Visual orientation in the Salticidae (Araneae)

T. J. BENNETT and R. D. LEWIS
Department of Zoology, University of Auckland, Private Bag, Auckland

Abstract

In both predation and escape behaviour, the jumping spiders *Trite auricoma* (Urquhart) and *Trite planiceps* Simon demonstrate open and closed loop visual orientation systems. Open loop visual orientation is mediated by the lateral eyes by visual stimuli occurring outside the fields of view of the anterior median (AM) eyes. Closed loop control with visual feedback through the anteriorly directed median eyes enables object location and recognition of stimuli falling within the field of view of these eyes.

Turning movements initiated by the lateral eyes result in object location by the AM eyes which control the animal's subsequent behaviour. Movement detection by the lateral eyes results in turning, by which action the object is brought within the range of the AM eyes. Visual stimuli located behind the body produce escape reactions without recognition and location by the AM eyes. Orientations involving turning movements include partial turns and tracking movements. There is some evidence to suggest that the spiders retain some memory of the previous turn.

INTRODUCTION

Jumping spiders (Salticidae) demonstrate very complex mechanisms of visual perception in prey-capture, escape, and courtship behaviour. These spiders have a large field of vision around their prosoma which enables them to detect objects moving in the surrounding environment (Fig. 1); with their ability for very dextrous movements they are actively predacious, leaping to capture their prey. Silk webs are used only for retreats, during moulting, and in the construction of brooding chambers.

The survival of these spiders depends on their ability to locate objects moving around them accurately. In order to do this the Salticidae use two methods of visual orientation. First, under closed loop conditions they receive visual feedback from the AM eyes which recognise the stimulus (Land 1972). Secondly, in the absence of visual feedback, they use the lateral eyes for open loop control where orientation occurs without perception of the spider's own movement (Land 1971).

The closed loop system enables the spider to follow its prey and to see the consequences of its own motion, and this system contributes to sensory information on which further movement is based (Hinde 1970; Kalmus & Wilkins 1966; Bullock & Horridge 1965).

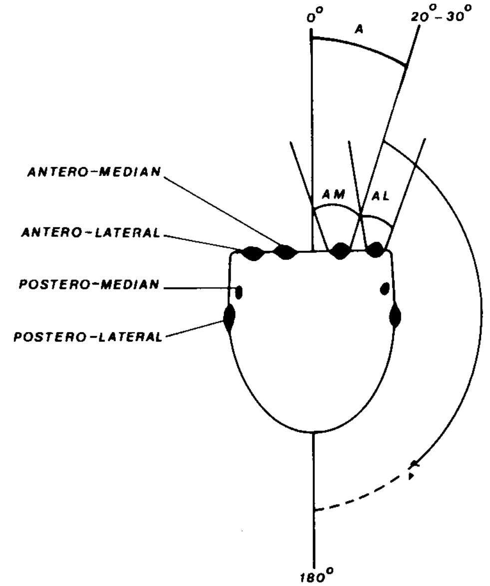


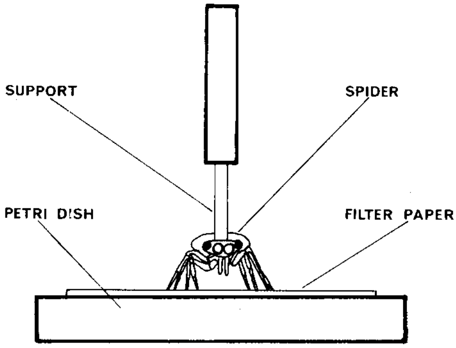
Fig. 1. Diagrammatic representation of the prosoma of a salticid spider showing the arrangement of the eyes, the possible fields of view for the antero-median (AM) eyes and antero-lateral (AL) eyes, the approximate range over which the open loop control operates marked B and that range for the closed loop control marked A.

