OCULAR TRACKING OF RAPIDLY MOVING VISUAL TARGETS BY STOMATOPOD CRUSTACEANS

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Summary

1. Ocular tracking in two species of stomatopod crustaceans, Squilla empusa (Say) and Gonodactylus oerstedii (Hansen), was studied by presenting animals with small targets moving to their right and left.

2. Squilla empusa showed no indication of ocular movement responses synchronized with the target's motion, whereas Gonodactylus oerstedii often tracked the target through large angular amplitudes.

3. The region of visual fixation in G. oerstedii is probably the ommatidial patches in line with the eyecup axis. This is suggested by the arrangement of ommatidial axes on the eye's circumference, and by the alignment of the eyes and the rotational motions they make as they observe an approaching target.

4. Tracking is irregular, probably because the animal pays attention to the target only intermittently. Targets are most stimulatory as they move nearly in front of an animal. Eye tracking responses become larger, more frequent and more accurate with increasingly anterior target positions.

5. During visual tracking, the eyes perform both smooth and saccadic tracking movements. Eye movements in the size range 7.5°–15° are made to near the position of the target at movement onset, but are less accurate relative to the target's position at the end of the movement.

6. During visual tracking, the two eyes apparently act with complete independence. Movements of one eye are uncorrelated with movements of the other, both for extreme and central locations of the moving target.

7. The existence of ocular independence during smooth pursuit and saccadic tracking in G. oerstedii may be possible because of the redundancy of visual fields existing in each eye, which could permit monocular measurements of distance to a viewed object. If so, each eye is capable of providing a complete description of the location of a target in space.

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Ocular movements of crustaceans have been well studied for over a century (reviewed in Wehner, 1981; Neil, 1982). Almost all the observations have been on decapod crustaceans, especially the crabs, lobsters and crayfishes (e.g. Horridge & Sandeman, 1964; Barnes & Horridge, 1969; Sandeman, 1978; Schöne et al. 1983; Okada & Yamaguchi, 1985). The mysids (Neil, 1975a,b) and euphausiids (Land, 1980) have also been examined. In general, this research has demonstrated that the stalked compound eyes of the decapods are well designed for stabilization of the visual field during changes in posture. These eyes also make optokinetic responses to movements of the whole visual field or parts of it, where the eye is driven by the rate of slip between it and the moving visual field. Under conditions of ocular stabilization or optokinesis, the eyes normally make conjugate movements (Barnes & Horridge, 1969; Nalbach et al. 1985), though in some species the eyes may exhibit a degree of independence (e.g. Palinurus interruptus, York et al. 1972). Tracking of moving targets on a stable visual background has not been reported.

Another major group of stalk-eyed crustaceans is the stomatopods, or mantis shrimps. Most stomatopod species are tropical, living in shallow, brightly lit marine environments. Their eyes are particularly interesting for two reasons. First, stomatopod eyes (with the exception of some deep-sea species) have triply overlapping visual fields for separate ommatidial groups in some directions of view (Exner, 1891; Demoll, 1909; Horridge, 1978; Schiff et al. 1986; Cronin, 1986b). This is possible because each oblong eye has a central band of 2–6 rows of ommatidia wrapping around it like an equator. The central band divides the eye into two halves, and its ommatidia share visual fields with groups of ommatidia in each half. Thus, the potential for range-finding exists in a single eye, though other advantages of such a design may also exist (Cronin, 1988). Second, stomatopod eyes have extreme freedom of movement. Unlike most decapod crustacean eyes, stomatopod eyes extend unobstructed from the extreme anterior end of the body. In some species they may move within at least a hemisphere of space. While moving, the eyes not only swing on their stalks but rotate on their axes through at least 90°. Rapid, apparently uncoordinated movements of the eyes in all three rotational degrees of freedom are immediately obvious to an observer (Milne & Milne, 1961; Cronin, 1986b). These two unique features of stomatopod eyes — monocular visual field redundancy and active, extreme mobility — may be functionally linked.

In spite of their unusual properties, stomatopod eye movements have been little studied. Schaller (1953) provided a qualitative account of ocular movement responses of Squilla mantis confronted with a moving target; both the eyes and antennules were reported to move actively under the conditions of his experiments. We report here experiments with two stomatopod species that possess eyes of different design and that inhabit very different visual environments. Squilla empusa, a species quite similar to Schaller’s (1953) S. mantis, is a coastal temperate species probably most active in dimly lit waters. Its eyes appear adapted
Visual tracking by stomatopod crustaceans

for vision in light-limited conditions (Cronin, 1986b). Gonodactylus oerstedii is a shallow-water tropical species, most active under well-lit conditions (Dominguez & Reaka, 1988). These two species were found to have very different ocular responses to moving targets.

Materials and methods

Squilla empusa was obtained from commercial fishermen in Beaufort, North Carolina, where we worked with it. It was kept in tanks supplied with running sea water and fed fresh shrimp meat. Gonodactylus oerstedii was collected in the Florida Keys and shipped to Catonsville, Maryland for study. It was maintained in aquaria in artificial sea water, supplied with small artificial burrows in which to live, and fed live or frozen shrimp.

