# THE VISUALLY CONTROLLED PREY-CAPTURE BEHAVIOUR OF THE EUROPEAN MANTISPID *MANTISPA STYRIACA*

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## Summary

Mantispids (*Mantispa styriaca*) are predatory insects; on bright sunny days, they wait in ambush for insect prey. The prey is captured as soon as it is within reach by means of lightning-speed strikes with the powerful forelegs. The strikes can take less than 60 ms. The mantispid accomplishes this almost as effectively as the larger praying mantis, which occupies a similar habitat, even though the praying mantis has apposition eyes with a high-resolution fovea, whereas the mantispid has unspecialized optical superposition eyes. *Mantispa styriaca* reacts to an item of prey when the latter covers a critical visual angle. The detection of prey immediately triggers adjustment reactions in the mantispid, which attempts to position the prey item in the visual field of both eyes and in the capture zone. Irrespective of the size of the prey, the capture reaction of the mantispid is always triggered if the distance to the prey falls below a certain critical value. As indicated by the analysis of individual video frames, immediately before an aimed strike, the item of prey is always positioned exactly in the centre of the binocular field of vision in the extended midsagittal plane of the mantispid's head. The strike may be triggered by the ommatidia of the left and right eyes, the lines of sight of which converge precisely on this region. The principal conclusion to be drawn is that the prey-capture behaviour of the mantispid appears to be based on a triangulation mechanism.

Key words: mantispid, *Mantispa styriaca*, compound eye, superposition eye, binocular vision, prey capture, binocular mechanism, triangulation.

## Introduction

If one comes upon a mantispid and is fortunate enough to discover it in the act of capturing prey, at first glance one might think it is a small praying mantis, so similar do the two insects appear, with their large compound eyes and their powerful raptorial pincers, which in both insects have evolved in a similar manner from the first pair of legs. However, they are not closely related, but belong to different insect orders: mantispids to the Planipennia and praying mantids to the Mantodea. This is reflected in the fact that mantispids are holometabolous or polymetabolous and undergo a complete metamorphosis with a pupal stage (Schremmer, 1959; Kral, 1989), whereas praying mantids are hemimetabolous and undergo incomplete metamorphosis. Accordingly, mantispids exhibit their prey-capture behaviour only during the relatively short adult stage of a few weeks, while in the case of praying mantids the behaviour is displayed even by the newly emerged larvae, which even at this stage look like small adults (Köck et al., 1993; Kral, 1998). In addition, the two insects have very different optical equipment: mantispids have refracting optical superposition eyes (Eggenreich and Kral, 1990; Kral et al., 1990), whereas mantids have simple apposition eyes with a frontal fovea (Horridge and Duelli, 1979; Rossel, 1979; Horridge, 1980). Nevertheless, both insects have extremely mobile heads and relatively large binocular visual fields with extensive horizontal overlap (Rossel, 1979; Kirmse and Kirmse, 1985; Eggenreich and Kral, 1990; Köck et al., 1993). Do the mantispid and the praying mantis use different or similar visual locating mechanisms to capture prey?

The aim of the present work was to address this question by analysing the prey-capture behaviour of *Mantispa styriaca* under conditions similar to those in the field, i.e. by using items of prey such as would be captured in the natural habitat and by ensuring that the lighting conditions in the experimental cage were as natural as possible.

## Materials and methods

### Animals

Twenty specimens of the European mantispid *Mantispa styriaca* (Poda) (Planipennia, Neuroptera) were studied. In early July 1999, an insect net was used to gather the mantispids from the upper branches of a pine, in a pine grove near Premantura on the Istria peninsula, Croatia. In the laboratory, the mantispids were placed individually in suitable terraria, where they were kept during the summer and fed with live flies or lacewings.

