MOVEMENTS OF THE RETINAE OF JUMPING SPIDERS (SALTICIDAE: DENDRYPHANTINAE) IN RESPONSE TO VISUAL STIMULI

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INTRODUCTION

Eye-movements play an important role in vision in most vertebrates, especially those with specialized foveal regions, and have been reported from invertebrates in cephalopods and a variety of crustacea. Homann (1928) and Kaestner (1950) found that the principal eyes of jumping spiders were also movable, and Dzimirski (1959) was able to show that in young, transparent spiders (Marpissa radiata) a typical optokinetic nystagmus could be induced by a moving pattern of stripes. These eyes are interesting because they present what is possibly the simplest case of true form vision in the animal kingdom; using them a jumping spider can make the difficult distinction between potential prey (flies, etc.) and potential mates (other jumping spiders) at distances of at least ten body lengths (5-10 cm.) (Heil, 1936; Drees, 1952). At such a distance the image of the target—spider or fly—covers at the most 100 receptors. The present inquiry sets out to determine the role of eye movements in the location and identification of targets in the field of vision of these eyes.

The development of a new ophthalmoscopic technique has made it possible to examine the retinae, and their movements in all directions, while at the same time presenting the retinae with a variety of visual stimuli. This has permitted the description and quantification of these movements and to some extent the assessment of their role in the animal’s normal behaviour. The most surprising discovery reported here is that in situations where pattern recognition can be presumed to be taking place, the retinae indulge in an elaborate and unique ‘scanning’ process, in which both retinae move back and forth across the target, while at the same time partially rotating about the visual axes of the eyes.

MATERIALS

Three species of jumping spider, Phidippus johnsoni (Peckham) Metaphidippus aeneolus (Curtis) and M. harfordi (Peckham), were collected locally. They were kept in Petri dishes containing pieces of damp cotton wool, and were fed on houseflies once a week until used. Adult P. johnsoni are 8–11 mm. in length and both Metaphidippus species are between 4.5 and 5.5 mm.
METHODS

Histology

Complete transverse and longitudinal series of sections were made of the heads of *P. johnsoni* and *M. aeneolus*. These were prepared from Bouin-fixed, paraffin-embedded material, and were stained with either Mallory's trichrome stain or haematoxylin and eosin. Reconstructions of the eye-muscles were made by photographing every section containing eye-muscle, enlarging it, and superimposing tracings of the photographs.

Ophthalmoscopy

To observe the retinae and their movements, an ophthalmoscope was designed and built (Text-fig. 1 a). The instrument consists of two parts: a stimulating light-path which illuminates the retinae, and in which targets to be seen by the retinae can be placed, and an observing path at right angles to stimulating path through which the observer can examine the retinae and record their movements. The two light-paths share the same final objective, and are separated behind it by a beam-splitter.

The stimulating path consists of a light source (a 6 V. car headlamp bulb) whose light is collimated by a condenser lens *L*₁; this light is focused at *x* by *L*₂, is collimated again by *L*₃, and is finally focused on the corneae of the eyes by the microscope objective *L*₄. *L*₂ and *L*₃ are arranged so that light from points on the stimulus plane *y* is collimated by *L*₂ and focused by *L*₃ on to the back focal plane of the objective *L*₄.
This light emerges from the objective as a series of parallel bundles from each point on \( y \), and the lens of the animal’s eye focuses this light to form an image of \( y \) on the retina. Thus the filament of the lamp is conjugate with \( x \) and with the cornea, and \( y \) is conjugate with the back focal plane of the objective and with the retina. The eye therefore sees any target placed at \( y \) against a uniform, circular Maxwellian field of view 29° in diameter (using a 16 mm. objective, N.A. 0.25). A series of aperture stops is placed at \( x \) to restrict the image of the filament on the animal’s head to just the area of the cornea, thereby minimizing stray light. Either four or two apertures can be used, permitting the target at \( y \) to be seen by both the antero-median (AM) and antero-lateral (AL) eyes (Text-fig. 2), or by the antero-median eyes alone. These aperture stops contain central black spots which just cover the areas of the corneal reflexes.

The viewing beam consists of a telescope \((L_5 \text{ and } L_6)\) focused on infinity. When the auxiliary lens \((L_7)\) is not in the light path, \(L_6\) forms an image of the cornea at \( z \), because the cornea is at the front focal plane of the microscope objective \(L_4\). However, with \(L_7\) in position, an image of the retinae is formed at \( z \), because \(L_7\) is focused on the back focal plane of \(L_4\), and this is conjugate with the retinae. Thus by moving \(L_7\) the observer can view either the cornea (for aligning the preparation) or the retinae. An aperture stop above \(L_6\) and an opaque dot between \(L_6\) and \( z \) help to occlude stray light, which comes chiefly from reflexions from the components of the microscope objective \(L_4\).

In the case of the antero-lateral eyes of jumping spiders, whose retinae have a simple structure and act as good diffuse reflectors, it is possible to make out not only the outlines of individual receptors, but also the image on the retina of any target placed at \( y \). In the antero-median eyes only the uppermost layer of receptors (layer 4; Land, 1969) reflects light well, but it is possible from the appearance of this layer to infer the positions of the other retinal structures (Pl. 1).

The stimuli used to elicit eye-movements were black dots and lines of various dimensions and orientations. More complex shapes were also used occasionally. They could be presented to any part of the spider’s field of vision by means of a manipulator at \( y \) to which the stimuli—opaque areas on transparent plastic plates—were attached. Movement of a lever on the manipulator brought the stimuli from outside the Maxwellian field to predetermined points within it in about \( \frac{1}{40} \) sec. Stimulus presentation was thus always accompanied by movement.

