

REACTIONS OF THE SPINY LOBSTER *PALINURUS VULGARIS* TO SUBSTRATE TILT

II. INPUT-OUTPUT ANALYSIS OF EYESTALK RESPONSES

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SUMMARY

1. The input-output properties of the eyestalk responses of *Palinurus vulgaris* to substrate tilt are described in both the time and frequency domains.

2. Trapezoidal substrate movements elicit phaso-tonic eyestalk movements which decay from the phasic peak to the tonic plateau with time constants of 9.2 s (tilt) and 6.1 s (return) (Fig. 1). Average eye excursions for tilt and return are equivalent (Fig. 2).

3. The relationship to tilt amplitude is non-linear (Fig. 3), and with step-wise tilts in opposite directions a marked hysteresis is evident (Fig. 4).

4. Sinusoidal stimuli produce consistent eyestalk responses (Fig. 5), and a frequency analysis reveals a high gain, phase-leading region below 0.25 Hz (Fig. 6). Around this frequency the eyestalk response is effectively a compensation with respect to both amplitude and phase position.

5. The results are considered in relation both to the experimental arrangement with fixed body and vision excluded, and to the normal biological situation.

INTRODUCTION

In common with many other ground-dwelling animals, decapod crustaceans orientate with respect to both substrate and gravity. (Alverdes, 1926; Kühn, 1914; Stein & Schöne, 1972). In the spiny lobster, *P. vulgaris*, forced movement of the substrate elicits equilibrium reactions in a number of different body appendages, as well as compensatory movements of the eyestalks (Schöne *et al.* 1976). These responses are initiated by stimulation of proprioceptors at the coxo-basal (C-B) joint of the leg, which monitor trunk-leg angle (Schöne *et al.* 1976; Clarac, Neil & Vedel, 1976). They are similar to the statocyst-controlled responses which occur when decapod crustaceans are displaced in the field of gravity (Schöne, 1954, 1975), and under normal circumstances these responses will reinforce each other, thus stabilizing the animal's position in space.

In order to understand the interaction of these sensory-motor systems in the control of orientation, it is necessary to determine the performance of each one alone under controlled conditions. Here we present quantitative data for the leg receptor-eyestalk system of *Palinurus* obtained by tilting the substrate while keeping the

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animal fixed in the field of gravity. The time course of the eyestalk reaction has been analysed during ramp-and-hold trapezoid stimuli, and its frequency response has been determined from sinusoidal substrate oscillations.

MATERIALS AND METHODS

The apparatus and recording techniques were, in the main, as described in a previous paper (Schöne *et al.* 1976). Fifteen animals were used in this study. Each was blinded and clamped in an upright position with all legs contacting a substrate board. Side-to-side movements of the board were produced by a variable-speed d.c. motor operating through a drive arm and connecting rod. Standard trapezoid movements consisted of a board tilt from the horizontal to 20° , hold for 60 s, return movement of the board and a further hold for 60 s. Sinusoidal oscillations of the board over a range of frequencies were produced by operating the motor continuously with different supply voltages.

Recording of data was, in most cases, by a filming technique, the relevant angles being measured from single frames, punched onto tape and processed by a digital PDP 1140 computer (Schöne *et al.* 1976). In later experiments (Fig. 6, 1977 data) board tilts, recorded potentiometrically, and eyestalk movements, recorded by a miniature angle transducer (Marrelli & Hsiao, 1976) were continuously monitored on a Philips oscilloscript paper chart recorder.

An estimate of the time constant, τ , of the eyestalk response was obtained as follows. A series of logarithmic curves was constructed on the computer with values of τ from 1–22 s. By comparing the response curve from the phasic peak to the asymptote with this series an estimate of τ was directly obtained. These values are only approximate, however, as the responses are not perfect logarithmic functions.

RESULTS

Control tests were performed to determine if water current produced by foot-board movements had any effect on the eyestalk response. At all stimulus velocities used in the experimental series such water currents were insufficient to displace the eyestalk directly, or to cause reflex activation through exteroceptive stimulation.

