INTRODUCTION

Jumping spiders (Salticidae) will often turn to face objects that move in the surrounding environment. This is the first step in a chain of events that may lead to prey-capture, mating or escape, depending on the nature of the object which caused the movement (Homann, 1928; Crane, 1949; Drees, 1952; Land, 1969a, b). This turn is mediated by the lateral eyes (Fig. 1) and generally results in the object being seen by the anteriorly directed principal eyes, which control the subsequent behaviour.

There are basically two ways in which such a turn could be executed. In the first case the animal, having detected the presence of a target to one side or the other, could turn towards it until the object was seen to lie directly ahead. This would be a 'closed' control system (see Mittelstaedt, 1962) since the animal relies on the visual consequences of its own motion, i.e. visual feedback, for the accurate execution of the turn. In the other case—'open' control—one of the spider's eyes might detect a target at, say, 80° to the animal's left, and the retina would issue a single instruction to the legs: 'turn left through 80° and then stop'. Here the magnitude of the turn made will not be affected by the relative movement of the target during the turn itself. Such a system would require that the central nervous system be well calibrated, so that the retinal position at which an event occurs is accurately translated into an appropriate spatio-temporal pattern of motor activity.

An example of a closed control system that is superficially very similar to the spider's case is the fixation response of the praying mantis. Here, according to Mittelstaedt (1957, 1962) the mantis turns its head towards its prey, which is continuously visible, and the visual and neck-motor systems operate 'to reduce the deviation of the prey from the eye axis as much as possible, preferably to zero, the fixed reference point of this loop'. On the other hand male fireflies employ an open mechanism for performing essentially the same function; an artificial flash, or the flash of a distant female, will cause the male to turn and fly rather accurately towards the source of the flash, even though the flash is over before the animal begins to turn (Mast, 1912).

To determine which kind of mechanism the spider employs it is necessary to 'open the loop', i.e. to prevent the animal from seeing the relative movement of the target during the turn itself. Then if the system is basically of the 'closed' type, this will drastically interfere with the execution of the turn; depending on the way the experiment is carried out the animal should either keep turning or not turn at all. If, however, the system is 'open', removal of visual feedback should have no effect on the accuracy of the turn. We shall see that this is what happens in the spider's case.
METHODS

Adult *Metaphidippus harfordi* and *M. aeneolus* were collected locally from the lower branches of redwoods (*Sequoia sempervirens*). They lived in Petri dishes until required, were kept moist with damp cotton wool, and were fed on a housefly or a few *Drosophila* each week. Individuals of both species are between 4.5 and 6 mm body length, and weigh between 10 and 20 mg. The results reported here were obtained from 85 individuals, mostly females.

![Diagram](image)

**Fig. 1.** Diagrammatic longitudinal section of the prosoma of *M. harfordi* showing fields of view of the eyes in the horizontal plane. For the right antero-median eye the field of view as it is extended by eye-movements is shown. Data from Homann (1928) and Land (1969a, b).

_Eliciting and recording turns under ‘open-loop’ conditions_

Mittelstaedt (1951) and Hassenstein (1951) investigated optomotor responses in insects by fixing their animals in space and providing them with freely movable ‘substrates’ which they could turn. The animals thus did not turn themselves, but their substrate; and in doing so they received none of the visual feedback or ‘re-afference’ which would normally accompany such a turn. An essentially similar method is used here.

A jumping spider will hold and freely manipulate a light card ring between its feet. It can walk forwards or backwards with the ring revolving underneath, or it can turn the ring to the left or right about a vertical axis. The spiders show amazing dexterity in this bizarre situation, although this is less surprising when one remembers that they normally live on thin twigs and leaflets, and are accustomed to dealing with narrow linear substrates.
Fig. 2 shows the apparatus used to evoke and measure turns. The spider is held rigid in space by a small piece of card waxed to the prosoma. The card is attached to a clip which is mounted so that the spider's view of objects in the horizontal plane is unobstructed. The spider is aligned carefully, and then given a ring of roughly its own weight (15 mg, 1 mm wide, 15 mm diameter) to hold.

The target used to elicit turns was usually a small black spot on the surface of a 12 cm diameter grey drum. The drum could be rotated around the animal so that the spot moved in short jerks of controlled length and velocity in the animal's horizontal (longitudinal) plane. Stimulus conditions which were found to be ideal for eliciting turns and which are those used here unless otherwise stated, employed a 5° square black target moved in 5° steps at a velocity of 25°/s relative to the animal. The drum was illuminated from above with diffuse tungsten light or in some experiments with light from a circular fluorescent lamp, in both cases giving a background luminance in the region of the target of between 3 and 5 lm/m², similar to normal room illumination. The position of the target relative to the spider was recorded automatically by a potentiometer coupled to the spindle of the drum, the output going to one channel of a pen-recorder.

