

## REGIONAL SPECIALIZATION FOR CONTROL OF OCULAR MOVEMENTS IN THE COMPOUND EYES OF A STOMATOPOD CRUSTACEAN

BY THOMAS W. CRONIN, HONG Y. YAN\* AND KAY D. BIDLE  
*Department of Biological Sciences, The University of Maryland Baltimore County, Catonsville, MD 21228, USA*

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### Summary

1. Regional specialization within the triple compound eyes of the gonodactylid stomatopod *Gonodactylus oerstedii* (Hansen) was studied by examining how ocular tracking of a small target was affected after occluding vision in particular ommatidial regions with black enamel paint.

2. Complete occlusion of one eye did not prevent the other eye from tracking, indicating that the two eyes act somewhat independently. However, following such treatment, the angular extent over which the seeing eye moved while tracking was reduced.

3. An eye was able to continue tracking a moving target even after occlusion of the anterior tip or after painting over all of its posterior surface except the anterior tip (restricting the visual field to a patch about 40° in diameter). Similarly, occlusion of only the midband, the medial half or the lateral half of an eye did not prevent tracking.

4. Tracking was also possible, although with decreased amplitude, when either the dorsal or the ventral hemisphere was occluded. However, when both the dorsal and ventral hemispheres were occluded, leaving only the midband for vision, the ability of an eye to track was abolished.

5. A computer model was used to investigate whether the midband alone had the potential to direct tracking in our experiments. The model's output predicts that, in spite of its restricted field of view, if the midband is oriented within 20° of the horizontal, an eye could track using the midband alone. Conditions favoring such potential tracking occurred in our experiments, but neither tracking nor targetting movements were observed.

6. We conclude that ommatidia of the dorsal and ventral hemispheres of each compound eye are essential for ocular tracking in *G. oerstedii*. The midband appears to play no major role in this activity.

\*Present address: Department of Zoology, The University of Maryland College Park, College Park, MD 20742, USA.

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### Introduction

The mantis shrimps, or stomatopod crustaceans, are active predators common in shallow subtropical and tropical marine waters. Members of the stomatopod superfamily Gonodactyloidea are particularly impressive in their technique of capturing prey by stunning or destroying it with a rapid strike of their raptorial appendages, directed under visual control (Caldwell and Dingle, 1975). As is typical of stomatopods, the eyes of gonodactyloids are very unusual. Each compound eye has a midband of six parallel rows of ommatidia, viewing a fairly narrow strip of space that divides the eye into two roughly hemispherical halves. Ommatidia in the midband share visual fields with groups of ommatidia in each hemisphere. This provides gonodactyloids with triply overlapping visual fields in some directions of view; the three regions mutually contribute to an acute zone located about  $15^\circ$  medial to the eyestalk axis (Horridge, 1978; Schiff and Manning, 1984; Cronin, 1986; Marshall, 1988).

This triple overlap appears to provide distance measurement by a form of 'monocular stereopsis', in which ommatidia of the dorsal and ventral hemispheres of the eye are used to triangulate a viewed object (Exner, 1891; Cronin, 1986; Schiff and Candone, 1986). Within the triple redundancy of these eyes, separate ocular regions have become adapted for particular tasks. Marshall and colleagues (Marshall, 1988; Marshall *et al.* 1991*a,b*) showed that ommatidia in the midband are structurally specialized, perhaps for color and polarization vision. Recently, Cronin and Marshall (1989*a,b*) demonstrated that, in the gonodactyloid species *Pseudosquilla ciliata* and *Gonodactylus oerstedii*, four of the ommatidial rows in the midband together constitute a remarkable spectral analysis system, including at least eight spectral classes of photoreceptors. The other two midband rows are apparently designed for multichannel analysis of polarized light (Marshall, 1988; Marshall *et al.* 1991*a*). The hemispherical regions of the eye, in contrast, probably have only two photoreceptor classes, one most sensitive to ultraviolet light and the other to light of medium wavelengths, near 500 nm (Cronin, 1989; Cronin and King, 1989; Cronin and Marshall, 1989*a,b*). It thus appears that ommatidia in the hemispherical regions cover a broad visual field with dichromatic vision at best, while those of the midband have a linear field of view which is analyzed for spectral and polarizational content.

In addition to their unique anatomy, stomatopod eyes are also capable of extreme freedom of movement. Unlike the compound eyes of most decapod crustaceans, stomatopod eyes extend unobstructed from the extreme anterior end of the body. In some species the eyes not only swing on their stalks but also rotate on their axes by  $90^\circ$  or more (Cronin *et al.* 1988, 1991; Land *et al.* 1990). In gonodactyloid stomatopods, one class of smooth eye movements contributes to optokinetic stabilization (Cronin *et al.* 1991). *G. oerstedii* can visually track a moving target on a stable background; during tracking the eyes act independently, performing both smooth and saccadic movements that presumably place the target's image on the acute zone (Cronin *et al.* 1988). Moreover, gonodactyloids perform a special class of scanning ocular movements. These are relatively small,

have moderate angular velocities, are performed roughly perpendicular to the plane of the midband and appear to be involved with vision in the midband (Land *et al.* 1990). Eye movements in these animals are therefore unusual in several aspects.

It is not at all clear how vision in the hemispherical regions and in the midband is ultimately coordinated, nor is it known how movements of the eye are directed for scanning, optokinesis, fixation and pursuit of visual targets. A hypothesis that is consistent with all current information is that the hemispherical regions are responsible for form vision and depth measurement, and that their ommatidia are used to direct the ocular movements involved with scanning and fixation. We report results from a series of experiments on visual tracking, during which various regions of the eyes were blinded with black paint, that support this hypothesis.

#### Materials and methods

Individuals of the study species, *Gonodactylus oerstedii*, were collected in the Florida Keys and shipped to our laboratory for study. The animals were maintained in aquaria in artificial sea water and fed frozen shrimps or fish. Prolonged periods (>1 month) of life in the laboratory generally led to apparent loss of motivation and vitality; therefore, the animals were normally used within 4 weeks of their arrival.

The experimental set-up for presenting a moving target to the animals and for making closed-circuit video recordings of eye movements followed that of Cronin *et al.* (1988). In the current study, we presented a target (a miniature yellow light bulb) moving horizontally within  $\pm 50^\circ$  of the animal's midline, and measured eye movements in the azimuthal plane alone. The target completed 12 cycles of movement in 30 s, with a maximum angular velocity (as seen from the position of the animal) of  $135^\circ \text{s}^{-1}$ , and was thus in a velocity range that was very effective in eliciting tracking responses in the earlier study (Cronin *et al.* 1988). In order to occlude particular regions of compound eyes, black enamel paint (Pactra X-1 gloss black) was applied with a single-hair paintbrush either to a whole eye or to a particular ommatidial region. The other eye of the animal was left untreated. In some cases, the same individual was used in several occlusion studies. This was possible because the enamel paint either spontaneously separated from the eye after a day or could be removed with fine forceps. We typically used 1–5 experimental animals for each treatment, usually videotaping the tracking responses about 10 times per animal.

