



Scanning and route selection in the jumping spider *Portia labiata*

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Jumping spiders *Portia labiata* were tested in the laboratory on three different kinds of detours. In one, both routes led to the lure. In the other variants, one of the routes had a gap, making that route impassable. When tested with only one complete route, *Portia* chose this route after visually inspecting both routes. An analysis of scanning showed that, at the beginning of the scanning routine, the spiders scanned both the complete and the incomplete route but that, by the end of the scanning routine, they predominantly scanned only the complete route. Two rules seemed to govern their scanning: (1) they would continue turning in one direction when scanning away from the lure along horizontal features of the detour route; and (2) when the end of the horizontal feature being scanned was reached, they would change direction and turn back towards the lure. These rules 'channelled' the spiders' scanning on to the complete route, and they then overwhelmingly chose to head towards the route they had fixated most while scanning.

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Jumping spiders (also known as salticids) have a well-developed visual system used in prey capture (Homann 1928; Foelix 1982). The majority of jumping spiders are active foragers, walking through their environment and relying on their sense of vision to alert them to the presence of prey. A jumping spider will slowly creep towards any prey it has seen, sometimes circling around so that it can attack from behind (Freed 1984). When close enough, it will leap on to the prey and inflict a venomous, subduing bite. By relying on stealth and a sudden attack, a jumping spider can often bring down prey several times larger than itself.

Many salticids live in a three-dimensional environment made topographically complex by floor clutter and the stems, branches and leaves of surrounding vegetation (Jackson & Blest 1982a; Jackson & Hallas 1986). The complex geometry of their environment means that a salticid may often see a prey item that it cannot reach simply by walking towards it. In such situations, it must take a circuitous route (called a detour) to reach a position from where it can attack the prey (Heil 1936; Hill 1979; Jackson & Wilcox 1993). *Portia fimbriata*, an araneophagic jumping spider from Queensland, Australia, can complete complex detours (Tarsitano & Jackson 1997) and, in this paper, we examine how its congener, *P. labiata*, selects a detour route for reaching prey.

Unlike insects, all salticids have four pairs of simple (i.e. camera-like) eyes: a pair of very large anterior median (AM) eyes and, around these, three pairs of smaller secondary eyes (Homann 1928; Foelix 1982) which differ from the AM eyes in both function and morphology (see Land 1985 for a review). Behavioural experiments suggest that the secondary eyes are involved in motion detection, but not in the detection of small stationary objects (Homann 1928; Heil 1936; Land 1971, 1972; Duelli 1978). The combined field of view of the secondary eyes encompasses an area nearly 360° around and above the salticid (Homann 1928; Land 1969a; Forster 1977; Jackson & Pollard 1996). This field of view and the sensitivity to movement of these eyes make them the salticid's principal sense organ for prey detection. When moving prey is detected with these eyes, the salticid executes a precise turn that brings the prey into the field of view of its AM eyes (Homann 1928; Land 1971).

The AM eyes are used primarily to identify objects. With these eyes, some salticid species can distinguish between different types of motionless prey, threats and conspecifics from up to 300 mm away (Homann 1928; Jackson & Blest 1982b; Jackson & Tarsitano 1993). Each eye acts as a Galilean telescope, with the objective lens embedded in the cuticle of the cephalothorax (Williams & McIntyre 1980; Blest 1985; Blest et al. 1990). Behind the objective lies the relatively long eye tube. An indentation in the walls near the back of the eye tube acts as a focusing and magnifying lens (Williams & McIntyre 1980; Blest 1985) and behind this indentation lies the retina. The design of the AM eye means that its field of

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Table 1. Effect of position of rampways on *Portia's* behaviour

	Leave on left, arrive at left	Leave on left, arrive at right	Leave on right, arrive at right	Leave on right, arrive at left	N
Rampway to the left	8	1	1	0	10
Rampway to the right	1	0	8	0	9
Two rampways	5	1	4	0	10

Spiders could leave on the left or right of the starting platform and arrive at the left or right support pole; see Fig. 1.

view in the majority of salticid species examined is only 5° wide at the 'fovea' at the centre of the retina (Homann 1928; Land 1969a). In *Portia*, this field of view is <2° (Land 1985).

Salticids can move the eye tubes of their AM eyes to point them at objects up to 30° on either side of the midline of their cephalothorax and up to 30° above the horizontal plane without having to change the orientation of their cephalothorax (Homann 1928; Kästner 1950; Dzimirski 1959). When we examine an area, we turn our head to the area to be searched, then make a series of fixations, each punctuated by a quick saccade, at each of the different objects in our field of view (Land 1995). The reason behind this strategy is that we attempt to hold the retinal image stationary to avoid blur. Salticids use a different strategy (Land 1995). When examining an area, such as a prey item or a detour route, a salticid continually sweeps its AM eyes back and forth and up and down within its 60 × 30° range of motion (Land 1969b, 1972, 1995). This behaviour is called 'spontaneous activity' (because it occurs even in the absence of visual stimuli). Once an object is found, however, the salticid switches to a 'scanning' behaviour, whereby it restricts the movements of its eyes to sweeping over the image of the object it has seen. These movements provide salticids with an 'extended retina' (Dawkins 1996) with which they can see motionless objects.

Salticids seem to use this complex visual system to examine their environment before starting a detour. A salticid first performs a distinctive behaviour called 'scanning' (not to be confused with the above-mentioned eye movement; Tarsitano & Jackson 1994, 1997). Scanning consists of a series of body turns between each of which the salticid pauses with its cephalothorax rigidly pointed in one direction. These pauses are called 'fixations'. By the time it has finished scanning, a salticid will usually have fixated most of the objects in its environment. Preliminary experiments (M. S. Tarsitano, unpublished data) suggested that salticids change their scanning behaviours in response to what they are fixating, either by making repeated fixations towards part of a detour route or by changing their direction of turning while scanning. After scanning, the salticids generally choose the correct route for reaching prey (Tarsitano & Jackson 1994, 1997), suggesting that the key to understanding how salticids select detour routes lies in their scanning behaviour.

