The influence of substrate contact on gravity orientation. Substrate orientation in Spiny Lobster V

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The Influence of Substrate Contact on Gravity Orientation

Substrate Orientation in Spiny Lobsters V

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Summary. Tilting of the animal with respect to gravity results in compensatory eyestalk movements and in leg counterforce reactions which vary with the number and sequential position of legs touching the body-fixed substrate board (Figs. 2, 3). The gravity response is reduced with increasing number of legs touching the substrate. The results fit an interpretation that the weight of the substrate input interacting with gravity signals results from superposition of the weighted effects of the single legs involved (Figs. 2, 4).

Introduction

Spiny lobsters, as many Crustacea, live in a rocky habitat, they walk and climb on inclined or vertical surfaces and hide in crevices where they sometimes cling to the vertical walls. Therefore the substrate is a very important reference. Its importance, however, is reduced, if the animal loses contact with the wall and is suspended free in the water. Then it relies upon the gravity input. This paper contributes to the understanding of the mechanism of interaction of the two input systems involved.

Gravity input is mediated by the statocysts, substrate input by proprioceptors in the basal joints of the legs (Schöne et al., 1976) and other leg receptors responding to changes in the geometrical leg-to-body relation (Scapini et al., 1978). It has been shown that the gravity input interacts with the substrate input; normally both signals are taken into account. When the substrate is tilted against the animal the compensatory eyestalk response is larger in animals with no statoliths than in animals with normal functioning statocysts (crayfish: Stein and Schöne, 1972; spiny lobster: Schöne and Neil, 1977). Other results show that the substrate-modulated eye response is different at different body positions to gravity, indicating that the "weight" of the gravity input is variable (Stein and Schöne, 1972). Another arrangement of the two inputs was investigated here: Substrate position was constant with respect to animal (with different numbers of legs making contact), and gravity input was modulated. The reactions monitored were compensatory eyestalk movement and leg counterforce.

Materials and Methods

The experimental animals (*Palinurus vulgaris*) were imported from the Thyrrenian coast of Italy and maintained under semi-natural conditions in the lab.

Apparatus and general procedure have been described before (Schöne et al., 1976; Neil and Schöne, 1978). The animal was fixed with its dorsal side to a holding device, which was combined with a footboard. The framework could be tilted with respect to gravity (Fig. 1). Position was recorded by means of a potentiometer, eye movement by a miniature angle transducer (Marrelli and Hsiao, 1976), force by a strain gauge (Grass FT 0.3 °C), all signals being continuously recorded on a chart recorder (Philips oscilloscript).

The board was fixed in relation to the body. The legs could be lifted off the board by strings fastened to the framework. Body plus board were oscillated from 0° to 30° left side down tilt about an axis running along the midline of the board.

Thus the main point of the procedure is to tilt the animal together with its substrate reference against gravity.

Data points were derived from the original records by averaging of 6 to 10 cycles, the variability of response amplitude being small.

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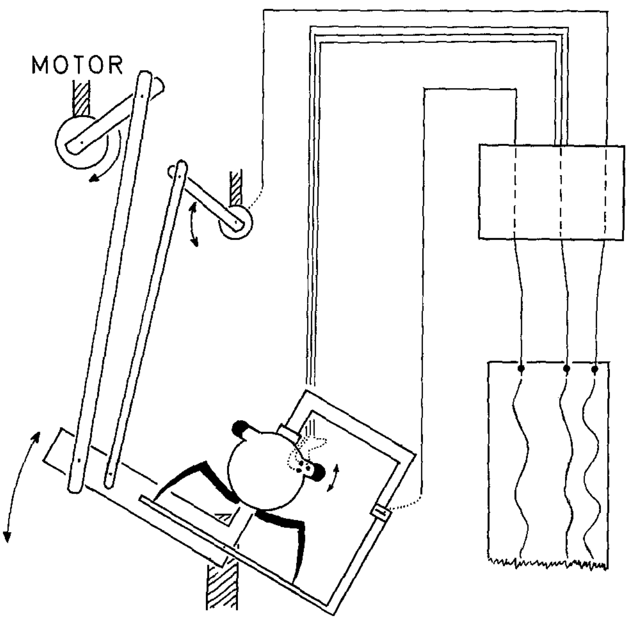