Because of the great mobility of the eyes, we had to establish a standard reference position for definition of the regions we occluded. When an individual of *G. oerstedii* is aroused, its eyes quickly assume a characteristic posture with the two midbands held nearly horizontal, but with a slight downward tilt medially (Fig. 1A). We therefore followed the system of Marshall (1988), and considered the eye to be divided by the midband into dorsal and ventral hemispheres (see Fig. 1). Medial and lateral eye halves were defined by a division made perpendicu-

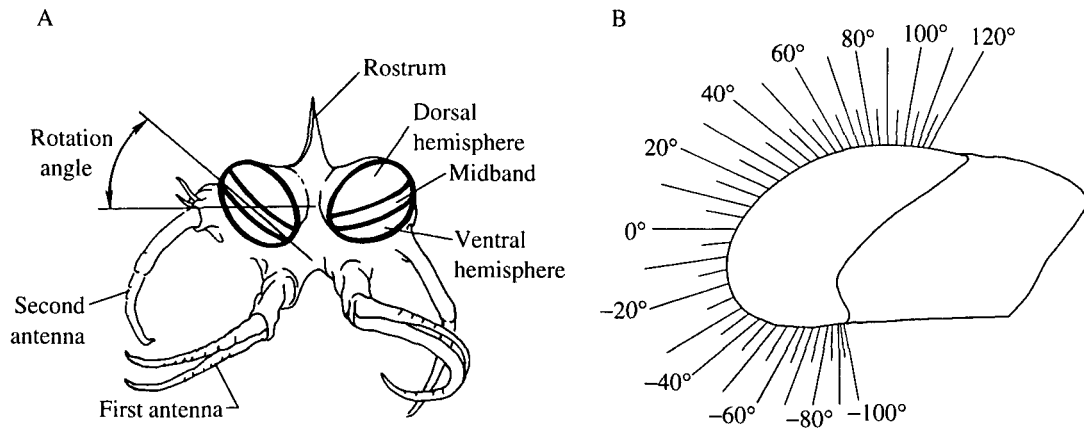


Fig. 1. (A) Line drawing illustrating the posture of the compound eyes of *Gonodactylus oerstedii* during arousal and the location of the ocular hemispheres and the midband. The animal is viewed from directly ahead, and the rotation angle of the right eye is indicated. Medial and lateral halves are defined by an imaginary plane passing perpendicular to the midband at the point where the eyestalk axis intersects the cornea. (B) Dorsal view of the right eye, showing the projected optical axes in the transverse plane of ommatidia in the midband (which lies at the border of the eye in this view). Angles are referenced to the axis of the eyestalk. Patches of ommatidia in the dorsal and ventral hemispheres adjacent to the midband share identical optical axes (modified from Cronin *et al.* 1988).

lar to the midband in line with the eyestalk axis. We regard this as an improvement on the description we used earlier (Cronin *et al.* 1988), in which we considered the midband to divide the eye into medial and lateral hemispheres. In each experiment, one of the following regions of the cornea of one eye was occluded: entire eye, anterior half of the eye, posterior half, posterior three-quarters, lateral half, medial half, midband, ventral hemisphere, dorsal hemisphere or dorsal plus ventral hemispheres.

Measurements of eye angles (see Cronin *et al.* 1988) were made directly from stopped frames of replayed video images at intervals of 0.1 s. The image of a computer-generated cursor was directly superimposed upon the eye image using a computer/video signal combiner (Telecomp 2000, Avas Co. Hackensack, NJ, USA). Target angles were calculated from the geometry of the image and the times when the target passed directly in front of the experimental animal.

Ocular tracking in *G. oerstedii* is a remarkably variable behavior; results vary even between successive trials with the same animal (see also Cronin *et al.* 1988). Before analyzing the data, we therefore reviewed the resulting videotapes and selected for analysis one or more runs from each series of experiments in which repeated movements of at least one eye were clearly expressed. As an objective measure of whether or not tracking occurred, we calculated product-moment correlation coefficients between eye angles and target angles (Sokal and Rohlf, 1979); a significant ( $P < 0.05$ ) value of the correlation coefficient ( $r$ ) was taken as an

Table 1. Product-moment correlation coefficients ( $r$ ) between eye position and target position measured at 0.1-s intervals during an experimental run of 28.4 s

Treatment (region occluded)	Relevant figure	Pretreatment		Treated eye	Treatment	
		$r_r$	$r_l$		$r_r$	$r_l$
Whole eye	2	0.314**	0.434**	R	<u>-0.048</u> NS	0.417**
Anterior half	3	0.473**	0.554**	R	<u>0.191</u> **	0.244**
Posterior half	4	0.501**	0.585**	R	<u>0.374</u> **	0.506**
Posterior three- quarters	4	0.501**	0.585**	L	<u>0.319</u> **	<u>0.351</u> **
Lateral half	4	0.501**	0.585**	L	0.286**	<u>0.175</u> **
Medial half	4	0.501**	0.585**	L	0.152*	<u>0.315</u> **
Midband	5	0.303**	0.158**	R	<u>0.270</u> **	0.189**
Dorsal hemisphere	6	0.443**	0.291**	L	<u>0.207</u> **	<u>0.190</u> **
Ventral hemisphere	7	0.738**	0.765**	R	<u>0.181</u> **	0.105 NS†
Dorsal and ventral hemispheres‡	8 (left)	0.203**	0.471**	R	<u>-0.033</u> NS	0.497**
		0.203**	0.471**	R	<u>-0.048</u> NS	0.514**
	8 (right)	0.820**	0.616**	R	<u>0.108</u> NS	0.476**
		0.820**	0.616**	R	<u>0.003</u> NS	0.514**

Correlation coefficients computed for eye positions lagged one point (0.1 s) behind target position. Pretreatment: control runs with eyes not occluded.

Treatment: occlusion of stated region of either the right (R) or left (L) eyes.

$r_r$ , value for right eye;  $r_l$ , value for left eye.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; NS, not significant.

For time series of this length (283 points), critical values of  $r$  are 0.118 ( $P < 0.05$ ) and 0.154 ( $P < 0.01$ ).

In the column labelled Treatment, the value for the treated eye is underlined.

†  $P < 0.1$ . If computed for no lag of eye position vs target position,  $r = 0.127$ ,  $P < 0.05$ .

‡ Two repeats of each treatment.

indicator of the occurrence of ocular tracking. In control runs (neither eye treated),  $r$  usually reached its maximum value if the eye data were lagged by 1 interval (0.1 s) behind the target data, so all correlation coefficients were computed at this same lag.

## Results

As described previously (Cronin *et al.* 1988), eye movements during tracking were variable, bilaterally uncoupled and idiosyncratic. Owing to their anterior location, eyes could track a target effectively both ipsilaterally and contralaterally. In many cases, only the first few passes of the target elicited tracking behavior. Experimental outcomes are summarized in Table 1. Overall, the results of analyses were unequivocal. In control runs, correlation coefficients were always significant at the 0.05 level for both eyes; this was also true for the untreated eye in experimental runs except in one case (ventral hemisphere occluded;  $0.05 < P < 0.1$ ). Correlation coefficients for treated eyes were either highly signifi-

cant ( $r > 0.154$ ;  $P < 0.01$ ) or near 0, suggesting that the ability to fixate and pursue a target was either left intact or completely lost.

When an eye was totally occluded with opaque paint it ceased to track the moving target, while the control eye was virtually unaffected (Fig. 2, Table 1). This result confirms the earlier observation that the eyes track independently (Cronin *et al.* 1988). It further demonstrates that loss of function in one eye does not significantly inhibit tracking movements in the other and that tracking movements of one eye only minimally influence the activity of the other. Note, however, that, although the correlation coefficient was essentially unchanged in the seeing eye, the amplitude of its tracking was reduced (Fig. 2). This suggests that the lack of vision in the blinded eye could have interfered with the seeing eye's activity to some extent. In the experiments that follow, in which only a part of the visual field was occluded, we treat the two eyes of an experimental animal as being virtually independent in function.

