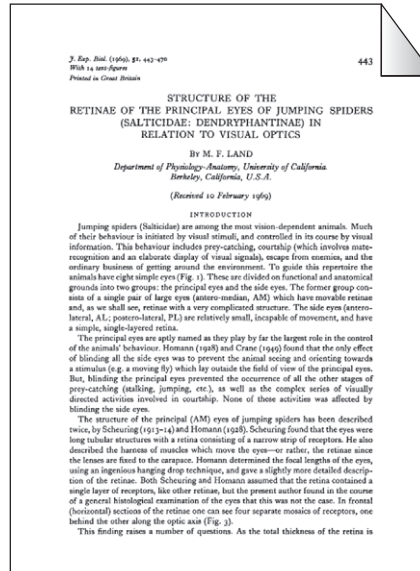


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JEB CLASSICS

ONE SMALL LEAP FOR THE JUMPING SPIDER BUT A GIANT STEP FOR VISION SCIENCE



Robert R. Jackson and Duane P. Harland discuss Mike Land's 1969 back-to-back papers entitled: 'Structure of retinæ of the principal eyes of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics' and 'Movements of the retinæ of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli'.

Copies of the papers can be obtained from <http://jeb.biologists.org/cgi/content/abstract/51/2/443> and <http://jeb.biologists.org/cgi/content/abstract/51/2/471>.

Weasels may be cunning, we might admire the intelligence of dogs and cats, but we can be forgiven for expecting the jumping spider, a diminutive predator with a brain not much bigger than a poppy seed, to be one of Descartes' automatons. Yet, jumping spiders, also known as salticids, alternate between entertaining and alarming us by planning prey-capture tactics ahead of time, adjusting their hunting behaviour in accordance with how the prey responds and giving us other examples of un-spider-like acumen (reviewed by Harland and Jackson, 2004). Underlying salticid behaviour, there is a more basic defiance of common sense. We may think that spider-size eyes are simply not suitable for seeing a lot of detail, but salticids seem to be telling us to think again. Here we have a celebrated example of how seeing with high spatial acuity can be achieved at a high level by a lowly animal working under severe size constraints.

The salticid-eye literature has its classics, a pair of papers that came out of Berkeley back in the turbulent 1960s when Berkeley's nickname was 'Berserkeley' and a young Englishman at the University of California, Mike Land, was carrying out his

staggeringly elegant research on salticid eyes. In 1969, the year when, 380,000 miles away, people were walking on the Moon, these papers appeared as 51 back-to-back pages in the *Journal of Experimental Biology* (Land, 1969a; Land, 1969b) and they have defined how we think about salticids ever since.

Hans Homann (Homann, 1928), along with Ludwig Scheuring (Scheuring, 1913-1914) and others, had already shown us the basics of how spider eyes are structured, and the behavioural studies of Karl Heil (Heil, 1936), Jocelyn Crane (Crane, 1949) and Oskar Drees (Drees, 1952), along with George and Elizabeth Peckham in the 19th century (Peckham and Peckham, 1887), had already told us that there was something special about salticid vision. These earlier researchers were the giants on whose shoulders Land stood when he saw further into what is special about how salticids see.

Berkeley settled down, people stopped walking on the moon and Land went to the University of Sussex where he got busy becoming a foremost authority on animal eyes (Land and Nilsson, 2002). Yet the style of research that became Land's hallmark was already abundantly evident in 1969 – comprehensive, with a clear focus on linking structure to the visual tasks that in turn support the animal's behaviour in its natural habitat.

Salticids, like most spiders, have eight eyes, the front-most pair (anterior-medial) being called 'principal eyes' and the rest being called 'secondary eyes' (Fig. 1A). Salticids have unusually large principal eyes and, before Land came along, it was already known that these eyes are especially important for discerning details about the appearance of the objects being viewed. These are the eyes Land considered in the 1969 classics.

The most striking discovery in the first paper was that the principal-eye retina is organized into four tiers of receptors (Fig. 1C), with light passing first through Layer 4 and then successively through Layer 3 and 2 before finally reaching Layer 1. In fact, what Land gave us, derived from serial 10 µm thick wax sections along the anterior-posterior and dorsal-ventral axes, was a remarkably detailed 3-dimensional understanding of the internal structure of the principal eye and he also showed that primary neural fibres from the receptors of each layer of the retina terminated in layer-specific areas in the part of the brain to which the optic nerve is attached.