Hill (1979) suggested that when no direct route to a lure exists, a salticid selects a 'secondary objective' (such

as a branch of a tree) to head towards, and then chooses a direction of movement that would bring it closer to this secondary objective. The choice of immediate objective is subject to physical constraints; in other words, a salticid on the stem of a tree can either run up or down, and it will choose whether to go up or down according to which direction brings it closer to the secondary objective it has selected. After reaching this secondary objective, the salticid then reorients towards the lure and chooses another secondary objective to head towards. Each completed detour therefore consists of a series of smaller segments of pursuit towards secondary objectives. While Hill (1979) provided no evidence for his proposals, Tarsitano & Jackson (1993, 1994, 1997) showed that salticids will choose the appropriate objectives to head towards for completing a detour when no direct route to a lure exists. However, conclusive evidence that salticids choose secondary objectives through scanning is still lacking. In this paper we analyse *Portia's* scanning and discuss its role in the selection of secondary objectives.

METHODS

We used adult female *P. labiata*, a species from Sri Lanka. Standard housing and maintenance procedures were used (Jackson & Hallas 1986).

We tested salticids on three different detours. Either nine or 10 salticids were tested on each detour (Table 1); to minimize any learning effects, each spider was tested only once. In all, we tested 29 spiders. All three detours began at the top of a plastic cylinder (the 'starting platform'), 50 mm high × 50 mm in diameter (Fig. 1) placed in the centre of a board of pine wood 300 mm wide × 300 mm in length (the 'base'). A 'starting hole' 15 mm in diameter and 15 mm deep was drilled into the centre of the top of the starting platform. At the start of each test, we placed a single salticid in this starting hole, which was covered with a piece of plastic to prevent immediate fleeing. Once the spider became quiescent, the plastic was removed and the test begun. Salticids that still fled from the starting platform were retested later that same day.

Directly in front of, and 200 mm distant from, the base of the starting platform was a vertical pole 100 mm high × 10 mm wide suspended 11 cm above the base of the apparatus. Before each test, a lure consisting of an artificial spider (spiders being *Portia's* preferred prey) was attached halfway up the pole (the 'prey pole'). Two detour routes led to the prey pole, one to its left and one

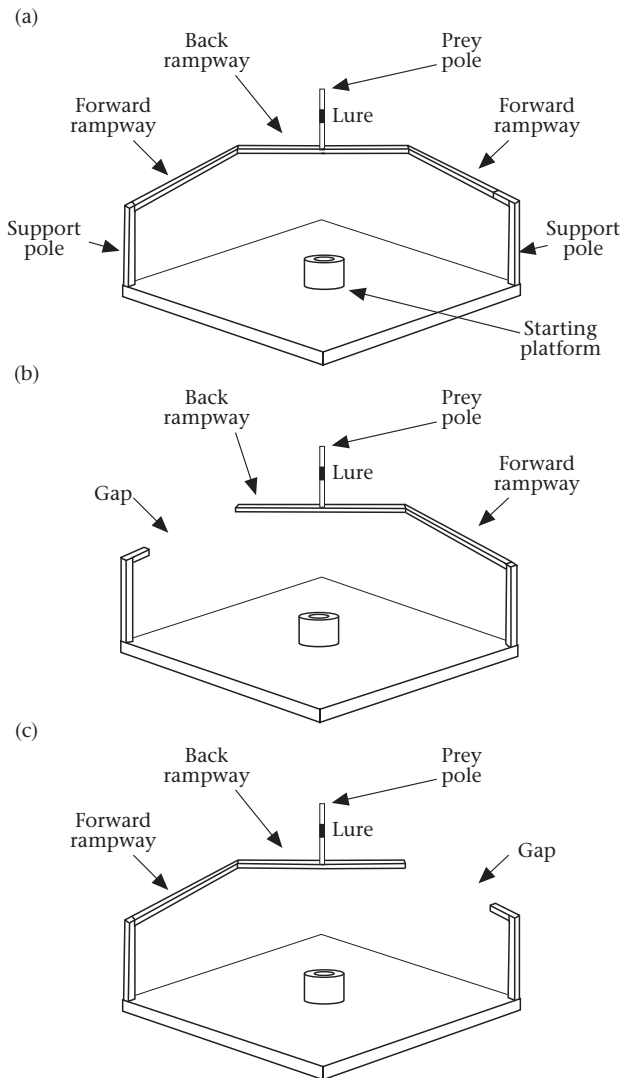


Figure 1. The detour set-ups. (a) Detour apparatus with two complete routes. (b) Detour apparatus with the forward rampway of the left route missing. (c) Detour apparatus with the forward rampway of the right route missing.

to its right. A salticid trying to get from the starting platform to the base of the prey pole (and thus the lure) could do so only by walking along one of the two detour routes.

We used an artificial spider for these experiments because lures made from real spiders tend to dry out and change shape with time; using an artificial spider standardized the lure for all tests. We made the artificial spider by gluing two small metal balls of different sizes (the ‘cephalothorax’ and ‘abdomen’ of the spider) next to each other on a piece of cork, and attaching metal wires bent into the shape of spider legs on either side of the smaller ball (i.e. the ‘cephalothorax’). The entire lure was then painted dark brown.

Each detour route consisted of three parts. The part extending from the base of the prey pole (the ‘back rampway’) was 100 mm long \times 10 mm wide and raised 100 mm off the base. A second rampway (the ‘forward

rampway’) was 180 mm long \times 10 mm wide and also raised 100 mm off the base; it lay at a 130° angle to the end of the back rampway (Fig. 1). A pole, 100 mm high \times 10 mm wide (the ‘support pole’) supported the rampway and provided access to it. Each support pole was placed approximately 180 mm from the starting platform, and the angle made between a support pole, the starting platform and the lure was approximately 80°.

In only one of the three set-ups did both detour routes lead to the lure (Fig. 1a). In the other set-ups, one of the two routes, either the one to the left or the one to the right, lacked most of the forward rampway (Fig. 1b, c). The support pole on the side with the missing forward rampway (the ‘incorrect support pole’) was connected to a 30-mm segment of rampway separated from the back rampway by a gap, while the other support pole (the ‘correct support pole’) led to the beginning of a complete forward rampway. The set-up where both routes led to the lure was used as a control.

