

SPONTANEOUS AND EVOKED EYE MOVEMENTS IN *POLYPHEMUS PEDICULUS* (CLADOCERA: CRUSTACEA): A CASE OF OPEN-LOOP TRACKING?

BY STEPHEN YOUNG AND VICTORIA A. TAYLOR

*Department of Pure and Applied Biology, Imperial College, Silwood Park, Ascot,
Berks SL5 7PY*

Accepted 7 April 1987

SUMMARY

1. *Polyphemus* eye movements were recorded in both pitching and yawing planes, both in a static visual environment and with a sinusoidally moving stimulus.
2. Spontaneous eye movements (average amplitude 1.7°) had different properties in the two planes, with trembling movements predominating in the pitching plane. A contour-sharpening function is proposed for these movements.
3. An attempt to analyse the eye movement response system using a Bode diagram shows a very poor fit to the data, leading to the conclusion that a closed-loop control system is an inappropriate model in this case.
4. The evoked eye movements are most convincingly represented by a model in which the time the stimulus takes to traverse a restricted sensitive zone in the central region of the eye controls the duration of a subsequent constant angular velocity saccade. The direction of the response movement follows the direction of the stimulus. A small-object tracking function is proposed for these movements.

INTRODUCTION

Crustacean visual systems are relatively simple, and have been extensively studied. The use of eye movements to keep moving objects in the field of view of the central eye region ('tracking') is common, as is the stabilization of the animal's visual world during turning manoeuvres by eye movements in response to large-field stimuli (optokinetic nystagmus).

In both these cases the eye movements are thought to be controlled by a visually mediated negative feedback loop (Horridge, 1966; Horridge & Sandeman, 1964; Wehner, 1981). Our observations of the eye movements made by the cladoceran *Polyphemus pediculus* in response to moving stimuli cannot be satisfactorily explained by this mechanism, and we present here an alternative model which does not involve continuous control of the eye position by visual feedback.

Polyphemus pediculus is a planktonic predator some 3 mm long, common in lakes and ponds in southern England in the summer and autumn months. Its morphology is dominated by a single large compound eye with 130 ommatidia, secured inside the

Key words: *Polyphemus*, Cladocera, eye movement, open-loop, control.

transparent head capsule by muscles capable of rotating it like a ball in a socket. We recorded eye movements in both the horizontal and vertical (sagittal) planes. The long axis of the animal's body is horizontal during swimming, so eye movements in the horizontal plane are yawing movements, and those in the vertical plane are pitching movements.

Eye movements in both these planes occurred constantly even in a static environment, but if a moving stimulus was introduced these apparently random, trembling movements were replaced by larger, steadier movements which followed the direction of the moving stimulus.

The eye movements in response to a sinusoidally displacing target were recorded for a range of frequencies and amplitudes, allowing an attempt at an analysis of the system as a linear servo-mechanism (McFarland, 1971; Montgomery, 1983). This model, essentially a continuous negative feedback system with closed-loop control, has proved a poor fit to the data, compared to a mechanism involving ballistic response movements (open-loop saccades) fired off after a brief experience of the stimulus. The target chosen for the major part of this study was a narrow, dark, vertical bar viewed against a uniform bright background, but some observations were made with a bright bar seen against a dark background, and with a single bright/dark boundary.

MATERIALS AND METHODS

Animals

Our *Polyphemus* were collected from Virginia Water lake (Surrey, England), and maintained in pond water in the laboratory at a constant 20°C with a 12 h:12 h L:D cycle with gradual dawns and dusks. They were fed on young stages of *Bosmina* sp. and *Daphnia* sp., and cultures could be maintained for several weeks.

Experimental animals were immobilized by glueing to a small cover slip with 'Daphnia cement' (red sealing wax dissolved in a little alcohol: Scourfield, 1900), rinsed well with pond water, and positioned in the centre of a plastic Petri dish (36 mm in diameter) containing 6 ml of pond water, placed on the stage of an inverted microscope. A 50× long-working objective produced a large image of the eye on the tube of a video camera, positioned at the microscope phototube. No eye-piece or camera lens was used, and an infra-red pass filter in front of the microscope lamp prevented any visible light reaching the animal's eye from that source. Animals were positioned on one side to measure pitching movements, and either dorsally or ventrally for yawing movements.

Visual stimulus

A horizontally mounted circular fluorescent tube (Philips type TLE, 22 W) surrounded the Petri dish and provided a bright evenly-lit background, whose height subtended 21° at the animal's eye. The tube was connected to a 240-V d.c. power supply in series with a resistive ballast, adjusted to give a current through the tube of 65 mA, corresponding to a light intensity at the animal's eye of 2.73 W m^{-2} ,

measured from 350 to 680 nm with a radiometrically corrected PIN photodiode (Young, David & Gibson, 1987). The luminance (apparent brightness) of the fluorescent tube surface, measured with a spot photometer, was $6.0 \text{ W sr}^{-1} \text{ m}^{-2}$. For comparison, measurements taken with the same photometer out of doors on a bright but lightly overcast February day at 11.00 h showed a sky luminance of $44 \text{ W sr}^{-1} \text{ m}^{-2}$ at the zenith and $14 \text{ W sr}^{-1} \text{ m}^{-2}$ near the horizon. These readings were calculated from photometric units using conversion factors of 360 lm W^{-1} for the lamp and 197 lm W^{-1} for the sky light. Each tube heater was kept warm throughout with a separate small mains transformer rated at 6 V a.c. This method of operation eliminated all 100 Hz flicker from the light.