To many, though not all, movements of the target the animal responds by turning its ring about a vertical axis in a single rapid action. If the target lies to the animal's left the ring is turned to the right (clockwise when seen from above), and vice versa (Fig. 3). In other words the movement the spider makes is in the direction which, in the 'real world' would have brought it round to face the target. Since the animal is not itself turning, the image of the target remains stationary on its retina, and the spider does not obtain the visual feedback appropriate to its turn. The spider produces turns only in response to moving targets; a stationary spot, unless it lies within the field of view of the antero-median eyes (Fig. 1) evokes no response whatsoever.

Movements of the ring were recorded by means of a pointer geared to a second potentiometer. The pointer and the ring are seen together by the observer by means of a half-silvered mirror directly above the animal, and the centre of rotation of the pointer is made to coincide with the vertical axis of rotation of the ring (which passes through the spider's prosoma). When the ring has stopped moving after a turn, the observer aligns the pointer with the new position of the ring. The size of the turn the animal has made is then read from the pen-recording (Fig. 4) by comparing the old and new positions of the ring. Ring position is recorded in this way with an accuracy of better than ± 2°.

In most experiments the stimulus spot was initially positioned directly behind the animal, and then advanced in one direction, with intervals of at least 2 s between each successive 5° movement. In 72 such movements the target completely circles the animal, and the direction of rotation is then reversed. In this way each part of the retina is presented with a stimulus only twice in each 'run', a situation which minimizes habituation and permits the animal to make up to a thousand successive turns before it stops responding. This contrasts with the situation where stimuli are confined to one part of the visual field, when the spider habituates after at the most 15 target movements, and usually only one or two (Fig. 10).

It was found that covering the principal eyes with a mixture of wax and soot had no effect on the production of turns to briefly moving objects. However, when the
principal eyes were left uncovered responses were occasionally produced which were quite different in character from those to be described here. *Stationary* targets within the field of vision of the principal eyes (up to 35° on either side of the axis (see Fig. 1)) sometimes evoked a series of up to six small (15–20°) turns in rapid succession, and this pattern of behaviour persisted after waxing over the lateral eyes. This behaviour

Fig. 2. (a) Diagram of the apparatus used to elicit and record turns. See text. (b) Arrangement for producing drum movements of controlled velocity and duration.
Turning in jumping spiders was rare, easily recognizable, and confined to stimuli in front of the animal. Because of the ease with which turning mediated by the principal eye and by the lateral eye could be distinguished, the principal eyes were not routinely covered.

![Diagram](image)

**RESULTS**

*Turns made by unrestrained animals*

Anyone who has watched jumping spiders can confirm that they turn to face moving objects in one of two ways. They either make a single complete turn which results in the spider’s axis pointing straight towards the source of the movement (fixation), or they will make one or more much smaller turns of 10–20° which may or may not result in fixation. Sometimes one sees a combination of the two, with a small turn followed by a much larger one. If the spider makes a turn which does not result in its axis coming to within about 30° of the target, nothing more happens, unless the target moves again, in which case another turn may be made. If the turn does result in fixation many things may happen: the spider may creep towards it, turn and run away, or begin a sexual display if the target turns out to be another jumping spider.
The spider may follow the target closely if it continues to move, or ignore it completely.

Homann (1928) and Crane (1949) showed that blinding all the lateral eyes had no noticeable effect on the co-ordination of these activities, provided the stimulus initially appeared close to the animal's axis; however, no orienting responses were made to objects behind or to the side of the spider. Conversely, animals with their principal eyes blinded would orient perfectly normally to objects around them, but having oriented they failed to do anything else, and thus were unable to feed, mate or escape. I have confirmed these findings. Orientational turns of the kind that concern us here are thus mediated by the four lateral eyes (the postero-medial eyes are minute and probably vestigial), whereas the principal eyes are responsible for identifying and tracking objects which the lateral-eye mechanism has brought into their field of view (see Land, 1969b).

**Turns made under open-loop conditions**

Fig. 3 shows diagramatically the difference between orientational turns made by a spider (a) sitting on a twig in the 'real world', and (b) in the experimental situation where the substrate, but not the spider, is free to move. It illustrates the general result of the experiments to be described, namely that in the experimental situation the animal makes a turn which is similar in both direction and size to the one it would have made in the 'real world'. The spider appears to move its substrate, the ring, in the 'wrong' direction, which is precisely what one would expect if it was making the same leg-movements in both situations.

