

Specialised use of working memory by *Portia africana*, a spider-eating salticid

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Abstract Using expectancy–violation methods, we investigated the role of working memory in the predatory strategy of *Portia africana*, a salticid spider from Kenya that preys by preference on other spiders. One of this predator’s tactics is to launch opportunistic leaping attacks on to other spiders in their webs. Focussing on this particular tactic, our experiments began with a test spider on a ramp facing a lure (dead prey spider mounted on a cork disc) that could be reached by leaping. After the test spider faced the lure for 30 s, we blocked the test spider’s view of the lure by lowering an opaque shutter before the spider leapt. When the shutter was raised 90 s later, either the same lure came into view again (control) or a different lure came into view (experimental: different prey type in same orientation or same prey type in different orientation). We recorded attack frequency (number of test spiders that leapt at the lure) and attack latency (time elapsing between shutter being raised and spiders initiating a leap). Attack latencies in control trials were not significantly different from attack latencies in experimental trials, regardless of whether it was prey type or prey orientation that changed in the experimental trials. However, compared with test spiders in the no-change control trials, significantly fewer test spiders leapt when prey type changed. There was no significant effect on attack frequency when prey orientation changed. These findings suggest that this predator represents prey type independently of prey orientation.

Keywords Expectancy–violation · Predatory versatility · Prey classification · Categorisation · Mental rotation · Representation

Introduction

In casual language, ‘cognition’, ‘thinking’ and ‘mind’ are often used interchangeably. Now that the philosophical problem of ‘the mind’ is being rapidly supplanted by scientific questions about various specialised ‘kinds of minds’ (Dennett 1996), there is a growing interest in understanding cognitive specialisation from the perspective of evolution by natural selection (Shettleworth 2010). Representation is often envisaged as a key attribute at the boundary between what does and does not qualify as cognitive (Maunsell 1995; Markman and Dietrich 2000; Burge 2010; but see Epstein 1982). Although it may be tempting to discuss representation in the context of vision, as though there are mental pictures in an animal’s head (Neiworth and Rilling 1987; Kosslyn et al. 2003; but see Pylyshyn 2003a, b), our concept of ‘representation’ needs to be more basic and more easily applied to other sensory modalities. For example, Gallistel (1989, 1990) argued that ‘representation’ refers to a functioning correspondence, or isomorphism, between an animal’s psychological processes and the salient objects and events in the animal’s environment.

Understanding how animals use representation when deploying working memory (Baddeley 2012) is of particular interest, where ‘working memory’ refers to the mechanisms by which priority information is made immediately accessible to other cognitive processes, including selective attention (e.g. Kamil and Bond 2006), object permanence (e.g. Gómez 2005), problem solving (e.g. Collett 1982) and making plans (e.g. Roberts and

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Feeney 2009). Expectancy–violation methods are particularly relevant for ascertaining the role of representation in working memory. In typical expectancy–violation experiments, a test subject observes a scene consisting of an item or a collection of items that disappears behind a screen, and then the individual’s gaze duration (‘looking time’) is recorded after the view of the scene is restored (Shettleworth 2010). During the time when the test subject’s view is blocked, alterations can be made to the scene. After the view is restored, instances of test subjects spending more time gazing at an altered scene than at an unaltered one serves as evidence that the subject has detected a mismatch between the current scene and the representation of the scene that had previously been loaded into working memory.

Expectancy–violation methods have been used in research on pre-verbal infants (e.g. Wynn 1992), non-human primates (e.g. Hauser et al. 1996) and even parrots (e.g. Pepperberg and Kozak 1986). However, as long as the methodological details are tailored to the biology of the particular species being investigated (see Pepperberg 2002; Shettleworth 2010), expectancy–violation methods should be applicable to a wide taxonomic range of animals. Yet, expectancy–violation methods have not featured in the literature on arthropods, despite arthropods being the largest animal phylum. Although there is evidence that working memory has a role in governing arthropod behaviour, this evidence has come primarily from research showing that honey bees and bumble bees can perform delayed matching-to-sample (DMTS) tasks after being trained to choose a scene that they had earlier observed (Giurfa et al. 2001; Brown and Sayde 2013).

Jumping spiders (Salticidae) are only distantly related to bees, and yet they have also been of particular interest in the context of animal cognition (Jakob et al. 2011). Salticids have complex eyes that support exceptional spatial acuity (Harland et al. 2012), spatial vision being the foundation for precise visual object identification (Land and Nilsson 2012). Moreover, some of the previous experimental findings from salticid research pertain specifically to working memory (Jackson and Cross 2011). However, instead of being based on DMTS tasks, findings related to working memory use by salticids have come from experiments pertaining to vision-based and olfaction-based selective attention (Cross and Jackson 2009, 2010a, b) and from experiments where salticids gained access to prey by following pre-planned detour routes during which the target’s location went temporarily out of view (Tarsitano and Jackson 1997; Tarsitano and Andrew 1999). As prior training was not part of the experimental procedure, these findings suggest that innate systems for deploying working memory have a primary role in salticid biology.