Throughout the paper, we use the phrase ‘a detour set-up’ to refer to the type of detour the salticid was tested on: the set-up where both routes led to the lure; the set-up where the route to the left of the starting platform led to the lure; or the set-up where the route to the right of the starting platform led to the lure. ‘Detour route’, however, refers to the entire route, consisting either of the back rampway, forward rampway and support pole (in the case of a complete route to the lure) or the back rampway, the gap and the incorrect support pole (in the case of an incomplete route to the lure).

To minimize stray vibrations, each test set-up was placed on a table whose legs stood on foam rubber pads and which had a steel plate measuring 600 \times 300 \times 10 mm placed on its top. Four walls (1000 \times 1000 mm) made from white stiffened paper prevented the spiders from seeing anything but the upper parts of the walls and the ceiling of the laboratory and provided a uniform backdrop against which the spiders could see the detour routes. The area within the blind was called the ‘test arena’. A video camera was placed approximately 1500 mm above the centre of the test set-up with a 100-W incandescent light bulb beside it. Additional ambient lighting was provided by overhead fluorescent ceiling lamps.

Because the pedicle joining the cephalothorax to the abdomen allows salticids to bend at this joint, only the orientation of the cephalothorax accurately reflects the possible orientation of the AM eyes. We used a computer-generated cursor superimposed over the video image of the spider to record the exact position and orientation of its cephalothorax whenever it paused in its turning while scanning. For convenience, these pauses while scanning are called ‘fixations’, even when the cephalothorax was not oriented towards any part of a detour route. ‘The direction of fixation’ refers to the orientation of the salticid’s cephalothorax; ‘direction of turning’, however, refers to the direction (left or right) that a salticid turns while scanning. Direction of turning is given either as to the right (clockwise) or to the left (anticlockwise). The direction of fixation was taken as an

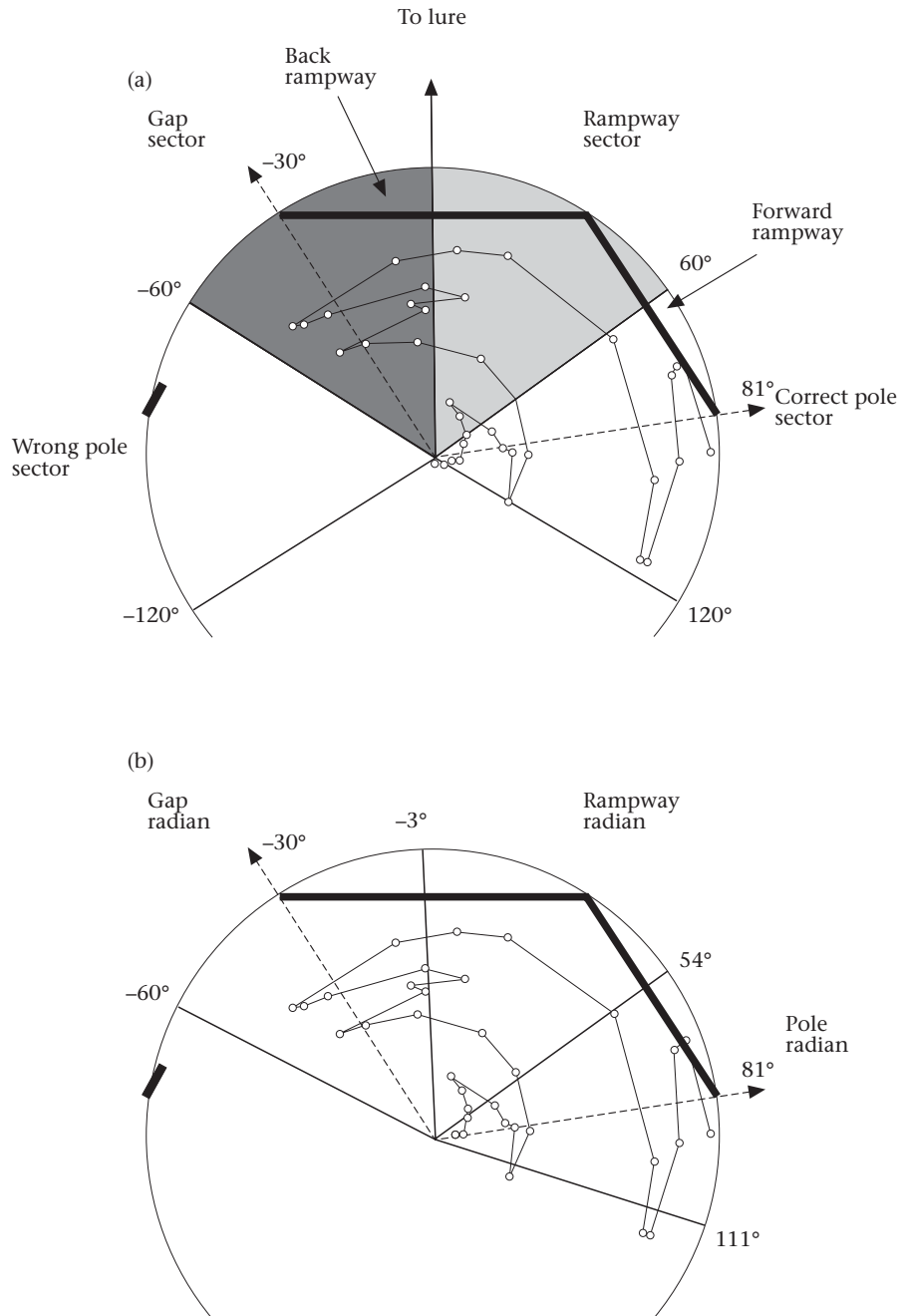


Figure 2. (a) The categorization of *Portia*'s directions of fixation into four sectors (the wrong pole, gap, rampway and correct pole). Each dot represents *Portia*'s direction of fixation during the pauses it made while scanning. The sequence of fixations made during scanning is plotted from the centre outwards: the dot closest to the middle of the circle represents the first fixation and each succeeding dot moving outwards from the middle represents the next fixation in the scanning sequence. The line connecting the dots is the sequential 'path' of fixation directions *Portia* made while scanning, and gives the direction *Portia* was turning between each fixation. (b) Radians used in the analysis to examine whether what a *Portia* could potentially see influenced its tendency to change the direction it was turning while scanning. In both (a) and (b) the angles forming the boundaries between each sector are given (—), as are the angles to the beginning of the gap and the correct support pole (---).

angular measure, in which the zero direction was towards the lure and in which negative angles always refer to directions towards the route with the gap, regardless of whether the gap was part of the right route or the left (Fig. 2). The junction between forward and back rampways lay at +30°. On the other route, the gap began at

-75° and extended to -30°. The incorrect and correct support poles lay at -81 and 81°, respectively.

