VISUAL DISTANCE DISCRIMINATION BETWEEN STATIONARY TARGETS IN PRAYING MANTIS: AN INDEX OF THE USE OF MOTION PARALLAX

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Summary

1. When larvae of the praying mantis *Polyspilota* sp. and *Tenodera sinensis* want to leave an exposed position and can choose to move between stationary objects at different distances, they usually choose the nearest. Their ability to select the nearest object is greatest when the background has horizontal stripes and is least when it has vertical stripes. Object preference is based on a successive distance comparison, which may involve content-related memory processes.

2. Mantid larvae can determine the absolute distance to a stationary object. Vertical contrasting borders play an important role in this process.

3. Side-to-side head movements (peering) are directly involved in the distance measurement, as shown (i) by the peering behaviour itself and (ii) by the fact that mantids can be deceived in distance measurement by arbitrary movements of target objects during the peering movement.

It is supposed that the distance measurement involves the larger and faster retinal image shifts that near, as opposed to more distant, objects evoke.

4. Mantid larvae can distinguish a black-and-white rectangle in the foreground from a black-and-white striped background, even when both are similar with respect to luminance, contrast and texture. The ability to distinguish between figures and background could be explained by motion parallaxes, i.e. by the fact that during peering movements the nearer object moves faster and by a larger angle than the background structure.

5. From birth onwards, even when the eyes have yet to develop foveal specialization, mantids are capable of this visually controlled behaviour.

Key words: insect, praying mantis, spatial vision, distance estimation, image motion, motion parallax, *Polyspilota* sp., *Tenodera sinensis*.

Introduction

The behaviour of some insects shows that they are capable of visual distance measurement (for reviews, see Wehner, 1981; Schwind, 1989). During some of these behavioural activities, such as orientational flights by honeybees (Srinivasan *et al.* 1990; Srinivasan, 1992) or landing flights by houseflies (Wehrhahn *et al.* 1981), distances are under constant visual control; for others, such as jumps or strikes at prey, this is only possible to a limited degree or not at all, since all visual parameters must have been determined in order for the absolute distance to be estimated before the behavioural reaction occurs. When a wingless locust larva makes an aimed jump that follows a ballistic course, the jumping-off speed and angle must be adjusted for the distance to the goal (e.g. Wallace, 1959; Heitler and Burrows, 1977*a,b*). For fast strikes at prey, the absolute distance to the prey must also be known. For example, this is the case when the dragonfly larva (Baldus, 1926) and the beetle *Stenus* (Weinreich, 1968) extend their labia, when the bulldog ant snaps its claws shut (Via, 1977) and when the praying mantis (Corrette, 1990) and mantispid (Eggenreich and Kral, 1990) strike with their powerful

forelegs. The observer can thus see, on the basis of jump and capture behaviour, whether and how well the insect is able to measure distances and which visual parameters are necessary for it to do so. The mechanism involved in distance measurement can be studied by changing certain parameters in such a way as to deceive the senses of the insect, causing a measurable error in distance estimation. Rossel (1983) used prisms with a praying mantis, causing the insect to mis-estimate the distance to prey and providing the first evidence that insects had stereoscopic depth perception. When peering locusts were confronted with artificial movements of the target object, they mis-aimed their jumps, which proved that motion parallax plays a role in distance estimation (Sobel, 1990).

The aim of this work was to determine whether the eyes of a praying mantis, which are suitable for stereoscopic vision (forward-looking and with foveas; Rossel, 1979), can also evaluate motion parallax, which has been shown so far only in insects whose eyes look towards the side. This question was studied using peering and jumping behaviour in young mantid larvae, a logical continuation of previous studies by Walcher

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and Kral (1994). Our aim in this study was to determine (1) whether distance measurement to stationary targets is possible when they are outside the range of optimal stereoscopic vision, and the role of the background in this process; (2) how precise relative and absolute measurements can be under these conditions; (3) whether the development of the fovea (Köck *et al.* 1993; Leitinger, 1994) during the first larval stages affects distance measurement; and (4) the role of peering, i.e. side-to-side head movements, in distance measurement.

Materials and methods

Animals

The behavioural experiments involved the first two mobile instars (second and third) of praying mantids, *Polyspilota* sp. ex Durban and *Tenodera sinensis* Saussure (both species are very similar). Adult females of *Polyspilota* were collected some 40 km north of Durban, South Africa, in December 1993, and fertilized eggs, laid in the laboratory, were raised individually under controlled conditions with a daily cycle of white light (500–800 lx) from 6:00 to 18:00 h and darkness from 18:00 to 6:00 h at 28 °C and 55 % relative humidity. Eggs of *T. sinensis* were obtained from the Carolina Biological Supply Company, Burlington, NC, USA. The larvae were fed with wingless adult *Drosophila*.

