EXTERNAL DESIGN AND FIELD OF VIEW OF THE COMPOUND EYES IN A RAPTORIAL NEUROPTERAN INSECT, *MANTISPA STYRIACA*

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Summary

Visual fields and ommatidial angles of the compound eyes of *Mantispa styriaca* were determined using luminous pseudopupil and histological–anatomical techniques. The maximal horizontal overlap averaged 42.7° in females and 52.4° in males; females had only one overlap maximum, whereas males had two. In the dorsoventral direction, the binocular field had an overlap of 135.2° in the female and 142° in the male.

In light-adapted eyes, optical acceptance angles reached values of 2.0°, and they reached 3.6° with dark adaptation; interommatidial angles were between 1.8° and 2.3°. The angles were very similar over the entire eye; no acute zone was found in the frontal part of the eye, as the large binocular overlap would suggest. The results are compared with those for the praying mantis: this animal is in no way related to *Mantispa* but resembles it in appearance and capture behaviour.

Introduction

A first glance at *Mantispa styriaca*, a predatory insect of the neuropteran family Mantispidae, suggests a small praying mantis. There are large bulbous eyes and a stalked prothorax bearing spiny forelegs which are powerful prehensile claws. The two distal members of the foreleg can be snapped against the next member, like a jack-knife. We have seen that *Mantispa* prefers to spend its time in trees or bushes, where it lies motionless in wait of prey. If a small insect comes within range, *Mantispa* moves in its direction and fixes it with its eyes. Then the two claws are extended with a sudden forward jerk of the body and the insect is caught. When the capture effort fails, it can happen that *Mantispa* 'follows up' its prey. We have also seen that even while *Mantispa* is eating its prey, held in the mandibles, it may reach out with its two free extremities after another insect scurrying along at its side, but this effort usually fails.

Though *Mantispa* and the praying mantis show similarities in capture behaviour, they are different in life cycle. The praying mantis shows hemimetabolous development and even the very small first-instar larvae show the same prey-

capturing behaviour with success rates similar to those of the large adult animals (Mittelstaedt, 1957). *Mantispa*, in contrast, is polymetabolous with two very different larval stages (Brauer, 1852, 1869). The first larval stage is slender and motile, and has suckers which it uses to penetrate the egg cocoons of the wolf spider. It then eats the eggs and young spiders and later moults into the second maggot-like larval stage which pupates in a cocoon it spins for itself within the spider cocoon (Hungerford, 1936; Schremmer, 1959, 1983). Only the adult insect that emerges from the metamorphosis has the powerful forelegs. Field observations show that the praying mantis hunts in the daytime and that the males mate at twilight and at night (Rossel, 1979). Similar behaviour is probably shown by *Mantispa* (New and Haddow, 1973).

In this paper we investigate whether the capture of prey by *Mantispa* is optically directed in a way similar to that in the praying mantis (Roeder, 1959; Levin and Maldonado, 1970; Maldonado and Barros-Pita, 1970; Maldonado *et al.* 1970; Rossel, 1979, 1980, 1983*a,b*, 1986), i.e. with a forward-looking acute zone, an adaptation for enhanced acuity of fixation, and fields of view of the two compound eyes with a large overlap. We approached this problem by measuring the total visual and binocular field size of both compound eyes and by surveying the optical parameters of single ommatidia with simple optical methods, such as the pseudopupil method.

Materials and methods

Animals

Adult females and males of *Mantispa styriaca* Poda (Planipennia, Neuroptera) (Fig. 1) were obtained from the southernmost tip of the Istrian peninsula near Premantura, Yugoslavia. The insects were collected early in July in the late afternoon and early evening in a pine wood. All the females came from a community of more than 80 individuals in one tree; males were found only occasionally on other nearby pines. All animals were about the same size. They were kept under controlled laboratory conditions (15 h:9 h light:dark cycle) in individual cages and were fed fruit flies in the evening.