For study, animals were placed in a small aquarium (15 cm x 30 cm x 18 cm deep) placed in a box lined with dark-blue paper. The environment was illuminated with fluorescent lighting. Experimental animals were in the planes of focus of two closed-circuit television cameras, one looking down from directly above the animal’s rostrum, and the other aimed horizontally from straight in front of the animal at eye level. We chose video techniques to observe eye movements because experiments were conducted in sea water under naturalistic conditions and because mantis shrimps poorly tolerate manipulations to their eyes, such as would be necessary to attach coils, magnets or wires. Experimental stomatopods were not confined or restrained; however, once accustomed to the experimental tank, S. empusa remained in the desired location throughout an experimental run. In the case of G. oerstedii, in some experiments the animals were tested in their artificial burrows, from which the eyes extended. In others, the animals were placed on a small circular platform with parallel rails on it separated by slightly greater than the stomatopod’s body width. Experimental animals readily inserted themselves between the rails, extending their anterior ends beyond them. The experimental platform could be placed inside a cylindrical chamber within the larger aquarium to isolate the animal from mechanical or other non-visual stimuli during an experiment.

A visual target was mounted on a transparent 3.0-mm diameter Lucite rod and moved at constant speed along a horizontal path. Experiments with S. empusa, and early experiments with G. oerstedii, used a plastic model shrimp about 2 cm in length as a target. In all experiments with G. oerstedii reported here, however, the target was a miniature yellow light bulb (filament length 2 mm). The light bulb occupied a much smaller visual angle than the plastic shrimp, making the interpretation of the angular data of the experiment more straightforward. The target was driven by an x–y recorder under analogue control from a microcomputer. When the light bulb was used it was monitored by a photodiode; when the bulb was switched on the computer immediately began providing signals for its movement. In some experiments, the target approached the animal from directly in front of its rostrum (Fig. 1). In other experiments, the target oscillated
horizontally to the right and left of the experimental animal 3–4·5 cm in front of and 0·2–1·0 cm above its rostrum (Fig. 1); the lighted filament subtended 2·5°–3·8° at its closest approach. During each experiment, video outputs from the two cameras were stored on videotape together with a common time signal to align their records and enable unique identification of each frame. The times when the target crossed the animal's midline were noted and used to compute the target's position throughout the experiment.

Angles of eye altitude and eye and body axis azimuth were measured directly from stopped frames of replayed video images at experimental intervals of 1 s (S. empusa) or 0·1 s (G. oerstedii). The television cameras were placed such that the raster orientation was horizontal in the front view, and perpendicular to the target track in the overhead view; thus, these orientations served as the baselines for measured angles. For S. empusa, measurements of the eyecup azimuth were made by hand using a protractor. Eye altitude angle was estimated by measuring the height of the video image of each eye and taking the inverse cosine of the value: (measured height)/(height when the eye was perpendicular to the camera). This method could be applied because Squilla's eye is tall and roughly cylindrical with hemispherical ends (see photograph in Cronin, 1986a).

Analysis of the data from G. oerstedii was performed using a video digitizer, which placed the image of a cursor on the replayed frame. The cursor was moved under computer control, and its current location could be stored when desired.

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**Fig. 1.** A schematic illustration of the experimental arrangement. For simplicity, the antennules of the mantis shrimp (in this case Gonodactylus oerstedii) are not drawn. The target moved along one of the indicated paths at a constant velocity. Experimental animals varied in size, but a rough indication of scale can be obtained by noting that the distance from the rostrum of the animal to the point where the oscillating target crossed the midline was 3–4 cm.
Eye azimuth was computed from the digitized locations of the centres of the eyecup base and tip in the overhead view, and the body azimuth was computed from the position of the rostrum and the position of the midline of the cephalothorax near its junction with the abdomen. Eye altitude was taken as the inverse sine of the ratio: \(\text{current eye height (centre of tip minus centre of base)}/\text{total eye length (eye tip to eyecup base when the eye axis is perpendicular to the camera axis)}\), as seen in the front view. Eyecup rotation angles (along the axis of the eyecup) were computed from the digitized positions of the dorsal and ventral ends of the eye’s central band of ommatidia, as seen from the front of the animal. These measurements were possible only when the eye was pointed nearly at the anterior camera.

Eye maps of \(\text{Gonodactylus oerstedii}\) were made using standard pseudopupil techniques (Horridge, 1978). An isolated right eye of an animal was placed on a two-axis goniometer in sea water. The eye was first lightly sprayed with black enamel paint to provide landmarks for later measurement. The eye was photographed at 5° intervals of visual space along the length of the central band (consisting of six rows of ommatidia). At each photographed position, the eye was rotated as required in the plane perpendicular to the plane of the photographic series so that a pseudopupil was always visible in the central band as well as the two hemispheres of the eye. The resulting photographs were analysed for the distance along the central band corresponding to each direction of view.

