FOVEAL VISION IN THE PRAYING MANTIS

AN ELECTROPHYSIOLOGICAL AND BEHAVIOURAL ANALYSIS

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A thesis submitted for the degree of Doctor of Philosophy of the Australian National University

Canberra, April 1980
DECLARATION

I declare that all the work presented in this thesis to be my own.

Part A has been published in J. Comp. Physiol. 131, 95-112 (1979) and Part B has been submitted for publication in the same journal.

S. Rossel
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ABSTRACT

The functional organisation of the compound eye of the praying mantis *Tenodera australasiae* has been analysed in terms of both photoreceptor performance (Part A) and visually mediated behavioural responses (Part B).

Part A - In the compound eye of the mantis *Tenodera* there are large regional differences in interommatidial angles, forming a fovea near the centre of the binocular field. The acceptance angles of light adapted photoreceptors are almost equal to the interommatidial angles across the whole eye. Estimations of the entrance aperture of ommatidia, and measurements of the quantum capture efficiencies of their photoreceptors, suggest that diffraction limits the acceptance angles in the fovea, while the angular acceptance function of the rhabdom is the limiting factor in the peripheral eye. The study also includes measurements of the changes of the acceptance angles in dependence of the adaptation state and time of day, spectral sensitivities, and absolute and relative sensitivities for dark and light adapted photoreceptors. Combined with the measurements of interommatidial angles this allows a complete description of the neural image erected by the retina from a stationary environment.

Part B - The fovea, an eye region specialized for high spatial acuity, is used to locate, track and identify objects of interest, particularly prey, after they have been detected by the peripheral eye and transferred to the fovea by ballistic saccadic head movements. *Tenodera* does not continuously inactivate the visual stabilisation (optomotor).
reflex during tracking. Consequently, when following a target against a disrupted background, the head is stationary for most of the time and tracking is accomplished through a series of saccades. Smooth or continuous tracking only occurs when the target moves against a homogeneous background. Remarkably, saccadic tracking is predictive, i.e. the saccades have adequate amplitudes to bring the fovea right on target at the instant the saccade is completed. Many of the problems that have been considered and examined such as the role of position and velocity information during tracking, and the similarities and differences between smooth tracking and optokinesis, are of fundamental interest because they are of similar importance in the foveate primates.
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INTRODUCTION

In this thesis I shall describe the functional organization of the compound eye of the grasshopper in terms of both photoreceptor performance and visually mediated behavioral responses. My topic originated from studies which were in progress in this laboratory on my arrival in Canberra three years ago. Prof. Snyder, Dr. Graverges, and Dr. Leaughlin were working on a theoretical paper dealing with the optimum design of compound eyes in relation to particular aduity tasks and varied environmental light intensities (Snyder, 1977; Snyder et al., 1977) and, based on this theory, Prof. Horridge was examining anatomical eye parameters in a variety of insects and crustaceans, in an attempt to clarify their adaptive significance in relation to behaviour and habitat (Horridge, 1978). None of these studies, however, could base its assumptions and conclusions on a comprehensive assessment of the imaging performance of compound eyes, derived from combined measurements of photoreceptor spacing and sensitivities. Such an analysis is extremely important because it is the pattern of receptor signals within the retina that governs and limits all subsequent visual processing and finally the behaviour of the animal. In addition, measurements of the receptor performance can be used to test the validity of theories which predict the imaging performance of the eye from its optical and anatomical dimensions.

In many respects the greying grasshopper appeared to be an attractive preparation for a thorough study of retinal function in a compound eye. Notably, the varied regional differences in interommatidial angles and retinial size
In this thesis I shall describe the functional organisation of the compound eye of the mantis *Tenodera* in terms of both photoreceptor performance and visually mediated behavioural responses. My topic originated from studies which were in progress in this laboratory on my arrival in Canberra three years ago. Prof. Snyder, Dr. Stavenga and Dr. Laughlin were working on a theoretical paper dealing with the optimum design of compound eyes in relation to particular acuity tasks and varied environmental light intensities (Snyder, 1977; Snyder et al. 1977) and - based on this theory - Prof. Horridge was examining anatomical eye parameters in a variety of insects and crustaceans, in an attempt to clarify their adaptive significance in relation to behaviour and habitat (Horridge, 1978). None of these studies, however, could base its assumptions and conclusions on a comprehensive assessment of the imaging performance of compound eyes, derived from combined measurements of photoreceptor spacing and sensitivities. Such an analysis is extremely important because it is the pattern of receptor signals within the retina that governs and limits all subsequent visual processing and finally the behaviour of the animal. In addition, measurements of the receptor performance can be used to test the validity of theories which predict the imaging performance of the eye from its optical and anatomical dimensions.

In many respects the praying mantis appeared to be an attractive preparation for a thorough study of retinal function in a compound eye. Notably, the marked regional differences in interommatidial angles and ommatidial size
in relation to the formation of a fovea in the frontal eye (Hesse, 1908), and the adaptation mechanisms to changing illuminance, which were supposed to be functioning during the dramatic colour changes of the eye at dusk (Frieza, 1929), were findings described in the literature which manifested the potential of the mantis eye for the study of a variety of basic problems concerning the design and function of compound eyes.

Part A of this thesis is an account of my efforts to record intracellularly from mantis photoreceptors and to measure interommatidial angles optically from the pseudo-pupil. The study describes all aspects of receptor performance required to predict the intensity measurements performed by the retina from a stationary environment. Significant insights into the design of the mantis eye are obtained from the comparison of the receptor characteristics in the fovea and the peripheral eye.

Admittedly, the adaptive value of many findings will remain unclear because of the lack of adequate behavioural experiments. However, the functional significance of the most impressive feature of the mantis eye, the fovea, is evident. It is an adaptation to the predaceous life style of these insects. Moving prey has first to be located, tracked and identified before it can be caught, and it is obvious that the increased spatial acuity of the fixation region, combined with binocularity, is advantageous for the performance of all these visual tasks. There are few insects which demonstrate eye movements so impressively as the praying mantis when it uses its fovea to fixate and track
potential prey. This must primarily be attributed to the fact that most mantids are sedentary insects. They wait in ambush and respond to movements of prey mainly by movements of the head. This makes observations particularly easy, even on unrestrained animals in their natural habitat. While on collecting trips during the course of the electrophysiological measurements I had several opportunities to observe the prey catching behaviour of Tenodera in the field, and it was following these observations that I decided to study the visual behaviour, and particularly the foveal fixation and tracking of prey, more carefully under controlled conditions in the laboratory. I report about my observations in Part B of this thesis.

The approach taken in this study was to separate and analyse the regional effect across the eye of two relevant visual stimuli, background and prey, in an effort to establish the interactions of eye regions and stimuli in the natural behavioural context. So far, a detailed analysis of the functional organisation in terms of behaviour, has not been available for any compound eye with a fovea and my investigation offers a number of new insights of how foveate insects use their eyes. My behavioural work on the praying mantis was strongly stimulated by a paper published by Collett and Land (1975) on visually guided eye movements in another foveate insect, the hoverfly. There are many parallels in the visual behaviour of these two insects. More fascinating, however, are the striking similarities between the types and function of eye movements in mantids and hoverflies on the one hand, and eye movements in foveate
vertebrates, particularly primates, on the other. Thus many of my findings will be discussed in the light of the extensive work carried out on eye movements in vertebrates.
PART A: REGIONAL DIFFERENCES IN PHOTO-RECEPTOR PERFORMANCE IN THE EYE OF THE PRAYING MANTIS
The compound eyes of *Tenodera* (frontal view). The prominent pseudopupils are used in the following study to measure interommatidial angles and the visual field of the compound eyes, and to identify the recording site during electrophysiological measurements.
SUMMARY

1. Photoreceptor spacing, and angular, spectral, absolute and relative sensitivities have been measured across the compound eye of the praying mantis *Tenodera australasiae* using optical and electrophysiological techniques.

2. Together, the two compound eyes cover virtually all spatial directions. The huge binocular fields extend vertically 240° with a maximum horizontal overlap of 35° in the frontal part of the eye (Fig. 2).

3. Interommatidial angles (Δφ) range from 0.6° in the frontal eye region up to 2.5° in edge regions of the eye (Fig. 5; Table 1). The eye region with minimum Δφ-values is defined as a fovea.

4. The acceptance angles (Δρ) of light-adapted photoreceptors are almost equal to the interommatidial angles over the whole eye (Δρ is 0.7° in the fovea and 2.5° in the edge of the eye) (Fig. 6; Table 1). The measured values of Δρ are close to those predicted by the theories of Snyder (1977) and Horridge and Duelli (1979) from the optical and anatomical dimensions of the eye. In this context, the facet diameters are larger and the crystalline cones are longer in the fovea than elsewhere, whereas the rhabdom diameters are smaller. It is concluded that diffraction limits Δρ in the fovea, whereas the acceptance function of the rhabdom limits Δρ in eye regions outside the fovea (Fig. 16).
5. The angular sensitivity depends on the state of light adaptation and the time of day. In a defined foveal region the photoreceptors have mean acceptance angles of 0.74° (S.D.=0.1°) when light-adapted, 1.1° (S.D.=0.2°) when dark-adapted in daytime, and 2° (S.D.=0.4°) when dark-adapted at night. The corresponding angles for a defined dorsal eye region are 2.4° (S.D.=0.3°), 3.2° (S.D.=0.3°), and 6° (S.D.=0.5°) (Fig. 10).

6. All units recorded from have similar spectral sensitivities, with a maximum in the wavelength range 500 nm to 520 nm, and a weak secondary peak around 370 nm (Fig. 12).

7. Dark-adapted photoreceptors produce bumps whose mean amplitude varies from cell to cell from 1 to 3 mV. Retinular cells in the defined foveal and dorsal eye regions have almost identical quantum capture sensitivities (defined as number of bumps per incident peak axial photons per cm²). Consequently foveal photoreceptors must have a lower quantum capture efficiency (defined as the number of bumps per incident peak axial photons per facet), because their ommatidia have larger facet diameters. The quantum capture efficiencies are 0.04 (S.D.=0.02) in the fovea and 0.10 (S.D.=0.02) in the dorsal eye (Fig. 13; Table 2). This finding supports theoretical predictions that the acceptance function of the rhabdom of foveal photoreceptors is narrowed to decrease $\Delta \rho$. 

8. Absolute and relative sensitivities of photoreceptors, defined as the reciprocal of the quantal flux required to generate a voltage response of 50% maximum, were determined in the defined foveal and dorsal eye regions. To a point source dark adapted retinula cells from both eye regions have almost identical sensitivities (Fig. 14b, c; Table 3). However, to a large diffuse source, dark-adapted foveal photoreceptors with their relatively small acceptance angles are less sensitive than receptors in the dorsal eye with their large Δρ-values, and retinula cells of both eye regions are more sensitive at night than during the day because their fields of view are broadened (Fig. 14d, e; Table 4).

9. The primary visual task of the praying mantis is the recognition and localization of prey moving against a disrupted background. Prey capture mainly occurs during the day, while the sexual behaviour takes place at night. Some relations between the eye performance and the visual behaviour are discussed.
I. INTRODUCTION

Part of the function of any visual system is the selection of biologically relevant features from the complex of information in the optical environment of the animal. This filtering process is performed mainly by the peripheral sense organs, the eyes. A knowledge of the photoreceptor properties, therefore, provides important indications of the function of the visual system as a whole. Several receptor characteristics are of interest, notably the receptor spacing, angular-, spectral- and absolute sensitivities.

The receptor spacing and the angular sensitivity are of primary importance. The imaging of spatial details requires a suitable angular density of visual axes, which in compound eyes is measured by the interommatidial angle, $\Delta\phi$; the contrast quality of the retinal image is influenced mainly by the size and shape of the receptive field, which may be defined as the width of the photoreceptor's angular sensitivity function at 50% sensitivity, $\Delta\rho$ (Götz, 1964). The smaller these two fundamental angular parameters, the greater the capacity of the eye for seeing spatial detail and contrast.

However, limitations on visual performance are set by both the wave and particle nature of light, manifested in the diffraction at the entrance aperture (given by the facet diameter D) of the ommatidia and the photon noise which dictates a minimum mean intensity at the receptor level necessary to guarantee an adequate signal-to-noise ratio (Barlow, 1964; Snyder et al., 1977). Therefore, a compound eye that optimises its information capacity has to compromise
spatial resolution and contrast sensitivity for the particular range of environmental intensities to which the animal has adapted (Snyder et al., 1977).

The above physical constraints are inescapable, but some flexibility in eye design is still left with respect to a regional variation in parameter values; where, of course, in an eye of fixed size any local improvement of the visual performance is at the expense of other regions. Eye specializations characterized by decreased interommatidial angles, usually correlated with an increased ommatidial size, have been reported for many insects and crustaceans (Horridge, 1978). Investigations so far, however, have been limited to measurements of optical and anatomical eye features and lack essential information on regional differences in receptor angular and absolute sensitivities.

In this study, new ground has been broken by making a comprehensive attempt to analyse the receptor performance all over the compound eye of an insect. This survey opens the way to the understanding of the functioning of an eye as a whole. Eye maps demonstrating the regional variation of the interommatidial angles, the acceptance angles and the facet diameters in the praying mantis Tenodera are presented. Furthermore, the angular sensitivity, the spectral sensitivity, and absolute and relative sensitivities in terms of both photon capture and voltage output, as a function of the adaptation state and the time of day, have been investigated in two selected eye regions which differ most in interommatidial and acceptance angles.
There were good reasons to choose the praying mantis for this type of study. Mantids are predators depending on vision for the location and capture of prey. Preliminary cross-sections through the prominent eyes revealed a considerable regional variation in the ommatidial size, which should provide the potential for interesting insights into the correlation of the various parameters across the eye. Finally, the visual behaviour of the praying mantis has attracted considerable interest, and studies have already been published on prey recognition, fixation, tracking and distance estimation (Mittelstaedt, 1957; Rilling et al., 1959; Maldonado and Levin, 1967; Maldonado and Barrós-Pita, 1970; Maldonado and Rodriguez, 1972; Levin and Maldonado, 1970; Maldonado et al., 1970; Lea and Muller, 1977). A behavioural background thus exists that should allow some functional interpretations of the results presented in this study.
II. METHODS

1. Animals
All experiments were performed on *Tenodera australasiae*, one of the two Australian species of this cosmopolitan genus. The animals were caught in the vicinity of Canberra or Bundaberg. Collecting trips were particularly successful at night when the mantids displayed a striking locomotory activity. The animals were kept in large cages until use. The animal house was illuminated by UV- and daylight fluorescent tubes (Philips).

2. The Mapping of the Facets
A small but very distinct cuticular nipple between the base of the antenna and the border of the eye was taken as a reference point to count the facet rows along the three directions of the hexagonal facet mosaic (Fig. 1). The eye was then divided into 31 fields bordered by z- and x-rows. Most fields are defined as groups of 10 by 10 facets but larger fields were used in the most ventral, lateral and dorsal eye parts, where irregularities in the facet mosaic prevented accurate counting of the rows (Fig. 3). The average values of the interommatidial angles ($\Delta\phi$), the acceptance angles ($\Delta\rho$) and the facet diameters (D) were then determined for each field as described below.

3. The Measuring of Facet Diameters
For measuring the facet diameters a varnish (spray pack, Dulux) was sprayed on the eye surface. After drying, the varnish was peeled off to give an exact copy of the eye
Figure 1 a-c

Lateral (a), dorsal (b) and frontal (c) view of the mantis head. A small cuticular nipple between the antenna and the borderline of the eye (see b and c) was used as a reference point to count the facet rows along the three axes (x, y and z) of the facet mosaic.
surface. This replica was photographed under the microscope. The short-diameters of the hexagonal facets were used as a measure of the facet size. (This method was developed by W.A. Ribi in this laboratory.)

4. The Measuring of the Interommatidial Angles

Most mantids have a well-defined pseudopupil, manifested as a small black spot with a diameter of only a few facets when viewed with a microscope with a narrow aperture. The pseudopupil has previously been used in many arthropods to estimate interommatidial angles and visual fields of compound eyes. A detailed description of the method was given by Horridge (1978). In the study presented here the mantis head was rotated in $5^\circ$ intervals and the interommatidial angle was calculated by dividing the step of rotation by the number of ommatidia between two neighbouring pseudopupil positions. In order to determine the visual field of the eye, the mantis head was rotated perpendicular to its sagittal plane and the angle on the goniometer scale was read off when the center of the pseudopupil reached the border of the eye.

5. Electrophysiological Measurements

a) Preparation of the Retina and Recording Technique

A major requirement for valid recordings from photoreceptors is a careful preparation of the retina to prevent any optical and mechanical deterioration. While starting to record from the eye of the praying
mantis, a new gentle preparation technique was developed for the retina. The intact mantis was secured with wax to a rotatable platform and centered in a perimeter device. A sharpened tungsten needle with a diameter of about 50 µm was mounted on the holder of the electrode micromanipulator and carefully pushed through the cornea. The penetrating tip probably compressed the corneal material in a sidewards direction, although under the microscope neither compression nor depression of the cornea could be observed. The tiny corneal hole, which was made as far as possible away from the intended recording site, prevented any spillage of blood and collapse of the underlying retina. After withdrawing the needle the opening was sealed with a speck of grease in order to avoid dehydration of the tissue. Finally the tungsten needle was replaced by a glass micropipette filled with 3 M KCl and a resistance of 80-200 megohms. Because the insertion of the electrode required a suitable illumination, a light guide had to be positioned in such a way that the corneal hole and the electrode tip were clearly visible under the microscope. This technique results in stable recordings and only a small scatter in angular and absolute sensitivities of photoreceptors from identical eye regions. All recorded cells were healthy and met the criterion of a saturated response of at least 40 mV.

b) Stimulation

Light was delivered by a 900 W Xenon arc via quartz optics
terminating in a quartz fiber optic light guide. Intensity and spectral composition were controlled by a set of neutral density filters covering a range of 6.25 log units and 16 narrow band spectral interference filters ranging from 333 nm to 634 nm. The transmission of the filters was measured periodically with a Radiant flux meter (Hewlett Packard). The absolute accuracy of the measurements was checked twice by repeating the calibration procedure with a second instrument. After a receptor cell was penetrated, the tip of the light guide, mounted on a Cardan arm device, was moved until it was accurately positioned on the optical axis of the unit. Light flashes of increasing intensity (0.25 log unit steps) were delivered in order to determine the intensity response function to which most calculations of sensitivity were related. The flashes were 100 ms in duration and normally separated by intervals of 6 s. At high intensity levels the interstimulus intervals often had to be extended to allow the cell to recover to the resting potential.

c) Sensitivity Measurements

Angular Sensitivity. White light was used to measure angular sensitivities because the Xenon arc lamp has a colour temperature close to that of sunlight. Neutral density filters were inserted until the cell response was situated in a medium range. The light source subtending an angle of 0.1° to 0.2° at the eye was then moved horizontally and vertically in 0.5° or 0.25° steps,
according to the receptor's expected field size. Note that the two directions of movement of the stimulus are relative to the perimeter device and not to the preparation. The latter had to be rotated until recording from the desired eye region was possible. The majority of angular sensitivity measurements were carried out on light-adapted preparations. For this purpose a second light guide mounted on the Cardan arm, projected white light onto a reflector around the test light subtending an angle of about 15°. The intensity of the adapting light was attenuated by a second set of neutral density filters to give at least a saturating transient response in dark-adapted photoreceptors. To examine angular sensitivities under dark-adapted conditions, the mantids were kept in complete darkness for at least three hours.