The stimulus activator was made from a meter movement mounted with its spindle vertically above the animal's eye, so the tip of the pointer described an arc centred on the eye. A black card strip subtending 6° at the animal's eye was fastened hanging down from the end of the pointer to provide the actual stimulus. Its lower end came very close to the microscope stage. When a sine wave oscillator was connected to the meter coil, the black strip described regular movements in the horizontal plane in an arc centred on the animal's eye, just outside the circular dish containing the animal. A bright stimulus bar could be produced by suspending a cut-out mask from the meter needle, and occluding the majority of the lamp circumference with black paper. A single-edge stimulus was improvised by moving a black cardboard mask by hand, using a pair of tweezers.

Recording

The microscope stage and stimulus bar were viewed from above by another video camera, whose image enabled the stimulus position to be read off against a protractor scale engraved on the stage. The central part of this camera's picture was occupied by a disc of black material, to allow the image of the *Polyphemus* eye from the second camera to be superimposed electronically. The mixed outputs from the two cameras thus provided a registered image of both the eye and the stimulus. Because the stimulus was seen from the 'wrong side' it was necessary to compensate for the left/right inversion of the picture by reversing the horizontal scan coil connections on the second camera. We set up the cameras without the stimulus in place, using a Perspex plate with a large cross-shaped graticule pattern, and positioning the cameras so that the magnified image of the centre of the graticule from the lower camera exactly overlaid the macro image of the whole graticule from the upper camera. We checked that the sense of rotatory movements of the images was the same for both cameras.

After mixing, the video signal was connected *via* a time-marker box to a National video recorder. Fig. 1 shows a typical single frame from the video tape. At the beginning of each run an animal was positioned in the dish with the central region of its D-shaped eye directed towards the stationary stimulus bar, and 15 min was allowed for adaptation to the stimulus conditions. Video recording then began, with a 30-s recording period for each of a range of stimulus amplitudes and frequencies, and for control periods with the stimulus bar stationary. The amplitude of the

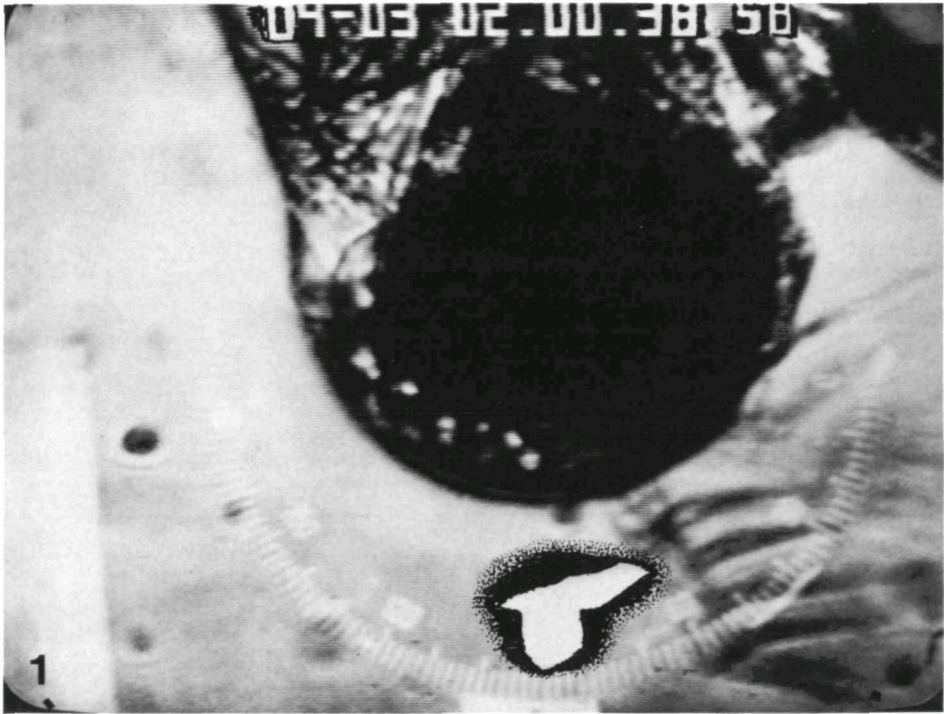


Fig. 1. Photograph of a single video frame, showing the time marker at the top, and the image of the eye superimposed on a view from above of the stimulus bar (emphasized) and the protractor scale.

response to a fixed low-frequency stimulus was checked at the end of each run so that any adaptation or fatigue could be detected.