Our goal here is to examine the role of working memory in salticid predatory strategies more directly than has been the case in the past. As an important step, we have developed salticid-specific expectancy–violation methods. In particular, these methods were developed for research using *Portia africana*, a salticid known to engage in extensive prey classification. Unlike most salticids, which are often envisaged as preying primarily on insects (Jackson and Pollard 1996), all species studied from the salticid genus *Portia* are known to be ‘araneophagic predators’, meaning that they specialise at preying on other spiders. Besides pertaining to an active preference for spiders as prey, ‘specialising’ also pertains to *Portia* adjusting prey-capture tactics to specific innately identifiable prey spider categories (‘predatory versatility’; see Curio 1976). Our primary hypothesis is that *P. africana* is innately predisposed to load into working memory, in the absence of lengthy prior observation, accurate representations of some of the particular types of spider prey that are common in its natural environment.

Our experiments were based on using four common prey species from *P. africana*’s natural habitat (see Fig. 1). We used *Portia*-specific expectancy–violation methods for examining some of the characteristics of these four prey species that are important to *P. africana* in the context of loading representations of prey type into working memory. Our experiments differed from more conventional research on working memory because we were interested in representations that did not need to be acquired by learning (i.e. ‘innate prey-type representations’). For this reason, there was no training of *P. africana* before use in our experiments and *P. africana* was only given brief exposure to the prey in each trial. Moreover, no individual of *P. africana* used as a test subject had any prior encounters with the prey types we used in our experiments.

In research on vertebrates, expectancy–violation methods have typically taken advantage of the animal’s predisposition to continue looking when an object of interest goes out of view and then to reach out for that object when it later comes back into view (Shettleworth 2010). With our *Portia*-specific methods, we instead relied on an inclination of these salticids to attack their spider prey by making a well-aimed leap from a few body lengths away (Jackson and Pollard 1996). With our methods, we could ascertain whether *P. africana*’s inclination to leap at a prey spider was affected by specific mismatches between initially seen and later seen prey. We propose that the mismatches that matter pertain to prey type but not to prey orientation. The rationale for this hypothesis is that prey individuals may often move and change their orientation when they are out of view. It would, therefore, be advantageous to render into working memory representations of prey type that allow for change in orientation.

Methods

General

All individuals of *Portia africana* used as test spiders were taken from laboratory cultures (2nd and 3rd generations) started from specimens collected in Mbita Point (Kenya), and all prey spiders were collected as needed from the same habitat as *P. africana*. Standard spider laboratory rearing and testing procedures were adopted (e.g. Cross et al. 2008), with each individual that we used as a test spider being reared in isolation from other conspecific individuals. No test spiders or their parents had any prior contact with the prey species that we used in experiments (Fig. 1), nor with our experimental apparatus or our experimental procedures. Moreover, as salticids readily identify and respond to lures (dead prey mounted on a cork disc), we could standardise the stimuli available to *P. africana* during encounters with prey and avoid the possibility of our conclusions being confounded by uncontrolled prey behaviour influencing *P. africana*'s response (see Jackson and Cross 2011). No lure or test spider was used more than once.

The spiders we used as prey when rearing *P. africana* were juveniles of *Achaearanea* (Theridiidae), *Leucauge* (Araneidae) and *Nephilengys* (Nephilidae). This meant that the prey used for rearing and the prey used for making lures were never the same. Feeding took place 3 days per week,

with each *Portia* individual being allowed to feed to satiation. During rearing, roughly equal numbers of each of these prey types were given to *Portia*. The spiders used as maintenance prey did not, to human observers, bear especially close resemblance to the prey spiders we used in experiments. Approximately once per week, this maintenance diet was supplemented by the addition of insects: male mosquitoes (*Anopheles gambiae* s.s.) and both sexes of a non-biting midge species (*Nilodorum brevibuca*). The mosquitoes came from stock cultures, but all other prey were collected locally from the field when needed.

All testing was conducted between 0900 and 1300 h (laboratory photoperiod 12L: 12D, lights on 08:00 h) using adult virgin females of standard body length (9 mm). These females reached maturity 2–4 weeks before being used in experiments. As in earlier studies (e.g. Cross and Jackson 2009), we standardised the hunger level of test spiders by adopting a 7-day pre-trial fast. This fast ensured that test spiders were motivated to feed during the trials.