Spectral Sensitivity. From about every third receptor cell recorded from, the spectral sensitivity was determined. Spectral runs were carried out under the same conditions of adaptation as the angular sensitivity measurements described in the previous section.

Absolute and Relative Sensitivities. Absolute and relative sensitivities of photoreceptors were obtained by recording quantum bumps and measuring intensity/response functions (for definitions of sensitivity see "Results", Sect. III. F.).

Dim monochromatic light at peak wavelength delivered from a point source (0.1°) carefully positioned on the optical axis of the unit was used to elicit bumps.
Periods of illumination (approx. 30 s) were followed by equally long intervals of complete darkness. Bumps were recorded at four levels of light intensity covering a range of 0.7 log units and producing bump frequencies up to 4 bumps/s at the highest level of intensity.

Intensity/response functions were measured by delivering monochromatic light flashes at peak wavelength from a point source (0.1°) and a large diffuse source subtending an angle of approx. 20°. The broad stimuli source was achieved by placing a diffusing screen made from lens tissue in front of the light guide.

d) Identification of the Recording Site

After a recording was successfully completed from a cell, the test light guide was removed from the Cardan arm to allow the preparation to be sighted from behind the light guide holder. Viewing through the small opening with the aid of a magnifying lens, the pseudopupil was clearly visible. A fine needle mounted parallel to the eye surface on a micromanipulator was moved across the eye until the needle tip was exactly on the centre of the pseudopupil. Then the position of the needle tip on the eye surface was marked by puncturing the cornea with a second needle. Afterwards, the recording site was localised by counting the facet rows from the defined reference point. The accuracy of the method was checked by repeating the adjustment of the magnifying lens, the centering of the needle and the marking of the needle.
tip several times for the same pseudopupil position. The resulting markers were scattered by not more than two facets around a central marker. Because this method requires sufficient illumination, it could not be used on dark-adapted preparations and a different method had to be applied. Investigations on dark-adapted photoreceptors were limited to a frontal- and a dorsal eye region. Before dark adaptation, the corners of the selected eye region were marked with small white dots. Position and angular subtense of the particular eye region with respect to the coordinate system of the perimeter device were then determined by looking through the holder of the test light guide and moving the Cardan arm so that the pseudopupil moved just within the marked eye region. Recordings were only made from cells with visual axis within the angular limits of this eye region.
III. RESULTS

A. Applicability of the Facet Mapping Method to Different Individuals

Before the measurements were started, two alternative mapping methods were considered, based on angular or facet coordinates. I decided for the latter, mainly because the localisation of the investigated eye region was easier to perform by counting the facet rows, than by mounting the preparation on a goniometer and measuring the angular position of the region. The facet method, however, would be less useful if the individual variability in the number of ommatidia of the eyes were considerable, leading, for example, to individually different positions of the borderline of the binocular field when determined in facet coordinates. (The borderline of the binocular field is shown in Fig. 2.) Therefore, the intersection of this line with the facet row \( z = -10 \) was determined in 8 individuals, and a scatter ranging from \( x = 23; z = -10 \) to \( x = 28; z = -10 \) was observed, which seems to be tolerable. Four animals of this sample with nearly coincident border lines of the binocular field (\( x = 25; z = -10 \)) were chosen for measuring the interommatidial angles, facet diameters and visual field of the compound eye. The electrophysiological work required a large number of mantids and a careful selection was not possible.

B. The Visual Field of the Mantis Eyes

Taken together, the two compound eyes of *Tenodera* cover nearly all spatial directions. There is only a small blind
Binocular field and blind spot of the mantis eye. The head was mounted in a goniometer so that the pseudopupils were symmetrically arranged and aligned with the reference points (v=0, h=0). Then the angular deviation between the optical ommatidial axis on the borderline of the binocular field (a) and the edge of the eye (b) was measured by rotating the mantis head perpendicular to its sagittal plane. Dotted area: binocular field; hatched area: blind spot.
spot in the neck region of the eyes. There are huge binocular fields extending about $240^\circ$ in a vertical direction and with a maximum horizontal overlap of $35^\circ$ in the frontal eye regions (Fig. 2).

### C. Eye Maps of the Interommatidial Angles, Acceptance Angles and Facet Diameters

The eye was subdivided into 31 areas (Fig. 3) and the average interommatidial angle ($\Delta \phi$), acceptance angle ($\Delta \rho$) and facet diameter (D) were determined in each area (Table 1). These values were then plotted as a function of their position along the three directions of the facet rows. An example with $z=-15$ is given in Fig. 4. The next step was the transformation of eye points with identical parameter values (isopoints) into a frontal and a lateral eye projection of the left eye. The isopoints were then connected, leading to the eye maps of the three parameters, $\Delta \phi$, $\Delta \rho$ and D (Figs. 5, 6 and 7).

#### Interommatidial Angles (Fig. 5)

The smallest interommatidial angles were localised in the frontal eye region, where they were as small as $0.6^\circ$. This region, with minimum $\Delta \phi$-values is defined as a fovea, by analogy with many vertebrate eyes. The fovea is slightly inward looking; its centre points to the sagittal plane approximately 4 cm in front of the mantis head. In all directions away from the centre of the fovea the interommatidial angles increase, reaching values of more than $2^\circ$ near the edge of the eye and in large areas of the dorsal and
Figure 3

Left eye shown from a frontal and lateral direction is divided into 31 fields. Note position of reference point (●). Fields 1-27, bordered by z- and x-rows, contain 10 times 10 ommatidia each. Fields 28-31 are larger. Average interommatidial angle, acceptance angle and facet diameter were determined for each field (Table 1).
Table 1

Average interommatidial angles ($\Delta \phi$), acceptance angles of light-adapted retinula cells ($\Delta \rho$) and facet diameters (D) from 31 regions that subdivide the compound eye (Fig. 3). For measuring $\Delta \phi$, fields 17, 18, 19 and 20 were subdivided once more using the central x-row ($\Delta \phi$ values in brackets). Measurements from fields 28, 29, 30 and 31 were classified as belonging to a border region or to a more central area of the eye (values in brackets).
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(1.1/0.8)  (0.78/0.62)  (0.64/0.79)  (1.0/1.05)  (2.1/1.6)  (35/30)  (2.5/2.3)
Figure 4

Plots of interommatidial angles (●), acceptance angles (■) and facet diameters (▲) along the facet row z=-15. Figures along the abscissa give the x-row number intersecting with z=-15. Analogous plots for every tenth facet row along the 3 coordinate axes were made to determine eye points with identical parameter values, finally leading to the eye maps presented in Figs. 5, 6 and 7.
lateral eye. The interommatidial angles presented in the eye maps are average values for each point of the eye, obtained from measurements along the three facet row directions. However, in eye zones which surround the fovea the interommatidial angles measured along the x-, y- and z-facet axes for the same ommatidia are different (Fig. 8). An explanation for this dissimilarity has been given by Horridge and Duelli (1979).

Acceptance Angles (Fig. 6)

The maps of the acceptance angles are based on recordings from light-adapted preparations. Acceptance angles are approximately equal to interommatidial angles in all parts of the eye as can be seen by comparing Figs. 5 and 6, and the values in Table 1. Acceptance angles around 0.7° were found in the foveal eye region, whereas units with $\Delta \rho$-values extending beyond 2° were recorded near the edge of the eye and in dorsal and lateral eye regions. Typical recordings from a foveal and a dorsal eye region (field nos. 19 and 31, Fig. 3) are shown in Fig. 9. For technical reasons (see "Methods") it was not possible to measure angular sensitivities along the different axes of a coordinate system of the preparation. However, measurements of $\Delta \rho$ around the two rotational axes of the perimeter device indicate that the receptor fields are approximately circular across the whole eye.

Facet Diameters (Fig. 7)

The decrease of the interommatidial angle and the acceptance angle toward the frontal eye region is roughly correlated
Figure 5

Eye maps representing variation of interommatidial angles across the left eye (frontal and lateral projection; note position of reference point (•)). The thick line crossing the frontal eye in a vertical direction borders the binocular field; the thick line running across the lateral eye covers the ommatidia which look in the same direction as the ommatidia along the edge of the right eye. Isolines connect eye points with identical interommatidial angles. $\Delta \phi$ values vary between 0.6° in a frontal and 2.5° in edge regions of the eye. Note that the fovea points slightly inwards.
Eye maps representing the variation of the acceptance angles across the left eye. (More detailed information about the general characteristics of the eye maps are given in the text to Fig. 5). All measurements were obtained from light-adapted retinula cells. $\Delta \rho$ values vary from less than $0.7^\circ$ in a frontal up to $2.5^\circ$ in edge regions of the eye. Note one-to-one correlation between acceptance angles and inter-ommatidial angles (Fig. 5).
Figure 7

Eye maps representing variation of facet diameters across the left eye. (More detailed information about the general characteristics of the eye map are given in the text to Fig. 5). D values vary between 30 µm and 55 µm and are roughly negatively correlated with the interommatidial angles (Fig. 5) and acceptance angles (Fig. 6), but the biggest facets are slightly shifted to the lateral eye.
Figure 8a and b

Interommatidial angles in the x-, y- and z-direction along the borderline of the binocular field (a) and the horizontal line through the fovea centre (b). The two lines intersect at eye point z=-12; x=25. Particularly in eye regions which border the centre of the fovea, ommatidial axes are not arranged in a regular hexagonal pattern.
Figure 9a and b

Typical recordings from a foveal (a) and a dorsal eye (b) photoreceptor used to determine their angular sensitivity function. Light source was accurately positioned on optical axis of the cell. Then the adapting light was briefly turned off to estimate maximum response of the unit by means of a 10 mV calibration pulse and a strong saturating light flash. After a longer period of dark adaptation the maximum responses of the photoreceptors would have been increased by approximately 15% relative to the responses shown in this figure and the subsequent adapting light would have saturated the receptors. A neutral density series incrementing in 0.25 log units followed. Finally the stimuli source was moved in two perpendicular directions in 0.25° and 0.5° steps (a) or in 0.5° steps (b) according to field size of the photoreceptor.
with an increase in the facet diameters, which range from 30 µm to 55 µm. However, the eye region with the largest facets does not correspond to the region with the smallest interommatidial and acceptance angles but looks slightly sideways, as can be seen by comparing Figs. 5, 6 and 7. In a large eye region (fields 1-27; Fig. 3) the facets are arranged in a regular hexagonal pattern. Extra facet rows are inserted in ventral lateral and dorsal regions of the eye (field nos. 28-31; Fig. 3).

D. The Dependence of Angular Sensitivity upon Adaptation State and Time of Day

With encroaching dusk the compound eyes change their colour. The pale green of the eye intensifies and this is accompanied by a pronounced enlargement of the pseudopupil. At night, the eyes become completely black, but the colour of the body remains unchanged. If the mantids are kept in darkness throughout the night and examined the following morning, the colour of the eyes and the size of the pseudopupil have returned to the state characteristic for dusk. It is reasonable to assume that this phenomenon reflects pigment movements in the eye which adjust the sensitivity of the visual system to the changed light conditions of the environment.

One possible adaptation strategy is to increase the receptor fields with decreasing illuminance to achieve an increased photon capture. In this set of experiments, the angular sensitivity of photoreceptors was measured in a foveal eye region (field nos. 13 and 19; Fig. 3) and in a
dorsal eye region (field no. 31; Fig. 3), under the following conditions: The majority of recordings from light-adapted retinula cells were performed between 0800 hours and 1600 hours. Before 1700 hours, the adapting light was turned off, and the preparation was kept in complete darkness. At 2000 hours the recordings were resumed with the compound eyes now darkly pigmented. On finishing recording before midnight a new electrode was inserted and the preparation was kept dark-adapted. At 0800 hours the next morning, measurements on dark-adapted receptors were continued until noon.

The following results were obtained: in the defined foveal region, light-adapted units had mean acceptance angles $\Delta\rho=0.74^\circ$ (S.D.=$0.1^\circ$; n=31). In the same region $\Delta\rho$ increased to $2^\circ$ (S.D.=$0.4^\circ$; n=18) when dark-adapted at night and narrowed down to $1.1^\circ$ (S.D.=$0.2^\circ$; n=15) when dark-adapted in day-time. The corresponding values for the dorsal eye region were $2.4^\circ$ (S.D.=$0.3^\circ$; n=30), $6^\circ$ (S.D.=$0.5^\circ$; n=15) and $3.2^\circ$ (S.D.=$0.3^\circ$; n=18) (Fig.10).

The findings presented indicate the influence of a circadian rhythm upon pigment migrations and angular sensitivities. However, at any time of the day the dominant influence appears to come from the illumination. After one or two hours of light adaptation at night (half an hour in daytime), the eye colour returned to the pale green and the receptor fields narrowed down to the same size observed in light-adapted preparations during daytime. This is demonstrated in Fig. 11 for two foveal photoreceptors which were recorded over several hours.
Figure 10a and b

Dependence of angular sensitivity upon adaptation state and time of day in a defined foveal (a) and a dorsal eye region (b). The mean angular sensitivity curves from dark-adapted photoreceptors at night (●, ■), dark-adapted receptors during day (●, ○) and light-adapted receptors during day (○, □) were plotted and fitted with normal distributions having the appropriate half-width.
The same two foveal retinula cells (●, ■) were recorded over a period of several hours to measure angular sensitivities in a light-adapted state during the day (1630 hours) and at night (2300 hours), and in a dark-adapted state at night (2000 hours). The eye colour changed from green to black between 1700 hours and 2000 hours and returned to green between 2030 hours and 2300 hours. This is accompanied by a considerable variation in angular sensitivity.
E. Spectral Sensitivity

Spectral sensitivity was measured in the foveal and dorsal eye regions and under the same adaptation conditions as defined for the angular sensitivity measurements in the previous section (i.e. field nos. 13/19 and 31 (Fig. 3); light-adapted in daytime and dark-adapted during day and at night). All recorded retinula cells had similar spectral sensitivity functions with a major peak in the range 500 nm to 520 nm and a secondary peak around 370 nm (Fig. 12). Only a few units had sensitivities fitting the theoretical rhodopsin absorbance calculated from the Dartnall nomogram. The majority had broader spectral sensitivity functions. No significant differences could be seen in the spectral sensitivities when considering the influence of adaptation and the recording site (Fig. 12). Intracellular recordings employed in this study gave similar spectral sensitivity functions to those from ERG-measurements carried out by Sontag (1971) in the compound eye of *Tenodera sinensis*.

F. Absolute and Relative Sensitivities

The variation of the facet diameters across the eye raises the question whether the larger size of the foveal facets increases the sensitivity of photoreceptors in addition to improving the resolution. Sensitivities were measured in terms of both quantum capture and voltage output in the same foveal and dorsal eye regions in which the angular and spectral sensitivities were measured (field nos. 13/19 and 31; Fig. 3).
Figure 12a and b

Spectral sensitivities of photoreceptors in a defined foveal (a) and a dorsal eye (b) region measured under light-adapted conditions (white adapting light) during the day (O, n=7; □, n=9) and dark-adapted conditions during the day (●, n=13; ▪, n=10) and at night (●, n=13; ■, n=8).
a) Quantum Capture Sensitivity
and Quantum Capture Efficiency

After approximately half an hour of dark adaptation the receptor cells produced quantum bumps when exposed to dim light. All bump measurements reported in this study were performed at night, after 3 h of dark adaptation, using monochromatic light at the most efficient wavelength (513 nm) delivered from a point source on the visual axis of the photoreceptor (see "Methods"). The mean bump amplitude varied from cell to cell from 1 to 3 mV (Fig. 13a). Periods of complete darkness revealed that "spontaneous" bumps are rare (less than 10 bumps per hour). The bump frequency is a linear function of the intensity. About half of the cells recorded from showed two types of quantum bump, one typical, the other slower in time course and smaller in amplitude.

These findings are very similar to those obtained from locust photoreceptors (Lillywhite, 1977, 1978). These detailed investigations led to the following conclusions:
First one absorbed photon generates only one bump (Lillywhite, 1977); Secondly, only large bumps (L-bumps) are initiated from the recorded unit. Small bumps (S-bumps) are derived from large bumps transmitted from neighbours by electrical coupling (Lillywhite, 1978). For the calculation of the quantum capture efficiency (see below) and the separation of large from small bumps in mantis retinula cells, it is assumed that the above statements are also valid for mantids.

The bump frequency can be plotted versus the peak axial photons per cm² per s or per facet per s. Both intensity
scales are useful and lead to separate important findings. The bump frequency as a function of the peak axial photons/cm²/s reveals the absolute effectiveness of photoreceptors, while the bump frequency correlated with the incident photons/facet/s provides more specific information about the effectiveness of the dioptrics and the photoreceptors. We define two separate terms in order to distinguish the two measures: the quantum capture sensitivity which is the number of bumps produced by a retinula cell per incident peak axial photons per cm², and the quantum capture efficiency as the number of bumps produced by a retinula cell per incident peak axial photons per facet. Quantum sensitivities and efficiencies for the whole ommatidia could not be determined because it is not known how the 8 retinula cells contribute to the rhabdom.

The analysis of bump recordings from the two particular eye regions reveals that the photoreceptors in the dorsal eye are by no means less sensitive than foveal receptors with their larger facets and - as sections show - rhabdons with nearly twice the length (Fig. 13b). This interesting result implies that the dorsal-eye photoreceptors are more efficient in capturing photons (Fig. 13c). Estimated values of quantum capture sensitivities and efficiencies are given in Table 2. A few recordings from the lateral eye (field no. 30; Fig. 3) revealed almost identical quantum capture sensitivities for this eye region as for the fovea and the dorsal eye. Because the facet diameters are only slightly larger in the lateral eye compared with the dorsal eye
Bump measurements performed to estimate the quantum capture sensitivity and efficiency of photoreceptors in a defined foveal and dorsal eye region. a) Train of quantum bumps recorded from a foveal retinula cell of Tenodera. b) Plot of the mean bump frequency versus the stimulus intensity given in peak axial photons per cm²/s. The slope of the regression lines gives quantum capture sensitivities for the two eye regions. c) Bump frequency as a function of the incident photons per facet/s. Facet diameters are 50 µm in the foveal and 32 µm in the dorsal eye region. Slope of regression lines gives quantum capture efficiencies for the two eye regions.
Table 2

Mean quantum capture sensitivity and quantum capture efficiency of retinula cells in the defined foveal and dorsal eye regions.

