walkway B connected the Platform to Box B. When a test spider moved across the Platform from the bottom of the Tower to S3, it encountered the beginning of Walkway B before it encountered the beginning of Walkway A. Box A and the beginning of Walkway B were on the side of the Pan's midline closer to S4. Box B and the beginning of Walkway A were on the other side of the Pan's midline closer to S2 (Fig. 1).

From the Platform, a test spider could climb a Vertical Segment of a Walkway and then reach a Box by walking across three successive Horizontal Segments. Each Vertical Segment was 160 mm tall and 10 mm × 10 mm in cross section. The Horizontal Segments (10 mm wide, 2 mm thick) were ramps of various lengths. For Walkways A and B, we used abbreviations for the four Segments and the five Intersections that joined successive Segments. Intersections A1 and B1 joined the Vertical Segments (A1–A2, B1–B2) to the Platform, whereas Intersections A2 and B2 joined the Vertical Segments to the first of the Horizontal Segments (A2–A3, B2–B3). The next Horizontal Segments were A3–A4 and B3–B4, followed by A4–A5 and B4–B5. The Walkways ended at Intersections A5 and B5, where Segments

A4–A5 and B4–B5 joined the Boxes. Intersection A5 was at Box A's front lower left corner and Intersection B5 was at Box B's front lower right corner.

Segments A2–A3 and B2–B3 were parallel to S1 and S3 of the Pan. Both of these Segments were 130 mm long, both extended 70 mm over the Platform, and both extended 60 mm over the water. Segments A3–A4 (180 mm long) and B3–B4 (130 mm long) were parallel to S2 and S4. Segments A4–A5 and B4–B5 were both 45 mm long and both were parallel to S1 and S3. Support Poles (10 mm × 10 mm in cross section, 180 mm tall) held A3, A4, B3, and B4 above the water in the Pan.

During trials, there was a Holder (16 mm × 16 mm) made from 1-mm thick brown wood positioned in the Window of each Box. There was a Prey Scene (four lures) on one Holder and a Control Scene (four pieces from green leaves; cut to similar size as prey) on the other Holder. The oecobiids used for making the lures for the Prey Scene had been preserved in 80% ethanol, but the green leaves used for the Control Scene were fresh (i.e., they had not been preserved in ethanol). On the day before they were used, the oecobiids were removed from the ethanol and allowed to dry, after which we secured them on the Prey Holder by putting a small drop of sticky gum (Tanglefoot® Pest Barrier) on the underside of each oecobiid's abdomen. This sticky gum was also used for securing the leaf pieces to the Control Holder. Each oecobiid faced the centre of the Prey Holder, with the posterior end of its anal tubercle being 1 to 2 mm from the nearest corner of this Holder. The closest edge of each leaf piece was 2 to 3 mm from the closest corner of the Control Holder. For preservation and for holding the prey spider or leaf piece firmly in place, we sprayed the Holder, along with the prey spiders and leaf pieces, with a transparent plastic adhesive (Crystal Clear Lacquer, Atsco Australia Pty).

When the Holder was positioned in the Window of a Box, its four sides were parallel to the four edges of the Windowsill. The mounted oecobiids and leaf pieces were on the side of the Holders facing the Platform. A block of Styrofoam (16 mm × 16 mm, 20 mm deep) was glued to the back of each Holder and one end of a rigid metal Pin (diameter 3 mm) was inserted in the centre of the Styrofoam block. The other end of the

Pin extended through the open back of the Box and through the matching opening in S1. A Stand behind S1 held each Pin in place. The Stand was connected to a single lever-operated device that was used for making the two Holders move up and down in unison.

### Procedure

We had a number of prerequisites for accepting a trial as successful. Whenever one of these prerequisites was violated, the trial ended and the test spider was not used again. It was replaced by another test spider from our stock culture. However, no more than 20% of the trials for any species were ever unsuccessful.

Before a trial began, the Lid confined the test spider to the Pit at the top of the Tower for 10 to 15 min. By sliding the Stand forward, the front sides of the Holders were positioned 5 mm in front of the Box Windows, with the lower side of each Styrofoam block resting on the Windowsill below. After removing the Lid, a trial began when the test spider spontaneously left the Pit. Our criterion for recording that a test spider had left the Pit was seeing its first pair of legs positioned on the rim of the Tower. Starting when the Lid was removed, we used the lever-operated device to move the two Holders in unison, every 15 s, up 7 mm and then immediately down 7 mm. The Styrofoam on each Holder's rear side hit the Windowsill of the Box at the top and then at the bottom. The time taken for each up-and-down cycle was about 0.5 s.