Expectancy–violation testing

The apparatus (Fig. 2) was a stainless steel ramp (15 mm wide \times 150 mm long) and three white wooden walls (front wall 200 mm long \times 200 mm high, each side wall 250 mm long \times 200 mm high, wood thickness 2 mm). The ramp angled up by 20° so that its higher end was even with the centre of a square window (40 \times 40 mm) that was



Fig. 1 Prey spiders used in expectancy–violation experiments. **a** *Argyrodes* sp. 1 facing left with legs up; **b** *Argyrodes* sp. 1 facing up with legs right; **c** *Argyrodes* sp. 1 facing right with legs down; **d** *Argyrodes* sp. 1 facing down with legs left; **e** *Argyrodes* sp. 1 facing up with legs left; **f** *Argyrodes* sp. 2 facing left with legs up;

g *Pycnacantha tribulis* facing down with legs left; **h** *Arachnura scorpionoides* (brown morph) facing down with legs left; **i** *Arachnura scorpionoides* (yellow morph) facing down with legs left; **j** *Arachnura scorpionoides* (yellow morph) facing up with legs right

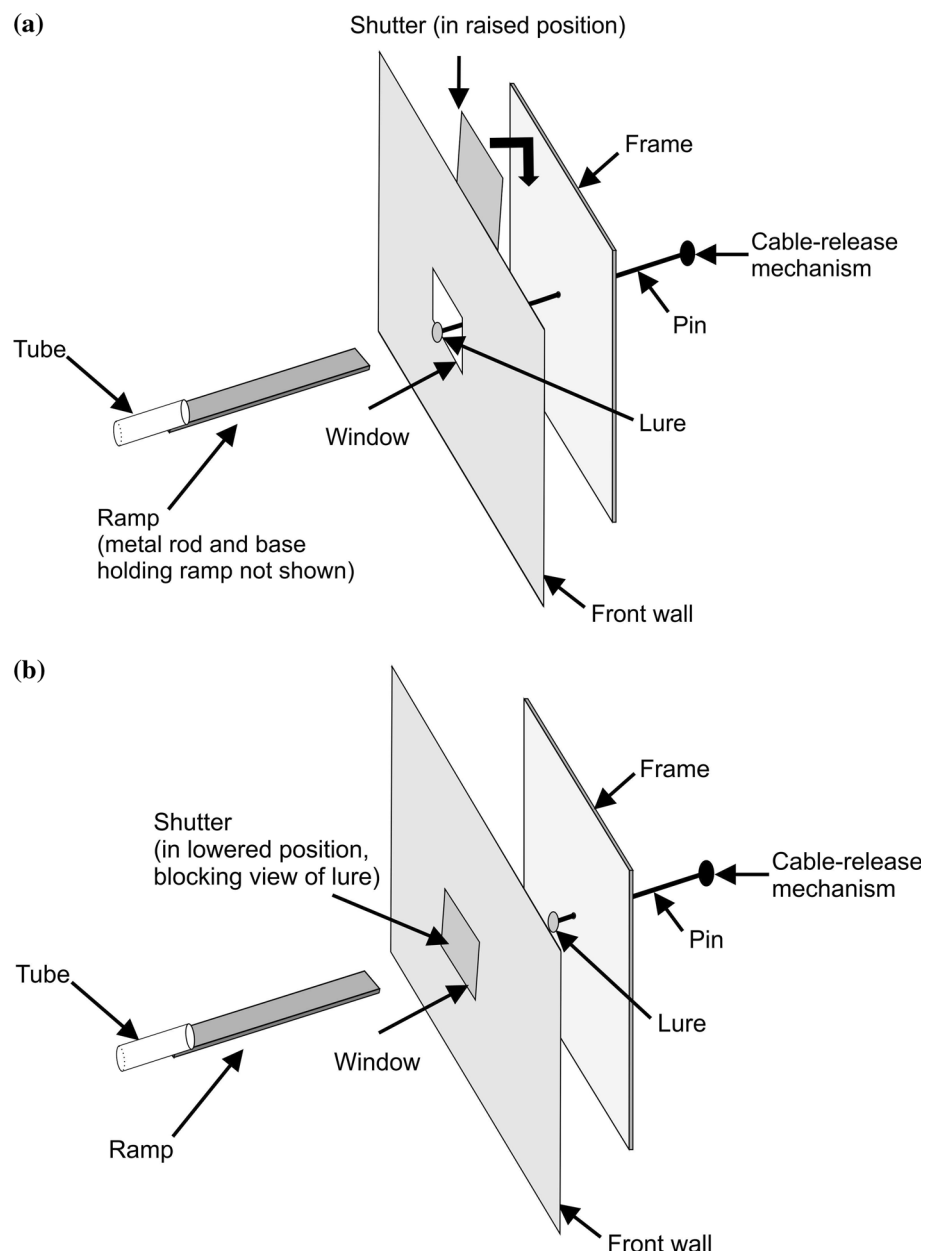
cut out of the centre of the front wall. The higher end of the ramp was 60 mm away from the window. The ramp was held in place by an assembly consisting of a metal rod (diameter 5 mm) with one end welded to the centre of the bottom of the ramp and the other end welded to a strong metal base that sat on the bench top. The side walls were parallel to, and alongside, the ramp. The two side walls were 200 mm apart, each being 100 mm from the centre of the ramp. A white wooden ceiling (200 × 200 mm) was fastened to the tops of the walls.