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(Table 1), photoreceptors in the two eye regions also have similar quantum capture efficiencies.

b) Sensitivities at the 50% Vmax Voltage Output Point

With increasing light intensity the quantum bumps fuse together and add up non-linearly to produce the receptor potential. The intensity/response function then is a plot of the membrane potential versus the logarithm of the light intensity. Intensity/response functions are important for the characterisation of photoreceptors because they are used to calibrate them for all calculations of angular, spectral and polarisation sensitivity and define their voltage range for any given state of adaptation.

In this study, intensity/response functions were measured using different stimuli and under different adaptation conditions. Sensitivity is defined as the reciprocal of the intensity necessary to produce a voltage response 50% of the maximum response (50% Vmax) of dark-adapted photoreceptors.

Sensitivity of Dark-Adapted Retinula Cells to a Point Source. In this set of experiments, sensitivity was measured by recording intensity/response functions from dark-adapted photoreceptors during the day and at night using on-axis parallel rays of monochromatic light at peak wavelength (point source, $\phi=0.1^\circ$). The results show that the intensity/response functions fall into nearly the same intensity range for both day and night curves and for the two eye regions (Fig. 14b, c). Absolute sensitivities are summarized in Table 3. A few recordings from the lateral eye (field no. 30; Fig. 3) showed almost identical absolute sensitivities for
this eye region as for the fovea and the dorsal eye. No
increase in absolute sensitivity was observed when either
the duration of the flash (usually 100 ms), or the minimum
period of dark adaptation (usually 3 h) was extended.

**Sensitivities of Dark-Adapted Retinula Cells to an
Extended Source.** Because of the considerable regional and
temporal variation in angular sensitivities (Fig. 10), one
might expect sensitivities to differ both across the eye
and with time of day, when the retina is stimulated from
monochromatic light at peak wavelength delivered from a
large diffuse source ($\phi=20^\circ$). Indeed, foveal units with
their relatively small acceptance angles are less sensitive
than those in the dorsal eye, and retinula cells of both
eye regions are more sensitive at night when their fields
of view are broadened (Fig. 14d, e; rs-values, Table 4).
Sensitivities to the point source and extended source were
measured from the same retinula cells. The former are nearly,
but not exactly, identical during the day and at night for
each eye region, as can be seen from Fig. 14b, c and Table 3.
Therefore, to estimate the variation of relative sensitivities
as a function of time of day and angular sensitivity, the
relative shifts of the intensity/response functions with
respect to the two stimuli sources were also taken into ac-
count for each eye region. These results (rs-values, Table 4)
are close to calculated ones (cRs-values, Table 4), where it
has been assumed that the sensitivity to a large diffuse
source is a function of $\Delta \rho^2$.

**Sensitivities of Light-Adapted Retinula Cells to a
Point Source.** Relative sensitivities of light-adapted retinula
Average intensity/response functions of photoreceptors from a foveal and a dorsal eye region, used to determine sensitivities at the 50% Vmax voltage output point under different adaptation and stimulus conditions. Adaptation and stimulus conditions are: a) Light-adapted during the day. Adapting light: large diffuse source; test light: point source. b) Dark-adapted during the day. Test light: point source. c) Dark-adapted at night. Test light: point source. d) Dark-adapted during the day. Test light: large diffuse source. e) Dark-adapted at night. Test light: large diffuse source.
Table 3

Absolute sensitivities to a point source from photoreceptors dark-adapted during day and at night for the defined foveal and dorsal eye regions. Sensitivity is defined as the reciprocal of the quantal flux (on axis, peak wavelength) required to generate a transient response of 50% maximum. (S.D.; t.s.: standard deviations and total scatters of the samples of intensity/response functions (at 50% Vmax) along the log I scale).

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<tr>
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Table 4

Relative sensitivities (rs, t.s, crs; see text) to a large diffuse source from photoreceptors dark-adapted during day and at night for the defined foveal and dorsal eye regions. (S.D.; t.s.: standard deviations and total scatters of the samples of intensity/response functions (at 50% Vmax) along the log I scale).

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<td>0.5</td>
<td>10</td>
<td>3.5</td>
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cells were obtained from the intensity/response functions used to calibrate the cells when measuring angular sensitivities during daytime. The white adapting light was emitted from a large diffuse source (ϕ=15°) that covered most of the visual field of the photoreceptors. The absolute adapting intensity, which was sufficient to evoke a saturation response in dark-adapted photoreceptors, was the same for both eye regions. However, dorsal eye receptors with their large visual fields catch more photons from a large diffuse source than foveal receptors with their narrow fields (Fig. 14d, e). The retinula cells were then tested with light delivered from a point source. The results show that under these stimulus conditions the foveal receptors are significantly more sensitive than their counterparts in the dorsal eye (Fig. 14a).
IV. DISCUSSION

The imaging performance of the compound eyes of the praying mantis has been analysed with respect to the regional variation and correlation of fundamental parameters including receptor spacing, angular, absolute and spectral sensitivities. The results have demonstrated the following major points: (1) There is a correlated variation of the interommatidial angles and acceptance angles across the eye, forming a fovea in the forward-looking eye region (Figs. 5, 6; Table 1). (2) Dark-adapted retinula cells have identical sensitivities to a point source over the eye (Figs. 13b, 14b, c; Table 2, 3). Consequently, there must be a decreased quantum capture efficiency in the fovea, because its larger facets receive more light (Fig. 13c; Table 2). (3) There is a dependence of the angular sensitivity upon the adaptation state and time of day (Fig. 10). This correlates with a variation of sensitivity to a large diffuse source (Fig. 14d, e; Table 4). (4) All photoreceptors recorded have similar spectral sensitivities (Fig. 12). These results will be discussed in the following respects: First, the receptor performance and its possible implications for the design of the mantis eye, and secondly, the relations between eye performance and behaviour and habitat.

A. Receptor Performance and Design of the Mantis Eye

1. The Optical and Anatomical Basis of the Fovea

In Tenodera the fovea, i.e. the frontal eye region with...
decreased interommatidial angles and increased ommatidial sizes, is formed by a local flattening of the eye surface and by tilting the ommatidial axes so that they are no longer normal to the cornea surface, particularly in eye regions which border on the centre of the fovea. The optical effect of skewed ommatidial axes is the refraction of the incident light at the eye surface in such a way that the optical ommatidial axes deviate, relative to the anatomical ones, towards the centre of the fovea (Horridge and Duelli, 1979). Thus the fovea is more curved anatomically than optically and a compact eye shape can be maintained in spite of the relatively broad eye region with decreased interommatidial angles and increased facet diameters.

2. The Optical Basis of the Angular Sensitivity

The field of view of a photoreceptor in an apposition eye arises from a combination of the properties of the dioptric system and of the acceptance characteristics of the rhabdom. Therefore, it should be possible to predict the size of the receptor fields from the anatomical and optical dimensions of the eye and compare the result with the measured field widths. Agreement of the predicted and experimental values of $\Delta \rho$ would then give a first hint of the validity of the optical theories.

The basic concept underlying the theory of Snyder (1977) is that a diffraction-limited lens generates, from a distant point source, a blurred image known as the Airy disc, at the tip of the rhabdom, and that this image sweeps across the rhabdom as the point source is moved. The angular sensitivity
function then derives from the convolution of two functions, both assumed to be Gaussians. The first describes the intensity distribution of the Airy disc, taking the angular width at half-height as \( \lambda/D \) (where \( \lambda \) is the wavelength of the most effective light and \( D \), the diameter of the lens, taken as the facet diameter), and the second, the acceptance profile of the rhabdom, taking the angular width at half-height as \( d/f \) (where \( d \) is the rhabdom diameter and \( f \), the distance from the posterior nodal point to the distal tip of the rhabdom). \( \Delta \rho \) is then given by:

\[
\Delta \rho^2 = (\lambda/D)^2 + (d/f)^2.
\]

Experimental values of \( \Delta \rho \) are now compared with predicted ones based on estimations of the single optical parameters and using the formula above. The regional variation of the light-adapted acceptance angles from the lateral and median eye to the fovea is quite marked in the mantis eye (Fig. 16). According to the theory, the decrease in the values of \( \Delta \rho \) should be the effect of either reduced values of \( \lambda/D \) or reduced values of \( d/f \) or both. The measurements show that \( \Delta \rho \) and \( D \) are in fact correlated, but the differences in \( D \) cannot account for the differences in \( \Delta \rho \) (Fig. 16). Evidence for a corresponding variation of \( \Delta \rho \) and \( d/f \) comes from the following physiological and anatomical measurements: (1) The lower quantum capture efficiency (to a point source) in the fovea relative to the dorsal and lateral eye presumably indicates that the angular subtense of the rhabdom has been narrowed relative to the angular dimensions of the Airy disc. (2) Cross-sections through the eye of *Tenodera* show that the rhabdom diameter, and the
combined cone length and corneal thickness, to which the
distance of the posterior nodal point from the rhabdom tip
might be related, are inversely correlated, where the
rhabdom diameter is the smallest and the cone length plus
corneal thickness, the largest in the fovea (Fig. 15; un­
published measurements by Duelli). Similar anatomical
findings have been made in the mantis Ciulfina by Horridge
and Duelli (1979). These authors also presented the theoret­
ical background for the estimation of the value of f from
the anatomical data, by showing that f is approximately
equal to the length of the dioptric system (crystalline
cone length plus corneal thickness) divided by the average
refractive index inside the eye (assumed to be 1.4). Pre­
dicted values of d/f and Δρ for Tenodera are plotted in
Fig. 16. A comparison of predicted and measured acceptance
angles show that the theory in general terms generates
acceptance angles close to those actually measured. However,
the predicted values are slightly smaller than the measured
ones over most of the eye. At present, it is not possible to
say whether this is due to errors in the optical principles
assumed, in the measured values of Δρ or in the estimated
values of D, d or f. If the theoretical assumptions are in
fact significant in determining the receptor fields, a
comparison of the measured values of Δρ, λ/D and the pre­
dicted values of d/f suggests the following conclusions
(Fig. 16): (1) The large facets of foveal ommatidia are
essential for the generation of their small acceptance
angles, because Δρ in this eye region is smaller than the
limit set by diffraction for ommatidia over most of the
Measurements of optically significant anatomical parameters along the facet row $z=-15$ which runs through the fovea (Duelli, unpubl.). Crystalline cone length, facet diameter and rhabdom length are larger in the fovea than elsewhere, whereas rhabdom diameter is smaller.
Figure 16

Measured and predicted acceptance angles, $\Delta \rho$ and $\Delta \rho'$, plotted along facet row $z=-15$ which runs through the fovea. $\Delta \rho'$ has been calculated with its two components, angular subtense of the rhabdom, $d/f$, and angular subtense of the Airy disc, $\lambda/D$, both estimated from anatomical data (Fig. 15). $d/f$ is a prediction of angular subtense of the rhabdom deduced from measured values of $\Delta \rho$ and $\lambda/D$. Note that in the fovea acceptance angles are limited by diffraction whereas outside the fovea they are dominated by angular width of the rhabdom.
rest of the eye. (2) Diffraction is limiting the acceptance angles in the fovea ($\lambda/D > d/f$), whereas the acceptance function of the rhabdom is the limiting factor in eye regions outside the fovea ($d/f > \lambda/D$).

3. The Correlation of $\Delta\phi$, $\Delta\rho$ and D

The interommatidial angles, acceptance angles and facet diameters are closely, but not perfectly correlated, and in particular, the D-isoline-pattern is shifted relative to the $\Delta\phi$- and $\Delta\rho$-pattern (Figs. 5, 6 and 7). Histological sections show that the tilt of the ommatidial axes relative to the eye surface reaches a maximum in the eye region where the facets are largest. The effective light catching area of these facets is therefore smaller than predicted from the anatomical measurements. Consequently, a better match in the relationship between $\Delta\phi$, $\Delta\rho$ and D might be expected when D is the effective rather than the anatomical facet diameter. The sections show furthermore that the length of the dioptric system (to which the value of f might be related) is correlated with the interommatidial angles and not with the facet diameters. The position of the ommatidia with the smallest acceptance angles between the centre of the fovea and the eye region with the largest facets, presumably reflects the significance of the optical parameters, f and D, in influencing the acceptance angle.

At present, it is not known whether the discrepancies in the relationship of relevant parameters have any functional significance or whether they represent inescapable
compromises in the overall design of the compound eye. These compromises do not only concern receptor spacing and sensitivities, but also eye shape and size, visual field, regularity of the facet mosaic and the development of the compound eye over several instar stages to the adult eye.

4. Absolute and Relative Sensitivities to a Point Source

In this study, photoreceptor sensitivity to a point source was measured and defined in several ways, over a range from the quantum capture sensitivity at threshold conditions to the sensitivity in the light-adapted domain. The results of the measurements from dark-adapted and light-adapted retinula cells will be discussed separately.

Dark-Adapted Retinula Cells. Sensitivity measurements of dark-adapted preparations were made with on-axis parallel rays of monochromatic light at peak wavelength. Because the angular and spectral sensitivity of mantis retinula cells are known, the sensitivity measurements under these well-defined stimulus conditions enable one to establish retinula cell responses for any intensity, spatial distribution of corneal irradiance and chromaticity and to compare receptor sensitivities with those of other animals.

The absolute sensitivities of dark-adapted photoreceptors at the 50% Vmax voltage output point are considerably higher in *Tenodera* than those in other insects examined and exceed the values available from dragonflies (Laughlin, 1976), flies (Hardie, 1977) and locust (Horridge and Tsukahara, 1977) by one or more log units. *Locusta* is of special interest.
because it shows approximately the same quantum capture efficiency, facet diameter and bump size (Lillywhite, 1977) as the dorsal eye of Tenodera. Obviously further investigations under strictly comparable conditions will have to be directed to the transduction processes which generate the intensity/response functions in order to explain the relatively high absolute sensitivity in mantis retinula cells.

At present, the functional significance of ommatidia having the same sensitivities across the eye with respect to a point source, whatever their facet diameter and acceptance angle, cannot be assessed. However, it is reasonable to assume that the decrease in the quantum capture efficiency towards the fovea is the result of narrowing the acceptance function of the rhabdom in order to adapt receptor directionality to receptor spacing (see Sect. IV. A. 2).

Light-Adapted Retinula Cells. Foveal photoreceptors are more sensitive than dorsal eye receptors when light-adapted with a large diffuse source and tested with a point source (Fig. 14a). To explain this observation one has to consider the angular extent of the stimuli sources in connection with the regional variation of the angular sensitivity. For a number of arthropod photoreceptors, it has been found that an increase in background intensity increasingly affects the sensitivity by shifting the intensity/response function along the intensity axis towards higher values. At background intensities which saturate dark-adapted photoreceptors, sensitivity becomes inversely proportional to the change in
background intensity and the plateau depolarization resulting from the background remains constant (Laughlin and Hardie, 1978). In the present case, both eye regions were exposed to the same absolute background intensity. The effective intensity at the photoreceptor level, however, must have been different because the dorsal eye receptors, with their large fields, catch more photons from an extended source than foveal receptors, with their narrow fields (Fig. 14d, e). One would expect the extra photons caught by the dorsal eye receptors to have the same effect on their sensitivity to a point source as an increase in the background intensity in the fovea would have. This would then shift the intensity/response function further along the intensity axis towards higher values for the dorsal cells than for the foveal ones which in fact has been observed. Because dark-adapted photoreceptors in both eye regions have almost the same sensitivity to a point source and were saturated by the adapting light, the sensitivity shift between the two eye regions is expected to be inversely proportional to the difference in the number of effective adapting photons. Further consideration suggests that at the high light adaptation levels employed, the sensitivities in the two eye regions should be the same when the photoreceptors are both adapted and also tested with an extended source, because the differing angular sensitivities must in this case affect equally the number of effective photons from both the adapting and test light. Therefore, under bright daylight conditions the retinula cells all over the eye presumably have similar voltage outputs with respect to the diffuse environmental illuminance.
5. Adaptation of the Mantis Eye to the Low Intensity Levels at Night

A visual system that operates in daylight and at night must have powerful adapting mechanisms, since the environmental intensity between moonlight and sunlight covers a range of 8 to 10 log units, whereas the operating range of an insect retinula cell defined by its intensity/response function is not more than 4 log units for a given state of adaptation. One possible adaptation strategy is a decrease in angular sensitivity with decreasing intensity, as the mean number of photons absorbed by a photoreceptor from a diffuse light is proportional to the square of its acceptance angle, at least when the acceptance function of the receptor is dominated by the acceptance function of the rhabdom (Snyder, 1977). The light-adapted fovea presumably does not satisfy this condition (see Sect. IV. A. 2). A comparison of the shift of sensitivities to a large diffuse source of dark-adapted photoreceptors with the corresponding variation of the acceptance angles as a function of the time of day, however, roughly confirmed the relation outlined above for both eye regions (Table 4).

If we consider now the widening of the acceptance angle in retinula cells of Tenodera from a light-adapted state in daytime to a dark-adapted state at night, we note an increase of $\Delta \theta$ by a factor of 2.9 in the foveal and 2.4 in the dorsal eye region. These figures represent an expected additional photon capture of $2.9^2$ and $2.4^2$ respectively, which results in a sensitivity gain of less than one log unit for both eye
regions. This result suggests that the variation in angular sensitivity plays only a modest role as an adaptation strategy. Moreover, it has to be noted that the retinula cells' sensitivity to a point source is not influenced by the diurnal rhythm which varies the acceptance angles.

In conclusion, although retinula cells vary the angular sensitivity as a function of adaptation and time of day, additional physiological adaptation mechanisms must be functioning if the receptors are to operate effectively both in daylight and at night (e.g. Laughlin and Hardie, 1978; Dvorak and Snyder, 1978).

The anatomical mechanisms which underly the changes in receptor fields are numerous, but mostly include movements of pigment granules (Walcott, 1975). Pigment migrations in the compound eyes of mantids which are underlaid by a diurnal rhythm and result in dramatic colour changes of the eyes, have been investigated by Friza (1929). That study, however, is incomplete and a thorough histological investigation is underway.

