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## Leg Resistance Reaction as an Output and an Input

### Reactions of the Spiny Lobster, *Palinurus vulgaris*, to Substrate Tilt VI

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**Summary.** 1. Substrate tilting consistently elicits both an eyestalk response and a resistance reaction by the legs in the spiny lobster *Palinurus vulgaris*.

2. These two responses differ from each other in terms of their phaso-tonic form, frequency response and strength of bilateral linkage.

3. Changing the relationship between imposed leg movement and the force of leg resistance demonstrates that force changes alone lead to eyestalk movements. However this eyestalk response is greatly enhanced when leg displacement also takes place.

4. It appears that the detection of substrate orientation has a multisensory basis distributed between different leg proprioceptors.

mental procedures are described elsewhere (Schöne et al., 1976; Neil and Schöne, 1979). The footboard mass was in most cases brought into balance about its turning axis, and in all cases the forces during lifts without the animal present were subtracted from the values obtained during the experiment. The forces in the system were measured using the arrangement shown in Fig. 1. A strain gauge (Grass type FT.03C) was incorporated in the drive system which operated either directly onto the footboard, or through an interposed spring. The springs employed had the following compliances:

Spring No.	Compliance ( $\text{g} \cdot \text{cm}^{-1}$ )
37	50
38	11
39	4
42	125

### Introduction

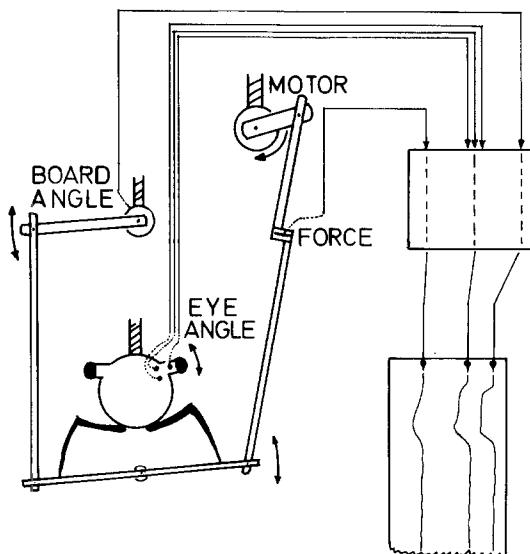
The righting responses which serve to restore and maintain normal posture are important components of the reactions induced by substrate tilt in the spiny lobster, *Palinurus vulgaris* (Schöne et al., 1976). The resistance reactions of the legs against the substrate fall into this category, and have been measured under a variety of experimental conditions (Scapini et al., 1978; Schöne et al., 1978). Here we present an analysis of the resistance reactions of the legs as an output of the equilibrium system, and report that in the absence of movement itself changes in the forces acting on the legs provide an adequate input to the leg receptor system controlling eyestalk movement.

### Material and Methods

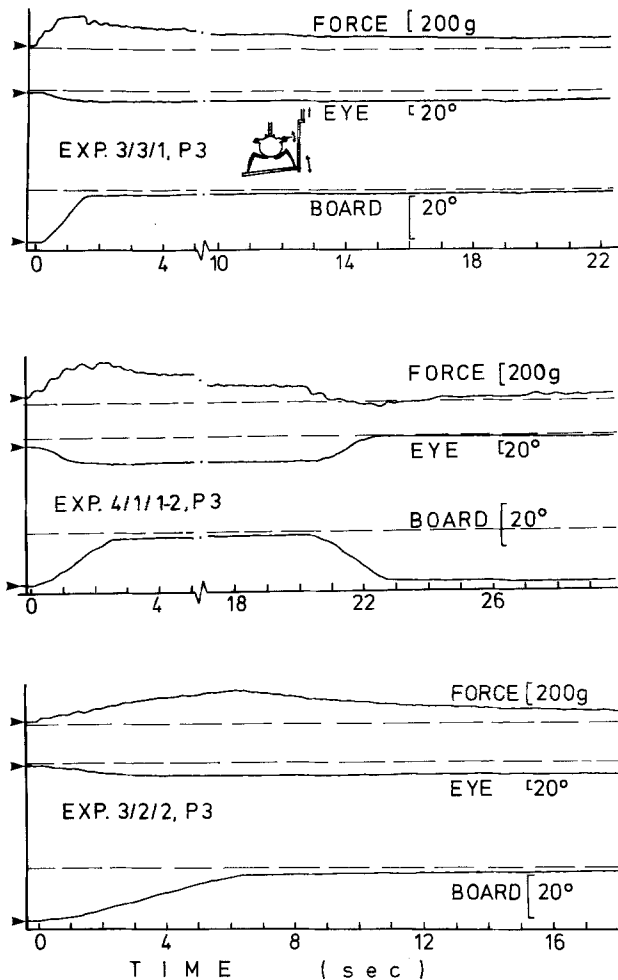
Spiny lobsters (*Palinurus vulgaris*) from the Tyrrhenian coast were kept under semi-natural conditions. Apparatus and general experi-