During testing, a lure was positioned 10 mm in front of the centre of the window (i.e. 50 mm from the upper end of the ramp). A metal pin (diameter 1 mm) held the lure in place, with one end of the pin pushed into the back of the

cork. The other end of the pin went through a hole (diameter 1.5 mm) in a white wooden frame that was 40 mm behind the front wall and 100 mm away from the ramp. The frame's dimensions (200 × 200 mm) matched the dimensions of the front wall. The end of the pin that was most distal from the ramp was connected to a cable-release mechanism that was used during trials for moving the lure forward by 5 mm and then back to its normal position 50 mm from the frame. A clamp and stand was used for holding the cable-release mechanism in place at the height of the hole in the frame.

The lure, the centre of the window, the hole in the frame, and the higher end of the ramp were all 100 mm above the table top. During the pre-trial period, the lure was kept

Fig. 2 Apparatus (not drawn to scale) used in expectancy–violation experiments. Metal rod and base (not shown) hold ramp in place. Side walls and ceiling are not shown. Start of trial: test spider leaves glass tube and walks along ramp towards lure. Cable-release mechanism moves lure forward and backward during trial. **a** Apparatus configuration at start of trial, and also when prey was restored later in trial. Lure (situated in front of window) in test spider's view because shutter is raised. **b** Apparatus configuration during 90-s period in which prey is hidden. Test spider's view of lure blocked because shutter is lowered. Lure pulled back behind window and removed from pin. Different lure then attached to pin (experimental trials) or same lure re-attached to pin (control trials)



hidden from the test spider's view by a white wooden shutter (60 × 60 mm, wood thickness 2 mm) situated behind the window (lure pulled back to 25 mm behind the window; centre of lowered shutter 10 mm behind centre of window). The shutter was held in place by a clamp and stand, with a long flexible arm between the clamp and stand being used for lowering and raising the shutter.

Before each trial, the test spider was held for 15 min in a glass tube (diameter 16 mm, length 50 mm). The tube was positioned centred on the top of the end of the ramp farthest from the lure. There was a rubber stopper in each end of the tube. Transparent sticky tape was used for holding the tube in place on the ramp, with only the higher 20 mm of the tube touching the ramp. At the beginning of each trial, the shutter was raised fully away from the window, the lure was moved into place in front of the window, and the stopper was removed from the end of tube that was facing the lure. The test spider was allowed 5 min to walk slowly out of the tube and on to the ramp.

Whenever the test spider failed to move out of the tube after 5 min, the other stopper was removed and a soft brush was pushed through this opening. When gently touched with the brush, the test spider always walked slowly out on to the ramp. This procedure was necessary in no more than 5 % of the trials for any one treatment.

Once the test spider was on the ramp, the lure was moved forward 5 mm and backward 5 mm once every 15 s. The time taken for the lure to move forward and then backward was 0.5 s. We adopted this procedure for moving lures because stationary lures were considerably less effective at eliciting responses in preliminary trials. During successful trials, the spider walked along the ramp, stopped at the end and remained there, facing the lure for 30 s. Once this 30-s interval had elapsed, the lure was moved back to the pre-trial position behind the window and the shutter was lowered (i.e. the lure was no longer visible to the test spider). Trials were aborted on the rare occasions when the spider attacked the lure or left the end of the ramp before the 30-s interval had elapsed. The shutter remained lowered for 90 s and, during this 90-s interval, the lure was removed from the pin. A different lure was put in its place in experimental trials, and the same lure was returned to the pin in control trials.

The ceiling and the two side walls blocked the test spider's view of the experimenter moving the shutter and the lures. After the shutter was raised again, the lure was returned to its position 10 mm in front of the window and the test spider was allowed 300 s (i.e. 5 min) to leap at the lure. If the test spider leapt at the lure, we recorded the time elapsing between the lure having been moved in front of the window and the spider's leap. Spiders that leapt at the lure usually landed on it (no more than 5 % missed for any treatment). Whenever a spider remained at the end of the

ramp for 300 s without leaping or else moved away before 300 s had elapsed, the trial ended and we recorded this as an instance of not attacking the prey.

Testing was aborted and no data were collected whenever the test spider left the ramp before reaching the end, longer than 3 min elapsed between the test spider leaving the tube and reaching the end of the ramp, the test spider reached the end of the ramp and then leapt before 30 s had elapsed with the test spider facing the lure, the test spider left the ramp while the shutter was down. No more than 10 % of trials for any given treatment had to be aborted, and test spiders from aborted trials were not used again.

Lures and prey species

Lures were made from individuals of four spider species (Fig. 1): *Argyrodes* sp. 1 and sp. 2 (Theridiidae), *Pycnanantha tribulis* (Araneidae) and two colour morphs of *Arachnura scorpionoides* (Araneidae). *Arachnura* and *Pycnanantha* build their own orb webs (Scharff and Coddington 1997), but the two *Argyrodes* species that we used are normally found in other spiders' webs where they feed as kleptoparasites on insects caught in the host's web (see Whitehouse 2011).

Prey spiders were first immobilised with CO₂ and then placed in 80 % ethanol the day before they were used for making lures. For preservation and for holding the dead prey on a cork disc (thickness of disc, 3 mm), the lure was then sprayed with a transparent plastic adhesive (Crystal Clear Lacquer, Atsco Australia Pty). The diameter of the cork disc was small enough that the disc was not visible to the test spider while viewing the prey spider. Prey spiders were mounted in lifelike posture, with 'lifelike' corresponding to the normal rest posture of each species used for making a lure.