Fig. 4 is a record obtained from an actual experiment. The lower trace shows the position of the target, which is being moved in 5° steps around the animal in a right-to-left direction. The upper trace shows the positions to which the spider turns the ring, as monitored by the matching pointer. The trace is arranged so that when the spider turns the ring to the left (equivalent to a 'real' right turn and so designated 'right') the line moves upwards by an amount equal to the angle of the turn. For turns in which a given pole of the ring crosses the axis behind the animal the line disappears and reappears at the top or bottom of the record, as the recording potentiometer goes from its maximum to minimum value, or vice versa. The record is thus really continuous.

The record shows the following. (i) When a response occurs it consists of a single rapid turn. (ii) When the stimulus is on the right all the turns made are 'right' turns, and vice versa. It can be seen that as the stimulus crosses the spider's midline the direction of the turns changes from 'right' to 'left'. (iii) The greater the stimulus angle, i.e. the angle between the stimulus and the animal's body axis, the greater the amplitude of most of the turns. (iv) For large stimulus angles some of the turns are of very small amplitude (10–30°), whereas others are approximately equal in amplitude to the stimulus angle. In most records the proportion of these small-amplitude turns is greater than it is here. (v) Not all movements of the target result in any turn at all. In this case there are 55 responses to 72 stimuli, and this is an exceptionally high proportion.

Two additional conclusions, not apparent from the trace, can also be given. (vi) Turns made to target movements of the extent and duration used here (5°, 200 ms) are always single and discrete. Continuous turning is never seen, even when the target
Turning in Jumping spiders

moves continuously, but additional discrete turns are sometimes seen if the target is still moving after the first turn is complete and the animal is still. (vii) Stationary targets never evoke turns. In the present experimental situation the target is present in the spider's field of view the entire time, but turns are made only when it moves; the system behaves as though it were completely blind to stationary objects.

This experiment has shown that turns initiated by moving targets in the visual environment stop of their own accord, even when the spider receives no feedback from the relative movement of the target across its retinas. This does not itself show that the system operates as an open system in the 'real world', although it strongly suggests this. However, if it can be shown that turns produced in the experimental situation are sufficiently accurate to permit accurate fixation under ordinary circumstances, we can assume that the mechanism is an open system in normal operation.

'Complete' and 'partial' turns

As mentioned in (iv) above, some of the turns made in response to targets at large stimulus angles are very small. This is shown more clearly in Figs. 5 and 6. In Fig. 5, which is a plot of the record shown in Fig. 4 plus its companion run in the opposite direction, it can be seen that most responses have magnitudes close to the stimulus...
angle (i.e. they lie along a line passing through the origin with a slope of 1) and that the remaining 15 turns are all of less than 30° (see also Fig. 7b), and their magnitudes do not seem to be related to the stimulus angle. Fig. 6 shows the results of a much more extensive experiment on a single spider, in which turns to the left and right of

Fig. 5. Plot of the angle the spider turns the ring against the stimulus angle (see Fig. 3). The stimulus angle is taken as the position of the leading edge of the black square at the midpoint of each movement. Closed circles are plotted from the record shown in Fig. 4. Open circles from the companion run to this with the target moving in the opposite direction (left to right).

the animal have been pooled. The histogram shows essentially the same features as Fig. 5, and confirms that for stimulus angles of 60° or greater there are two quite distinct kinds of turns (the histograms of numbers of turns versus angle turned become bimodal). In over a hundred repetitions of this experiment this result was confirmed: turns are either close in magnitude to the stimulus angle or they are small.

These two kinds of turns will be referred to in future discussion as complete and partial turns respectively. For convenience, a complete turn will be defined as one whose amplitude is greater than half the stimulus angle, and a partial turn less than half. Where the stimulus angle is less than 60° it does not seem possible to draw this distinction, since the histograms of number of turns versus angle turned are unimodal (Fig. 6).

Notice that complete turns are those which, in the ‘real world’, would have brought the spider’s body axis to within a few degrees of the target, and thus resulted in fixation. Partial turns, while always in the direction of the target, would not result in
fixation. This result precisely parallels the observations made on unrestrained animals, where turns to moving objects were either small and ineffective, or resulted in accurate fixation.