After removing the Lid, we allowed 10 min for the spider to leave the Pit. Test spiders could move in and out of the Pit any number of times, but one of our criteria for a successful trial was that at least 10 min had to elapse between the test spider leaving the Pit and leaving the top of the Tower. While on top of the Tower, the test spider had to fixate its gaze on both Windows and on each Segment of each Walkway at least once (see Tarsitano & Andrew, 1999). Its gaze also had to be fixated on the Prey Holder for a total of at least 60 s and on the Walkways for a total of at least 240 s.

Test spiders were allowed a maximum of 30 min to leave the top of the Tower. In successful trials, "leaving the top of the Tower"

meant that the test spider walked on to one of the four sides of the Tower and remained off of the top of the Tower for at least 30 s (i.e., if it returned to the top before 30 s had elapsed, then we ignored that it had been off of the top for this time). Once the test spider met the criteria for recording that it was on a side of the Tower, we allowed a maximum of 120 s for it to walk down to the Platform. A trial was unsuccessful if a test spider exceeded this time.

We were certain that the only time a test spider could see the Holders was while it was on top of the Tower because, when it left the top of the Tower, we moved the Holders completely out of the Boxes and through the matching openings in S1. This was achieved by sliding the Stand that held the Pins and Holders in place back and then to the side so that the Holders were taken well away from S1, making them no longer visible to the test spider.

Once on the Platform, the test spider had 15 min to move away from the Tower and choose A1, B1, or S3. By "choose" we mean that the test spider moved all of its legs on to A1, B1, or S3 and then did not return to the Platform for the next 30 s. Whenever a test spider chose S3, the trial was recorded as unsuccessful. Whenever a test spider chose the beginning of A1 or B1, we also recorded its postchoice behavior. It was given 15 min to cross each Segment of Walkway A or B. This meant that the test spider had a maximum of 60 min in which to complete the full journey from A1 to A5 or from B1 to B5.

Another requirement for a successful trial was that the test spider had to approach the beginning of a Walkway (A1 or B1) directly (see Tarsitano & Jackson, 1994). However, we still used the data of test spiders that approached A1 or B1 indirectly, as we were interested in comparing how direct and indirect approaches influenced a test spider's initial choice of Walkway.

We recorded a test spider's approach as *indirect* when, before choosing A1 or B1, it walked farther than 20 mm beyond A1 or B1. This distance was measured along a line parallel to S2 and S4, and refers to the distance from the side of A1 or B1 that was closest to S3. We also recorded a test spider's approach as indirect whenever it went on to A1 or B1 after any instance of having had its gaze

oriented more than 45° away from this Intersection for more than 60 s. These requirements minimized any possibility of the test spider viewing the extent of a Walkway from the Platform to a Box before going on the Walkway.

Our apparatus was designed to ensure that test spiders could not clear any of the critical distances by leaping. These critical distances were from the Tower to any side of the Pan, from the Tower to a Box, from any side of the Pan or the Platform to a Box, from the Platform to S1, S2, or S4, from the Platform to any horizontal Segment, from the Platform to any Support Pole of a Walkway, and from any part of a Walkway to any side of the Pan. We also recorded trials as unsuccessful whenever a test spider leapt from the Tower, regardless of whether it landed in the water in front of the Tower or instead landed on another part of the Tower or on the Platform.

Trials ended and were considered to be unsuccessful whenever a test spider chose S3. Whenever a test spider made a choice by moving on to A1 or B1, we also recorded as additional data how far the test spider advanced along the Walkway (i.e., the data we took from the trials included the choice the spider made plus how far it went on the Walkway after making a choice). Sometimes a test spider reached A5 or B5. However, there were other times when the trial ended sooner because the test spider doubled back, let more than the allowed times elapse, left the Walkway by leaping or dropping off, or moved from the Walkway onto a Support Pole. *Doubling back* meant that a test spider had moved from its current location on a Walkway to a previously-visited Segment and then failed to return to its current location within 30 s. These were all instances of successful trials.