The species we used adopt different resting postures. The two *Argyrodes* species are normally positioned horizontal in the web, with the ventral sides of their bodies facing up. *Arachnura* normally rests facing down. *Pycnanantha* rests facing horizontal with ventral side up or it rests facing down. When resting, *Argyrodes* sp. 1 holds its first pair of legs extended forward, with the other legs flexed in close to the body. The other three prey species keep all legs flexed in close to the body. *Argyrodes* sp. 2 holds its first pair of legs so that the last two segments (metatarsus and tarsus) are positioned directly in front of the spider's face and perpendicular to the horizontal axis of the body. In some experiments (see Fig. 1), the orientation of the spider's body departed from the normal rest posture. However, leg posture remained consistent with the spider's normal rest posture.

Each prey spider used for making a lure was an adult female or a large juvenile of standard body length. Each

individual of *Arachnura* was 14 mm in body length when paired with another *Arachnura* and 8 mm when paired with *Pycnacantha*. For the other three species, we always used individuals that were 5 mm in body length. All lures were displayed so that the test spider saw the prey spider side on.

We adopt specific definitions for the terms ‘prey type’, ‘prey orientation’, ‘hide prey’, ‘restore view of prey’, ‘attack frequency’ and ‘attack latency’. Prey type: one of two particular colour morphs of *Arachnura* or one of the four particular prey species. Prey orientation: various rotations of the lure by 90° or 180°, but with leg posture staying the same (Fig. 1). Hide prey: lowering the shutter to block the test spider’s view of the lure type. Restore view of prey: lifting the shutter to bring the same or a different lure into the test spider’s field of view. Attack frequency: the number of test spiders that leapt at prey after view had been restored. Attack latency (hesitation time before leaping on the prey): the time elapsing between restoring view of the prey and the test spider leaping at the prey.

Data analysis

One series of tests was designed to determine how test spiders responded to prey-type changes when prey orientation remained constant (see Table 1), and another series was designed to determine how test spiders responded to prey orientation changes when prey type remained constant (see Table 2). The changes in prey type were between *Argyrodes* species 1 and 2, between *Pycnacantha* and *Arachnura* and between the yellow and brown morphs of *Arachnura*. Whenever we tested for effects of changing prey orientation, the prey used was *Argyrodes* sp. 1 or the yellow morph of *Arachnura* (see Fig. 1).

As our data often did not meet the assumptions required for parametric data analyses, we used Mann–Whitney *U* tests for comparing attack latency data from different treatments (null hypothesis: latencies for compared treatments equal). We used χ^2 tests of independence for comparing attack frequency data from different treatments. Bonferroni adjustments were applied whenever there was repeated testing of the same data sets (alpha 0.05, adjusted alpha 0.017). For details about statistical procedures, see Howell (2002).

Results

When prey type was the variable and orientation was held constant (Table 1; Fig. 3a), attack frequency was significantly lower in experimental trials than in control trials. However, when prey orientation was the variable and prey type was held constant (Table 2, Fig. 4a), attack

Table 1 Response by test spiders (*Portia africana*) to change in prey type

Condition	Orientation	Experimental trials		Control trials		χ^2 test of independence	Mann–Whitney <i>U</i> test
		First lure	Second lure	First lure	Second lure		
1.	Facing left, legs up	<i>Argyrodes</i> sp. 1	<i>Argyrodes</i> sp. 2	<i>Argyrodes</i> sp. 1	<i>Argyrodes</i> sp. 1	17.88, $p < 0.001$	$Z = 0.77$, $p = 0.442$
2.	Facing left, legs up	<i>Argyrodes</i> sp. 2	<i>Argyrodes</i> sp. 1	<i>Argyrodes</i> sp. 2	<i>Argyrodes</i> sp. 2	7.93, $p = 0.005$	$Z = 1.07$, $p = 0.285$
3.	Facing down, legs left	<i>Pycnacantha</i> sp.	<i>Arachnura</i> sp. (brown morph)	<i>Pycnacantha</i> sp.	<i>Pycnacantha</i> sp.	23.03, $p < 0.001$	$Z = 1.15$, $p = 0.250$
4.	Facing down, legs left	<i>Arachnura</i> sp. (brown morph)	<i>Pycnacantha</i> sp.	<i>Arachnura</i> sp. (brown morph)	<i>Arachnura</i> sp. (brown morph)	32.20, $p < 0.001$	$Z = 1.94$, $p = 0.052$
5.	Facing down, legs left	<i>Arachnura</i> sp. (brown morph)	<i>Arachnura</i> sp. (yellow morph)	<i>Arachnura</i> sp. (brown morph)	<i>Arachnura</i> sp. (brown morph)	7.62, $p = 0.006$	$Z = 0.61$, $p = 0.541$
6.	Facing down, legs left	<i>Arachnura</i> sp. (yellow morph)	<i>Arachnura</i> sp. (brown morph)	<i>Arachnura</i> sp. (yellow morph)	<i>Arachnura</i> sp. (yellow morph)	6.13, $p = 0.013$	$Z = 0.16$, $p = 0.873$