**Results**

### Eye movements in azimuth and altitude

**Squilla empusa**

Eye movements of \(\text{Squilla empusa}\) in response to a horizontally moving target are plotted in Fig. 2A. The plot shows the paths in space viewed by ommatidia looking perpendicular to the vertical axis of the eye (corresponding to the central viewpoint of the eye’s triple acute zone, see Cronin, 1986b) and parallel to the eyecup axis. During the 195 s of the experiment, both eyes moved about 30° horizontally and about 15°–20° vertically, but there was no apparent attempt to follow the target with the eyes. In some trials, the eyes exhibited apparent startle responses to the target’s initial movements, but in all experiments, with targets at distances from 5 to 20 cm, and moving with speeds from 1 to 5 cm s\(^{-1}\), no greater movements than those of Fig. 2A were noted. In this species, at least, ocular localization of objects in visual space seems not to require prominent fixation movements. In the absence of prominent responses, we did not evaluate ocular tracking in \(\text{S. empusa}\) further.

**Gonodactylus oerstedii**

\(\text{Gonodactyloid stomatopods have ovoid compound eyes on the ends of cylindrical eyecups (see Fig. 1). In contrast to \(\text{S. empusa}\), movements of the eyes of \(\text{G.oerstedii}\) in response to a horizontally moving target were frequently dramatic}\)
Fig. 2. Eye movements of mantis shrimps plotted as the points viewed in space by an animal situated at the centre of a sphere of visual space. Circles of altitude and azimuth are drawn at 30° intervals. Movements of the right eye (dark irregular trace), left eye (dotted trace) and target (dark smooth trace) are plotted. The animal faced directly towards the nearest point of the spherical surface; its right (R) and left (L) axes are indicated. (A) *Squilla empusa*. Azimuth is the extension of the eyecup axis, and altitude is the normal to the vertical axis of the eye. The target was located 4.0 cm in front of the animal and 0.2 cm below eye level, and it moved on a 9.6-cm path at 1.0 cm s⁻¹ for 10 cycles. (B) *Gonodactylus oerstedii*. Azimuth and altitude are both the extension of the eyecup axis. The target was 3.0 cm away and 1.0 cm above the animal at closest approach and moved at 5.2 cm s⁻¹ for eight cycles. (These data correspond to cycles 5–12 of the experiment of Fig. 6.)

(Fig. 2B). Although there were vertical excursions of the eyes, most of the eye movements were in the horizontal (azimuthal) plane. Since we confined stimulus movements to the azimuthal plane, henceforth we will discuss only eye movements in this plane.

Under the conditions of our experiments, visual tracking responses of *G. oerstedii* were remarkably idiosyncratic, and varied not only among animals, but even among successive runs with the same individual. On the first presentation of the target, apparent tracking responses were almost always observed, but they often continued for only a few cycles of target oscillation. Although we have observed such tracking in dozens of individuals in our experiments, we normally analysed only those experiments which on replay of the videotape record appeared to include fairly vigorous and continuous responses. These were best evoked by very rapidly moving targets (angular velocities up to 100° s⁻¹). Because each experimental run is unique, we prefer not to average among experiments. Instead, the results of selected experiments will be presented independently and analysed as if they formed a single data set.

*Eye movements in the horizontal plane*

The visual space of a gonodactyloid stomatopod compound eye includes most of
a spherical surface, so it was first necessary to determine whether there is an eye region that functions primarily for fixation of an object. For example, each eye might possess an acute zone serving this function. Because of the triple organization of the eye, we expected such an acute zone to occur, if at all, such that three ommatidial patches would contribute to it. Except at the borders of the cornea, sizes of individual facets vary only slightly across eyes of this species. Accordingly, we mapped locations on the surface of the eye, in the slightly twisted plane of the central band of ommatidia, viewing successive 5° intervals of space (Fig. 3). Although there is a noticeable spreading of visual axes between ±40°, a marked acute zone is not present. The general symmetry of ommatidial arrangement about 0° (the axis of the eyecup) suggests that the eyecup axis itself could define the vector of visual fixation.

This hypothesis is supported by observations of visual tracking during the anterior approach of a target (Fig. 4A). When the target was about 5 cm from the stomatopod, the two eyes moved to orientations roughly parallel to the target’s track and remained there throughout the rest of its approach. While in this position, each eye rotated rapidly on its axis. In some cases, only one eye appeared to track the target; again the tracking eye performed large, rapid rotations (Fig. 4B). Such actions also suggest that the fixation zone looks parallel to the eyecup axis, for if it were located eccentrically on the eye’s surface, rotational movements would move its visual field through a conical region of space. We observed sustained periods of large and rapid rotations of the eye like those plotted in Fig. 4 only during ocular tracking.