(1) *Ramp-and-hold tilts*

The phaso-tonic response

The eyestalk response to standard stimulation is phaso-tonic in form (Fig. 1), the initial peak (p) reached during footboard movement decaying in an approximately exponential manner to a tonic plateau (t). Records up to 5 min show that the tonic deviation is usually maintained at a constant level over this period. On the return tilt the eyestalks again respond phaso-tonically (Fig. 1 p' , t') and their final positions coincide with their initial positions (i.e. $t = t'$). The data from ten animals demonstrate that the mean phasic and tonic values for tilt and return are equivalent (Fig. 2).

Estimates of the time constant of the decay from phasic peak to tonic stage for a

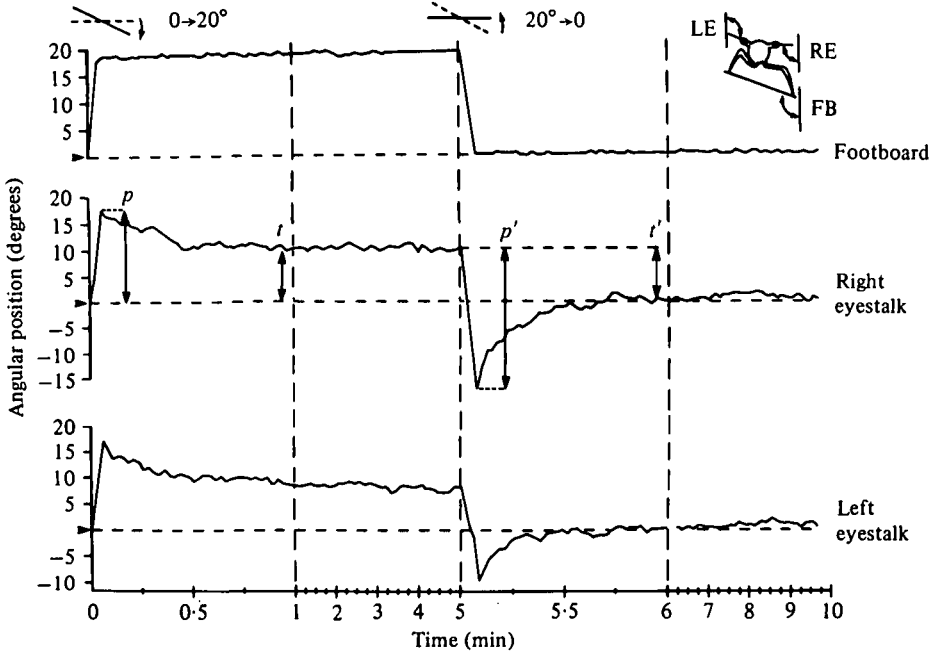


Fig. 1. Response of left eyestalk (LE) and right eyestalk (RE) to trapezoid footboard tilt (FB) as a function of time (note changing time scale). This plot has been reconstructed from single frame film analysis. Upward on ordinates corresponds to increase in angles indicated on right-hand inset figure (stylized front view of animal standing on footboard). *p*, Phasic response to initial tilt; *t*, tonic response to initial tilt; *p'*, phasic response to return tilt; *t'* tonic response to return tilt. Arrowheads, start position.

