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Optokinesis in gonodactyloid mantis shrimps (Crustacea; Stomatopoda; Gonodactylidae)

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Summary. 1. We investigated optokinetic eye movements in 3 species of stomatopod crustaceans *(Odontodactylus scyllarus, Pseudosquilla ciliata,* and *Gonodactylus oerstedii),* all of which are members of the superfamily Gonodactyloidea, by making video recordings of their behavior when placed at the center of a rotating striped drum. Results from these species were sufficiently similar to permit a general description of optokinesis in gonodactyloid stomatopods.

2. Within the range of drum speeds tested (0.40 to 33.6° s^{-1}), the eyes frequently moved smoothly in the direction of the drum's rotation. The movements of the 2 eyes were only weakly coordinated, and optokinesis occurred with an irregular and intermittent time course.

3. Closed-loop gains varied with the drum's speed of rotation, ranging from 0.4 to near 1.0. The gain did not depend on the orientation of the eye in space, remaining relatively constant as the eye swung on its point of attachment to the anterior end of the animal or rotated on the eyestalk axis.

4. In *O. scyllarus* (the only species tested), optokinetic eye movements in the animal's vertical, dorsoventral plane occurred with characteristics similar to those in the horizontal plane.

Key words: Optokinesis – Eye movements – Mantis shrimp – Stomatopod – Orientation

Introduction

The stomatopod crustaceans, or mantis shrimps, have compound eyes that are unique in structure, and probably in function as well. Each eye has 3 distinct regions, two extended arrays of ommatidia (termed the hemispheres) and a midband between them which contains a linear array of 2 or 6 rows of ommatidia. Visual fields of the hemispheres overlap to some extent, and the ommatidia of the midband view a smaller strip of space, roughly 5° wide, within the region of overlap (Horridge 1978; Schiff and Manning 1984; Cronin 1986; Marshall 1988).

Of the 4 modern superfamilies of stomatopods, the Gonodactyloidea contain the species that have eyes with the greatest mobility and most extreme functional specialization. Midbands in the compound eyes of gonodactyloid mantis shrimps include 6 parallel ommatidial rows, each of which is anatomically distinct (Marshall 1988). The structural specializations apparently permit this part of the retina, and only this part, to perform a detailed analysis of the spectral and polarizational content of light (Marshall 1988; Cronin and Marshall 1989a, b). The remaining parts of the retina, which cover by far the bulk of the total visual field, are more like the retinae of other crustaceans, having extended spatial coverage but more limited abilities to analyze for wavelength or polarization.

Thus the eye is faced with a conundrum. To use the peripheral, hemispheric retinae, the eye should be stabilized relative to the visual world. But since the midband's field of view is linear, eye movements are necessary to bring its ommatidia onto objects of interest and to integrate spatial with spectral and polarizational information. The problem is apparently solved by time-sharing; the eye alternates between immobility and performing characteristic scanning movements that translate the fields of view of the midband ommatidia across a part of the visual world (Land et al. 1990). As in most other visual animals, during the stationary phases the eyes' immobility may be maintained by an optokinetic feedback loop that actively opposes image slip (Land et al. 1990).

In the gonodactyloids, the compound eyes are able to move with unusual freedom on all 3 rotational axes. They can swing horizontally (in azimuth) and vertically (in elevation) through 120° or more, and can rotate on the eyestalk axis by at least 70° (Cronin et al. 1988; Land et al. 1990). To stabilize an eye in all 3 degrees of freedom demands a flexible control system. Crustacean optokinetic systems typically operate with quite different charac-

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teristics in each of the 3 rotational planes (Nalbach et al. 1989a). Further complicating the issue is the ability of the 2 eyes to move independently, and frequently to occupy very different postures concurrently. This would seem to imply either that the eyes must trade off periods of stabilization or that they must be directed at least in part by separate optokinetic control centers. In other crustaceans, even though each eye has its own control center (Barnes and Horridge 1969; Nalbach et al. 1985), most eye movements during optokinesis are conjugate (review: Neil 1982). This emphasizes an overriding role for central control.

As a companion study to recent research we have been doing concerning eye movements during tracking and scanning activity, we examined optokinetic eye movements in 3 species of gonodactyloid stomatopods differing in habitat, eye morphology, and retinal anatomy (Caldwell and Dingle 1975; Manning et al. 1984; Schiff et al. 1986): *Odontodactylus scyllarus, Gonodactylus oerstedii,* and *Pseudosquilla ciliata. O. scyllarus,* a large (10–15 cm) Indopacific species, lives among corals and may be active at virtually any time of the day or night (R.L. Caldwell, personal communication). Eyes of *O. scyllarus* have an almost spherical cornea, and the compound eye is mounted on a short eyecup, so that its pivot point is only slightly proximal to the eye's center (see photographs in Land et al. 1990). The smaller *Gonodactylus oerstedii* (2–3 cm) and *Pseudosquilla ciliata* (3–5 cm) are native to the Caribbean (*P. ciliata* is a cosmopolitan species; our specimens came from the Caribbean). Both of these species live in shallow water and are diurnally active, but *G. oerstedii* lives on hard substrate, such as coral or calcareous algae, while *P. ciliata* lives on sandy or muddy bottoms among submarine grasses. Their corneas are ovoid, and the eyecups are long, so that the eyes swing a considerable distance through space when they move (see drawings in Cronin et al. 1988). All three species have complex retinae with tiered photoreceptors and intrarhabdomal filters, and the organization of the retina and its visual pigments is known in detail for *G. oerstedii* and *P. ciliata* (Marshall 1988; Cronin and Marshall 1989a, b).