The results of both the eye mapping study and the experiments involving

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Fig. 3. Angles of view in the twisted plane of the central ommatidial band of the right eye of *Gonodactylus oerstedii*, projected onto a medial view of the eye. The 0° axis is that of the eyecup, and positive angles are normally dorsal to the animal (depending on eye rotation). Each plotted ray shows the centre of the ommatidial patch making up the pseudopupil as seen from that viewpoint. Ommatidial patches in the medial and lateral hemispheres of the eye also view each of the plotted directions in visual space.
Fig. 4. Ocular tracking movements in the azimuthal plane and ocular rotations of *Gonodactylus oerstedii* as a target approached from directly ahead. Target movement began at the times indicated by the vertical dashed lines, and each trace ends when the target reached the animal. The target, a miniature light bulb, travelled at 1.4 cm s$^{-1}$ and was 1.0 cm above the level of the animal's eyes. In each part of the figure, the top panel shows the movements of the right (dark trace) and left (light trace) eyes, and positive angles are to the animal's right. The bottom panel shows the rotational angle of the central band of the right eye (dark trace) and left eye (light trace, part A only; eye azimuth angles were too extreme to measure left eye rotation in B) as seen from directly ahead. Positive angles are counterclockwise in direction and measured from the horizontal plane. (A) Binocular tracking of the approaching target. (B) Monocular tracking of the approaching target.

tracking of anteriorly approaching targets suggested that the orientation axis of the eyecup is in line with the fixation axis of the eye itself. Accordingly, we used this axis as an indicator of eye alignment in all further work.

**Tracking of oscillating targets**

Experiments with ocular tracking of targets oscillating to the animal's right and left reveal a variety of features of stomatopod visual responses to movement (see Figs 5–8). Our experiments with *G. oerstedii* initially used the model shrimp as a
target. This target elicited strong apparent tracking responses quite unlike the eye movements of *S. empusa*, but because the target was so large it was difficult to know which part of it served as a visual fixation point. A miniature light bulb was used for subsequent experiments because it provided a more discrete and defined stimulus. All data reported here were obtained with the light bulb target. In Fig. 5 the azimuth angles of both eyes and the target angle are plotted. When the target was immobile, the eyes exhibited uncorrelated movements of various sizes, and the left eye apparently continued to observe the target after it stopped. However, eye movements were very different when the target was in motion. The tracking responses were complex; at various times one eye, or the other, both, or neither appeared to track the target. Furthermore, ocular tracking, when it occurred, involved slow smooth movements, rapid smooth movements, and saccadic flicks lasting one or a few tenths of a second. Particularly abrupt or large saccades are indicated in Fig. 5 by arrows. Tracking appeared to be mainly ipsilateral, but at times an eye tracked the target on the contralateral side as effectively as when it was ipsilateral.

The additional experiments of Figs 6–8 (top two panels in each) are plotted on a

![Graph](image)

Fig. 5. Tracking of an oscillating target, plotted as the azimuthal positions of the right eye (solid trace), left eye (dashed trace) and target (dotted trace) in *Gonodactylus oerstedii*. The target was illuminated, and it began to move, at time 12 s. It was driven through 15 cycles of movement, after which it stopped but remained lit. Eye positions are plotted at intervals of 0.1 s (small dots), and every 1 s is indicated by a larger dot. Positive angles are towards the animal's right. Arrows indicate onsets of some large, abrupt saccadic eye movements. The animal was contained within a chamber that isolated it from nonvisual stimuli (see Materials and methods). The target was 4.5 cm in front of the animal at closest approach, and it travelled at constant linear velocity along a 10.5-cm path.
compressed time scale, but they include the same features: intermittent tracking, mixing of smooth and saccadic responses, and varying accuracy. A consistent and striking result is the apparent lack of coordination between the eyes. This is best revealed in the mathematical analysis below, but it is obvious on inspection of the raw data as well. For instance, in Fig. 6 during target cycles 5 and 6, the right eye tracked well, whereas the left eye showed little evidence of response to the target. In the same experiment, the situation reversed on cycles 9 and 10, when the left eye tracked more accurately.

The data of Fig. 6 were obtained from an animal within an artificial burrow, so movements of the body axis could not be observed. The measured eye movements could have been largely caused by swinging of the animal's body axis in phase with the movement of the target, perhaps in preparation for launching a strike. In the experiments of Figs 7 and 8 the experimental animal was placed on a platform, exposing the whole body and enabling body axis measurements to be made (Figs 7 and 8, bottom panel in each). Although the body axis often moved as the target passed, its movements had a much smaller amplitude than the eye movements and contributed only slightly to target tracking.

In the experiments of Figs 5 and 8, the experimental platform was enclosed in a vertical cylindrical chamber, isolating the animal from all but visual input from the moving target. Tracking occurred as in the other cases, and movements of the body axis were slight. Thus, visual stimulation alone is sufficient for ocular tracking.

Differential plots of eye movements (Figs 6-8, third and fourth panels) confirm that during tracking, eyes of *G. oerstedii* undergo both smooth and saccadic tracking movements. The differential plots reveal a constant background of jitter, mostly reflecting the error inherent in measurements made from the video screen, but also caused by small eye movements (<5°) in the planes of both azimuth and altitude as well as rotational movements around the axes of the eyecups. Against this background are seen brief waves of activity, consisting of successive movements up to 10° in amplitude (per 0.1 s). These waves indicate periods of smooth tracking, and are particularly obvious in Figs 7 and 8. The smooth tracking responses may include very rapid eye movements, but even faster saccadic responses are clearly evident as spikes of very large amplitude (up to 300° s⁻¹). Small saccades could also occur, but these would be difficult to distinguish within brief bursts of smoother movements.