Experimental design

Individual animals were placed on a small round island in the middle of an arena that was filled with water up to the edge of the island (Fig. 1A). Four different versions of the inner wall of the arena were presented: plain white, or white with horizontal, diagonal (45 °) or vertical black stripes, all with the same spatial frequency of 0.19 cycles degree^{-1}. This meant that a white and a black stripe together always had a visual angle as seen from the centre of the island of 2.6 °. This more than covered the visual angle of an ommatidium, which in turn meant that the stripes could be seen distinctly by the animal (see Rossel, 1979). Two or three black rectangular tiles were placed in the foreground as target objects (visual angles as seen from the centre of the island: 33.7 ° vertically and 66.8 ° horizontally) at right angles or at an angle of 120 ° to each other. The targets were within a range of distance within which (1) the vertical edges of the objects elicited distinct peering movements with subsequent flight reactions (aimed jumping or forward-stretching body movement) and (2) there was a distinct preference for the objects over the background. The distance of the individual objects from the island could be changed with a graduated rod (Fig. 1A) that was not visible to the animal. The diameters of the island (2–3 cm) and the arena (22–33 cm) were adjusted according to the size of the animal depending on its larval stage (body lengths between 7 mm and 10 mm); the arena was 20 cm high. The illumination of the striped background was between approximately 100 and 150 lx, measured from the middle of the arena. The plain background was more reflective, and when it was in place, illumination measured about 200 lx.
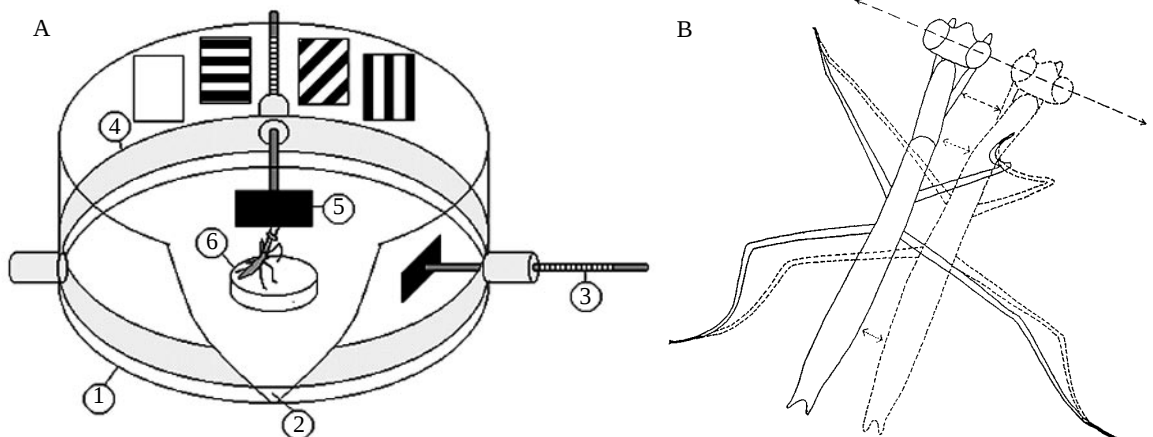
Recordings were made with a Sony CCD-VX1E Hi8 video camcorder under remote control to avoid disturbance by the experimenter; they were displayed on a PVM-1440QM 14 inch colour monitor.

Behavioural experiments

Analysis of the ability to discriminate distances to stationary targets

The first experimental series aimed to determine whether the animal always decides in favour of the nearest target when there are three targets at the same visual angle but at different distances. In the first experimental design, the distances of the three targets from the edge of the island were 1.5, 2 and 2.5 cm; in the next design confronting the animals, the distances had been pushed back by 5 mm and so were 2, 2.5 and 3 cm. The same was true for the third design, with distances of 2.5, 3 and 3.5 cm. This meant that the same distance occurred in at least two experiments and was accompanied by targets with different alternative distances. The attractiveness of the target was determined on the basis of the number of flight reactions

Fig. 1. (A) Experimental design: (1) arena, (2) water, (3) graduated rod to hold object, (4) holder, (5) black cardboard object, (6) island. Insets show the four backgrounds. Measurements are given in the text. (B) Schematic drawing of the horizontal peering movement of a mantid. Video analysis shows that peering begins as an accelerated movement. The head turns forward from a slightly sideways position, continues with a uniform translatory movement and ends with a delayed movement with the head turned slightly sideways. The smaller the peering amplitude, the smaller the non-uniform translatory movement component.

it elicited over a period of 30 min; this was then compared with results for a given distance, but when different alternatives were offered. If the tendency to jump or flee depended only on the absolute distance to a target, then the number of jumps or flight reactions (the time allowed was generous enough) towards a target at a given distance should not change much in the presence of distance alternatives.

The finding from this first series, that the most distant target in each experimental design was scarcely noticed or jumped at, while a target placed at exactly this same distance very often elicited jump or flight responses when the two alternative distances were larger, was the prerequisite for the second experimental series.

Analysis of the distance-discrimination threshold

The second experimental series determined the distance-discrimination threshold for mantids. This was carried out as follows. The distance to the first target was chosen so that it was just beyond the reach of the feelers and legs of the larva (foreleg length 6.8 mm in the second larval stage and 9.8 mm in the third stage) as it stood on the island, which maximized its readiness to jump. The distance of the target from the edge of the island was 1.5 cm in the second larval stage and 2 cm in the third stage. The second object was then placed at a distance that was 3 mm greater. The animal was then left in the arena until it had made six jumps. If five of the six jumps were to the nearer target, we interpreted this as meaning that the animal had recognized it as the nearer target. If fewer than five jumps were to the nearer target, then we concluded that the difference in distance had not been recognized. If at least five jumps were to the farther target, which was only the case in 11 of 480 studies, this was interpreted as an elevated motivation to flee and the animal was excluded from the evaluation.

When the first decision on distance discrimination had been made, the same animal was returned to the arena after a rest of at least 20 min. Depending on whether the animal had recognized the difference in distances in the previous experiment, the targets were either positioned closer to one another or farther apart. If, for example, the animal had recognized a difference of 3 mm, the distance was reduced by 1 mm and the test repeated. With every change in distance, the positions of the nearer and farther object were changed to prevent the animal from remembering the location of the nearer object. This process was repeated until the threshold of discrimination had been determined for every animal; the threshold was reached when two successive experiments produced different results (for example, difference at 4 mm recognized; difference at 3 mm not recognized; threshold therefore 4 mm). The threshold value was the smallest difference in distance between two targets that still elicited a distinct preference for the nearer target. The threshold value was determined for the four different background conditions. At least 20 animals were tested for each experimental design and their threshold values determined. Random checks were made to determine whether the established value remained

stable for a given animal on a particular day and this was found to be the case.

Analysis of peering behaviour

For scanning and peering analyses, a SVO9620P S-VHS hi-fi recorder and a PVM 1440QM 14 inch colour monitor were used. Peering parameters were calculated using single-image analysis. A peering movement was defined as a lateral movement of the head along a line that could not be interpreted as being part of a locomotory movement (Fig. 1B). The distance between the reversal points for this movement was called the peering amplitude. The points marking the beginning and end of each peering movement were marked on a transparent sheet mounted on the monitor screen. This distance was used to calculate the actual distance by relating it to the known diameter of the island, which was also shown on the screen. When the peering amplitude had been established, the duration of the peering movement was measured by counting the individual images on the video tape in which a point on the head appeared on the screen until the end point of the movement had been reached. The length of the peering movement was then calculated using the factor of recording or playing speed of the device in images s^{-1}. Velocity in mm s^{-1} could then be calculated from the length of the movement and the amplitude.

