

'Eight-legged cats' and how they see - a review of recent research on jumping spiders (Araneae: Salticidae)

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Recent research on the eyes and vision-guided behaviour of jumping spiders (Salticidae) is reviewed. Special attention is given to *Portia* Karsch. The species in this African, Asian and Australian genus have especially complex predatory strategies. *Portia*'s preferred prey are other spiders, which are captured through behavioural sequences based on making aggressive-mimicry web signals, problem solving and planning. Recent research has used *Portia* to study cognitive attributes more often associated with large predatory mammals such as lions and rarely considered in studies on spiders. In salticids, complex behaviour and high-spatial-acuity vision are tightly interrelated. Salticid eyes are unique and complex. How salticid eyes function is reviewed. Size constraints are discussed.

INTRODUCTION

When studying spiders, salticids are not easily mistaken for anything else. In English, the common name for salticids is 'jumping spiders' and many are indeed phenomenal leapers. However, jumping alone is not what distinguishes salticids from other spiders. Some other spiders can jump, but only salticids make accurate vision-guided leaps on to prey and other targets. What makes salticids special is their unique, complex eyes and acute eyesight, not leaping prowess. Salticids have large anterior medial eyes that give them an almost catlike appearance. No other spider has eyes like these and no other spider has such intricate vision-guided behaviour. The feline analogy is more than superficial (Land 1974), and a better common name for salticids would probably be 'eight-legged cats'.

As with a cat, a salticid uses more than its eyesight during prey-capture sequences. Chemoreception and other modalities also play a role. Like a cat, and unlike any other spider, however, a salticid locates, tracks, stalks, chases down and leaps on active prey, with all phases of these predatory sequences being under optical control (Forster 1982). Using optical cues, salticids discriminate

between mates and rivals, predators and prey, different types of prey, and features of non-living environment (Crane 1949; Drees 1952; Heil 1936; Jackson & Pollard 1996; Tarsitano & Jackson 1997). No other spider is known to see this well.

Resemblance between cats and salticids may go beyond having good eyesight. Animal intelligence, animal cognition and related topics, although long neglected by scientists studying behaviour, are now being taken seriously (Gallistel 1992; Griffin 1984). For cats, especially big cats such as lions, many scientists might be ready to concede that these topics are relevant, but cognition is not a conventional topic in spider studies. There may be compelling reasons for the traditional portrayal of spiders as simple, instinct-driven animals (Bristowe 1958; Savory 1928), and the very notion of discussing 'spider minds' might seem comical, if not scientifically disreputable.

Here we shall review recent work on salticids that challenges conventional wisdom. Of the salticids that are well studied to date, those with the highest optical spatial acuity (Williams & McIntyre 1980) and most complex behaviour (Jackson & Pollard 1996) are species in the genus *Portia* Karsch, 1878 (Wanless 1978).

Our review focuses on this genus.

PORTIA'S PREDATORY STRATEGY

Most salticids prey primarily on insects caught by actively hunting as opposed to building webs (Richman & Jackson 1982), but *Portia* not only hunts in the open but also builds a prey-catching web. Besides this, *Portia* also invades the webs of other spiders, where it feeds on other spiders' eggs, on insects ensnared within their webs and on the other spiders themselves (Figure 1). *Portia* is also unusual in appearance, not really resembling a spider at all, but cryptically resembling detritus in a web (Jackson 1996; Jackson & Blest 1982a).



Figure 1. *Portia* feeds on *Pholcus phalangioides*, a long-legged web-building spider.

Hunting in other spider's webs is dangerous and *Portia* has evolved complex, flexible behaviour that minimises risk. Instead of simply stalking or chasing down its victim, *Portia* generates aggressive-mimicry web signals (Tarsitano *et al.*; in press). *Portia's* preferred prey (Li *et al.* 1997), web-building spiders, have only rudimentary eyesight (Land 1985) and rely

primarily on interpreting web signals (Foelix 1996). Web signals are the tension and movement patterns conveyed through silk of the web, with the spider's web being almost literally a sense organ (Witt 1975).