Fig. 1. Setup for recording eyestalk responses and force responses of spiny lobsters when tilted against gravity with body-fixed substrate board. The animal is shown in a stylised front view with eyestalks and legs

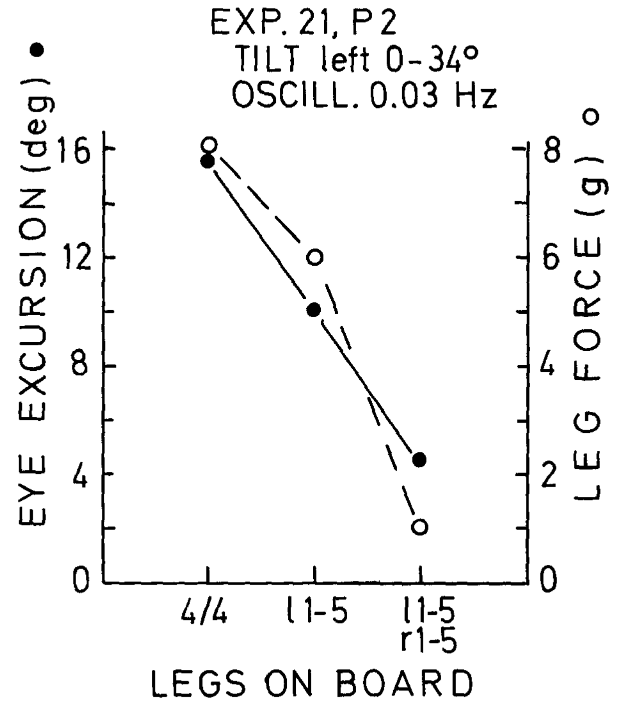

Fig. 3. Eyestalk reaction (solid line) and counterforce reaction of legs (dotted line) released by an oscillatory movement to gravity (left 0–34°) with varying numbers of legs touching substrate