Movements of the two eyes were not usually coincident in time, but movements of either or both eyes were much more probable as the target approached or crossed directly in front of the animal (see below). Often the initial movements of the target were strongly stimulatory. For example, in Fig. 7, the animal's right eye initiated a saccade as soon as the target was illuminated and began to move, though the target was about 90° to the left of the eye axis at that time. The same eye immediately went into smooth tracking after the saccade.

The frequencies of eye movements in various size classes were computed, for periods both of target immobility and target movement. The analysed data were
Fig. 6. Oscillating target. The target was 3·0 cm in front of and 1·0 cm above the animal (*Gonodactylus oerstedii*) at closest approach. The target was illuminated and began to move at 3·1 s, and it moved back and forth at constant linear velocity along a path 6·5 cm in length. Positive values are to the animal's right. Because the unrestrained experimental animal was not precisely centred along the path of the target, angular excursions of the target differed slightly on each side. Solid traces: eye movements. Dotted traces: target. Positive angles are to the animal's right. Top two panels: movements of the right eye and target, and left eye and target, in azimuth. Bottom two panels: angular movements of the right eye and left eye in each 0·1-s interval of the experiment. Each vertical line plots the change in azimuth in a single interval.
Fig. 7. Oscillating target. The experimental arrangement was identical to that of Fig. 6, although the data are from a different animal (*Gonodactylus oerstedii*). The top four panels are as in Fig. 6. Bottom panel: angular positions of the body axis (dark trace) and target (dotted trace) in azimuth.

from the experiments of Figs 5–8; results are plotted in Fig. 9. Even when the target was stopped, eye movements in all size classes up to 30° (per 0.1 s) were initiated, but almost 90% of the movements were of 2.5° or less. However, in the presence of the moving target the frequencies of larger movements increased substantially. The eyes moved 5° or more almost 40% of the time, and this
increased to nearly 50% when the target moved within 10° of its closest approach to the animal.

Inspection of the raw data suggested that each eye moved independently. We tested whether the eyes truly act independently using the following analysis (Table 1). Probabilities of eye movements of 0°, 2.5°, 5°, 7.5° or 10° (±1.25°) for the right eye, left eye, or both eyes in a single 0.1-s interval in all experiments were determined (columns 2–4 of Table 1). (Larger movements occurred too rarely to
Fig. 9. Frequencies of eye movements of various sizes in the presence or absence of a moving visual target in *Gonodactylus oerstedii*. Movements are grouped into size classes at intervals of 2-5° (±1-25°). Solid line: eye movements when the target was stationary (*N* = 812). Dashed line: eye movements while the target was moving (*N* = 2710). Dotted line: eye movements while the target was moving, but only for target positions within 20° of its point of closest approach to the animal (*N* = 856).

Also computed was the product of the probabilities of right and left eye movement (column 5). The analysis was conducted for periods when the target was immobile and for various extents of target travel. If the two eyes had coordinated movements, then whenever one eye moved by a given amount, the other should also move by that amount, and the value in column 4 should be near those of columns 2 and 3, and considerably greater than that of column 5. If the movement of one eye inhibited the movement of the other, the value in column 4 should be much less than that in column 5, and near 0. However, if the two eyes were fully independent, the values in columns 4 and 5 should be approximately equal. In fact, in all cases the probability of having both eyes move by similar amounts very nearly equals the product of their individual probabilities of movement by that amount, providing strong support for the conclusion that the eyes are coordinated weakly, if at all. Movements of one eye neither stimulate nor inhibit movements of the other. This conclusion holds whether or not the moving target was present, and for all target angles.

Properties of the system controlling ocular tracking movements were examined by determining how eye movement amplitude was related to eye error angle. Error angle was defined as the difference, in azimuth, between current eye angle and current target angle (see Fig. 1), and the eye movement angle was defined as the change in eye azimuth in the subsequent 0-1 s. Since we could not distinguish unambiguously between large smooth tracking responses and saccades, and since periods of effective tracking were interspersed with periods of little or no tracking,
<table>
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<th>Maximum target angle (number of intervals)</th>
<th>Size of eye movement ($\pm 1.25^\circ$)</th>
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<th>Left eye</th>
<th>Both eyes</th>
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<td>$\pm 10^\circ$ (210)</td>
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</tbody>
</table>

The probabilities for the right eye, left eye and both eyes are taken directly from the original data of the experiments of Figs 5–8 (Gonodactylus oerstedii). The column ‘Right eye $\times$ left eye’ is the product of the independent probabilities of a movement of the right and left eyes.
all movements while the target was moving were treated equally. The results are
given in Fig. 10, which plots each eye movement vs its associated error angle. Each
panel of Fig. 10 was constructed for target angles less than or equal to various
angular extremes (compared with the point nearest the animal), given in the upper
left corner. Thus, as the extreme angle decreases, eye movements to more
peripheral target angles are excluded; only responses to more and more central
locations of the target are plotted. The responses of the right and left eyes are
mixed in each panel.