Portia makes aggressive-mimicry signals by manipulating, plucking and slapping web silk with anyone or any combination of its eight legs and two palps. Each appendage can move in a great variety of ways, and movement patterns of any one appendage, however complex, can be combined with different movement patterns of any number of the other appendages (Jackson & Blest 1982a; Jackson & Hallas 1986). On top of all the signals made possible by moving legs and palps, *Portia* also makes signals by flicking its abdomen up and down, and abdomen movement can also be combined in various ways with the different patterns of appendage movement. The (net effect is that *Portia* has at its disposal a virtually unlimited array of different signals to use on the webs of other spiders (Jackson & Wilcox 1993a).

Portia uses aggressive mimicry against, and catches, just about every kind of web-building spider imaginable, as long as it is in a size range of from about 1/10th to twice *Portia's* size (Jackson & Hallas 1986). Being able to make so many different kinds of signals is important, because how *Portia's* prey, another spider, interprets web signals may vary considerably depending on the species to which it belongs, its sex, age, previous experience and feeding state.

An ability to make so many different signals, however, raises the next question. How does *Portia* derive the appropriate signals for each of its many victims from its enormous repertoire? Two basic methods appear to be critical (Wilcox & Jackson 1998): 1) using specific genetically pre-programmed signals when cues from some of its more common prey species are detected; and 2) flexible adjustment of signals in response to feedback from the prey (i.e., trial-and-error

derivation of appropriate signals). The first, using pre-programmed signals, is consistent with the popular portrayal of spiders as animals governed by instinct, but trial and error is an example of problem-solving behaviour and less expected in a spider.

How *Portia* uses the trial-and-error tactic may be most easily appreciated when *Portia* enters the web of a species of web-building spider for which it does not have a pre-programmed tactic. After presenting the resident spider with a kaleidoscope of different web signals, *Portia* eventually chances upon a signal that elicits an appropriate response from the victim, whereupon *Portia* ceases to vary its signals and concentrates instead on producing this particular signal (i.e., the signal that worked; Jackson & Wilcox 1993a). When *Portia* is larger than its intended victim, interpreting the predatory sequence appears to be straight forward: *Portia* homes in on signals that cause the resident spider to approach as though *Portia* were a small ensnared insect (Jackson & Blest 1982a; Tarsitano *et al.* in press). The function of signals often may, however, be subtler than this.

In encounters with a large and powerful spider in a web, simply mimicking a trapped prey and provoking a full-scale predatory attack would be highly dangerous, and *Portia* appears to adopt an alternate goal: fine control over the prey's behaviour (Jackson & Wilcox 1998). *Portia* may make signals that draw the prey spider in slowly, or *Portia* may pacify the prey with monotonous repetition of a habituating signal while moving in slowly for the kill.

Trial-and-error derivation of signals may enable *Portia* to manoeuvre a prey spider into a particular orientation before attacking. Species within the family Pholcidae, for instance, are especially dangerous spiders. They have very long legs and, once a leg is contacted, pholcids defend themselves and sometimes kill *Portia*

(Jackson 1990, 1992a, 1992b). The best way for *Portia* to catch a pholcid is to grab hold of its body without first hitting a leg. Using trial-and-error signal derivation, *Portia* may coax the pholcid into a position from which a clear shot at the body is possible.

Even during encounters with spiders for which *Portia* has pre-programmed signals, trial and error may still be relevant, as the role of the pre-programmed signal may be to initiate the predatory sequence in an optimal fashion, after which adjustments are made by using trial-and-error signal derivation (Jackson & Wilcox 1998). The victim spider may, for instance, start to approach slowly, then lose interest, become distracted, or begin approaching too fast. When, for any reason, pre-programmed signals fail, *Portia* switches to trial-and-error signal derivation.

Flexibility in *Portia's* predatory strategy is a factor not only when generating signals, but also during navigation, with detouring behaviour being the most extensively studied example of this (Tarsitano & Andrew 1999). *Portia* routinely reaches prey by taking indirect routes (detours) when direct paths are unavailable (Tarsitano & Jackson 1993), including reverse-route detours' (i.e., detours that require movement initially away from prey) (Tarsitano & Jackson 1994, 1997). In encounters with some of its prey, *Portia* takes detours even when direct routes are available (Jackson & Wilcox 1993b). For example, a species of *Scytodes* Latreille, 1804 (Scytodidae), a spitting spider from the Philippines, is particularly dangerous because its preferred prey are salticids (Li *et al.* 1999). By taking detours, Philippine *Portia* approach spitting spiders from the rear, the safer end (Jackson *et al.* 1998).