As Land unfolds the principal eye's design details in this paper, we are confronted with

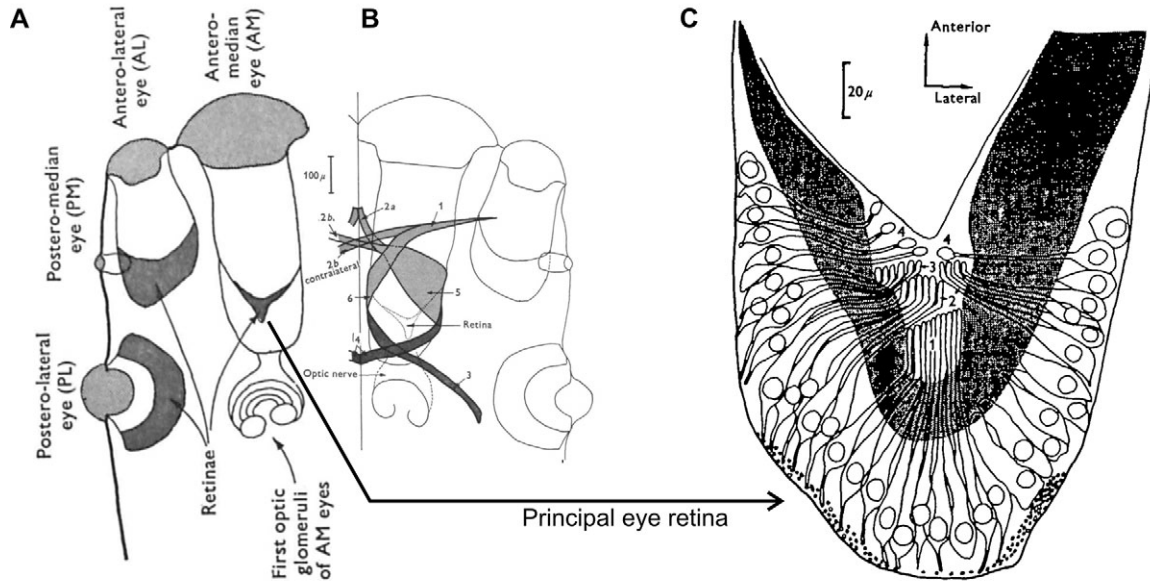


Fig. 1. Salticid eye structure. (A) General layout of salticid visual system as seen through left-hand side of cephalothorax. (B) Principal-eye tube muscles as seen through right-hand side of cephalothorax. (C) Section through central part of principal-eye retina showing receptor layers (numbered), pigmented matrix (dark) and intermediate segments (cell bodies with nuclei). A and C reproduced from Land (Land, 1969a). B reproduced from Land (Land, 1969b).

the vexing question of what on Earth these eyes are designed to do. Later Land studied the salticid's secondary eyes (Land, 1971) and their resolution is probably good enough to support a wide range of vision-guided behaviour, being comparable to that of typical vision-guided insects. It is just that the principal eye's spatial resolution is so much better, but for doing what?

If you want to know how good the principal eye's spatial resolution is, the answer depends on where you are in the salticid's principal-eye retina. The best spatial resolution (0.2 deg.) is in a central ('foveal') region in Layer 1. To put this into perspective, 0.2 deg. is the kind of resolution we might expect for a mammal or a bird eye but not for a small arthropod eye. Out of the details in this classic paper on the structure of the principal eye's retina, there emerges an unsettling suspicion that, with this unfamiliar design, the principal eye has an unusual, specialised role in vision. In the 1980s, this paper of Land's and the extraordinary spatial acuity of Layer 1 became the impetus for David Blest's laboratory at the Australian National University making major advances in our understanding of how salticids see.

Besides the conventional approach of making measurements from sectioned material when calculating Layer 1's spatial acuity, Land designed and built an experimental ophthalmoscope and this gave him a truly innovative way of directly determining the lens' focal point within the retina. Later, in Blest's laboratory, Land's

ophthalmoscope design was important when Williams and MacIntyre (Williams and MacIntyre, 1980) demonstrated that a pit at the rear of the principal-eye tube functions as a lens, turning the salticid principal eye into a Galilean telescope. By showing the salticid achieves even better spatial acuity than Land had demonstrated, this ranks as one of the most important post-Land salticid-vision discoveries.

Layer 1 is only a part of the salticid principal-eye story. Land also considered the evidence for two hypotheses concerning why the retina is in layers. He favoured the hypothesis that the tiered retina functions in colour vision, by taking advantage of chromatic aberration resulting from light passing through the corneal lens. Light of different wavelengths ends up in focus at different distances from the corneal lens and Land proposed that, by concentrating photoreceptors with corresponding sensitivities in different layers of the retina, the salticid would have an especially effective eye for the task of colour discrimination. The most elegant corroboration of Land's colour-vision hypothesis came later, again from Blest's laboratory, in a study based on optics and intracellular recording from receptors known to be located in different layers of the principal-eye retina (Blest et al., 1981). As predicted, peak sensitivity to specific wavelengths coincided with appropriate retinal layers.