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**Fig. 1.** Apparatus used to tilt footboard and to record leg resistance reaction and eyestalk response. A strain gauge is incorporated in the drive system, and when necessary springs can be inserted below the gauge. Outputs from the strain gauge, the board angle potentiometer and the eyestalk angle transducer are converted to analog signals and fed to a pen recorder



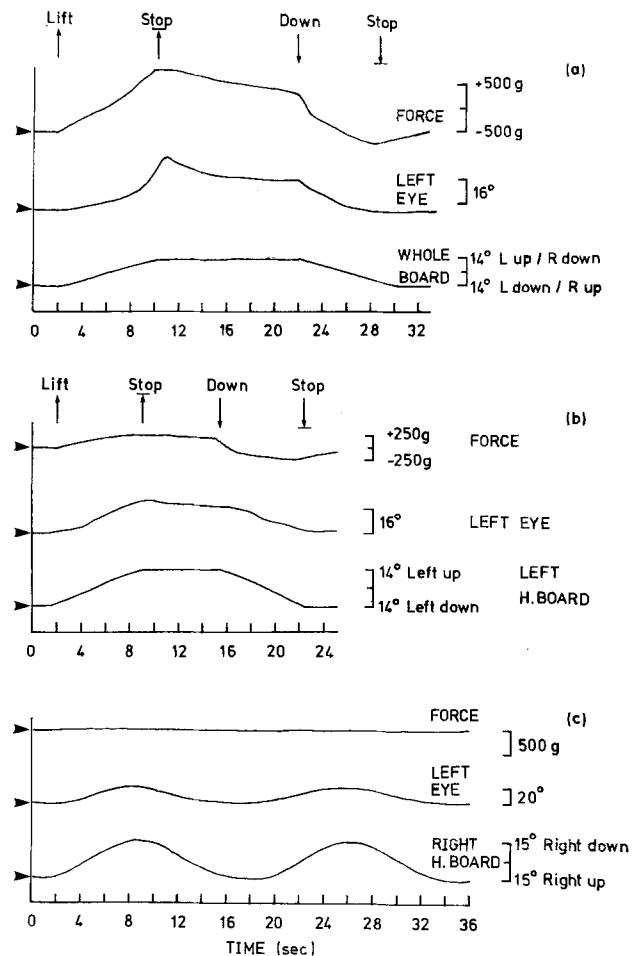
**Fig. 2.** Effect of changing angular velocity of footboard tilt on leg resistance reaction and eyestalk response. Outputs were monitored on left side of the animal (see inset figure). In each record upper trace is a force measurement (increasing force upwards), middle trace is movement of the left eyestalk (dorsal movement is downwards) and lower trace is board movement (lift is upwards). Arrows: starting values; dashed lines: horizontal position of the board and the average initial force and eyestalk values. Velocity of footboard tilt: top record,  $15.0^\circ \text{ s}^{-1}$ ; middle record,  $8.3^\circ \text{ s}^{-1}$ ; bottom record,  $3.3^\circ \text{ s}^{-1}$

For a given lift of the drive arm (routinely 10 cm, but in some cases 20 cm) the force acting on the board was a function of the strength of the spring. The lobster's leg reaction, by extending the spring, was capable of reducing board movement or preventing it completely. Eyestalk movements were measured using a miniature angle transducer (Marrelli and Hsiao, 1976) and recorded on a Philips Oscilloscript pen recorder.

## Results

### 1. Force as an Output

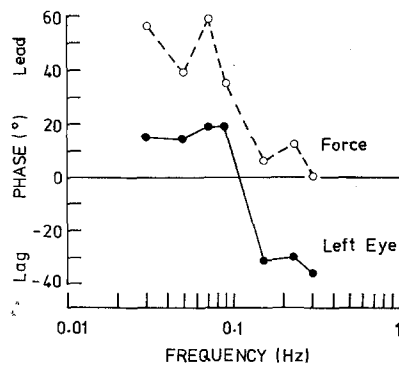
During ramp movements of the footboard with rigid drive (Fig. 1) the righting force of the legs increases



**Fig. 3a-c.** Leg and eyestalk responses with different footboard configurations. **a** Whole footboard, ramp movements. **b** Footboard split along long axis and halfboard ipsilateral to monitored outputs moved (ramp tilts). **c** Footboard split and halfboard contralateral to monitored outputs moved (sinusoidal tilts)

with displacement and can reach values exceeding 500 g (Figs. 2, 3a). When the imposed board movement stops the force exerted by the animal declines from this peak, but is still maintained at high values. The form of this response was found to be consistent over a range of tilt velocities (Fig. 2). The eyestalk response to these trapezoid board movements is of a phaso-tonic form, although the phasic peak which is reached before the end of the lift is not as distinct as previously found (Schöne et al., 1976).