Between successive trials, we cleaned the apparatus with ethanol and distilled water, and we replaced the water in the Pan. The rationale for this cleaning procedure was that many spartaeines respond to chemical stimuli from conspecific individuals and other spiders (Cerveira & Jackson, 2013; Jackson, Clark & Harland, 2002; Nelson, Warui & Jackson, 2012). Having a glass apparatus made it easier to remove potential chemical traces that might otherwise have influenced test-spider behavior and thereby might have confounded conclusions from our experimental findings.

No individual was used more than once as a test spider, and no individual oecobiid and no individual leaf piece was ever used in more than one trial. All testing was initiated between 0900 and 1200 hours (laboratory photoperiod 12 L:12D, lights on at 0700 hours). For standardizing hunger level and for ensuring that test spiders were motivated to respond to living prey, all test spiders were deprived of food for 7 days prior to testing, this being a routine procedure in research on salticids in our laboratory (Jackson & Cross, 2011). After each successful trial, the test spider was given access to a living oecobiid (prey) on the same day at 1500 hours. Any test spider that failed to feed on the prey was excluded from our data analysis. The rationale for this decision was that we were interested in choices made by test spiders specifically in the context of predatory sequences. However, no more than two individuals of any one species ever failed to feed.

### Definitions

With each of the 15 spartaeine species, we assigned the test spiders to one of two groups at random, with the Prey Scene being in Box A for Group A and with the Prey Scene being in Box B for Group B. In successful trials, the test spider chose A1 or it chose B1, and the choice could be correct or incorrect. We recorded a trial outcome as a correct choice when A1 was chosen and the Prey Scene had been in Box A or when B1 was chosen and the Prey Scene had been in Box B. We recorded a trial outcome as an incorrect choice when A1 was chosen and the Prey Scene had been in Box B or when B1 was chosen and the Prey Scene had been in Box A.

Besides recording the choice of A1 or B1 made by the test spider, and whether this choice was correct or not, we also recorded how far the test spider advanced along the chosen Walkway after making a choice. This was recorded as a score based on successive intersections reached on the Walkway. For example, when a test spider arrived at Intersection A1 and then failed to advance to the top (Intersection A2), its score was 1. The maximum score we recorded was 4, because every test spider that reached Intersection A4 or B4 continued on to Intersection A5 or B5, respectively, removing any need to distinguish

between a score of 4 and a score of 5. Arriving at Intersection A5 (score of 4) or Intersection B5 (score of 4) was recorded as completing the journey.

### Data Analysis

First, we focussed on all instances of test spiders choosing A1 or B1. By using chi-square tests of goodness of fit, we determined whether there might be a relationship between the test spider making a correct or incorrect choice of A1 or B1 and whether this choice was made directly (i.e., *successful trial*) or indirectly (i.e., *unsuccessful trial*). Next, using chi-square tests of independence, we considered whether individuals chose A1 or B1 correctly more often than they chose A1 or B1 incorrectly.

Completing the path along a Walkway (score of 4) was not a prerequisite for a successful trial. However, we used chi-square tests of independence for considering whether individuals that chose the correct Walkway completed the journey more often than individuals that chose the incorrect Walkway. We then used a Kruskal-Wallis test for comparing how far individuals from each of the 15 species advanced along the Walkway. We also used a Mann-Whitney *U*-test for comparing how far test spiders advanced along Walkways after making correct choices with how far they advanced after making incorrect choices. For further details about statistical procedures, see Howell (2002).

### Results

The number of test spiders in successful trials that made the correct choice by going directly to the beginning of the Walkway was significantly more than the number of test spiders in unsuccessful trials that made the correct choice by going indirectly to the beginning of the Walkway (pooled data,  $\chi^2$  test of goodness of fit:  $\chi^2 = 161.06$ ,  $p < .001$ ; Fig. 2). The opposite trend was found for test spiders that made incorrect choices: The number of spiders that made the incorrect choice by going indirectly to the beginning of the Walkway was significantly more than the number of test spiders that made the incorrect choice by going directly to the Walkway ( $\chi^2 = 8.00$ ,  $p = .005$ ).