Land's other hypothesis was that, owing to each layer receiving in-focus images from

objects at different distances in front of the eye, layering might function as a way to expand the eye's depth of focus. Later, once again in Blest's laboratory, this hypothesis was shown to work, but applied now to Layer 1 alone instead of to layering of the retina as a whole. Distal tips of light-guiding receptive segments in the fovea of Layer 1 form a staircase-like structure such that objects at a wide range of field depths will be in focus somewhere on the 'staircase' (Williams and McIntyre, 1980).

In short, Land's first paper showed us the surprising design features of the salticid's principal eyes, including the four-tiered retina covering a tiny field of view, and laid the groundwork for understanding how these unique eyes enable so small an animal to see with such remarkable spatial acuity.

The second of the classic papers (Land, 1969b) has also fundamentally transformed the way we think about the salticid's eyes. These eyes have elaborate ways of moving about. They have behaviour. Each principal-eye tube is shaped something like a windsock and, from wax sections, Land carefully reconstructed how three pairs of muscles are positioned around each eye tube (Fig. 1B) and, again with the ophthalmoscope being a key innovation, he characterized the intricacies of how the eye tubes move. With the ophthalmoscope, Land peered through the salticid's corneal lens while the salticid was gazing at simple stimuli silhouetted against a uniform, bright background. Imaged through the principal

eye's own optics, the field of view of the visible parts of the retina was directly observable with the ophthalmoscope (Fig. 2A).

Using painstaking 1960s technology, Land discerned details of the eye's behaviour by continuously turning knobs adjacent to the ophthalmoscope's eyepiece that caused a reticule to remain centred on the image of the retina (Fig. 2B) and gave him plotter traces that revealed four basic classes of eye-tube movement. During 'spontaneous movement', the eyes swept, apparently at random, either in tandem or not, across the scene. 'Saccades' were rapid shifts in the positioning of the eye tubes, resulting in fixation on different parts of the image that the spider was viewing. 'Tracking' was an in-tandem movement by which the retina

was kept oriented on a moving image. However, the most intricate class of movement was what Land called 'scanning', this being something that appears to be unique to salticids.

Consisting of a regular pattern of periodic horizontal movement simultaneous with slower rotational movement (Fig. 2C), scanning was typically preceded by a saccade to a new stimulus. Land concluded that this intriguing behaviour of the eye functions somehow as a mechanism for determining target shape or form. For example, he proposed that, after achieving a specific angle of rotation, horizontal movement of the lined-up retinas might function as a mechanism by which the eye searches for lines oriented at the specific angle to which the eye tubes have been

rotated (Fig. 2D), in this way enabling the salticid to find the key features (or sign stimuli) that identify the object being viewed.

We should remember that 1969 was not so long after the heyday of ethology when salticids were envisaged as instinct-driven animals that went through life making only simple decisions. Drees (Drees, 1952), for example, had experimental evidence suggesting that the salticid's sign stimulus for courtship and threat displaying was seeing legs (lines) at a particular angle to a body (i.e. representing a potential mate or conspecific rival), with anything else of similar size being a sign stimulus for attacking and eating (i.e. representing prey). Taking his lead from Drees, Land considered how scanning might be used for