In the compound eyes of *G. oerstedii*, ommatidial axes throughout the lateral surface of the cornea are skewed towards the eyestalk axis (see Fig. 1B). Painting over the anterior tip of the eye blocks vision from roughly 20° laterally to 50° medially. This region includes the acute zone, which lies about 15° medially along the midband (N. J. Marshall, in preparation). Nevertheless, the eye remains capable of tracking (Fig. 3, Table 1). The fact that an eye can pursue a target, even though the target itself cannot be seen when the eye is aligned with it, suggests that tracking in *G. oerstedii* proceeds as a series of refixations of gaze. In this case, control is exerted only when the target is perceived by peripheral ommatidia. The movements of the seeing eye were once again reduced in angular extent. The reciprocal treatments, allowing vision only in more-or-less circular regions within the sector from approximately 20° lateral to 50° medial ('posterior half'), or just from about 10° lateral to 30° medial ('posterior three-quarters'), also permitted tracking activity (Fig. 4, Table 1). Since our targets were presented anteriorly, they would rarely have been viewed by these posterior ommatidia once the eye had initially detected the target. The results demonstrate that, even when vision is restricted to small parts of the visual field, essentially normal tracking behavior can occur.

The animal in which we studied the effects of posterior occlusions was also used for treatments involving either the medial or lateral half of an eye. In these cases, ommatidia of both hemispheres and the midband were blocked on one half of the corneal surface. Occlusion of either half alone did not prevent the eye from tracking (Fig. 4, Table 1), although the magnitudes of the correlation coefficients (and the fidelity of tracking as seen in the figures) were notably reduced compared to the controls.

When the midband of an eye was completely occluded, tracking continued at a reduced amplitude (Fig. 5, Table 1). This demonstrates that the ommatidia of the midband are not required for the detection and pursuit of a moving target. Similarly, occlusion of either the dorsal hemisphere (Fig. 6) or the ventral hemisphere (Fig. 7) of an eye, which should prevent any monocular stereopsis, did

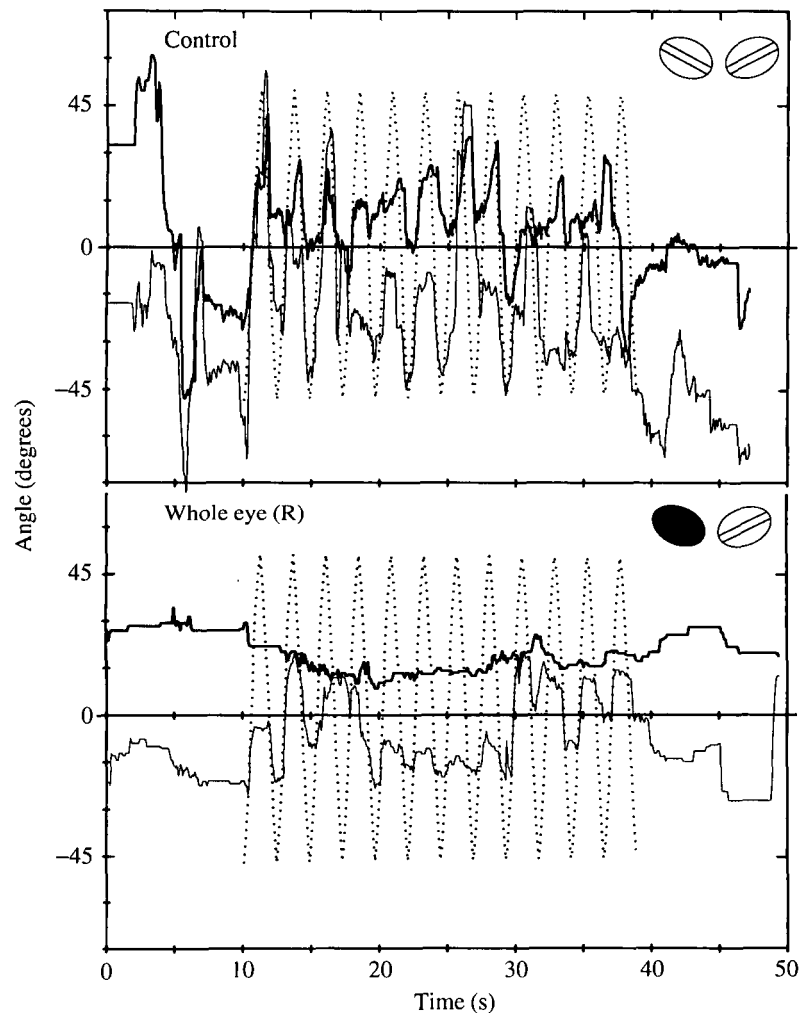


Fig. 2. Tracking of an oscillating target by a normal animal and by the same individual after painting over the right eye.  $0^\circ$  represents the position of the target at its nearest approach to the animal; positive angles are to the right. The bold trace plots the position of the right eye, and the light trace that of the left eye, at 0.1-s intervals. The dotted trace plots the position of the target during its movement. Each experiment began and ended with a period of about 10 s during which the target, a miniature light bulb, was not illuminated and did not move. In this and all figures that follow, the top panel is the control run, and the lower panels are the experimental runs for the same individual; the region occluded is printed on the relevant part of the figure. R, right eye; L, left eye. The small inset in the top right-hand portion of each panel illustrates the treatment, with the occluded region of the eye in black; these insets should be compared with Fig. 1.

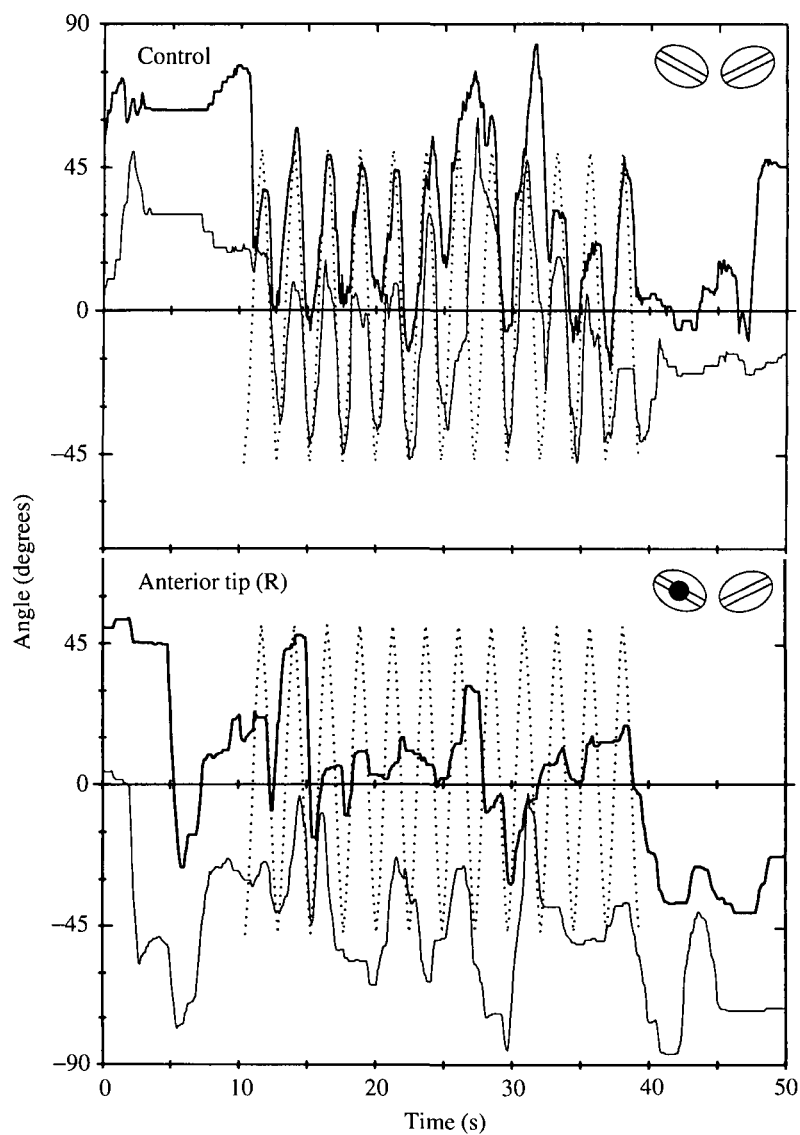


Fig. 3. Tracking of an oscillating target before (top) and after (bottom) painting over the anterior tip of the right eye. See text and caption of Fig. 2 for other details.