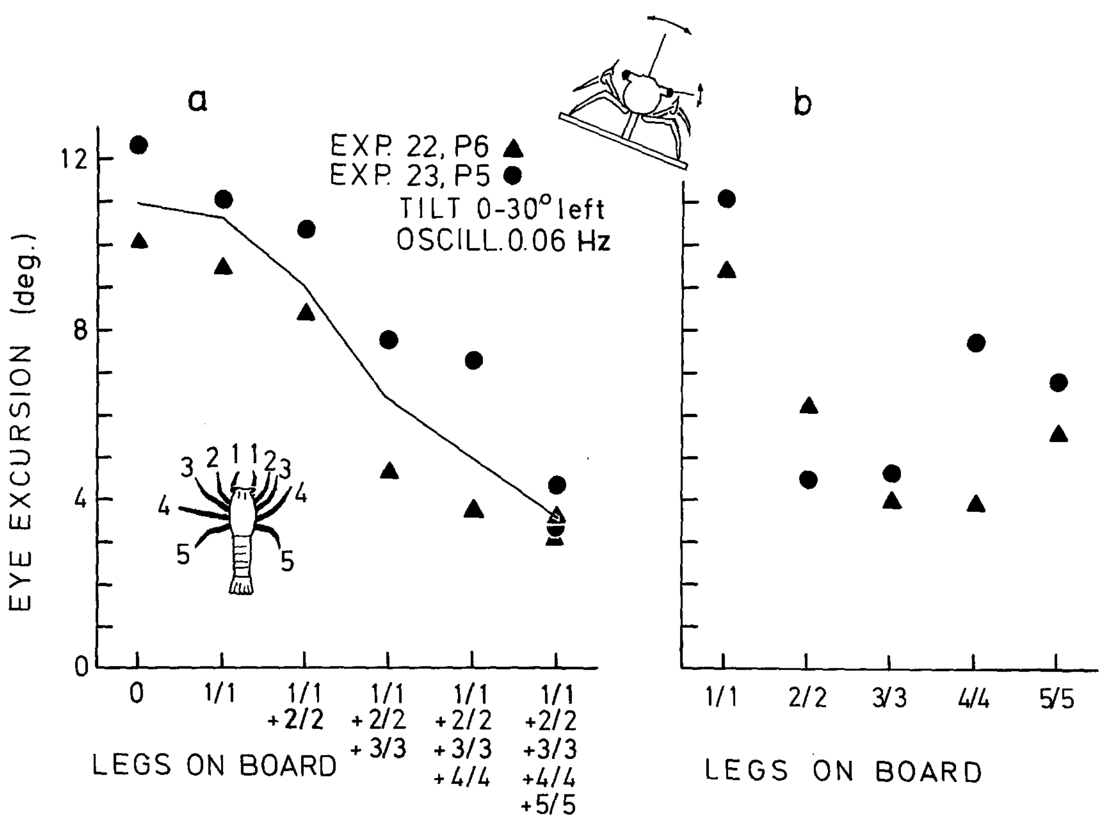

Fig. 2a and b. Eyestalk reaction to statocyst and substrate input. Oscillatory movement of animal plus board against gravity (0–30° left) with (a) increasing number of legs on board, (b) single pairs of legs on board. The line in a was calculated thus: taking into account a "weighting factors" (cf. text). The upper inset figure refers to a stylised frontview of the animal with some legs lifted from board, the left inset figure demonstrates a dorsal view with legs numbered

Results

Eye amplitude with no legs on the board represents the compensatory response to statocyst input. The eye response reduces as successively more legs contact the board. When all legs are down the response is reduced to 30% of initial amplitude (Fig. 2a).

Individual leg pairs were tested separately and results indicate that their modulation of statocyst response differs with leg number, the greatest effect being produced by legs 3 (Fig. 2b).

During body tilt the force imparted by all the legs onto the board is less than 10 g (Fig. 3). As the number of legs on the board is reduced the force produced in response to body tilt increases in proportionality with increase in eyestalk movement.

Thus the leg contact is "weighted" in its interference with the gravity input. This holds true for the compensatory eyestalk movements and for the counterforce (=righting reaction) of the legs.

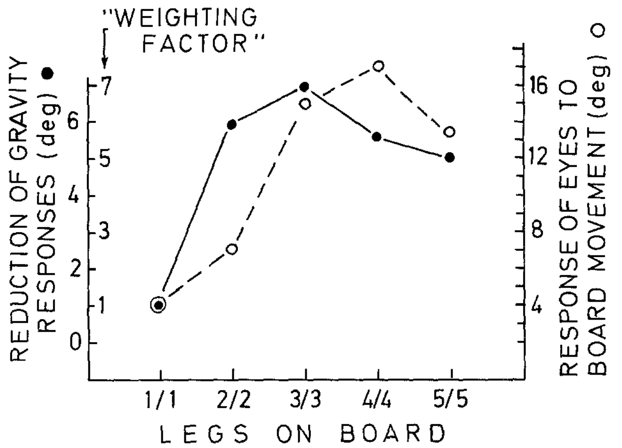

Fig. 4. Eyestalk reaction to oscillatory substrate movement of ±15° (dotted) affecting single legs (data from Schöne and Neil, 1977) and reduction of eyestalk response to gravity input (solid) as derived from Figure 2. The "weighting factor" scale refers to the reduction effect as scaled on left ordinate

Discussion

The results of the force measurements appear to be a paradox: The righting force exerted onto the board during body tilt is smallest when all legs touch the board, and increases as the number of contacting legs is reduced (Fig. 3). More legs should be capable of producing larger forces, but in fact produce smaller.

This contrasts to the finding that strong forces are produced by the animal, when either the substrate is tilted with respect to animal or when the animal is tilted with respect to substrate plus gravity (Schöne and Neil, 1977; Neil et al., 1978). Forces up to 500 g have been measured.

The paradox is resolved if we analyse the eye response which is also reduced in magnitude if the number of board-touching legs increases. That is in both cases the effect of the substrate input in reducing the gravity signal increases as the contact of the animal with the substrate gets larger. We see differences in the contribution of the individual leg pairs to this effect (Fig. 2b). A comparison can be made with the results of other experiments, where the leg movement released the eye response (Fig. 4). In each case the influence of a leg is of the same relative magnitude, leg 3 exerting a large influence. The combined effect of several legs is explained if we assume that in the neural computation "weighting factors" for each leg are incorporated, the values of which can be derived from Figure 4.

The sum effect of each leg combination can be calculated from addition of the effects of individual leg pairs weighted according to the results of Figure 2b, as replotted in Figure 4. The result of such a calculation is represented by the line in Figure 2a. It indicates that the weight of the substrate input interacting with the gravity signals results from superposition of weighted effects the single legs involved.

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