Observations were made on live, active animals. They were restrained by means of a small strip of card which was waxed to the top of the prosoma and attached to a micromanipulator, permitting the animal to be aligned exactly with the optic axis of the ophthalmoscope. The spider held a light card ring between its feet, round which it could walk at will without moving its body. The intensity of the light-source was adjusted so that the luminance of the Maxwellian field was similar to that of a white surface in diffuse sunlight \((10^4 \text{ cd./m}^2)\). The flux at the retina was approximately \(1.4 \times 10^{-3} \text{ lm./mm}^2\) or \(5 \times 10^{-9} \text{ lm. per } 2 \mu \text{m. diameter receptor. The system was calibrated using the method given in Westheimer (1966). Large changes in intensity (± 1 log unit) did not appreciably affect the kinds of eye-movements made by the spider.}

**Eye-movement recording**

Movements of the retinae of the antero-median eye were recorded by means of a graticule line in the image plane \((z)\) which could be moved laterally, or rotated about
the optic axis of the instrument (Text-fig. 1b). The observer manipulates two control levers and endeavours to move these controls in such a way that the graticule line is always between and parallel to the inner edges of the images of the two retinae (see Pl. 1a and Text-fig. 5). The controls are geared to potentiometers, which transduce their movements, and these movements are thence recorded on a two-channel pen-recorder. The records are calibrated by removing the spider, and replacing it by a scale at a large distance from $L_4$ (e.g. a centimetre scale at 57 cm.; 1 cm. = $1^\circ$).

This method of recording has obvious limitations, imposed mainly by the observer's inability to respond sufficiently quickly to rapid movements; in general, eye-movements which are faster than about $10^\circ$/sec. cannot be accurately recorded. This means that recordings of 'saccades' indicate accurately only their amplitude and the slow time-course of recovery, and recordings of 'spontaneous activity' indicate the frequency and approximate amplitude of this behaviour, but not its 'waveform'. Fortunately, in 'scanning', the eye-movements are slow, periodic and of small amplitude, and the records reproduce reasonably faithfully their frequency and amplitude. It is immediately clear to the observer when he can or cannot follow particular movements.

**Cinematography**

An alternative method of recording eye-movements is to photograph the moving eye-tubes in animals whose carapaces are sufficiently transparent for this to be possible. This was the method used by Dzimirski (1959). It has the limitation that only movements in the horizontal plane can be studied, but it provides a useful check on observations derived from ophthalmoscopy (Text-fig. 6).

**RESULTS**

**Anatomy of the eye-muscles**

The muscles which move the principal (antero-median) eyes have been described once before by Scheuring (1913–14). The present description confirms most of Scheuring's observations, but extends them with a description of the oculo-motor nerves, and with a re-evaluation of the contributions of the various muscles to the movements the eyes are now known to make. The numbering system used here differs from that of Scheuring as shown in Text-fig. 3. This description is based on serial sections of *M. aeneolus*, and on dissections of *P. johnsoni*.

There are altogether six muscles attached to each eye, and these can be divided into three pairs (Text-figs. 2, 3). A pair of muscles (1 and 2) are attached to the ventral surface of the eye-tube, about half-way between the lens and the retina. Both muscles insert into the carapace on the ventral internal surface of the clypeus, immediately in front of the falces; muscle 1 inserts laterally, while muscle 2 has two branches, one of which (2a) inserts close to the midline and the other (2b) crosses the midline and joins with the contralateral muscle 1, sharing the same point of insertion on the clypeus. A second pair of muscles (3 and 4) arises from the dorsal surface of the eye-tube behind the retina; muscle 3 inserts on the carapace laterally, just medial to the postero-lateral eye, and 4 inserts on the midline. In addition to these four muscles there are two thin but wide bands of muscle, designated 5 and 6, which encircle the eye-tube medially (6) and laterally (5), apparently joining the regions of attachment of
Text-fig. 2. Scale reconstruction of the muscles of the left antero-median eye of *M. aeneolus*, seen from above. The portions of those muscles lying beneath the eye, and which would not be visible, are shown in lighter stipple.

Text-fig. 3. Scale reconstruction of the muscles of the left antero-median eye of *M. aeneolus*, seen from in front. The numerals in parentheses indicate Scheuring's numbering system.
the dorsal and ventral muscles. In dissections the muscle system gives the appearance
of having only two distinct continuous parts, comprising muscles 1–6–3 and 2–5–4.
I am unable to confirm the presence of a ventral muscle joining the two eyes together
(Scheuring’s muscle 4).

Text-fig. 4. Diagram showing the paths of the six axons of the oculomotor nerve to the left
antero-median eye. The drawings on the right are transverse sections of the nerve (as viewed
from the anterior end of the animal) at the indicated levels.

All six muscles contain apparently unstriated fibres. The dorsal muscles each contain
about 12 fibres approximately 2 \( \mu \text{m} \) in diameter; in the ventral muscles the fibres are
of similar thickness, but are more numerous, with about 20 fibres in 1 and in each part
of 2. The circumferential muscle sheets are only 1–2 fibres thick.

Innervation

The eye-muscles are supplied by a pair of nerves (not previously described) which
originate in the posterior part of the brain just above the oesophagus (i.e. in the trito
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Each nerve passes anteriorly around the brain to a point just beneath the first optic glomerulus of the antero-median eye, and then it passes forward beneath the eye itself. When it leaves the brain each oculo-motor nerve contains only 6 axons, about 2 μm in diameter. The course of each axon was traced, section by section, from the brain to the point at which it entered an eye-muscle and became impossible to follow. It was found that although some of the axons divided once or twice before reaching their goals, all the branches of any one axon terminated in only one of the muscles described above (Text-fig. 4). In each of the four externally attached muscles (1–4) the axon entered the muscle close to its insertion on the eye; the remaining two axons entered the circumferential muscles (5 and 6) in their antero-ventral portion.