In this study, we wished to learn (1) the general pattern of optokinesis in the gonodactyloids, (2) whether the 2 eyes operate conjugately or independently during optokinesis, and (3) whether optokinetic stabilization varies in its effectiveness depending on eye posture.

Materials and methods

Animals. Odontodactylus scyllarus was obtained from local tropical fish dealers. *Gonodactylus oerstedii* and *Pseudosquilla ciliata* were supplied by collectors in Florida. Animals were kept in separate compartments in seawater aquaria at 25 °C, under a 12 h light: 12 h dark cycle.

Presentation of stimuli. During experiments, individual animals were restrained using rubber bands in a cylindrical Lucite tube, so that only the anterior end, rostrum, and eyes projected from the front of the tube and were free to move. The animal in the tube was mounted on a pedestal at the center of a drum 32 cm in diameter. The drum was marked with vertical black and white stripes of equal width; each pair of stripes spanned 30° in azimuth. To permit videotaping of the experimental animal's eyes, the drum was split horizontally into 2 equal halves separated by a 1.75-cm vertical gap level with the eyes. The total height of the drum, including the gap, was 18.0 cm, producing a vertical angle of 60° at the center. The drum was driven by a reversible electric motor through a geartrain, and its speed could be varied by changing the gear arrangement and by altering the voltage supplied to the motor. In these experiments, the drum's angular velocity varied from less than 0.5°/s to greater than 30°/s. The experimental chamber was brightly lit in all experiments; the typical light level was 150 cd m^{-2}.

Data collection and analysis. Videotapes were made and analyzed as described in Land et al. (1990), using a Sony DXC-101P CCD color video camera and a Panasonic AG 6200 videocasette recorder. A time signal was recorded onto the videotape throughout each experiment. The tape was played back at single frames for analysis, at intervals of 40 ms, 0.5 s, or 1 s. The video image was combined with a graphic 3-D model of the eye produced on an Acorn Archimedes 440 microcomputer. The model's image was manipulated by an observer, using a trackerball, until it matched the actual video image, at which time the angular coordinates of each eye were recorded. Angular values were recorded as azimuth, elevation, and rotation. These corresponded respectively to longitude, latitude, and bearing of Land et al. (1990). In some cases (experiments of Figs. 2, 3, and 7), videotapes were analyzed 3 times, producing a mean absolute accuracy of $\pm 5°$, and a repeatability of $\pm 2°$, on each axis (see Land et al. 1990). Other runs were analyzed only once.

Results

General features of optokinesis

The overall patterns of eye movements of our study species during typical bouts of optokinesis are illustrated in Fig. 1. In these experiments, the optokinetic drum rotated with an angular velocity of 6.4°/s and reversed its direction of rotation about halfway through the plot. The results for all 3 species illustrate features that are consistently observed during optokinesis. Both eyes have periods when they smoothly rotate in the direction of the drum, with angular velocities somewhat less than the drum's, intermingled with instances when one or both eyes make rapid flicks against or with the drum's direction, or by apparently spontaneous eye movements in other directions. Each eye has a distinctly individual time course of movement, and the 2 eyes are not closely coordinated in either the timing or the amplitudes of the movements.

These points are illustrated again, at a finer temporal resolution, in Figs. 2 and 3. (These data are from an experiment that also appeared in Land et al. 1990; see their Fig. 7c.) Periods of smooth optokinesis alternate with other movements varying in amplitude and velocity (Fig. 2A). During these smooth movements, only slight changes in elevation and rotation of the eye occur (Fig. 2B). In other words, although the eye may perform optokinesis at a variety of elevational positions and rotations, when doing so it is normally quite stabilized relative to the visual world at the current values of these angles. The tracks in visual space made by the projected eyestalk axes of the 2 eyes during this same experiment are plotted in Fig. 3. The tracks include stretches of purely, or almost purely, horizontal movements, repre-