Fig. 4. Tracking of an oscillating target (top) before treatment and after the following treatments: second panel, painting over the posterior half of the right eye; third panel, painting over the posterior 75% of the left eye; fourth panel, painting over the lateral half of the left eye; fifth panel, painting over the medial half of the left eye. See text and caption of Fig. 2 for other details.



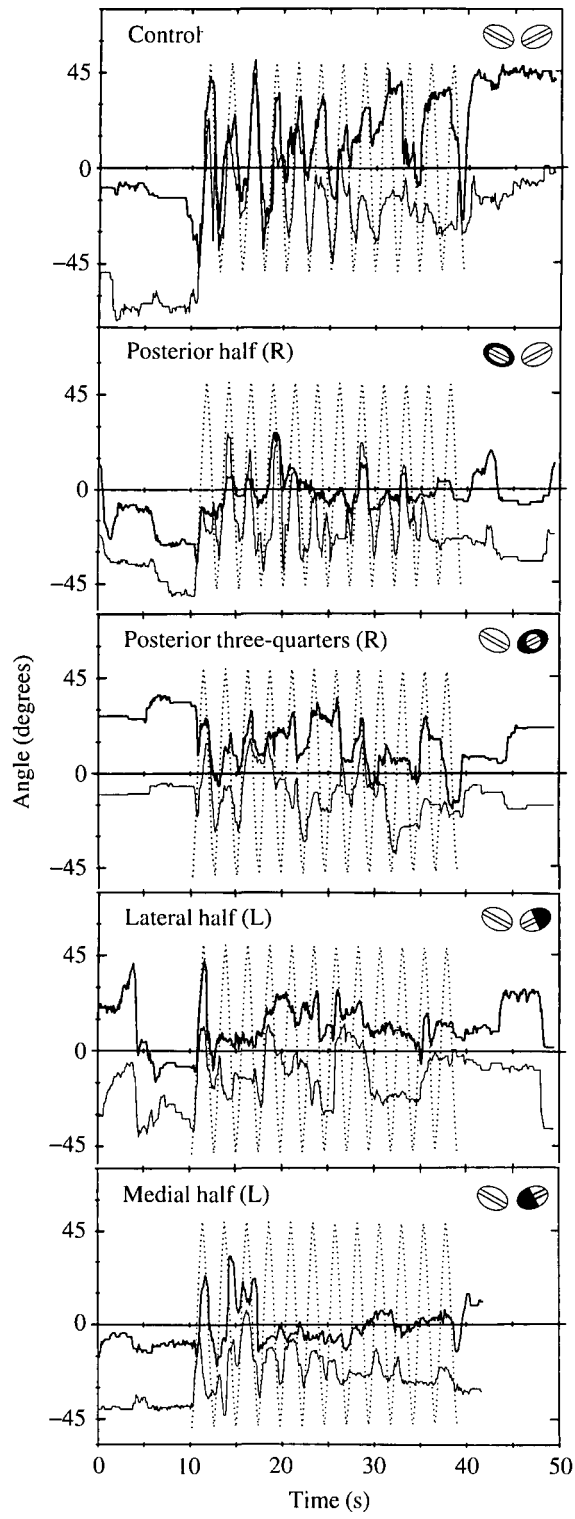


Fig. 4

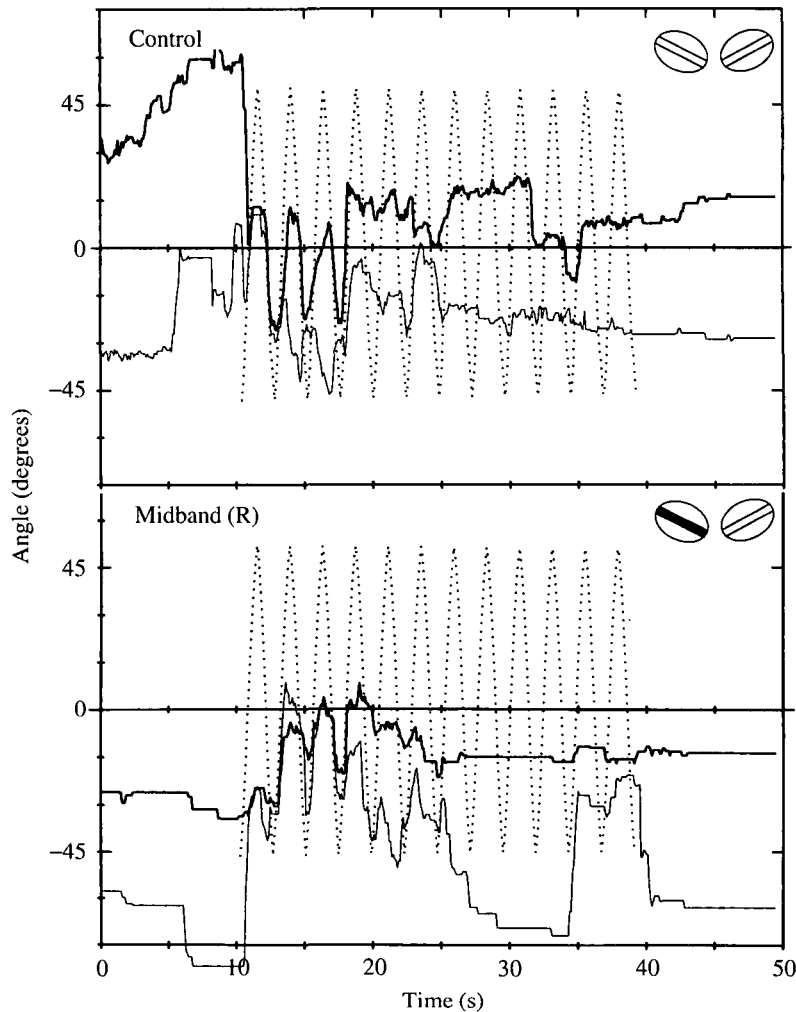


Fig. 5. Tracking of an oscillating target before treatment (top panel) and after painting out the midband of the right eye (bottom panel). See caption of Fig. 2 for other details.

not abolish the tracking response of the eye (Table 1). In these cases, tracking movements by both eyes showed decreased correlation with the target, and their patterns of movement were more irregular than in the companion control runs.