### Behavioural experiments

For the behavioural experiments, a rectangular cage was used, consisting of a thin frame (50 cm×45 cm×50 cm, length×width×height) covered with white transparent screening. The cage was illuminated by natural daylight, which entered the laboratory unhindered through open side windows and skylights; however, there was no direct exposure to sunlight. In the middle of the cage, the light intensity ranged between approximately 50 lx (under cloudy conditions) and 2400 lx, measured using a silicon photodiode (insensitive to the short-wave portion of daylight). The room temperature was approximately 27–31 °C.

Before the beginning of the experiment, a hungry (unfed for 2 days) mantispid was placed in the experimental cage. Approximately 20 min later, a fly (*Fannia*, *Musca*, *Lucilia*, *Calliphora* or *Sarcophaga* spp.), which had been caught outdoors with a fly trap, was released into the cage. When running about or fluttering against the bottom, walls or ceiling of the cage, the fly clearly acted as a strong stimulus with respect to triggering the prey-capture behaviour of the mantispid. This was the case regardless of whether the mantispid and the prey were on the same or different substrata, thus possibly excluding a role for vibration as a stimulus (see Devetak and Amon, 1997). To investigate whether the size of the prey influences prey-capture behaviour, flies of various sizes were offered to the mantispids.

### Video recording

Two Sony DXC-107 CCD video cameras with Sony VCL1106YM objectives (11.5–69 mm), two video monitors and S-VHS video recorders were used for the observation and recording of the prey-capture behaviour of *M. styriaca*. The cameras were mounted on movable tripods and were focused on the cage from the side or from above. One video camera was used to record a view of the whole cage, while the other was used for close-up views. The cameras recorded at approximately 30 frames s$^{-1}$. Measuring tapes with metric units were mounted in the cage to facilitate the determination of the spatial position of the prey relative to the mantispid. The experiments were carried out on sunny days between 10:00 and 17:00 h.

### Evaluation of the video recordings

The following equipment was used to evaluate the video recordings: a Sony SVO9620P S-VHS video recorder, a PVM-1440QM 14 inch colour monitor, an IBM-compatible computer and PC-supported image-analysis software programmed using Turbo C++ (Borland), described in detail by Kral and Devetak (1999). Actual frames of the video recording were translated into digital information using a WinCast (Hauppauge) video capture card. After calibration using an object of known size, distances were calculated on the screen using the *x*- and *y*-coordinates of the position of the cursor (controlled by the computer mouse).

GraphPad Prism and StatMate version 2.0 (San Diego, USA) were used for the statistical analysis (frequency distribution, $\chi^2$-test, $P<0.05$), nonlinear regression analysis and presentation of the data. In the nonlinear regression analysis, $r^2$ measures goodness of fit, with a value of $r^2=1.0$ indicating that all points are exactly on the curve; $\pm s_{y.x}$ is the standard deviation of the vertical distances of the points from the curve.

### Morphological and optical measurements

Important morphological variables relevant to the present study, such as the body length of the insects, interocular distances and the length of the raptorial legs, were determined using a stereo-microscope with the aid of a calibrated ocular micrometer. Optical variables, such as the visual field of the eyes and of the ommatidia, had been determined previously by means of the pseudopupil method (see Eggenreich and Kral, 1990). Interommatidial angles were measured using sections prepared from the eyes (see also Kral et al., 1990).

## Results
### General features of the prey-capture behaviour

*Mantispa styriaca* captures other insects; any that can be reached and caught seem to be suitable. Prey captured in the natural habitat range from various insects, even those larger than *M. styriaca*, such as lacewings and adult antlions, to flies of various sizes and Hymenoptera. The prey may be crawling, running or fluttering. A strong stimulus was found to be provided by running flies. Thus, the size of the experimental cage was chosen to encourage flies of all sizes to run rather than fly. During preliminary experiments with a larger cage (100 cm×70 cm×80 cm, length×width×height), it was found that flying flies did not attract the attention of the mantispid.