B. The Performance of the Mantis Eye in Relation to Behaviour and Habitat

1. The Visual Task of the Praying Mantis

The mantis Tenodera australasiae observed in the grasslands around Canberra is normally seen resting on wildflowers and feeding on pollinating insects, especially bees. The flowers are surrounded by sparsely distributed grasses. This habitat is protective in that mantids, which hang vertically on stalks of plants, are not easily recognised by the human
eye. From a teleological viewpoint, a mantis which occupies a habitat that guarantees food and protection has no longer to be concerned with the recognition of details of the stationary environment. Only factors which disturb this state are of interest and the main concern is the arrival of prey. As for most arthropod predators, the prey itself has only a few specific characteristics. Mantids are most readily attracted by objects which describe rapid jerky movements; object size and shape are less important (Rilling et al., 1959). The size of the prey within relevant limits of distance always exceeds the distance between the forward looking visual axes of the two eyes, but the prey is normally small enough to allow a complete coverage with both eyes owing to the large binocular field. My own observations on the prey capture behaviour indicate that low amplitude movements of a target (e.g. small rotational and translational movements of a fly) are not followed by head movements of the mantis. Consequently, even when the prey is fixated, it still causes some motion across the retina. Additional complications arise when larger movements of the prey require head or body movements of the mantis to keep the target in the fixation region of the eyes. In order to prevent disturbing interferences between the moving background and the moving target, mantids, like other insects, have adopted a specific tracking strategy in the form of rapid saccadic head movements, thereby limiting the blurring of the environment to short time intervals.

In summary, the primary visual task of the praying mantis is the recognition and localisation of small objects,
moving against a disrupted background. The following considera-
tions are an attempt to sort out the eye properties which are relevant for the accomplishment of this function.

2. The Use of the Fovea in the Praying Mantis

The most significant relation between eye structure and function concerns the fovea in the frontal eye region which is used to fixate and track objects of interest. Foveas are commonly found among insects which rely on vision for the accurate localisation of small objects such as sexual partners and prey (Collett and Land, 1975; Sherk, 1977, 1978; Horridge, 1977a, b and 1978), but the relation between the head movements towards the prey and the eye region of most acute vision is particularly impressive in the praying mantis and has been known for more than 70 years (Hesse, 1908). A thorough investigation of the prey capture behaviour of the mantis Stagmatoptera showed, however, that the eye region which is essential for a successful raptorial strike flanks the region with the largest facets and smallest interommatidal angles but does not include it (Maldonado and Barros-Pita, 1970; Barros-Pita and Maldonado, 1970). As pointed out by Collett and Land (1975), this area roughly corresponds to the projection of the outline of the centered prey. The importance of edges for the localisation of the normally dark prey is in fact obvious as they provide a reliable contrast against the bright background. If the distance between the target and the mantis increases, the silhouette of the target image on the retina moves towards the centre of the fovea. The shape of the fovea and its position relative to the sagittal plane of the mantis head (Fig. 5) are
presumably reflections of the typical prey in such a way that they represent a compromise to maximize the coverage of the prey edges for the relevant range of the prey distance.

3. The $\Delta \theta / \Delta \phi$ Ratio

One of the more striking facts to have emerged from this study is the constant one-to-one ratio of the acceptance angle and interommatidial angle across the light-adapted eye in spite of the large regional variation of both parameters, $\Delta \theta$ and $\Delta \phi$. For any environmental intensity there is an optimum $\Delta \theta / \Delta \phi$ ratio when a random contrast pattern has to be reconstructed by the compound eye (Snyder et al., 1977). Quantitative values of $\Delta \theta / \Delta \phi$, predicted by this theory for the eyes of diurnal insects are nearly twice as large as those measured in Tenodera. The reason for this dissimilarity is possibly the different visual task of the praying mantis. However, at present, we do not know why the interommatidial angles are large relative to the acceptance angles in an eye which looks for small objects moving against a disrupted background. Similarly to spatial acuity, motion acuity is a function of the density of the sampling stations, and the overlap of the visual fields of neighbouring ommatidia may differ according to the movement parameters to which the visual system has to be sensitive.

4. Mantids Are Active Day and Night

The variation of the angular sensitivity and consequently the absolute sensitivity to the diffuse environmental illumination as a function of a diurnal rhythm indicates that Tenodera
is active by day and night. This suggestion is confirmed by field observations which furthermore gave some evidence that the two periods of activity (day and night) serve two different functional goals - prey capture and mating.

Prey capture is the main activity Tenodera performs during daytime. Because of camouflage and remaining motionless in ambush, a mantis is probably seldom required to escape from enemies. Mating Tenoderas are frequently found at night when the animals show a striking locomotory activity. These observations are supported by Frauca (pers. comm.) who encountered Tenodera in the swamps and the grasslands around Bundaberg (Qld).

What possible reasons could there be to perform the feeding behaviour in daytime and the sexual behaviour at night? Presumably, an excellent visual performance, only available in bright daylight, is required to fulfill the visual task associated with the capture of prey. During daytime Tenodera are sparsely distributed throughout their habitat and distances between individuals are of the order of meters. Thus mating requires a considerable locomotory activity. It may be essential for the survival of the clumsily moving mantids that they perform all locomotory activity under the protection of darkness. During daytime a flying or stalking mantis would become an easy target for predators, particularly birds.

5. Conclusions and Outlook

The results presented in this paper include a comprehensive account of fundamental parameters and their regional
variation in a compound eye. The description of receptor performance and eye specialisations, however, is meaningless without reference to its function. It has to be admitted, as has been made clear in the discussion, that a full interpretation of the significance of eye properties in terms of behaviour and habitat is not possible at present. Not only for mantids, but for insects in general, we lack knowledge of how information is processed at the different levels of the visual pathways and what information finally has to be represented in the brain. Such knowledge is essential, as the eye design reflects what an insect needs to see. The situation in stationary mantids, however, which have to perform primarily one particular visual task (prey capture), is relatively simple compared to many other insects for which a variety of requirements may compete in the eye design. It is hoped that some of the answers to the questions still open will come from the behavioural experiments presently in progress.
PART B: Foveal Fixation and Tracking in the Praying Mantis
Most mantids are sedentary insects and the fixation and tracking of prey, which is the main theme of the following study, is primarily performed by the extremely mobile head.
SUMMARY

1. Visually guided head and body movements of restrained and freely moving mantids (Tenodera australasiae) have been studied by means of closed circuit television. Interest was concentrated on the association of visually evoked responses with the two regions which subdivide the eye, the fovea and the periphery (Part A).

2. The peripheral eye is mainly responsible for the detection of novel objects (preferably potential prey) and the generation of ballistic (open-loop) saccadic head movements (Fig. 3) which bring the target image to the fovea (Figs. 4, 5, 6, 7).

3. Measurements on monocular animals show that the fovea of each eye is encircled by a saccade sensitive periphery (Figs. 6, 7). In other words each eye is capable of measuring any retinal position of the target image in a coordinate system whose origin is at the fovea. Based on this finding, a hypothesis, which is outlined in section IV. 7, suggests that the binocular coordination during fixation, tracking and distance estimation is based on the comparison of angular coordinates extracted by each eye from the position vector of the target.

4. Moving targets which have been fixated are held in the fovea either by smooth or saccadic tracking eye movements. The degree to which either tracking strategy is employed depends mainly on the features of the background, but to some extent also on the velocity of the target.
5. Targets which move against a homogenous background are tracked by smooth eye movements (Fig. 8). Low target angular velocities are closely matched by the eye velocity. At high target speeds the head lags increasingly behind the target and saccades are periodically required to reduce the position error relative to the fovea.

6. Smooth pursuit eye movements, evoked either by a single target (Fig. 8) or a disrupted background (Fig. 9), are affected primarily by the velocity of the retinal image. While the effects of target and background are similar in this respect, they differ in others. Small objects in the foreground, subtending an angle of only a few degrees on the retina, evoke strong pursuit responses only when they resemble typical prey and project onto the fovea (Fig. 10). On the other hand, the image stabilisation of the background is a stereotyped response that can be evoked whenever a large part of the background moves across the visual field (Fig. 11a). Moreover, responses caused by a moving target in the fovea, and movements of the background in the periphery, are not combined additively (Fig. 11b). The foveal tracking response is weighted more strongly, but because the target is usually small, compared with the background, competing background motion can suppress smooth foveal tracking almost completely.

7. This limitation imposed upon the smooth pursuit system by the presence of a disrupted background (either a stripe pattern in the experimental set-up or grass and
other plants in a natural setting) is avoided by the adoption of a strategy of saccadic tracking (Figs. 12, 13, 16, 17). This also applies for the tracking which immediately precedes the catching of prey (Fig. 16). Therefore, the stabilisation of the target image in place on the fovea is not a prerequisite for a successful strike.

8. Up to target angular velocities of about 100°/sec, saccadic tracking is predictive, i.e. the saccades have adequate amplitudes to bring the fovea right on target at the instant the saccade is completed (Fig. 14). This implies that the saccadic system processes not only position information of the target but velocity information as well. It is suggested that this velocity information is provided by the smooth pursuit system. Saccadic tracking would then reflect interactions of two circuits, the velocity coding circuit which in the presence of a homogeneous background also generates smooth pursuit head movements, and the position coding circuit which in the absence of target movement is able to generate saccades on its own.

9. The visual behaviour of the praying mantis is of special interest because it has evolved very similar ways to move the eyes as vertebrates and particularly the foveate primates.
I. INTRODUCTION

The visually guided control of eye movements in vertebrates represents an impressive example of sensory motor integration of the nervous system and has been examined in considerable detail throughout this century (rev. Yarbus, 1967; Stark, 1971; Ditchburn, 1973; Robinson, 1977; Carpenter, 1977). A comparison with recent investigations on the visual behaviour in invertebrates has revealed remarkable parallels between the types and function of eye movements, in animals as different as men and insects* when performing comparable visual tasks (e.g. Kirmse and Lässig, 1971; Land, 1975; Land, 1977; Poggio, 1977).

Both vertebrates and invertebrates use rapid saccadic and smooth eye movements during the fixation and tracking of single objects of interest and during optokinetic responses evoked by movements of the whole visual surroundings. The saccades bring new parts of the visual field into the fixation region of the eyes, and also form a significant component of the tracking response by recentering the moving target whenever it deviates by some critical angle from the fixation region. By comparison, the smooth eye movements minimize the retinal slip of moving background or single target image patterns.

In addition to the parallels in the visually mediated behaviour there are also structural similarities in the sense

* Note that insects do not have movable eyes. Thus eye movements are exclusively brought forth by head and body movements.
that the fixation region of many vertebrates and insects corresponds with a fovea, which is a limited eye zone particularly designed for high spatial resolution. A thoroughly studied example is represented by the fovea of the praying mantis, Tenodera (Part A). These insects possess large compound eyes allowing them to see almost all around the head. Yet there is a considerable variation in the receptor spacing and receptor field width across the eye; the values of both parameters markedly decrease towards the front, forming a fovea near the centre of the binocular field.

While the previous study primarily dealt with the regional differences in the photoreceptor performance in the mantis eye, the aim of this investigation is to analyse its functional organisation, particularly with respect to the visual responses mentioned above. It is shown how accurately Tenodera utilizes its fovea while fixating and tracking potential prey. The regional differences in sensitivity across the eye to the different types of visual responses has also been studied. Corresponding measurements on monocular animals have been included as part of the analysis of the interactions between the two eyes. Next, efforts have been made to clarify the interactions between foveal and peripheral movement effects of the retinal image pattern by varying the target and background characteristics. Finally, the comparison of observations under controlled experimental conditions and natural conditions provides a deeper understanding about the way the eyes operate in the normal behavioural context.
The praying mantis is particularly well suited for the analysis of fixation and tracking phenomena. In fact, as an essential prerequisite for a successful strike, the accurate localisation of small, highly mobile prey is the primary visual task of these predaceous insects. Thus mantids have not only highly sophisticated fixation and tracking abilities but corresponding responses are also easily evoked when the experimenter confronts hungry animals with a fly, a cockroach or other adequate prey. Moreover mantids are sedentary; they usually lie in ambush and follow potential prey mainly by movements of the head and the thorax. The visual behaviour is consequently easy to monitor even on unrestrained animals in a natural setting.

Some aspects of the fixation and tracking behaviour in mantids have already been described by Mittelstaedt (1957), Levin and Maldonado (1970) and Lea and Mueller (1977). Other researchers examined the prey characteristics which release and control the strike (Rilling et al., 1959) and studied the role of binocular vision for the absolute localisation of objects in space (Maldonado and Levin, 1967; Maldonado and Barrós-Pita, 1970; Barrós-Pita and Maldonado, 1970; Maldonado et al., 1970; Maldonado and Rodriguez, 1972).
II. METHODS

1. Animals

The experiments were performed on adult and late nymph females of the large mantis *Tenodera australasiae*. The same species has been used in the previous study (Part A). The animals were collected in the vicinity of Canberra or Bundaberg, kept individually in in- or outdoor cages until use, and fed on a limited diet of 1 or 2 flies every second day. Mantids selected for the experiments were not fed for several days. This proved to be important because only hungry animals responded in a satisfactory manner to visual stimulation.

2. Experimental procedure

The visual behaviour was observed on mantids (adults only) fixed by the back of the thorax to a plastic holder, so that they could only move the head, and on animals (adults and late nymphs) allowed to walk freely on a vertical surface.

a) Fixed mantids

The mantids were fixed in the centre of a translucent glass globe (Philips) with a radius of 15 cm (Fig. 1). The globe was illuminated from outside by a number of lamps which provided a diffuse and homogeneous illumination inside. In order to get an idea of the light conditions inside the test arena the following measurements were performed: The globe was covered with a piece of black tissue, leaving only a square 3 x 3 cm on the
Figure 1

Diagram of the apparatus used to study the fixation and tracking behaviour of fixed mantids. The animal is centered in a translucent glass globe with a radius of 15 cm. Holes at the top (15°) and along the equator (7°, 10°, and 15°) of the globe allow the observation of the praying mantis by means of a closed circuit television set-up \((C_1, M_1; C_2, M_2)\). \(C_1\) is horizontally fixed to the platform which carries the globe and both can be rotated either by hand or by motor \((E_1)\) around the mantis which is fixed relative to the base plate. The target is represented either by the lens of the camera or by a living cockroach \((T_1)\) in front of it. The mantis platform can be rotated thus enabling a target presentation in any plane relative to the animal. The eye region used to fixate the target is determined from prepared maps which express the relationship between visual axes of the ommatidia in the centre of the pseudopupils \((S, S')\) and markers in defined positions along the border of the eye \((AB, A'B')\) in facet coordinates \((z, x)\) (see \(M_1\)). The camera mounted in a vertical position is used to study the tracking of a target \((T_2)\) which can be moved by motor \((E_2)\) at various velocities. A thin fibre projects from the target to a point 2 cm above the mantis head showing the direction of the target on the monitor \((M_2)\). Head and target directions are measured relative to the longitudinal axis of the thorax.
equator of the globe exposed to the external illumination. Next a spectroradiometer (In 790, International Light, Inc.) was mounted in the centre of the globe and directed towards the illuminated area. The photon flux/cm²/°/nm/°/arc (steradian) was then measured as a function of the wavelength, starting from 250 nm and proceeding in 10 nm steps up to 650 nm (Fig. A1). Finally, the function was integrated over the given wavelength interval, resulting in a total of 1 x 10⁵⁹ photons/cm²/°/nm/°/arc (steradian). It should be noted that this was not the reflected radiation from the globe itself, which during the experiments was also affected. A disrupted background was produced by the black stripes, random dot pattern, and dots from the natural habitat of the mantis, to the inner surfaces of the globe. The globe was orientated in the horizontal plane extending 20° and 8° holes along the equator at 10°, 15°, and 15° through which the polarisation of the stimulus could be observed by means of a gelled circular polariser set-up (C₁, M₁, C₂, M₂) (Fig. 1). The camera was either in a horizontal position or tilted 45° upwards on C₁. C was fixed to the platform which carried the globe and both could be rotated by hand or by motor (M₁) around the mantle, which was fixed relative to the base plate. The 0° direction of the optical axis of the camera lens coincided with the median plane of the mantle thorax.

Using a stereolens (Nikon 10x) in combination with bellows, the frontal area of the mantis head filled nearly the whole screen of the TV monitor (M₂). The
equator of the globe exposed to the external illumination. Next a spectroradiometer (JL 780, International Light, Inc.) was mounted in the centre of the globe and directed towards the illuminated area. The photon flux/cm²/sec/sr (steradian) was then measured as a function of the wavelength, starting from 350 nm and proceeding in 10 nm steps up to 650 nm (Fig. 2). Finally, the function was integrated over the given wavelength interval resulting in a total photon flux of $1.5 \times 10^{14}$ photons/cm²/sec/sr. Note that this value does not include the reflected light from other parts of the globe which during the experiments was also effective. A disrupted background was provided by sticking black stripes, random dot patterns or grass from the natural habitat of the mantis to the inner or outer surface of the globe. The globe had a hole at the top extending $15^\circ$ and 3 holes along the equator extending $7^\circ$, $10^\circ$ and $15^\circ$ through which the behaviour of the animals could be observed by means of a closed circuit television set-up ($C_1$, $M_1$; $C_2$, $M_2$) (Fig. 1). The camera was set either in a horizontal position ($C_1$) or in a vertical position ($C_2$), $C_1$ was fixed to the platform which carried the globe and both could be rotated by hand or by motor ($E_1$) around the mantis which was fixed relative to the base plate. The $0^\circ$ direction of the optical axis of the camera lens coincided with the median plane of the mantis thorax.

Using a macrolens (Nikkor 105 mm) in combination with bellows, the frontal area of the mantis head filled nearly the whole screen of the TV monitor ($M_1$). The
small sharp pseudopupils (8.0') were clearly visible, as were the tiny coloured dots glued at the border of the eye of A7A', at the ocularia, applied beside the antennae which are used as a reference point to count the facet rows ($x = 0, y = 0$), and at 9, 9.1 30 degrees below (for details of the facet model see Par. A).

The pseudopupil is always directed towards the observer, no matter how the head is turned, because the visual axis of the ocularia at the centre of the pseudopupil coincides with the optical axis of the lens. Therefore, when a small object is placed in front of the animal and the head is turned to the left, the pseudopupil will always be seen in the same region of the field of view as if the eye remained stationary. However, the image in the pseudopupil of an object, no matter how the eye is turned, could not be resolved by the eye. Therefore, an indirect method had to be used to define the position of pseudopupil in facet coordinates. Starting from the reference point A (left eye on monitor I, every 3° in the anterior eye region of bee animals was marked), a holder which carried the sample was rotated in the apparatus so that the marked facet after whether was centered in the pseudopupil. In each pseudopupil position the head was photographed from monitor I and the ratios $A8/A7'$, $A8'/A7'$ and $A8/A7$ were determined for the corresponding marked facet. Finally, the ratios for all marked facets were plotted. $A8/A7'$ versus $A8'/A7'$ and $A8/A7$ versus $A8'/A7'$. 