When all possible target positions were considered (Fig. 10, top left panel), the

![Fig. 10. Scatter plot of eye movement angles vs target error angles occurring in each
0.1-s interval of Figs 5-8. Each panel includes movements for target positions, relative
to closest approach, within the angular limits given in the upper left corner. (All: all
positions of the target.) Each point represents one eye movement, and all movements
of the right and left eyes are plotted. The error angle is defined as the separation in
azimuth between the eye angle and the target angle (see Fig. 1) at the beginning of an
interval. The product-moment correlation coefficient, \( r \), and the number of data points
in each panel, \( N \), are also given. All values of \( r \) are significantly (\( P < 0.01 \)) different
from 0. Note the difference between the horizontal and vertical scales. Positive values
are towards the animal's right.](image-url)
scatter plot consists of a cloud of points lying along the x-axis, together with a number of other points extending mostly into the first and third quadrants of the plot. The horizontal cloud presumably includes intervals of no response to the target, and most other points represent responses. The most notable change in the forms of the scatter plots as more and more anterior positions of the target are considered is the increased correlation between error angle and response angle (product-moment correlation coefficients are given in each panel of Fig. 10). The increased correlation is illustrated by the greater compression of points into quadrants 1 and 3, and by the disappearance of the cloud of points lying along the x-axis. When the target is within only 10° of closest approach, the estimated slope of the group of points, not including the cloud along the x-axis, is about +0.5, which suggests that on average the eye moves about halfway from its current location to the position of the target in a 0.1-s interval.

Average responses at error angles from −90° to +90° were calculated from the same data set (Fig. 11). The overall results corroborate the conclusions of the previous paragraph, but two additional aspects of gonodactyloid ocular tracking emerge on these plots. At small error angles (<15°) there is a close association between error angle and average response, with an estimated slope near +0.4. This is probably caused by smooth tracking responses when the eye is already following the target closely. The average response becomes irregular at larger error angles, but as increasingly anterior target positions are considered, the relationship between error and average response becomes closer and extends to larger error angles. The experimental stomatopods clearly tracked most faithfully when targets were near the extension of the anterior–posterior axis. These positions correspond to those within which raptorial strikes can be launched. Also, each eye moved most accurately when the errors were to its ipsilateral side. This is best seen for target angles within 10° of closest approach, when the left eye did better for negative than positive error angles (most points lie near the x-axis for errors >0), whereas the right eye did better at positive error angles. Each eye appears biased to move towards objects ipsilateral to it.

For the entire data set, error angles for all intervals when the target was moving averaged 24° (Fig. 12, upper left panel, solid horizontal line). The smallest eye movements were initiated on average at or near this error, supporting the hypothesis that these are not tracking responses, but instead are measurement errors or noise. Movements of intermediate sizes (7.5°–15°) were generally initiated at error angles slightly below the experimental mean, but the largest eye movements tended to occur at error angles well above the mean. Eye movements larger than 5° generally swung the eye towards the initial position of the target (Fig. 12, dotted traces). The eye error was less improved with respect to the position of the target at the end of the interval (Fig. 12, dashed traces), suggesting that little or no correction was made for target motion. However, in an average 0.1-s interval, the target moved 7.2°, although the separation between the curves plotting eye error following a movement (1) relative to initial target position (dots) and (2) relative to final target position (dashes) is less than this. This indicates that
eye movements do include some prediction of the moving target’s future position (or that the target’s position is sampled at intervals more frequent than 0.1 s). The two very large saccadic movements that occurred in this study (30° size class, Fig. 12, lower right panel) were directed accurately to target position at saccade onset, but included no correction for target motion during the saccade.

There was little association between eye movement angle and error angle in the overall data set (Fig. 12, upper left panel), but these angles became increasingly similar when the target was near the animal’s midline axis. For target angles within ±20°, eye movements of 10° or more are associated with error angles only slightly larger than the eye movement itself. Although the tracking system of gonodactyloid stomatopods is a sloppy one, it operates fairly effectively for target positions near the animal’s midline, particularly when the eye faces more than 10° away from the target’s position.

![Graphs](image-url)

**Fig. 11.** Averages of eye movements vs error angle (same data as in Fig. 10), plotted at 1° intervals of error angle. Each panel includes values for all target angular positions, relative to the point at nearest approach to the animal, within the limits given in the upper left corner. (All: all positions of the target.) (+) right eye averages; (O) left eye averages.
Discussion

Of the stomatopods, only *Squilla mantis* has had its ocular responses to moving objects examined previously. Schaller (1953) noted that this species, which is very similar to *S. empusa*, has pronounced movements of the eyes and antennules when a disk 1-0 cm in diameter is presented in motion at distances up to 15 cm from the eyes. He did not distinguish between tracking responses and alertness or startle responses, however. We have never seen *S. empusa* exhibit clear ocular
tracking movements, though we have noted that its antennules will sweep in the
direction of a large moving stimulus. The eyes of this species have limited freedom
of movement in azimuth, and their tall cylindrical shape could obviate the need for
fixation movements in that plane since the triple acute zone (Cronin, 1986b)
examines virtually the entire, almost horizontal, plane perpendicularly bisecting
the long axis of the eye. Azimuth may thus be encoded in the particular groups of
ommatidia viewing an object of interest. Squilla has no obvious means of
monitoring eye position, as its eyecups and eyestalks apparently lack propriocep-
tors (Sandeman, 1964), so a method for determining azimuth based on geometry
could very well out-perform one based on eye orientation.