To quantify the changes in the salticids' scanning behaviour before they started a detour, we first examined whether their tendency to concentrate fixations towards different parts of the detour set-up changed during the

course of the scanning routine. To do so, we divided the scanning routine into four consecutive 'epochs' and examined where the spider predominantly fixated during each epoch. The first epoch began when the salticid emerged from its starting hole and ended when it had fixated on the lure for the first time. We defined the second, third and fourth epochs by dividing into three equal portions the number of fixations the salticid made between fixating on the lure and leaving the starting platform. Each fixation was assigned to one of four sectors, each 60° wide, according to its direction: 0–60°, which included fixations in which the rampway could be seen; 61–121°, which included fixations in which the support pole could be seen; –60–0°, in which the gap could be seen; and –61––121°, in which the wrong pole could be seen (Fig. 2). Because spiders varied in how many fixations they made during their scanning routines ($\bar{X} \pm SD = 43.9 \pm 20.25$, $N = 29$), we normalized the number of fixations in each sector by finding the percentage of fixations made in each sector during each epoch. We then found the mean percentage of times the salticids as a group fixated in each sector for each epoch. Fixations outside of the four sectors (17.5% of the total) were not considered when calculating percentages.

When the salticids were tested with only one forward rampway, we additionally examined whether what the salticid could see while scanning influenced its decision to change its overall direction of turning while scanning. Although the above-described method of grouping fixations by their orientation gives equally sized sectors, and therefore allows us to compare corresponding parts of a distribution that is symmetrical about the lure, a small number of fixations in the 0–60° sector (for instance) might have allowed the salticid to see the support pole, if the AM eyes were maximally turned in that direction. Although this would have tended (if anything) to dilute out differences between the two sectors depending on what the spider saw, we nevertheless devised a second method of classification for examining whether what a salticid could see influenced its decision to change its direction of turning while scanning. This method of classification assigned fixations more strictly according to what a salticid could potentially see with each fixation. To avoid confusion with the sectors used in the epoch analysis, we called these sectors 'radians' (for reasons that will become apparent later; Fig. 2) as in the phrase, 'the rampway radian'.

The radians were designed to divide up fixations as clearly as possible according to what the spider could potentially see, taking into account the maximal possible excursion of the eyes. For instance, since the support pole was placed at 81° relative to the lure, and because the width of the salticid's extended retina is $\pm 30^\circ$, the salticid could see the support pole when facing in any direction between +51 and +111°. As a first step, therefore, a zone from +51 to +111° was chosen as the support pole radian (but see below). Similarly, since the start of the gap was at –30°, the salticid could potentially see the start of the gap when facing in any direction between –60 and 0°; this zone therefore became the gap radian. In the space in between 0 and 51°, the salticid could see

neither the gap nor the support pole; this zone therefore became the rampway radian, within which the spider could not be directly affected by visual input from the gap or the support pole. Furthermore, since the rampway could be seen from each radian, the effect of seeing the rampway on the salticid's tendency to change the direction it was turning while scanning was controlled for.

To produce equal-sized radians to facilitate subsequent analysis, the boundary between the rampway radian and the gap radian was moved 3° towards the gap, and the boundary between rampway and support pole radians was moved 3° towards the support pole. This gave three equal 57° radians, (and justified the term radian, since a geometric radian is 57.26°). These slight adjustments were so small that the results of our statistical analysis proved to be identical, whichever radian the fixations lying in the 3° zones were assigned to.

Casual observation suggested that the salticids changed their direction of turning while scanning according to the object they were possibly seeing. To find out whether what the salticid could see while scanning had an influence on its decision to change its direction of turning while scanning, we found the average percentage of times the salticids changed the direction they were turning while scanning in each radian. To do this, each time an individual salticid's direction of fixation entered a radian, we recorded whether that salticid kept turning in the same direction while scanning. A salticid was judged to have kept turning in the same direction when its direction of fixation eventually left the radian on the opposite side to that of its entry into the radian. A salticid was judged to have changed its direction of turning when its direction of fixation left the radian on the same side as that of its entry into the radian. We then divided the number of times that there was a change in turning direction in each radian by the total number of entries into each radian, yielding for each radian and spider the percentage of times in which there was a change in turning direction. These values were then used to calculate the average percentages of turning directions for the salticids as a group.

We conducted tests in the morning between 0800 and 1100 hours and again in the afternoon between 1500 and 1900 hours, the times when *Portia* is active in the field (Jackson & Hallas 1986). To ensure that each spider to be tested was active, we lightly tapped on the cage of each potential subject. Only those that responded to this stimulus by waving their palps (the typical *Portia* startle response; Jackson & Blest 1982a; Jackson & Hallas 1986) were tested. To motivate the spiders, each subject was deprived of food for 3–5 days prior to testing. Because salticids leave pheromones on the draglines they lay down while walking, we wiped both detour routes and base with acetone after each test to remove all traces of any trail the tested salticid may have left behind.

Tests were concluded when a salticid: (1) climbed the prey pole; (2) walked out of the field of view of the video camera; (3) stayed motionless for 30 min; or (4) abandoned the detour (i.e. turned around and returned along the route, or leapt off of the route on to the base of

the apparatus). Spiders that walked away from the detour routes and off of the base were removed and tested later on another day. Subjects were allocated at random to different experimental groups. All statistical tests used are in Sokal & Rohlf (1981).