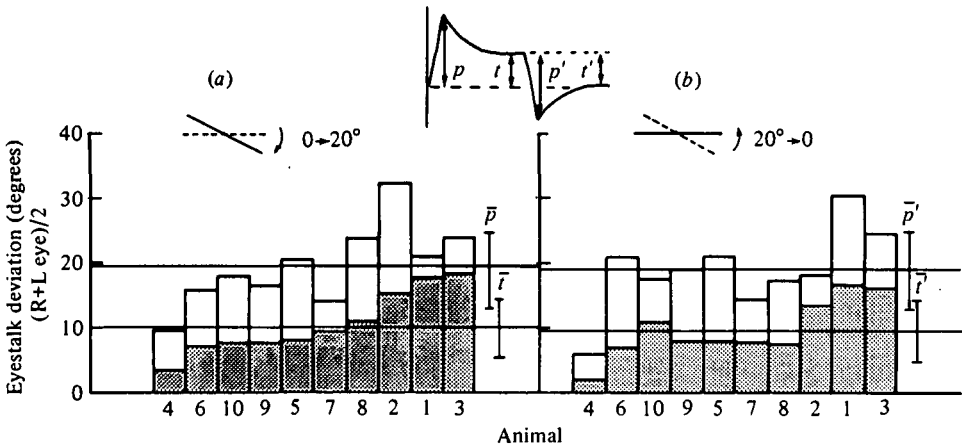


Fig. 2. Eyestalk responses of 10 animals (1-10) to standard trapezoid board tilt (tilt 0-20°, hold for 60 s, return 20-0°, hold for 60 s). Hatched bar, tonic component; open bar, phasic component. Horizontal lines represent means, and vertical bars two standard deviations, for phasic (*p*) and tonic (*t*) responses to (a) tilt and (b) return. Data are based on three experiments per animal, right and left eyestalk responses being averaged.

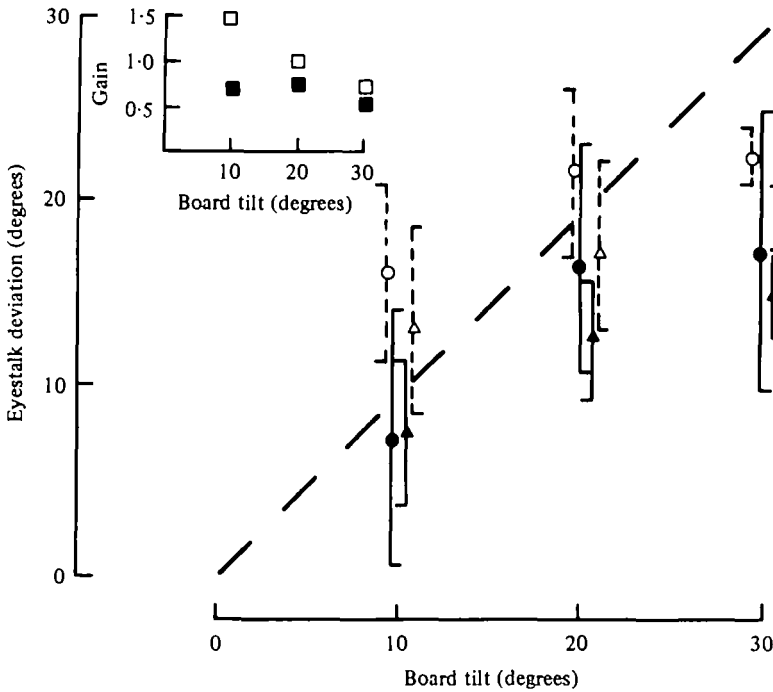


Fig. 3. Eystalk responses as a function of footboard tilt from horizontal to left side down. Diagonal line indicates correspondence of board movement (input) and eystalk movement (output). Inset: gain of response as a function of tilt. Open symbols, phasic responses; filled symbols, tonic response; squares, average of both eystalks; circles, left eystalk; triangles, right eystalk; vertical bars, two standard deviations.

ten animals yield mean values of $\tau = 9.2$ s (s.d. = 3.8 s) for tilt and $\tau = 6.1$ s (s.d. = 2.1 s) for return.

Relation to tilt amplitude

For a given tilt velocity, increases in tilt amplitude result in increases in amplitude of both the phasic and tonic components of the eystalk response (Fig. 3). This relationship is non-linear, as the gain (i.e. output amplitude/input amplitude) decreases with increasing amplitude. For small tilts (10°) the phasic values exceed the tilt angle and the tonic values approach it. For a 30° tilt however the response in many cases begins to saturate so that the gain is less than one.

Incremental tilts

Successive 10° steps with 30-second pauses at each position elicit progressively smaller responses, as measured both at the phasic and tonic levels (Fig. 4). There is a larger decrement at the final 30° tilt position than at preceding intermediate positions. On the return, subdivision of the board movement into 10° increments reveals a similar range effect. A large response to the initial step (30° to 20°) is followed by smaller responses to the successive steps, even though these bring the footboard closer to the horizontal position. As a result of these differences between the eystalk