In contrast to the situation in Squilla, ocular tracking movements like those of
Gonodactylus oerstedii have never previously been described. Stalk-eyed decapod
crustaceans have ocular movements of limited angular extent, and for effective
tracking the targets must move slowly — typically with angular velocities of
0.01°-1.5° s⁻¹ (Horridge & Sandeman, 1964; Barnes & Horridge, 1969; Okada &
Yamaguchi, 1985). With such stimuli, the eyes perform very slight movements
(<1°), which are normally conjugate and driven by a constant slip rate between
eye and target position (Horridge & Sandeman, 1964; Barnes & Horridge, 1969;
Sandeman, 1978). G. oerstedii, however, is well stimulated by targets having
angular velocities of nearly 100° s⁻¹, perhaps because such a fast-moving target
repeatedly acts like a novelty stimulus as it reverses course and moves back
towards the animal's midline axis (see next paragraph). Its responses reach
amplitudes exceeding 90°, and attain angular velocities during saccades of at least
300° s⁻¹.

Stomatopods may use motion-detecting systems unlike those of the decapod
crustaceans. In a study of single units in the optic nerve of Oratosquilla oratorio,
Ochi & Yamaguchi (1976) located no jittery motion fibres, yet these are common
in decapods (Wiersma et al. 1982). The only units responsive to movement were
fast movement fibres, which are infrequently encountered in decapods. Such
neurones could play a role in initiating the large and fairly accurate movements
characteristic of stomatopod ocular tracking. These fibres habituate rapidly (Ochi
& Yamaguchi, 1976), which correlates well with the irregular nature of gonodacty-
lid tracking. Each new set of responses to the oscillating target could occur because
the object is repeatedly perceived as a novel stimulus.

Some decapod crustaceans produce eye movements approaching those of
mantis shrimps in magnitude when they are stimulated to move their eyes in the
roll or yaw plane during whole-body orientation changes, movements of body
parts, or optokinetic stimuli in those planes (Neil et al. 1983; Varjú & Sandeman,
1982; Schöne et al. 1983). These responses are certainly employed to stabilize the
whole visual field and not to track part of it. Eye movements are invariably
conjugate during optokinesis, to the extent that an immobilized seeing eye will
drive the response of a freely moving but blinded eye (Horridge & Sandeman,
1964; Sandeman, 1977). The only crustaceans hitherto reported to swing their eyes
through angles larger than those we observed are midwater, vertically migrating
species. Their eye movements are used for orientation to the submarine light field, not for fixating individual objects (Land, 1980; Latz & Case, 1982).

In *Gonodactylus*, tracking is centre-weighted. When the target is within 20° of its point of closest approach, ocular movements are closely correlated with error angle, and the most frequent and accurate large tracking movements are initiated. This is in clear contrast to the optokinetic movements of the crab *Leptograpsus variegatus*, where lateral presentations consistently elicit the largest eye movements (Sandeman, 1978). The zone within which *G. oerstedii* can strike prey, competitors or predators extends anterior to the animal, and could define the region within which the most accurate ocular fixation is necessary.

The independence of the two eyes during observation of a single moving object is among the most remarkable aspects of stomatopod tracking behaviour. Independence of the activity patterns of the eyes of gonodactyloid stomatopods during scanning of the environment has been noted (Milne & Milne, 1961; Cronin, 1986b), but its occurrence during tracking was not suspected. Most descriptions of the eyes of these animals emphasize the involvement of both eyes in visual attention (Caldwell & Dingle, 1975; Manning et al. 1984a), often in stereotyped fixation positions. Yet fixation on an approaching target, which maintains a constant azimuth, is frequently monocular (e.g. Fig. 4B), and is normally accompanied by high-amplitude rotations of the eyes. Whether the stomatopods do coordinate their eyes in particular circumstances, and whether the eyes may simultaneously track separate targets moving on different paths, remain compelling questions for further research.

Among the other crustaceans, independent eye movements occur only in special conditions. Barnes & Horridge (1969) found that the two eyes of the crab *Carcinus maenas* were independent only during eye tremor (continuous movements <0.1°) or eye waving (associated with leg movements); even when each eye viewed a different stimulus their actions became synchronized. [This synchronization is strongest in very dim lighting conditions; it can be broken in bright light (Nalbach et al. 1985)]. More generally, stomatopods may be unique among animals with extensive binocular visual field overlaps. Chameleons are well known for the independent scanning movements of their turret eyes, but these eyes must show vergence for accurate location of an insect target (Harkness, 1977). Ocular independence should be more common in animals like fish, which have little binocular overlap. Nevertheless, many movements of the eyes of fish show temporal synchrony and binocular vergence (Fernald, 1985).