RESULTS

Choice of Routes

When tested with two complete routes, approximately equal numbers left from the left and right sides of the starting platform (Table 1). The salticids did not prefer either route. However, when tested with one complete and one incomplete route, the salticids preferred the complete route, both on the measure of the direction in which they left the starting platform and on which support pole they reached (Table 1; in both cases, Fisher's exact test: two-tailed $P < 0.001$).

Selection of Route while Scanning

In each of the test set-ups, the salticids predominantly chose to head towards the route they had fixated most during scanning. This was also the case for the salticids that, when tested with a choice between an incomplete and a complete route, chose the incomplete route (15 had the majority of fixations to the left, of which 13 went towards the left route; 14 had a majority of fixations to the right, of which 11 went to the right route, $N = 28$; Fisher's exact test: $P < 0.001$).

When tested with two forward rampways, the salticids tended to concentrate fixations at the start and at the end of their scanning routine towards the route they would eventually head towards (Fig. 3). Seven salticids tested with two complete routes fixated one route more often than the other during the first epoch. Of these seven, five began scanning with a majority of their fixations on the left route; all five of these concentrated their fixations towards the left route in the last epoch and headed for the left route after scanning. Two salticids began scanning with a majority of their fixations on the right route; both of these concentrated their fixations towards the right route in the last epoch and headed for the right route after scanning (Fisher's exact test of independence: two-tailed $P < 0.05$).

In tests with a gap to one side, the left/right distributions of fixations changed during the course of scanning. When tested with one complete route, the salticids' fixations during the first epoch were concentrated towards the gap or the rampway, with the gap being favoured (Fig. 4; first epoch, null hypothesis: fixations equally distributed between sectors; median test: $\chi^2_3 = 8.89$, $P < 0.05$). However, the distribution of fixations changed with each epoch, fixations being concentrated towards the rampway in the second epoch (Fig. 4; second epoch, null hypothesis: fixations equally distributed between sectors; median test: $\chi^2_3 = 10.55$, $P < 0.01$), but more or less evenly distributed in the third (Fig. 4; third epoch, null hypothesis: fixations equally distributed

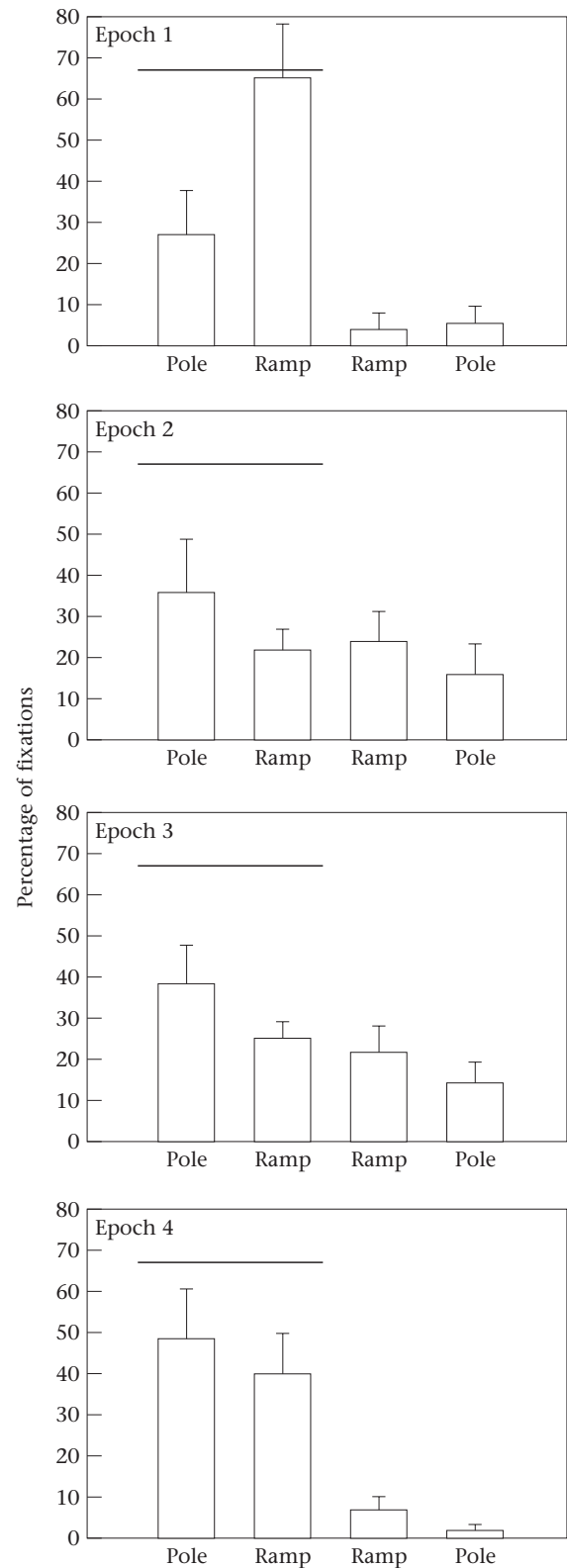


Figure 3. The distribution of the directions of fixation in each epoch of scanning, in the tests with two rampways. The mean \pm SE percentage of fixations within each epoch that were oriented in the support pole and rampway sectors (see Fig. 2) are shown. Data from 10 *Portia* were normalized according to which route they headed towards when they left the starting platform. Horizontal lines indicate sectors oriented towards the spiders' eventual detour route.