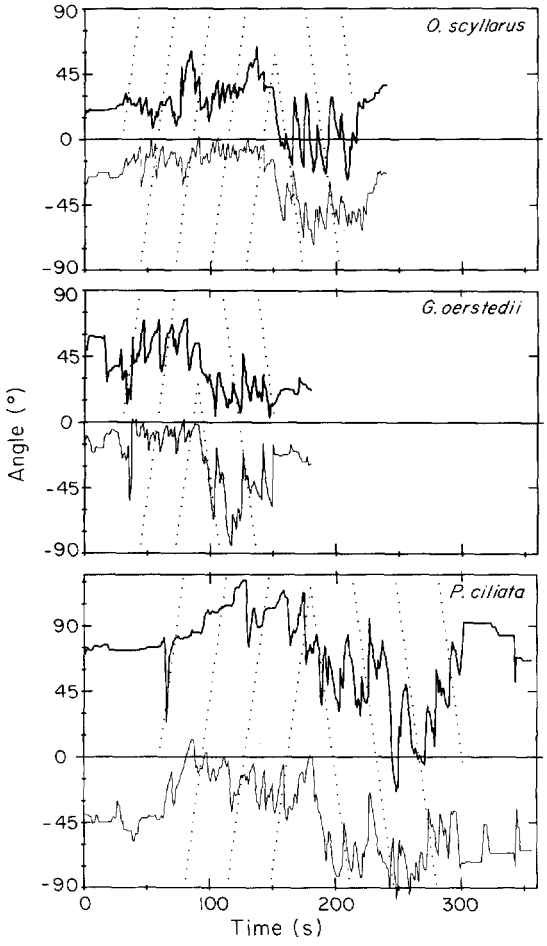

Fig. 1. Optokinesis in all 3 study species. Each experiment began and ended with a period during which the striped drum was stationary; during rotation the drum moved at 6.4°/s, reversing its course about halfway through the experiment. On all 3 panels, successive positions in azimuth of the right eye *(dark trace)* and left eye *(light trace)* are plotted at 1-s intervals. 0° represents the extension of the animal's midline and positive angles are to the animal's right. The dotted line indicates the overall movement of the striped drum, but does not identify the position of a particular white or black stripe. *Top panel: Odontodactylus scyllarus. Center panel: Gonodactylus oerstedii. Bottom panel: Pseudosquilla ciliata*

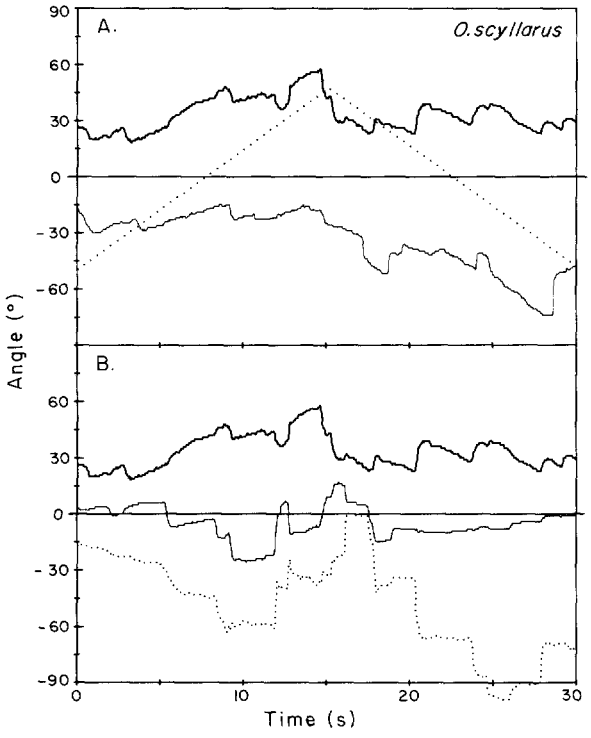

Fig. 2. *Odontodactylus scyllarus.* Optokinesis at a drum speed of 6.4°/s. Measurements made and data plotted at 40-ms intervals. The slight jitter seen in each trace is due to limits in the analytical technique and to the averaging of 3 records, and probably does not reflect small-amplitude eye movements from frame to frame. **A.** Movements in azimuth of the right eye *(dark trace)* and left eye *(light trace)*, plotted as in Fig 1. These data also appeared in Land et al. (1990, Fig. 7c). **B.** Movements of the right eye in azimuth *(dark trace)*, elevation *(light trace)*, and rotation *(dotted trace)*. Azimuth angles as defined for part A, elevation angles relative to the horizontal, and rotation defined as degrees clockwise from horizontal, with the acute zone medial to the extension of the eyestalk axis

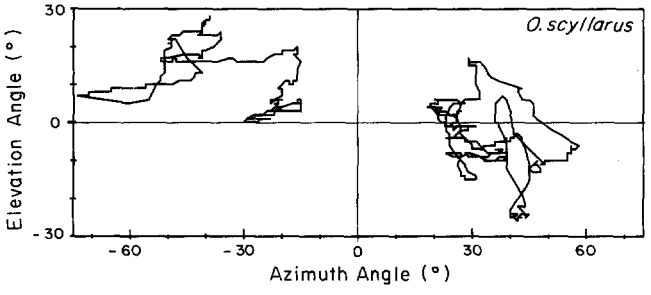

Fig. 3. *Odontodactylus scyllarus.* Tracks made by the right and left eyes in the experiment of Fig. 2. Successive positions (40-ms intervals) occupied in visual space by the extension of the eyestalk axis are connected with lines. The left eye occupies the part of the graph having negative values of azimuth, the right eye the positive values

senting optokinesis, separated by movements of various sizes in other directions. Each eye covered a separate region of space, and the overall patterns of movements of the eyes were very different. For example, the right eye tended to make many short optokinetic tracks with large excursions between them, while the left eye had much longer periods of stabilization, with generally smaller movements between these. A large proportion of the movements which are not clearly optokinetic are up-and-medial or down-and-lateral, and could represent scanning activity (Land et al. 1990). We shall return to this point later.