The results thus far demonstrate clearly that ommatidia throughout the dorsal and ventral ocular hemispheres can direct tracking movements. However, when both the dorsal and ventral hemispheres of an eye were occluded, leaving only the ommatidia of the midband with normal vision, tracking ceased entirely (Fig. 8; Table 1). The untreated eye continued to track the target. In each case, as the animal became aware of the target's presence, the treated eye assumed the characteristic 'alert' posture (see Fig. 1A). This event can be seen on most panels of Fig. 8 as an abrupt movement of the right (treated) eye towards the midline

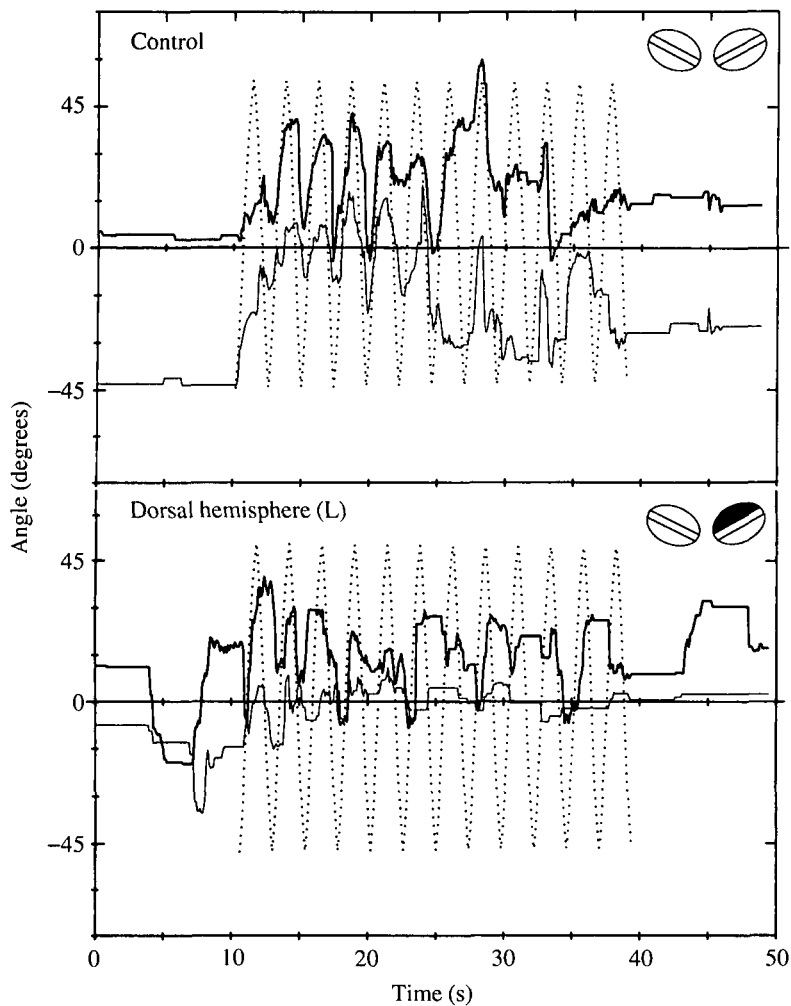


Fig. 6. Tracking of an oscillating target before treatment (top panel) and after painting over the dorsal hemisphere of the left eye (bottom panel). See caption of Fig. 2 for other details.

when the target began to move. In this position, the midband is nearly horizontal (see Discussion, below) and is therefore capable of imaging the moving target over a sector of its track. Nevertheless, the eye did not follow the target. Two large movements, resembling saccades, in the experimental panels of the right half of Fig. 8 are due to changes in the animal's posture and not to ocular fixation movements (see below).

Because tracking behavior was so persistent following all other partial occlusions, we were concerned that we might have overlooked the occurrence of weak or infrequent tracking. We therefore analyzed two different runs from each of two experimental animals, with consistent results. We conclude that at least some parts of the hemispherical regions of the compound eye of *G. oerstedii* must

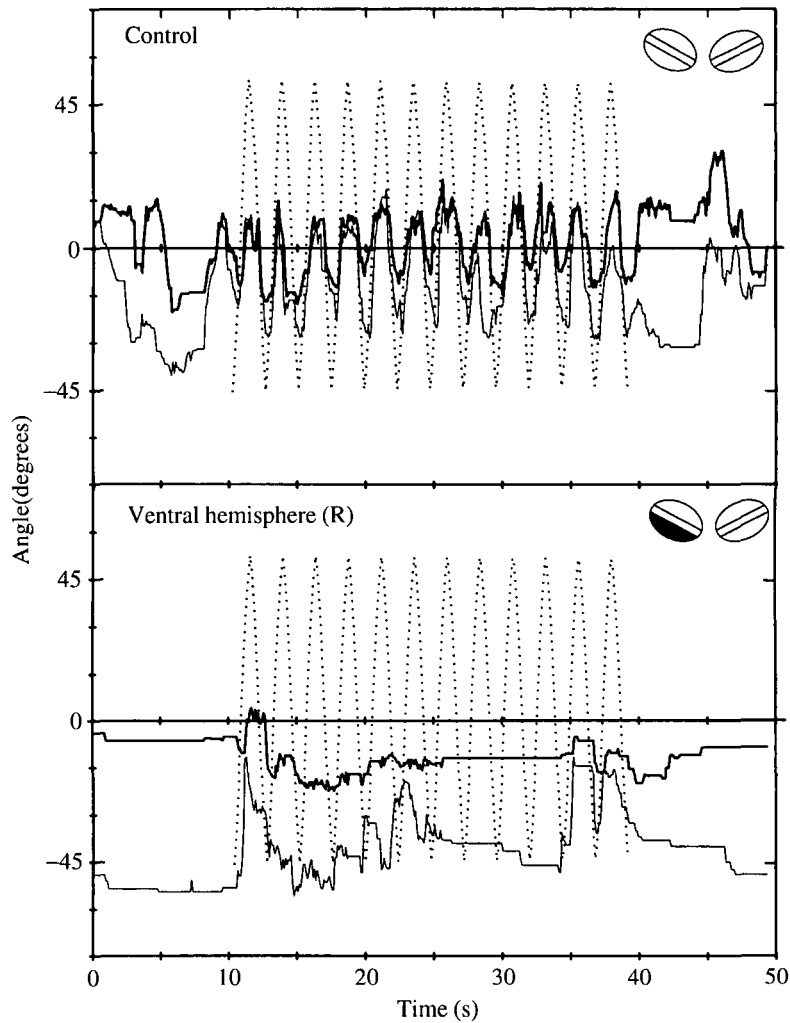


Fig. 7. Tracking of an oscillating target before treatment (top panel) and after painting out the ventral hemisphere of the right eye (bottom panel). See caption of Fig. 2 for other details.

retain normal vision to direct the eye towards a moving object. The midband alone is not sufficient.

To explore the properties that eye movements would possess when directed by the midband alone, we constructed a computer model of tracking behavior. Tracking by *Gonodactylus oerstedii* has the following three properties (Cronin *et al.* 1988). (1) Eye movements are generally saccade-like, with single movements tending to move the eye up to 50% of the angular distance to a target. (2) Eye movements are probabilistic; they may or may not occur in a given time interval. (3) The nearer that a visual target is to an animal's midline, the more likely it is to provoke eye movements; the maximum probability of a movement (as the target