A terrestrial insect predator, the praying mantis, captures prey under visual control using a raptorial strike much like that employed by the stomatopods. Visual tracking in one species has been extensively analysed by Rossel (1980), and it is instructive to compare his findings with our own. Praying mantis compound eyes have an acute zone surrounded by a saccade-sensitive periphery; when peripheral ommatidia view a target an accurate saccade is generated to move the head axis so as to place the image of the target on the acute zone. Gonodactyloid eye movements also tend to bring the eye axis towards the target position, but the
presence of the equatorial band of six rows of ommatidia (Horridge, 1978; Manning et al. 1984b; Schiff & Candone, 1986) must complicate the control of the movements. Targets located along the plane of the central band would be viewed by very different classes of ommatidia from those along the perpendicular axis. Perhaps one function of the rapid eye rotational movements during tracking is to correct for the radial asymmetry of the eye.

Rossel (1980) found that tracking by a praying mantis may be saccadic or smooth, depending on the texture of the stable background. In our work, G. oerstedii viewed a bright target against a relatively featureless background, and ocular tracking invariably included a mixture of smooth and saccadic phases. In both the praying mantis and the mantis shrimp, smooth tracking occurred with high angular velocities of the target (exceeding $90^\circ\text{s}^{-1}$). Saccades of the head (praying mantis) or eye (mantis shrimp) had angular velocities up to several hundred degrees per second, and had durations of less than $0.1\text{s}$ to several tenths of a second. Unlike mantis shrimp saccades, those of the praying mantis included an accurate prediction of the future position of a moving target. Though similarities exist, the insect and crustacean species appear to direct ocular tracking through very different control systems. The objectives of the strikes of these two animals also differ – the insect must actually capture its relatively small prey, whereas the crustacean need only impact a victim which is often large relative to itself.

The normal purpose of visual tracking is to minimize the displacement of the retinal image of an object moving in the visual field. Typically, the image is placed on a retinal region of greater than average acuity, such as a fovea or acute zone. Insects having sessile (fixed) compound eyes may perform foveal tracking by moving either the head or the whole body (Mittelstaedt, 1957; Collett & Land, 1975; Rossel, 1980; Lehrer et al. 1985). The presence of eyecups mounted on eyestalks would seem to offer advantages over such a tracking system. Gonodactylus, however, does not have a well-defined acute zone, though these are known in other stomatopod species (Horridge, 1978; Cronin, 1986b). Fixing the eyecup axis on the target does permit the rotational oscillations seen in this species, which could serve for accurate ocular alignment. The ommatidial regions brought to bear on a target may have some as yet unknown specializations as well. For instance, they could contribute to form vision, hue discrimination or polarization analysis. Nevertheless, since proprioceptors monitoring eye position have never been found in stalk-eyed crustaceans (Sandeman, 1964; Horridge & Sandeman, 1964), fixation alone cannot provide the central nervous system with complete information for determining the precise location of an object. If eye orientation is to be used for judging the location of an external object, the information may reach the central nervous system through other sensory systems. For example, the eye commonly contacts the anteriorly directed antennules, organs that are usually well supplied with proprioceptors. Conceivably, for critical directions of a possible target (e.g., directly anterior to the stomatopod), eye axis orientation is determined by its contact with them. It is clear that G. oerstedii has some internal representation of
Visual tracking by stomatopod crustaceans

eye and target coordinates relative to itself, since it responds particularly strongly to targets directly in front.

In summary, stomatopod ocular tracking of high-speed targets, at least in the gonodactyloids, includes a variety of features, some typical of visual tracking systems and others less so. As in many other animals, tracking involves a mixture of smooth and saccadic responses, both apparently in response to visual error angle (though some correction for target velocity may be included). More unusual aspects are that tracking is irregular, rarely accurate, centre-weighted and independent in each eye.

Why should a species like *G. oerstedii* operate its eyes in this fashion? Like other stomatopods, this species spends much of its time in a confined burrow entrance, from which only the eyes and antennules protrude, and scans its immediate environment for predators, prey and competitors. Ocular independence would extend the angular field within which it could track approaching objects without exposing itself, and could increase the volume of space inspected per unit of time. Furthermore, territorial aggressive interactions are common among stomatopods, and their powerful raptorial armament allows them to kill or seriously wound conspecifics even in brief encounters (Caldwell & Dingle, 1975). We have found in the field that up to 2% of individuals have lost one eye, apparently in encounters with competitors or predators. Mantis shrimp compound eyes have the potential for range-finding in a single eye (Horridge, 1978; Cronin, 1986b; Schiff et al. 1986), and we have seen monocular stomatopods accurately direct strikes. As in other crustacean stalked eyes, neural apparatus capable of considerable processing exists within the eyestalk, so each eye may be competent to assess the range and identity of an object it views. Mantis shrimps could thus possess a uniquely specialized visual system, in which a pair of separate and largely redundant sensors operate autonomously in a single individual. It remains to be seen how the central nervous system deals with this type of sensory input, as well as how eye position is monitored during visual tracking.

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