With visual inspection alone, it is difficult to assess how interdependent are the movements of the eyes during optokinesis. We therefore determined the cross-correlation coefficients of the movements of the 2 eyes of individual animals during periods of optokinesis, using standard techniques of correlation analysis (Sokal and Rohlf 1969). All 3 study species were analyzed, each at a variety of drum rotational speeds. Results are provided in Table 1. For movements in azimuth (the plane of the drum's rotation), cross-correlation coefficients (r) commonly lay between 0.1 and 0.5; in most cases these values

Table 1. Cross-correlation coefficients (r) for movements of the right and left eyes of the study species. The original data were taken from videotapes at sample intervals of 0.5 or 1.0 s, during periods when the optokinetic drum was in motion. The number of sample intervals included in each analysis (n) is indicated, as is the Figure number when the analyzed data also appear in a Figure. These data were also used for the computation of gains illustrated in Figs. 6 and 7.

Species	Drum speed ($°s^{-1}$)	n	r_{AZ}	r_{AL}	r_{RO}	Fig.
Odontodactylus scyllarus	1.8	285	0.131[a]	0.072 n.s.	−0.097 n.s.	
Odontodactylus scyllarus	6.4	182	0.567[b]	0.241[b]	0.025 n.s.	1
Odontodactylus scyllarus	6.4	315	0.376[b]	0.300[b]	0.033 n.s.	8
Odontodactylus scyllarus	13.2	90	0.788[b]	0.124 n.s.	0.242[a]	
Odontodactylus scyllarus	33.6	136	0.476[b]	0.181[a]	0.016 n.s.	
Gonodactylus oerstedii	1.8	120	0.067 n.s.	0.364[b]	0.155 n.s.	
Gonodactylus oerstedii	6.4	120	0.510[b]	0.142 n.s.	−0.086 n.s.	1,4
Gonodactylus oerstedii	13.2	120	0.474[b]	0.066 n.s.	0.041 n.s.	5
Gonodactylus oerstedii	33.6	120	0.438[b]	0.052 n.s.	0.159 n.s.	
Pseudosquilla ciliata	0.40	60	0.329[a]	0.293[a]	0.025 n.s.	
Pseudosquilla ciliata	0.84	75	0.461[b]	0.424[b]	0.379[b]	
Pseudosquilla ciliata	1.7	121	0.132 n.s.	0.253[b]	0.167 n.s.	
Pseudosquilla ciliata	6.4	241	0.185[b]	−0.120 n.s.	0.203[b]	1
Pseudosquilla ciliata	6.4	478	0.235[b]	0.146[b]	0.235[b]	7
Pseudosquilla ciliata	13.0	124	0.111 n.s.	0.081 n.s.	0.082 n.s.	
Pseudosquilla ciliata	21.8	119	0.085 n.s.	0.147 n.s.	−0.006 n.s.	
Pseudosquilla ciliata	33.5	121	−0.025 n.s.	−0.132 n.s.	0.061 n.s.	

r_{AZ}, cross-correlation coefficient for movements in azimuth; r_{AL}, cross-correlation coefficient for movements in altitude; r_{RO}, cross-correlation coefficient for rotational movements. The significance level of the correlation coefficient is indicated as follows: [a] $P<0.05$; [b] $P<0.01$; n.s., not significant

were significantly greater than 0. We therefore conclude that, in general, the eyes are coordinated in their movements. Nevertheless, the frequent incidence of low values of r indicates that coordination can be quite weak, or even completely absent. Cross-correlation coefficients for movements on the altitudinal and rotational axes were usually lower in value than those for azimuthal movements, emphasizing the independence of the drivers for each axis.

To illustrate the relationships between drum velocity and eye velocity, the results of 2 experiments with *Gonodactylus oerstedii* are plotted in Figs. 4 and 5. Eye positions in these experiments were measured at intervals of 1 s. Each experiment began with a 30-s period when the drum did not move, followed by 60 s of clockwise movement (to the animal's right), 60 s of anticlockwise movement, and a final 30 s of no movement. Angular velocities of drum movement were 6.4 and 13.2° s^{-1} in the 2 experiments, respectively. The amount each eye moved per second in azimuth was determined and is plotted in each figure for periods when the drum was stable (top), moving clockwise (middle), and moving anticlockwise (bottom).

When the drum was stopped, both eyes tended to remain immobile for most of the time; in about 80% of the intervals little or no movement occurred. This situation is described by Land et al. (1990; see their Fig. 7b). The relative immobility of the eyes is partly due to ocular stabilization relative to the striped drum, and probably also reflects the absence of any other interesting visual stimulus which might stimulate a fixation or scanning movement.

When the drum moved at 6.4°/s, the narrow distribution of movements just described broadened considerably, producing a histogram with a skewed shape and with a peak near the velocity of the rotating drum (Fig. 4, middle and bottom panels). The breadth of the distribution suggests that the optokinetic movements are not tightly clamped to the drum's movement, but may occur at a variety of speeds. In many intervals the eye moved very little. The distribution characteristically had a long tail extending in the direction opposite to that of the drum's rotation, representing nystagmic flickbacks of the eye, and often included a few very large movements – flickforwards – in the direction of the drum.

If the drum rotated at the higher velocity of 13.2°/s (Fig. 5, middle and bottom panels), the histogram of eye movements broadened even more and had a peak value below the actual drum speed. This shows that on average there was now a slippage between the velocity of the drum and that of the eye. Movements against the drum, however, occurred within the same size range as in the previous experiment.