A measure of the accuracy of complete turns can be obtained by measuring the ‘error’ of each turn (i.e. the angle turned minus the stimulus angle) and finding the mean and standard deviation of these errors. A plot of such errors for one animal is given in Fig. 7a. The mean indicates whether the spider tends to overshoot or undershoot the target, and the standard deviation indicates the probability of the spider making an error of a particular size. For this animal, which was typical of six others examined, the mean error for all turns was $-0.5^\circ$, which is negligible, and the standard deviation $16.2^\circ$. Since the errors appear to be normally distributed, this means that 50% of all complete turns would have resulted in the target appearing within $11^\circ$ of the spider’s midline, and 90% within $27^\circ$, had the spider been free to turn. Since the animal’s antero-median eyes, which need to see the target if the spider is going to respond to it further, cover when moving a field of up to $35^\circ$ on either side of the midline (Fig. 1), it is reasonable to conclude that virtually all complete turns would result in the target being ‘picked up’ by the antero-median eyes. Thus complete turns made in the absence of visual feedback from the stimulus are sufficiently accurate to ensure that the target is fixated by the antero-median eyes, and so presumably the system can operate effectively in this ‘open’ manner under normal circumstances.
A number of attempts were made to determine whether complete and partial turns were normally made in response to slightly different stimuli—perhaps the stimulus used here was somehow intermediate, and evoked both. However, varying the size and contrast of the target, or its distance and rate of movement, failed to produce any differences in the relative rates of occurrence of the two kinds of turn, and it is concluded that the decision as to whether a complete or partial turn is to be performed is not made on the basis of stimulus quality. The only factor which was found consistently to affect the relative proportions of complete and partial turns was the state of habituation of the system. In previously unstimulated animals the proportion of complete turns was higher (up to 80%) than in partially or nearly completely habituated animals (as low as 20%).

**Removal of all sources of visual feedback**

In the experiments so far described, visual feedback derived from movement of the target across the surface of the retiniae has been excluded, but there remains the possibility that the spider might gauge the size of its turn by observing the movement of the ring itself, or, even less likely, by watching its feet. These possibilities were excluded by using a fluorescent lamp to illuminate the drum, turning this lamp off immediately after the target had ceased to move, and keeping it off for approximately 1 s until the animals' turn was completed. Thus the animal saw the stimulus during the light, but turned in complete darkness. The spiders had no difficulty doing this; the accuracy of complete turns made in darkness was normal.

**Time course of turns**

The minimum latency of the turn has not yet been measured. Of 41 turns recorded on film, all but seven had begun within 100 ms of the time the target stopped moving,
and over half of these began before this. However, since the duration of the movement of the target itself was 200 ms, there is a problem in deciding on the instant in time to take as the ‘beginning’ of the stimulus; a stimulus cannot be regarded as such until the target has moved a certain distance, and that takes time. The shortest time observed between the beginning of movement of the target and the beginning of a turn was between 80 and 120 ms, but this must be re-examined using stimuli of shorter movement duration. More interesting was the fact that the seven turns that did not immediately follow the stimulus had latencies ranging up to 1 s. These turns were of normal accuracy, i.e. they were clearly directed to the preceding target movements. Thus information concerning the spatial position of the target can be stored in the spider’s brain for at least a second, before being acted upon.

The rate at which the spider turns the ring is enormously variable. The range of angular velocities seen so far in turns performed by one animal is from 164 to 1120°/s (total angle turned divided by total time taken) with the velocity from one frame of film to the next during the turn reaching 1775°/s. Two consecutive turns could be executed at quite different speeds, and both be accurate with respect to the stimulus angle. Turn duration varied from less than 0.1 to 1.6 s, depending on the size of the turn and the velocity of its execution. There was no obvious relation between the magnitude of a turn and its velocity; small and large turns could both be executed either fast or slowly.

The adequate stimulus

The effect of changing the size, contrast, velocity or extent of movement of the stimulus is to change the probability of a turn being made. This is the only parameter of the response which is affected. Thus a 0.5° target rarely evokes a response, but when it does the turn made is of the same size (if it is a complete turn) as it would have been if the target subtended 5°. In all cases the sizes of complete turns depend solely on the stimulus angle, i.e. on the specific position of the stimulus on the retina. Similarly the relative probabilities of a given stimulus evoking partial or complete turns do not seem to be influenced by the size, speed or other characteristics of the stimulus. There is no evidence, for example, that ‘less adequate’ stimuli (small, slow), which have a low probability of evoking any sort of turn, preferentially elicit partial turns, as might perhaps have been expected.

To determine the minimum size of target that the spider would respond to, a 10° black line target was used whose width was varied randomly in successive ‘runs’ (a ‘run’ consists of the target moving clockwise around the animal in 5° steps, followed by the same thing anticlockwise). Half an hour was allowed to elapse between runs to avoid excessive habituation, and thus each experiment took several days. For simplicity of interpretation only responses to stimuli in the fields of view of the posteralateral eyes (directly behind to 45° from the body axis) were recorded; these eyes have a nearly uniform receptor density over their entire field, the receptor spacing being very nearly 1° (Land, 1969a). The result of such an experiment is shown in Fig. 8; two other animals gave almost identical results. The figure shows that targets narrower than 0.4° do not elicit turns, between 0.4° and 1.1° the probability of a turn occurring increases, but thereafter there is little if any increase in turning probability with increasing target size. The ‘final’ response probability can be quite low (in Fig. 8 it
is 0.15) and it may differ from one animal to another or even from day to day in a single animal.