Tissue preparation

Whole eyes were fixed in a standard mixture of 2.5 % glutaraldehyde and 2.5 % paraformaldehyde in 0.1 mol l^{-1} sodium cacodylate buffer (pH 7.2) at 4°C for some hours. The tissue was then washed for 1 h in four changes of 0.1 mol l^{-1} cacodylate buffer. Postfixation was in 2 % osmium tetroxide buffered with veronal acetate buffer (pH 7.2) at 4°C for 2 h. Dehydration was through an ascending series of ethanol to propylene oxide; embedding followed in soft Epon 812. Semithin sections 1–2 μm thick were stained with Toluidine Blue or were left unstained. For scanning electron microscopy, (SEM), air-dried specimens were sputter coated with a 20–30 nm thick layer of gold and examined in a Cambridge scanning electron microscope.
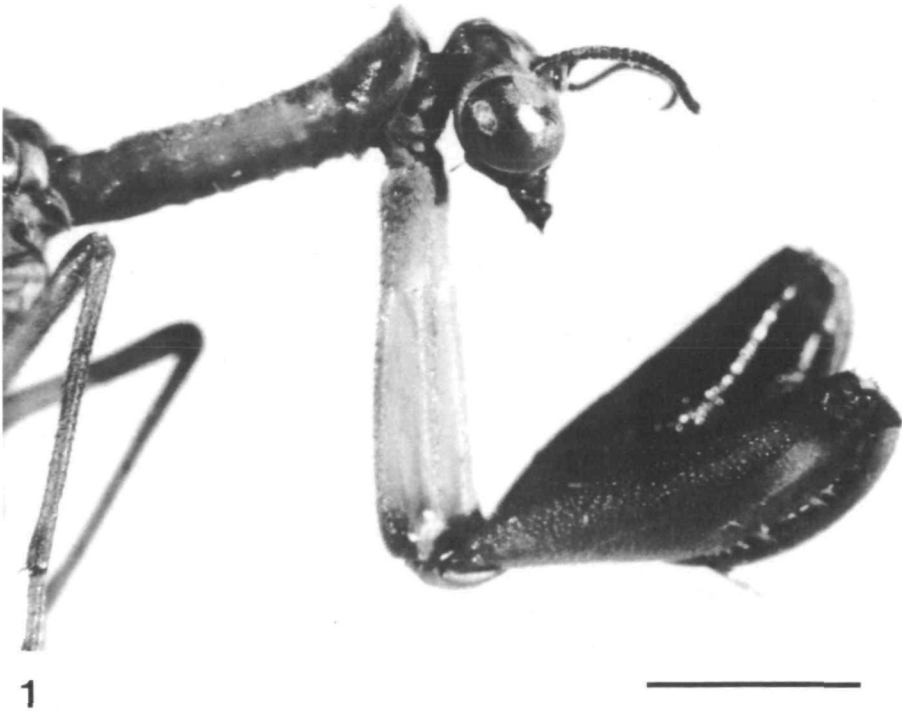
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Fig. 1. A female *Mantispa styriaca*. Note the narrow, elongated prothorax, the bulbous eyes and the powerful, extensible raptorial forelegs, similar to those of the praying mantis. The tibia can be snapped into the groove on the femur like the blade of a pocket knife. Scale bar, 2.5 mm.

Ommatidial measurement

Calculation of eye surface and mapping of the ommatidial pattern

Before the optical measurements began, a Wild M400 photomicroscope equipped with an ocular micrometer was used to record eye size and the smallest distance between the eyes. Mapping and counting of facets was on the basis of SEM photographs.

Determination of monocular and binocular visual fields

The visual fields were measured by using the luminous (corneal) pseudopupil caused by axially incident light (orthodromic illumination). The insect was mounted in the centre of a three-dimensional goniometer. The eucentric point corresponded to the middle point of the spherical coordinate system. The angle of each axis of the goniometer was measured to one decimal place by a linear recording potentiometer with digital display. The high-intensity, bluish-yellow, round pseudopupil (see Fig. 4) was allowed to wander around the marginal

ommatidia, starting from a reference point on the equator (defined by the smallest distance between both eyes, see Fig. 2A; fused rhabdoms are unrotated so there is no obvious equator; cf. open rhabdoms of flies). Meanwhile, the spherical coordinates of the goniometer were read at 10° intervals, as described extensively by Beersma *et al.* (1977). The spherical form of the eye ensured that measured optical axes were in accordance with real optical axes.