Since in the experiments just described, measurements were at 1-s intervals, and the durations of eye movements may be much briefer than this (Land et al. 1990), the larger movements were no doubt completed in only a fraction of a sampling interval. We wished to know whether the flickbacks or flickforwards were like saccades, which are incompatible with normal vision and have angular velocities in excess of 100°/s, or were more like the scans described by Land et al. (1990), which had velocities near 40°/s in *O. scyllarus*. Data from this species in the experiment of Figs. 2 and 3, where measurements of the position of both eyes were done every 40 ms, were used for accurate estimates of these velocities as well

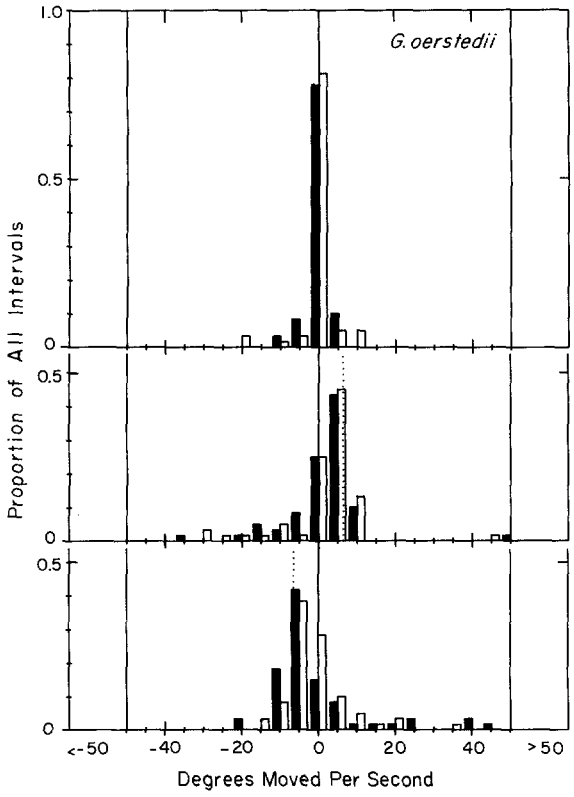

Fig. 4. *Gonodactylus oerstedii.* Histograms of eye movements in azimuth in the presence of a stationary drum *(top panel)*, or with the drum revolving with an angular velocity of 6.4°/s to the right *(center panel)* or the left *(bottom panel)*. The number of degrees each eye moved in each 1-s interval is grouped into bins centered at 10° increments. At each 10° position, the filled rectangle indicates the proportion of all left-eye movements and the open rectangle the proportion of all right-eye movements. The vertical dotted lines in the center and bottom panels indicate the angular velocity of the drum. These data are taken from the experiment illustrated in Fig. 1, middle panel

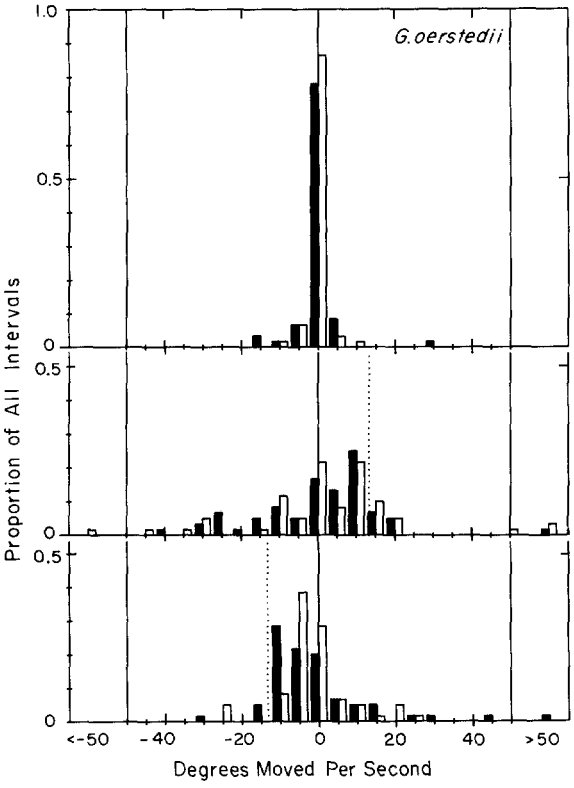

Fig. 5. *Gonodactylus oerstedii.* Histograms of eye movements in azimuth in the presence of a stationary drum *(top panel)*, or with the drum revolving with an angular velocity of 13.2°/s to the right *(center panel)* or to the left *(bottom panel)*. Otherwise as in Fig. 4

as the sizes and durations of the movements. Results are displayed in Table 2.

During optokinesis, the average great circle angle moved was about 6.9° and each movement lasted about 1.3 s with an average velocity just below drum speed. In contrast, the flicks were larger in size (9°–11°), were much briefer (near 0.3 s), and had velocities in a range near 35°/s. These values are typical of scanning movements (Land et al. 1990), suggesting that reasonably good visual function can be maintained throughout the entire cycle of nystagmus. The greatest velocity we observed during any 40-ms interval was 327°/s, which compares well with the maximum of 250°/s reported by Land et al. (1990).