The probability of a turn being made thus has two components: one is dependent on the size of the target movement, and the other is intrinsic to the animal and sets the maximum response probability that can be reached, however 'adequate' the stimulus. Fig. 8 shows that for a response probability of 50% maximum, the target must subtend about 0.7°, which is slightly less than the inter-receptor angle in the retina. This is roughly what one would expect; targets can be detected by individual receptors, although since movement is an essential stimulus component the sequential

![Fig. 8. Minimum target width required to evoke turns. The stimuli were black lines, 10° long and of varying width (the abscissa). The ordinate gives the proportion of target movements that evoked turns. The target was moved in 5° steps at 25°/s every 2 s; at stimulus angles from 45 to 180° (confined to the postero-lateral eye fields). Filled circles: vertical lines, 432 stimuli/point. Open circles: horizontal lines, 216 stimuli/point. Open arrow on abscissa indicates approximate target width which was half as effective as a maximal (5°) target in evoking turns. Closed arrow indicates receptor spacing. *M. aeneolus* (?), single animal.](image)

stimulation of several (i.e. at least two) receptors is needed if a response is to be produced. The minimum distance a target must move has not yet been investigated systematically, but turns can certainly be elicited by movements of 1°, indicating that the smallest 'movement-detecting unit' probably consists of two receptors. Stimuli which change in intensity without moving (i.e. go on and off) have not been found to elicit turning; change in intensity has to be accompanied by change of position.

Other factors that affect the chance of a target being detected are contrast and velocity of movement. These parameters have not yet been examined systematically. Targets may be lighter or darker than the background, and the chances of their being detected improves, as one would expect, as their contrast with the background is increased. There appear to be both lower and upper limits to the rate at which the target must move if a turn is to be evoked. Preliminary experiments indicate that this velocity range is approximately from 1 to 100°/s.
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Response probability and stimulus position

The chances of a suprathreshold stimulus evoking a turn vary with its position in the visual field, i.e. with the stimulus angle. Fig. 9 shows that for stimuli behind the animal the response probability is very low; it rises to a maximum which can approach unity for stimuli at about 45° from the body axis, and then falls drastically closer to the axis. The two graphs shown in Fig. 9 designated by squares were both obtained from the same animal, but on separate occasions 2 months apart. On the second occasion (open squares) the shape of the curve was the same as on the first, but the overall probability of obtaining a response was much lower for every stimulus position.

![Graph showing the probability of a turn being made as a function of stimulus angle.](image)

This experiment has been repeated on numerous occasions with different animals and the results were always similar. Sometimes the curves were less symmetrical than those in the figure, there being a higher probability of the animal making turns to the right rather than to the left, or vice versa. Another fairly common feature was the presence of a region of enhanced probability of response for targets at stimulus angles of about 150°, in an otherwise low-probability part of the visual field. The results given in Fig. 9 are not explicable as an habituation artifact resulting from the sequential method of stimulation, since targets moving from the axis towards the spider's posterior give identical curves to those obtained with targets moving in the opposite direction. Nor are they due to different parts of the various retinas requiring somewhat different stimulus characteristics in order to properly excite them, since similar curves are obtained whatever stimuli are employed. It has to be assumed that the variable probability of a response occurring as a function of stimulus position represents a 'decision'
on the part of the central nervous system only to respond to a set fraction of stimuli received, that fraction depending on the retinal site of origin.

Teleologically, the results might be explained by assuming that the spider is economizing on the production of large turns—the larger the turn it has to make the less likely it is to make it. The region of low response probability near the axis is the region in which the spider would not need to make turns anyway, since the principal eyes can be moved to view targets up to 35° from the axis (Land, 1969b).

Habituation

Stimuli delivered repeatedly to the same part of the visual field stand progressively smaller chances of evoking turns (complete or partial). This is illustrated in Fig. 10. In the lower curve the target was moved to-and-fro across the same 5° region of the field at 2 s intervals, and, except for the second such movement, there was a progressive decline in the probability of a turn occurring. On the other hand the upper curve shows that when the same stimulus encounters a different region of retina on each occasion (i.e. each movement advances it 5°) there is no decrease in the chance of a response occurring.

Fig. 10. Habituation to a target which moves to and fro at the same retinal location (filled circles) and to one which moves to a new part of the retina with each target movement (open circles). In both cases the stimuli (5° black squares moved 5° at 25°/s) were presented at stimulus angles between 55 and 95° to the left and right. For the closed circles they were moved back and forth at randomly selected locations, and for the open circles they were moved sequentially as in Fig. 4. The graph should be read as showing the proportion of turns (complete and partial not discriminated) made to the first, second, third, etc. target movement in each sequence of nine. Four spiders (Mesosa harfordi, 9) were used, and all showed the same marked habituation to stimuli presented at the same position, and lack of habituation to stimuli that changed position. 40 stimuli/point.