**Figure 2**

Light conditions in the centre of the test arena shown in Fig. 1. The photon flux, measured as a function of the wavelength, is given in photons per cm$^2$ per second per steradian.
small sharp pseudopupils (S,S') were clearly visible, as were the tiny coloured dots glued at the border of the eye; at A,A' at the cuticular nipples beside the antennae which are used as a reference point to count the facet rows (z = 0, x = 0), and at B,B' 30 z-rows below (for details of the facet mosaic see Part A).

The pseudopupil is always directed towards the observer no matter how the head is turned, because the visual axis of the ommatidia at the centre of the pseudopupil coincides with the optical axis of the lens. Therefore, when a small target is presented in front of the camera, and the mantis turns its head to fixate it, the pseudopupil phenomena provides a unique opportunity to observe eye movements and to measure the fixation region of the eye in facet coordinates. Single facets, however, could not be resolved by the television camera, so that an indirect method had to be used to define the position of pseudopupils in facet coordinates. Starting from the reference point A (left eye on monitor 1), every 5th facet in the anterior eye region of two animals was marked with a white dot which could easily be recognized on the monitor. The head was fixed to the body. Next the holder which carried the mantis was rotated in the apparatus so that one marked facet after another was centered in the pseudopupil. In each pseudopupil position the head was photographed from monitor 1 and the ratios AS/BS, A'S'/B'S' and AS/A'S' were determined for the corresponding marked facet. Finally the ratios for all marked facets were plotted, AS/A'S' versus AS/BS and AS/BS versus A'S'/
B'S'. Ratios of intermediate facets were estimated by interpolating the ratios of neighbouring marked facets. As a result, charts were available which allowed the determination of which ommatidia in the binocular eye region were looking towards the camera.

Note that there is some variability between individual animals with respect to the number of ommatidia. This leads, for example, to individually different positions of the forward looking ommatidia (borderline of the binocular field) when measured in facet coordinates (Part A). Therefore, the two animals, which were used for the preparation of the charts mentioned above, were carefully selected so that the borderline of the binocular field crossed the facet with the coordinates $z = -10, x = 25$ as in the eye maps of the interommatidial angles, acceptance angles and facet diameters presented in the previous study. This correspondence was important because the behavioural findings are to be compared with the maps of the eye parameters.

A transformation of facet coordinates into angular coordinates was obtained from eye maps of the interommatidial angles similar to the ones presented in the previous study. Due to the small interommatidial angles and the large facets in the anterior eye, the position of the pseudopupils and therefore the position of the head could be measured with an accuracy of $1^\circ$ with respect to a reference facet on the borderline of the binocular field.

The method of measuring pseudopupil positions was used
mainly to determine the eye region which fixates targets presented in different positions in the visual field. The target was sometimes merely the front lens of the camera itself, which was seen by the mantis as a black spot against a bright background after a white shutter, placed between the lens and the globe, had been opened. After the mantis had turned the head, a photograph was taken from the monitor in order to determine the pseudo-pupil positions. Then the shutter was closed and the camera (with the globe!) was moved into a new position by steps ranging between $20^\circ$ and $90^\circ$. Altogether 21 target positions $10^\circ$ apart were considered in a horizontal plane. With respect to the praying mantis the target presentation was in an anterior-lateral, dorso-ventral or intermediate plane depending on the rotation angle of the platform which carried the animal. Living targets which moved their body parts proved to be much more attractive than a plain black dot represented by the lens of the camera. Therefore a cockroach ($T_1$) which was mounted on a second shutter between the lens and the globe could additionally be presented until the mantis moved the head.

A different presentation of the target was employed to measure the saccade probability as a function of the position of the target relative to the head. A cockroach was fixed to a metal rod which could be moved on a slider pointing horizontally towards the $7^\circ$ hole in the equator of the globe. After the shutter had been opened the target was pushed forward from 15 cm (edge of the
globe) to 12 cm with respect to the mantis head and then backwards again all within 3 sec. The mantis was observed from above. The choice of target positions followed a random pattern.

For all tracking experiments the camera was positioned above the animal (C₂) and oriented so that the longitudinal axis of the thorax always pointed in a vertical direction on the monitor (M₂). A cockroach (T₂) mounted on a white painted metal rod which also carried a thin glass fibre to a point 2 cm above the mantis head, was moved by a motor (E₂) at various velocities in the horizontal plane. Target and head movements were recorded and later analysed frame by frame at 20 ms intervals by measuring the head position (given by midline of the head) and the target position (given by the direction of the glass fibre) relative to the longitudinal axis of the thorax.

In addition, some continuous recordings of head movements were obtained using the movement recorder described by Sandeman (1968).

b) Freely moving mantids

Mantids were allowed to move freely on a vertical grid (18cm x 25cm) which was part of the broad side of a plexiglass box (12cm x 40cm x 40 cm). The box was placed in the laboratory window usually exposed to direct sunlight. The background was provided by dry and green grass collected from the natural habitat of the mantis and arranged in and around the plexiglass box.
The visual behaviour of the mantids towards moving flies was then recorded by means of closed circuit television. On some occasions the flies were allowed to move freely, on other occasions they were fixed onto a thin wire and moved by hand or a motor drive. The camera was fixed to a tripod which could be moved parallel to the plexiglass box, keeping the optical axis of the lens perpendicular to the walking plane of the praying mantis. Attempts were made to keep the head and thorax of the mantis on the edge of the camera's recording area so that the mantid's frontal visual field, visible on the TV monitor, had a diameter up to 15 cm. Angular parameters, such as the position of the target relative to the mantis, and the head and body orientation of the mantis, were related to the vertical axis of the vertical walking plane of the test arena and could be measured to an accuracy of about $\pm 1^\circ$, providing that the median plane of the head and the body were perpendicular to the walking plane. Tracking runs which did not satisfy this condition were excluded.
III. RESULTS

A. Fixation

1. Saccadic head movements

The praying mantis fixates attractive objects in its visual surroundings primarily by means of rapid saccadic turns of the head (Fig. 3) (Mittelstaedt, 1957; Levin and Maldonado, 1970; Lea and Mueller, 1977). As in other animals, the saccadic movements in mantids are ballistic events; this means that once a saccade is initiated it follows a predetermined course. In mantids, evidence for this characteristic is based on the observation that the final head orientation is the same whether the target is removed immediately before or during the execution of the saccade, or whether the target is still present after completion of the saccade (Lea and Mueller, 1977). Own measurements confirm this observation. In addition it could be shown that displacement of the target during the saccade also does not affect its preprogrammed excursion. It was arranged for the target to move off with constant angular velocity (230°/sec - 270°/sec) in a lateral direction after it was initially presented for a fraction of a second in a stationary position between 45° and 60° away from the mid-line of the head. From a great number of trials 6 saccades (2 examples are shown in Fig. 3b) coincided with the onset of the target movement and the subsequent analysis showed that on the average these saccades stopped 4° short of the stationary target position which was realized before the head started to move, but 25° short of the moving target.
Figure 3a and b

a) Continuous recording of the time course of two saccadic head movements which fixate targets presented 35° and 15° in the lateral visual field. b) 3 saccades analysed frame by frame from the TV monitor. The first saccade is towards a stationary target, the two others towards a target which moved off with constant velocity during the execution of the turn. Note that the saccades only correct for the position of the target realized before the head started to move.
Table 1

Comparison of (i) peak angular velocities of saccades with their amplitudes, (ii) peak angular velocities of saccades in the presence of either a homogeneous or disrupted background and (iii) the angles the saccades fell short of target when the head moved against a homogeneous or disrupted background respectively. The target was presented at 30° and 65° in the lateral visual field. It evoked saccades with amplitudes ranging from 25° to 35° and 55° to 70° respectively, providing that the mantis was initially looking straight ahead. The disrupted background consisted of a vertically-oriented, black and white striped pattern (stripe width = 7°). Movements of the background evoked strong optokinetic responses (see below).

<table>
<thead>
<tr>
<th>Saccade amplitude</th>
<th>Saccade peak angular velocity</th>
<th>SD</th>
<th>n</th>
<th>Final head position short of target</th>
<th>SD</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>homogeneous</td>
<td>25° - 35°</td>
<td>470°/s</td>
<td>95°/s</td>
<td>20</td>
<td>3°</td>
<td>3.1°</td>
</tr>
<tr>
<td>background</td>
<td>55° - 70°</td>
<td>560°/s</td>
<td>85°/s</td>
<td>20</td>
<td></td>
<td></td>
</tr>
<tr>
<td>disrupted</td>
<td>25° - 35°</td>
<td>480°/s</td>
<td>90°/s</td>
<td>20</td>
<td>3.6°</td>
<td>3.5°</td>
</tr>
<tr>
<td>background</td>
<td>55° - 70°</td>
<td>550°/s</td>
<td>75°/s</td>
<td>20</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
at the instant the saccades were completed. In control measurements (Fig. 3b), where the target has not been displaced, the average undershoot was $3^\circ$ which is not significantly different from the $4^\circ$ measured above.

The peak angular velocities and durations of saccades are positively correlated with the saccade amplitude. There is no significant difference in peak angular velocities and final head positions when the eyes move against either a homogeneous or disrupted background (Table 1).

2. The fixation region of the eye

Under the experimental conditions presented in Fig. 1, the angular range over which a target can be fixated is limited, partly because the animal is fixed by its thorax to the centre of the test arena. It is important, therefore, to determine the point of fixation in the environment of the fixed animal from which head movements are most easily made in all directions, and in doing so, to determine the fixation region of the eye. The fixation point in the environment mentioned above obviously lies in the median plane of the animal and the target was consequently first presented here. The target position was related to the longitudinal axis of the thorax ($p' = 0^\circ$; upward positions are positive, downward positions negative; Fig. 4a) and the retinal locations which centre the target in 20 different positions covering a range of $190^\circ$ (from $p' = +60^\circ$ to $p' = -130^\circ$) were determined in facet coordinates (see Sect. II.2.a). The frontal eye projection of the left eye presented in Fig. 4b illustrates the results. The retinal locations which come
The fixation region of the eye and the fixation point in the environment of the restrained animal from which head movements are most easily made in all directions. The target was presented first in the dorso-ventral plane of the mantis at 20 different positions each 10° apart. The positions are related to the longitudinal axis of the body (p' = 0°, Fig. a). The eye locations which centre the target in each position are then expressed in facet coordinates as shown in a frontal eye projection of the left eye in Fig. b. Over a large range of target positions (p' = 0° to p' = -90°) the fixating facets are concentrated in a small area which apparently represents the preferred fixation region of the eye. Its centre has the facet coordinates z = -12, x = 25. Next the angular separation (e) of fixating facets is plotted versus the target position (p') (Fig. c). The point of fixation in the environment from which head movements are most easily made in an up and downward direction is defined as the point from which object fixation 90° above and 90° below results in the smallest possible angular separation of the two facets involved. This point is 42° below the longitudinal axis (p' = -42°). The point p' = -42° gets the new specification p = 0° (Fig. a, c). In Fig. d the angular separation (e) of fixating facets is plotted versus the different positions of a target which has been presented in the anterior-lateral plane of the animal containing p = 0. Finally, Fig. c and d also include the standard deviation of the scatter of individual fixation points for each target position. Standard deviations have been calculated along z-rows (dotted lines) and x-rows (solid lines) of the facet mosaic.
to bear on the target in the different positions are scattered along the median plane at the eye (border line of the binocular field). Yet for a large range of target positions (from about $p' = 4^\circ$ to $p' = 24^\circ$) the fixation facets are concentrated in a small area which apparently represents the preferred fixation region of the eye. The centre has the facets coordinates $x = 3$ and coincides with the eyes as shown below. Targets presented at extreme by or downward positions ($90^\circ, p = -60^\circ$, $p = -90^\circ$) are still looked at, but there is a fixation area with respect to the fixation centre of the eyes. This is demonstrated by plotting the target position $x$ and $y$ at $p' = 42^\circ$, $p = 90^\circ$ and $p = -90^\circ$ (Fig. 4b). As the head movements are possible only in the horizontal plane which fixate targets in these two positions are separated by the smallest possible angle. According to Fig. 4b, the point of interest is at $42^\circ$ below the longitudinal axis of the body. Note that in all following considerations the target position $p' = 42^\circ$ has the new specification $p = 90^\circ$ (Fig. 4c, d), i.e. the target positions are now related to this newly defined reference point. Target positions upward from $p = 90^\circ$ are positive, lower positions downward from $p = 90^\circ$ are negative. $p = 90^\circ$ also defines the reference point above which, in general, targets are fixated.
to bear on the target in the different positions are scattered along the median plane at the eye (border line of the binocular field). Yet for a large range of target positions (from about \( p' = 0^\circ \) to \( p' = -90^\circ \)) the fixating facets are concentrated in a small area which apparently represents the preferred fixation region of the eye. Its centre has the facet coordinates \( z = -12; x = 25 \) and coincides with the fovea as shown below. Targets presented at extreme up or downward positions (e.g. \( p' = +60^\circ \), \( p' = -130^\circ \)) are still looked at, but there is a fixation error with respect to the fixation centre of the eye. This is also demonstrated by plotting the angular separation \( (e) \) of the visual exes of the fixating facets along the median plane of the eye as a function of the target position \( (p') \) as in Fig. 4c. In addition, the resulting graph has been used to define the point of fixation in the environment from which optimum head movements are possible in an up and downward direction. It is the point from which object fixation \( 90^\circ \) above and \( 90^\circ \) below involves the smallest possible eye region, or in other words, the visual axes of the facets which fixate targets in these two positions are separated by the smallest possible angle. According to Fig. 4c the point of interest is \( 42^\circ \) below the longitudinal axis of the body. Note that in all following considerations the target position \( p' = -42^\circ \) has the new specification \( p = 0^\circ \) (Fig. 4a, c), i.e. the target positions are now related to this newly defined reference point. Target positions upward from \( p = 0^\circ \) are positive, target positions downward from \( p = 0^\circ \) are negative. \( p = 0^\circ \) also defined the reference point when
the target was presented in an anterior-lateral plane of the mantis so that a target $90^\circ$ to the left or $90^\circ$ to the right has the specification $p = 90^\circ$. Fig. 4d shows the result of head movements which have been evoked by targets presented in this anterior-lateral plane. Again there is a slight error in fixation of targets deviating considerably from the favourable position $p = 0^\circ$. The saccade direction relative to $p = 0^\circ$ has little effect on the final head position. Thus head movements away from $p = 0^\circ$ may undershoot the target by the same amount as turns towards $p = 0^\circ$ overshoot the target. The retinal locations which are centered on the target in various positions as in Fig. 4b, c and d represent average values of 10 to 15 head movements to each target position. The standard deviation of the angular scatter of the individual fixation points of the eye with respect to each target position has also been calculated along the z-facet rows (dotted lines) and along the x-facet rows (solid lines) and is included in Figs. 4c and d.

The effect of target size on the accuracy of fixation has been tested by presenting alternatively targets subtending $7^\circ$, $10^\circ$ and $15^\circ$ at various positions (from $p = 0^\circ$ to $p = 90^\circ$) in the anterior-lateral plane (Fig. 5). It appears that the scatter of the individual fixation points is slightly greater for larger targets (Fig. 5a). Generally, however, the scatter is small and if one locates, from a number of head movements, the points on the target which come to lie on the fixation centre of the eye (Fig. 5b), it becomes quite clear that the mantis tries to centre the target as a whole and not its edges.
3. The saccade probability

The probability of the occurrence of a saccade depends on the position of the target image on the retina (Fig. 6). Targets presented in the fixation centre rarely provoke saccadic head movements independently of the head orientation relative to the body. Increasing target displacement in the anterior-lateral and dorso-ventral direction increases the saccade probability and maximum is reached in an eye zone at 20° to 40° from the fixation centre. Beyond this range the saccade probability function drops off. With respect to two distinct planes, target positionally, head movements are evoked if the target deviates from the fixation point in either of the visual fields. The saccade probability functions are very similar when binocular (Fig. 6a) and monocular (Fig. 6b) animals are compared.

Figure 5a and b

a) Standard deviation of the scatter of individual fixation points of the eye with respect to 10 target positions (p = 0° - p = 90°) in the anterior-lateral plane of the mantis and 3 different target sizes subtending 7°, 10° and 15°. Dotted lines: SD-values along the z-facet rows, solid lines: SD-values along the x-facet rows. b) A number of head movements have been evoked by targets which were laterally positioned at p = 30° and subtended three different angles (7°, 10° and 15°). The dots on the targets mark the intersections of the direction of view of the fixation centre of the eye after completion of the saccadic movement.
3. The saccade probability

The probability of the occurrence of a saccade depends on the position of the target image on the retina (Fig. 6). Targets presented in the fixation centre rarely provoke saccadic head movements independently of the head orientation relative to the body. Increasing target displacement in the anterior-lateral and dorso-ventral direction increases the saccade probability and a maximum is reached in an eye zone about 20° to 40° from the fixation centre. Beyond this range the saccade frequency drops again. Although detailed saccade probability functions have been measured with respect to two distinct planes of target position only, head movements can be elicited for any direction of target deviation from the fixation centre. The most sensitive eye region is within the binocular field. But remarkably enough the values of saccade probability and the shape of the saccade probability functions are very similar when binocular (Fig. 6a, b) and monocular (Fig. 6c, d) animals are compared. Therefore it can be concluded that the fixation zone of each eye is encircled by a zone which generates saccades, or in other words the fixation zone is the eye region with a lower probability of producing saccades than the rest of the eye.

Without affecting this central finding, many factors influence the absolute values and shape of saccade probability functions, notably the motivation of the animal and the characteristics of the target. Most unpredictable is the motivation factor. Generally head movements
Figure 6a - d

Saccade probability as a function of target deviation from the fixation centre (0°). Binocular (a, b) and monocular (c, d) animals fixated targets presented in the anterior-lateral (a, c) and dorso-ventral (b, d) plane.
occurred only when the mantis was in a state of hunger, i.e. not fed for several days. Some animals then displayed 50 or more saccades; others habituated earlier and it was up to the experimenter to interrupt the measurements when the responsiveness diminished. Objects subtending an angle of approximately $10^\circ$ are more attractive than larger or smaller ones (Maldonado and Rodriguez, 1972). Target size could affect the shape of the saccade probability function in the sense that larger targets presented close to the fixation centre, and possibly including it, are less frequently centred than smaller ones in corresponding positions. A flickering circular black dot of $10^\circ$ presented in the eye region which is most effective in initiating saccades produced them with a frequency of less than 0.2. There was no significant difference when the circular black dot moved with constant velocity to and fro over an angular range of $10^\circ$. The saccade frequency increased to 0.4 when the target was a stationary living cockroach which moved its body parts in a characteristic manner, and an additional increment of 0.2 units was observed when the cockroach was moved by hand, describing lateral jerky movements (maximum amplitude $10^\circ$). The most effective stimulus and the one used to determine the saccade probability functions was a living cockroach moved towards the mantis, thus increasing its visual angle equally from $7^\circ$ to $10^\circ$ in all directions (see Sect. II.2.a). In all these measurements the target was visible for 3 seconds and the interval between successive target presentations was about 30 seconds or more. A longer presentation of the target naturally increases the saccade frequency but to some extent
the interval between successive target presentations is also important. Ten or more saccades could sometimes be elicited in a row when the target appeared in short time intervals of approximately 1 second, which might indicate that for some time after a saccade has been completed the threshold for a following one is decreased.