A search for other nerves supplying the eye muscles failed to reveal any, and so it can be concluded that each of the six eye-muscles is a single motor unit, whose functional boundaries are similar to those given in the anatomical description, and whose state of tension is controlled by the activity in a single axon.

Function

Ophthalmoscopic observation of the retinae in the live animal shows that there are basically two kinds of eye-movements; displacement and torsion. In displacements the retinae are moved from one position to another in a vertical plane at right-angles to the optic axes of the eyes (or more correctly over part of a sphere centred on a pivot-point close to the back surface of each lens). These movements may be in a dorso-ventral or latero-medial direction, or along any vectorial combination of the two. It is obvious that these movements are performed by the four muscles (1–4) that are attached to the carapace. It can be seen from Text-fig. 2b that, as a first approximation, one can regard these muscles as being arranged as two antagonist pairs (1 and 4, 2 and 3) operating at right angles to each other. Any change in the pattern of tension in these four muscles (or in the pattern of activity in the four axons supplying them) will result in a displacement of the retina, and the new pattern will be reflected in the new position which the retina adopts, approximately according to a parallelogram of forces rule. The dorsal and ventral muscles will not have to contract to the same extent to produce displacement movements of the same aptitude, because the dorsal muscles (3 and 4) insert on to the eye about 2.5 times as far from the pivot-point as do the ventral muscles (2 and 3) (the eye-tube pivots from a point about 50 μ behind the rear surface of the lens). To produce a 1° displacement of the retinae a dorsal muscle must contract by approximately 7.7 μ, but a ventral muscle by only 3.1 μ (in M. aeneolus).

Torsion movements are defined as those in which the retina rotates about an axis joining the centre of the retina to the nodal point of the eye (i.e. about the axis of the eye-tube). They occur during ‘scanning’ (see p. 484) and may be as great as 30° in either direction. They could be mediated either by the circumferential muscles (5 and 6) or possibly by the translational muscles contracting in pairs (1 and 4, 2 and 3). The latter suggestion, however, is unlikely because it implies that torsion ought to accompany certain displacement movements, especially during ‘saccades’ and ‘scanning’ (p. 482); one does not, however, observe the kinds of torsional movements that this suggestion would predict. The other reason for thinking that the circumferential muscles are involved in torsional movements is that there is nothing else they could be doing—their only other possible function would be to change the length of...
the eye-tube (accommodation), but such changes, which would be readily detected by ophthalmoscopy, have not been observed. The mode of operation of the circumferential muscles would be as follows: the antero-ventral end of each muscle band, being nearest to the lens, will be relatively rigidly fixed with respect to the eye-tube axis, compared with the postero-dorsal end, so that the effect of contraction of one of the muscle-bands will be to twist the eye-tube drawing the postero-dorsal part of the eye (and hence the retina) down and round—clockwise or anti-clockwise depending on which muscle (5 or 6) is active.

It is concluded that six muscles move each eye, with each muscle controlled by a single axon. Four muscles are attached to the carapace and displace the retina, while the two encircling bands twist the eye-tube, causing torsional movements.

EYE MOVEMENTS

Fields of view of the retinae

The movements of the AM eyes of jumping spiders differ from those of vertebrates in that the optical system does not move with the retina. The lenses are a fixed part of the carapace, and they produce a pair of fixed images which are scanned by movable retinas.

The retinae of the AM eyes are boomerang-shaped structures, whose convex edges are directed laterally (Homann, 1928; Land, 1969). The portion of the environment from which each retina receives its image will have the same shape as the retina, but will be reversed and inverted when compared to the geometry of the retinae as they lie in the head (Text-fig. 5a). Thus the combined fields of view of the two retinae will have something like the shape of a diagonal cross, the left and right halves of which are seen by the right and left eyes respectively. This cross pattern can be thought of as the shape of the movable 'window' through which the AM eyes view the environment.

The most convenient way of specifying the position of any point on the retina, at rest or during eye-movements, is to specify its direction of regard, i.e. the direction, relative to the animal's body axis, of the nodal ray joining the retinal point to its conjugate image at infinity. Two angles specify its direction: the angle in the horizontal plane between the ray and the animal's sagittal plane, and the angle in the vertical plane between the same ray and a horizontal reference plane containing the optic axes of the eyes.

Text-figures 5a and b illustrate how the direction of regard is related to the ophthalmoscopic image. Because all light from a single point on the retina emerges as a parallel bundle, and because all rays whose direction is the same are imaged at a single point on the ophthalmoscopic image, this image can be used to determine directly the direction of regard of those parts of the retinae that this technique makes visible. It is clear from Text-fig. 5b that the ophthalmoscopic image has the geometry of the combined field of view of the retinae, rather than of their configuration in the head. Further, the angles that specify the direction of regard of points on the retina can be obtained directly by calibrating and making measurements on the ophthalmoscopic image. Eye-movements cause changes in the direction of regard of the retinae, and these too can be measured directly in degrees, using the ophthalmoscope. Angular measurements made in this way will be used throughout the remainder of this paper.
To convert these angular measurements into distances on, or moved by, the retinae, they must be converted to radians and multiplied by the focal lengths (posterior nodal distances) of the eyes. In *M. harfordi* and *M. aeneolus* the focal lengths of the AM eyes are between 500 and 600 μm. (Land, 1969), which means that a distance of 10 μm. measured in the plane of the retinae, corresponds to a visual angle of very nearly 1°.

**Text-fig. 5.** Relation of the fields of view of the retinae to the ophthalmoscopic image. (a) Approximate fields of view of the AM retinae, projected onto a sphere at infinity (see text). (b) Image formation by the ophthalmoscope objective. The image has the same configuration as the fields of view of the retinae (see Pl. 1).