Effective acceptance angles of the ommatidium

The effective acceptance angles of ommatidia ($\Delta\rho$), which determine the size of the ommatidial visual field, were estimated in monocular and binocular eye regions by measuring the angular span in which the luminous pseudopupil remains in the ommatidium (similar to Nilsson and Odselius, 1982, who, however, used a true pseudopupil). This optical measuring method defines the angle at which the distal rhabdom on the lens surface remains fully visible. In contrast, with electrophysiological determination, the acceptance angle is defined as the half-width of the ommatidia's or receptor's acceptance function. The general agreement of $\Delta\rho$ (light-adapted) and interommatidial angle ($\Delta\phi$) confirms the suitability of the optical measuring method.

Determination of facet diameter and eye radius for the calculation of interommatidial angles

Interommatidial angles ($\Delta\phi$) were determined from R (the distance between the midpoint of the corneal surface of an ommatidium and the imaginary intersection of its optical axis with the optical axis of a neighbouring ommatidium) and the diameter D of the regular hexagonal facet, determined in semithin sections (Fig. 3) in the horizontal plane (x,z) and in the sagittal plane (y,z). Eight different sections of the eye were measured (see Table 3). The interommatidial angles were calculated according to Snyder (1977) using the D/R formula.

Results

The external design of the compound eyes

The emerald-green eyes of adult *Mantispa* are almost hemispheres, covering a large part of the rather simple head capsule (there are no ocelli) (Figs 1, 2A). The eye surface measures about $1.2\,mm^2$ and contains some 3500 ommatidia with a regular hexagonal shape, though those at the edges can be irregular. The surface of the ommatidia and the interommatidial area are covered with numerous hemispherical corneal nipples that are considerably lower on the cupola of the lens than on the surrounding mantle (Fig. 2B).