Analysis

Tapes were analysed frame by frame, reading off the stimulus position directly from the engraved protractor scale, and measuring the eye position angle by superimposing a drawing (itself traced from the monitor screen onto acetate sheet) mounted on a circular protractor. Fig. 2 shows the use of a sheet of neutral-density Perspex as a half-reflecting mirror to view the drawing in the plane of the monitor screen. The protractor was centrally pivotted on a piece of plywood resting against the parallel ruler on a drawing board, so the drawing could be moved sideways and up and down the screen without twisting. This allowed for slight movements of the animal's head; records with large head movements were discarded.

Three sets of measurements were made for each condition: the clock time from the video time marker, the stimulus angle, and the eye angle. For stationary controls, only the eye angle was recorded. These data files were analysed by using autocorrelation to measure the stimulus frequency, cross-correlation between stimulus and response to measure the lag, and averaging of repeated cycles to measure stimulus and response amplitudes. At least six cycles of stimulus and

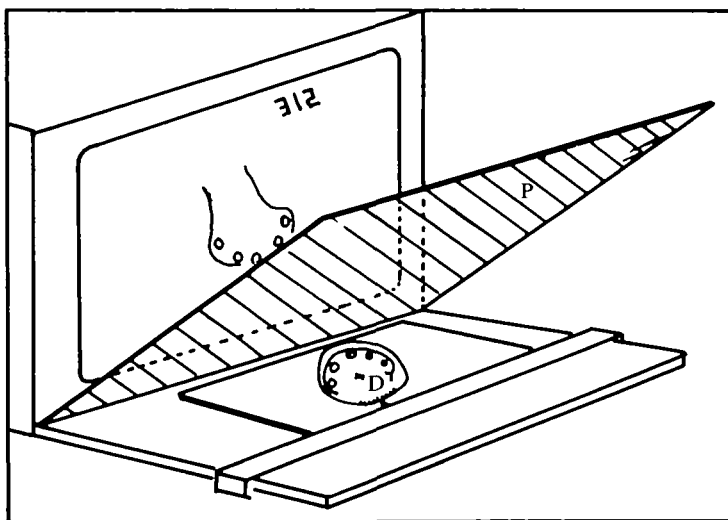


Fig. 2. Equipment for digitizing the video record. The observer sits in front of the monitor and looks at the screen. The tracing of the eye (D) is reflected in the neutral Perspex sheet (P), and appears to be drawn on the monitor screen.

response were digitized in each case. The eye's slew rate (rotational angular velocity), and the speed of the stimulus relative to the eye while passing the centre of the eye were determined by subtracting each value in the relevant column from its predecessor, thus converting positions into velocities.

For the control records with the stimulus bar stationary, the spontaneous eye movements were analysed by manually identifying successive maxima and minima, thus dividing the record into individual movements whose duration and size could be computed. These records were also individually subjected to a Fourier transform using a fast Fourier transform subroutine to produce spectrograms: plots of the relative contributions to the eye movement signal of sine wave components of differing frequencies.

RESULTS

Spontaneous movements

Pitching movements of the eye showed a large amount of trembling, while yawing movements had periods of stationary fixation, as can be seen in two 10-s sample records in Fig. 3. The significance of these differences was confirmed by a statistical analysis of the seven records available for yawing movements, and the five for pitching movements. The average amplitude (\pm S.E.) for pitching movements was $2.22 \pm 0.072^\circ$, while that for yawing movements was $1.26 \pm 0.090^\circ$, the difference being significant ($P < 0.001$, F -test on an analysis of variance with animals as blocks, standard errors of means based on residuals). The average time interval for

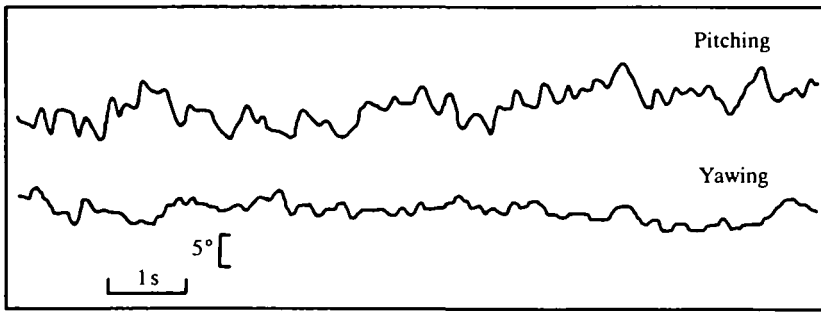


Fig. 3. Two complete 10-s samples of spontaneous eye movement behaviour, with the angular position of the eye plotted against time. The upper record is for an animal immobilized lying on one side, and hence shows movements in the pitching plane; the lower record is from an animal immobilized on its dorsal surface, with movements in the yawing plane being recorded. Digitization interval, 20 ms.

pitching movements was 130 ± 5 ms and for yawing ones was 147 ± 6 ms. The difference is just statistically significant, $P < 0.05$. Thus spontaneous movements in the pitching plane (i.e. vertically in the animal's normal swimming position) were around 80 % larger and 10 % faster than those in the yawing (horizontal) plane.