**Resting position**

When the animal is not active, and the eyes are not in motion, the retinae adopt a characteristic resting position. This is shown in Pl. 1. The only structures in the retina which are made visible by ophthalmoscopy are the intermediate segments of the receptors in the most superficial layer of the retina (layer 4, see Land, 1969, fig. 7);
however, the positions of the other parts of the retinae can be inferred from the known anatomy.

Plate 1 shows the ophthalmoscopic appearance of the two retinae. It can be seen: (i) that the fields of view of the two retinae do not overlap; their inner edges are separated by a narrow gap which in all three species is between 1 and 2 degrees wide. (ii) Each retina has the form of a narrow vertical strip with a bend of approximately 30° in the centre. The detailed organization of receptors within this strip is given in Land (1969). Between them the fields of view of the retinae form a diagonal cross; the angle between the upper arms of the cross (in object space) is always somewhat greater than that between the lower arms—40°–45° as opposed to 15°–20° (Text-fig. 5).

Text-fig. 6. Drawings of frames taken from a ciné film of a semi-transparent female M. harfordi during spontaneous eye-movements. The nodal points of the eyes, and the positions of the centres of the retinae, have been reconstructed from data given in Land (1969) for the optically similar M. aeneolus. (a) Frame taken during a conjugate eye-movement. The directions of regard of the centres of the retinae maintain the same angular separation (5°) as in the resting position (b). (b) Retinae in the resting position. Note that the optic axes of the eyes make a larger angle with each other (18°–20°) than do the directions of regard of the retinae. (c) Non-conjugate (disjunctive) activity. Here the left retina leads the right by approximately 25°. The left retina is shown in its extreme medial position, making an angle of 28° between the body axis and the direction of regard of the retinal centre. The corresponding extreme angle with the retinae displaced laterally is always less than this, about 20°.

During most of the eye-movements about to be described, this cross-pattern is preserved. This means that most eye-movements are highly conjugate—any movement made by one retina is exactly paralleled by a movement made by the other. This even extends to 'scanning' (p. 484), where the retinae rotate about the optic axes of the respective eyes (torsion); again both retinae rotate through the same angle and in the same sense. The only exception to this rule occurs during 'spontaneous' activity (see p. 481) where one retina may lead the other by up to 25° (Text-fig. 6c)—so that the two halves of the cross-pattern become separated. This, however, is relatively uncommon. The two eyes are not mechanically linked in any way, nor do they share the same anatomical innervation. Thus the high degree of conjugation observed results from similar patterns of activity in the axons to the complementary, but not bilaterally homologous, muscles.
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Types of eye-movements

Four kinds of activity can be distinguished. These are: (i) spontaneous activity, (ii) saccades, (iii) tracking, (iv) scanning.

The first kind can occur whether or not there is any structure in the animal's field of view; the remaining three are only observed when the eyes are stimulated by the presence of a newly presented target, such as a black dot (Text-fig. 11). All four kinds of activity have been observed by ophthalmoscopy in each of the three species, and they have also been observed by direct microscopy in females of *M. harfordi*. Females of this species are sufficiently transparent for horizontal movements of the AM eyetubes to be seen directly through the carapace (Text-fig. 6).

Spontaneous activity

In a normally active, unstimulated animal the eyes alternate between periods of quiescence and periods of activity. This activity occurs in bouts of variable duration, usually lasting 1–10 min., separated by intervals of longer duration. Bouts of eye-movement activity are usually associated with other activities, such as locomotion and palp waving, and they thus appear to indicate periods of increased alertness of the animal. An inactive animal can be provoked into starting eye-movement activity by touching it, removing its substrate or similarly disturbing it. Repeated visual stimulation of various kinds can initiate activity, but is usually much less effective than tactile stimulation.

Spontaneous activity consists of rapid, periodic side-to-side movements of the retinae (Text-figs. 6, 7a). These vary enormously in frequency, amplitude and regularity. The maximum excursions made by the retinae occur during this kind of activity and are between 45 and 50° in the horizontal plane (measured by filming activity in transparent animals, and reconstructing on single frames the positions of the retinae and nodal points of the eyes). During excursions of this amplitude the retinae actually cross the midline of the animal (Text-fig. 6a). Towards the beginning and end of bouts of activity the amplitude of the excursions is usually less than their maximum, frequently less than 10°.

The frequency of movements in the horizontal plane range from slightly greater than 1 Hz. down to about 0.05 Hz. The lower frequencies usually occur at the beginning and end of bouts of activity (Text-fig. 7a), and in many cases the animal appears to break from a slow rhythm into a fast rhythm quite suddenly. The total range of retinal angular velocities (combining data from films and ophthalmoscopy) is from 100°/sec. down to 2°/sec.

Ophthalmoscopic observation shows that most spontaneous activity consists of movements in the horizontal plane, but that successive horizontal movements may differ in their vertical displacement by up to 35°, the limit of movement in the vertical direction. Vertical displacements cannot be recorded with the present instrument, but observation indicates that the vertical component of these eye-movements is not periodic to anything like the same extent as the horizontal component. A common pattern of scanning would consist of about five horizontal cycles with the retinae in a low position followed by five cycles in a high position, but the pattern is very variable.

These eye-movements are irregular in that successive cycles do not always have
similar periods or amplitudes, and they are frequently asymmetric, with the retinæ spending more time on one or the other side of their resting axes.

Spontaneous activity can occur when all the eyes have been blinded (by painting over the corneæ with a mixture of carbon and shellac), or when the field of view of the AM eyes is completely blank—a white card or an empty Maxwellian-field. They are also seen in juvenile spiders before their second moult—i.e. before the corneæ and lenses are fully formed. This kind of activity does not appear to be affected by the contents of the field of view; the spontaneous eye-movements made by an animal looking at a pattern of stripes are indistinguishable from those made by one looking at a blank field. When there is a single small target in the field—a dark line or spot—the retinæ may come to rest on that spot momentarily, and may begin to ‘scan’ (see p. 484). But during periods of rapid spontaneous activity these interruptions usually last less than 2 sec.