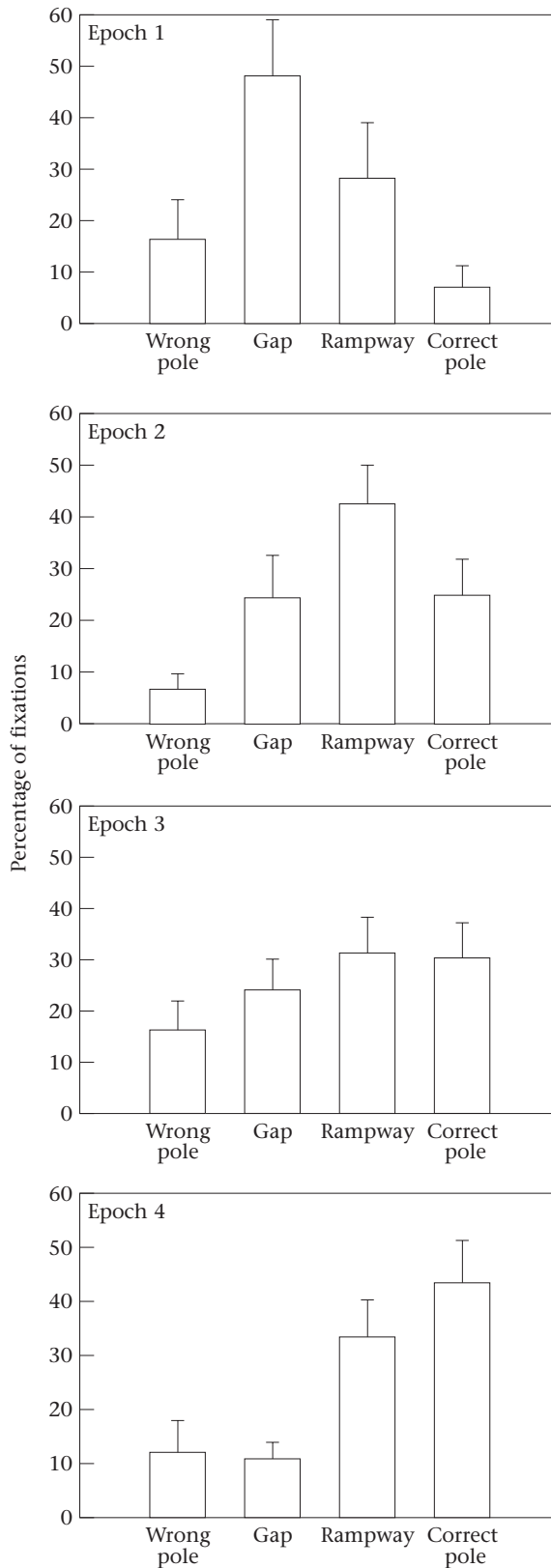


Figure 4. The distribution of the directions of fixation in each epoch of scanning, in the tests with one rampway. The mean+SE percentage of fixations within each epoch that were oriented in the wrong pole, gap, rampway and correct pole sectors (see Fig. 2) are shown. Data are from 19 *Portia*.

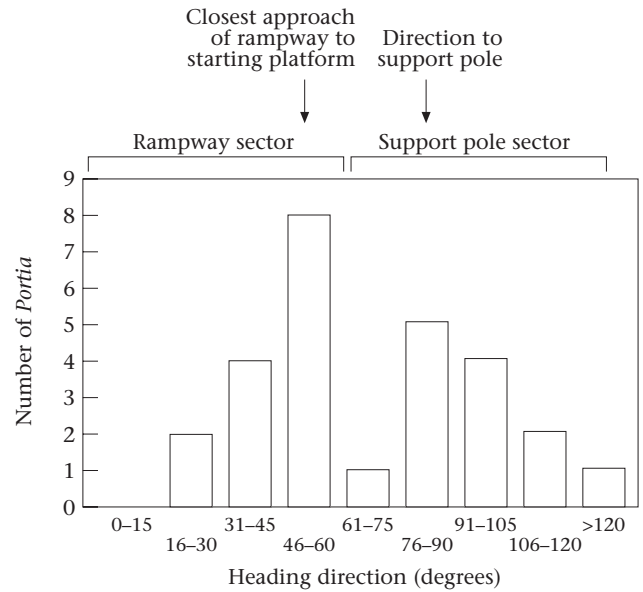


Figure 5. Frequency distribution of *Portia*'s initial direction when leaving the starting platform. The direction is given as a circular measure in degrees centred on the starting platform; the zero direction was towards the lure.

between sectors; median test: $\chi^2_3=6.46$, NS). By the end of the scanning routine (fourth epoch), the salticids' fixations were directed towards the side of the complete route, which is also the route that the spiders overwhelmingly chose (Fig. 4; last epoch, null hypothesis: fixations equally distributed between sectors; median test: $\chi^2_3=15.32$, $P<0.005$).

We next examined whether the direction of the salticids' fixations in the last epoch correlated with their heading direction after leaving the starting platform. Such a positive correlation would suggest that during the scanning process they had chosen which part of the detour route to aim at. This question could be asked of all three types of test. All three showed the same distributions and are therefore pooled here. The resulting distribution (Fig. 5) was bimodal; 14 spiders headed towards the forward rampway (initial median direction 50° , lower quartile 37° , upper quartile 59°), and 13 towards the support pole (initial median direction 95° , lower quartile 87° , upper quartile 107°). These data do not include the two salticids that went left from the starting platform heading towards the incorrect route. However, at the end of the scanning routine these spiders also fixated the object they were heading towards (i.e. one to the gap, the other to the incorrect pole). The distribution of fixations in the final epoch reflects the distribution of directions taken by the salticids after leaving the starting platform: 83% of the spiders (Table 2, data from all groups, $N=23$) that left the starting platform on course towards a complete route headed towards the part of the detour route (i.e. either the forward rampway or the support pole) that they fixated most during the last epoch of scanning (Table 2; Fisher's exact test: two-tailed $P<0.001$).

Table 2. The direction in which *Portia* headed after fixating on either the support pole or rampway during the last epoch of scanning

Object fixated most often during last epoch of scanning	Heading direction at start of detour	
	Support pole	Rampway
Support pole	10	2
Rampway	2	9

Data do not include four spiders that had an equal number of fixations in the rampway and support pole sectors during the last epoch of scanning.

Of the 14 salticids that left the starting platform and headed towards the rampway of a complete route, 13 changed course during their approach so that they arrived at the support pole leading to that rampway. The one exception changed course to arrive at the incorrect support pole. All salticids that left the starting platform and headed towards the support pole of a complete route arrived at that support pole without changing course.