### Watching for prey

It was found that both in the experimental cage and in the terraria, a mantispid preparing to capture prey would move upwards to where the light was brightest. Upon arrival at the brightest region of the cage, the mantispid immediately assumed a 'lookout' position, either standing upright or hanging upside-down. The raptorial legs were drawn up close to the body, and the antennae continually oscillated back and forth. In this 'ambush' position, the mantispid remained motionless except for repeated raising of the head and thorax or stretching and turning of the head and thorax or the whole body in another direction. From time to time (usually after a few minutes), the mantispid moved to another location, then again assuming the lookout position.

### Detection of prey and movement to within striking distance

Upon detecting an item of prey, the mantispid turned its head towards it; this was accompanied by a perceptible tensing of the whole front part of the body. This behaviour could be triggered by a large fly (10–12 mm) running about at a distance of up to 180 mm from the mantispid or by a medium-sized (7–9 mm) or small (4–6 mm) fly at a distance of up to 140 mm if the fly entered the visual field of both eyes of the mantispid (Fig. 1A). However, the majority of large flies (82 %) were first
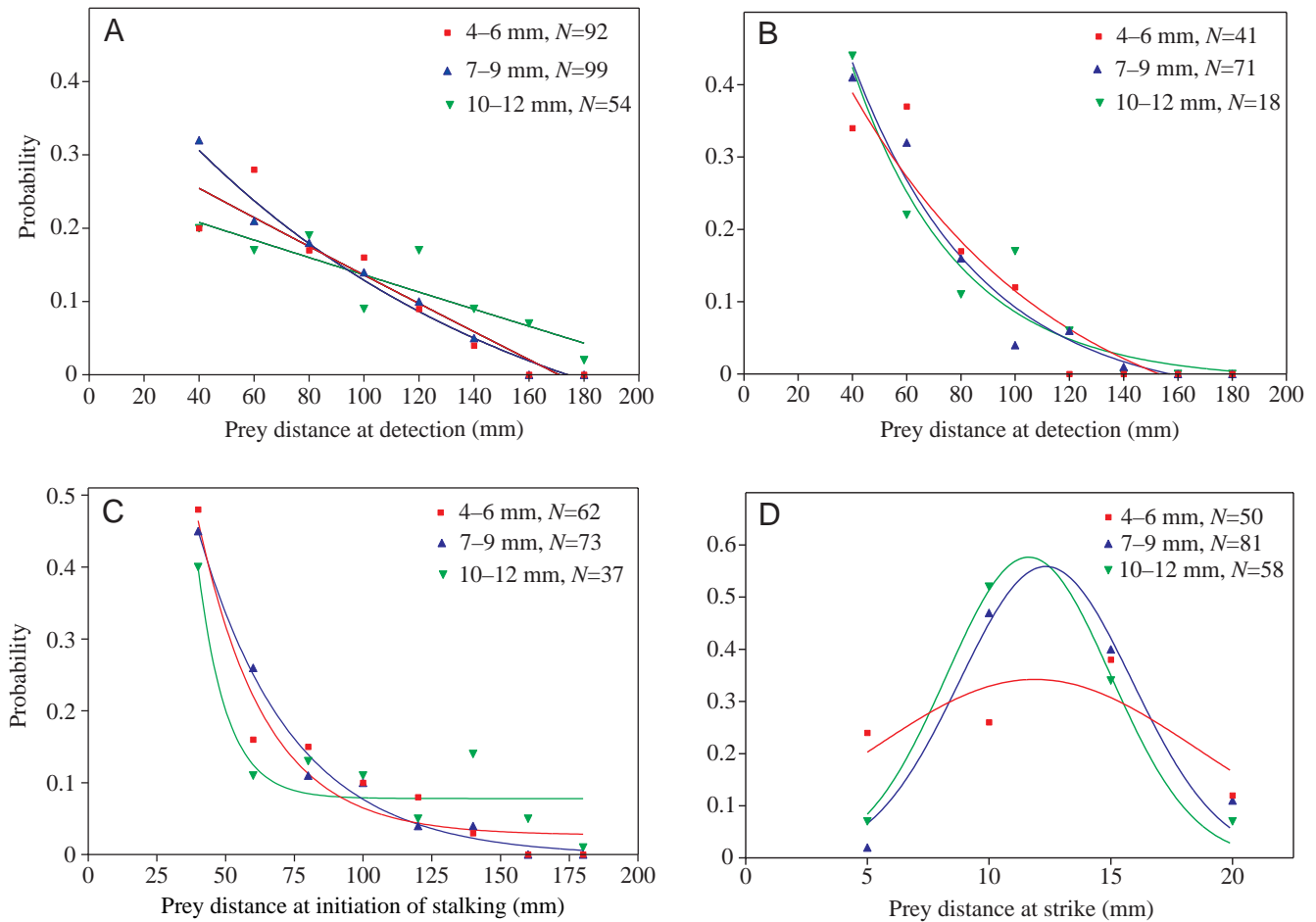
Fig. 1. Relationship between the size of an item of prey (a fly) and the distance at which it triggered a reaction, with respect to the various behavioural responses of *Mantispa styriaca*. (A,B) Frequency distribution showing the distance from the mantispid to the prey when it was first detected by the mantispid if the prey entered the visual field of both eyes (A) or if the prey entered the lateral visual field of only one eye (B). (C) Frequency distribution showing the distance from the mantispid to the prey when the mantispid began to stalk it, i.e. became active. (D) Frequency distribution showing the distance from the mantispid to the prey that invariably triggered a lunge and strike by the mantispid. The measurements were made for small (4–6 mm), medium-sized (7–9 mm) and large (10–12 mm) flies, for 14, 19 and 13 mantispids, respectively. The solid curves were determined by nonlinear regression. The functions plotted are those that best fit the data; for more information, see Results.