Prey orientation constant for each condition. Experimental: second prey type different from first prey type. Control: first and second prey types the same. χ^2 tests of independence used for determining whether change in prey type influenced attack frequency (see Fig. 3a). Mann–Whitney *U* tests used for determining whether change in prey type influenced attack latency (see Fig. 3b)

Table 2 Response by test spiders (*Portia africana*) to change in prey orientation

Condition	Prey type	Experimental trials		Control trials		χ^2 test of independence	Mann–Whitney <i>U</i> test
		First lure	Second lure	First lure	Second lure		
7.	<i>Argyrodes</i> sp. 1	Facing left, legs up	Facing up, legs right	Facing left, legs right	Facing left, legs up	0.05, <i>p</i> = 0.816	<i>Z</i> = 0.99, <i>p</i> = 0.322
8.	<i>Argyrodes</i> sp. 1	Facing up, legs right	Facing left, legs up	Facing up, legs right	Facing up, legs right	1.15, <i>p</i> = 0.284	<i>Z</i> = 1.16, <i>p</i> = 0.248
9.	<i>Argyrodes</i> sp. 1	Facing left, legs up	Facing right, legs down	Facing left, legs up	Facing left, legs up	0.69, <i>p</i> = 0.407	<i>Z</i> = 0.14, <i>p</i> = 0.892
10.	<i>Argyrodes</i> sp. 1	Facing right, legs down	Facing left, legs up	Facing right, legs down	Facing right, legs down	4.20, <i>p</i> = 0.040	<i>Z</i> = 0.84, <i>p</i> = 0.401
11.	<i>Argyrodes</i> sp. 1	Facing down, legs left	Facing up, legs left	Facing down, legs left	Facing down, legs left	0.85, <i>p</i> = 0.357	<i>Z</i> = 1.73, <i>p</i> = 0.084
12.	<i>Argyrodes</i> sp. 1	Facing up, legs left	Facing down, legs left	Facing up, legs left	Facing up, legs left	1.15, <i>p</i> = 0.284	<i>Z</i> = 0.31, <i>p</i> = 0.756
13.	<i>Arachnura</i> sp. (yellow morph)	Facing down, legs left	Facing up, legs right	Facing down, legs left	Facing down, legs left	0.16, <i>p</i> = 0.692	<i>Z</i> = 0.17, <i>p</i> = 0.868
14.	<i>Arachnura</i> sp. (yellow morph)	Facing up, legs right	Facing down, legs left	Facing up, legs right	Facing up, legs right	2.70, <i>p</i> = 0.100	<i>Z</i> = 0.55, <i>p</i> = 0.584

Prey type constant for each condition. Experimental: second prey orientation different from first prey orientation. Control: first and second prey orientations the same. χ^2 tests of independence used for determining whether change in prey orientation influenced attack frequency (see Fig. 4a). Mann–Whitney *U* tests used for determining whether change in prey orientation influenced attack latency (see Fig. 4b)

frequencies in the experimental trials were not significantly different from attack frequencies in the control trials.

Regardless of whether testing pertained to prey type (Table 1, Fig. 3b) or prey orientation (Table 2, Fig. 4b), attack latencies in control trials were never significantly different from attack latencies in experimental trials.

Testing for prey preferences was not an explicit objective, but we realised that any distinct preferences that might have been expressed by our test spiders would have complicated interpretation of our experimental outcomes. Comparing attack frequencies in the control trials gave us a way of determining whether preference for a prey type was a variable affecting test spider response. When we made these comparisons, there was no evidence of *P. africana* expressing prey preferences in our experiments: The