Turning Direction and Fixation Radian

When the salticids turned away from the lure while scanning, the frequencies at which they would change turning direction towards the lure were statistically different from radian to radian (average percentage of change in direction versus radian of fixation; median test: $\chi^2_2=9.11$, $P<0.01$). When turning away from the lure, the salticids had a greater tendency to change turning direction when oriented towards the gap and the correct support pole radians than when oriented towards the forward rampway radian (Fig. 6a; median test of average percentages of changing turning direction when the salticid was fixating in the rampway radian versus the gap radian: $\chi^2_1=9.81$, $P<0.005$; median test of average percentages of changing turning direction when the salticid was fixating in the rampway radian versus the support pole radian, median test: $\chi^2_1=8.93$, $P<0.005$). There was no statistical difference in the salticids' tendency to change turning directions back towards the lure when they were fixating in the gap versus the support pole radians (i.e. the two ends of the horizontal feature: median test of average percentages of changing turning direction when the salticid was fixating in the support pole radian versus the gap radian, median test: $\chi^2_1=1.03$, NS).

When the salticids turned towards the lure while scanning, the frequencies at which they would change turning direction away from the lure were not statistically different from radian to radian (Fig. 6b; average percentages of changing turning direction when the salticid was turning towards the lure versus radian of fixation; median test: $\chi^2_2=0.261$, NS). The average percentage of time the salticids changed turning directions was approximately 45% for each radian.

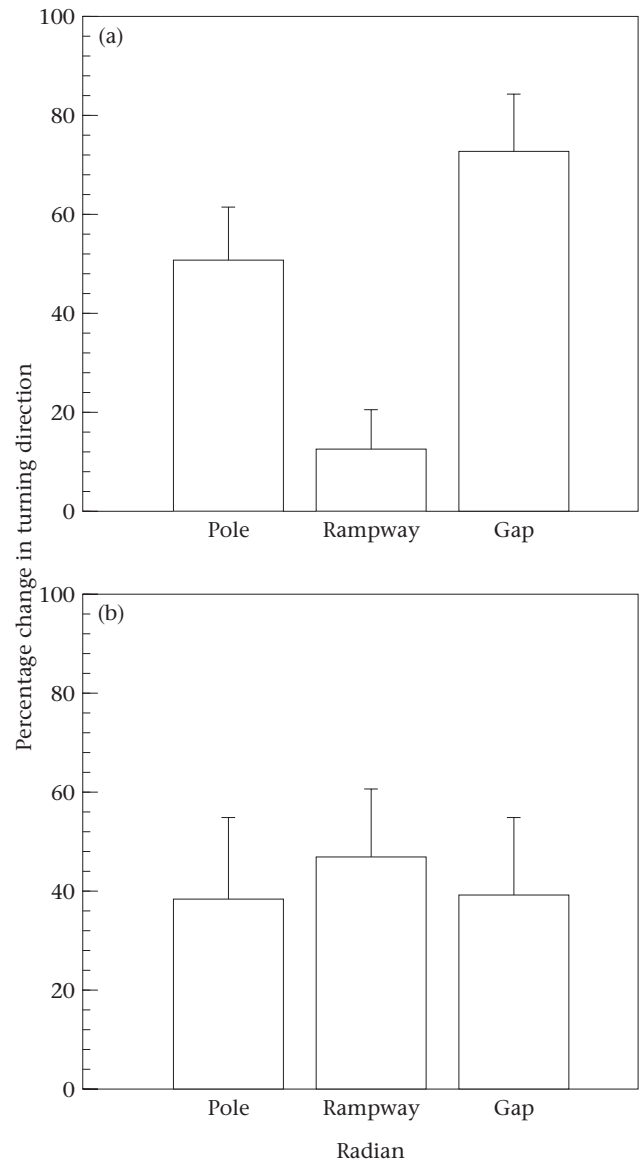


Figure 6. The mean percentage change+SE in the direction of turning when *Portia* fixated in the gap, rampway and support pole radians, in tests with only one complete route. (a) Percentage change when *Portia* turned away from the lure. (b) Percentage change when *Portia* turned towards the lure.

DISCUSSION

Choice of Routes

When given the option of two complete detour routes to a lure, approximately equal numbers of salticids headed towards the left or the right route. However, when tested with only one complete route, nearly all of the salticids left the starting platform on the same side as the complete route, regardless of whether the complete route was to the left or to the right of the starting platform. Therefore, when tested with one complete and one incomplete route, *P. labiata* was able to select the complete route while scanning.

Rules Governing Selection of Detour Routes

When tested with only one complete route, how the salticids selected the complete route can be seen by following the progressive changes in the distribution of where the salticids fixated while scanning. At the beginning of the scanning routine, they had a slight preference for the gap. By the end of the scanning routine, they preferred to fixate the support pole or the rampway of the complete route. The scanning routine therefore seems to be 'channelled' on to the complete route during the scanning routine. The salticids then overwhelmingly chose to head to that route they had fixated most while scanning.

How Scanning is Channelled

What the spider probably saw from each radian affected its decision to change the direction it was turning while scanning. When turning towards the lure, *Portia* tended to have about a 45% chance of changing its turning direction in each radian. However, when turning away from the lure, *Portia* had a much greater tendency to change turning direction when facing in the gap or support pole radian than when facing in the rampway radian. In other words, while facing in the rampway radian, a radian where a horizontal line continuous with the lure is seen, the salticids had a tendency to keep turning in one direction (i.e. away from the lure). In contrast, when oriented in the gap or support pole radians, radians where an end to the horizontal feature being scanned can be seen, turning away from the lure tended to be replaced by turning back towards it. These behaviours can be summarized by a simple set of rules: (1) continue turning in one direction when scanning away from the lure along horizontal features; and (2) when the end of the horizontal feature being scanned is reached (either the salticid sees the actual end of the horizontal feature or scans out into open space), turn back towards the lure (Fig. 7). These two rules allow *Portia* to trace out multiple horizontal routes leading back to the lure, and lead to a concentration of fixations on to the complete route.

Selection of 'Secondary Objectives' while Scanning

The salticids headed to the specific object they fixated most during the last epoch of scanning: the majority of those salticids that concentrated their fixations towards a forward rampway during the last epoch of scanning headed towards that forward rampway; the majority of salticids that concentrated their fixations towards a support pole during the last epoch of scanning headed towards that support pole. Because the part of the detour route at which they would subsequently aim emerged during scanning, it would seem that the salticids selected that part of the detour route while scanning. This result confirms Hill's (1979) suggestion that salticids choose secondary objectives to head towards when they make a detour.