perceived at a distance of 40–120 mm, and the majority of medium-sized (85 %) and small (81 %) flies at a distance of 40–100 mm. The tendency of the detection distance for small and medium-sized flies to be shifted towards lower values than those measured for large flies was statistically significant ($\chi^2$-test; $P<0.05$, d.f.=7).

In the case of flies that entered the visual field of only one eye, large or medium-sized flies approached to a distance of 120 mm, and small flies to a distance of 100 mm, before being noticed by the mantispid (Fig. 1B). Thus, prey approaching from the side had to be closer to the mantispid to be detected than prey approaching from the front. Apart from this, the differences in the frequency distributions of the detection distances for prey detected with one eye and prey detected with two eyes (Fig. 1A,B) were not statistically significant ($\chi^2$-test). It was also found that these frequency distributions for the three different sizes of prey did not differ significantly (Fig. 1B). From calculations based on the size of the prey and

the detection distance, visual angles covered by flies of approximately 4–6° in the frontal visual field and of approximately 4–10° in the lateral visual field seem to be sufficient for the detection of prey.

In general, the probability of detecting an item of prey decreased with increasing distance (Fig. 1A,B). This relationship was analyzed using nonlinear regression. It was found that there was an exponential relationship between detection probability and distance. The function fitted the data best in the case of medium-sized flies that entered the visual field of both eyes ($r^2=0.98$, $s_{y.x}=\pm1.83$) or one eye ($r^2=0.96$, $s_{y.x}=\pm3.55$). For the other two size categories of prey, an exponential correlation between prey detection and distance was more or less evident in the case of small flies down to a distance of 60 mm ($r^2=0.97$, $s_{y.x}=\pm2.09$ for both eyes; $r^2=0.98$, $s_{y.x}=\pm2.65$ for one eye), and for large flies entering the visual field from the side ($r^2=0.93$, $s_{y.x}=\pm4.64$). It was striking that, in every case, regardless of its size or spatial position, a fly