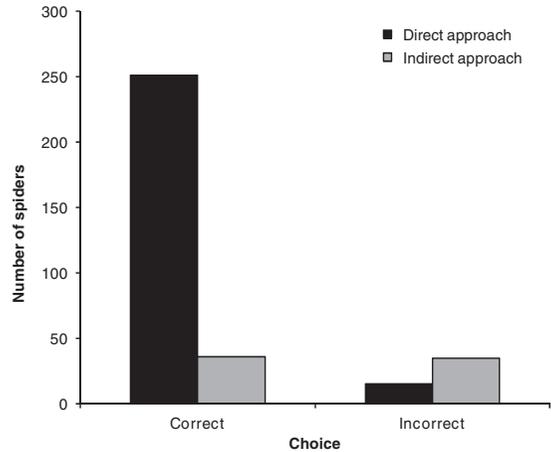


Fig. 2. Total number of test spiders (pooled data) that made a correct or incorrect choice after approaching a Walkway directly or indirectly (see text for definitions).

When considering only those test spiders that went directly to the beginning of the Walkway (i.e., only successful trials), the number that made the correct choice was significantly more than the number that made the incorrect choice (pooled data,  $\chi^2$  test of goodness of fit:  $\chi^2 = 209.38$ ,  $p < .001$ ). However, when considering only those test spiders that went indirectly to the Walkway (i.e., unsuccessful trials), the number that made the correct choice was not significantly different than the number that made the incorrect choice ( $\chi^2 = 0.14$ ,  $p = .906$ ; Fig. 2). As only a few test spiders indirectly approached a Walkway, the remainder of our data analysis is limited to the individuals that directly approached a Walkway.

Next, we considered each species separately and found for each species that the number of test spiders that made the correct choice was significantly more than the number that made the incorrect choice (Table 2). We also found, for each species, that the number of test spiders that completed the journey after making the correct choice (i.e., the number that reached the Box that had held the prey when the test spider was on the Tower) was significantly more than the number that completed the journey after making the incorrect choice (Table 3).

Scores (i.e., how far test spiders advanced along the Walkway) were not significantly different among species when we only considered individuals that made the correct choice

Table 2

For each of the 15 spartaeine species, data analysis ( $\chi^2$  test of independence) for individuals that chose a Walkway. Individuals chose the correct Walkway significantly more often than individuals that chose the incorrect Walkway.

Species	Prey were in Box A		Prey were in Box B		$\chi^2$ value	<i>p</i> value
	Chose Walkway A	Chose Walkway B	Chose Walkway A	Chose Walkway B		
<i>Brettus adonis</i>	8	2	2	7	6.34	.012
<i>Brettus albolimbatus</i>	6	0	1	8	11.43	< .001
<i>Cocalus gibbosus</i>	9	2	0	8	12.44	< .001
<i>Cyrba algerina</i>	5	0	0	7	12.00	< .001
<i>Cyrba ocellata</i>	9	0	1	10	16.36	< .001
<i>Cyrba simoni</i>	7	1	0	7	11.48	< .001
<i>Gelotia lanka</i>	6	0	0	7	13.00	< .001
<i>Meleon solitaria</i>	8	0	0	9	17.00	< .001
<i>Neobrettus nangalisagus</i>	9	1	0	6	12.34	< .001
<i>Portia africana</i>	9	0	1	12	18.28	< .001
<i>Portia albimana</i>	6	0	0	4	10.00	.002
<i>Portia fimbriata</i>	12	0	0	9	21.00	< .001
<i>Portia labiata</i>	10	0	2	13	18.06	< .001
<i>Portia cf occidentalis</i>	10	1	0	12	19.30	< .001
<i>Portia schultzi</i>	8	1	0	8	13.43	< .001

Table 3

For each of the 15 spartaeine species, data analysis ( $\chi^2$  test of independence) for individuals that completed detours. Individuals completed the correct Walkway significantly more often than individuals that completed the incorrect Walkway.

Species	Prey were in Box A		Prey were in Box B		$\chi^2$ value	<i>p</i> value
	Completed Walkway A	Completed Walkway B	Completed Walkway A	Completed Walkway B		
<i>Brettus adonis</i>	6	0	0	5	11.00	< .001
<i>Brettus albolimbatus</i>	7	0	0	4	11.00	< .001
<i>Cocalus gibbosus</i>	5	0	0	5	10.00	.002
<i>Cyrba algerina</i>	4	0	0	2	6.00	.014
<i>Cyrba ocellata</i>	5	0	0	4	9.00	.003
<i>Cyrba simoni</i>	4	0	1	4	5.76	.016
<i>Gelotia lanka</i>	4	0	0	6	10.00	.002
<i>Meleon solitaria</i>	6	0	0	6	12.00	< .001
<i>Neobrettus nangalisagus</i>	4	0	1	6	7.54	.006
<i>Portia africana</i>	10	1	0	6	13.25	< .001
<i>Portia albimana</i>	3	0	0	4	4.80	.029
<i>Portia fimbriata</i>	7	0	0	10	17.00	< .001
<i>Portia labiata</i>	10	1	0	9	16.36	< .001
<i>Portia cf occidentalis</i>	7	0	0	7	14.00	< .001
<i>Portia schultzi</i>	6	0	0	6	12.00	< .001