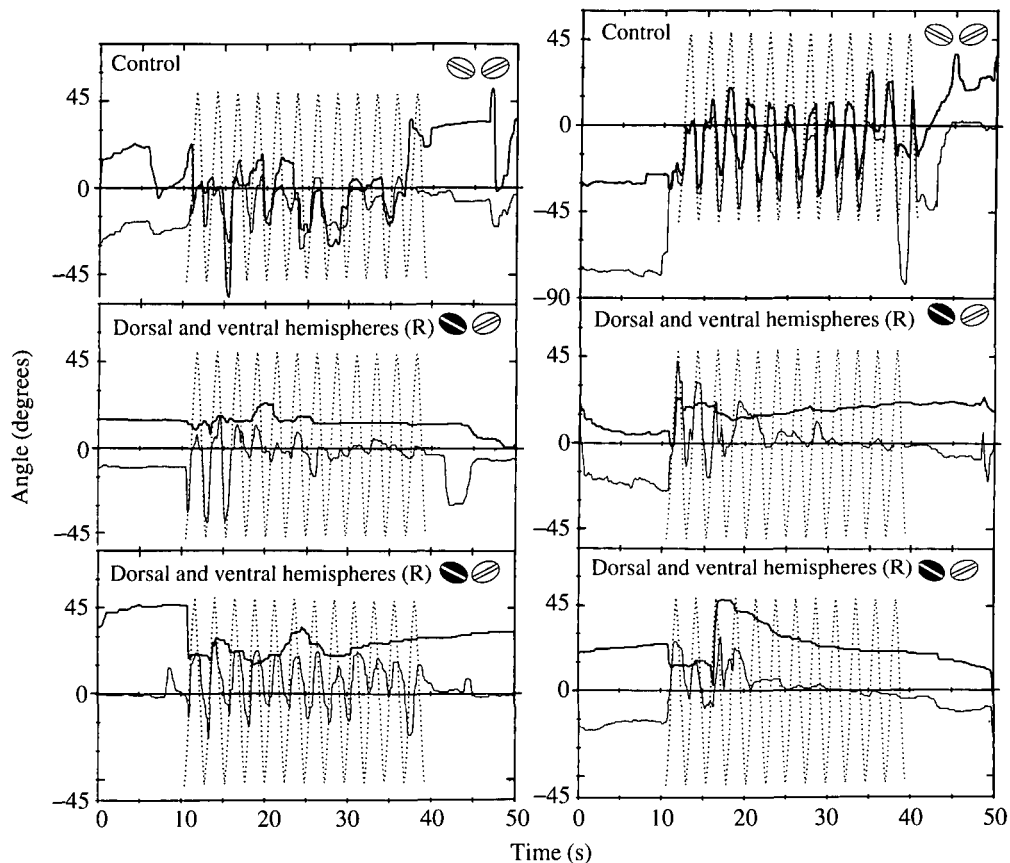


Fig. 8. Tracking of an oscillating target before treatment (top panel in each group) and after painting out both the dorsal and ventral hemispheres of the right eye (middle and bottom panels). Each group of three panels represents the results (one control, two tests) from a different animal. See text and caption of Fig. 2 for other details.

crosses the midline) is about 60%. Therefore, in the model the probability of a tracking movement was linearly reduced from 60% at a target azimuth of 0° to 10% for target azimuths at or beyond 50°. If a movement occurred, it reduced the current error angle by 40% (i.e. the gain was set to 0.4). To estimate the integration time for a single movement, we noted that, in the large gonodactyloid *Odontodactylus scyllarus*, eye movements are complete in as little as 50 ms (Land *et al.* 1990). Therefore, in the model, eye positions and target positions were evaluated at intervals of 50 ms. Finally, the visual field width (in azimuth) of the midband was calculated for various angles of eye rotation. Ommatidia of the midband accept light from a strip of space that varies in width from 5° at the acute zone to 15° at the margins of the eye (Marshall, 1988). We used the mean value of 10° in combination with eye tilt angles ( $\rho$ ) from 0° to 40°; horizontal halfwidths of the field of view of the midband corresponding to these are given in Table 2. The

Table 2. Results of runs of the model (described in the text) of eye movements in *Gonodactylus oerstedii*

Rotation angle, $\rho$	Field halfwidth	Random movements	$r_{\min}$	$r_{\max}$	$r_{\text{mean}}$	% Occurrences $P < 0.05$
0°	60°*	–	0.678	0.860	0.765	100
0°		+	0.570	0.823	0.751	100
10°	28.8°	–	0.150	0.684	0.432	100
10°		+	0.204	0.658	0.408	100
20°	14.6°	–	0.024	0.381	0.125	53
20°		+	–0.111	0.315	0.105	39
30°	10°	–	–0.067	0.314	0.077	25
30°		+	–0.095	0.138	0.034	7
40°	7.8°	–	–0.084	0.251	0.060	16
40°		+	–0.132	0.169	0.008	4

Results are given for various eye rotation angles,  $\rho$  (see text and Fig. 1A), with or without the addition of random eye movements.

Field halfwidth, angular extent of the field of view of the midband (width 10°) from its midpoint, defined as  $5^\circ/\sin(\rho)$ .

Two hundred runs of the model were completed for each rotation angle; 100 without the addition of random movements (–) and an additional 100 with random movements included (+). Movements were added at random to 20% of the intervals; movements were assigned a value of  $1000 \times (R - 0.5)^7$ , ( $R$  is a pseudorandom number from 0 to 1) and thus ranged from 0° to 7.8° in a 50-ms interval.

Minimum ( $r_{\min}$ ), maximum ( $r_{\max}$ ) and average ( $r_{\text{mean}}$ ) values of  $r$  for each group of 100 trials are given, as is the percentage of occurrences in which  $r$  was statistically significant at the 0.05 level.

For time series of the length created by the model (288 points), statistical significance is attained at  $r > 0.117$ ; by definition, 5% of uncorrelated runs should achieve significance.

\* At 0° rotation, the midband's field of view extends to the margins of the cornea. In earlier work with intact eyes, very few targetting movements were observed at offsets greater than 60°, so field halfwidth was arbitrarily set to this value.

Eye movements at  $\rho = 0^\circ$  are, in principle, equivalent to movements of intact eyes.

eye was assumed to be aligned with the target in elevation (see below for a discussion of this assumption).

Computation proceeded as follows. First, the eye was assigned an initial azimuth of 15° and a rotation angle, and the horizontal field width of the midband was determined. Positions of a model target, moving exactly like the real targets used in the experiments, were provided at intervals of 0.05 s. Once target movement began, in each interval the probability of an eye movement (dependent upon target azimuth, as described above) was assessed and compared to a pseudorandom number between 0 and 1 generated by the computer. If the value of the pseudorandom number was lower than the evaluated probability of movement, and the target's position fell within the lateral range of vision of the midband (i.e. the difference between the target azimuth and eye azimuth was within the

field halfwidth), the eye was assigned a new azimuthal position 40% closer to the target. If not, no eye movement occurred. In some runs, random, small eye movements were added (see Table 2). Following the completion of each run, correlation coefficients were computed for positions of the eye and target at 0.1-s intervals, for comparison with the previous data. One hundred runs of the model were carried out for each eye rotation angle, with and without the addition of random eye movements. Results are summarized in Table 2, and samples of the model's output are plotted in Fig. 9.

When the midband was horizontal (a situation equivalent to vision with an untreated eye, since vision was panoramic in the horizontal plane), model eye movements were very much like those observed during the experimental controls in both amplitude and pattern, and correlation coefficients were similar to the highest ones observed in control eyes (Tables 1 and 2). The lesser correlations of most controls simply reflected the failure of some animals to track the target throughout the entire experiment. At a rotation of  $10^\circ$ , correlation coefficients were invariably statistically significant, even in the presence of random eye movements (Table 2). Vision in this case was restricted to a horizontal zone approximately  $58^\circ$  wide. This situation is analogous to the cases when the posterior part of the eye was occluded, and the output of the model resembles results obtained with such treatment (compare Tables 1 and 2; Figs 4 and 9). If the eye was rotated  $20^\circ$ , its movements became smaller and less frequent, but its position remained significantly correlated with that of the target in nearly half the trials. At rotations of  $30^\circ$  and beyond, eye movements became essentially uncorrelated with the target, particularly in the presence of random movements (Table 2). In summary, the model predicts that, for eye rotations of  $20^\circ$  or less, the midband alone could in principle direct ocular tracking; for angles of  $30^\circ$  and above, midband tracking is impossible.