Extent of the visual field and binocular overlap

Figs 5 and 6 and Table 1 show the extent of the areas of binocular, monocular and blind visual field as a percentage and in mm^2 (all values are mean±S.D.). The
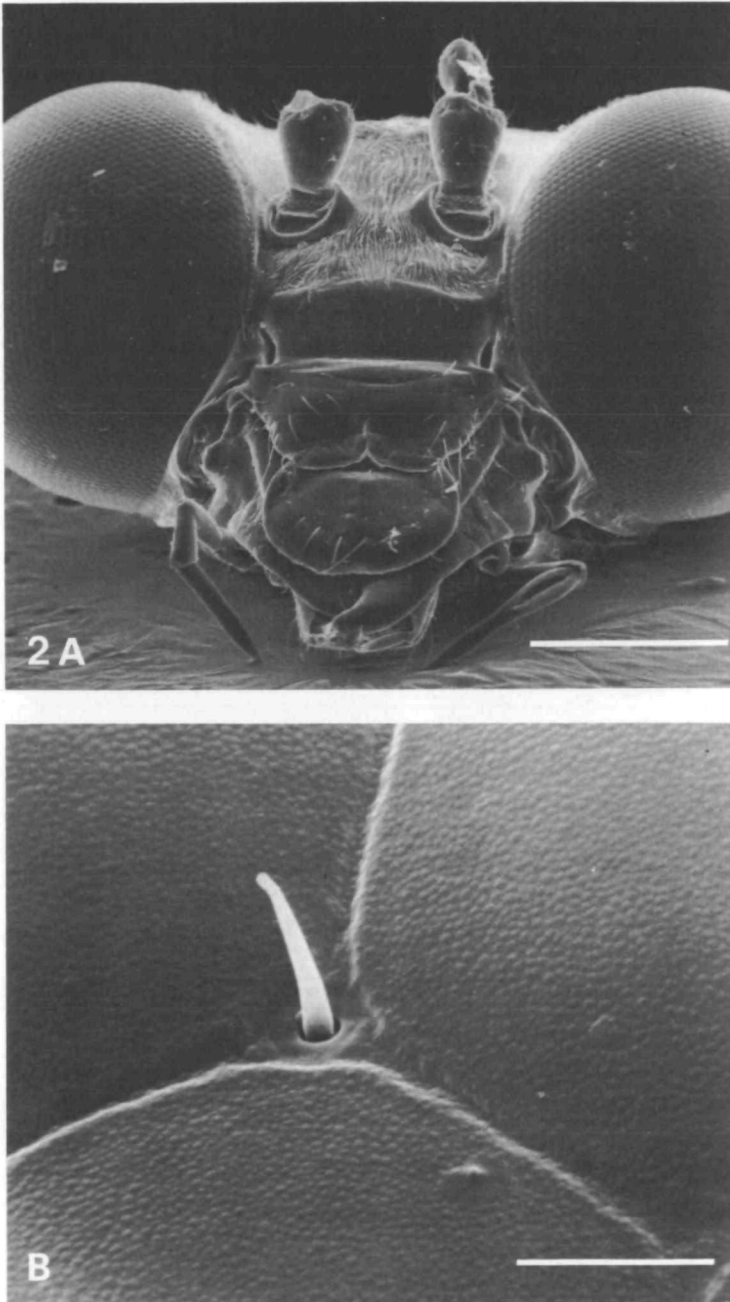
Fig. 2. Female *Mantispa styriaca* in SEM view. (A) Frontal view of both compound eyes. Hypothetical equator is determined by the smallest interocular distance. Scale bar, 0.4 mm. (B) The surface of the faceted cornea is covered with nipples; there is a short bristle between three facets, as also occurs in mantis (Zack and Bacon, 1981). These may be airflow receptors. Scale bar, 5 μm.
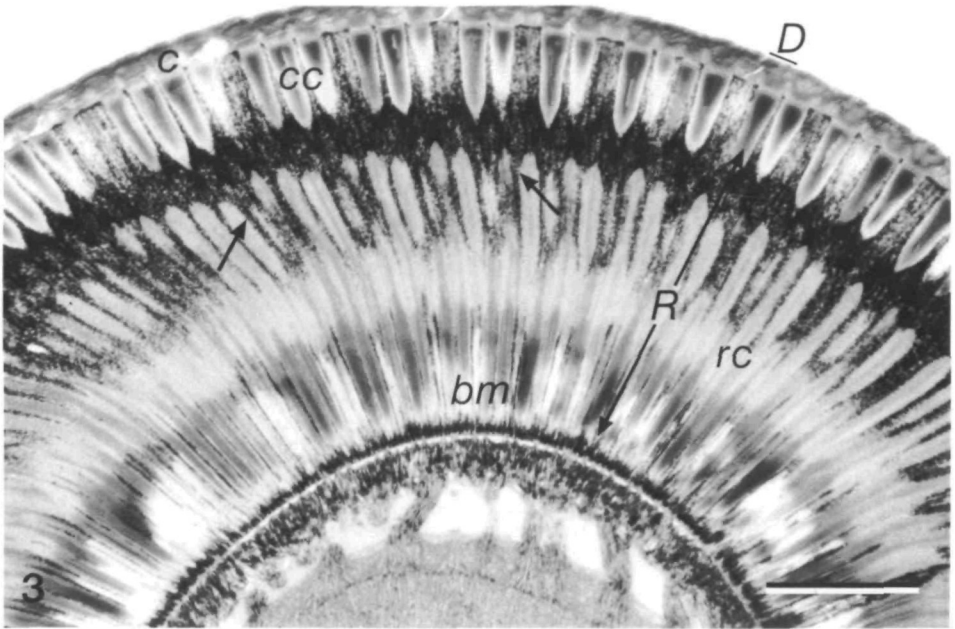
Fig. 3. Longitudinal semithin section through the light-adapted compound eye of *Mantispa styriaca* in the horizontal plane near the equator, as used to determine $\Delta\phi$. It is evident that, in contrast to mantis eye cone length, R and D are generally constant throughout the section. Abbreviations: *c*, cornea; *cc*, crystalline cone; arrows, pigment cells; *rc*, retinula cells; *bm*, basement membrane region with reflecting tapetal layer. Scale bar, 150 μm.

extent of the binocular visual field was 6.6 % in females and 8.2 % in males, the 20 % greater area in males producing a reduction in the blind spot. In contrast, the monocular field was about the same size in both sexes. The maximum extent of the binocular visual field in the dorsoventral direction was 135.2° in females and 142° in males (Figs 5, 6). The maximum horizontal overlap averaged 42.7° in females and 52.4° in males; in males there was a suggestion of two maxima in the dorsoventral direction at about 0° and 30°.