Attempts to determine whether peering is directly involved in distance measurement to stationary objects

This series used essentially the same experimental arrangement as described above, but with a target that could be moved in all three dimensions with an MM33 micromanipulator (HSE, Germany) and a stationary reference object which was outside the jumping range (the targets were rotated by 90°; visual angles of both targets were 33.7° horizontally and 66.8° vertically). The reference object encouraged the mantids to compare distances and repressed spontaneous decisions based on only a single means of escape. The background was white and unstructured. We examined jump readiness and/or accuracy in peering mantids (third instars) under the following conditions: (1) the target was not moved and when the mantids jumped, the optimal jump distance was measured (3 cm) and (2) as soon as the animal began to peer at an object, the target was moved at about the same speed either in the same direction or counter to peering. If the animal uses retinal image speed to measure distances, then the target ought to appear farther away than it actually is. The apparently too great distance should prevent the animal from trying to escape by jumping. However, if retinal image movement does not play a part in distance measurement, the mantids could have recognized that the target was being moved and refused to jump at a moving object. For this reason, a further experiment was performed in which the target was moved in the opposite direction when peering commenced. This would give the animal the impression of a lesser distance, and so it should react by jumping even if the target was outside the jumping range (5 cm).

The experiments were filmed and studied for changes (compared with peering movements using objects that were really stationary), such as synchronous movement of the head with the target. This should show whether mantids can detect target movement after they have begun their own movements. The disadvantage of manual movement of the target is that it requires great concentration on the part of the experimenter as well as ample experience with peering behaviour to match object and peering movements precisely. To prevent misinterpretations, only those trials in which this was successfully accomplished were evaluated, so that a large number of trials and large numbers of animals were needed to produce useful results.

Results

Ability to discriminate distances to stationary targets

The ability to discriminate distances to stationary targets was studied in the second and third instars of the praying mantis. It should be noted that, although the acute zone for greater spatial resolution (fovea) in the frontal eye region is scarcely developed in younger larvae, it is relatively well developed in older larvae (Köck *et al.* 1993; Leitinger, 1994). It can be said at the outset that this age-dependent difference in the degree of development of the fovea did not have any detectable effects in our findings.

Recognition of the nearest target

When mantid larvae (*Polyspilota* sp.) were given a choice of three black rectangular targets at the same visual angle but at different distances in front of a white, unstructured background, a comparison of distances showed that there was a clear preference for the nearest target. The possibility that the animals might have a spatial preference was excluded by ensuring that each target was sited closest to the animal in individual experiments (Figs 2, 3).

Threshold of distance discrimination

Fig. 4 shows that mantid larvae of *Polyspilota* sp. were able to discriminate the distance between two targets better when the background consisted of horizontal stripes (means ± S.D.; discrimination threshold: second instar 3.6±1.0 mm; third instar 3.5±0.7 mm); discrimination was poorest with vertical stripes (second instar 4.3±0.9 mm; third instar 4.6±0.7 mm). The distance to the nearest target was 1.5 cm in second instars and 2 cm in third instars. The difference in acuity of discrimination between horizontal and vertical background stripes was about 16 % in second instars (Student's *t*-test; $P<0.005$) and 24 % in third instars ($P<0.0001$). With the diagonally striped background, it seems that the distance between two objects at varying distances from the animal must be somewhat greater than with the other backgrounds if the animal is to recognize the nearer object. The values for the difference in acuity of discrimination for diagonal stripes in the second instar and for an unstructured background in the third
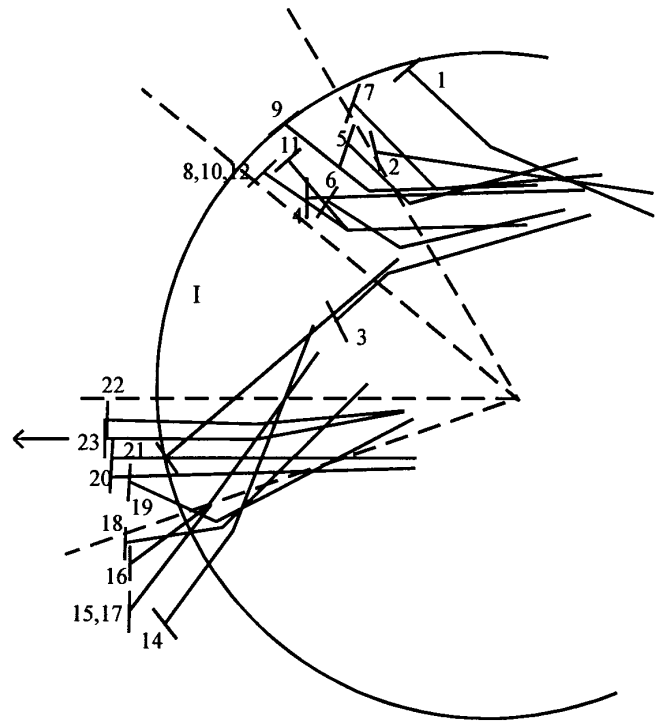
Fig. 2. Reconstruction of the movements by which the mantis (*Tenodera sinensis*) attempts to find the nearest object, to adjust its body for a jump and to determine the absolute object distance. This represents a typical case for a mantid larva on the island arrangement (duration of sequence approximately 3 min). The median sagittal plane of the head (short line) and the longitudinal axes of the thorax and abdomen are drawn. In this example, the mantid turns to two objects in succession whose edge positions are shown with dashed lines. The object closest to the bottom of the sketch is the nearer one. The edge of the island (I) is drawn as a circular outline. The mantid first tries to get as close as possible to the more distant object (movements 1–9). This is followed by peering movements (8–12, repeated bobbing of thorax and head). For movements 2, 3 and 4, the second (nearer) object is already within the mantid's visual field and the animal turns immediately to the nearer object after peering at the more distant one. Here the animal also attempts to get as close as possible, and with this nearer object, it leans farther over the edge of the island than it did for the more distant object. Movements 14–18 and 20–23 can also be seen as peering movements directed towards different edges of the same object (position 13 is not shown). Two different peering techniques can be distinguished here: for movements 14–18, translation of the head is due primarily to movement of the thorax–abdomen joint; movements 19–23 are based on bending of the legs, i.e. a lateral shift of the entire animal. The jump (arrow) occurs immediately after movement 23.

instar were approximately midway between the values for the horizontal and vertical patterns ($P<0.05$).