Average spectrograms for the two groups of records (Fig. 4) were identical for low-frequency components, but diverged at higher frequencies as the increased intensity of the trembling movements in the pitching plane made a contribution.

All occasions for which the eye was stationary for more than 60 ms were noted. On average the eye was stationary for 1.4 ± 0.4 s of each 10-s sample (14 % of the time) for the pitching plane, and for 3.6 ± 0.4 s of each sample (36 % of the time) for the yawing plane. The difference between these means is statistically significant ($P < 0.01$, *t*-test).

Responses to moving stimuli – linear analysis

Fig. 5 shows plots of corresponding stimulus and eye positions for three samples of digitized video record, one with a dark bar stimulus, one with a bright bar stimulus, and one with a single bright/dark boundary stimulus. In each case the eye position clearly responds to the movements of the stimulus. One possible mechanism which could account for this sort of result is a position/position servo, with the eye moving under constant visual control using an eye position/stimulus position difference signal to compensate for stimulus movements. Other possibilities are velocity/velocity and position/velocity servos, in which the angular velocity of the eye is controlled by the angular velocity and position of the stimulus, respectively. For our data the average (\pm S.E.) of the peak values for the correlation between stimulus position and eye position, obtained by performing a cross-correlation between stimulus and response on each of the 68 records, was 0.635 ± 0.024 . For the stimulus velocity/eye velocity cross-correlations the average peak value was 0.455 ± 0.022 , and for stimulus position/eye velocity it was 0.445 ± 0.024 . Thus we have no

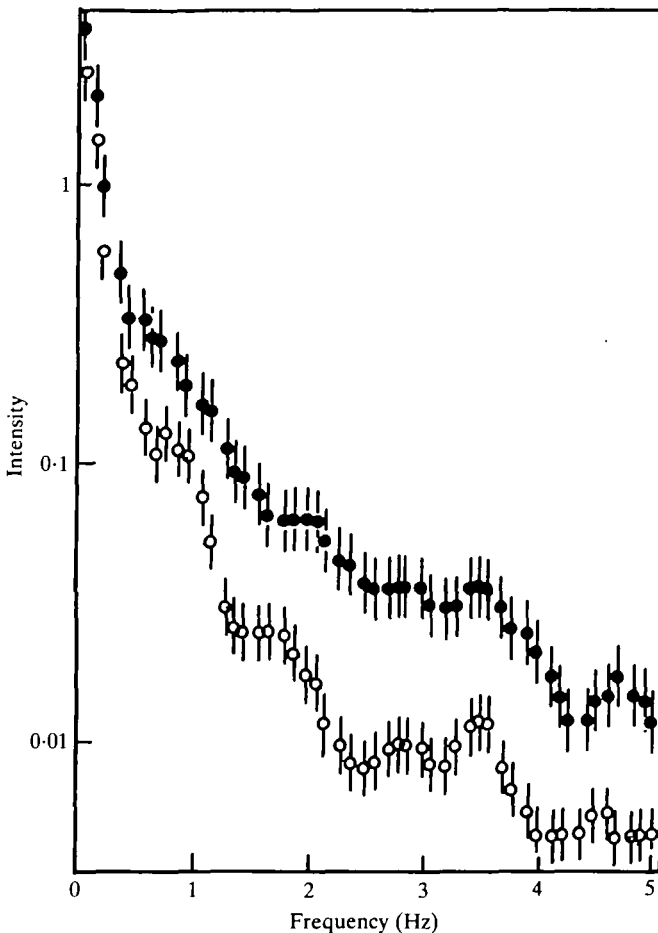


Fig. 4. Average spectrograms for spontaneous eye movements: solid circles for side-immobilized animals ($N=7$), and open circles for dorsally or ventrally immobilized animals ($N=5$). Log intensity (sum of squares of Fourier components) is plotted against frequency. Error bars are derived from analysis of variance residuals. The intensity measure gives an indication of what contribution oscillations of a given frequency make to the total pattern of eye movements.

evidence to prefer either a position/velocity or a velocity/velocity model over a position/position servo.

The simplest possible servo-engineering account of a stable negative-feedback controlled system of this sort is a *single first-order model*. In essence the output of the system should look like the input put through a one-stage low-pass filter, with output amplitude falling off above a certain frequency, and output phase lagging progressively as output amplitude decreases. This model has had considerable success in accounting for control phenomena in visual systems (Montgomery, 1983; Ditchburn, 1963). Its applicability in a given case can be assessed by plotting a Bode diagram as in Fig. 6, in which the lefthand graph is a log/log plot relating the gain to