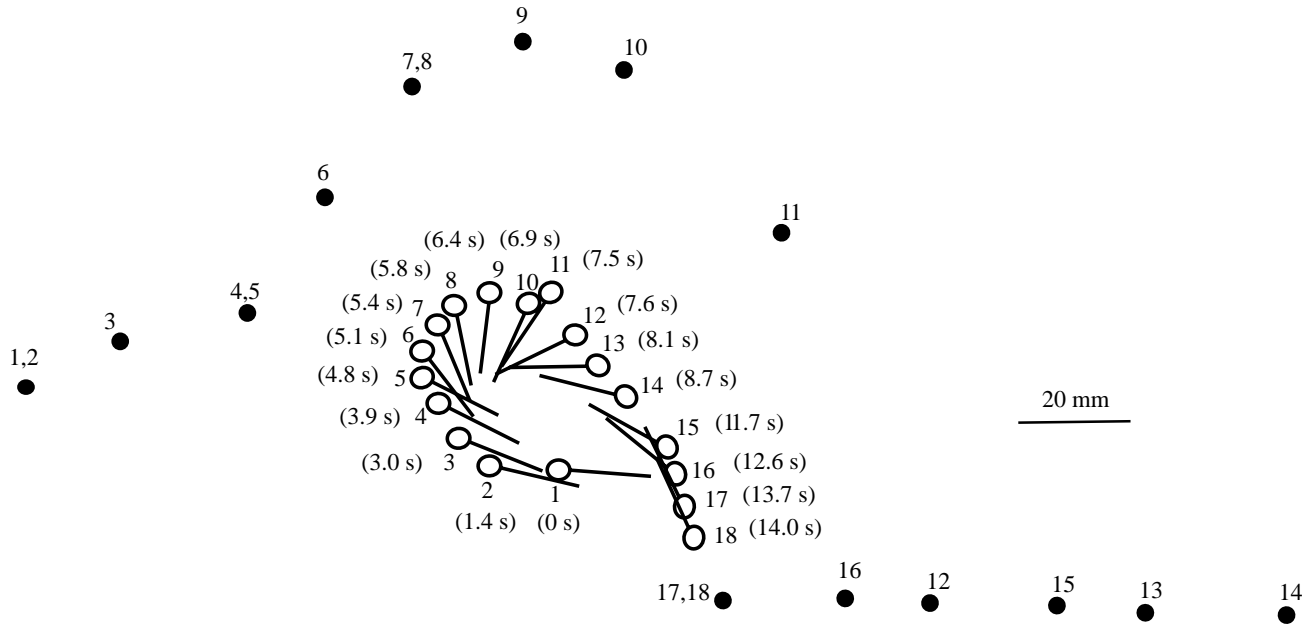
Fig. 2. Changes in the location of a running fleshfly *Sarcophaga* sp. and the adjustment movements executed by a *Mantispa styriaca* to move the fly into the centre of its field of vision and into the capture zone. The lines represent the longitudinal body axis of the mantispid, the open circles represent the position of its head and the filled circles represent the location of the fly. Numbers in parentheses give the elapsed time corresponding to each position. Point 1, first visual detection (defined as the first detected increment of the mantispid's head); point 2, first turning reaction; points 3–16, stalking and adjustment movements; points 17 and 18, fixation and strike.

could approach only up to a distance of 40 mm before being detected by the mantispid (Fig. 1A,B). At this threshold distance, the stalking behaviour was often triggered immediately (Fig. 1C).

On detecting a fly, the mantispid instantly turned towards it and, as soon as the prey approached to within a certain distance, cautiously attempted to move nearer to it (see Fig. 2). Large flies could trigger this stalking behaviour at greater distances (160–180 mm) than medium-sized or small (140 mm) flies; for the majority of the latter (92 and 89 %, respectively), stalking began at distances of 40–100 mm (Fig. 1C). This relationship between the behaviour of the mantispid and the size of the prey is apparent in the frequency distribution of the distances at which stalking began (Fig. 1C). The differences in the frequency distributions between small/medium-sized flies and large flies were statistically significant ($\chi^2$-test; $P<0.02$, d.f.=7). Although the probability of initiating stalking behaviour decreased exponentially with increasing prey distance (Fig. 1C), the function fitted the data well only in the case of medium-sized ($r^2=0.99$, $s_{y.x}=\pm1.97$) and small ($r^2=0.97$, $s_{y.x}=\pm1.49$, down to 60 mm) flies.