Text-fig. 7(a). Spontaneous activity recorded ophthalmoscopically. This record (traced from the pen recording) shows the horizontal (lateral-medial) movements of the fields of view of the retinæ, during a bout of rapid movement (approx. 0.5 Hz.) preceded and followed by periods of slower activity. This record, and those in Text-figs. 8–10, were made by keeping the graticule line midway between the inner edges of the two fields of view (see Pl. 1). The dotted portions of the record are inferred—the retinæ were outside the field of the ophthalmoscope; no reliance should be placed on the ‘waveform’ of the rapid portion of the record, but the periodicity is accurately represented. (b) Saccades evoked by small movements of a stimulus (3° black spot) in the left-hand side of the field of view. Each movement immediately evokes a saccade consisting of a rapid conjugate movement towards the stimulus, followed by a very slow return to the resting position. Stimulus visible to both AM and AL eyes. Calibrations as in (a). Both (a) and (b) were recorded from an adult male M. harfordi.

Saccades

In order to observe the eye-movements made in response to small targets, without the added complication of spontaneous activity, it is necessary to get the animal into a state where it is responsive, but its eyes are still. This is conveniently and repeatedly done by removing and restoring the animal’s substrate (a card ring); this induces a bout of spontaneous eye-movement, often accompanied by locomotion, at the end of which the animal is inactive but very responsive. If the animal is left undisturbed for more than about 10 min. it is often found to be unresponsive to visual stimuli which normally evoke activity. Mechanical disturbance restores the animal’s responsiveness.
When a small target (e.g. a 3° black dot) is introduced into an outlying part of the field of view of either the antero-lateral (AL) or the AM retinae, the retinae of both AM eyes move towards the target so that their central regions superimpose on the image of the target. Thus if the image falls on the upper end of the retina of the left AM eye, both retinae move upwards and slightly to the left, bringing the target to the centre of the cross formed by the two limbs of each retinal projection. This response is exactly analogous to a human saccadic eye-movement, which brings a target seen by the peripheral retina on to the fovea. Saccades are rapid, too rapid to record accurately by ophthalmoscopy, but films of transparent animals show that large saccades of 15° are complete within 0.1 sec. The retinae move along the most direct route to reach the stimulus, whether this requires a vertical, horizontal or an oblique movement. Saccades have not been seen to overshoot the target, but after several presentations of a target to the same part of the retinae at 20 sec. intervals the system apparently becomes fatigued so that saccades are initiated in the right direction, but they fail to reach the target. After further presentations saccades are abolished altogether, although presentation of the target to a different part of the retina will continue to elicit some response. The number of presentations required to abolish saccadic movements varies unpredictably from 1 to about 10, presumably due to variations in the animal’s central ‘alertness’ which are not directly controllable by the experimenter. Stationary targets never initiate saccades, although small movements of targets already within the retinal fields of view are effective stimuli. The direction in which the target is moved is irrelevant, the direction of the saccades is affected only by the target’s location on the retinae.

A saccade can have one of two outcomes. It can lead to ‘scanning’ (p. 484), or the retinae can return slowly to their resting position. Which of these is more likely to occur is largely out of the control of the experimenter, but again the more ‘alert’ the animal (by other criteria) the more probable it is that scanning will ensue. When scanning does not occur, the retinae remain ‘fixated’ on the target for 1–2 sec., and then begin to drift back, rapidly at first and then more slowly. For a saccade of moderate amplitude (e.g. 10°) in any direction this return takes 10–15 sec. Text-fig. 7b.

Tracking

The retinae will track a moving target. Once the retinae have acquired the target by a saccade any subsequent movement of the target causes the retinae to move with it, so that they always remain centred (or fixated) upon it. Targets in the form of small spots can be tracked vertically or horizontally by the retinae over angles of at least 25° (the effective field of view of the ophthalmoscope). Such tracking is apparently smooth. No attempt has yet been made to determine the range of speeds over which tracking is possible; these observations refer to target speeds of less than 10° per second. Tracking can occur whether or not the antero-lateral eyes can see the target.

It was shown by Dzimirski (1959) that it was possible to evoke nystagmic eye-movements in transparent juvenile jumping spiders (M. radiata), by moving a pattern of stripes in front of the AM eyes. These movements were similar to nystagmus in vertebrates, slow tracking movements alternating with rapid saccades back to a stripe closer to the resting position. Similar eye-movements have been seen in the ophthal-
moscope, using a moving pattern of 2° stripes spaced at 5° intervals. The retinæ followed single stripes for a few degrees, and then moved saccadically back to the next stripe. However, this kind of nystagmus usually lasted for only a few cycles and frequently led to a more random pattern of spontaneous activity.

Text-fig. 8 (a) Movements of the fields of view of the retinæ during scanning. The horizontal and torsional movements are simultaneous. (b) Recording of horizontal (upper) and torsional (lower) activity during a long bout of scanning, which follows a period of slow spontaneous activity. The horizontal size (3°) and position of the stimulus relative to the resting position of the retinæ (horizontal line) are shown at right. The same time calibration applies to both records. Male *M. harfordi*.

**Scanning**

Scanning is by far the most interesting kind of activity revealed by ophthalmoscopy. It occurs after the retinæ have made a saccade to a new stimulus, and consists of a regular pattern of periodic horizontal movements, associated with a rather slower pattern of rotation movements. It has been observed in both males and females of all three species. An unusually long, but otherwise typical record of such activity is shown in Fig. 8. The following description of scanning is based on over 100 recordings, mainly from *M. harfordi*, supplemented by observations in which recordings were not made.