Trigonometry, using the angular data and the interocular separation, showed that the projected optical axes of marginal ommatidia intersected in the area of maximal overlap in the sagittal plane of the animal at 1.017 mm in males and 1.305 mm in females. This 'critical' distance amounts to some 10–20 % of the length of the extended forelegs. The convergence angle with an interocular separation of 1.07 mm in males and 1.09 mm in females corresponded to the overlap area in degrees and was 32.4° on average in males and 38.3° in females. The blind spot in the neck region had a dorsoventral extent of 224.8° in females and 218.3° in males on average.
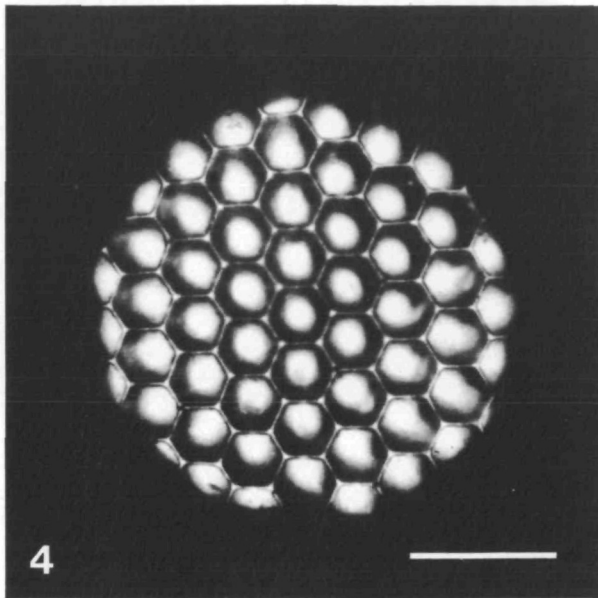
Fig. 4. Photograph of luminous corneal pseudopupil (orthodromic illumination) in the anterior eye of a female *Mantispa styriaca*. When the spot of light is exactly in the middle of the facet, the facet is directed precisely at the viewer. Scale bar, 50 μm.

Table 1. *Visual field areas of compound eyes of* Mantispa styriaca *in relative and absolute terms*

Sex	Binocular area	Monocular area	Blind area
	(%)	(%)	(%)
Female (*N*=12)	6.57±1.13	80.20±1.74	13.23±1.74
Male (*N*=2)	8.20±1.42	80.20±2.26	11.60±0.85
	(mm²)	(mm²)	(mm²)
Female	0.30±0.05	3.63±0.41	0.60±1.74
Male	0.33±0.03	3.19±0.35	0.46±0.85

N, number of specimens.
Values are mean±S.D.

Ommatidial parameters

Effective acceptance angle of the ommatidium

Horizontal measurements in the binocular region near the equator produced average values of $\Delta\rho$ of 1.9° in the light-adapted eye ($\Delta\rho$LA) and $\Delta\rho$ in the dark-adapted eye ($\Delta\rho$DA) of 3.6°, and $\Delta\rho$LA of 2.0° and $\Delta\rho$DA of 3.6° in the monocular region of the lateral part of the eye. Table 2 summarizes the calculated values and Fig. 7 shows the dependence of the effective acceptance angle of a single
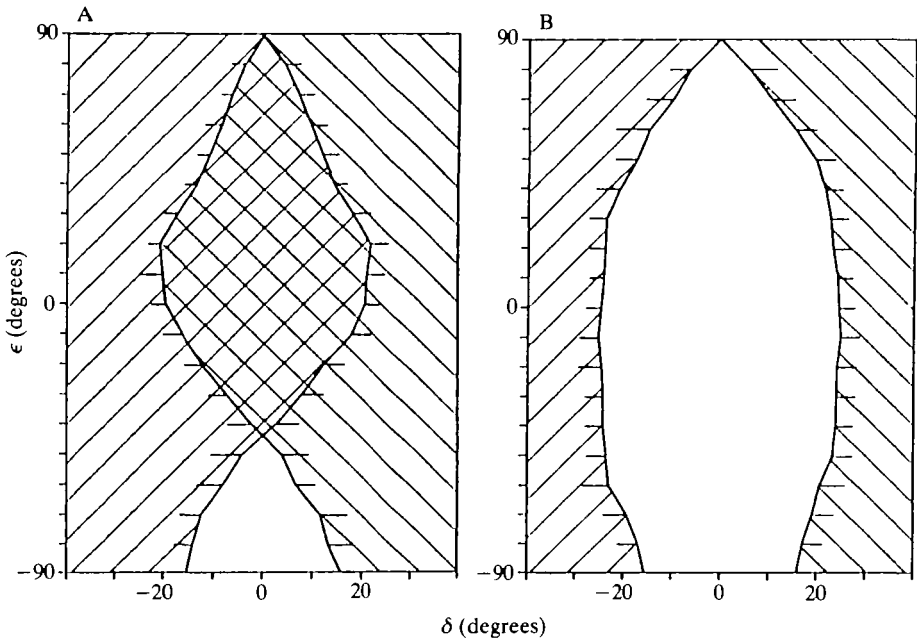
Fig. 5. The extent of monocular (striped) and binocular (cross-hatched) visual fields and the blind areas (unshaded) of the two compound eyes in female *Mantispa styriaca*. (A) Looking forwards; (B) looking backwards; δ is the angle between the optical axis of a marginal ommatidium and the vertical symmetry plane. When $\delta=0°$ the optical axis of the border ommatidium between monocular and binocular visual fields is parallel to the vertical bodily plane of symmetry. ϵ is the angle of the same axis with the horizontal symmetry plane. The equator is at $\epsilon=0°$. Error bars+s.D. ($N=12$).