The stalking behaviour was dependent on the movements of the fly that was fluttering and running about. If the prey moved directly towards the mantispid, the latter remained motionless; however, if the prey moved past or away from the mantispid, the mantispid attempted to move at the same time, often turning about its own axis (Fig. 2). As indicated by analyses of the video recordings, the mantispid attempted to keep the prey within the field of view of both eyes by means of these tracking movements (Fig. 2). If the prey then moved away, the

mantispid again attempted to follow; however, as soon as the prey paused, the mantispid also stopped, sometimes executing side-to-side and nodding movements of its head and thorax. The movements of the mantispid were therefore dictated by those of the prey as the former attempted to approach the latter. However, this stalking behaviour ceased if the prey moved too far away. If the prey moved farther than the distance at which stalking behaviour was triggered, but was still within the range of distances at which it could be perceived by the mantispid (Figs 1, 2), the mantispid continued to execute following motions with the head and thorax. When the prey moved beyond this distance, the mantispid performed a consistent behavioural sequence: alternately stretching its raptorial legs forward a couple of times and then cleaning its antennae.

*Prey-capture attempts*

Upon reaching striking distance of the prey, the mantispid instantly ceased its stalking behaviour and immediately assumed a position in which its raptorial legs, head and thorax formed a straight line pointing exactly towards the centre of the item of prey (see Fig. 2). Similarly, if the prey moved directly towards the mantispid, the latter froze, and as soon as the prey came within striking range the mantispid aligned itself as described above. At this point, immediately before the lunge and strike, the distance between the mantispid and the prey was a maximum of 20 mm (Fig. 1D). For the majority of small flies (88 %), the distance was 5–15 mm; for the majority of medium-sized and large flies (87 and 86 % respectively), the distance was 10–15 mm (Fig. 1D). This was expressed as statistically significant differences in the frequency distributions of the

distance values for small compared with medium-sized flies ($\chi^2$-test; $P<0.0001$, d.f.=3) and small compared with large flies ($P<0.001$, d.f.=3). Thus, although the critical distance at which the lunge and strike could be triggered was never larger than 20 mm for prey of any size (Fig. 1D), within the critical range of distances, a relationship between distance and size was



A

B

C

D

E

F

10 mm

Fig. 3. Lateral views taken from sequential frames of a video recording of *Mantispa styriaca* and a fleshfly illustrating the fixation and strike of the prey-capture behaviour (corresponding to points 17 and 18 in Fig. 2). (A) Fixation of the prey; (B) beginning of the strike; (C–F) lunge and capture of the prey. The vertical line is given as a reference to show the forward movement of the mantispid (compare with praying mantis; Corrette, 1990, p. 157). The interval between frames is approximately 30 ms.

apparent, in that the mantispid could be closer to small flies than to medium-sized or large flies. However, small flies could also elicit strikes when they were up to 20 mm away (Fig. 1D). Note that the data in Fig. 1D follow a Gaussian distribution; in the case of medium-sized and large flies, the distribution is bell-shaped, with the best fit being for medium-sized flies ($r^2=0.99$, $s_{y.x}=\pm0.02$).

Once the prey was within striking distance, if it moved, the mantispid lunged forward and executed a strike with both raptorial legs (Fig. 3). The time elapsed between the alignment of the mantispid towards the prey and the execution of the strike ranged from less than 30 ms to 300 ms, depending on the movement of the prey (Fig. 2). The capture behaviour (lunge and strike) could take less than 60 ms (Fig. 3); the speed was therefore of the same order of magnitude as has been found for the praying mantis (Corrette, 1990). Regardless of the size of the prey, only one in four or five strikes hit the target. A relationship between capture success and the distance from the prey was obvious. All the successful strikes (for all sizes of prey) occurred at distances of 10–15 mm. Of the missed strikes, 50 % (for small flies), 84 % (for medium-sized flies) and 82 % (for large flies) were executed within this range of distances. The other missed strikes were executed at distances of 20 mm (17 %, small flies; 13 %, medium-sized flies; 9 %, large flies) and 5 mm (33 %, small flies; 3 %, medium-sized flies; 9 %, large flies; see Fig. 1D). The mantispid missed its prey occasionally because of distance miscalculation, but more often because of escape flight by the prey (0.4–0.7 m s$^{-1}$).