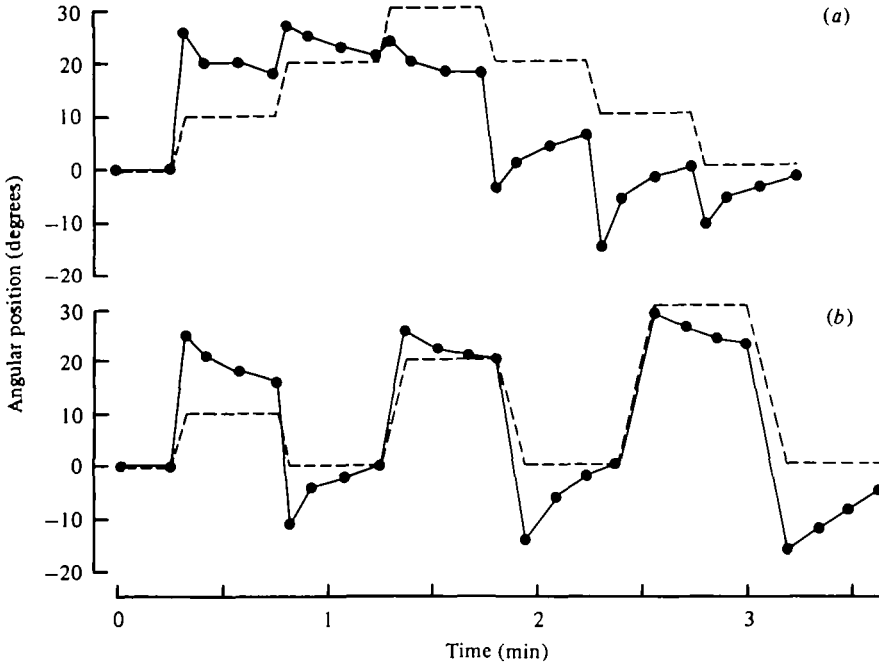


Fig. 4. Eyestalk response (solid line) to different angles of footboard tilt (broken line) as a function of time. (a) Interrupted tilt, (b) single step tilts. Records of left eyestalk for tilts from horizontal up to 30° left side up, and return.

responses to tilt and return, a marked hysteresis is evident in the shape of the response curve, even when values measured at 30 s after each tilt movement are considered (Fig. 4).

(2) Sinusoidal footboard tilts

Input-output relationships

At the employed frequencies (0.002–0.8 Hz) and amplitudes ($+/-7^\circ$ to $+/-20^\circ$) continuous oscillation of the footboard elicits consistent compensatory movements of the eyestalks, with no apparent adaptation (Fig. 5). At (and below) the frequency illustrated the response phase-leads the stimulus and non-linearities are evident in the shape of the eyestalk response curves. These deviate from a sinusoidal form in that the slopes following the midpoints are relatively steeper, those preceding them relatively shallower, than the corresponding portions of the board curve. This relationship indicates a velocity gain in the response.

Frequency analysis

An analysis of the frequency response of the system in terms of the gain and phase relationship between input and output is illustrated in Fig. 6 as a Bode plot. The phase of the response is frequency-dependent and below 0.25 Hz leads the stimulus (Fig. 6a) by an amount which reaches 35° at 0.002 Hz, the lowest frequency tested. Above 0.25 Hz a phase lag develops more rapidly with frequency, reaching 35° at 0.8 Hz.