Scanning is a spontaneous activity in the sense that once the target has entered the field of view and has been fixated by the retinæ, this activity proceeds on its own without requiring any further movement on the part of the stimulus. However, unlike ‘spontaneous activity’ as described above, scanning is dependent on the presence of a target. Also, while ‘spontaneous activity’ is unpredictable and rather chaotic, the detailed time-course of scanning is largely predictable; repeated presentations of the same stimulus evoke responses which are similar in every respect except their duration.
The horizontal component of scanning consists of regular movements of the retinæ across the target. The amplitude of each scan depends on the horizontal width of the target (Text-fig. 9). For targets less than 10° wide the scan amplitude and target width are very nearly the same, although for larger targets the retinæ fail to scan across it completely, and tend to remain intermittently closer to one end than the other. The amplitude of horizontal scanning does not become smaller than 2° even for targets 10° wide. The duration of each scan also depends on target width; in

![Graph showing the effect of stimulus width on scanning](image)

**Text-fig. 9.** Effect of stimulus width on scanning. Recording as in Text-fig. 8. As stimulus width increases, the amplitude of horizontal scanning increases by approx. the same amount, and the frequency decreases slightly. Torsional movements and bout duration are not affected. Adult female *M. harfordi*.

*M. harfordi*, viewing a 2° or smaller target, each cycle lasts 1.1–1.3 sec., while for 11–12° targets the period increases to 2.0–2.4 sec. This rhythm varies very little from presentation to presentation, or from animal to animal. The fact that the scan period varies by a factor of only 2 while the amplitude varies by a factor of 5 rules out the simplest possibility that the retinæ move at constant velocity until they meet an edge, and then return. The amplitude and period of horizontal scanning are unaffected by the height of the stimulus.
While the retinae are scanning horizontally they also undergo torsion. Both retinae rotate simultaneously and in the same sense so that at all times the resting cross-shaped configuration of the retinal projection is preserved. The average amplitude of a complete torsion cycle is between 40 and 50°, with the retinae rotating 20–30° clockwise then returning through the resting position to an inclination of 20–30° in the opposite sense. In a typical response the period of successive rotation cycles increases from 5 to 8 sec. for the first to about 15 sec. by the fourth or fifth cycle, by which time the response has usually become irregular. The amplitude of each cycle shows no such dependence on elapsed time. In each cycle the retinae remain in one extreme inclination for 2–5 sec, then take about 2 sec. to rotate to the other extreme position. Neither the amplitude nor the frequency of rotation is affected by the size or shape of the target (adding oblique lines to the sides of a 3° spot, for example, does not affect rotation).

Text-fig. 10. Decay of scanning with repeated stimulus presentation. Stimuli (3° dots) were presented each minute for 15 min.; every second record is shown here. Bouts become progressively shorter until in the last two records only the initial saccade remains. It is not possible to say to what extent the decreasing response strength is due to habituation rather than to spontaneous change in responsiveness. Adult male *M. harfordii*.

The third component of scanning is the preservation of fixation. In saccades which do not lead to scanning the retinae drift back to the resting position. However, when scanning is initiated the retinae remain locked to the target (as they do during ‘tracking’) and remain there until scanning is complete.

The duration of a bout of scanning varies enormously from one presentation of a target to the next. The shortest and longest bout durations recorded were 5 sec. and 94 sec., with most responses in the range 20–40 sec. For the first 10–20 sec., the pattern of scanning is very regular as described, but after this it becomes increasingly ragged. What usually occurs is that both retinae break away from the target, and move to another part of the visual field for a few seconds, during which time scanning activity ceases. The retinae normally return to the target and scanning resumes, and for the remainder of the bout scanning and break-away movements alternate, with the proportion of the time spent scanning decreasing (as in Text-fig. 8). Finally the retinae either break into ‘spontaneous activity’ or more commonly return to the resting position.
The three activities which constitute scanning—horizontal displacement, torsional movements and fixation maintenance—all begin and end at the same time. This is true of even the longest responses, but is most clearly shown in Text-fig. 10, where successively shorter bouts of scanning are evoked by repeated presentation of the same stimulus. In each case, horizontal and torsional movements start and cease together, and the retinae either break-away from the target, or return to the resting position. In the last pair of records scanning has ceased completely, and only the initial saccade remains (cf. Text-fig. 7 b).

A diagram summarizing the four kinds of eye-movements is given in Text-fig. 11.

Text-fig. 11. Diagram summarizing the four kinds of eye-movements, see text for explanation. Open arrows indicate movements made by retinae, and the thin solid arrow—movement of the stimulus (black square).
Functions of eye-movements

Jumping spiders are carnivores, like other spiders. However, instead of relying on a web to catch their prey, they catch flies by stalking them, as a cat would stalk a bird, and then jumping on them when the range is sufficiently close (1–2 cm.). It is known that every stage in this behavioural sequence is directed by the eyes (Heil, 1936; Drees, 1952).

Such a way of life demands that the visual system be capable of: (i) detecting potential prey; (ii) distinguishing between objects that are edible (e.g. flies) and closely similar objects that it would be inappropriate to eat (e.g. other jumping spiders); (iii) supplying the animal with the information required for accurate navigation towards the object seen, and finally for accurate jumping.

Detection (i) and identification (ii) pose slightly different problems for the animal. Detection involves recognizing novelty; objects of interest to most animals are those that move relative to the background—i.e. other animals—and a retina organized neurally as an array of movement detectors would be sufficient for the task of simply detecting prey. Identification on the other hand is the much more complex task of distinguishing between objects which are similar in size and in the way they move, but which differ only in their detailed geometry; such a task clearly requires much greater neural sophistication.