(Kruskal-Wallis:  $H(14, 250) = 12.812, p = .541$ ; Fig. 3). Sample sizes for individuals that made incorrect choices were too small for making a similar comparison using a Kruskal-Wallis test. However, when we pooled the data for all species, we found that test spiders advanced significantly farther along Walkways after making correct choices than after making incorrect

choices (Mann-Whitney *U* test:  $Z = 3.044, p = .002$ ; Fig. 4).

**Discussion**

We were interested in whether the spiders in our experiments behaved in a way that is “genuinely cognitive” in the same sense as

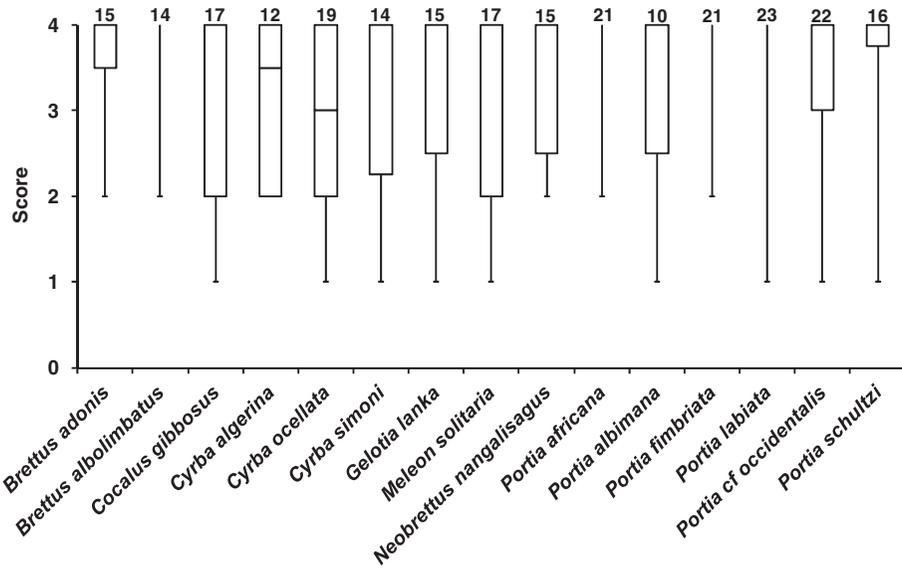


Fig. 3. Score (i.e., how far individuals progressed along Walkway before trial ended) for each species tested. Score (1–4) indicates Intersection reached before trial ended (see Methods for details). For example, score 1: spider reached Intersection A1 when Walkway A was correct or B1 when Walkway B was correct. All spiders that reached Intersection 4 continued to Intersection 5. Boxes show medians plus upper and lower quartiles. Whiskers show minimum and maximum values. For four species, the median and both quartiles is 4. Sample size (number of test spiders that made a correct choice of Walkway) indicated for each species.

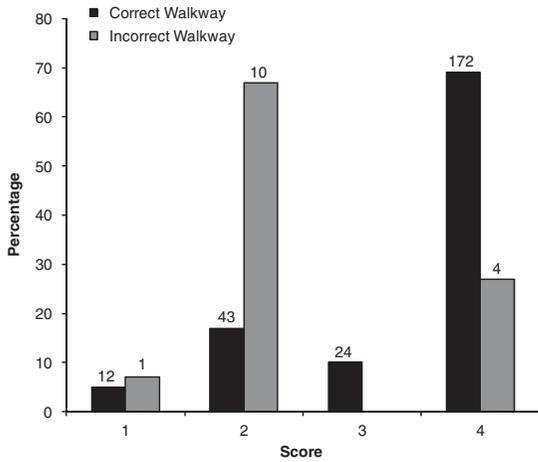


Fig. 4. For all individuals tested (pooled data), progress along Walkway before trial ended. Each spider was given a score (1–4) that corresponded to Intersection reached before trial ended (see Methods for details). For example, Score 1: test spider reached Intersection A1 or B1 before trial ended. All spiders that reached Intersection 4 continued to Intersection 5. Percentages calculated separately for test spiders that chose correct Walkway and individuals that chose incorrect Walkway. Number of test spiders that chose correct Walkway and number of test spiders that chose incorrect Walkway shown above bars.