Were conditions during the actual experiments such that midband-directed tracking could have occurred? Using videotapes of eye movements as seen from directly ahead of the animal (the view in Fig. 1A), we measured the angle of rotation in the treated eye by taking the tangent to the midband at the point of the projection of the eyestalk's axis (see Fig. 1A), with a correction for eyestalk azimuth. The treated eye in both experimental animals was the right eye; rotation angle was defined as the counterclockwise angle of the midband with the horizontal, seen from the animal's point of view. Eye elevation angles were small, and no correction was applied for elevation.

Results of these measurements, together with values for azimuth, are plotted in Fig. 10. Except for the experiment of the top right-hand panel, the midband was within  $20^\circ$  of the horizontal for at least some part of each trial; in both bottom panels eye rotation angles were small most of the time. If the actual experimental rotation angles are fed into the model, tracking occurs in almost all runs of the two experiments of the bottom panels ( $P < 0.05$  more than 90% of the time), but rarely in the other two experiments. The predictions of the model differ from the experimental results in another important way. Movements of eyes with occluded

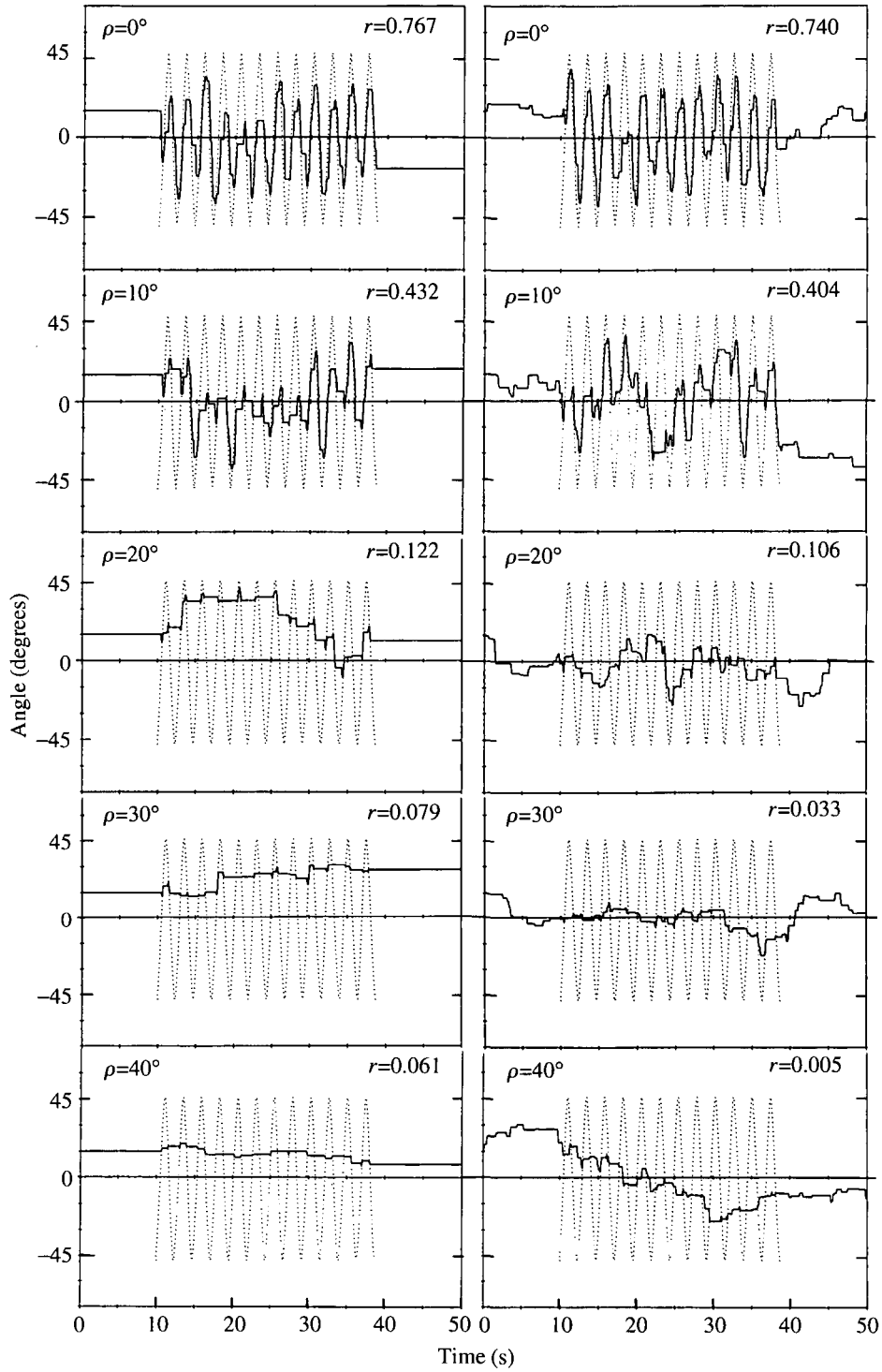


Fig. 9



Fig. 9. Sample traces of eye movements produced by the model described in the text. Each panel includes target azimuth (dotted line, plotted only when the target was moving) and eye azimuth (solid line). The rotation angle ( $\rho$ ) and correlation coefficient ( $r$ , calculated for 0.1-s intervals when the target was moving) are given on each panel. Model outputs producing typical correlation coefficients for each condition were selected for display. Random movements were not included for runs plotted on the left-hand side but were included for those of the right-hand side. See text for further discussion.

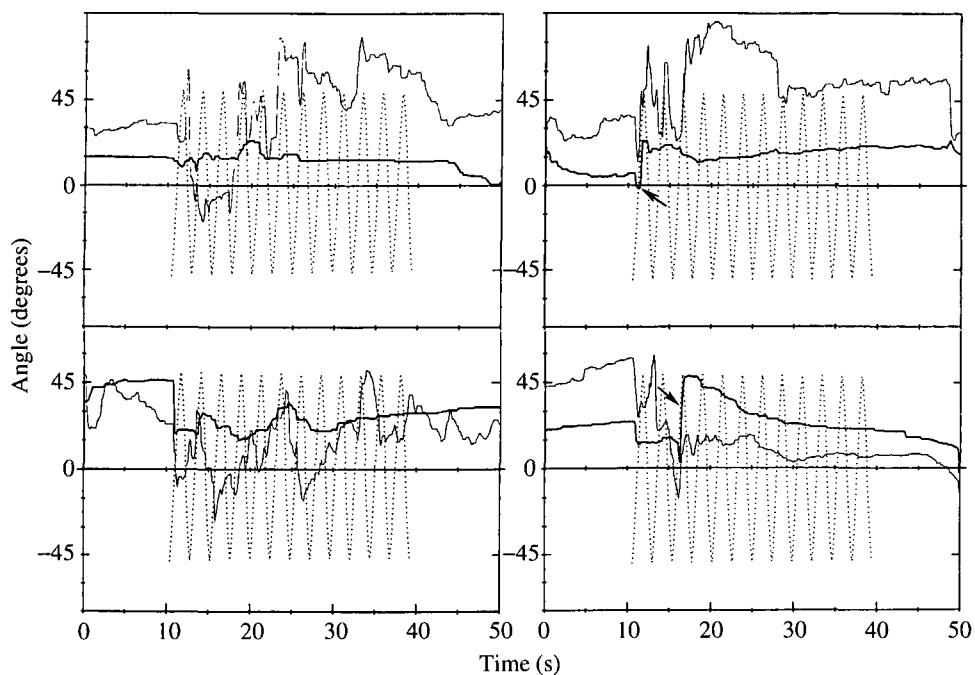


Fig. 10. Eye rotation angles for eyes in which only the midband was able to see. These experiments correspond to those of Fig. 8. Each panel includes target azimuth for intervals when the target was moving (dotted trace), azimuth of the experimental (right) eye (bold solid trace) and rotation angle, as defined in the text (light solid trace). Arrows indicate large, rapid changes in eye azimuth due to shifts in the posture of the experimental animal.

dorsal and ventral hemispheres were invariably slow after the initial saccade to the 'alert' posture. Only two other large movements occurred (indicated by arrows in Fig. 10), and both of these were due to changes in the animal's posture, not to movements of the experimental eye. All other experimental and control runs, and all outputs of the model for rotation angles of  $20^\circ$  and below, include numerous large, rapid movements associated with targetting (Figs 2–9). Apparently, ommatidia of the midband cannot command such movements.