Optokinetic gain

The results of the experiments of Figs. 4 and 5 indicated that optokinetic gain varies, as expected, with drum speed. We therefore carried out a series of additional experiments to learn more completely the relationship between gain and drum speed in our study species. Eye positions were analyzed at intervals of 0.5 or 1 s, and sections of each experiment's results in which the eye smoothly moved for several consecutive intervals in the direction of the drum were selected for computation of the gain.

In all species, the closed-loop gains (eye speed/drum speed) were between 0.8 and 1.0 when the drum rotated at velocities near 1°/s and declined at greater speeds (Fig. 6). Gains also decreased at very low drum speeds in *P. ciliata,* the only species for which we have data on optokinesis at these speeds. We might have underestimated the optokinetic gain at the extreme drum

Table 2. Characteristics of eye movements of *Odontodactylus scyllarus* during optokinesis. Data obtained from both eyes in the experiment of Figs. 2 and 3. Given are the mean and standard deviation for each class of movement. The speed of the drum was 6.4°/s in this experiment

Type of movement	*n*	Great circle angle (°)	Duration (s)	Angular velocity ($°s^{-1}$)
Optokinesis	26	6.87±3.95 SD	1.32±0.67 SD	5.54±1.96 SD
Flickback	15	10.98±6.24 SD	0.31±0.15 SD	39.11±20.13 SD
Flickforward	7	9.12±6.07 SD	0.26±0.14 SD	33.57±13.56 SD

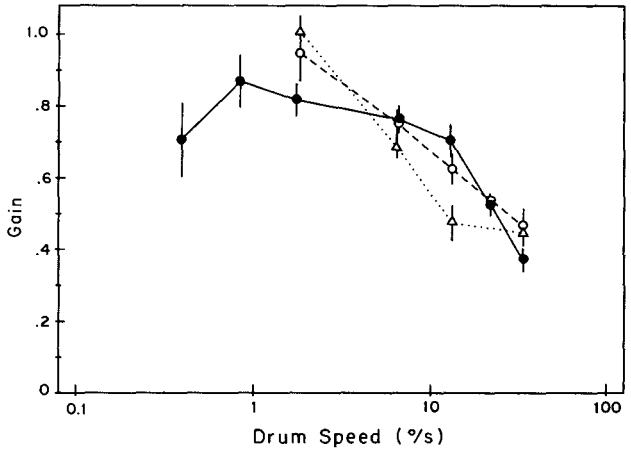

Fig. 6. Optokinetic closed-loop gains, computed as the ratio of the movement of an eye per s, in azimuth, to the angle rotated by the optokinetic drum in the same interval. Drum speeds are plotted on a logarithmic scale. Vertical lines indicate standard errors of the means. *Solid line, filled circles: Pseudosquilla ciliata. Dashed line, open circles: Gonodactylus oerstedii. Dotted line, open triangles: Odontodactylus scyllarus*

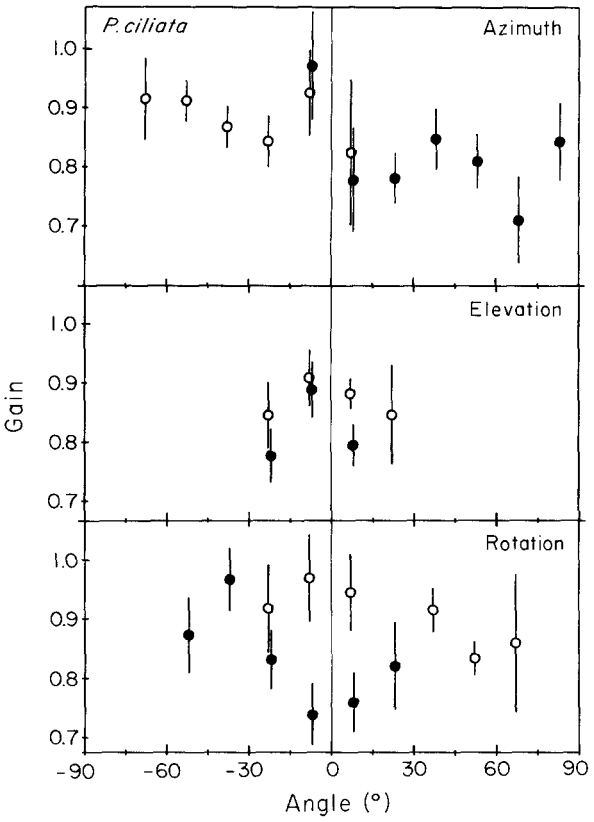

Fig. 7. *Pseudosquilla ciliata.* Optokinetic closed-loop gains, computed as in Fig. 6. Drum speed: 6.4°/s. Results are grouped into bins at 15° intervals, as described in the text. Vertical lines indicate standard errors of the means. *Closed circles:* right eye. *Open circles:* left eye. *Top panel:* Gains plotted vs. eye azimuth. 0° is the extension of the body axis; positive values are to the right. *Middle panel:* Gains plotted vs. eye elevation. 0° is directly horizontal at the level of the eyes; positive angles are above the horizontal. *Bottom panel:* Gains plotted vs. eye rotation. Angles are those of the midband, measured up from the horizontal with the acute zone of each eye located medially to the extension of the eyestalk axis

speeds, since at very low drum speeds the eye had to remain moving for several seconds before its angle changed sufficiently to be measured, while at very high drum speeds an eye may have completed a single optokinetic sweep in a very few measured intervals, but this does not qualitatively affect our conclusions.