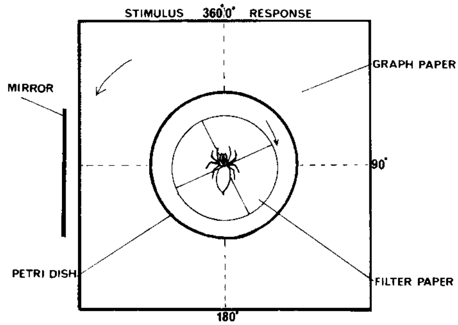
In closed loop orientation there can be correction for deviation and error, and the animal relies on visual feedback for orientation. An example of a closed system that is superficially very similar to the spider's situation is the fixation response of the praying mantis (see Hinde 1970). Here the mantis turns its head towards the prey which is continuously visible and the animal reduces the deviation of the prey from the eye axis as much as possible, preferably to zero, the fixed reference point for the closed loop.

The open loop control involving the lateral eyes is typical of many rapid movements, especially predatory strikes, e.g., the cuttlefish, Messenger (1968), and there is obviously a great need for precise calibration of the nervous system for accurate translation to motor activity. Some fireflies also employ an open loop mechanism during courtship behaviour where the flash of a distant female causes the male to turn and fly towards the source. It receives no visual feedback during turning, as the flash is over before the animal begins its movements (Mast 1912).

In order to understand the systems operating in the orientation of these spiders it becomes necessary to interfere permanently with the feedback system. The removal of visual feedback prevents the spider from seeing the relative movement of the stimulus during the turn itself. In the experiment to be described the spider is physically fixed in such a situation to prevent visual feedback. If the spider is orientating by a closed loop mechanism this will drastically interfere with the response. If, however, the system is an open one the absence of visual feedback should have no effect on the turn. The experiment will therefore provide information on the control system used in visual orientation in jumping spiders, and will illustrate how and when these systems operate. Combined with observations and experimentation in the natural situations, it should provide information as to how the spider's visual mechanisms are employed.

In natural conditions, jumping spiders turn to face moving objects with combinations of both complete and individual turns which may or may not result in prey location by the AM eyes. Once this object location has occurred, however, the spider may behave in one of several ways. For instance, if it is prey, the spider may crawl towards it and jump and grasp it with the pedipalps and the first pair of legs. The spider may creep towards or run away from an object or begin a particular display if the object is another jumping spider. Even when starved these spiders often show no interest in prey and at other times they will follow an object incessantly. At all times the spiders are extremely agile and the





Figs 2,3. 2. Lateral view of an experimental animal set up in open loop conditions. 3. Plan view of an experimental set up. The larger arrow indicates the direction of the applied stimulus, and the smaller one the direction of the response in open loop conditions. The point of attachment of the spider to the support is shown by the black bar.

positioning of prey relative to the horizontal axis of the spider makes little difference in location.

METHODS

Adult *Trite planiceps* and *T. auricoma* were collected locally and maintained in dry petri dishes and fed on a housefly or a few adult *Drosophila* each week. The experimental design to prevent visual feedback was similar to the one designed by Land (1971) and modified by L. M. Forster (personal communication).

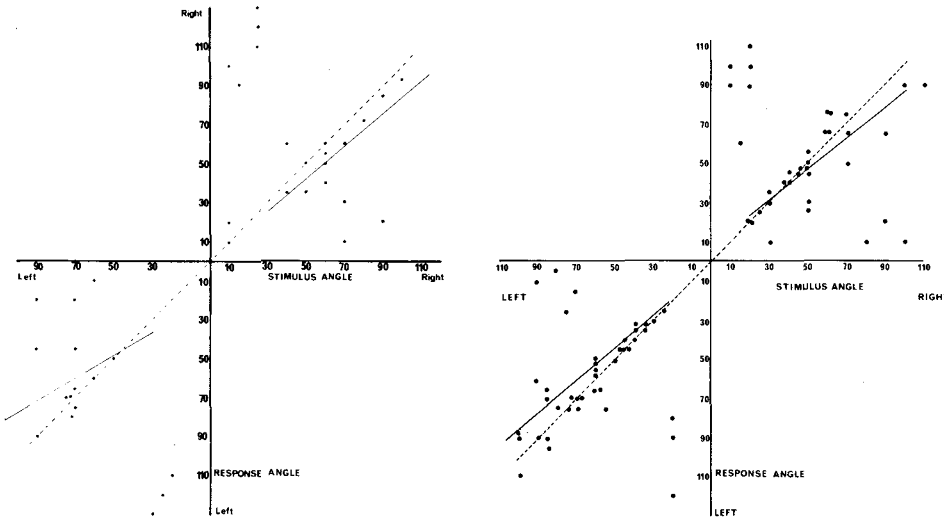
The spider was suspended in space by cementing balsa wood to the prosoma with paraffin wax. It was mounted so that the spider's horizontal view remained unobstructed (Fig. 2). To record the spider's response a circular filter paper was waterproofed, marked into quadrants and allowed to float freely in a petri dish full of water, this in turn lay on a graph paper marked into appropriate angles. The apparatus was arranged so that the suspended spider was just able to reach the filter paper with its legs and move it forwards, backwards or in a circular fashion (Fig. 3).