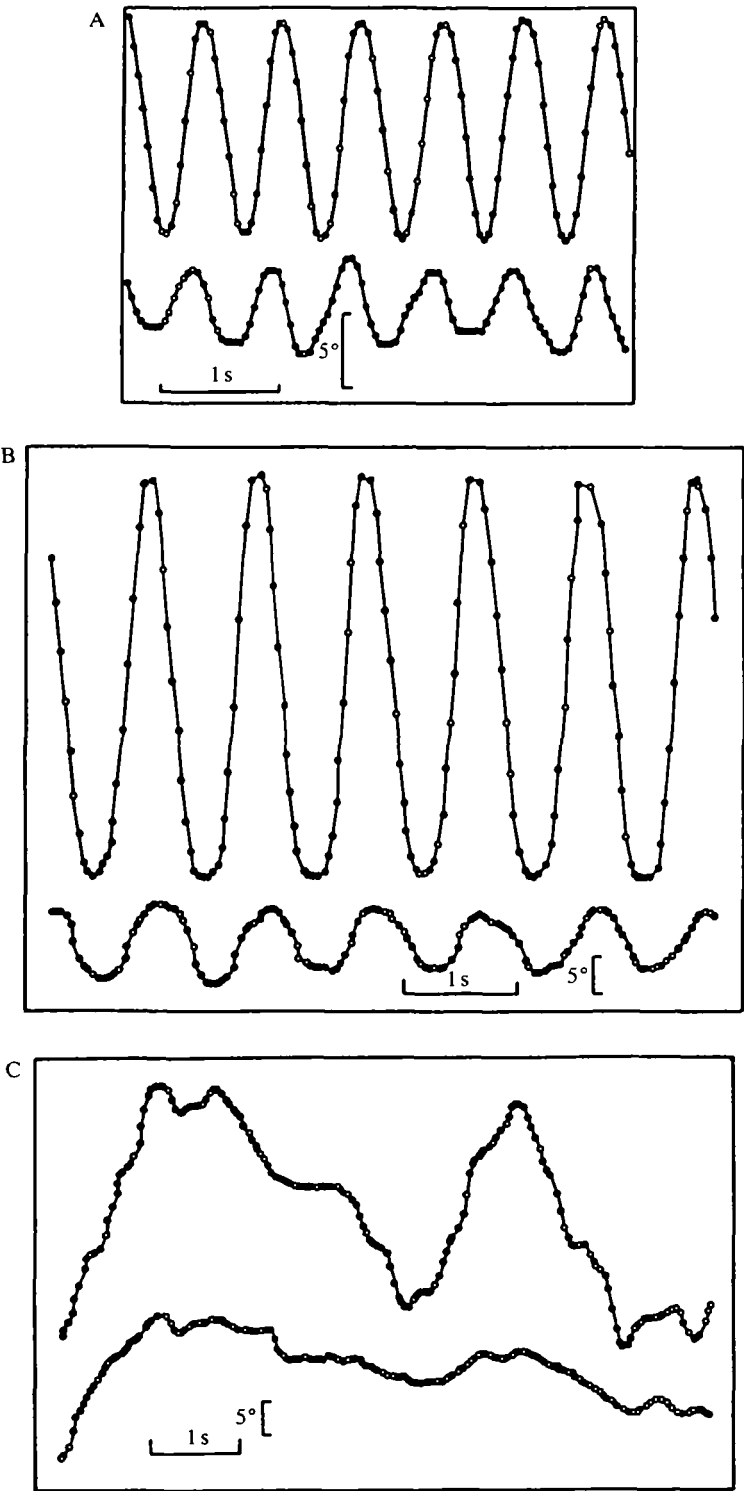


Fig. 5

the stimulus frequency, while the righthand one gives the corresponding phase lags (McFarland, 1971). In this context 'gain' means the closed-loop gain: the response amplitude as a proportion of the stimulus amplitude.

Fig. 6 is a plot of the combined data for all 68 trials with a dark stimulus moving against a bright background. The lefthand plot appears to show characteristics of a single first-order model, with a significant negative correlation ($r = -0.292$, $P < 0.019$) between gain and log frequency, though the peak gain at low frequencies is only around 17%. The righthand plot, however, fails to show the expected significant correlation between phase and log frequency ($r = -0.137$, NS), and the data points are a poor fit to the expected curve, even with the most favourable assumptions. Some values for the phase parameter are leads, implying response peaks preceding stimulus peaks, which can never happen with a first-order model. Fig. 5A gives an example of a phase lead, with peaks in the response trace preceding those in the stimulus trace.

Moreover, for any given frequency, the gain is dependent on the stimulus amplitude, with a statistically significant negative correlation ($r = -0.297$, $P < 0.01$) between stimulus amplitude and response amplitude. These results have led us to reject the model that the response is under constant visual control, and instead to investigate the possibility that it is being built up from a series of individual eye movement responses to briefly sampled stimuli.

Open-loop model

For each sample, the angular velocity of the target relative to the centre of the eye was calculated from the records of eye and target position by subtracting each value for the angular position of the target relative to the centre of the eye from the value for the preceding sample. The distribution of these relative velocities (ignoring signs) showed a bunching at high values with a tail of low values. Since the stimulus amplitude was generally considerably greater than the eye amplitude, relative velocities when the stimulus passed the centre of the eye were characteristic of the high-velocity segments of the stimulus movement, rather than its slower turns. We have estimated this high stimulus velocity experienced by central regions of the eye by taking the median of the upper half of the relative velocity values (their upper interquartile). Given the nature of the distribution, the actual estimation method makes little difference. We call this measure the 'maximum stimulus velocity'.