Due to their extreme mobility, gonodactyloid eyes become stabilized optokinetically in a great variety of postures, as is well illustrated by the data of Figs. 2 and 3. We wished to learn whether the stabilizing mechanisms operate equally effectively for any eye position, or whether there is a systematic variation in optokinetic gain with change around one or more of the angular axes. The experiment was performed with *Pseudosquilla ciliata,* at a drum speed of 6.4°/s (which should produce a gain near 0.8, see Fig. 6), by allowing optokinesis to continue for over 20 min. A section of the videotape record 500 s in length was taken from within this long run, analyzed 3 times at 1-s intervals, and the results were averaged. From the averaged data set, 149 optokinetic tracks were selected. Throughout each of these tracks, in every interval, the eye position along all 3 rotational axes was noted and the amount the eye moved in the next 1 s was determined. Thus it was possible to compute closed-loop gains for every eye position occupied during optokinesis throughout the analyzed section of the tape. Data were gathered into groups separated by 15° for the computations of means and standard errors, and the results are displayed in Fig. 7.

Although each panel of Fig. 7 includes gain values ranging from about 0.75 to 0.95, there is no systematic variation in gain with eye position. In cases where there appears to be a relationship between gain and eye angle in one eye, the other eye expresses a different association, and the overall results are essentially constant. Thus, gain remains near 0.8 for eye azimuth values from about 10° contralateral to 80° ipsilateral, for elevations between ±30°, and for roughly 90° of rotation of either eye. Since each eye is controlled by at least 3 drivers (Land et al. 1990), all of these must be reasonably well corrected for eye position, producing an extraordinarily flexible optokinetic system. Furthermore, the gain constancy with angle of rotation implies that these drivers must interact in a complex fashion, such that appropriate optokinetic responses can be generated by ommatidial rows making all possible angles with the eye surface. Similar results were obtained from less exhaustive experiments with the other species.

Optokinesis on other axes relative to the body

The observation that optokinetic gain varies little with eye orientation suggests that optokinesis could occur with similar characteristics along many axes relative to the animal's body. We tested this by mounting an individual of *O. scyllarus* in the optokinetic apparatus with its right side down. The drum rotated at 6.4°/s in the

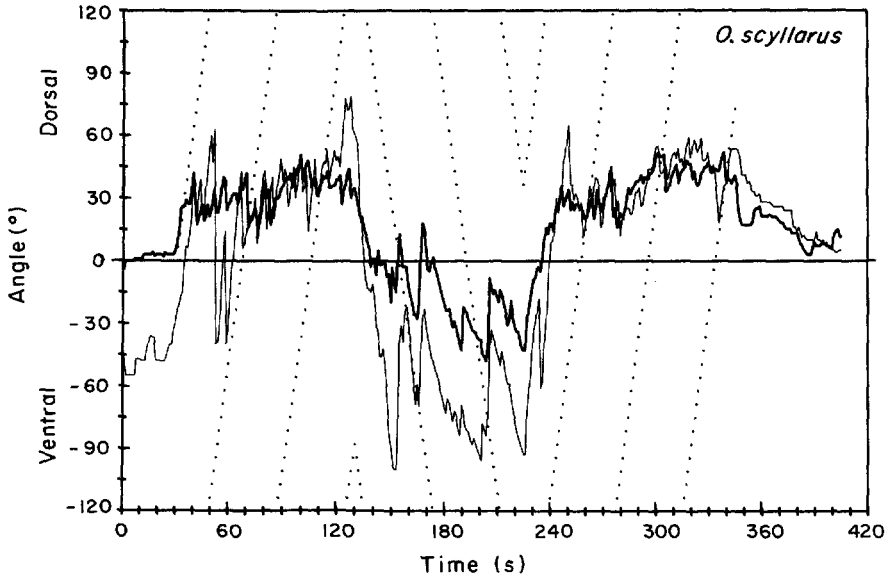

Fig. 8. *Odontodactylus scyllarus.* Optokinesis in an animal mounted with its right side facing downwards, so that movements of the drum occurred in the animal's dorsoventral plane. The plotted angles are in the plane of the drum's rotation; positive slopes, indicating rotation to the right, are in the animal's dorsal direction. Drum speed: 6.4°/s. The drum's rotation is indicated by the dotted lines; its direction of rotation reversed twice during the course of the experiment. *Dark trace:* position of the right eye. *Light trace:* position of the left eye

horizontal plane, thus acting as an optokinetic stimulus in the animal's dorsoventral plane. Results (Fig. 8) were very similar to those obtained when the animal was mounted in its normal, horizontal posture (compare Fig. 8 with the top panel of Fig. 1). The movements of the 2 eyes were now primarily dorsoventral, and their cross-correlation coefficients were similar to those obtained when the animal was mounted normally (Table 1). Note that because of the 90° rotation of the animal, azimuthal and elevational movements are now controlled by the drivers that actually deal with movements in the animal's dorsoventral and right-left planes, respectively. Periods of smooth responses of variable length alternated with times in which the eye movements were apparently independent of the drum's rotation. Closed-loop optokinetic gain in this experiment, measured during the smooth phases, was 0.79. This is similar to the values obtained at the same drum speed when the animal was mounted normally (Fig. 6, Table 2).