Habituation is not to be explained by fatigue in the motor part of the system since all turns in the same direction share the same muscles, and yet it is only stimuli to the same part of the retina that cause habituation. On some occasions during to-and-fro stimulation the spider did not respond at all, however long the stimulation was continued, but nevertheless responded promptly as soon as the target was advanced to
the next 5° sector. In this case habituation had clearly occurred without any response, again excluding the motor system.

Even when the target is moved to a new part of the retina each time, habituation does eventually occur. Fig. 11b shows that after a number of complete ‘runs’ the probability of a response occurring falls to zero. The number of runs required to bring this about varies from animal to animal, from one or two to as many as 20. The upper curves in the figure show that, even when the response probability has fallen to near zero, the sizes of the few turns that are made are not diminished; again there is no sign of motor fatigue.

![Graphs showing habituation](image)

Fig. 11. Two examples of habituating responses showing (a) the effect of repeated stimulus presentation on the probability of a turn being made, and (b) on the average size of complete turns made. Each run consisted of 96 target movements (stimulus angles between 60° and 180° left and right) under the conditions of Fig. 4. In (b) the ordinate is the percentage error of the responses, i.e. a 120° turn to a 150° stimulus angle or a 60° turn to a 75° stimulus angle would both give a value of 80%. Each run immediately follows the preceding one in time. Both $M. \text{harfordi}$.

Complete recovery from habituation takes many hours, but its time course has not yet been determined. Routinely, habituation can be minimized by allowing half an hour for recovery between each stimulus run, but even under these conditions there is some decline in responsiveness that is not attributable just to the passage of time. Dishabituation is sometimes observed. It may occur spontaneously; in a series of stimulus runs during which the probability of turning is decreasing, there may be some in which responsiveness is considerably greater than in those preceding or succeeding. Alternatively, dishabituation can reliably be induced by mechanical stimulation (such as briefly removing the spider’s ring) just before a stimulus run. These observations imply that the site of habituation and dishabituation is central to the retina and movement-detecting neural machinery, since it is affected by spontaneous fluctuations not of visual origin, and also by modalities other than vision.
Fields of view of the lateral eyes

The estimates of the fields of view of each of the lateral eyes given in Fig. 1 were derived from the anatomical and optical measurements of Homann (1928) and Land (1969a). They can easily be checked physiologically by blinding each eye in turn (with wax) and determining in which regions of the complete visual surround stimuli are no longer effective in producing responses. Fig. 12 shows the results of an experiment in which this was done. Blinding the left postero-lateral eye had the effect of abolishing all responses to stimuli in the range 170–50° left, while blinding the right antero-lateral eye abolished responses in the range 20–35° right. The remaining left antero-lateral eye thus had a field of view from 45° left across the midline to 15° right, and in the contralateral part of this field it was capable of eliciting right turns. The extent of overlap between the fields of the antero-lateral and postero-lateral fields is...
very small, and covers the range 40–45° right and left. These results precisely confirm
the earlier optical findings.

No responses of any kind were produced when only the tiny postero-median eyes
remained open.

Other responses mediated by the lateral eyes

In addition to making turns towards moving objects the spider makes three other
kinds of responses to targets in the field of view of the lateral eyes.

(i) Stimuli seen by the antero-lateral eyes cause the movable principal eyes to
saccade to the source of the stimulus (Land, 1969b). For targets up to 30° off the axis
this saccade results in fixation by the centres of the retinæ of the principal eyes.
However, in semitransparent females and juvenile specimens of *M. harfordi*, where
one can watch the activity of the principal eyes, saccade-like responses can be seen
to targets which lie in the field of view of the postero-lateral eye, i.e. more than 45°
off the axis. These saccades are sometimes accompanied by a turn, but not always.
They do not, of course, result in fixation by the principal eyes, and their occurrence
seems to serve no useful purpose.

(ii) Occasionally a spider sitting on the edge of a leaf will double under the leaf
with a sideways movement when something moves above or behind it. This response
is not often seen, turning towards the stimulus being much more common. However, *M. aeneolus*, in the apparatus, occasionally shows a very similar manoeuvre, when
instead of turning toward the target it jerks the ring up sideways until it is nearly hori-
zontal; in the real world this would have placed the spider behind or beneath what-
ever it was sitting on. This is presumably a defensive response to flying predators.

(iii) When a spider is being chased by, for example, a biologist’s pencil, it con-
tinuously adjusts its track so as to keep the stimulus directly behind. This is a par-
ticularly interesting response in that it represents a completely opposite interpretation
by the motor system of sensory data which would, under happier circumstances, result
in a turn to face the target.

All three kinds of responses are made to moving objects only, and so presumably
their pathways share the same peripheral neuro-sensory machinery as the more
common fixating type of turn.