The eye's responses are easier to quantify, because, as the record in Fig. 5 shows, the eye movement records approximate to a series of truncated triangles, with intervals of constant angular velocity rotation interrupted by near static intervals. Eye angular velocities were calculated by subtracting each eye angular position data point from the next one in the record, to give the angle moved per sampling period. Values below 0.75° per 40-ms sampling period were eliminated because they

Fig. 5. (A) Typical records for the angular position of the dark bar stimulus (upper trace) and the corresponding angular position of the eye (lower trace) for a *Polyphemus* immobilized on its side. Digitization interval, 40 ms. (B) Similar plot for a bright bar stimulus. (C) Similar plot for a bright/dark boundary stimulus, moved manually.

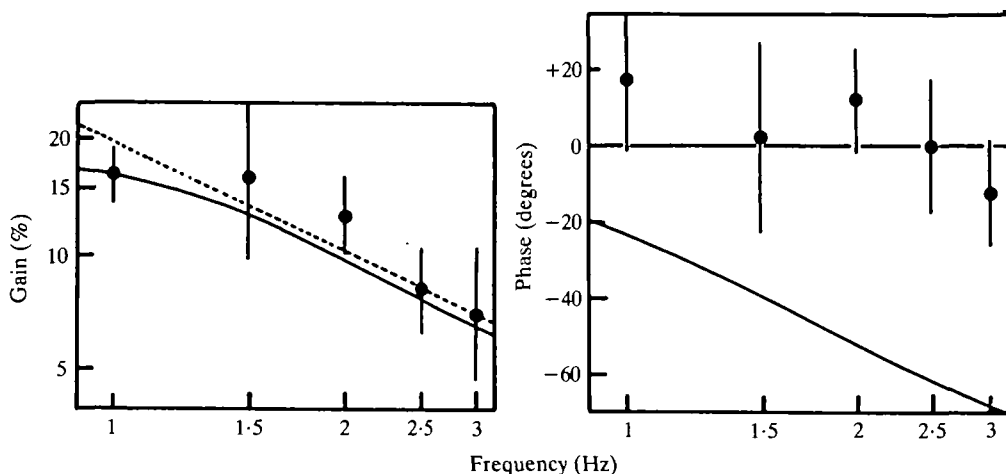


Fig. 6. Bode diagram for *Polyphemus* eye movement response. The lefthand graph is loggain (response amplitude divided by stimulus amplitude) plotted against log frequency (Hz). The righthand graph shows the corresponding phase difference between response and stimulus. The points are means for experimental data (\pm S.E. from one-way analysis of variance residuals); the broken line shows the theoretical behaviour of a single first-order model, assuming the asymptotic low-frequency gain to be unity. Corresponding phase lags for this model are between -70 and -85° , i.e. off the bottom of the righthand graph. The solid lines assume the observed gain at 1 Hz is asymptotic.

corresponded to the static phases between the constant-velocity movements, and the remainder were averaged to give the measure we call slow rate. The differences in mean slow rates between animals were large, ranging from 33 to 58°s^{-1} , and were highly statistically significant (using a nested design analysis of variance, the F ratio for the animal main effect was 10.6 , corresponding to $P < 0.001$). However, the differences between the means for the various stimulus frequencies within animals were not significant (the F ratio for the animal.frequency interaction was 1.03 , NS). Thus the slow rate for a given animal is little affected by the stimulus frequency, but differences between individuals are large.

Dividing response amplitude by slow rate gives the measure we have called the 'response time' – the time during which the eye muscles are 'switched on' to complete a single, steady, slewing eye movement. The response time proved to be strongly negatively correlated with maximum stimulus speed (Fig. 7), with the plot of response time against the logarithm of the reciprocal of the maximum stimulus speed being linear.

The reciprocal of the maximum stimulus speed represents the time during which an ommatidium in the central region of the eye will receive stimulation as eye and stimulus bar pass one another. This stimulus time, probably averaged across a group of ommatidia forming a sensitive zone in the central region of the eye, is the effective stimulus controlling the length of the eye's next slewing movement, which must be in the same direction as the stimulus movement. Thus slow-moving objects evoke larger responses than do fast-moving ones, and objects moving with the direction of