## Discussion

The behavioural experiments indicated that *Mantispa styriaca* first reacted to an item of prey when the latter covered a visual angle of at least 4–10 ° per eye (corresponding to 2–5 ommatidia if one takes into account the ommatidial angle of 2 °; Eggenreich and Kral, 1990). (The visual angle was greater for the lateral region of the eye than for the frontal region.) It should be noted that Collett and Land (1975) estimated that a female hoverfly *Syritta pipiens* subtends an angle of less than 2 ° (corresponding to three ommatidia) on the eye of a pursuing male at the time of initial visual contact, and Vallet and Coles (1993) found that drone honeybees *Apis mellifera* responded to objects that subtended an angle smaller than that corresponding to a single ommatidium. The present experiments also showed that the probability of detecting an item of prey increased with decreasing distance, down to a critical distance at which an item of prey was always perceived. This relationship was more-or-less exponential (Fig. 1A,B).

In addition, the behavioural experiments suggested a direct relationship between the size of the prey approaching from the front and the distance at which it was detected (Fig. 1A). For prey approaching from the side, this was not clearly evident (Fig. 1B). One reason for this could be a difference in the spatial resolving power of the frontal and lateral regions of the eye. It is possible that the difference in size among the three
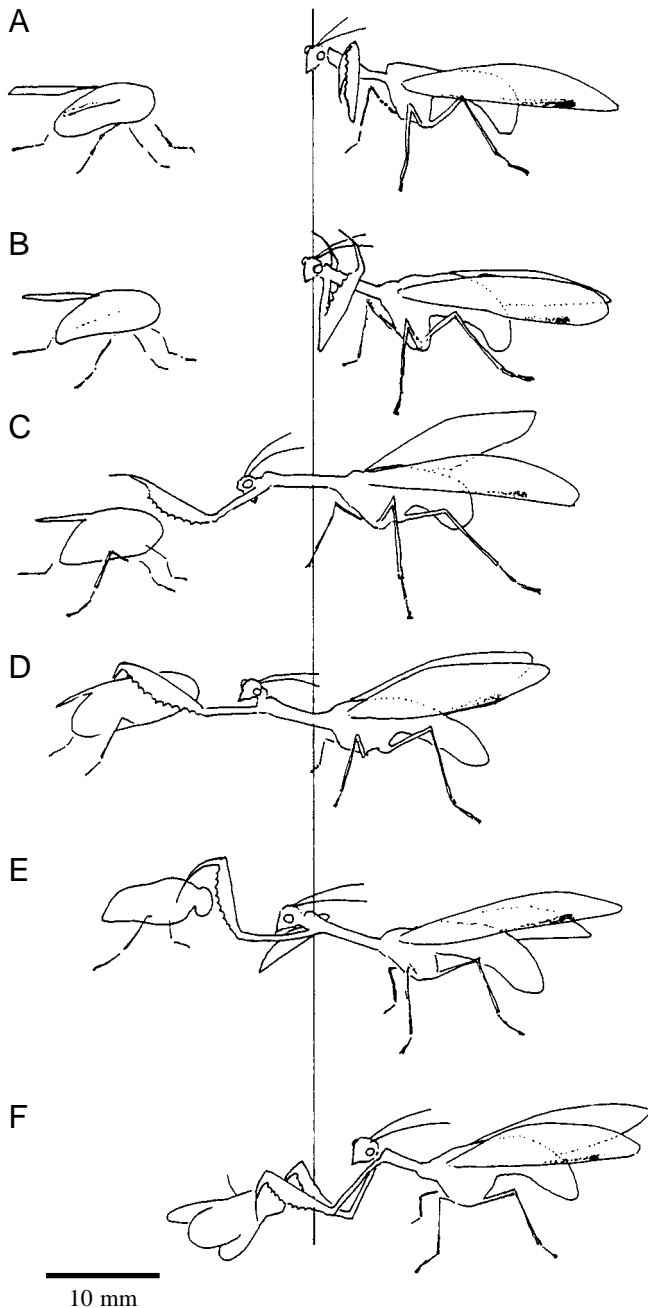
categories of prey might have been too small to be perceived by the mantispid when the prey approached from the side. But the difference between the frontal and lateral retina with respect to size preference could also be a difference in triggering features, possibly, for instance, biased more towards motion in the lateral than in the frontal retina. This question needs to be addressed by further experiments.