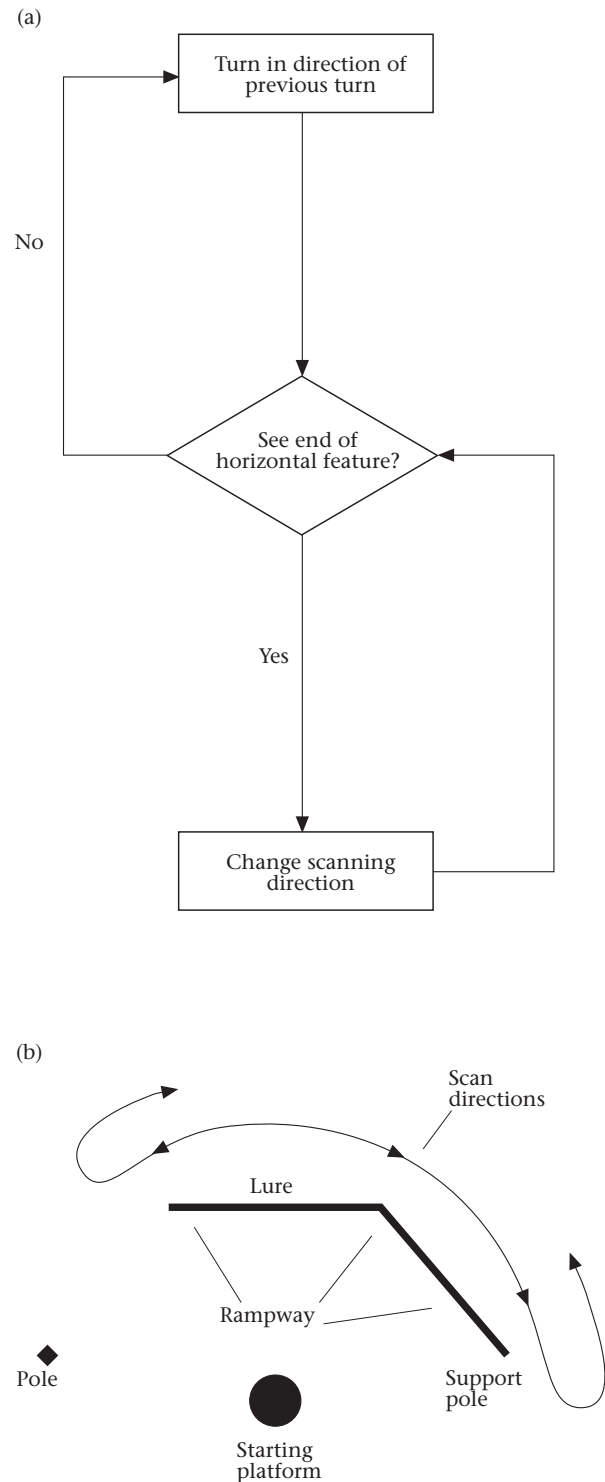


Figure 7. (a) Flow chart illustrating the proposed rules governing *Portia*'s scanning behaviours. (b) How these rules may serve to concentrate *Portia*'s scanning on to the complete route to the lure. The direction of turning while scanning tends to continue to be away from the lure so long as *Portia* is facing the rampway. At the ends of the rampway, however, *Portia* tends to change its turning direction towards the lure. Although *Portia* does not automatically turn towards the lure when it comes to the ends of the rampways, its greater tendency to do so means that, with time, *Portia* concentrates its fixations on to the correct route.

The initial mean direction of those salticids that left the platform and headed towards the rampway was 49°, the angle that has them heading towards the part of the rampway closest to the starting platform. This suggests that the salticids could judge the distance to the rampway. Therefore, our results imply that the salticid visual system is sophisticated enough to allow the salticid not only to see and identify prey, but also to judge distances to objects for the purpose of selecting secondary objectives for making a detour.

How Salticids Choose Detour Routes

The salticids may be using a very simple general rule for deciding which route to head for to complete a detour, namely, to head towards that detour route fixated most while scanning. However, this rule cannot explain how the salticids were able to select the complete route over the incomplete route. To see how they did this, one has to look at the rules governing their scanning routine.

As stated above, the rules governing scanning seem to be: (1) continue turning in one direction when scanning away from the lure along horizontal features; and (2) when the end of the horizontal feature being scanned is reached, turn back towards the lure. These two rules result in *Portia* concentrating its fixations on to the complete route, and thereby ensure that the correct route receives the most fixations. Since *Portia* heads to the route fixated most during scanning, these two rules also allow it to select the correct route while scanning.

Some of the salticids that headed for a complete route headed for the support pole, whereas others headed for the point of the rampway closest to the starting platform. It is difficult to find any reason as to why some salticids chose one secondary objective, and the others another. The only indication of which secondary objective they would head towards was where they were fixating during the last epoch of scanning.

What is clear is that an object does not have to be itself accessible in order for the salticid to choose it as a secondary objective. In other words, the salticids do not necessarily have to have found 'the complete solution' (i.e. heading towards an object, the support pole, that would get it to the lure) in order to start on the detour. A partial solution is good enough to begin with. Yet the salticids that left the starting platform heading towards the rampway eventually changed course towards the correct support pole, and thereby solved the detour problem. While the salticids were heading towards the rampway, the correct support pole was not within the field of view of their AM eyes, suggesting that it was an inability to reach the rampway directly (unless they reoriented towards it) that triggered the salticid to head for the support pole. Therefore, these salticids did not seem to solve the detour 'all at once', but rather in a stepwise fashion, changing secondary objectives when the immediate secondary objective could not be reached.

Because of the complex environment in which *Portia* lives this may be the optimal way to solve detours. The salticid's complex environment might make solving a detour all at once too difficult for its limited nervous

system. Selecting new secondary objectives when the immediate secondary objective cannot be reached gives the salticid a way to complete complex detours in a complex environment without having to pay a high cost in complex cognitive processing in the central nervous system.

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