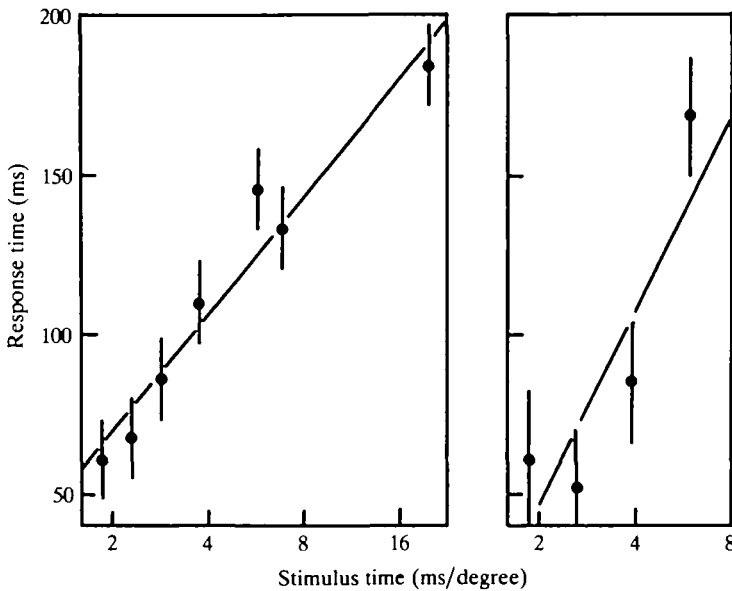


Fig. 7. Separate plots for side-immobilized (left, $N = 42$) and dorsal- or ventral-immobilized animals (right, $N = 26$) showing the linear relationship between the time during which the eye is actually moving for each individual response and the logarithm of the time the image of the stimulus bar took to traverse 1° across the central region of the eye. Correlation coefficients ($r = 0.85$ for the pitching plane movements shown in the left plot and $r = 0.81$ for the yawing plane movements shown in the righthand plot; $P < 0.01$ in both cases), are based on a statistical modelling analysis. Error bars show standard errors based on residual sums of squares from the modelling analysis.

an on-going eye movement evoke larger responses than objects moving against the eye movement.

DISCUSSION

In a stationary visual environment, the *Polyphemus* eye shows a pattern of constant, small, trembling movements superimposed on periodic slower changes in average position, which are presumably changes in fixation. In the yawing plane, the tremor movements are much less prominent, and steady fixations interrupted by saccadic jerks are clearly visible in the records. The preponderance of trembling movements in the pitching (vertical) plane is unlikely to be a contingent feature of the neuromuscular anatomy, because responses evoked by moving stimuli in this plane are, if anything, larger than those evoked by the same moving stimulus in the yawing plane.

There are two possible functions for tremor movements. First, to scan the visual world, by using an eye with a small overall field of view or a small high-resolution fovea like a pair of binoculars. Land (1982) provides an excellent example of this process in a molluscan eye, and reviews the literature. Second, to enhance the perception of edges, presumably by generating a flickering illumination of a crucial

receptor site; Horridge (1966) has demonstrated edge-enhancing tremor in *Carcinus*.

Polyphemus eyes do have a small foveate region (Nilsson & Odselius, 1983) of high visual resolution, so scanning cannot be ruled out solely on the basis that the roughly spherical *Polyphemus* eye has an all-encompassing field of view. In our view, contour enhancement is a much more likely candidate. *Polyphemus* eye movements are small in amplitude, and follow a symmetrical time course, in contrast to the large-amplitude, sawtooth pattern movements reported by Land (1982).

Moreover, the visual world of *Polyphemus* is dominated by Snell's window, the circular pool of light (about 90° across) seen on all water surfaces viewed from below, due to total internal reflection. It is frequently argued that planktonic animals with no statocysts maintain their orientation by using the fact that an eyeline to the edge of Snell's window is always at a constant angle to the vertical (Harris, 1953; Young, 1981). Hence one would expect to find edge-enhancing tremor in the pitching plane movements, which cut across the edge of Snell's window, and not in the yawing plane movements, since the latter pivot *around* a vertical axis directed through the centre of Snell's window and produce no movement of the edge across the eye. This prediction is borne out by our results, strengthening the case for an edge-enhancing role for tremor movements. In contrast, in *Carcinus* tremor movements are most pronounced in the horizontal plane (Barnes & Horridge, 1969), presumably representing the different visual priorities of an animal with knowledge of its orientation provided by statocysts and by substrate contact.

Another view of tremor movements is that they are an artefact of a jittery position servo-mechanism (Sandeman, 1978). We would argue that this is unlikely to be the case for *Polyphemus*, because no negative feedback mechanism is needed to account for its evoked eye movements.

The responses we observed to moving stimuli seem most likely to be part of a system for tracking small objects. They were evoked by a single moving object, a stripe whose width was equivalent to the subtense of three ommatidia in the most acute region of the eye (Nilsson & Odselius, 1983), and are thus unlikely to contribute to a wide-field optokinetic nystagmus response. We cannot eliminate the possibility that this system tracks the edge of Snell's window, because the response can be evoked by moving a single light/dark boundary. However, a tracking system specializing in Snell's window would be expected to be restricted to the pitching plane, and to have a sensitive zone on the dorsal surface of the eye, rather than in the central region.

On the basis of data representing responses to a stimulus oscillating sinusoidally at a range of amplitudes and frequencies, we have proposed a ballistic response model, which has as inputs the direction of motion of the stimulus through a restricted central 'window' on the eye plus the time it takes the stimulus to pass through the zone, and as output the time during which the eye's slew rate is constant. Output movements are in the same direction as the stimulus, and response time is proportional to the logarithm of stimulus time, which implies that the effectiveness

of the stimulus is inversely proportional to the time since it entered the window. The model requires the visual system to be able to detect movement, but does not need any sort of velocity measurement.