That *Portia* makes pre-planned detours has been corroborated in laboratory experiments. For example, when choosing between two routes on

artificial vegetation in the laboratory, only one of which leads to a prey spider, *Portia* consistently takes the appropriate path, even when this means initially moving away from the prey, where the prey is temporarily out of view, and going past where the inappropriate path begins (Tarsitano & Jackson 1997). Lions have been observed making comparable detours when hunting their prey (Schaller 1972). The taking of detours by lions, although not studied experimentally, has also been interpreted as demonstrating planning ahead. Lions, however, are much bigger animals with much bigger brains, and they are mammals.

Salticids may have comparatively larger brains than other spiders (Meyer *et al.* 1984), but the salticid brain is still minute when compared to the much larger brains of mammals. We might envisage a brain as something more or less like a computer, and common sense tells us that a complex computer needs a lot of components. Miniaturising a computer requires miniaturised components, but miniature animals, such as spiders, do not have miniaturised neurons. As a rule, smaller animals simply have fewer neurons (Alloway 1972; Menzel *et al.* 1984), and an elementary engineering problem would seem to work against animals in the salticid's size range. With so few components, how can they orchestrate complex and flexible behaviour?

One of our long-term objectives has been to clarify how *Portia*, despite operating with a miniature nervous system, adopts a predatory strategy that rivals a lion's. *Portia's* acute eyesight raises a parallel question: how can *Portia*, a spider with eyes that are minute compared with the eyes of a cat or a person, see so well? Understanding how salticid eyes work is currently more tractable than understanding how salticid brains work, but the kinds of answers that apply to small eyes may also apply to small brains.

HOW WELL DOES *PORTIA* SEE?

In *Portia*, complex behaviour and acute vision

are tightly interrelated. For example, planning and executing detours is based primarily on seeing features of the environment (Tarsitano & Andrew 1999) and *Portia's* complex, flexible prey-capture tactics rely on using optical cues for resolving the identity and behaviour of prey from a distance (Jackson 1995; Li & Jackson 1996; Li *et al.* 1997). For example, recent research has shown that *Portia* can readily distinguish between an insect and a spider, regardless of whether the two prey are in or out of webs. Finer distinctions are made as well between different types of spiders (and different types of webs) against which species-specific prey-capture tactics are deployed. *Portia* can also distinguish between egg-carrying and eggless spiders, and the orientation of the spider. For example, *Portia* tends to approach eggless spitting spiders from the rear, whereas egg-carrying spitting spiders are approached head on.

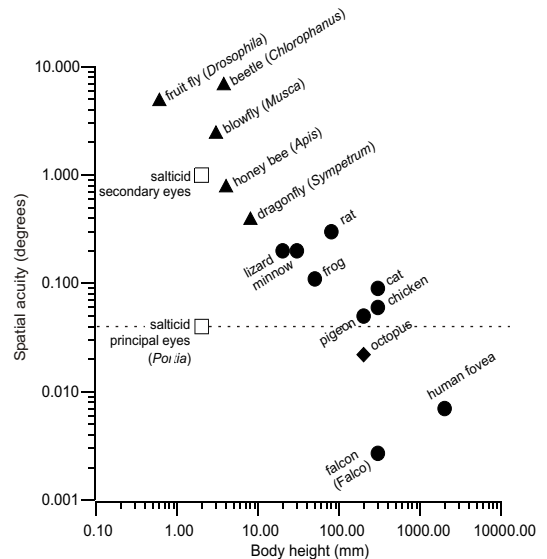


Figure 2. Spatial acuity of *Portia's* eyes compared with that of other animals. Spatial acuity (expressed approximately as minimum inter-receptor angle) plotted against body height (logarithmic scale on both axes). Triangles: insect compound eyes. Squares: salticid eyes. Circles: vertebrate eyes. Diamond = cephalopod eyes. Modified after Kirschfeld (1976). Data from Kirschfeld (1976), Land (1985, 1997) and Snyder & Miller (1978).