The experimental findings clearly indicated that, as soon as it had identified a fly as an item of prey, *Mantispa styriaca* attempted to position the prey in the visual field of both eyes and to hold it there (Fig. 2). This behaviour is similar to that of other insects that attempt to fixate a moving prey item or a mate (for reviews, see Wehner, 1981; Schwind, 1989). This is also true for mantids, for example *Mantis religiosa* (e.g. Zänkert, 1939) and *Empusa fasciata* (Gombócz, 1999).

The present experiments also showed that an item of prey entering the binocular visual field of *Mantispa styriaca* caused the latter to execute typical visual fixation behaviour, very similar to that of praying mantids (Zänkert, 1939; Gombócz, 1999) and other visual predatory insects, such as aeschnids (Baldus, 1926; Etienne, 1969) and various beetles (Weinreich, 1968; Bauer, 1977; Betz, 1998). It was found that, irrespective of the size of the retinal image, the strike occurred only when the prey was located in the extended midsagittal plane of the mantispid's head, at a certain fixed distance from the mantispid. It is possible that this critical distance was determined by means of triangulation (see Burkhardt et al., 1973), with the stimulus falling on a binocular trigger zone. If this is the case, then the ommatidia involved are likely to be those of each compound eye with visual axes converging on points lying in the extended midsagittal plane of the mantispid's head, from a distance of 10–15 mm from the mantispid (Fig. 1D). Triangulation has also been postulated for praying mantids (Barros-Pita and Maldonado, 1970; for a review see, Kral, 1999) and the other predatory insects mentioned above (e.g. Bauer, 1981, 1985).

An important question arising from this study is whether *Mantispa styriaca* is able to incorporate information from the binocular disparity of retinal images in its determination of prey distance. Binocular attributes, such as a horizontal binocular overlap of approximately 50 °, could perhaps provide prerequisites for this ability (Eggenreich and Kral, 1990). However, the distance between the forward-directed ommatidia of the two eyes (1.1 mm) is relatively small compared with that of mantids and would yield only relatively small binocular disparities which may be adequate only for accurate determination of close distances. However, the lack of a fovea is not sufficient reason to exclude the possibility of stereoscopic vision. Although a reference system for the measurement of retinal positions is required for distance determination by means of the disparity of retinal images, this does not necessarily have to be provided by a fovea. Direct evidence of stereopsis could perhaps be obtained if the head position of the mantispid were fixed during prey-capture experiments, as has been done in the case of the praying mantis *Tenodera australasiae*, in which highly controlled stimuli were required to demonstrate the ability of the mantis to determine distances by means of horizontal disparities (Rossel, 1983, 1986).

If all the findings are taken together, it becomes evident that the prey-capture behaviour of mantispids is similar in principle to that of praying mantids and may be based on a similar underlying mechanism, even though the types of eye are quite different. However, the difference in eye type has implications for the kinds of prey that can be caught; mantispids will not be able to perceive and capture prey that can move as rapidly as prey captured by mantids.

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