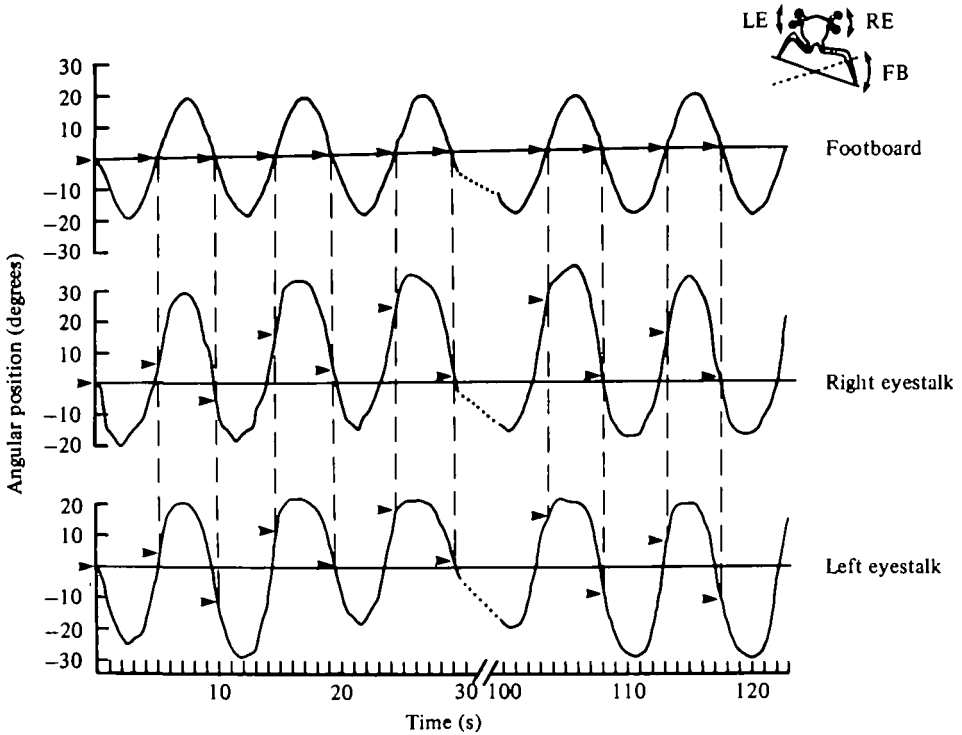


Fig. 5. Eyestalk movement in response to continuous sinusoidal oscillation of the footboard at ca. 0.1 Hz. The record, which has been reconstructed from single frame film analysis, is interrupted for seven cycles (70 s) to show the persistence of the response. Arrowheads indicate the horizontal positions of the board, and the corresponding eyestalk positions. Note the phase-lead of the response.

The amplitude gain of the system shows a humped maximum in the range 0.01–0.05 Hz. Unity gain occurs around 0.25 Hz, corresponding to the frequency at which phase position is zero, and falls away sharply from this value with increasing frequency. The intercept of high frequency and low frequency asymptotes occurs at 0.13 Hz, which corresponds to the value of 7.7 s for the time constant of the system. This value is in fairly good agreement with those calculated from the phaso-tonic decay (9 s and 6 s for tilt and return respectively).

Data obtained from experiments using three different input amplitudes over a restricted frequency range (cf. Fig. 6b) demonstrate non-linearities of the system since the gain at input amplitudes of 20° (square symbols) is lower than that for an input of 12–15° (triangles) or 7° (circles).

DISCUSSION

The compensatory eyestalk response in *Palinurus* is under the control of three main sensory systems: visual, statocyst and proprioceptive (i.e. substrate contact). An understanding of this compound system requires a detailed knowledge of the response characteristics of each subsystem. The data presented here define the over-
input-output properties of the subsystem based on leg proprioceptors. Our aim in