When only the halfboard ipsilateral to the monitored eye is moved both the leg reaction and the eyestalk response are reduced to approximately half the values for whole board movement (Figs. 3a, b).



**Fig. 4.** Phase relationships of eyestalk and leg responses to sinusoidal movements of a whole footboard over a restricted range of frequencies (0.02–0.2 Hz)

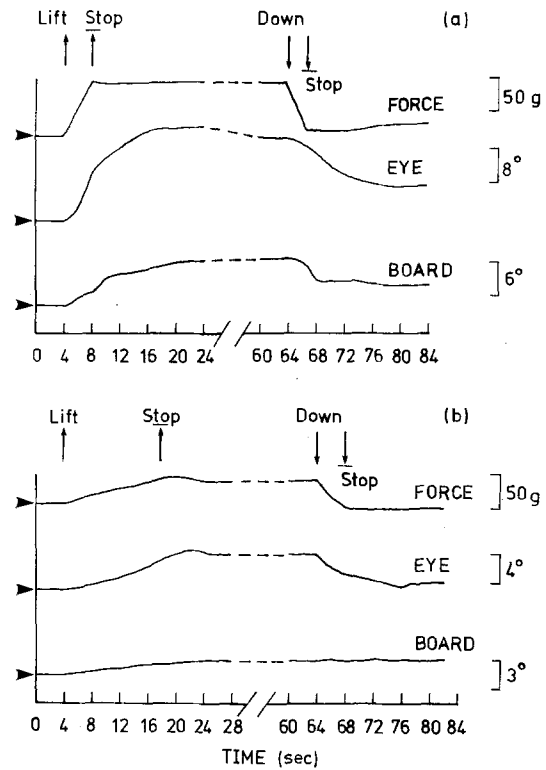
When legs contralateral to both monitored outputs are moved on a halfboard the eyestalk movement is reduced by a further 25%, while the resistance reaction of the legs (standing on a stationary halfboard) almost completely disappears (Fig. 3c).

The phase angles of eyestalk responses relative to oscillatory whole board movements are consistent with previous measures (Neil and Schöne, 1978) but the phase of the leg reaction leads the eyestalk response over the range of frequencies tested (Fig. 4).

## 2. Force as an Input

The above results demonstrate that leg resistance reactions always accompany footboard movements, and thus the possibility exists that it is in fact these force changes rather than changes in leg joint angles which underlie the measured eyestalk movements. In an attempt to investigate this possibility the relationship between the imposed board movement and the resulting leg righting force was altered by inserting different springs into the driving system (see Material and Methods). The profile of the leg reaction is essentially unchanged during lifts with an interposed spring compared with the rigid drive, but the magnitude of board movement is reduced to a small drift which continues beyond the lifting phase (Fig. 5). The eyestalks respond strongly during the lift, which corresponds to the period of increasing leg force, but continue to move when the lift is completed and the force is declining, as long as the footboard continues to drift (Fig. 5a). Similar results were obtained during the return phase (drive motor reversed).

In many experiments, and with different stimulus configurations (whole board, halfboard, three-leg