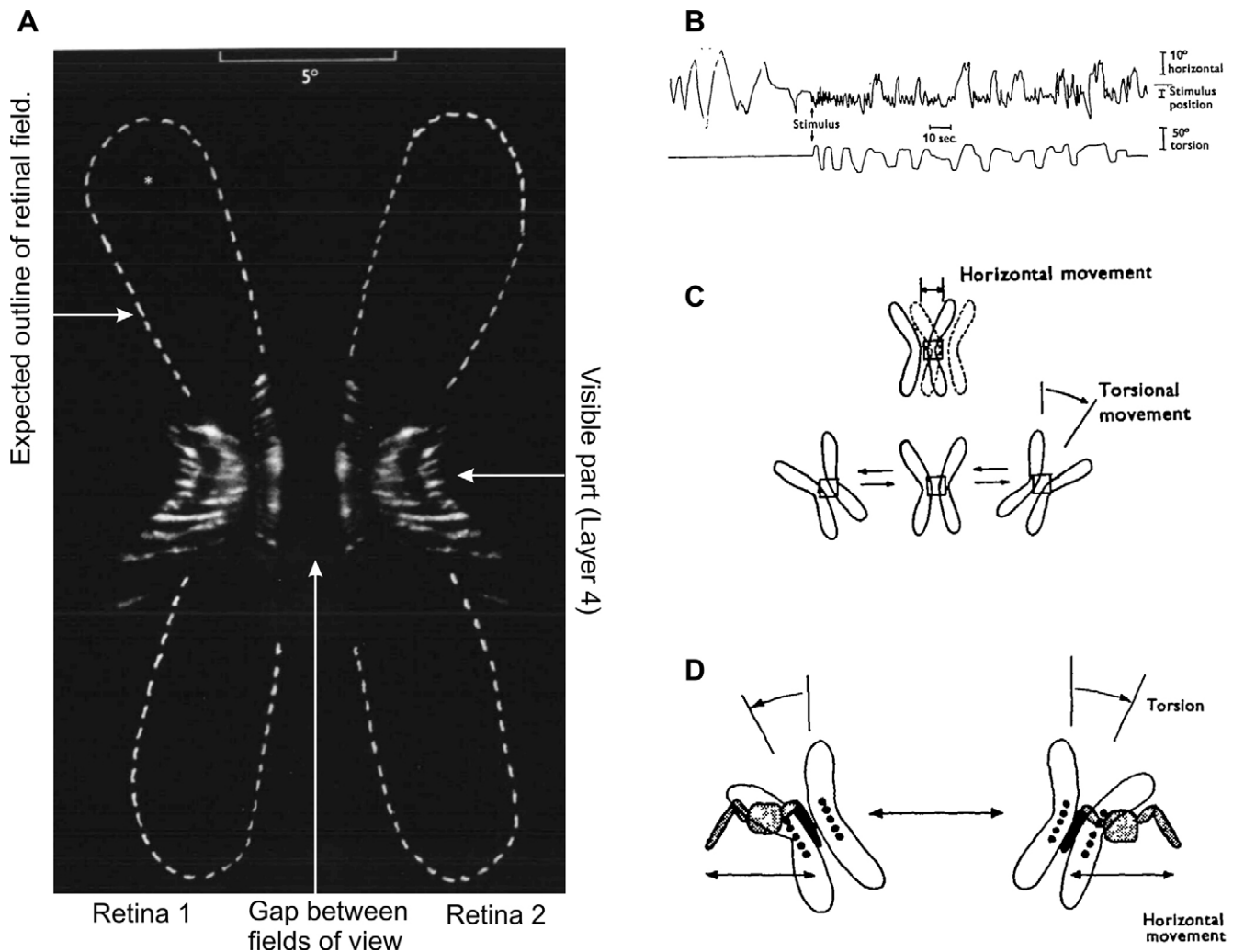


Fig. 2. Salticid eye movement. (A) Principal-eye retina photographed through ophthalmoscope. Visible features primarily intermediate segments from Layer 4. Full extent of retina (not visible in photograph) indicated by dashed line. Note: in cross-section each retina is shaped like a boomerang and there is a gap (blind spot) between the two retinas. (B) Example of trace plotted from ophthalmoscope while salticid views line-and-dot drawings. (C) Salticid scanning with principal eyes while viewing a simple stimulus (a square). Note: scanning, the most elaborate of four categories of eye behaviour discerned by Land, is based on two modes of movement (translational, which is horizontal in this example, and rotational or, to use Land's expression, torsional). (D) Illustration of Land's hypothesis concerning how salticid might be using scanning to search for legs (lines) at specified angles. (From Land, 1969b.)

distinguishing between something to display at and something to eat. Yet it is interesting that, even way back in 1969, Land acknowledged that the salticid's task could not really be that simple, and he was right.

What we now know about salticid vision-based behaviour goes beyond what Drees, and Land, could have sensibly considered 40 years ago. For example, we now appreciate that, by sight alone, salticids can distinguish between many different categories of prey and, while relying on subtle visual cues, salticids adjust their prey-capture behaviour in response to their prey's behaviour and orientation. Yet Land's scanning hypothesis continues to be the most elegant and well-supported proposal for how the salticid might be using its unique mobile eyes in its day-to-day life, but we should now be considering whether there are intricacies in the principal-eye scanning routines that correspond to different categories in the salticid's intricate prey-classification scheme.

One of us (R.R.J.) still remembers long ago, in Berkeley, when Land casually said something about how watching a salticid scan feels almost like watching it think. Talking about animals thinking was taboo back then, making it easy to dismiss this classic Land remark as facetious. Four decades later, maybe it no longer sounds that way.

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