A mirror provided the stimulus to the spider and this was rotated around the edge of the petri dish. It was moved through small turns to provide a target stimulus by reflection of the spider's own image. An alternative stimulus could be provided by fixing a large live housefly by the thorax and wings in place of the mirror; the movement of the legs was sufficient to provide a moving stimulus to the spider.

The spider would respond to a stimulus by attempting to turn. Unable to do so, the spider would rotate the filter paper in an opposite direction to the intended turn. Thus it was possible to record both the angle of stimulus and the direction and magnitude of the desired orientation. Since the orientation of the body axis of the spider remained the same even after an attempted turn, the spider could receive no visual feedback in turning. The spider would only respond to a moving target, if disturbed by noise or vibration it would draw up its legs and remain stationary. In general any one spider could remain attached and respond for several hours. If too many stimuli were applied in quick succession the animal failed to respond.

RESULTS AND INTERPRETATIONS

A total of 4 individuals of *T. planiceps* and 6 individuals of *T. auricoma* gave the results presented graphically in Fig. 4 and Fig. 5. Each result is given by a stimulus angle and a response angle. Regression lines are drawn and the dashed line indicates a 1:1 orientation where response angle is equal to stimulus angle.



Figs 4,5. Relationship between stimulus angle and animal response. The solid lines are the regression lines for the regions of open loop control, and the dashed line indicates the 1:1 orientation where response angle is equal to stimulus angle. At large stimulus angles there are 2 groups of partial turns, and at low stimulus angles there are 2 groups of closed loop turns. 4. *Trite planiceps*. 5. *Trite auricoma*.

Open loop control

From the results it can be seen that both species are able to orientate accurately in the absence of visual feedback, and thus this is an open loop control system. The spiders use this mechanism during orientation only when the stimulus is in the field of view of the lateral eyes; i.e., with stimulus angles greater than 20° to the body axis for *T. auricoma*, and 30° to the axis of *T. planiceps*. The accuracy of the orientation depends on the angle of the stimulus. At large angles, i.e., greater than 100°, the orientations are less accurate than for small stimulus angles. Note that although the spider needs to orientate by the lateral eyes only to within the field of view of the AM eyes where recognition can occur, the accuracy of the open loop orientation is far greater than strictly required thus reducing the total number of turning movements required for location.

Closed loop orientation

The spiders exhibited a series of small turns when the stimulus was applied close to the body axis, i.e. within 20° either side of the body axis for *T. auricoma*, and 30° for *T. planiceps*. They continued to turn towards the stimulus in an attempt to retain a constant image of the object, i.e. they required the visual feedback that the design of the experiment prevented; this is described as a closed loop system. Any orientation within these fields was thus controlled by a closed loop mechanism and produced turns of large angles, often associated with forward steps whereby the spider attempted to bring the stimulus directly in front of the mid-line axis.

Partial turns

In approximately 5% of the trials partial turns were exhibited. Here the animal in response to a stimulus of large angle demonstrated incomplete turning. This involved small turns of about 10° or 20° followed by either forwards or backwards steps or in some cases a large angle turn. This correlated with observations made in the field where they were found to produce similar "test" turns which would result later in prey location.

Escape reactions

When a stimulus of large angle was applied an escape reaction was produced. Here the spider turned through large angles in the same direction as the stimulus, followed by stepping movements forwards and backwards. In the natural habitat it was found that anything moving directly behind the spider caused it to move rapidly away. Strong light or vibration would also produce escape reactions.