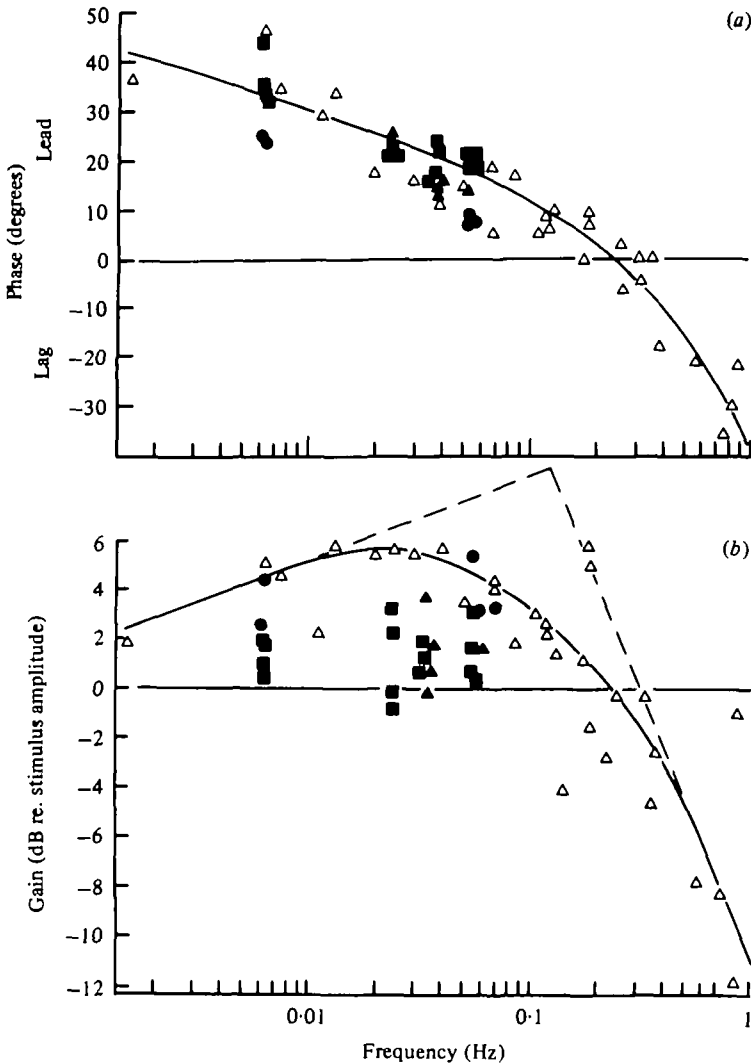


Fig. 6. The frequency response of the left eyestalk to sinusoidal footboard movements, presented as a Bode Plot. Footboard movement amplitudes: circles, $\pm 7^\circ$; triangles, $\pm 12-15^\circ$; squares, $\pm 20^\circ$. Data obtained from 4 animals in 1975 (filled symbols) and 5 animals in 1977 (open symbols). Each point represents the mean value derived from at least 5 cycles of oscillation. The curves have been fitted to the 1977 data alone. Broken lines in (b) indicate high and low frequency asymptotes. These intersect at the corner frequency, $\omega = 0.13$ Hz. The time constant, $\tau = 1/\omega = 7.7$ s.

this approach is ultimately to describe such overall performance in terms of the individual transfer characteristic of the system elements. This approach has been successfully applied in related orientational systems (Precht, 1978; Sandeman, 1977).

The responses to ramp-and-hold stimuli (Fig. 1) demonstrate a marked dynamic component, with overshooting phasic peaks which decay to tonic levels with a time constant of several seconds. Such dynamic effects probably reflect properties at the sensory rather than the motor level. Certainly the leg proprioceptors involved, which

include the CB chordotonal organ (Clarac *et al.* 1976) have been shown to respond appropriately to dynamic components of displacement (Bush, 1965; Clarac, Vedel & Bush, 1978).

The frequency response indicates that the system acts as a lowpass filter, gain falling away rapidly above 0.25 Hz. The phase lead at low frequencies indicates that some time integral of the stimulus, i.e. velocity or acceleration, is being coded. This corresponds to the dynamic phase of the eyestalk response to ramp inputs. The eyestalk compensates most effectively in the frequency range around 0.25 Hz, where the output has both the same amplitude and the same phase position as the input. It is tempting to suggest that this may be of biological significance and indicative of a preferred operating range around this frequency.

Considered in relation to the normal behaviour of *Palinurus* it appears that the leg receptor-to-eyestalk system is well adapted. It is designed to operate dynamically and provide effective compensation for continuing body displacements, thus fitting the biological demands of spiny lobsters. These are active exploratory animals which are often subjected to repeated water movements and show the ability to detect and orientate to water currents using proprioceptive cues (Herrnkind & McLean, 1971).

In evaluating the finding that at low frequencies the final eyestalk response phase leads and overshoots a compensatory relationship to the initial substrate movement, it must be taken into account that in these experiments visual input was excluded. Normally the leg receptor system will act in combination with the optomotor feedback system, which serves to match output to input in terms of phase and gain, and which is known to operate optimally in the low frequency range in crustaceans (Sandeman, 1977).

The contribution of statocyst input is also known to be important (Schöne & Neil, 1977), and preliminary experiments suggest that these gravity responses of the eyestalks have different frequency characteristics from those of substrate responses. Thus the substrate responses of *Palinurus* are to be understood only if taken as component elements of a system which normally operates on the basis of a multi-sensory input.

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