4. The retinal position of fovea, fixation centre and saccade sensitive surround

The characteristics of the mantis fovea have been described in detail in Part A. Measurements from this study have been used to demonstrate the regional variation of the interommatidial angle ($\Delta \phi$) and the acceptance angle ($\Delta \rho$) in the frontal projection of the right eye shown in Fig. 7a. Both parameters range from less than 0.7° in the anterior eye to more than 2° in the periphery. The facets which centre the target at $p = 0^\circ$, $p = 60^\circ$ and $p = 90^\circ$ in the anterior-lateral, dorso-ventral and intermediate plane are plotted in a frontal projection of the left eye (Fig. 7b). Assuming that the absolute values and the shape of the saccade probability functions (Fig. 6) are not confined to the two planes of target presentation examined, Fig. 7c is a map of the regional differences of the saccade probability across the left eye.

In comparing the eye charts in Fig. 7 we find a good correlation between the fovea and the fixation centre. In addition, the following points should be noticed: When measuring the saccade probability in monocular animals it became clear that saccades in either eye centre the target
a) Frontal projection of the right eye demonstrating the decrease of the interommatidial angle (solid lines) and the acceptance angle (dotted lines) towards the anterior region, forming a fovea near the centre of the binocular field. The thick line which crosses the frontal eye in a vertical direction covers the ommatidia whose visual axes are parallel to the median plane of the head (borderline of the binocular field) (Part A). b) Facets of the left eye which centre a target which was located at $p = 0^\circ$, $60^\circ$ and $90^\circ$ in the anterior-lateral, dorso-ventral and intermediate plane. The dotted lines mark the outline of a circular target image subtending an angle on the eye surface of $5^\circ$ and $10^\circ$, respectively. c) Regional differences of the saccade probability across the left eye based on the data presented in Fig. 6. Isolines connect eye points which produce saccades with the same probability. Note the correspondence of fovea (a) and fixation centre (b, c).
on the most forward looking ommatidia. Although the target appeared at considerable distance from the mantis eye (12 to 15 cm) one might suppose that this result is the same when the target is presented closer to the eyes. On the other hand, binocular mantids possibly attempt to centre the target in the median plane of the head. In this case the retinal position of the fixated target would also depend on its distance because the eyes are widely separated. Note, however, that fixation in the median plane is only possible when the target appears within the binocular field. This is because saccades are ballistic responses, so that the eyes must interact before the execution of the saccade (see Sect. IV.7.).

B. Tracking

Depending on the features of the background and to some extent on the type of movement of the target, mantids can display smooth or saccadic tracking, as demonstrated in the following sections.

1. Smooth tracking

Smooth pursuit head movements are mainly employed when a target moves against a homogeneous background (Fig. 8). A closer examination, however, reveals that the head movements are not entirely smooth but may also include small amplitude jerks (Fig. 8a). The relative contribution of smooth and jerky components recorded under constant stimuli conditions differs from one tracking run to another. The frequency and amplitude of jerks appears to increase with
Figur~ 8

Targets travelling in an otherwise homogeneous environment are tracked by smooth head movements. Note that the latter may also include small amplitude jerky components (a). Tracking runs over large angular ranges have been examined relative to targets moving with different velocities in the dorso-ventral plane (b) and anterior-lateral plane (c, d, e) containing $p = 0^\circ$. Saccades are marked with short arrows.
increasing head velocity but this has yet to be properly explored. Jumps are not induced by the weight of the eyes stuck to the head to record its movement with the head, but by the movement of the eyes' image on the retina.

At an apparent range of 20°, the mantis was moved after it had been fixated by a decade. As the mantis moved forward from 20° to 0° to 0°, it was fixated on the target. The data shown was taken from a target with a velocity of 8°/s, 12°/s, 35°/s, and 95°/s. During the experiment, the mantis was fixated on the target, which was displayed on a distinct small amplitude jump, which was obviously not able to keep the target in the fixation period.

The mantis was positioned for instance to the right of the target. The data shown was taken from a target with a velocity of 8°/s, 12°/s, 35°/s, and 95°/s. During the experiment, the mantis was fixated on the target, which was displayed on a distinct small amplitude jump, which was obviously not able to keep the target in the fixation period. The mantis was fixated on the target, which was displayed on a distinct small amplitude jump, which was obviously not able to keep the target in the fixation period.
increasing head velocity but this has yet to be properly explored. Jerks are not induced by the weight of the wire stuck to the head to record its movement with the capacitor device, nor by the movements of the body parts of the cockroach because they can also be observed directly on the monitor when the unloaded head follows a dead target or a striped pattern.

Head movements following the target over large angular ranges have been examined for a variety of target speeds (Fig. 8b, c, d). The target, initially positioned at $p = 0^\circ$ or $p = 90^\circ$, was moved after it had been fixated by a saccade. At low target velocities there can be considerable angular ranges over which the head closely follows the target, but for higher target velocities the head lags increasingly behind the target and saccades are periodically required to reduce the error angles. The saccade frequency also appears to increase when the target does not move with constant velocity as for instance a freely running fly or cockroach. The fact that positional corrections are not accomplished by smooth head movements provides a first indication that the smooth tracking is primarily a response to the target velocity rather than to its position. In this context it is important to note that the small amplitude jerks observed during smooth tracking are not microsaccades in the sense of correcting position errors relative to the fovea. In the tracking run presented in Fig. 8e, for instance, the mantis displayed very distinct small amplitude jerks, which were obviously not able to keep the target in the fixation centre so that the increasing error angle had finally to be corrected
Optokinetic responses have been evoked by vertically-oriented, horizontally moving striped patterns (pattern wavelength = 14°). The pursuit responses are periodically interrupted by fast movements which realign the head with the body (a) or a stationary target (cockroach) laterally positioned (b).
by a saccade.

Smooth head movements with similar characteristics are also part of the typical optokinetic response when the animal follows movements of the whole visual surroundings (Fig. 9). The pursuit responses are periodically interrupted by fast movements which realign the head with the body (Fig. 9a), but the fast phase can also be directed towards stationary attractive objects positioned anywhere (Fig. 9b). There is, however, a difference in that the fast phases directed towards the midline are often considerably slower, than fast phases which refixate a target (Fig. 9a, b).

Eye regionalisations: Moving targets elicit smooth pursuit responses only when the target image projects on to the fovea. Details of the regional characteristics of the smooth tracking system have been examined by measuring the ratio of head to target angular velocity as a function of the target position with respect to the fixation centre of the eyes. Note that the ratio of head to target angular velocity examined in this study, defines the overall (closed loop) gain of the system, in contrast to the forward (open loop) gain which relates the slip velocity of the retinal image to the resultant eye velocity (e.g. Carpenter, 1977).

A living cockroach subtending an angle of about 10° was oscillated with constant velocity (10°/sec) and amplitude (10°) at varying positions in the anterior-lateral plane and dorso-ventral plane. The average angular velocity of head and target was then measured for a medium range of the head
and target oscillations.

As expected, the eye region with the highest overall gain (the eye velocity is close to that of the target) coincides with the fixation zone. Beyond this range the gain drops sharply and no head movements have been obtained when the target image moved beyond 35° from the fixation centre. Note that the gain of the smooth tracking system also depends on the velocity of the target but this has not been quantified in this study. Gain profiles for smooth tracking responses are essentially the same for binocular (Fig. 10a, b) and monocular (Fig. 10c, d) mantids. Yet in all monocular animals tested the gain function obtained from target positions and movements in an anterior-lateral plane were slightly shifted towards the lateral eye. Combined with the spatial separation of the two eyes, this provides a wider range of high gain for binocular mantids and this might explain the observation that monocular animals always used more saccades when tracking targets over large angular ranges. Monocular animals also performed worse in other respects. Many could not stabilize the head in the rotational plane of the target and the tracking movements were accompanied by head rotations around the head-target axis which quickly caused loss of the target.

The fact that the head moves in phase with the target, independently of its position within the fovea, provides further evidence that smooth tracking is a response to the velocity of the target. The difference between smooth head movements and saccades which correct position errors relative
Regional differences in the overall gain (ratio of head to target velocity) of the smooth tracking system (bell-shaped graphs). The gain is plotted versus the average position of the oscillating target relative to the fixation centre (0°). Head movements of binocular (a, b) and monocular (c, d) animals have been considered. The target was positioned and oscillating in the anterior lateral (a, c) and dorso-ventral (b, d) plane. The saccade probability functions (Fig. 6) have been plotted again to demonstrate the power of the peripheral eye to evoke saccadic head movements, in comparison to the fovea which evokes smooth tracking movements.
to the centre of the fovea can best be demonstrated when a target out of the centre of the fovea moves towards or away from the centre. If the initial fixation deficiency is between $10^\circ$ to $15^\circ$, the target image falls within an eye region capable of generating both types of head movements (Fig. 10). Target movements towards the centre of the fovea then either cause a saccade, which throws the head towards the target thus reducing the position error, or the head moves smoothly in the opposite direction thus reducing the velocity error. Target movements away from the fovea may also induce smooth head movements but the latter can only match the velocity of the target and the initial positional error again has to be corrected by a saccade.

A larger eye region is involved in the optokinetic responses that are evoked by movements of the large field background. No, or only minor, head movements can be evoked when a striped pattern (stripe width = $7^\circ$) which oscillates with constant velocity ($10^\circ$/sec) and amplitude ($10^\circ$) stimulates the back region of the eye (Fig. 11a). However, using the ratio of head to target velocity as a measure of the overall gain of the optokinetic system, we note that the response increases when the pattern covers more and more of the anterior eye region. The specific regional effect is evident because 3 black stripes presented in front of the head are sufficient to evoke the same optokinetic response as a disrupted background surrounding the whole eye. The gain profiles are similar in shape and extension when the median plane of the mantis is either parallel or perpendicular to the stripe orientation.
A stationary background has a profound effect on the smooth tracking response to a single moving target in that the ratio of head to target angular velocity declines when the background increasingly occupies the anterior visual field (Fig. 11b). The interaction, however, is not a simple summation of the effects due to the pattern presented by the background in the periphery on the target in the focus, as can be deduced when comparing the responses presented in Figs. 11a and b. Although the homogeneous field of 90° around the target is sufficient to elicit a visible optokinetic response to target movements (Fig. 11a), when a stationary background, without the target, still elicits a visible optokinetic response (Fig. 11b), it is possible that the stationary background tends to "sleep" the head, and decreases smooth tracking responses that would otherwise be evoked by a moving target in the immediate background. Smooth head movements, however, occur without delays, but are unaffected by the background. Figure 11a and b

Regional effect of the background. a) The ratio of head to background angular velocity is plotted as a function of the angular subtense (β) of a frontal homogeneous field bordered by a vertically-oriented, horizontally oscillating striped pattern (wavelength = 14°). Median plane of the mantis is parallel (○) or perpendicular (■) to the striped pattern. b) A target oscillated horizontally (perpendicular to the median plane of the animal) in the frontal visual field. The ratio of head to target velocity is plotted versus the angular subtense (β) of a frontal homogeneous field, bordered by a vertically-oriented, stationary striped pattern (wavelength = 14°). The resulting graph shows that the tracking response weakens when the stationary disrupted background covers increasing parts of the anterior visual field.
A stationary background has a profound effect on the smooth tracking responses to a single moving target in that the ratio of head to target angular velocity declines when the background increasingly occupies the anterior visual field (Fig. 11b). The interaction, however, is not a simple summation of the movement effects induced by the background in the periphery with that induced by the target in the fovea, as can be deduced by comparing the graphs presented in Fig. 11a and b. Although a homogeneous field of 60° around the target is sufficient to evoke a maximum response to target movements (Fig. 11b), movement of the same background, without the target, still causes considerable optokinetic response (Fig. 11a).

2. Saccadic tracking

It has been shown above that a stationary structured background tends to "clamp" the head, and suppresses smooth tracking responses that would otherwise be evoked by a target moving in the foreground. This limitation is overcome by adopting a saccadic tracking strategy. The moving target is tracked using a sequence of saccadic head movements to recentre the target image onto the fovea (Fig. 12). If the background provides a strongly contrasting pattern, only minor head movements occur between neighbouring saccades. Moreover, tracking is still saccadic, and saccades have the same amplitude, when the trajectory of the target is free of contrast in the background. Saccades, therefore, are not induced by masking effects of contrasting elements in the immediate background. Smooth head movements, however, occur
Saccadic tracking in the presence of disrupted backgrounds. A continuous recording is shown in (a). Tracking runs over large angular ranges comprise target movements in the dorso-ventral plane (b) and anterior-lateral plane (c, d) containing $p = 0$. 

**Figure 12a - d**
Figure 13

Comparison of responses to a target subtending different angles depending on its distance from the mantis head and moved in front of either a homogeneous or a disrupted background. Note that there are fewer saccades when the target subtends a large angle because it travels close to the catching distance.
between saccades when the contrast of the background is sparse (e.g. dry grass; Fig. 12c, d) or when the size of the target is increased, for instance, by moving the target closer to the eyes (Fig. 13). Together, a sparse background and a large target may well lead to smooth head movements over considerable angular ranges. The effect of varying the contrast of the backgrounds has not been examined in detail, yet all backgrounds used in this set of measurements were effective enough to evoke an almost saturated optokinetic response.

So far, saccades have been considered to be ballistic position-correcting events (Fig. 3). If this is true, then positional information sampled from a moving target just before the execution of the turn must be out of date when the head reaches its final pre-programmed position. Therefore, a more sophisticated system would include information of the movement of the target (e.g. its velocity) and the performance would be improved by using this movement information to predict the target position at the time the saccade has been completed. Is this what happens during the saccadic tracking in mantids? To investigate this question a number of saccadic tracking responses evoked by targets moving with different velocities have been examined, comparing various parameters such as the error angle ($\alpha_p$) immediately before the head starts to move, the saccade amplitude itself ($\alpha$) and the theoretical saccade size ($\alpha_s$) expected to be generated by a "predictive" tracking system which takes information of the target position and velocity into account (Fig. 14a). All measurements were performed on mantids allowed to
move freely in a natural setting (see Sect. II.2.b) because they were more motivated to track than animals fixed in the test apparatus. Note that freely moving mantids displayed the same tracking behaviour as animals in the test apparatus, i.e. saccadic tracking when the target was tracked against a disrupted background (e.g. grass and other plants) and smooth tracking when the target was viewed against a homogeneous background (e.g. the sky), although only the first case was of interest in this set of measurements. Only those responses have been considered where the body orientation was kept constant so that the head alone was responsible for tracking. This was usually the case when the target moved far beyond the catching distance, so failing to provoke an alignment of the raptorial forelegs (for the latter see the following section). Altogether an approximately equal number of saccade sequences were selected which were directed either towards or away from the median plane of the body. The tracking range was limited to a frontal visual field of 90°. Some saccades have been obtained by using freely moving flies but in most cases the flies were stuck to a thin wire and moved by hand or by motor. Only the latter produced constant target velocities. Where the velocity was not constant the value used was the average velocity measured between successive saccades.

The amplitude of saccades (a) varies considerably for a given target velocity, but generally the amplitude is greater for faster moving targets (Fig. 14b). A relationship can be established between the position error (a_p) existing immediately before the execution of the saccade
Figure 14a - e

Predictive saccadic tracking. The following parameters are compared (Fig. a): the velocity of the target (v), the error angle ($\alpha_p$) which is the angular difference between head and target direction at the instant the saccade starts, the saccade amplitude ($\alpha$) and the theoretical saccade amplitude ($\alpha_s$) expected to be generated by a predictive tracking system which includes the average velocity of the target between consecutive saccades. Results: The average saccade amplitude ($\alpha$) increases with increasing target velocity (v) (Fig. b). Error angles ($\alpha_p$) are positively correlated with the saccade amplitude ($\alpha$) (Fig. c). However, saccade amplitudes ($\alpha$) overshoot the error angle ($\alpha_p$) as a function of the velocity (v) (Fig. d). At least up to target velocities (v) of about 100°/sec, this overshoot is just adequate to bring the fovea on target ($\alpha = \alpha_s$) (Fig. e). Saccadic head movements are directed towards (●) or away (■) from the median plane of the body.
and the decade amplitude of itself (Fig. 14d). The amplitude amplitude, however, increasingly overshoots the position error (\( a_p \)) with increasing target velocities up to about 100°/s (Fig. 14d). Beyond this point the overshoot appears to be constant and possibly decreases again at speeds exceeding 100°/s, but this small amount of data does not allow a firm conclusion. For a calculation necessary to confirm this point, more data are immediately needed. The error amplitude is measured immediately after the resetting of the position of the target large into adequate negative or positive target. The position is indicated as a function of the target velocity. The important point is, however, the amount of overshoots.

In the lower range of the target velocities the target amplitudes were measured as a function of the target velocity. The real position of the target was indicated as a function of the target velocity. The target amplitudes were measured as a function of the target velocity. The position was indicated as a function of the target velocity.

To the natural habitat of the praying mantis, the tracking responses of the praying mantis is adapted, targets are usually seen against a rich visual background. Therefore according to the
and the saccade amplitude ($a$) itself (Fig. 14c). The saccade amplitude, however, increasingly overshoots the position error ($\alpha_p$) with increasing target velocities up to about $100^\circ$/sec (Fig. 14d). Beyond this range the overshoot appears to be constant and possibly decreases again at speeds exceeding $200^\circ$/sec, but the small sample of data does not allow a final judgement on this point. The calculation necessary to transform retinal position of the target image into adequate motor actions presumably requires some reaction time. From this point of view the error angle measured immediately before the start of the saccade presumably overestimates the value actually computed by the saccadic system, and it is obvious that any time delay must increase the overshoot presented in Fig. 14d as a function of the target velocity. The important point is, however, that the overshoot, at least in the lower range of target velocity, is just adequate to allow the saccade to catch up with the target (Fig. 14e) thus providing strong evidence that mantids utilize information about the motion of the target to predict its future position. This information certainly includes the velocity, because predictive tracking is possible with respect to targets moving with uniform speed. It is not yet clear whether accelerations of the target can also be used for predictive tracking because accelerating targets have not been used.