DISCUSSION

When a jumping spider turns to face a moving object behind it or to the side, it
does so accurately whether or not it receives visual feedback, i.e. whether or not the
image of the target moves across the retinæ as the turn is made. This means that
the retinæ tell the central nervous system not only that a stimulus exists, but also
precisely where it has been seen, and this information is translated into a set of instruc-
tions to the legs to turn the animal by the appropriate amount. Once initiated, a turn
is not further influenced by the stimulus. It follows from this that each small region
of the retina is capable of issuing a different instruction to the legs from each adjacent
region. The interesting question which now awaits investigation is the problem of
calibration: how do the various instructions issued by the retinæ, representing spatial
positions, come to be translated accurately by the nervous system into the fairly
complex patterns of muscular activity which constitute the turns.
Partial turns

In practice the spider has three main options open to it when a moving stimulus appears. It may (i) do nothing, (ii) make a partial turn of about 20°, the size of such turns being independent of the stimulus position (Fig. 5, 6), or (iii) make a complete turn of the kind just discussed, where the size of the turn is approximately equal to the stimulus angle. These are in addition to the three other special kinds of responses mediated by the lateral-eye and described in the last section of Results. The most enigmatic of these responses is the partial turn, since such a turn does not result in fixation by the antero-median eyes, and is thus apparently not useful to the spider. Partial turns are not artifacts of the experimental situation since unrestrained animals also show them.

A possible teleological explanation for their presence is that they give the spider a second chance of responding fully to a stimulus. Fig. 10 shows that when a target is seen by the same part of the retina repeatedly, the chance of a turn—partial or complete—being made falls rapidly to a low value. If, however, the target appears on a different part of the retina when it moves again, the probability of a turn being made is not diminished (the probability remains close to 50% in the example shown in Fig. 10). Thus a small turn in the direction of the target will permit the spider to respond a second time should the target move again. Further, since the stimulus angle decreases following each partial turn, and the probability of a response occurring increases as the stimulus angle decreases (Fig. 9), the chance of a second turn being made will actually increase, for stimuli more than about 60° from the body axis.

Partial turns can thus perhaps be regarded as a way of minimizing the amount of work done by the spider, enabling it to avoid making too many large turns to possibly irrelevant objects, while not preventing responses to insistently important ones—those that move several times.

Sensory, central and motor aspects of turning

The problem of how the spider's nervous system is organized to perform the task of turning can be divided into three parts. These correspond roughly to the contributions of the three traditional divisions of the nervous system—sensory, central and motor—and the questions that need answers are: (i) what are the characteristics of stimuli which lead to their detection by the retinae, and how do the 'movement detectors' of the retinae work? (ii) What is the nature of the central decision-making process which permits some stimuli to result in turns, while other identical stimuli do not? (iii) How is the information from the retinae, specifying position, translated into appropriate neuromuscular activity?

These questions will be discussed in turn.

Sensory factors

Some stimuli consistently result in turns while others do not. It is reasonable to suppose that the retinae and their associated neural machinery are organized in such a way as to respond, by passing on spatial information, only to a restricted range of stimuli, possessing perhaps the characteristics of potential prey or mates.

The conditions that have so far been shown to be essential for the initiation of turns
Turning in jumping spiders

are, first, that the target moves—stationary objects or those that merely change in
intensity at a single position are not effective—and secondly that the smallest dimen-
sion of the target must exceed about three-quarters of the distance between receptors.
Other factors which are important, but have yet to be properly explored, are contrast
and the rate and distance of the stimulus movement. What emerges from this is that
the ability to detect small targets is limited, at least in part, by the dimensions of the
receptors themselves as well as by the connexions of their associated neuropile. It is
too early at present to attempt the task of producing a formal minimal model of the
system responsible for movement detection, like that proposed by Reichardt (1962)
for optomotor responses of beetles, but careful analysis of stimulus conditions should
make this possible.

It is interesting that the use of a target with a complex outline, as opposed to a
plain dot, does not improve the chance of a turn being made. This contrasts with the
situation in the praying mantis (Rilling, Mittelstaedt & Roeder, 1959) where strike
release is considerably affected both by the complexity of the outline of the target,
and by the detailed nature of the movements that it makes. ‘Form vision’ for the
lateral eyes of salticids apparently means no more than the detection of movement
by objects subtending an adequate visual angle; the movement of a hand, or a car on
the street seems to be as ‘adequate’ a stimulus for eliciting turns as more appropriate
stimuli—a fly or another jumping spider. The elucidation and identification of pattern
is performed by the principal eyes, after the spider has made its turn (Land, 1969).

Central factors

Even when the stimulus is optimal in size, contrast and velocity of movement, the
spider often fails to respond to it; in fact under most circumstances it fails to turn to
it most of the time. The same stimulus in the same position may fail to evoke a turn
at one time but may evoke one at the next presentation. This is not due to a failure of
the retina to detect the stimulus, but to a ‘veto’ imposed centrally, somewhere between
the retina and the motor part of the nervous system that executes the turns.