Animals differ in the way their visual systems are organized to perform these two functions. In man, and probably in most other vertebrates which have foveae, the peripheral retina is very sensitive to movement (detection), but is not capable of supplying the information required to evaluate the object detected. The region competent to do this is the fovea, which is small compared with the peripheral detecting field. In order to use the fovea to examine an object detected by the peripheral retina, a movement of the retina is required, whose magnitude and direction is specified by the position on the retina, relative to the fovea, of the object detected. In primates this movement is achieved by a saccadic movement of the eyes, in birds of a head-movement, and in most fish by a movement of the whole body. In other animals, for example amphibia and the majority of arthropods, the distinction between detecting and evaluating regions of the eyes is less clear cut; there is no anatomically distinct fovea and often no region of the retina upon which stimuli are fixated, and presumably in these animals a limited degree of stimulus evaluation is carried on throughout the retina.

In the functional organization of the visual system jumping spiders are remarkably similar to mammals, and quite unlike most arthropods. When a novel stimulus is presented to the outer parts of the retina of either of the antero-median eyes, it causes a saccadic movement of both retinæ which brings their central regions to rest on the stimulus. This is essentially a foveal system, and as in vertebrate foveæ the regions of the retinæ upon which stimuli are finally fixated are anatomically specialized; the receptor density in the centre of these retinæ is nearly ten times that in the periphery, and the centre contains four layers of receptors as opposed to two in the periphery (Land 1969). The field of view of the detecting part of the system is extended by the fixed antero-lateral eyes; movement of a target on their retinæ similarly evokes a
saccade by the antero-median retinae bringing the target to their centres. It is further extended by the postero-lateral eyes which also detect movement. However, when a stimulus is seen by these eyes it evokes a series of leg movements which bring the animal’s whole body round to face the stimulus, which is then picked up by the antero-median retinae. This turn has properties in common with saccadic eye-movements in that it is not controlled by visual feedback, the animal making a single turn of appropriate magnitude whether or not the stimulus remains in the field of view (unpublished experiments).

Thus the division of labour in the visual system of jumping spiders is similar to that in man, with the largest area of retina (the side eyes and outer parts of the antero-median retinae) devoted to detecting movement, and to initiating body and eye-movements appropriate to bring the detected stimulus on to the small evaluating region (the centres of the antero-median retinae). Blinding the antero-median eyes completely prevents prey/spider recognition and stimulus-directed navigation (Homann, 1928; Crane, 1949), whereas blinding the side eyes does not affect ‘post-detection’ behaviour. Thus the antero-median retinae are solely responsible for stimulus evaluation.

When a detected stimulus finally reaches the antero-median retinae, they begin to ‘scan’ it in a regular, repeatable manner that is without parallel in any other visual system (Fig. 8). The only other case of an eye which shows regular scanning activity is the copepod *Copilia* (Gregory, Ross & Moray, 1964), but in that animal the retinae are so simple (three cells) that it is difficult to imagine what the significance of this activity might be.

Scanning in jumping spiders appears to be an important part of the process the animal uses to identify objects that have entered its visual environment. This is clear from the context in which it occurs. In an animal ‘at large’ the first action in the normal sequence of events leading to prey-capture or courtship is detection, accompanied by a turn or a saccade as the position of the stimulus may warrant. The spider then watches the target, face-on, for a variable period of time, usually in the range 1–10 sec., after which it embarks on one or a number of courses of action. It may: (i) creep towards and capture the target (ii), raise its first pair of legs and begin a courtship dance (if male), (iii) remain still and watch (if it is a female that has seen a male), (iv) turn and run, (v) walk away. Because scanning is the only activity which reliably follows detection and the ensuing saccade in the restrained animal, it is highly probable that it occurs during normal behaviour during the period of ‘watching’ which follows detection and precedes prey-catching, etc. It would thus be during scanning that the identity of the stimulus (prey/mate/enemy/indifferent object) is determined.

Scanning—a rapid side-to-side motion of the retinae coupled with a much slower conjugate torsion (Fig. 8)—is a complex and highly structured activity, and there must be a reason for its pattern. Is it possible to relate this pattern to the specific recognition tasks the retinae are performing?

It is hard to see why ‘indifferent objects’ or ‘enemies’ would require a special mechanism like scanning for their identification. The former are distinguished by their immobility, or by being ‘prey’ when the animal is not hungry or ‘mate’ when it is not sexually active, and ‘enemies’, probably, are distinguished by movement and largeness. However, the distinction between a potential prey and potential mate is a
considerably more complex feat, and depends principally on the geometry of the stimulus. Following Drees (1952), spiders (*Epiblemum scenicum*) will attack any small dark object that has just moved, unless the object possesses a pair of oblique lines ('legs') on either side of a central spot (the 'body'). Such an object (Text-fig. 12) is treated as another jumping spider, and will elicit a courtship display from a male spider. An important task that the retinæ are performing during scanning is therefore going to be the detection of lines or contours with particular orientations and in appropriate positions.

![Text-fig. 12. Stimuli found by Drees to evoke courtship (a) and prey capture (b) in male jumping spiders (*Epiblemum scenicum*). The numbers beneath each figure in (a) are the percentage of trials on which courtship was evoked. After Drees (1952).](image)

If we make the reasonable assumption that scanning is related to the performance of this task, the movements of the retinæ become comprehensible. Suppose that each retina contains a row of receptors arranged as a ‘line detector’, so that a higher-order cell is stimulated only when a contour crosses all the cells in that row nearly simultaneously (such a line detector would have properties similar to ‘simple’ cells of the visual cortex of the cat (Hubel & Weisel, 1959)). Then, if the eyes are looking at a stationary target, such a detector would only be able to detect relevant contours if (i) it is correctly oriented, with the receptor row parallel to the contour(s) in the target, and (ii) the detector moves in a direction approximately (but not critically) at right angles to itself and to the contour in the target.