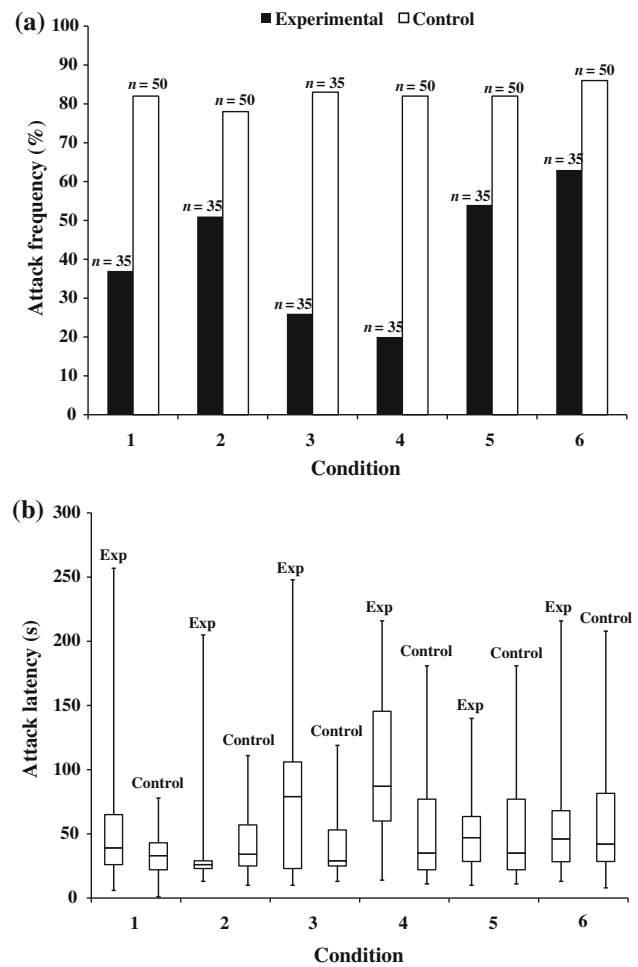


Fig. 3 *Portia africana* tested with different prey types. Prey orientation constant for each condition. **a** Attack frequencies (percentage of test spiders that leapt at the prey). **b** Attack latencies. Experimental: second prey type different from first prey type. Control: first and second prey types the same. See Table 1 for prey types used in each condition. Total number of test spiders (*n*) shown above bars in **a**. Boxes in **b** show medians and upper and lower quartiles, and whiskers show minimum and maximum values

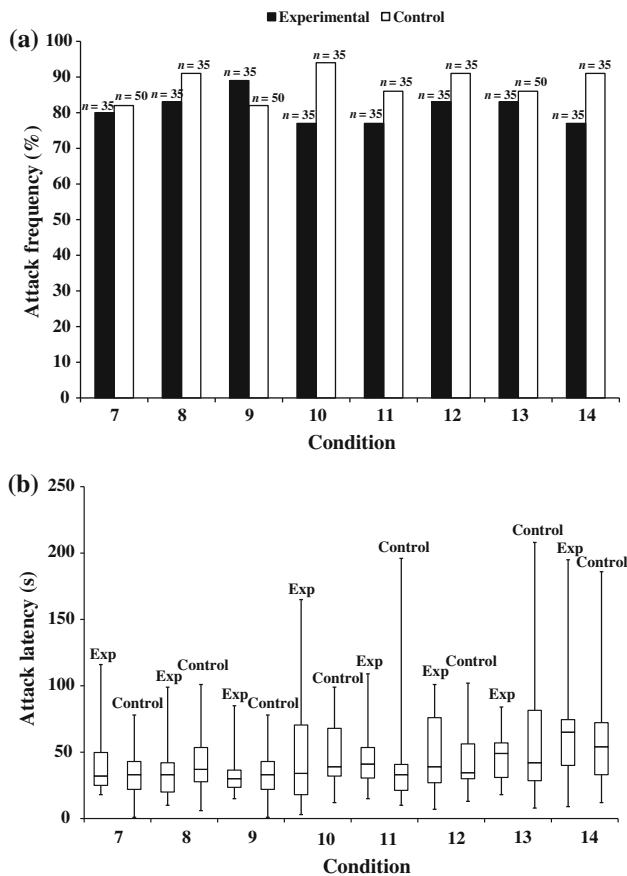


Fig. 4 *Portia africana* tested with different prey orientations. Prey type constant for each condition. **a** Attack frequencies (percentage of test spiders that leapt at the prey). **b** Attack latencies. Experimental: second prey's orientation different from first prey's orientation. Control: first and second prey's orientation the same. See Table 2 for prey orientations used in each condition. Total number of test spiders (n) shown above bars in **a**. Boxes in **b** show medians and upper and lower quartiles, and whiskers show minimum and maximum values

controls for the different prey types were not significantly different from each other (between *Argyrodes* sp. 1 and *Argyrodes* sp. 2: $\chi^2 = 0.25$, $p = 0.617$; between *Pycnanantha* sp. and *Arachnura* sp.: $\chi^2 = 0.01$, $p = 0.920$; between *Arachnura* sp. (brown morph) and *Arachnura* sp. (yellow morph): $\chi^2 = 0.30$, $p = 0.584$).

Discussion

Expectancy–violation

In research on pre-verbal infants and non-human primates, it is conventional to use looking time, or gaze duration, as data for showing expectancy–violation effects (Shettleworth 2010). In our experiments, *P. africana*'s attack latency might seem comparable to looking time, but our analysis of attack latencies revealed no evidence of

expectancy–violation. On the other hand, we did find evidence of expectancy–violation from comparing attack frequencies, where spiders made all-or-none decisions (i.e. to leap or not leap), rather than simply hesitating. When prey type changed during a trial, *P. africana* leapt significantly less often than when prey type stayed the same. Preference appears not to be a confounding variable because we always presented *P. africana* with a potential meal from its preferred prey category, namely other spiders. Moreover, we found no evidence to suggest that *P. africana* preferred any one of the spider prey types we used over another.