This can be demonstrated in two ways. First, as one increases a particular stimulus
parameter, e.g. size (Fig. 8), the probability of a turn being made increases, but only
up to a certain point, and after this there appears to be nothing one can do with the
stimulus that will improve its chance of evoking a turn. Thus only part of the failure
to respond can be attributed to stimulus inadequacy, the rest being due to other
factors, presumably operating central to the retina. In fact in the experiment shown
in Fig. 8 the maximum probability of turning attained by stimulus manipulation was
about 15% (rather lower than usual) leaving 85% of ‘failures’ unaccounted for.
Secondly, if one examines the movements of the principal eyes while presenting
stimuli to the lateral eyes one finds that target movements often evoke saccades in
these eyes without simultaneously causing turns. There is thus no question of the
stimuli not being detected; rather, the central nervous system does not transmit the
findings of the retina to the legs, although it does transmit them in this case to the
muscles of the principal eyes.

One way of looking at this problem, which brings together conceptually the findings
reported here, is to suppose that each position-specifying ‘line’ from the retina to the
motor system contains a device of unknown nature which permits the passing on of
a given proportion of instructions from the retina, while vetoing the remainder. The ‘setting’ of each device, i.e. the proportion of retinal instructions that it will pass, can be different from the settings of those in other lines, and can be altered in various ways. Factors which would affect the setting of each device include: (i) the retinal location to which it is connected (Fig. 9); (ii) the number of instructions it has recently received (habituation, Fig. 10); (iii) long-term variations in ‘central state’. Fig. 10 shows that the probability of a response occurring may be higher or lower on different occasions for stimuli in all positions. Factors, so far unexplored, which might have this general effect include hunger and thirst, time of day, sexual state and stage of moult. (iv) Dishabituation. Noxious mechanical stimulation would reset all devices in the direction of increased probability of passing instructions.

For the moment the idea of a probability-setting device must be regarded as a convenient fiction. There is no reason to suppose that each of the four kinds of probability variation occur at a single stage in the neural ‘throughput’—much less at a single synapse with appropriate magical properties. Nevertheless, the idea is useful in defining the role of the neural structures intervening between the detecting and executive machinery.

A second decision is also made by the nervous system, namely whether a turn is to be partial or complete. At present little can usefully be said about it, except that it has the same probabilistic character as the decision whether to turn at all, and that factors such as habituation which decrease the probability of any turn being made also tend to decrease the ratio of complete to partial turns.

**Motor factors**

The task of the ‘motor end’ of the nervous system is to obey the instructions from the retinae. This is a more complex task than it appears at first sight. Inspection of Fig. 4 will show that the position of the spider’s body with respect to the substrate (the ring) prior to each turn depends upon an historical accident—the position attained at the end of the previous turn. Examination of cine records of turning shows that the positions of the legs, like the positions of the ring, are quite different at the beginnings of each succeeding turn. There can thus be no single ‘fixed action pattern’ or ‘motor tape’ corresponding to each retinal instruction. A turn of 80° to the left must be executed quite differently, in terms of leg movements, when the legs are in one starting position rather than another. The motor nervous system must not only execute the retinal instruction, but must make this execution independent of the positions of the legs at the outset.

**SUMMARY**

1. Jumping spiders turn to face moving objects. These turns are mediated by the lateral eyes. They can be accomplished accurately whether or not the spider sees the relative movement of the stimulus across the retinae which would normally result from such a turn.

2. The spider’s response to an adequate stimulus may be: (i) to make a ‘complete’ turn resulting in fixation by the antero-median eyes; (ii) to make a ‘partial’ turn of 10–20°, whose magnitude is independent of stimulus position, and which does not result in fixation, or (iii) to ignore it.
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3. To be seen, a stimulus must subtend more than 0.7° (slightly less than the distance between receptors) and must move through a minimum angle of about 1°.

4. The probability of a turn being made is greatest for stimuli 40–90° from the spider's front, and decreases to a low value for stimuli behind the animal, and immediately in front of it.

5. Repeated presentation of a stimulus to one part of the retina results in a rapid decrease to zero of the probability of a turn being made, but turns can still be evoked by moving the stimulus a few degrees to a previously unstimulated part of the retina. Habituation does not affect the sizes of the few turns that are made. Dishabituation can be caused by mechanical stimulation, or it may occur spontaneously.

6. The fields of view of the lateral eyes have been measured in the horizontal plane by blinding each eye and determining the parts of the visual field from which turns could not be evoked.

7. Three kinds of response mediated by the lateral eyes, in addition to turns towards the stimulus, are described.

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