In this scheme the torsional component of scanning would be concerned with the orientation of the detectors; the two extreme positions adopted by the retinæ (25° clockwise and anti-clockwise) would then become the two orientations in which a given receptor row ‘samples’ the stimulus (Text-fig. 13a). The horizontal component of scanning would serve to provide the relative motion of target and detector required for stimulation to take place. Given the movements observed, one would expect such a detector to respond strongly to patterns like those Drees used, whenever the retinæ are rotated fully in either sense—i.e. during about two-thirds of the time that the animal spends scanning.

It is worth noting that rapid ‘tremor’ and ‘flick’ movements, like those observed in man (Ditchburn, 1955) and in crabs (Horridge & Sandeman, 1964; Horridge, 1966) where they are responsible for sharpening and maintaining edge-perception, are not seen in jumping spiders. Rather it seems likely that the scanning movements observed
Eye movements of jumping spiders

here themselves generate the relative movement of stimulus and retina, necessary for the continuous detection of spatial stimulus characteristics by phasic receptor systems.

As it stands, the hypothesis outlined in Text-fig. 13a is certainly too simple to account for spider-recognition as it normally occurs. In the first place both Drees' observations and my own show that jumping spiders can recognise other jumping spiders, or spider-like targets, when these are rotated through 90° and 180° (upside down), without much difficulty. The specific angles made on the retinæ by the contours of such targets will be quite different from those made when both animal and

![Text-fig. 13. (a) Proposed function of scanning eye-movements in stimulus identification. It is supposed that each retina contains rows of receptors arranged as edge or line detectors (black dots). These detectors are used to sample the image of the target for contours in certain positions. The rotational component of scanning serves to align the detectors at predetermined inclinations, while the horizontal movements provide the required relative motion between detector and stimulus-image (here shown as a highly simplified spider). (b) Tracing of a photograph of a female jumping spider (P. johnsoni) in a typical resting posture, showing the preponderance of contours making angles of 25–30° with the vertical.]

target are horizontal, and to account for this it would be necessary to propose that several alternative sets of line-detectors are present. Secondly, in real spiders the angles that the various parts of the different visible limbs make with the vertical (strictly, with the animal's sagittal plane) vary between 10° and 45° (measured on photographs of P. johnsoni like that copied in Text-fig. 13b) and it is not clear that a detector that simply sampled the target for lines inclined at 25° to the vertical would succeed in identifying a real spider. Finally, in behavioural experiments on Phidippus and Metaphidippus species it was found that targets like those used by Drees were much less
effective in eliciting courtship displays than were real spiders, and again it seems likely that the pattern of contours that constitutes 'spideriness' is more complicated than has so far been supposed.

Until the behavioural effectiveness of different spider-like stimuli has been examined in greater detail, it will not be possible to make any precise statements about the orientation or number of receptor rows that probably contribute to spider-recognition. However, this does not detract from the general conclusion that an identification procedure based on the detection of contours by oriented receptor rows seems to be the most plausible explanation for the retinal movements observed during 'scanning'.

**SUMMARY**

i. Movements made by the principal eyes of jumping spiders (*Phidippus* and *Metaphidippus* spp.) have been investigated using an ophthalmoscopic technique which permits simultaneous observation and stimulation of the retinal surface.

2. The eye-movements are produced by six muscles. Four are attached to the cara-pace, and displace each retina latero-medially and dorso-ventrally. The remaining pair are thin bands of muscle which encircle the eye-tube. These twist the eye-tube, rotating the retina about the visual axis (torsion).

3. The nerve supplying these muscles contains only six axons. Each axon terminates in one of the six muscles.

4. Four types of eye-movements are observed. These are spontaneous activity, saccades, tracking and scanning. All movements are usually conjugate.

5. Spontaneous activity consists of a very variable, periodic side-to-side motion of the retinae. It is associated with states of high excitability, and occurs whether or not there is any structure in the field of view.

6. Saccades occur when a small stimulus (e.g. a dark dot) is presented to, or moved upon, the retinae of either the principal eyes or the antero-lateral eyes. In a saccade the retinae move towards the image of the target so that they come to rest with their central regions fixated on the target.

7. If the target moves the retinae track it, maintaining central fixation.

8. Scanning normally follows a saccade. It consists of an oscillatory, side-to-side movement of the retinae across the stimulus, with a period of 1–2 sec., and a simultaneous torsional movement in which the retinae partially rotate about the visual axes, through an angle of approximately 50° and with a period of 5–15 sec.

9. Jumping spiders distinguish other jumping spiders from potential prey by the geometry of their legs. It is suggested that scanning is a pattern-recognition procedure in which the torsional movements are concerned with the spatial alignment of line or edge detectors, and the horizontal component with providing relative motion between these detectors and the stationary stimulus.

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REFERENCES


EXPLANATION OF PLATE

(a) Photograph of the retinae of the principal eyes of P. johnni, taken through the ophthalmoscope. The only visible part of the retina is layer 4, where the receptors are oriented at right-angles to the incident light. The outline of the rest of the retina (layers 1 and 2) is shown by the broken line, which was constructed from the histological description given in Land (1969). This plate was actually made using a single photograph of one retina, which was reversed and positioned to provide the pattern of both eyes. Normally both retinae are visible ophthalmoscopically, but for purely technical reasons it is easier to photograph one than both. As shown here, the retinae are as they appear when in the resting position. The relation of the ophthalmoscopic image to the position of the retinae in the head is explained in Text-fig. 5. (b) Transverse section through the head of M. aeneolus at the level of the retina. Because the section is slightly oblique, only the ventral and central parts of the retinae can be seen; however, the central bend and the laterally directed convexity of each retina can be seen. Corresponding parts of the (morphologically) right retinae in (a) and (b) are indicated with an asterisk (*). The oculomotor nerve is shown by an arrow.