expressed by Grush (1997). More specifically, we were interested in whether test spiders, after leaving the Tower, used representations that they had derived while on top of the Tower. Another way of saying this is that we were interested in whether our findings have at least a rudimentary correspondence to Geffner’s (2013) thinking-before-acting characterization of planning.

Our experiments began with a test spider on a Tower from where it could see two Walkways, only one of which led to prey situated in a Box. Reaching the location of the prey required an indirect journey of leaving the Tower, walking across a Platform, arriving at the beginning of the correct Walkway, and then following this Walkway to the Box. Going from the Tower to the beginning of the Walkway required moving 180° away from the location of the prey, with the entire journey after leaving the Tower having to be taken with the prey no longer in view. There were many other places the test spiders could have gone after leaving the Tower, including leaving the apparatus altogether and yet individuals usually went to the beginning of the correct

Walkway. Moreover, they succeeded in a single trial, after no prior experience with the apparatus or with the experimental protocol—quite a feat of planning.

We propose that, while on the Tower, the test spider determined by sight which of the two Walkways led to the correct Box and that, after leaving the Tower, it arrived at the beginning of the correct Walkway by relying on a plan it had made while on the Tower. Owing to the findings from the research of Tarsitano and Andrew (1999) on *Portia labiata*, we may be arriving at a precise understanding of how these route-choice plans are made.

Their experiments differed from ours and from earlier experiments using *P. fimbriata* (Tarsitano & Jackson, 1997) by giving test spiders the opportunity to continue seeing the prey while executing detours. However, all of these experiments shared a basic design by which a test spider viewed two paths (walkways) with only one leading to the prey. By analyzing video recordings, Tarsitano and Andrew (1999) documented how *P. labiata* used stepwise whole-body movements (i.e., with intermittent pausing) to shift its gaze systematically along the walkways. In this slow, laborious manner, *P. labiata* spent more and more time repeatedly tracing out the path from the prey to the beginning of the correct walkway and eventually went to the beginning of the walkway where it had spent the most time visually inspecting.

Following Tarsitano and Jackson (1997), Tarsitano and Andrew (1999) used the expression *scanning* for these orienting-and-pausing sequences; however, we now see that this expression was ill-advised in both cases because ‘scanning’ already has a considerably different, well-established meaning in the literature on salticid eyes (Land, 1969). We advise using ‘scanning’ exclusively for a specific type of eye behavior and using *visual inspection* for the whole-body behavior used by *Portia* when viewing alternative paths to prey.

Recent reviews of *Portia* detouring behavior (Barrett, 2011; Wilson & Golonka, 2013) illustrate the importance of making this distinction. For example, Barrett (2014) referred to the “vibrating eyes” of salticids, but “vibrating” is not an appropriate description of the slow, methodical eye behavior that Land (1969) called scanning. More importantly, scanning by the eyes is not what the findings from the

experiments of Tarsitano and Andrew (1999) are about.

Salticids have eight eyes, with a pair of large, forward-facing eyes, called the *principal eyes*, being responsible for the kind of visual discrimination that requires especially good spatial resolution (Blest, O’Carroll & Carter, 1990). Salticid principal eyes are roughly analogous to the foveae in the retinas of human eyes and, like the human fovea, the entire retina in the salticid’s principal eye has a small field of view. Human eyes can move within their sockets, but the corneas of salticid eyes are fixed in place on the carapace. However, the principal-eye retinas are located at the ends of long, slender eye tubes that extend deep into the salticid’s cephalothorax; these eye tubes can rotate and move side-to-side in the intricate movement patterns that Land (1969) called *scanning*. A related hypothesis is that the scanning behavior of these eyes is an integral part of the process by which salticids identify lines as a step toward the perception of visual objects (Land, 1969; Harland et al., 2012).