Table 2. *Average effective acceptance angle of a single ommatidium of* Mantispa styriaca

Eye region	$\Delta\rho_{DA}$ (degrees)	$\Delta\rho_{LA}$ (degrees)
Monocular	3.63±0.11	1.91±0.09 ($N=7$)
Binocular	3.61±0.12	1.99±0.07 ($N=7$)

N, number of eyes.
DA, dark-adapted; LA, light-adapted.
Values are mean±s.D.

ommatidium in the binocular and monocular areas on the duration of illumination. The curves are quite similar; there is no significant difference between the monocular and binocular areas (*t*-test).

Diameter and R *value of the facets*

    In the frontal equatorial region, the diameter D of the facets averaged 21.3 μm.

In the anterior dorsal area it was 20.9 μm and on the outer margin of the eye, 20.1 μm; thus it was quite constant over the entire eye. There were slight variations in the values of R, between 450 and 550 μm.
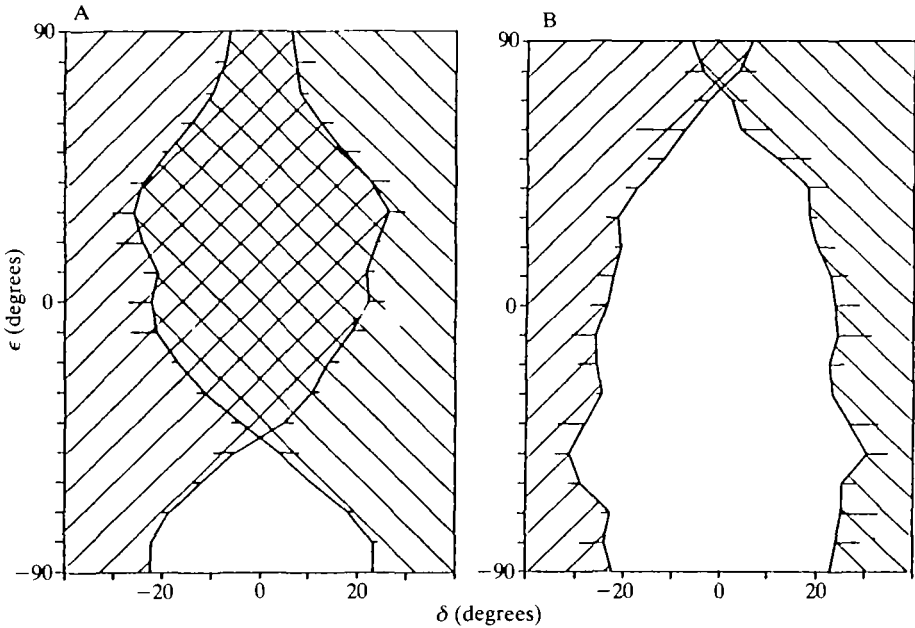