Peering at stationary targets

There was a close relationship between peering and object comparison, object choice and aimed jumping. Regardless of the background, mantid larvae on the edge of the island peered preferentially at the vertical edges of objects. When the animal peered at two or three objects at different distances, peering
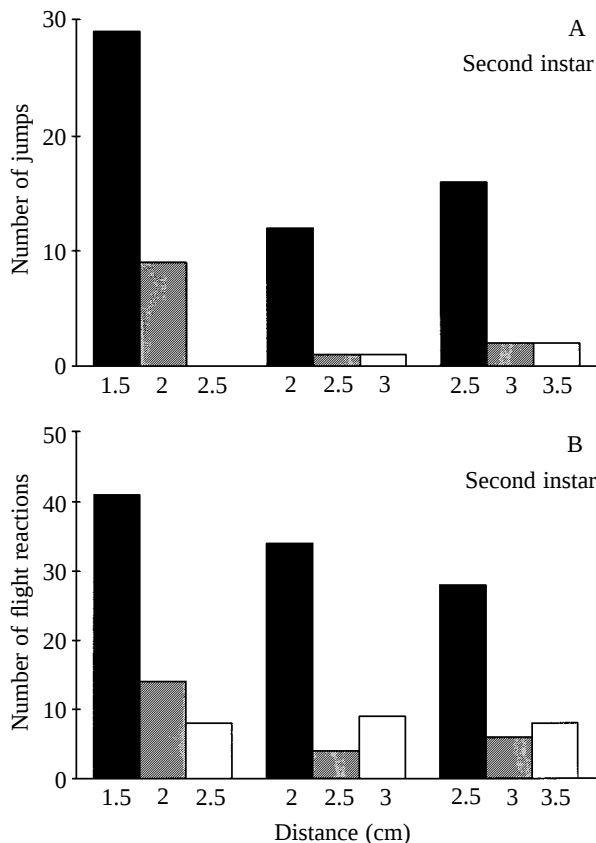
Fig. 3. Diagrams showing the absolute numbers of (A) aimed jumps and (B) flight attempts, i.e. forward stretching of the body, for a total of 14 animals in the second instar of *Polyspilota* sp., aimed at one of three identical rectangular black targets at various distances (in cm) in front of a white, unstructured background.

amplitude was adapted to the distance to whichever target was under consideration at that moment. Object-related peering was also seen immediately before an aimed jump.

Peering velocity

The velocity range for object-related peering was $0.6–4.2\,\mathrm{mm\,s^{-1}}$ in the second instar and $0.6–4.1\,\mathrm{mm\,s^{-1}}$ in the third instar of *Polyspilota* sp. Individual peering speeds could vary considerably during an experimental run; however, if the mantid made an immediate distance comparison, then the peering speed was usually adjusted to a rather constant value. For jump-eliciting peering, the velocity was generally higher for all background conditions than when peering did not lead to a jump (see Fig. 5; Table 1). With object-related peering that was not followed by an aimed jump, there was no significant difference in peering velocity between the nearer and farther object with all background conditions (except for vertical stripes in the third instar, $P<0.05$) (Fig. 5B).

Peering velocity immediately preceding an aimed jump to the nearer object was lower in the second and third instar with an unstructured than with a structured background. There was no distinct trend in the two larval stages for an effect of the three structured backgrounds, but the peering velocity was
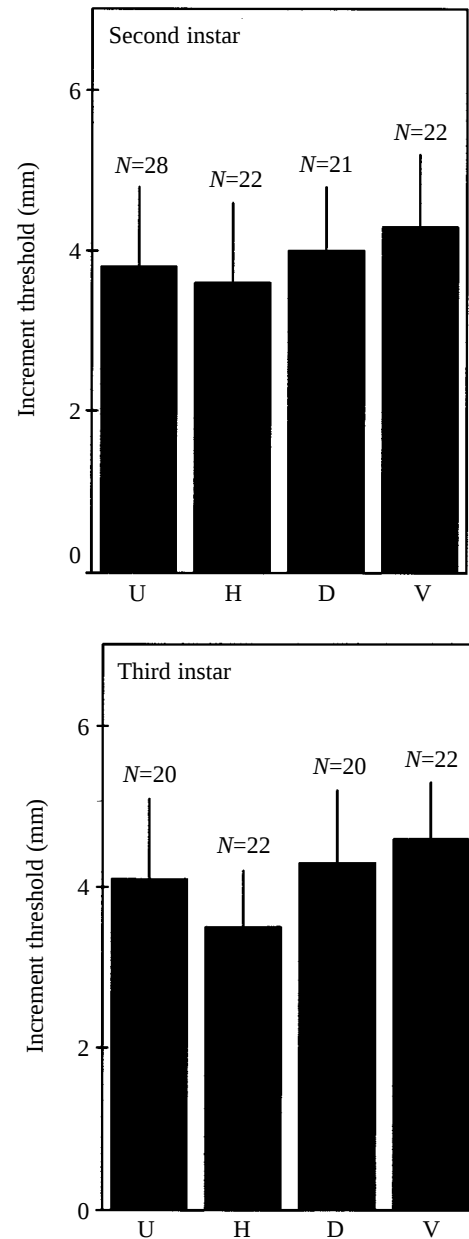
Fig. 4. Diagrams showing the smallest average differences in distance (increment threshold; mean + S.D.) from two black rectangular targets at the same visual angles at which the experimental animals (*Polyspilota* sp.) clearly, i.e. with a jump ratio of 5:1, chose the nearer target, as a function of background type. U, unstructured background; H, horizontal stripes; D, diagonal stripes; V, vertical stripes. For significance levels, see text.

somewhat higher with vertical than with horizontal stripes (about 10 %).

Mean peering velocity increased significantly from the second to the third instar with all four background conditions (e.g. for peering prior to a jump: unstructured 24 %, $P<0.01$; horizontal stripes 27 %, $P<0.05$; diagonal stripes 74 %, $P<0.0001$; vertical stripes 35 %, $P<0.001$).

Table 1. *Difference between the average peering speed of* Polyspilota *sp. before a jump to the nearest target (V_{nj}) and average peering speed when no jump was attempted (V_n) expressed as a percentage*

$V_n - V_{nj}$	Unstructured	Horizontal stripes	Diagonal stripes	Vertical stripes
Second instar	−5%*	−20%*	−19%; $P<0.05$	−30%; $P<0.01$
Third instar	−35%; $P<0.0001$	−13%*	−12%; $P<0.05$	−32%; $P<0.0001$

Significance level (*t*-test) $P<0.05$; * not significant.