Do the assumptions of the model apply to the conditions of our experiments? In

constructing the model, we omitted a consideration of eye elevation. In our experiments, the center of the target (the filament of a miniature light bulb) was at an elevation of between  $12^\circ$  and  $18^\circ$  (depending on azimuth). When an animal was alert, the eyes extended either horizontally or tilted slightly upwards. They drooped downwards when the animal was apparently resting, disinterested or unmotivated; this posture was often observed when the target was stationary or when the seeing eye ceased tracking. The target housing, which was also visible to the animal, extended several degrees above and below the filament, and the target was suspended on a long vertical rod. We consider that even at the smallest tilt angles, as long as eye elevation was  $0^\circ$  or greater, the image of the target (and certainly of its housing and support rod) would have fallen on ommatidia of the midband during part of its travel. The other assumptions of the model are derived from extensive work with normal, untreated animals, and its output is closely similar to what is observed in the controls. In a further test of the model, we found that simulations in which vision in the anterior region of the eye was blocked (as in the experiment of Fig. 3) consistently produced tracking, at a lower level of correlation than controls – as was actually observed. Therefore, we believe our model provides a reasonable description of visual tracking in *G. oerstedii*, and that the failure of experimental animals to track or even to exhibit fixation movements is due to the inability of ommatidia of the midband to direct such movements.

### Discussion

Throughout this work, tracking by the control animals repeated the results of our earlier work (Cronin *et al.* 1988) in all essential regards. Eyes tracked intermittently, the two eyes of an individual had rather different time courses of movement, and tracking was a mixture of smooth and abrupt movements. It now appears that not all gonodactyloid stomatopods track moving objects with smooth movements. *Odontodactylus scyllarus*, when presented with an oscillating target viewed against a striped background, tracks with a series of discontinuous movements (Land *et al.* 1990). These movements appear to be a mixture of refixations and scans, and are quite distinctive in character when compared to the results of our experiments with *G. oerstedii*. The disparate results could well reflect differences in the way these quite different animals use their eyes. Alternatively, they may arise from differences in the background (unstructured *vs* vertically striped) against which the target was viewed; Rossel (1980) obtained similarly different tracking behaviors with praying mantises; tracking depended upon the background behind the moving target. Another possibility is that *G. oerstedii* performs a series of small rapid refixations while tracking. The acuity of the video system we used in these experiments is too limited both temporally and spatially to resolve this matter, but it appears that, under the conditions of our experiments, *G. oerstedii* can track smoothly.

In the experimental animals, the untreated eyes continued to track the target, often with equivalent fidelity to the controls. But in many cases eye movements

were more irregular and of lower amplitude than in the controls. We suspect that this is partly due to the animals' being disturbed by the handling required for painting the treated eye, but it remains possible that lack of normal vision in the experimental eye interfered with or inhibited movements of the untreated eye. In gonodactyloid stomatopods, knowing when or how much one eye moves provides little or no predictive power concerning movements of the other eye (Cronin *et al.* 1988; Land *et al.* 1990). The eyes could nevertheless influence each other; for example, alterations in the frequency or amplitude of movement of one eye may well be reflected in the behavior of the other, even though individual movements remain uncoupled. If this is so, it would provide another explanation of the reduced amplitude of movements of the untreated eyes in the experimental animals. The data required to understand interactions between the eyes do not exist. Stomatopod oculomotor control contrasts sharply with the situation in decapod crustaceans. For example, during stomatopod optokinesis the eyes are mainly independent (Cronin *et al.* 1991), whereas in the decapods such eye movements are almost invariably conjugate (see Barnes and Horridge, 1969; York *et al.* 1972; Nalbach *et al.* 1985).

The most significant finding of this study is that only the ommatidia of the hemispherical regions of the eye direct the tracking of a target. The midband is not required for such tracking and, if vision is restricted to the midband alone, the eye cannot follow the target. Such results strongly suggest that the triple eye is regionally specialized.

In gonodactyloid stomatopods, visual fixation (aligning the eye with a viewed object) and visual pursuit (following a moving object) may be very similar events. If so, the ocular regions that control tracking probably also direct visual fixation. Gonodactyloids fixate viewed objects with an acute zone typically located about 15° along the midband, medially from the extended axis of the eyestalk (N. J. Marshall, in preparation; see also Fig. 1B). In our experiments, it is difficult to determine where the acute zone is actually looking, since we measured only eye azimuth, and the eye is also changing its elevation and rotation angles. It seems likely that in *G. oerstedii*, as in the praying mantis (Rossel, 1980), the zone of fixation is surrounded by an annulus of ommatidia in the hemispherical regions (extending perhaps to the rim of the cornea) that generate saccades to direct the eye towards an object of interest. The situation is necessarily more complicated in a mantis shrimp than in a praying mantis, because the symmetry of the stomatopod eye is more complex than that of the insect, and the eyes are more mobile and independent, but a study of visual fixation should produce very interesting and informative results.

Wehner, in his synoptic 1981 review, discusses many insect species that perform some type of foveal tracking. In these cases, peripheral ommatidia are surely responsible for placing the eye's acute zone onto the visual target. Examples from crustaceans, however, are rare. In a study of target tracking by the single compound eye of the water flea *Polyphemus*, Young (1988) concluded that the system operates in an open loop; eye movements were related to the length of time

the image of an object remained within the field of view of an anterior patch of ommatidia. Another cladoceran, *Daphnia magna*, is capable of smoothly tracking a moving light at about half the target's velocity. This behavior is directed by a group of dorsal ommatidia and is used for control of body orientation (Consi *et al.* 1990). These are the only reports that we can locate concerning tracking by a specialized ocular region in any crustacean other than mantis shrimps. Regional specialization of function, however, is common in crustacean eyes, generally for control of optokinetic activity for ocular stabilization. For example, in crabs, optokinetic stimulation of lateral ommatidia produces the strongest responses (Sandeman, 1978; Nalbach and Nalbach, 1987; Barnes, 1990). These responses exist not to direct the eye towards an object, but instead to separate flow fields due to rotation from those due to translation. In the case of *D. magna*, cited above, distinct regions of the compound eye control 'flicking', fixation and tracking (Consi *et al.* 1990). Again, these responses are used for body orientation, not vision.

The triple compound eye of stomatopods is a unique visual organ, with a compartmentalization of function within its various parts. The hemispherical regions specialize in extended vision; in analysis of form, motion and position; and possibly in rangefinding as well. They direct the eye towards an item of visual interest and direct the tracking of a moving object. They probably also control ocular scanning movements (Land *et al.* 1990). In contrast, the midband appears to have no involvement in the control of eye movements. Its speciality is the analysis of spectral and polarizational properties of imaged objects, which it executes during the scans. The result of this regional specialization is a very compact, polyfunctional sensory organ that can be supported by relatively modest neural machinery. At this point, the means by which the several distinctive aspects of visual function are united in the stomatopod central nervous system remain a tantalizing mystery.

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