Good eyesight might mean a variety of things, but it is perception of shape and form that is especially relevant for understanding *Portia's* predatory strategy. Seeing shape and form depends critically on an eye's spatial acuity. Comparing *Portia* with insects, there is no known rival. *Sympetrum striolatus*, a dragonfly, has the highest acuity (0.4°) known for insects (Labhart & Nielsson 1995; Land 1997). The acuity of *Portia's* much smaller eyes is 0.04° (Williams & McIntyre 1980), exceeding that of the dragonfly by tenfold. Yet the compound eyes of the dragonfly are comparable in size to *Portia's* entire cephalothorax. The human eye, with acuity of 0.007° (*vide* Land 1981), is only five times better than *Portia's*. In practical terms, acuity of 0.04° means that *Portia* may be able to discriminate, at a distance of 200 mm, between objects spaced no more than 0.12 mm apart. Spatial acuity of other salticid eyes tend not to be far behind that of *Portia* (Harland *et al.* 1999; Jackson & Blest 1982b).

Explaining how *Portia* can see with spatial acuity more similar to that of a mammal rather than that of an insect (Figure 2) is not a trivial problem. The size difference is enormous; There are more than 150 million photocells in the human retina, but the photocells in a salticid's eyes number only in the thousands (Land 1969a).

THE DESIGN OF SALTICIDEYES

Salticids have eight eyes (Figure 3). Six of these, the secondary eyes, are positioned along the sides of the carapace and function primarily as movement detectors (Land 1971). However, it is a pair of large forward-facing antero-medial eyes (called the 'principal eyes') that give salticids their catlike appearance, and these eyes are responsible for acute vision.

Compound eyes, as found in most insects, are absent in spiders. Spiders have what are known as 'camera eyes', Mammals also have 'camera

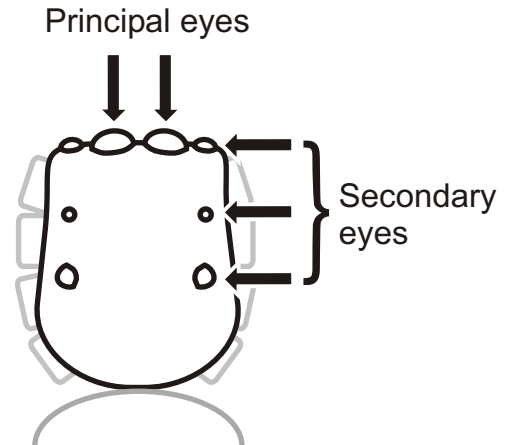


Figure 3. Salticid eyes. Secondary eyes alert salticid to nearby movement. Principal eyes, with high spatial acuity, allow salticid to detect fine details and identify distant objects.

eyes', but salticids' principal eyes are, in their details, very different from the camera eyes of mammals or any other animals. Many of these details appear to be solutions to the problem of accommodating a high-resolution eye in a small body, as neither compound eyes nor spherical humanlike eyes would seem to be feasible for a spider. Compound eyes with acuities approaching those of *Portia's* principal eyes would not be supportable on a body of *Portia's* size, and there is insufficient space inside *Portia's* body for humanlike spherical camera eyes of equivalent acuity (Land 1974).

What we know about the structure of the principal eye and the function of its components can be illustrated by following the path taken by light passing into the eye. On the outside are the two large corneal lenses. These lenses have long focal lengths (i.e., they are good at magnifying distant objects). Having binocular overlap, the combined field of view of the two corneal lenses covers an ambit of roughly 90° in front of the salticid. However, a retina that could sample this whole field at once with the kind of acuity implied by salticid behaviour would have to be so large that it could not begin to fit inside the

salticid's principal eye. The solution is surprising. There is a long, narrow eye tube behind each corneal lens, with a small retina at the end (Figure 4). The retina's horizontal field of view is only 2-5° (Land 1969b), much less than the 90° taken in by the corneal lenses.

On the basis of appearance this pair of corneal lenses and pair of long eye tubes resembles a pair of binoculars. This resemblance is more than superficial. Just before reaching the retina, light passing down the eye tube encounters a second lens (a concave pit) that augments the magnifi-

cation of the corneal lens. This means salticid principal eye is a telephoto system because the corneal lens has a long focal length and a second lens at the rear of the eye tube magnifies the image from the corneal lens (Williams & McIntyre 1980).