We devised this model in the first instance because orthodox servo-mechanism accounts were a poor fit to our data. Most small-object tracking systems are position/velocity servos (Wehner, 1981), but in our case the peak position/velocity correlation is much lower than the peak position/position correlation. The Bode plot is unconvincing, and the eye angular velocity is virtually a constant, unaffected by stimulus velocity. However, the maximum stimulus velocity during its sinusoidal travel proved to be a very good predictor of the response amplitude, and the current model is a version of this relationship which produces a linear plot with a high correlation coefficient (Fig. 7).

An even simpler account would result if the behaviour could be explained by the total dimming experienced by the sensitive zone when the stimulus interrupts its illumination. However, since the response is bi-directional, and also works with a bright target on a dark ground, postulating some sort of movement detector seems inevitable.

None of the elements of our current model are anatomically or behaviourally improbable: Nilsson & Odselius (1983) have demonstrated anatomically and optically differentiated central regions in the *Polyphemus* eye which they describe as a fovea (size about $12^\circ \times 20^\circ$), with high resolution, and a subfovea (about $45^\circ \times 60^\circ$), of medium-resolution receptors. Either of these zones could function as the window needed by our model, but trials with the moving stimulus well to one side of the eye make the larger subfovea seem more likely.

Only limited regions of *Carcinus* eyes can be stimulated to evoke eye movement responses (Horridge & Sandeman, 1964; Sandeman, 1978), suggesting the existence of a sensitive window in this species, though in this case it is positioned at the sides of the eye, rather than frontally.

Logarithmic relationships between input stimulus intensity and response size of the sort required for our model have been found in *Carcinus* (Nalbach, Thier & Varjú, 1985).

The mechanism we propose would serve the same functional purpose as a classical foveal tracking mechanism – to keep likely prey or mates in view without the delay or energy expenditure of turning the whole animal, and would do so without the need for elaborate neural feedback connections. The main cost to the animal is that the crude nature of the mechanism means that only objects within a limited range of angular velocities will be effectively tracked – perhaps just those objects that a *Polyphemus* would have a reasonable chance of catching?

We thank Miss C. Getty for dedicated digitizing of video tapes, the NERC for a grant supporting the project, and Drs J. Brady, C. David and G. Gibson for comments on the manuscript.

REFERENCES

- BARNES, W. J. P. & HORRIDGE, G. A. (1969). Two dimensional records of the eyecup movements of the crab *Carcinus*. *J. exp. Biol.* **50**, 673–682.
- DITCHBURN, R. W. (1963). Information and control in the visual system. *Nature, Lond.* **198**, 630–632.
- HARRIS, J. E. (1953). Physical factors involved in the diurnal migration of plankton. *Q. Jl microsc. Sci.* **94**, 537–550.
- HORRIDGE, G. A. (1966). Perception of edges versus areas by the crab *Carcinus*. *J. exp. Biol.* **44**, 247–254.
- HORRIDGE, G. A. & SANDEMAN, D. C. (1964). Nervous control of optokinetic responses in the crab *Carcinus*. *Proc. R. Soc. Ser. B* **161**, 216–246.
- LAND, M. F. (1982). Scanning eye movements in a heteropod mollusc. *J. exp. Biol.* **96**, 427–430.
- McFARLAND, D. J. (1971). *Feedback Mechanisms in Animal Behaviour*. London: Academic Press.
- MONTGOMERY, J. C. (1983). Eye movement dynamics in the dogfish. *J. exp. Biol.* **105**, 297–303.
- NALBACH, H.-O., THIER, P. & VARJÚ, D. (1985). Light-dependent eye coupling during the optokinetic response of the crab *Carcinus maenas* (L.). *J. exp. Biol.* **119**, 103–114.
- NILSSON, D.-E. & ODSELIUS, R. (1983). Regionally different optical systems in the compound eye of the water-flea *Polyphemus* (Cladocera, Crustacea). *Proc. R. Soc. Ser. B* **217**, 163–174.
- SANDEMAN, D. C. (1978). Regionalisation in the eye of the crab *Leptograpsus variegatus*: eye movements evoked by a target moving in different parts of the visual field. *J. comp. Physiol.* **123**, 299–306.
- SCOURFIELD, D. J. (1900). The swimming peculiarities of *Daphnia* and its allies. *J. Queckett microsc. Club*, series 2 **7**, 395–404.
- WEHNER, R. (1981). Spatial vision in arthropods. In *Vision in Invertebrates, Handbook of Sensory Physiology*, vol. VII/6c (ed. H. Autrum), pp. 287–616. Berlin: Springer-Verlag.
- YOUNG, S. (1981). Behavioural correlates of photoreception in *Daphnia*. In *Sense Organs* (ed. M. S. Laverack & D. J. Cosens), pp. 127–135. Glasgow: Blackie.
- YOUNG, S., DAVID, C. T. & GIBSON, G. (1987). Light measurement for entomology in the field and the laboratory. *Physiol. Entomol.* (in press).