When the shutter was lifted, our test spiders could apparently determine whether the prey seen was the same as (expected) or different from (unexpected) the previously seen prey. Nonetheless, the unexpected prey was still a spider, and there appears to be an interesting question here concerning why test spiders would forego an opportunity to feed on prey from their preferred category. However, a design feature of our apparatus may have been an important factor related to why attack latency did not reveal expectancy–violation. The apparatus we used included an exposed platform. After detecting an unexpected prey, the test spider may have been faced with a choice between remaining exposed while determining whether the prey belonged to the preferred category ('spider') or leaving and therefore minimising the risk associated with being exposed. One of our goals for future experiments is to modify the apparatus to provide test spiders with cover and then determine whether the test spiders become more willing to invest time in making and acting on decisions to attack an unexpected prey. With these modifications, we predict that attack latencies will reveal expectancy–violation.

Loading innate representations into working memory

Training has been a common feature in expectancy–violation studies using other animals, but we did not train our test spiders prior to use in experiments, and no test spider was used more than once. Moreover, we found expectancy–violation effects despite *P. africana* never before encountering a prey item of the particular type used in the experiment and even though the initial opportunity to see this particular prey item was only the 30-s interval at the top of the ramp and no more than 3 min while walking up the ramp. It may be conceivable that, during this short exposure, *P. africana* discerned and remembered the features of this particular prey type despite no reinforcement and that it compared this acquired prey-type representation with the prey it saw later. However, an alternative hypothesis seems more realistic. The prey types we used are common in *P. africana*'s habitat and we propose that

even brief exposure to an individual from one of these prey types triggers the loading of an innate representation of that particular prey type into working memory. There is other evidence from research on another two salticid species, *Portia fimbriata* (Jackson et al. 2002) and *Evarcha culicivora* (Cross and Jackson 2009), that salticids can rely on pre-formed (innate) representations of specific prey types in the absence of any prior experience with the particular prey type in question. The way this works is that olfactory cues prime *P. fimbriata* and *E. culicivora* to become selectively attentive to the appearance of never-before-seen prey and visual cues prime *E. culicivora* to become selectively attentive to the odour of never-before-smelt prey.

Criteria by which *Portia africana* defines prey type

Portia africana leapt significantly less often when, during a trial, the prey changed between *Argyrodes* species 1 and 2, between *Pycnacantha* and *Arachnura* and between the yellow and brown morphs of *Arachnura*. The two prey items were always presented to *P. africana* sequentially (i.e. they were presented before and then after the shutter blocked the window), not simultaneously (i.e. they were not presented side by side). These findings suggest that, after the shutter was raised, the test spider compared the second prey with a representation of the type of prey seen first. We propose that a mismatch between the prey-type representation in working memory and the prey now in view was an expectancy–violation that made the test spider less inclined to leap.

Expectancy–violation experiments may be especially suitable for research aimed at understanding the prey features that, for *P. africana*, innately define prey types. Our findings suggest that *P. africana* relies on features of general morphology when identifying the prey types we used in our experiments. This includes colour when the prey was *Arachnura*. However, determining more precisely the prey features that matter to *P. africana* will require additional research. For example, size differences might have mattered especially when the change was between *Pycnacantha* (body length 5 mm) and *Arachnura* (body length 8 mm). Moreover, although *Argyrodes* species 1 and 2 were of standardised body length (5 mm), they differed in surface area and contour length. There may also have been differences in markings and colouration that mattered to *P. africana* when these four different prey species were paired in different combinations in our experiments.

Yet we standardised general morphology (including body size) especially tightly when we paired the brown and yellow morphs of *Arachnura*. In this particular instance, it is reasonable to propose that colour was a specific feature

that mattered to *P. africana*. There is considerable evidence that salticids, in general, have good colour vision, with this evidence having come from determining photoreceptor sensitivities and from experiments based on behavioural responses to colour (Jackson and Cross 2011; Harland et al. 2012). However, it was not one of our objectives in this study specifically to demonstrate colour vision, and we cannot at this stage rule out the possibility that *P. africana* distinguished between *Arachnura* morphs on the basis of other features, such as relative brightness.

Prey-type discrimination independent of prey orientation

It might be tempting to suggest that the representations *P. africana* loads into working memory are analogous to photocopies that get used like overlays, and yet our findings appear to rule out this simplistic hypothesis. If this hypothesis had been correct, then changing the orientation of the prey should have caused expectancy–violation. Contrary to this hypothesis, we found no evidence to suggest that *P. africana*'s attack frequency was influenced by changing the orientation of the prey while keeping prey type the same.

For a less simplistic version of the overlay hypothesis, we can consider the possibility that *P. africana* mentally rotates visual objects held in working memory. There is evidence suggesting that mental rotation can be an important part of day-to-day life for some non-human animals (Peissig and Goode 2012; but see Delius and Hollard 1995), as well as for humans (Shepard and Metzler 1971). There is also evidence to suggest that, for humans at least, mental rotation is a task analogous to rotating physical objects, with a rotated representation of an object being used as an overlay to determine whether it matches another object that is in view (see Palmer 1999). However, in our study, we found no significant effects on attack frequency or attack latency when orientation changed but prey type stayed the same. Our findings suggest instead that *P. africana* has considerable capacity for representing prey type in a manner that is independent of the prey's orientation.

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