Light imaged through the telephoto-lens comes into focus on a complex retina. The human retina is arranged in a single plane, but the salticid receives light successively on four layers of receptors, stacked along the light path. This tiered arrangement functions critically in colour

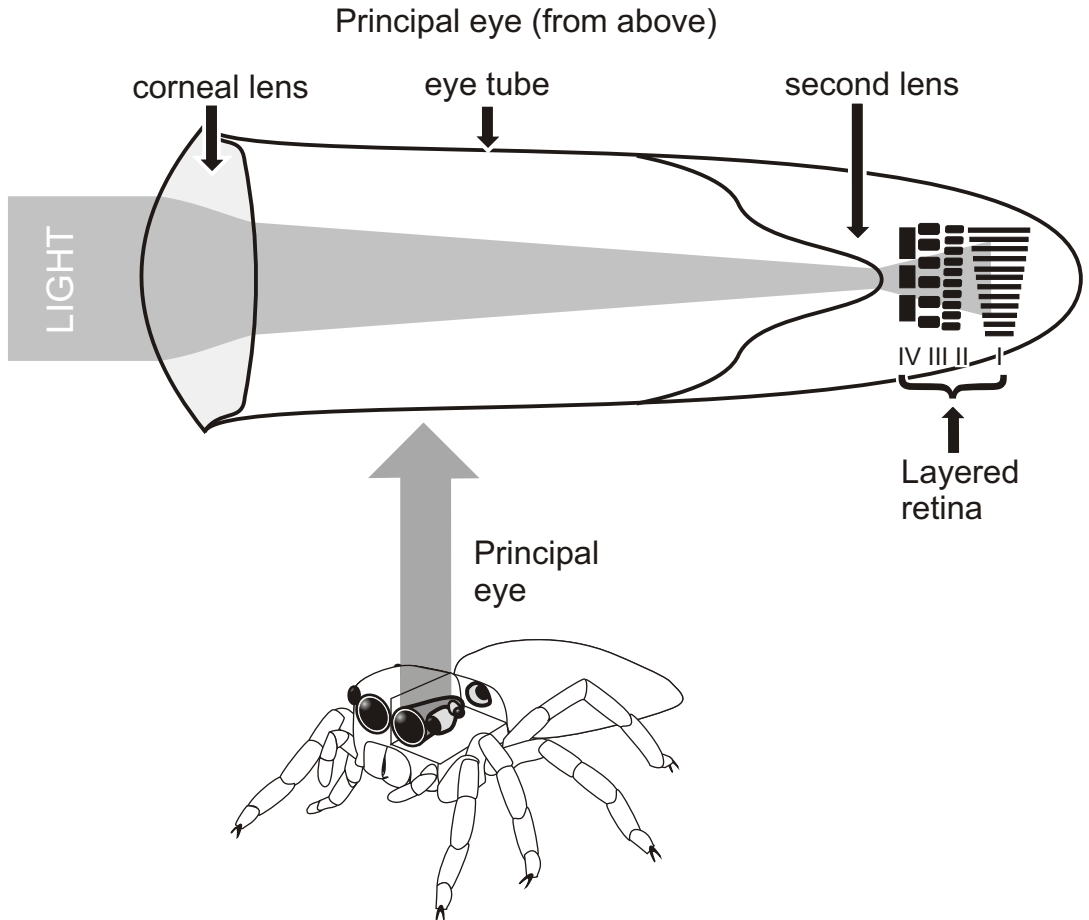


Figure 4. Internal structure of the salticid principal eye. Below: position of eye in cephalothorax: Above: light passes through a corneal lens and down an eye tube where it is magnified by a second lens before falling onto a four-layered retina. Layers II-IV function in colour vision. Layer I functions in high-acuity perception of shape and form.

vision (Land 1969a). Light entering each principal eye is split into different colours (chromatic aberration) by the corneal and secondary lenses. Different wavelengths (colours) of light come into focus at different distances, and these distances correspond to the positions of different layers in the retina. Using this system, salticids discern green, blue and ultraviolet (Blest *et al.* 1981).