Salticid-specific ophthalmoscopes are required for identifying specific eye-tube movement patterns; however, using ophthalmoscopes has not been part of the procedure in any of the detouring experiments nor would it have been particularly relevant. The systematic visual-inspection routines identified by Tarsitano and Andrew (1999) are not automatic consequences of scanning, even though scanning optimally may depend on pausing. Moreover, we do not see a convincing case for concluding that this visual-inspection routine fully explains why individuals usually went to the correct walkways. Nevertheless, the data from Tarsitano and Andrew can give us an eerie impression of witnessing a spider planning the choice it will act on after leaving the tower. This impression is analogous to how we can almost see the process of planning from neurophysiological recordings of rats preparing to take a novel route through a maze (Johnson & Redish, 2007).

Although we do not have video detail for the other 14 spartaeine species we investigated here, it is reasonable to suggest that our test spiders used visual-inspection routines similar to *P. labiata*’s. We propose that, while on the Tower, our test spiders traced out the paths from the prey to the beginning of the correct

Walkway; indeed, we may have ensured this possibility by setting, as a criterion for a successful trial, a minimum time that test spiders had to remain on top of the Tower as well as stipulating that each test spider had to fixate its gaze on both Windows and on each Segment of each Walkway at least once.

Proposing that test spiders relied on a plan after leaving the Tower does not require proposing that test spiders memorized every twist and turn in the path leading to the prey. Moving to the correct Walkway and then following the path to the end might suffice. Yet, the variety of detour-related problems confronting salticids in the field must be enormous and probably includes problems that are considerably more complex than the ones we simulated with our experiments.

For example, one of the hypotheses suggested by observations in the field (Jackson & Wilcox, 1993) was that *P. fimbriata* can plan ahead of time to follow a detour path that, owing to obstructions, cannot be seen in its entirety at the time when the plan is being made. In these situations, a salticid might not plan everything ahead of time and instead make a series of navigational decisions as needed *en route* to the prey (e.g., Tarsitano, 2006). *Phidippus*, for example, is a genus of non-spartaeine salticids that often prey on the insects encountered on herbaceous plants; these salticids are exquisitely proficient at compensating, in a three-dimensional environment, for their own movement relative to the prey (Hill, 1979).

We deliberately simplified the test-spider's task in our experiments because our goal was to determine whether test spiders relied on representations after leaving the Tower. The alternative was that test spiders relied solely on what Grush (1997) called *presentations*. In other words, the alternative was a stimulus-response chain in which seeing the prey triggered a visual-search routine that, in turn, triggered going to the correct path. Such a strategy precludes the test spider using representations as part of a plan related to accessing prey. When reviewing the experiments of Tarsitano and Andrew (1999), Barrett's (2011) conclusion appears to be that *Portia* relies solely on presentations.

The prey remained visible in Tarsitano and Andrew's (1999) experiments; however, the prey were hidden from view when the test

spider left the Tower in our experiments, thereby removing any possibility that test spiders were influenced by seeing the prey while they executed detours. Nevertheless, this does not rule out the possibility of stimulus-response chains. It could be argued that test spiders went to the beginning of the correct Walkway simply because their visual-search routines, while on top of the Tower, resulted in spending more time fixating on the correct Walkway instead of fixating on the incorrect Walkway. If this were the case, then it could be argued that it is misleading to propose test spiders planned to reach the beginning of the correct Walkway with a goal of accessing prey.

However, a goal of accessing prey would appear likely from how we offered prey to the test spider after the trial ended. These prey, and the prey seen from the Tower, were of the same type and we had stipulated that trials were recorded as successful only if test spiders later captured and ate these prey. However, there was also an interesting difference between spiders that chose the correct Walkway and spiders that chose the incorrect Walkway, with these observations suggesting more about what the test spider represented during the execution of the detour.

Most spiders that chose the beginning of the correct Walkway continued their journey and reached the Prey Box. However, a few chose the beginning of the incorrect Walkway and, instead of continuing on to the Control Box, they usually ended the trial without advancing further than the first horizontal Segment. These findings cannot be explained as being a consequence of the preys' absence, because the prey were absent regardless of which Walkway was chosen. Yet, these findings do suggest something related to the prey as the goal. We propose that test spiders arriving at the beginning of the incorrect Walkway were expecting to see a path laid out differently. More specifically, we propose that test spiders expected to see a path leading to the Prey Box instead of to the Control Box, despite both Boxes now being empty. We also propose that the Prey Box mattered to the test spider specifically because this had been the location of the prey when seen from the Tower.