Table 2. *Difference between average peering amplitude in* Polyspilota *sp. before a jump to nearer target (A_{nj}) and peering without a jump to nearer target (A_n) or peering without a jump to the farther target (A_f) expressed as a percentage*

	Unstructured	Horizontal stripes	Diagonal stripes	Vertical stripes
$A_n - A_{nj}$				
Second instar	+34%; $P<0.0001$	+42%; $P<0.0001$	+23%; $P<0.01$	+11%*
Third instar	+17%; $P<0.05$	+54%; $P<0.0001$	+39%; $P<0.01$	+22%; $P<0.01$
$A_f - A_n$				
Second instar	+14%; $P<0.05$	+18%; $P<0.05$	+20%; $P<0.01$	+19%; $P<0.05$
Third instar	+17%; $P<0.01$	+17%; $P<0.01$	+21%; $P<0.01$	+25%; $P<0.05$

Significance level (*t*-test) $P<0.05$; * not significant.
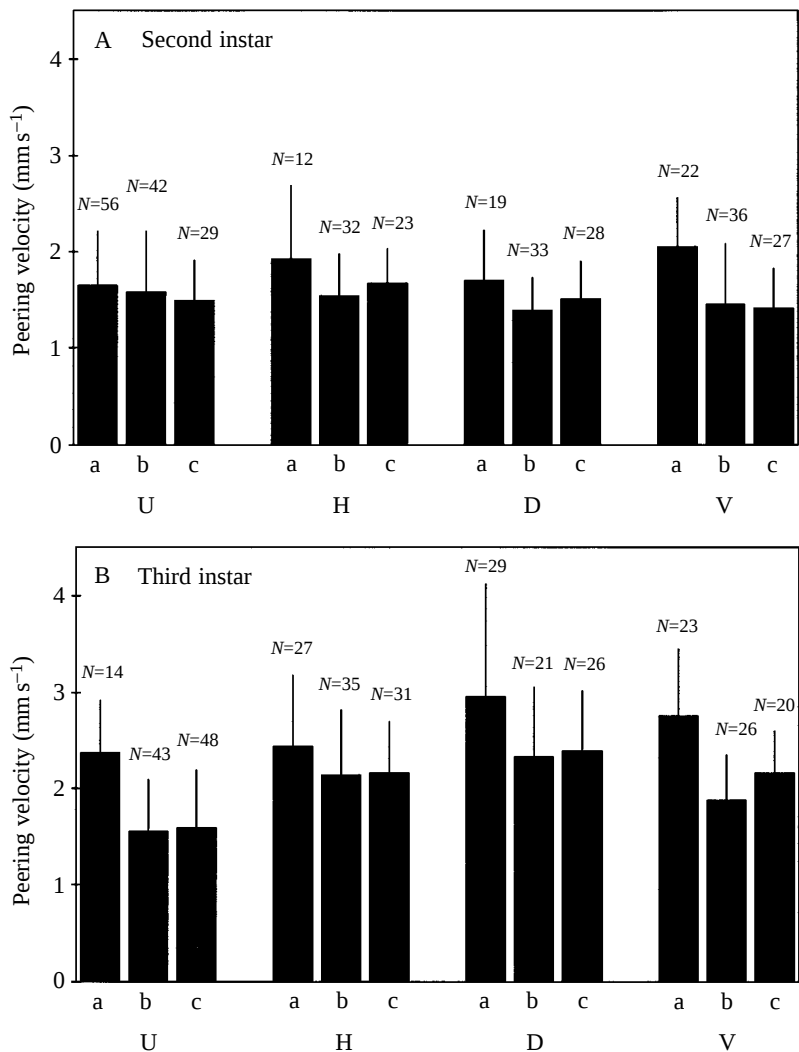
Fig. 5. Mean velocity of target-related peering movement (+ s.d.) for (a) a nearer target with a subsequent jump, for (b) a nearer target without a jump and for (c) a more distant target without a jump, as a function of the type of background. U, unstructured background; H, horizontal stripes; D, diagonal stripes; V, vertical stripes. (A) second instar and (B) third instar of *Polyspilota* sp. For significance levels see text and Table 1.

Peering amplitude

Peering amplitudes could be divided into two categories: relatively large amplitudes while the animal was scanning the surroundings, and smaller amplitudes when the animal had focused on nearby objects.

Fig. 6 shows that mean peering amplitudes prior to an aimed jump towards the nearer object were of about the same order of magnitude within the relatively narrow range for the first two motile instars of *Polyspilota* sp. with all background conditions. They averaged 1.9–2.1 mm in the second instar and 2.1–2.7 mm in the third. Fig. 6 also shows that when the animal peered at the nearer object but did not jump, the peering amplitude was greater than when it did jump (see Table 2, upper section). When the animal peered at the farther object, the amplitude was greater than when it peered at the nearer one (Table 2, lower section). However, within the relatively narrow range of distances (a few millimetres), no relationship was measurable between peering amplitude and distance to the object for peering ending in an aimed jump (see below).

Fig. 6 shows that the background influences peering amplitude, although the differences tend to be statistically insignificant. In both larval stages, the amplitudes with jump-eliciting peering were greater when the background was unstructured than when it was structured: by 5–10 % in the second instar and by approximately 10–22 % in the third instar. This difference in amplitude could also sometimes be seen when peering was not followed by a jump and was most evident between unstructured and vertically striped backgrounds in second instars (about 20 %; *P*<0.001) (Fig. 6A). The amplitudes for jump-eliciting peering were about the same with the three striped backgrounds in the second instar, but in the third instar they were highest with vertical and lowest with horizontal stripes. When there was no following jump, this tendency is reversed. Values were highest with horizontal, or sometimes diagonal, stripes but always lowest with vertical stripes.

There was a general tendency for peering amplitudes to increase after the moult from one instar to the next one (throughout postembryonic development).