Role of the lateral eyes

It was found that when the lateral eyes were blinded the animal was only able to respond to stimuli applied close to the body axis, and only able to catch prey that landed directly in front of the body. The animal could still however, show recognition of stimuli, i.e., respond to different stimuli selectively, and perception of distance. When the AM eyes were covered this ability was lost and responses could only be elicited by moving stimuli within the field of view of the lateral eyes. Here the spiders became unable to locate and capture prey. Covering the small postero-median eyes had no effect on orientation.

Feedback from the legs

In the absence of visual feedback, information concerning the orientation must come from the legs (Land 1972). The spiders were able to orientate accurately when several of the legs had been amputated. Orientation would proceed as long as the spider was able to turn the filter paper. Accurate turning also seemed to be independent of the original starting position of the legs.

Tracking movements

Also demonstrated with individual spiders of *T. auricoma* were "tracking movements" with the lateral eyes. The response occurred with stimuli from 30° to 70° angles where the animal having already responded, for example, to a 50° turn would make a small 5° turn when the stimulus was moved 5°, i.e., rather than reorientate to a 'new' stimulus at 55°, and would follow an object in this manner over a range of degrees with small turning increments. If any time lag occurred between the stimuli the spider would reorientate to zero. This implies that the animal has a short term memory of the previous turn, but this may only be a consequence of the experimental design.

DISCUSSION

The relevance of the above results can be considered in relation to the natural behaviours of these spiders. The Salticidae have a large field of vision around their body, and by using both open and closed loop visual systems are able to orientate precisely or react swiftly to an object within this range. This is important when considering the environmental situation, with the high probability of predation and the need to conserve energy. The combination of the two types of orientation provides for considerable behavioural versatility with respect to capture, mating, and escape.

The lateral eyes consisting of both the postero-lateral and the antero-lateral eyes control the open loop system and enable the spider to locate prey, produce escape reactions, and allow subsequent recognition by the principal eyes. The open loop system prevents distraction from objects around the spider in the visual field, for the spider will only respond to the initial stimuli, and ignore others in the course of the turn. AM eyes enable the spider to track and follow, to recognise objects, and to carry out very precise manoeuvres.

Turning movements also include successive or partial turns which mean the animal can test a possible sighting or make turns where the environment limits manoeuvres (here the importance of memory is obvious as it enables the animal to complete a partial turn).

The animal can now be seen as a formidable predator. The spatial arrangement of four pairs of eyes permits considerable visual specialization, with each set of eyes coordinating a particular response. The Salticidae are extremely perceptive and agile and are capable of a large number of patterned behaviours. Physically they have powerful legs, a highly mobile opisthosoma, and strong palps and chelicerae. However, while the basic design of the visual orientation system has enabled these spiders to become successful active predators, their behavioural plasticity is reflected in a wide variety of species-specific courtship displays.

ACKNOWLEDGMENT

The authors wish to acknowledge the invaluable help of Mrs L. M. Forster, Dunedin in the design of the experiments and the preparation of the manuscript.

REFERENCES

BULLOCK, T. H.; HORRIDGE, G. A. 1965: *Structure and Function of the Nervous System of Invertebrates.* Volume 1, Freeman, 798 pp.

HINDE, R. A. 1970: *Animal Behaviour: a Synthesis of Ethology and Comparative Psychology.* 2nd ed. McGraw-Hill Kogakusha. 876 pp.

KALMUS, H.; WILKINS, B. R. 1966: Physiological control systems. *In* Kalmus (ed.) *Regulation and Control in Living Systems.* Wiley. 468pp.

LAND, M. F. 1971: Orientation by jumping spiders in the absence of visual feedback. *J. exp. Biol. 54:*119-39.

—— 1972: Stepping movements made by jumping spiders during turns mediated by the lateral eyes. *J. exp. Biol. 57:*15-40.

MAST, S. O. 1912: Behaviour of fireflies, with special reference to the problem of orientation. *J. anim. Behav. 2:*256-72.

MESSENGER, J. B. 1968: Visual attack of the cuttlefish, *Sepia officinalis. Anim. Behav. 16:*342-57.