Fig. 6. The extent of monocular (striped) and binocular (cross-hatched) visual fields and the blind areas (unshaded) of the two compound eyes in male *Mantispa styriaca*. (A) Looking forwards; (B) looking backwards; Error bars+s.d. ($N=2$).
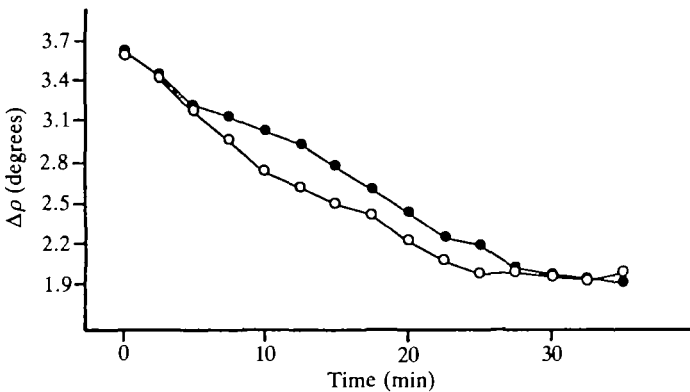

Fig. 7. The two curves represent the mean values of effective acceptance angle of a single ommatidium ($\Delta\rho$) in monocular (closed circles) and binocular (open circles) areas depending on the duration of illumination with white light. According to the *t*-test, there is no significant difference between the two functions (for values see Table 2).

Table 3. *Interommatidial angles and calculated eye parameter* p *from eight different eye regions in* Mantispa styriaca

Eye region	$\Delta\phi$ (degrees)	p
Dorsal	2.17±0.011	0.77±0.008 (N=3)
Dorsofrontal	2.24	0.818
Dorsolateral	2.131	0.739
Dorsocaudal	2.155	0.756
Frontal	2.175±0.043	0.77±0.024 (N=3)
Lateral	2.269±0.190	0.839±0.139 (N=2)
Caudal	1.804±0.075	0.53±0.045 (N=3)
Ventral	1.917	0.598

N, number of eyes; for each optical region, measurements were made of some 20 ommatidia; the s.D. was small enough to be neglected.

$p=D^2/R$, where *D* is facet diameter and *R* is the distance between the midpoint of the corneal surface of an ommatidium and the imaginary intersection of its optical axis with the optical axis of a neighbouring ommatidium.

Values are means±s.D.

Interommatidial angles

Values of $\Delta\phi$ measured in the horizontal sections of the eye from median to lateral near the equatorial plane, and from ventral to dorsal in the sagittal plane, were generally constant and ranged from 1.8° to 2.3°. Table 3 demonstrates the uniformity of the angular values and the significant decrease in the angular values in the mediofrontal part of the eye, where the binocular overlap was greatest. Table 3 also shows the eye parameter p (D^2/R).

Discussion

Our results lead to the conclusion that the ommatidia of the eyes of *Mantispa* have a high light-gathering capacity, owing to an anti-reflection system made up of corneal nipples and a reflector consisting of tracheal tapetal layers on the base of the ommatidia. The corneal nipples increase in height from the periphery to the centre of the lens to compensate for the increase in the angle of incident light and the related degree of reflection. Furthermore, it is possible that the higher nipples operate on longer wavelengths, while the lower ones would be most effective for the shorter wavelengths received by the photoreceptors (see Bernhard *et al.* 1970). The striking tracheolar tapetum is similar to that of the closely related *Chrysopa* (green lacewing) (Ast, 1920; Horridge and Henderson, 1976) and is formed from thick tracheal ridges at the base of each rhabdom. As in the eyes of butterflies (Horridge *et al.* 1972; Ribi, 1979), it probably serves to return light that has already passed the rhabdom, thus effectively doubling the rhabdom's length.

In *Mantispa*, the visual field and the binocular overlap are relatively large. *Mantispa* is similar in appearance and mode of capture of prey to the praying

mantis, and it is therefore of interest to compare the present results with those obtained in mantids (*Ciulfina*, *Mantis*, *Tenodera*: Horridge and Duelli, 1979; see also Horridge, 1980; Rossel, 1979, 1986). The horizontal overlap of the visual fields in *Mantispa* is of a magnitude similar to that of mantids, i.e. 48–70°. The praying mantis has a vertical binocular field of 240° compared with only 135.2° and 142° in *Mantispa*, which results in a reduction of the posterior blind spot (the area that the animal cannot see) in the praying mantis.