Discussion

We selected for study 3 species of gonodactyloid stomatopods that have quite different habitats, ecological niches, overall eye shapes and sizes, and details of retinal anatomy (Caldwell and Dingle 1975; Manning et al. 1984; Schiff et al. 1986; Marshall et al., unpublished). Yet their optokinetic systems have a number of similar properties. In all species, optokinesis in each eye occurs somewhat independently, closed-loop gains are roughly equal at similar angular velocities of the environment, nystagmus is irregular and fairly sloppy, and optokinesis appears to be unaffected by either eye position or the orientation of the animal. Taken together, these results indicate the presence of an ocular stabilization system that has similar gains along both rows and columns of ommatidia, that is insensitive to the direction the eye may be currently pointing, and that can operate each eye individually. Such a system is not only flexible, but also in some ways unlike any other yet described, particularly in the way the 2 eyes are handled.

Eye movements resembling those of optokinesis may be initiated in many crustaceans by non-visual sensory systems, for example by the statocysts or by movements of the legs (see review of Neil 1982; also Nalbach et al. 1989b). Crabs, for instance, usually orient the eyes and their movements to the vertical axis. We do not yet know whether similar control systems exist in stomatopods (which lack statocysts), but they seem likely to be absent in the gonodactyloids. These animals may adopt almost any posture while in their burrows, and the eyes constantly perform spontaneous movements that appear to be either scans or voluntary refixations. In these circumstances, the stabilizing influence of optokinesis would best be left under the influence of purely visual input.

In other crustaceans, the eyes are invariably coupled during optokinesis (review: Neil 1982). The amount of coupling may vary among species (e.g. Barnes and Horridge 1969; York et al. 1972) or under different environmental lighting conditions (Nalbach et al. 1985), but it is always present. This produces a characteric optokinetic nystagmus (see the description in Horridge and Sandeman 1964), in which both eyes together drift slowly in the direction of visual field movement and at regular intervals simultaneously and rapidly flick back to their original positions. A graphical plot of such activity produces similar sawtooth patterns for both eyes. To break the coordination, Nalbach et al. (1985) had to provide different optokinetic stimuli to each eye; even under these conditions one eye frequently became locked to the movements of the other.

We were stimulated to study the eye movements of gonodactyloid mantis shrimps because even casual observation of these animals reveals a bewildering amount of apparently independent ocular activity. It now appears that this initial impression of independence is largely correct, at least in the visual behaviors of optokinesis,

spontaneous relocation of gaze, tracking (and presumably visual fixation), and scanning (Cronin et al. 1988; Land et al. 1990). In the gonodactyloid stomatopods, the eyes seldom, if ever, become tightly linked, even when they view the same stimulus simultaneously.

The concordance of results obtained with the quite distinct visual behaviors of tracking, scanning, and optokinesis must point to the operation of two central control centers for ocular activity, which in most situations interact only weakly. Nevertheless, the visual fields of the 2 eyes overlap extensively, and for some eye positions virtually completely, so the central nervous system must somehow combine their inputs in forming an internal representation of the visual world. Onto this representation are presumably painted the spectral and polarizational information inputs from the ommatidia of the midband during ocular scanning. The overall picture is of an extremely odd and complicated visual center, and at this point it is difficult to know – or even predict – its structure or properties.

These experiments were performed under closed-loop conditions; in other words, the movements of the eyes directly affected the animal's view of the world. A common technique used with crustaceans to open the loop (so that the movements of the eye cause no change in vision) is to immobilize an eye that is allowed to view a moving scene, and monitor the movements of the second eye, which has been blinded (Horridge and Sandeman 1964). Preliminary results suggest that similar techniques can be applied to mantis shrimps, although their interpretation is complicated by the weakness of intraocular coupling. Open-loop experiments might also be attempted with the eye attached to an immobile torque meter so that the torque produced by the muscles of the eyestalk could be monitored.

The large degree of ocular independence, together with the great mobility of mantis shrimp eyes, implies that the visual system is concerned with finding objects of interest, particularly those that contrast with or move against the background. With the eyes stabilized, even if they view disparate regions of the visual world, moving objects would stand out. But the incoming information must also be compiled into a useful representation of the world and its spatial organization with respect to the animal. There is some evidence that mantis shrimps have an awareness of the locations of visual objects relative to their bodies (Cronin et al. 1988), and their predatory strikes could only be launched accurately under visual control if such an internal map of visual space existed. Yet there are probably no proprioceptors associated with the eyestalk or eyecup (Sandeman 1964). This leaves monitoring of efference to the optomotor system as the only reasonable means of knowing eye position – unless the purpose of the uncoupled eye movements is to allow one eye to watch the other to see where it is pointed!

Ultimately, we still seek an explanation for the extreme mobility and independence of these eyes. It is difficult to conceive how the apparent sloppiness could benefit stomatopod vision. A proper understanding of optomotor design and control in mantis shrimps will require the integration of additional laboratory work on ocular movements with appropriate studies of relevant aspects of their behavior and ecology.

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