Distance measurement when the object was moved during the peering movement

The diagrams in Fig. 7A show that *Tenodera sinensis* in the third instar made an aimed jump 76.5±10.0 % (s.d.) of the time
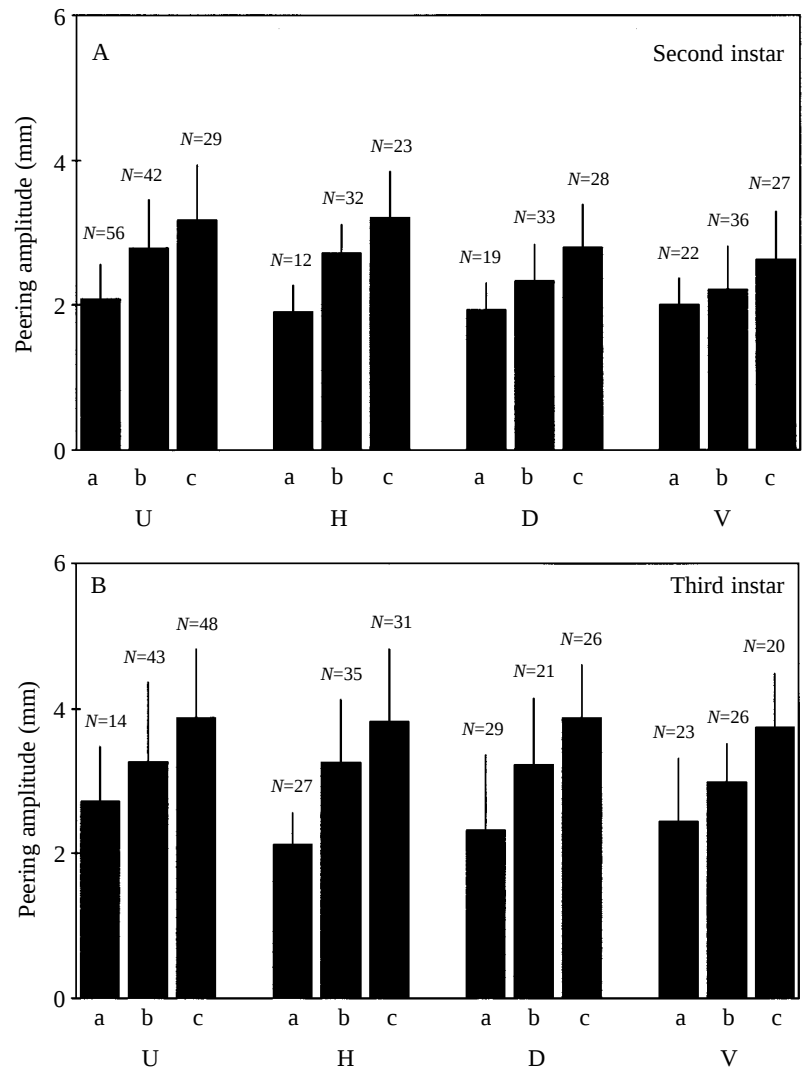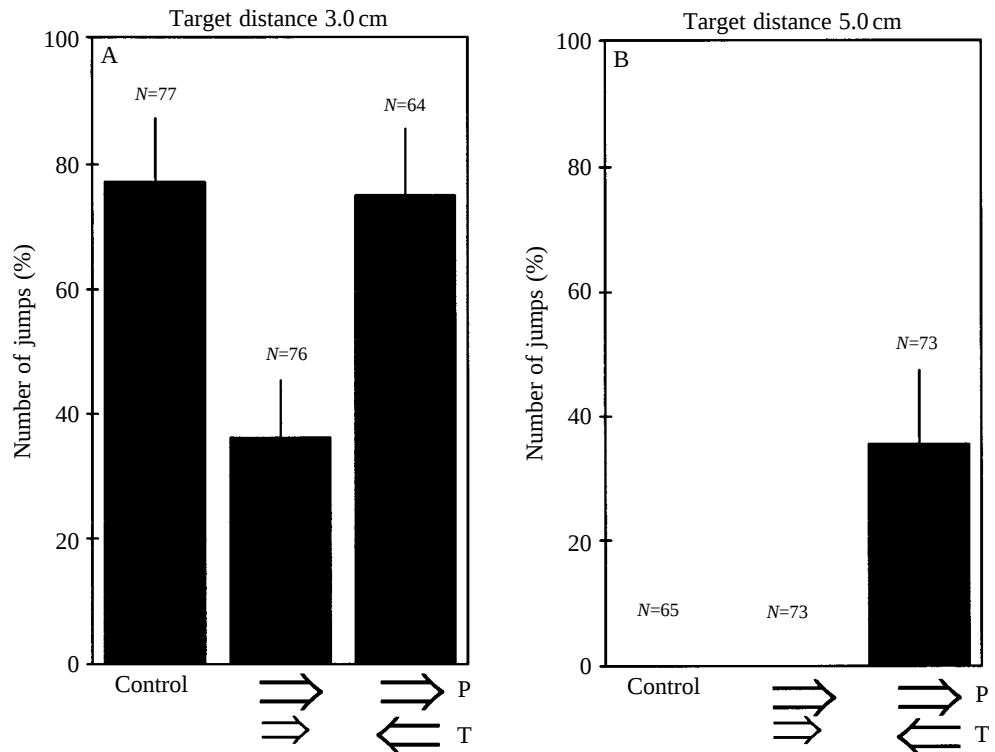
Fig. 6. Mean amplitude of target-related peering movement (+ s.d.) for (a) a nearer target with a subsequent jump, for (b) a nearer target without a jump and for (c) a more distant object without a jump, as a function of the type of background. U, unstructured background; H, horizontal stripes; D, diagonal stripes; V, vertical stripes. (A) second instar and (B) third instar of *Polyspilota* sp. For significance levels see Table 2.

Fig. 7. Diagrams showing the percentage of jumps after an animal has turned to an object, focused on it and peered at it when the object is stationary (control; no arrows), when the object moves in the direction of peering (two arrows pointing the same way) and when the object moves counter to peering movements (arrows going in opposite directions) (A) at a distance that is within the optimal jump distance (3 cm) and (B) at a distance at which jumps rarely occur (5 cm). The vectors (arrows) give the direction of movement and the speed component for a constant distance covered by the peering movement (P) and the target (T). Third instar of *Tenodera sinensis* (*N*=9 animals). For significance levels, see text.

to a stationary object at a distance of 3 cm, i.e. within the optimal range, after turning towards it, fixing on it and peering at it. If the object was moved at about the same speed and in the same direction as the peering movement, the jump rate decreased to 36.2±9.2 % (Student's *t*-test: *P*<0.0001). In contrast, if the object was moved during the peering movement at the same speed but in the opposite direction to the peering movement, the jump rate was 74.6±10.4 % and so, although a little lower than in the controls, was not significantly different from that of the controls. If the object was outside the jump range (5 cm) and was stationary, there was no jumping activity; if this object moved in the same direction as the peering movement, there were again no jumps, but if it moved in the opposite direction, there were 35.5±12.0 % jumps (Fig. 7B). Sometimes jumps could be elicited with target movement in the direction opposite to peering at distances which were very far outside the jumping range (about 8 cm).