For understanding perception of shape and form, it is the rearmost layer (i.e., the green layer; called 'layer I') that matters because only here are receptors spaced close enough together to support high-acuity vision (Blest *et al.* 1990). There is a central region of layer I, called the 'fovea', where receptors are especially close together (inter-receptorspacing of about 1 micron). Spacing at 1 micron seems to be optimal. The telephoto optical system is precise enough to let the retina sample at this resolution, but spacing any closer than this would reduce the ability of the retina to sample the image because of quantum-level interference between adjacent receptors (Blest & Price 1984; Williams & McIntyre 1980).

Two factors critically influence the acuity of an eye, the quality of the receptor mosaic and the quality of the image (Land 1981). One problem with maintaining a good image quality is that objects at different distances in front of the eye come into focus at different distances behind the lens. This means that, when a close object is in focus, a more distant object is likely to be out of focus. Ability to accommodate (by changing the shape of the lens) solves this problem in our own eyes, but this is not the solution adopted by salticids. Unlike our own eyes, or a pair of binoculars, the salticid principal eye cannot be focussed. Instead, a clever arrangement of the layer I receptors makes focal adjustments unnecessary. Different parts of layer I are positioned on a 'staircase' at different distances from the lens. This means any object, whether only a few centimetres or many metres in front of

the eye, will cast an in-focus image on some part of the layer-I staircase (Blest *et al.* 1981). Another surprising feature of the salticid principal eyes makes this solution work. The eye tubes can swing side to side while the corneal lenses remain static. This means that the salticid can sweep the staircase of each retina across the image generated by the corneal lens. However, eye-tube movement may have significance that goes beyond solving the focussing problem.

The human eye and the salticid principal eye are similar in that a high-acuity central region (a fovea) is used for resolving fine detail, but there is a major difference in scale. The fovea in each of *Portia's* principal eyes has a field of view only 0.6 degrees wide and contains only a few hundred receptors, yet *Portia* somehow uses this miniature system for routinely making the fine-scale distinctions necessary to sustain its complex vision-guided behaviour. How this is achieved is not fully understood, but eye-tube movement may be the key.

Six muscles attached to the outside of each principal eye tube allow the same three degrees of freedom (horizontal, vertical, and rotation) as in each of our own eyes (Land 1969b). Using these muscles, the salticid sweeps the two eyes' fields of view in complex patterns over the scene coming into the eye from the telephoto lens system.

Eye-tube movement enables the salticid to sample from the larger image projected by the corneal lens, and patterns of movement can be complex. This suggests that eye-tube movement patterns are intimately involved in how salticids process visual information, serving as critical steps in the perception of shape and form (Land 1969b). One intriguing possibility is that, by using specific patterns of eye-tube movement, a salticid may search images for particular pieces needed for arriving at perception of specific objects.

PORTIA'S LIMITATIONS

Extensive sampling may be the salticid's answer to the problem of how to see details of shape and form within the constraints imposed by small size, but speed of perception may be a primary limitation. From many years of studying *Portia*, our impression is that, although these spiders' feats of discrimination are impressive, they are often strikingly slow on the uptake. It may be that *Portia* can see more or less what we can see, but achieves this by means of a slow scanning process. Part of what it means to say an animal 'sees well' should perhaps be that it perceives what is out there quickly. On this criterion, *Portia* may see only poorly.

Another potential limitation is that the small size of *Portia's* fovea may limit perception of large objects. Images of small features of animals (e.g., a palp, leg or eye of a spider) may be more or less easily sampled by the salticid fovea, whereas sampling critical body parts of larger animals may be exceedingly difficult. When *Portia* scans with its foveas across smaller objects, such as its usual spider prey, piecing together a 'picture' of what it is looking at may be much more feasible than when scanning in a 'picture' of a larger animal such as a bird, a frog or a large mantis, all of which are relevant to *Portia*. Mantises, for instance, readily prey on *Portia*, yet *Portia* typically shows no evidence of taking appropriate precautions when coming face to face with these deadly foes. Our impression is that *Portia* often looks at large mantises and then fails to discern what they are.

When it comes to seeing, it seems that *Portia* has made efficient use of its limited materials and overcome many, but not all, of the limitations imposed by small size. The same basic principle may apply to cognition. It may be that by making efficient use of limited brain resources (neurons), *Portia* can achieve considerable cognitive skills, such as problem solving and planning ahead, all the while suffering limitations

comparable to those that apply to seeing. For example a big difference between *Portia* and cats may be the speed at which problems are solved.

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