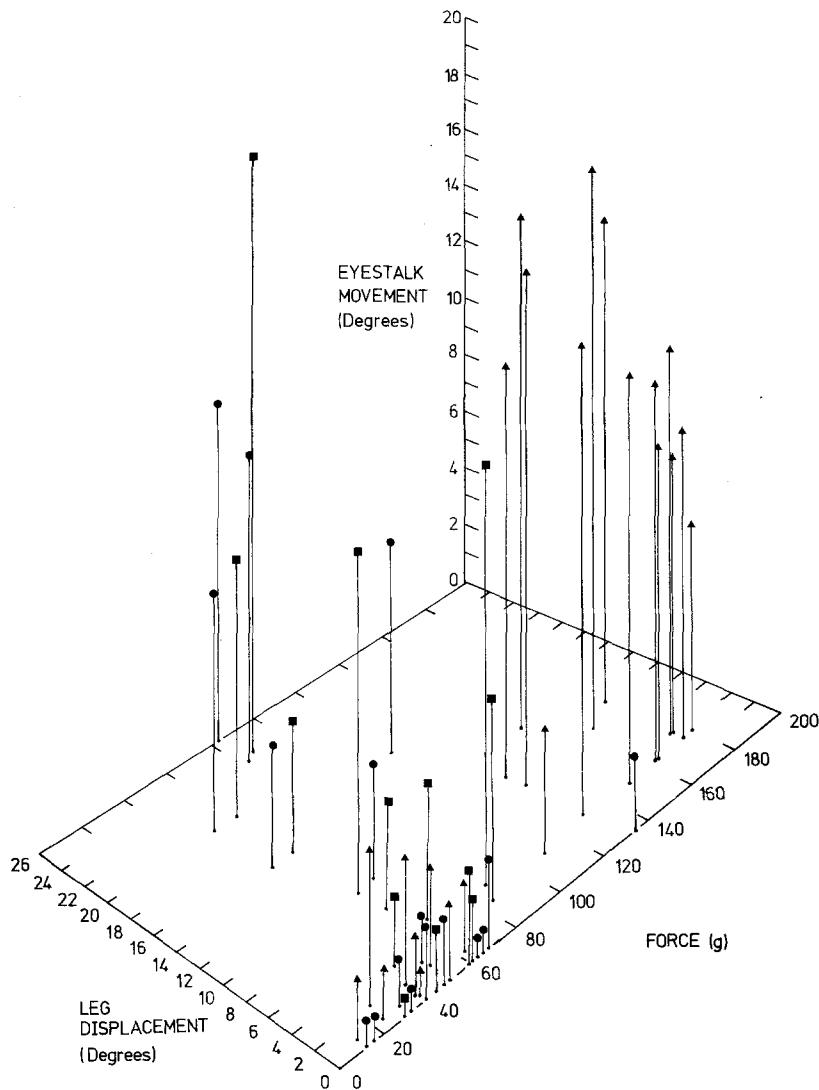


**Fig. 5a and b.** Typical examples of experiments with interposed springs in the drive system. In each case the drive arm moves the upper end of the spring through ca. 10 cm. Periods when the drive motor is operating indicated by arrows. In **a** (spring 38) both spring extension (lift) and release (down) result in a leg resistance reaction, although in each case there is an accompanying board movement. In **b** (spring 39) leg reaction is again present, but here almost completely prevents board movement during the lift. On return the leg reaction subsides but no board movement occurs. However, a clear eyestalk response is still present

group) eyestalk movements of up to 4° were measured in the complete absence of footboard movements (Figs. 5b, 6). In each case, however, leg righting forces in the range 10–130 g were recorded (Fig. 6). This indicates that force alone, in the absence of leg movement, is an input parameter to the eyestalk control system. Nevertheless, movement of the leg joints is an additional and more powerful input, as is demonstrated in Fig. 6. For a given force of leg reaction the eyestalk response increases with increasing footboard displacement, and reaches values which greatly exceed those recorded with force changes alone.

## Discussion

Several differences emerge between the responses of legs and eyestalks to stimulation of leg receptors on a moving substrate. The leg resistance reaction continues as long as there is an imposed force, whereas



**Fig. 6.** The relationship of the eyestalk response to leg displacement and leg resistance force, plotted in 3 dimensions. Data from 3 experimental arrangements:  $\blacktriangle$  = whole footboard (springs 37, 38);  $\bullet$  = halfboard (springs 37, 38, 39, 42);  $\blacksquare$  = group of three legs held in cradle spanning meri (springs 38, 39). When no leg displacement occurs the eyestalk response appears to be a function of the force generated by the leg reaction. However, for a given force eyestalk response increases in proportion to amount of leg displacement

the eye response reaches peak values before the end of board movement (Fig. 2). The different phase relationships with sinusoidal inputs (Fig. 4) are also indicative of different input-output transformations. A clear difference exists in the strength of the contralateral effect, the eyestalk response being a little less than the ipsilateral value while the leg reaction is effectively absent (Fig. 3). Such differences may be related to the natural functions of these output systems. The eyestalk reaction compensates for the shift of the visual surroundings, and is therefore expressed by both eyes. The leg reactions contribute to righting and may be organised mainly in terms of reflexes within individual appendages which react to particular external forces and movements acting upon them.

The finding that eyestalk movements accompany changes in the leg resistance reactions in the absence of leg movement itself raises questions about the sen-

sory basis of this effect. Candidates as receptors include stress detectors in the cuticle (e.g. campaniform sensilla, CSD's) (Laverack, 1976; Clarac, 1976) and muscle tension organs (Macmillan, 1976). The effect of such force detecting systems acting alone is limited, however, resulting in eyestalk displacements of less than  $5^\circ$ . This compares with eyestalk responses of greater than  $20^\circ$  when changes in particular leg joint angles (especially at C-B, see Schöne et al., 1976) also occur (Fig. 6). It therefore seems probable that a compound sensory input from force detectors and position detectors (e.g. chordotonal organs, strand organs) normally drives the eyestalk response to forced changes in leg-to-body position. Although the nature of this interaction is at present unknown, it is becoming increasingly clear that intra- and inter-segmental leg reflexes in *Palinurus* are based on multiple proprioceptive effects rather than on simple reflex re-

sponses to the stimulation of individual sensory receptors (Clarac et al., 1976; Bush et al., 1978; Clarac et al., 1978; Scapini et al., 1978).

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