When the point of landing was compared with that of control animals with stationary targets, we had an indication as to whether the distance had been over- or underestimated. Overestimation occurred when the object moved in the same direction as the peering movement, and underestimation when the object moved in the opposite direction. When the animal landed too late, it tended to hit the vertical edge and be turned to the rear of the target, where came to rest in a sitting position. When the landing was too early, the animal would barely reach the edge of the target with its relatively long legs and often hung upside down from it or fell into the water. When the distance was 5 cm, the mantids never jumped far enough when the object moved counter to peering. Water landings usually occurred in
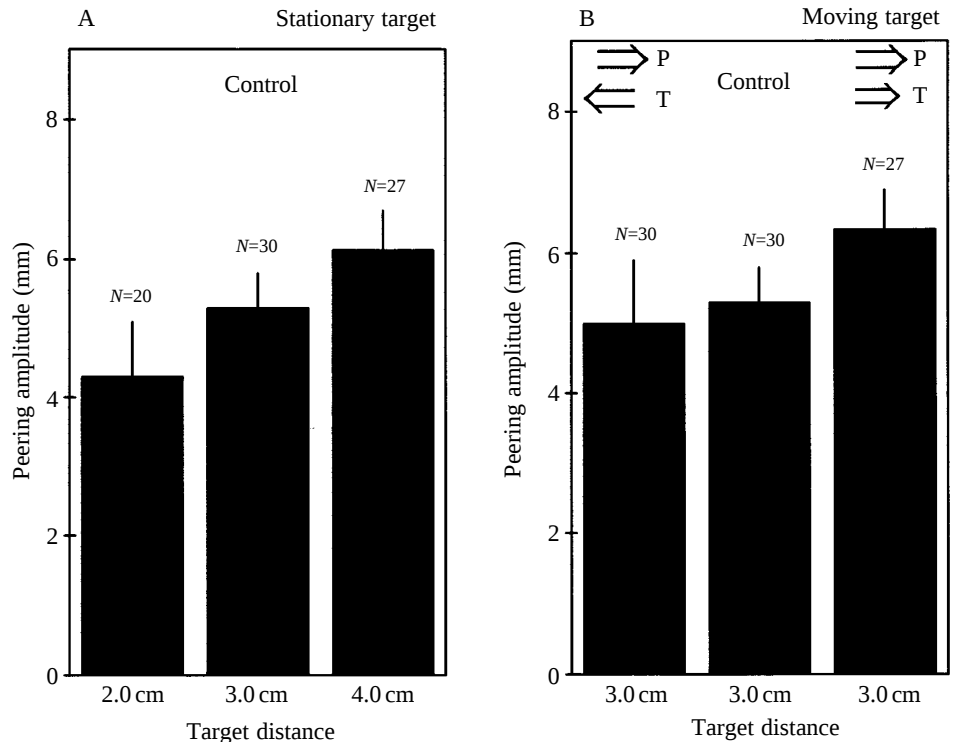
the last third of the jump, and well in front of the object. Because jumps were fast and rather short, take-off speed could not be quantified as a parameter for distance measurement.

Peering parameters

Before a jump at a stationary target, peering amplitude increased with distance to target; this is clearly shown in Fig. 8A with the three distances used, one of which sufficed to cause the animal to jump, one of which was in the optimal jumping range and one of which was barely within jumping range (*Tenodera sinensis*, third instar). The amplitude increase as distance increases is about one-fifth of the peering amplitude for the nearest target (*P*<0.0001). Fig. 8B shows the effect of target movement on peering amplitude when jumping distance is optimal. When the target was moved counter to peering movement, peering amplitude decreased slightly, but not significantly, compared with the situation with a stationary target. When the target was moved in the same direction as the peering movement, amplitude increased significantly compared with controls (20 %; *P*<0.01). If we assume that, for the animal, counter movement apparently decreases the distance and movement in the same direction apparently increases the distance, then the trend in Fig. 8B fits well with that in Fig. 8A.

Peering speed, however, was generally constant, both for the different distances and for the different moving conditions; slight variations were not significant. It should be emphasized that the target was moved manually while the movements were followed on the monitor; automatic target movement is planned to make more precise measurements of the movement.

Fig. 8. Mean peering amplitudes immediately prior to a jump (+ S.D.) (A) at target distances of 2, 3 and 4 cm and (B) at a target distance of 3 cm when the object was moved counter to peering movement (arrows going in opposite directions), when the object was stationary (control; no arrows) and when the object was moved in the direction of peering (two arrows pointing the same way). The vectors (arrows) give the direction of movement and the speed component for a constant distance covered by the peering movement (P) and the target (T). Third instar of *Tenodera sinensis* (*N*=9 animals). For significant levels, see text.

Discussion

Relative distance estimation to stationary targets

The island-in-the-arena experiments showed that when confronted with stationary targets at different distances but at the same visual angle, mantid larvae can clearly determine the nearest object, whether or not the background is structured. They can do this from birth, but after training for several days their ability to estimate distances improved considerably (Walcher and Kral, 1994). Their ability to discriminate distances is very acute compared with that of other insects under similar conditions (locust hoppers *Schistocerca gregaria*: Wallace, 1959; wood crickets *Nemobius sylvestris*: Goulet *et al.* 1981).

The preference for the nearest object is based on a comparison of distances. This was seen when the number of jumps to an object at a given distance was compared with the number directed at alternative objects at various greater distances. The objects were arranged in such a way as to show that the comparisons were successive, i.e. object for object; two or more objects were not compared at the same time. Whether or not the animal was peering, there was normally only one object, or two at most, within its visual field at the same time. Parallel processing would thus only be possible for a maximum of two objects. Fig. 2 shows this with a chronological series of numbered turning reactions to the edges of spatially separated objects. A successively operating mechanism of comparison, however, needs memory to retain the information on the distance to an object long enough for the next distance to be measured and for a comparison to be made. This leads us to consider whether not only distance to the object but also object position are retained. Mantid larvae

always find the nearest object very quickly when they first investigate the island. This could happen when both the distance and the position of an object in relation to other objects are compared in the animal's memory. Content-related memory of this sort has been demonstrated in other insects (e.g. beewolf or sphecid wasp *Philanthus triangulum*, Tinbergen, 1932; desert ants *Cataglyphis*, Wehner and Srinivasan, 1981; honeybees, Collett, 1992). Walcher and Kral (1994) showed that finding the nearest object is possible with only one intact eye, with only the frontal or the lateral visual areas or without a fovea. Essentially the same has been found for locusts (Wallace, 1959).