While the size and characteristics of the binocular field in *Mantispa* and the praying mantis are similar with regard to horizontal overlap, they differ in vertical overlap. As far as the size of ommatidial angles and their relationship to the part of the eye are concerned, there is a striking difference between the two species. In *Mantispa*, both the effective acceptance angles and the interommatidial angles seem to be rather constant over the entire eye. It should be noted that $\Delta\rho$ of light-adapted ommatidia and $\Delta\phi$ correlate very well, indicating a 1:1 ratio. Eye mapping in the equatorial plane also fails to show significant decreases in $\Delta\rho$ and $\Delta\phi$ in the inner frontal eye region. Therefore, the situation in *Mantispa* is different from the situation in the praying mantis. In *Tenodera*, Rossel (1979) recorded a $\Delta\rho$LA of around 2° near the edge of the eye and in the inner frontal regions. The same is true of the interommatidial angles, which are of about the same order of magnitude as the acceptance angles. Similar values were found for *Ciulfina* (Horridge and Duelli, 1979). Thus, the praying mantis, unlike *Mantispa*, has a distinct acute zone in the frontal eye area.

This difference is especially apparent when one compares longitudinal sections through the eye in the horizontal plane in the equatorial region in *Mantispa* (Fig. 3) and the praying mantis (Horridge and Duelli, 1979; Horridge, 1980; Kirmse and Kirmse, 1985). In *Mantispa*, *R*, ommatidial diameter and cone length are constant throughout the entire section (Fig. 3), while in the praying mantis there is an enormous difference in *R* and cone length between the inner frontal region and the rest of the eye. The mantispid eye seems to be homogeneous from the optical and anatomical points of view, while the mantis eye shows extreme regional specialization. It is likely that mantispid eyes are too small and spherical to have a fovea.

Numerous reports on behaviour and optical measurements in praying mantis (e.g. Mittelstaedt, 1957; Maldonado and Barros-Pita, 1970; Rossel, 1979, 1980, 1983a,b, 1986) suggest that, in this animal, the acute zone is an important prerequisite for the binocular triangulation needed to estimate distances to prey.

Behavioural experiments under physiological conditions would be necessary to provide evidence of binocular vision in *Mantispa*. The prey-capturing behaviour of *Mantispa* under natural conditions and in the laboratory shows fixation and following movements (i.e. target following of the prey) which give the impression that prey capture is mainly binocularly controlled. It is interesting to note that *Mantispa* can catch not only prey located on a projection of its longitudinal body axis, which requires binocular distance estimation, but also prey considerably to the side of that axis. In this situation, *Mantispa* also uses both forelegs to strike,

while the mantis often uses only one. Movement parallax may play a role in this behaviour, as it does in the praying mantis (see Rossel, 1983a,b, 1986).

Both *Mantispa* and the praying mantis show a distinct dependence of acceptance angles on adaptional state. In *Mantispa*, the effective acceptance angles of single ommatidia in both monocular and binocular regions decrease by a factor of 1.9 with illumination of the eye. In *Tenodera* (Rossel, 1979), mean $\Delta\rho$ in the light-adaptated eye is 0.7° in the acute zone in the frontal region, and 2.0° under dark adaptation at night. In the dorsal eye region, $\Delta\rho$ increases from 2.4° to 6° with dark adaptation. In *Mantispa* and praying mantis (Stavenga, 1979) massive pigment shifts in the ommatidia are probably the reason for the illumination-dependent change in angle. Rossel (1979) tried to explain these pronounced adaptional changes on the basis that *Tenodera* uses its eyes in the daytime for hunting and at night for mating. In *Mantispa* this also seems to be true (McKeown and Mincham, 1948; New and Haddow, 1973), as we saw in Istria and in the laboratory, as well as in insects captured with light traps. When *Mantispa* is flushed from its roost into broad daylight, it flies immediately to the protection of another bush or tree. At night, the males seek mates and the females gather at a laying site; the latter often have to fly some distance to get there. *Mantispa* thus needs eyes that can perform specialized tasks around the clock. In this context, it is interesting that in *Mantispa* there is a distinct difference in binocularity between male and female. As our data reveal, *Mantispa* males have a degree of overlap in the dorsal direction that is greater by a factor 1.2 in the horizontal and by 1.1 in the vertical direction than in females. In the male, there is a second, more pronounced, overlap maximum above the equator. No such gender-specific differences are known from praying mantis, but Kirmse and Kirmse (1985) briefly mention that, in *Mantis*, males have a greater percentage area of frontal acute zone than do females. The reason for sexual difference in *Mantispa* could be that the male uses binocular vision not only to capture prey but also to find a mate.

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