For making this hypothesis more precise, we could propose that the test spiders that found themselves on the wrong Walkway expected to

see the Prey Box specifically on the left or on the right side of the Tower, depending on whether the prey had been on the left or the right when seen from the Tower. We could also propose that the test spider compared what it saw from the first horizontal segment of the Walkway with a representation, held in working memory, of what it had seen while on top of the Tower. We could then propose that, when there was a mismatch between the two, the test spider experienced an expectancy violation and became disinclined to continue. There is evidence of expectancy violation from other research on salticid behavior (Cross & Jackson, 2014; also see Cross & Jackson, 2009), which makes proposing expectancy violation in the context of executing detours seem all the more reasonable. Using an expression from Clark and Toribio (1994), we could say that expectancy-violation effects are “representation hungry”.

Our detour experiments join a vast literature on the detouring behavior of animals, but we need to emphasize differences in design and objective. Our objective pertained specifically to questions about planning and representation but these are not the objectives most often considered in the literature on other animals (see Atkinson, 2003; Shearer & Atkinson, 2001). For example, animals taking detours have been incorporated into research on laterality (Baragli, Vitale, Paoletti, Sighieri, & Reddon, 2010; Bisazza, Pignatti, & Valortigara, 1997; Wynne & Leguet, 2004), social learning (Pongrácz et al., 2001; Rørvang, Ahrendt, & Christensen, 2015; Wilkinson, Kuenstner, Mueller, & Huber, 2010), and the way different cognitive traits are correlated (Boogert, Anderson, Peters, Searcy, & Nowicki, 2011) without the question pertaining to representation being emphasized.

It is common in this other detouring research to let the test subject view a target of interest (e.g., food) that cannot be accessed directly because it is behind a see-through barrier (e.g., a glass sheet or a wire fence; Smith & Litchfield, 2010). Typically, the test subject makes repeated unsuccessful attempts to access this target directly and, when it finally succeeds, it is only by moving around the barrier. Seeing this switch in behavior makes it easy to propose that the test subject is suddenly accepting that its efforts to go directly to the target are futile and that it then recognizes

the workable alternative. However, with our experiments, there were no repeated efforts by test subjects to achieve something impossible followed by a switch to doing something that would be successful. For this reason, the suddenness of the switch in behavior seen in experiments on other animals suggests something that is not suggested by our experiments.

The basic design of conventional experiments on animal detouring is often attributed to Köhler (1927); however, Köhler's primary interest was in animals being insightful, not in animals making plans. In more conventional experiments, where the subject views a target behind a see-through barrier, suddenly moving around the barrier can suggest that the subject has an “aha” or “eureka” moment during which it reformulates the problem and finds the solution (Chronicle, MacGregor & Ormerod, 2004; Jones, 2003). The influence of Köhler may make it easy to expect as a general rule that any experiment pertaining to detouring must be somehow designed to test for insight. Perhaps this is why Barrett (2011, 2014) got the impression that Tarsitano and Jackson (1997) had proposed *P. fimbriata* has a eureka moment when it chooses a detour path.

The problem is that, in our experiments, as well as in the earlier experiments of Tarsitano and Jackson (1997), nothing fitting that description was ever seen. In fact, we seriously doubt that *Portia*, or any salticid we have studied, ever has eureka moments, whatever such moments might be, when taking detour paths to prey. Indeed, the slow, meticulous way *P. labiata* laboriously traces out detour paths while choosing a walkway (Tarsitano & Andrew, 1999) is almost the antithesis of a eureka moment.

There is often an assumption that genuine cognition involves something that is complex and difficult, but we are not proposing anything about complexity here. Still, we now know that, whatever the underlying processes might be, they are not unique to the two previously studied species from the salticid genus *Portia*.

We had a specific rationale for choosing the species we used in our experiments, as it has been proposed that expertise at implementing planned detours is related to specializing at preying on other spiders (Jackson & Cross,

2011). Earlier findings from research on *Portia labiata* (Tarsitano, 2006; Tarsitano & Andrew, 1999) and especially *P. fimbriata* (Tarsitano & Jackson, 1997; also see Jackson et al., 2002) were consistent with this hypothesis. We have now gone further by investigating 15 species and, for all of them, found evidence of proficiency at solving a detouring problem. It seems likely that a capacity for planned detouring is unlearned and widespread, if not universal, among araneophagic spartaeines.

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