Absolute distance estimation to stationary targets

These experiments also showed that mantids are able to measure absolute distances to stationary objects from birth. Accurate aimed jumps are a clear indicator for absolute distance measurement. It should be mentioned that in 88 % of jumps, the landing was directly on the vertical edge of the object, otherwise it was near the edge, but in no case was it in the middle of the object. It was found that two fully intact eyes (i.e. including the frontal visual field, but without a fully developed fovea) are essential for absolute distance measurement (Walcher and Kral, 1994); monocular mantids can sometimes be mechanically provoked by the experimentor into making a jump but these are always unaimed attempts to escape. It is remarkable in this context that, unlike mantids, locusts (*Schistocerca americana*) also jump towards the object when an eye is fully occluded; however, they overestimate the distance (Sobel, 1990). This does not seem to be the case with grasshoppers (*Phaulacridium*

vittatum); according to Eriksson (1980) they reach their target even when one eye has been blinded.

Is stereopsis involved in distance measurement to stationary targets?

Binocular object localization is seen in mantids not only from the observation that only animals with two intact eyes jump, but also because they organize their jump to the vertical edge of a chosen target so that it is located exactly between the two eyes, i.e. on the extended median plane of the head. The presence or absence of a background is irrelevant. Similar stabilization behaviour with respect to a target object has been seen in other insects that move while they are making absolute distance measurements. The hawk moth *Macroglossum stallatarum* tries, while approaching and hovering, to hold the target (a dummy flower) exactly in the middle of the ventral binocular visual field, i.e. where the binocular overlap is greatest (Pfaff and Varjú, 1991). This type of behaviour suggests to the authors that, in this case, distance measurement could involve stereopsis; Farina *et al.* (1994) restricted this to the case where the dummy flower is closer than the maximum proboscis length of 2.5 cm.

Can mantid larvae stereopsis be precluded under these conditions? In the third instar with a distance between the eyes of 1 mm, there is a maximal horizontal binocular overlap of 52.7° and medio-frontal interommatidial angles $\Delta\phi$ of some 2° (acceptance angles $\Delta\rho$ of 2° light-adapted) (Leitinger, 1994), producing a distance range of from 1 mm to a maximum of 10 mm, beyond which there is unclear depth perception because the considerable increase in overlap of the relevant ommatidia in the visual field would decrease to an extent at which distance discrimination on the basis of triangulation would not be possible (see Burkhardt *et al.* 1973). However, the mantid views a target with several ommatidia and hence might perform some interpolation when determining the position of the retinal image. This, in turn, would provide the insect with a more accurate signal than would be expected from the interommatidial angle. Some evidence for such a mechanism is given by Maldonado *et al.* (1970) and Rossel (1986). It seems possible that stereopsis could provide distance information significantly beyond the range that is important for prey capture.

Is peering involved in distance measurement to stationary targets?

When mantid larvae focus on a target to determine its distance, they always make object-related peering movements; this suggests that peering must have something to do with distance measurement (see also Horridge, 1986). This is also indicated by the peering behaviour itself, which adjusts peering parameters depending on the visual conditions, such as a homogeneous or a structured background, as well as on different kinds of background structures.

A simple methodological trick (Wallace, 1959; Sobel, 1990) provided a direct indication that retinal image shifts caused by peering play a role in distance measurement in locust. Sobel (1990) studied the effect of lateral object movements both in the direction of, or counter to, the peering movement on take-off speed. The experiments showed that locusts are deceived by movement and perceive an object movement counter to the peering direction as a larger relative movement than that obtained with a stationary object, and so they underestimate the distance to it.

We used this idea to study the hypothesis of retinal image shift as a means of distance measurement in mantids. The findings shown in Fig. 7 support the following: the decreased jump frequency when the object moves in the same direction as the peering movement is because (1) the mantids are disturbed by the movement of the object and thus do not jump or (2) a distinct decrease in image motion produces the effect of a distance outside their jump range. The tendency for late landing indicates overestimation of distance. Increased jumping frequency when the object moves counter to the peering movement indicates (1) that jump motivation is increased and (2) that increased image motion makes the object appear to be nearer than it actually is. An underestimation of the distance is indicated by the too-short jumps and by landing in the water.

There is thus reason to believe that, in distance measurements, mantids use the fact that nearer objects cause larger and faster retinal image motion than farther ones. If retinal image motion actually does have an effect on distance discrimination, what are the possible measurement strategies? The direct connection between peering amplitude and object distance and the lack of correlation between peering speed and object distance (also seen outside the arena in the structured laboratory: the farther away the object focused on, the more pronounced the peering movements are with rather constant speed) support the supposition that estimated distance may be calculated from both the image movement (dependence of speed on distance) and from the peering movement (holding image displacement constant with distance). The results summarized in Fig. 8 clearly suggest a strong relationship between image movement and peering movement; it seems as if image movement (speed) controls peering movement (amplitude).

The assumption based on all these facts, that the animal's own movements are involved in distance measurement, i.e. that the animal must also be aware of its own movement, is indirectly supported by the observation that mantids never jump at moving objects when they themselves are not moving.

How can the foreground target be distinguished from the background?

From all of the above results and from the findings that mantids can only distinguish foreground and background contours that are similar with respect to contrast, shade of grey and pattern when they make peering movements, we conclude that absolute and relative movement parallax might be used. The necessary prerequisite for this, i.e. the evaluation of retinal image motion for distance estimation, has been demonstrated here. This would put mantids in the company of some other insects that are generally believed to use movement parallax in spatial orientation (e.g. locusts, Collett, 1978; Sobel, 1990;

Collett and Paterson, 1991; grasshopper, Eriksson, 1980; honeybee, Srinivasan *et al.* 1990). Further studies will be necessary before a final word can be said on this subject.

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