3. Tracking preceding the catching of prey

In the natural habitat to which the tracking mechanism of the praying mantis is adapted, targets are usually seen against a rich visual background. Therefore according to the
findings presented so far, smooth tracking would be little
used under natural conditions. However, stabilisation of
the target image on the retina might be essential for a
successful strike, since this requires an accurate locali-
sation of prey. Measurements on restrained animals showed
that tracking is still dominated by saccades when the target
moves close to the catching distance and a sufficiently
contrasting background is provided (Fig. 13). However, this
finding might be questioned on the ground that the labora-
tory conditions, and in particular the physical restraint
of the animals might have severely affected not only their
natural movements but their general catching motivation as
well. Therefore the tracking behaviour preceding the catching
of freely moving flies has been studied under conditions
which closely imitated the natural setting (see Sect. II.2.b),
but still allowed an accurate measurement of important para-
meters such as the target position and distance relative to
the mantis, and the head and body orientation of the mantis
(Fig. 15). Altogether 26 recordings have been analysed. Two
typical examples and one less frequent but interesting case
are the subject of the following considerations.

24 of the analysed tracking runs were similar in one
way or another to the two examples shown in Fig. 16a and b.
When the fly moved from a lateral position, towards the
median plane of the mantis, the prey was fixated and tracked
mainly by saccadic head movements ($\phi_h$) and caught when it
came within the catching distance, preferably in the frontal
visual field (Fig. 16a). After the initial fixation by a
saccade, there were also body movements ($\phi_b$) which aligned
Figure 15

Parameters used to describe the tracking behaviour of freely moving mantids: $\psi$, position of the target relative to the mantis head; $d$, distance mantis - target; $\psi_h$, head orientation; $\psi_b$, body orientation; $\psi_{h-b}$, angular deviation of head with respect to body. $\psi$, $\psi_h$ and $\psi_b$ are related to the vertical axis ($0^\circ$) in the vertical walking plane.
Two tracking runs, a and b, which preceded the catching of prey.

The measured parameters are explained in Fig. 15. For details see text (Sect. III. B.3).
the raptorial forelegs with the target particularly when the target moved slowly or stopped in a lateral position. Pronounced body movements ($\phi_b$) always made essential contributions to the tracking when the target moved close to the catching distance away from the median plane of the mantis (Fig. 16b). The head then counterrotated relative to the body ($\phi_h-b$) but periodically caught up with the target by means of saccadic movements.

In conclusion, tracking which precedes the catching of prey is also dominated by saccadic eye movements. The stabilization of the target image on the fovea is consequently not a prerequisite for a successful strike.

On two occasions Tenodera approached and caught a resting fly which only occasionally moved its legs or wings. Particulars of one case are given in Fig. 17. A fly landed about 10 cm from the mantis (Fig. 17a, 1), which responded with a saccadic head movement towards the potential prey. During the next 4 minutes (Fig. 17a, 2; b) the mantis slowly approached the fly periodically displaying swaying movements of the body which resulted in translational and rotational movements of the head. A sequence of 10 sec of these swaying movements is shown in Fig. 17c. The translational movements of the head are measured in mm and split into two components, side to side movements (first trace) and back and forth movements (second trace). Note that the actual movement is a superposition of both traces. The third trace demonstrates the rotational movements of the head in degrees. Sometimes the head slightly counterrotated relative to the body.
Figure 17a - f

Approach and capture of a resting fly. For details see text (Sect. III.B.3).
Nonetheless there is a considerable displacement of the retinal image of the target as shown in the fourth trace which has been obtained by combining trace one (side to side movements) and trace three (rotational movements) with the distance of the fly from the mantis head. The occurrence of such eye movement is not dependent on the presence of potential prey. They are also easily evoked when the mantis is placed in a new environment. The described eye movements possibly have similar functions as the scanning movements in jumping spiders (Land, 1969) and the peering movements in locust (Wallace, 1959; Collett, 1978). Scanning has been assigned an important role in identifying objects that have entered the visual field and peering is thought to provide motion parallax information for judging the distance of objects. After the mantis had approached within a distance of about 6 cm the fly started to walk away, visually tracked by the mantis (Fig. 17a, 3; d). The analysis of head and body movements revealed that the saccadic movements of the head relative to the body ($\phi_{h-b}$) are superimposed upon smooth body movements ($\phi_{b}$) (Fig. 17d). The fly finally stopped and the mantis resumed its approach periodically displaying swaying movements of the body (Fig. 17a, 4; e). Fig. 17f shows a sequence of 10 sec. For the meaning of the 4 traces see Fig. 17c. After reaching the catching distance the swaying movements continued for about 1 min before the fly was struck and caught. Interestingly no movements of any sort could be monitored from the resting fly during the last minute preceding the strike. However, motion of the prey is usually important for
the release of the strike. In three other instances mantids lay in ambush in front of the resting fly for minutes at a time and the strike was released only when the fly suddenly took off. Take off is an extremely rapid movement and in all cases the mantis missed the fly.

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1. Detection of prey

Although the range of visual stimuli detected by the peripheral retina of the praying mantis has not been studied in detail, targets which subtend an angle of about 15° (Heldon and Rodriguez, 1977) and describe jerky movements or rapidly approach the eyes are particularly attractive because they resemble potential prey (see Sect. III.A.3). Object detection and localization, however, is not confined to particular movement patterns of the visual stimuli. In fact, stationary, flying, or targets, and therefore signals modulating processes from single retinal points, are sufficient to evoke fixation movements (see Sect. III.A.3) (Lee and Mueller, 1977). The same applied to flies (Pitts, 1974) but apparently not in jumping spiders where motion of the target is essential to evoke a turning response (Land, 1971).
IV. DISCUSSION

The investigation of visually guided eye movements in the praying mantis yielded the following major results:

1. Detection of prey

Although the range of visual stimuli detected by the peripheral retina of the praying mantis has not been studied in detail, targets which subtend an angle of about 10° (Maldonado and Rodriguez, 1972) and describe jerky movements or rapidly approach the mantis are particularly attractive because they resemble potential prey (see Sect. III.A.3). Object detection and localisation, however, is not confined to particular movement patterns of the visual stimuli. In fact, stationary flickering targets, and therefore signal modulation processed from single retinal points, are sufficient to evoke fixation movements (see Sect. III.A.3) (Lea and Mueller, 1977). The same applies in flies (Pick, 1974) but apparently not in jumping spiders where motion of the target is essential to evoke a turning response (Land, 1971;
The need for selectivity in the detecting mechanism in mantids may have its cause in the often difficult conditions under which prey has to be detected. *Tenodera* inhabits grassland and is often found on wild flowers catching bees and other pollinating insects. In frequent windy conditions the environment appears as a complex moving pattern where numerous contrasting elements move rhythmically back and forth. Therefore, to guarantee an economical and efficient behaviour, the detecting mechanism might be expected to distinguish the typical pattern of moving potential prey from moving and flickering parts of the background. Form vision, in the sense of detecting the typical outline of prey, presumably does not play a significant role, if only for the reason that the interommatidial angles are relatively large in the peripheral retina compared with the angular extension of approaching prey. For instance, freely moving mantids sometimes turned the head towards laterally moving flies which subtended an angle of only about $3^\circ$. By comparison the interommatidial angles in the lateral eye are about $2.3^\circ$ (see Part A). A close examination of spatial detail of the target is apparently the function of the fovea and in fact, objects which simulate the typical contour of prey increase the frequency of the strike release (Rilling, Roeder and Mittelstaedt, 1959).

2. Saccadic fixation movements

Rapid saccadic eye movements constitute the basic fixation response in many animals and particularly in those which have a fovea (vertebrates: rev. Fuchs 1971, Carpenter
1977; arthropods: e.g. Land 1971, Collett and Land 1975, Lea and Mueller 1977). Clearly, high response velocity, which in mantids, as in other animals, may reach some hundred degrees per second (Table 1, Fig. 3), is important in bringing newly detected objects as quickly as possible to the fovea for detailed visual analysis. In addition, one may ask to what extent high response velocity helps to overcome the optokinetic reflex which normally prevents movements of the background relative to the eyes, but - as shown in Table 1 - has no significant effect during saccades. Are the eye movements fast enough to make the background image sufficiently blurred so that the optokinetic system is no longer provided with movement information, or is there a special mechanism of central or peripheral origin which suppresses visual stimulation during saccades as suggested in man (rev. Carpenter, 1977), locust (Zaretsky and Rowell, 1979) and fly (Heisenberg and Wolf, 1979)? In arthropods the optokinetic behaviour with respect to rapid movements of the environment has only been examined in flies (Fermi and Reichardt, 1963) in which the optokinetic responses do weaken, but do not completely vanish, at the rapid background movements which are normally encountered during saccadic head movements in flies; e.g. the head velocity is at least 500°/sec during saccades, (Land, 1973), but optokinetic responses can be evoked by background velocities exceeding 1000°/sec (Fermi and Reichardt, 1963). This is probably the reason why flies do in fact need a mechanism which suppresses the visual input during rapid saccadic turns of the body as demonstrated by Heisenberg and Wolf (1979). However, for the fly, which
performs rapid aerial manoeuvres, an image stabilizing system that is sensitive to stimuli of high velocity is presumably more important than for the sedentary mantis. Thus the two species are not strictly comparable and experiments similar to those performed in flies, are required in the praying mantis to receive a satisfactory answer to the two questions outlined above.

Considering the inevitable impairment of vision during rapid saccadic fixation movements, it is not surprising to find that no visual feedback guides the target image to its final position on the fovea (Fig. 3). Therefore, as has been mentioned by others (Land, 1971; Collett and Land, 1975) who have studied saccadic movements in arthropods, each point of the peripheral retina and its subsequent neuronal machinery must be capable of predicting the pattern of muscle activity required to produce turns of correct amplitude and direction with respect to the fovea. Unfortunately, very little is known about the mechanisms that translate the retinal position of incoming visual signals into adequate motor actions. A first clue, however, of how the saccade amplitude is generated in primates, has been derived from studying the activity of their occulomotor neurons (Fuchs and Luschei, 1970; Schiller, 1970). The recordings revealed that a spike burst of variable duration, but constant frequency, determines the saccade amplitude, followed by a less intense but maintained activity which holds the eyes in the new position. Equally, the investigation of the mechanical properties of the extraocular muscles and the eyeball came to the conclusion that saccades are produced by a pulse-step combination of
forces applied to the eye, where the pulse rotates the eye and the step holds it in the new position (Robinson, 1964). In turn, the question has been asked what kind of system is capable of converting temporal duration into spatial extent, resulting in hypothetical models of the spatial-translator element of the saccade generator (for details see Carpenter, 1977).

Saccades in vertebrates and mantids share the property that the amplitude is a function of the velocity and the duration. Since this characteristic reflects the application of corresponding mechanical principles — in both vertebrates and mantids, an inertial mass (the eyes in vertebrates and the head in mantids) is driven and fixated by muscle force — one might suppose that the underlying neural activity is also similar. Therefore, quantitative measurements of saccadic head movements in the praying mantis, combining both the dynamic properties of saccades and the activity of the driving muscles and motoneurons would be a useful first step in a further comparative approach to the mechanisms which generate saccades in foveate animals. The problem of how position information is obtained in mantids is raised again in the last section when discussing interactions between the two eyes.

3. Fixation errors

Mantids show systematic fixation errors which do not depend on the saccade amplitude but on the target position relative to the body axis of the animal (Fig. 4). Error angles have also been observed by Mittelstaedt (1957) and
Lea and Mueller (1977). Mittelstaedt attributed them to the interaction of two feedback systems; a visual circuit tending to minimize the position error of the target and a proprioceptive circuit tending to keep the head aligned with the body. The two circuits then oppose each other or act together depending on the relationship between body, head and target orientation, resulting in undershooting or overshooting saccades (Fig. 4). Visual feedback does not seem to be involved during saccadic head movements (Fig. 3; Lea and Mueller, 1977) but the proprioceptive loop could in fact be active according to Mittelstaedt's observation that disconnection of the afferent nerves serving the servical hair plates in the neck region diminishes the error angles. A notable difference between the measurements presented in this paper and the earlier ones by Mittelstaedt and Lea and Mueller concerns the extent of the error angles. Fig. 4 shows that for a large range of target position in an anterior-lateral plane the error angles are almost negligible and increase only to about 5° with respect to targets 90° to the side. On the other hand, the authors mentioned above observed a linear relationship between error angle and target position, leading to a fixation deficit of about 30° when the target is 90° to the side. Large error angles are possibly induced when the target presented in an anterior-lateral plane does not have the optimum inclination relative to the longitudinal axis of the body. This critical angle was not determined in those earlier studies. Whatever the cause of fixation deficits in this or the other studies might be, they apparently play no significant role in the natural
visual behaviour. Ultimately, prey is of interest when there is a chance to catch it, and in this case aligning movements of the body with the prey are required which then allow the recentring and tracking of the target in the frontal visual field where, as shown in this study, the fixation deficits are small.

4. Tracking of prey

Tied in with their function as fixation movements bringing novel objects to the fovea, saccades form a significant component of the tracking response. In fact, in the praying mantis, the tracking movements are almost exclusively composed of saccades when the target travels in front of the usually disrupted background in a natural environment (Figs. 12, 13, 14, 16, 17) and only the rare conditions of a homogeneous background, for instance when the mantis views the target against the sky, reveal the existence of a smooth tracking mechanism (Figs. 8, 13). This is in contrast to what we know from primates (rev. Capenter, 1977), hoverflies (Collett and Land, 1975) and tethered flying houseflies (Virsik and Reichardt, 1976) which are reported to track smoothly when there is a contrasted background, although the effect of the latter has been studied systematically only in the housefly. These insects show a target induced torque response which increases as a function of the target angle relative to the forward direction. Interference of the background then leads to an equilibrium between the position dependent, target induced torque and the opposing forces which tend to stabilize the retinal image of the background.
The result is a smooth tracking response with the eyes lagging constantly behind the target (Virsik and Reichardt, 1976).

This kind of interaction between the movement effects of target and background might be an adequate solution for the housefly which, in contrast to the praying mantis, lacks a distinct fovea. Because the praying mantis, similar to the fly, has no mechanism which continuously neutralises the opposing effect of the background during tracking, it has to employ a predictive saccadic tracking strategy if it wants to make use of the fovea (Fig. 14). In conclusion, the housefly can afford to give image stabilisation of the target priority because it is not so important that the target projects on to a particular eye region but the praying mantis has to sacrifice image stabilisation in order to benefit from the sophisticated visual abilities of the fovea.

Since, in mantids, the use of smooth tracking is extremely limited and, moreover, saccadic tracking allows the performance of all the visual tasks required for the catching of prey, it needs to be explained why mantids have a smooth tracking mechanism at all. Before answering this question we must ask whether smooth tracking is an independent response, directed towards particular objects of interest in the environment, or whether smooth tracking represents a simple optokinetic response in the sense of an indiscriminate stabilising reflex elicited by any contrast element moving relative to the eyes.
5. Similarities and differences between smooth tracking and optokinesis

In the praying mantis both smooth tracking and optokinetic response stabilise the movement of the retinal image independently of its position on the retina (Figs. 10, 11). Yet image stabilisation is not perfect, because the velocity of the eyes is usually slightly smaller than the velocity of the stimuli (Figs. 8, 9, 10, 11). These characteristics are typical of the optokinetic responses studied in a wide range of animals (e.g. rabbit: Collewijn, 1969; fly: Mittelstaedt, 1951; crab: Horridge and Sandeman, 1964) and it is generally agreed that the retinal slip velocity is the effective stimulus which generates the pursuit movements. This view has been strengthened by the discovery of directionally selective, velocity sensitive neurons whose activity is in good correlation with the optokinetic behaviour (rabbit: Oyster et al., 1972; fly: McCann and Foster, 1971; locust: Kien, 1974a, b; crab: Sandeman et al., 1975a, b).

Velocity is also important for smooth tracking of small targets in the foveate primates (Rashbass, 1961) although more recent studies demonstrated position effects as well; for instance, position errors relative to the fovea are sometimes reduced entirely by smooth tracking movements rather than through saccades (rev. Young, 1971; Carpenter, 1977). An additional problem in accepting that velocity information is solely responsible for tracking, is that at least in vertebrates there appears to be no measurable difference between target and eye velocity at low target
speeds (Young, 1971). This observation led Robinson (1971) to propose a relative position tracking system which keeps the target in place on the retina and, after slipping, resumes relative position tracking around a new retinal location. According to Robinson the same system could then also account for the holding of the target after it had stopped moving. In this context it is interesting to note that in mantids the position system which holds the eyes on a stationary target does not require visual stimulation. When a target is removed, after it had been fixated, the mantis keeps the head in the same position, even when there is no contrasted background that could possibly stabilise the head. On the other hand, the small amplitude jerks observed during smooth tracking (Fig. 8) and optokinetic responses in mantids could be interpreted as correcting for relative position. However, the existence of rapid jerky eye movements does not contradict the possibility that the primary visual information is provided by movement. Evidence from studies on the optokinetic system in other animals suggests that the velocity error signal is integrated over time at some stage of signal processing along the sensory-motor pathway so that the behavioural output in a sense resembles corrections of relative position errors (vertebrates: rev. Carpenter, 1977; invertebrates: e.g. Kien, 1977). In other respects, the question of what is correction of relative position and velocity respectively is, at least for this consideration, rather academic. The important point is that the praying mantis is capable of responding to the velocity and direction of a moving target, or contrast elements of the background, independently of their position.
relative to the fovea - in contrast to the saccades which correct position errors relative to the fovea independently of the movement direction of the target (see Section III. B.1).

While smooth tracking and optokinetic response are similar in that both minimize the slip of the retinal image, they differ in other respects. Small objects in the foreground, subtending an angle of only a few degrees on the retina, evoke strong pursuit responses only when they represent typical prey (and possibly predators) and project onto a foveal eye region (Fig. 10). On the other hand, the image stabilisation of the background is a stereotyped response that can be evoked whenever a large part of the background moves across the visual field (Fig. 11a). Moreover, responses caused by a moving target in the fovea and movements of the background in the periphery are not combined additively (Fig. 11b). The tracking response is weighted more strongly, but because the target is usually small, compared with the background, competing background motion can suppress smooth tracking movements almost completely. A major difficulty, however, in quantifying the interaction of competing target and background movement, arises from the intervention of complex visual phenomena such as the momentary attention towards one or another part in the visual field and particularly the selective attention towards potential prey. In Fig. 9b, for instance, it has been demonstrated that the mantis head follows the background but periodically jumps back to the stationary target located in a lateral position of the visual field. In most cases, however, refixation did not
occur, but in a few examples the mantis ignored the motion of the background and kept the fovea firmly on target. External factors such as movements of the body parts of the target influence its attractiveness, but there can be little doubt that central factors as yet not understood also effect the visual responses in a way which is difficult to control or to measure.

6. The possible role of the smooth tracking system

The fact that the smooth tracking response can be distinguished from the optokinetic response strengthens the necessity to search for its possible role under natural conditions, i.e. when there is a contrasted background. A reasonable possibility is that the smooth tracking system has a supportive role in the generation of saccades, in providing the velocity information required in combination with position information to predict the future position of a target during saccadic tracking (Fig. 14). Predictive saccadic tracking could then reflect interactions of two systems, the velocity coding system, which in the presence of a homogeneous background also generates smooth tracking movements (Figs. 8, 10), and the position coding system which in the absence of target movement is able to generate saccades on its own (Figs. 6, 10).

Alternatively, based on the finding that velocity information can be integrated by the nervous system one might suggest that the smooth pursuit system has a more dominant role in the generation of saccades. What the smooth pursuit system might do in the presence of a disrupted background
is to integrate the velocity signal from the monitored retinal slip of the target and periodically discharge - at a threshold somehow dictated by the background - in the form of rapid head movements which correct for the position error developed during the sampling period. However, for various reasons the exclusive use of velocity information would not guarantee stable foveal tracking. Notably one has to consider that the initial saccadic fixation movements are not accurate enough to provide a relative position tracking system with a reliable start (Figs. 4, 5). Moreover, the integrator would be expected to work very precisely to guarantee accurate corrections of relative positions, and this could be difficult when the jerking movement pattern of typical prey is considered. Thus it appears likely that intervening position computations relative to the fovea would sooner or later be required.

In appreciating the need for position and velocity information for saccadic tracking, it should be pointed out that we do not know how the extraction of either stimulus parameter is connected to the other. It is true that velocity and position dependent responses can be demonstrated separately, and it is then convenient to propose two different systems acting together during saccadic tracking that reflects the effects of both stimulus parameters. However, in considering the present knowledge, it is equally justified to consider the tracking response and to ask to what extent the separated position and velocity effects are manifestations of one and the same system. The same reservations must then also apply when tracking and optokinetic
responses are compared.

Finally it should be pointed out that position and velocity information have very similar functions in other foveate animals such as primates and hoverflies. In primates both stimulus parameters interact to predict adequate saccade amplitudes (Barmack, 1971) where the velocity component is thought to derive from the smooth pursuit system (e.g. Robinson, 1973). During tracking the chasing hoverfly Syritta is primarily guided by the position of a leading conspecific and it uses this information for both smooth and saccadic tracking (Collett and Land, 1975) - in contrast to the housefly where velocity information has a supportive role at least, in providing further stability during smooth tracking eye movements (Land and Collett, 1974; Reichardt and Poggio, 1976; Poggio and Reichardt, 1976). However, the hoverfly clearly uses velocity information as well when it computes an interception course with approaching objects (Collett and Land, 1978) and this represents a predictive task similar to that of mantids and primates during saccadic tracking.

7. Collaboration between the two eyes

So far, little consideration has been given to the fact that the mantis Tenodera benefits from huge binocular fields extending vertically 240° with a maximum horizontal overlap of 35° in the frontal part of the eye (for details see Part A). This binocular overlap allows a complete coverage of fixated and tracked prey with both eyes. Although the present experiments were not particularly designed to elucidate the
interactions between the two eyes, some considerations can still be made with respect to binocular coordination during fixation and tracking and also in the estimation of the target distance.

In fact it has often been suggested that distance estimation is the most essential role of binocularity in insects - and particularly in predators (Demoll, 1910; Baldus, 1926; Friederichs, 1931; Maldonado and Barrós-Pita, 1970; Barrós-Pita and Maldonado, 1970; Burkhardt et al., 1973; Cloarec, 1979). Where experiments have been carried out, including in the praying mantis by Maldonado and his coworkers, it has been found that monocular animals cannot strike their prey and it has been concluded that this deficiency is caused by the upset of a binocular mechanism of distance estimation. However, the explanation of the possible nature of this mechanism caused considerable difficulties. Generally it has been hypothesized that the visual system establishes the position of a point in 3-dimensional space, by determining the two ommatidia, in opposite eyes, whose visual axes intersect at this point. However, as pointed out by Pichka (1976) this would require a complex binocular retinal projection involving all possible pairs of ommatidia of the two eyes whose visual axes intersect in space. As mentioned by Pichka this requirement can hardly be accounted for by the limited number of neurons that connect the two optic lobes in insects. Fewer interactions between the two eyes would be required if binocular correlation is restricted to the ommatidia which intersect in the median plane of the head, and, in fact, this special case has preferably been
considered by most authors mentioned above. In considering the points made by Pichka (1976), Horridge, (1977, 1978) suggested that the distance of a target, once it is centered in the median plane, could be estimated by either eye so that no binocular coordination between the two eyes would be necessary. However, it is doubtful whether fixation and distance estimation can be separated as implied by Horridge. Obviously, the centering of prey in the median plane of the head needs both eyes because the disparities of the target image on the two eyes depend on the target distance. Limiting distance judgements to the median plane would be severely disadvantageous for the praying mantis. Since it does not track smoothly when there is a contrasting background, the moving target is centered in the median plane (or close to it) only for a short time interval after completion of a saccade, while the strike is usually released when the target projects onto the edge region of the binocular field. The following considerations suggest a binocular mechanism which is not restricted to the median plane of the head and yet enables range estimation to be performed simply.

The basis of the theory is the experimental finding that each eye has the neuronal machinery to relate position of a target image at any retinal point to the centre of its forward looking fovea, as revealed by saccadic fixation movements (Figs. 6, 7). In other words position measurements are related to one reference point on each eye.

Consider a frontal projection of the mantis head (Fig. 18a). Parallel rectangular coordinate systems \( (\alpha_1 \beta_1; \alpha_2 \beta_2) \) whose origin coincide with the fovea of each eye are projected
a) Frontal projection of the mantis head. Parallel rectangular coordinate systems \((a_1, \beta_1; a_2, \beta_2)\), whose origin coincide with the foveas, are projected onto the eye surface. \(s_1, s_2\); position vectors of the target images on the two eyes. b) Dorsal projection of the mantis head. The target is positioned in the horizontal plane defined by the visual axes of the two foveas. \(a_1, a_2\); error angles of the target relative to the foveas. \(\alpha\); error angle of the target relative to the median plane of the head. The target distance \((d)\) is related to the rotation point of the head.

Figure 18a and b
onto the eye surface. Thus the position of the target image on each eye is given by a vector, \( \mathbf{e}_1 \) for the left eye and \( \mathbf{e}_2 \) for the right eye. These vectors are defined by the corresponding angular coordinates \( \alpha_1 \) and \( \alpha_2 \). We must also consider the target distance \( d \) and the angular deviation of the target \( \alpha \) from the median plane of the mantis head. Both parameters, \( d \) and \( \alpha \), are related to the rotation point of the head (neck) as shown in the dorsal view in Fig. 18b.

First let us examine the special case where a target is positioned or moving in the horizontal plane defined by the visual axes of the forward looking foveas of the two eyes. The vectors \( \mathbf{e}_1 \) and \( \mathbf{e}_2 \) are then simply defined by the angles \( \alpha_1 \) and \( \alpha_2 \) respectively (Fig. 13b). If a target is at infinity, both eyes perceive the same error angle relative to the foveas and position information from either optic lobe would enable accurate centering of prey with respect to the foveas and the median plane of the head. However, if the target moves closer to the mantis, the eyes measure increasingly different position errors relative to the foveas and the question arises as to whether a saccade centres the target on one or the other fovea, or whether the two optic lobes act together in order to arrange for the target image to be symmetrically mapped on the two eyes with respect to the median plane. Figure 19a illustrates the problem for two targets, one moves in the median plane (\( \alpha = 0^\circ \); upper graph) the other along (\( \alpha = + 20^\circ \); lower graph). In both cases the distance ranges from 150 mm to the catching distance of 25 mm. For the sake of revealing the kind of
Figure 19a and b

a) The target moves along $\alpha = 0^\circ$ (upper graph) and $\alpha = +20^\circ$ (lower graph) from $d = 150$ mm to $d = 25$ mm ($d =$ target distance from the mantis head). The error angles of the target relative to the foveas ($a_1$, $a_2$) and the average of the two error angles ($a_1 + a_2/2$) are plotted as a function of $d$. b) The difference of the error angles ($a_1 - a_2$) as a function of $d$. Target moves along $\alpha = 0^\circ$ and $\alpha = \pm 20^\circ$. 
interactions between the two eyes, the second case is more interesting, because laterally located or moving targets evoke saccades with high probability and a comparison of saccade amplitudes between binocular and monocular animals could in fact reveal whether or not the different position signals from the two eyes are compared. Such measurements would also have to include angular saccadic tracking, because it is possible that during tracking coordinated interactions between the two eyes are more important than during the fixation of novel objects, where quick reaction might be the governing factor. If aligning of the target in the median plane is what the position system attempts to do, the most simple operation would be to average the different position signals derived from the two eyes. As shown in Fig. 19a (lower graph) the saccades would then slightly overshoot the target, but the error is small and would decrease even more when the target is initially closer to the median plane. In this context it should be pointed out that $\alpha = \pm 20^\circ$ represents an extreme target deviation in two respects. First, in Tenodera the maximum horizontal binocular overlap is only about $35^\circ$ (Part A). Thus for typical prey which subtends an angle of about $15^\circ$ at the catching distance, $\alpha = \pm 20^\circ$ would just allow a complete coverage of the prey with both eyes which is important when the position system of each eye has to measure the centre of gravity of the target (Fig. 5). Secondly, during tracking the saccade amplitude rarely exceeds $20^\circ$, so that most of the time the target is closer to the median plane (Fig. 14b).

If a comparison of position signals is possible between
the two eyes, a simple operation using the same position information from each eye could account for the judgment of the target distance. While for the saccadic system the average of two position signals might be important (Fig. 19a), the distance could simply be coded by their difference (Fig. 19b). One may quickly notice that the distance coding signal also depends on the angular deviation of the target from the median plane. Yet the signal variation for constant distance, but varied $\alpha$, is small and would hardly affect the accuracy of the strike. For instance, the distance of prey at the catching distance would be underestimated only by about 2 mm at $\alpha = \pm 20^\circ$, compared to the judgement at $\alpha = 0^\circ$ (Fig. 19b). Naturally, the sensitivity of the system in measuring absolute distances and distance differences increases with the steepness of the function so that the best performance is achieved at close range. This, and the dependence of the overall performance on the interocular distance, are, of course, determined by geometrical principles similar to those outlined by Burkhardt et al., (1973) in their "intersection theory". In conclusion, the only information to be coordinated between the two eyes are two angles and their sign (+ - ). As mentioned in an earlier section, for the saccadic system, angles are possibly coded by the duration of a burst of action potentials, as in the vertebrate oculomotor system, but we do not know how continuous position information - if it is continuous - is transmitted.

Let us turn back now to the general case illustrated in Fig. 18a. We notice immediately that the visual system has to code the position of the target, i.e. the vectors
\( \vec{r}_1 \) and \( \vec{r}_2 \), by its angular coordinates \( \alpha_1 \beta_1 \) and \( \alpha_2 \beta_2 \) if the interactions between the two eyes are to be as simple as they were in the special case outlined above. \( \alpha_1 \) and \( \alpha_2 \) would then interact as before, using the same neural pathways, in order to determine the angular deviation of the target from the median plane and to provide a measure of its distance. The saccadic system would additionally require the angular coordinates \( \beta_1 \) and \( \beta_2 \) to bring the target image as close as possible to the foveas. At this point one might object that such a vector analysis is a further complication for the visual system. However, such an objection mistakenly takes the mapping of the target position in the visual system for granted, and one would then have to answer the question how the position has been measured in the first place, in a way that differs from the framework of a coordinate system. In fact, position and its coordinates are in a sense not separable and the question is only whether the visual system uses a coordinate system which is appropriate to fulfil the visual tasks outlined in our model. One might suppose that the natural coordinate system defined by the regular hexagonal array of the facets is more important to define retinal position than the rectangular coordinate system which has been introduced before. We will return to this problem below. First, however, we must consider how position information is transmitted to the muscle system of the neck because the aspect of muscle coordination presumably represents the most clear manifestation of the vector analysis carried out by the visual system.
Levereault (1938) has localized 8 pairs of muscles (8 on each side of the neck) in the Carolina mantis, but it seems likely that not all participate in rotating the head around the two axes (dorso-ventral, medio-lateral) which are primarily relevant for saccadic head movements. Therefore, a fine tuning between the limited number of muscles is required to turn the head with respect to an unlimited number of possible target positions, and this can be achieved only when the position vectors $\mathbf{e}_1$ and $\mathbf{e}_2$ are decomposed into components which correspond to the direction of forces of the participating muscles. It is important to recognize that each optic lobe has not only to perform a vector analysis, but the coordinate systems of the two optic lobes must also be parallel because both transmit position information to the same muscle system. Consider, for instance, a target at infinity so that $\mathbf{e}_1$ equals $\mathbf{e}_2$. If one or the other eye is blinded, either optic lobe must code the position vector with the same angular coordinates because there is only one muscle system. It is obvious that parallel coordinate systems, and this has been assumed in Fig. 18a, are also a prerequisite for the neuronal coordination between the two optic lobes. Only when there is a uniform binocular coordinate system, can corresponding angular coordinates be compared.

The direction of forces of the individual muscles define the coordinate axes of the muscle system and one might suppose that they are parallel to the coordinate axes used by the visual system to extract position information from the retinal image, because in this case it is possible to
convey position information through the sensory motor system without any transformation of coordinates. Thus it would be interesting to compare the coordinate axes of the muscles with the ones defined by the hexagonal facet mosaic, whose striking regularity, particularly in the foveal eye region, may provide the anatomical basis for precise location of the target image on the retina. At present such a comparison is not possible. What can be examined, however, is whether a hexagonal coordinate system can determine the angles that are required for the proposed interactions between the two eyes.

It is obvious that in any insect the facet mosaics of the two eyes are arranged symmetrically to the median plane of the head. In the hypothetical facet coordinate system in Fig. 20a we additionally assume that one facet coordinate, $\beta_1$ ($\beta_2$), coincides with the median plane of the eye so that pairs of coordinate axes from the two eyes are parallel ($\beta_1 \beta_2; a_1 y_2; y_1 a_2$). As mentioned before this arrangement of coordinate axes is a prerequisite not only for muscle coordination, but for binocular coordination of visual information as well. To get a measure of the angular deviation of the target (given by the vector $\vec{e}_1$ ($\vec{e}_2$)) from the median plane of the eye, either component, $a_1$ or $y_1$ ($a_2$, $y_2$) could be used. If the $\beta_1$-(\(\beta_2\))-coordinate is neglected the angle of interest could still be measured by adding the $a_1$- and $y_1$- ($a_2$, $y_2$) components together. Of course, it does not matter that the measured angles, $a_1$ or $y_1$ ($a_2$, $y_2$), are not perpendicular to the median plane of the eye because the position signal for the saccadic system, for instance, always
Figure 20a and b

a) Hexagonal coordinate systems \((a_1 \beta_1 \gamma_1; a_2 \beta_2 \gamma_2)\), whose origin coincide with the foveas, are projected onto the eye surface. Pairs of coordinate axes are parallel \((\beta_1 \beta_2; a_1 \gamma_2; \gamma_1 \alpha_2)\). On each eye the position vector of the target image \((e_1, e_2)\) can be defined by any pair of coordinate axes. 

b) Frontal view of the left eye. Every tenth x-, y- and z- facet row is plotted. The thick line which crosses the fovea (marked with a black dot) covers the ommatidia whose visual axes are parallel to the median plane of the head. This line corresponds with the \(\beta_1\)-coordinate axis in Fig. a. Note that in the fovea and the ventral eye - but not in the dorsal eye - \(\beta_1\) runs parallel to the x-facet rows, so that in this eye region at least, pairs of facet-coordinate axes are parallel as in Fig. a.
includes a second coordinate and, for the estimate of range, only the differences between the angles measured by each eye are important. Thus it can be concluded that the information required for the considered interactions between the two eyes can equally be extracted in a hexagonal coordinate system.

Some indication of how the real facet mosaic of the mantis eye suits the concepts which have been developed above are provided by Fig. 20b which shows a frontal projection of the left eye. Every tenth x-, y- and z-facet row is marked. - It should be noticed that a proper consideration would not consider the facet lines but the lines defined by the visual axes of the ommatidia. In the mantis eye (and also in the fly, Franceschini, 1975) the two are not exactly identical because (i) the regional variation of the facet diameters and the interommatidial angles across the eye are not exactly correlated (Part A) and (ii) the anatomical and optical ommatidial axes do not correspond, particularly in the eye region which surrounds the fovea (Horridge and Duelli, 1979; Part A). - The thick line which crosses the fovea (marked with a black dot) in a vertical direction covers the ommatidia whose visual axes are parallel to the median plane of the head. It consequently corresponds with the $\beta_1$-coordinate axis in Fig. 20a. By comparing the $\beta_1$-coordinate with the arrangement of the facet mosaic, we note that in the fovea and the ventral eye, $\beta_1$ runs approximately parallel to the x-facet rows so that at least in this eye region the favourable arrangement of pairs of parallel coordinate axes of the two eyes is realized.
However, in the dorsal eye the x-rows increasingly deviate from the $\beta_1$-axis so that the whole facet coordinate system is rotated towards the median plane of the head. It is obvious that in this eye region the facet coordinate axes of the two eyes are no longer parallel and it would be useless to compare corresponding angular coordinates from the two eyes unless the rotation of the coordinate system is taken into account. In other words, each optic lobe would have to perform a coordinate transformation so that interactions between the two eyes could be performed on the basis of a uniform binocular coordinate system. In this context it should be pointed out that a coordinate transformation would also be required when the head is initially rotated around its longitudinal axes. In this case the coordinate systems of the visual and muscle system are rotated to each other and the proprioceptive system of the neck would possibly have to make the appropriate corrections. Normally, however, a mantis waiting in ambush or tracking prey, has its head well balanced with respect to the body and distinct rotations around the longitudinal axis occur only during the process of feeding.

In summary, as revealed by saccadic fixation movements in monocular animals, each eye is able to extract position information in a coordinate system whose origin is at the fovea. Based on this finding, and the assumption that the coordinate systems of the two eyes are parallel - an arrangement which must also be favoured with respect to muscle coordination - it is hypothesized that the collaboration between the two eyes during fixation, tracking and distance
estimation is restricted to the comparison of the angular coordinates which define the position vector on each eye.
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