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Leg-to-Body Geometry Determines Eyestalk Reactions to Substrate Tilt

Substrate Orientation in Spiny Lobsters IV

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Summary. The effect of oscillatory movement of single legs (about C-B axis) on compensatory eyestalk reactions and on leg counterforce as normally produced by substrate tilt has been investigated with the legs at different states of flexion (M-C joint) and leg-to-body orientation (T-C joint). Eye response and force reaction released by standard C-B movement increase with increasing angle of M-C (Figs. 2, 4) and decrease with decrease of T-C angle (Fig. 3). The effects demonstrate a multiplying influence of M-C signal and T-C signal on C-B signals. The stump of an autotomized leg releases eye responses of similar magnitude to unimpaired single legs (Fig. 5).

The data are discussed in relation to neurophysiological findings and with respect to the geometrical implications for the mechanism of substrate orientation (Fig. 6).

Introduction

Decapod crustacea show compensatory eyestalk movements and equilibrium reactions in response to stimulation of leg proprioceptors on a tilting substrate (Schöne et al., 1976). The basic elements of the sensory system involved are the individual legs which have different effects on the eye response (Schöne and Neil, 1977) and which contribute accordingly to the interaction of leg receptor input and statocyst input (Schöne et al., 1978). We are now in a position to consider how each leg operates to produce a biologically meaningful output. Available evidence suggests that movements of the C-B joint are of particular importance in producing the observed responses (Schöne et al., 1976; Clarac et al., 1976). Here we report experiments which investigate geometrical relationships at other joints within the leg and between leg and body in relation to the compensatory eyestalk response.

Materials and Methods

Spiny lobsters (*Palinurus vulgaris*) from the Thyrrenian coast were kept under seminatural conditions. Apparatus and general experimental procedure have been described in a previous paper (Schöne et al., 1976; Neil and Schöne, 1978). Special techniques concern the moving device for single legs (Fig. 1). Plexiglas cradles were

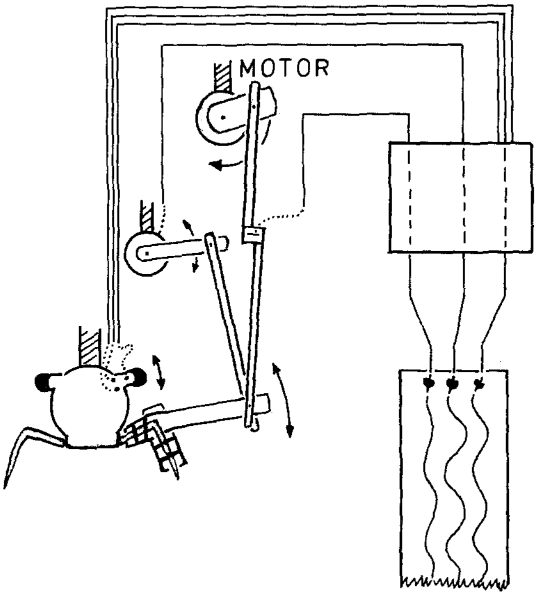

Fig. 1. Setup for moving single legs or groups of legs and recording displacement, eye response and the force exerted by the legs. The animal is shown in a stylised frontview with eyestalks and legs. The same holds true for the inset drawings in the other figures

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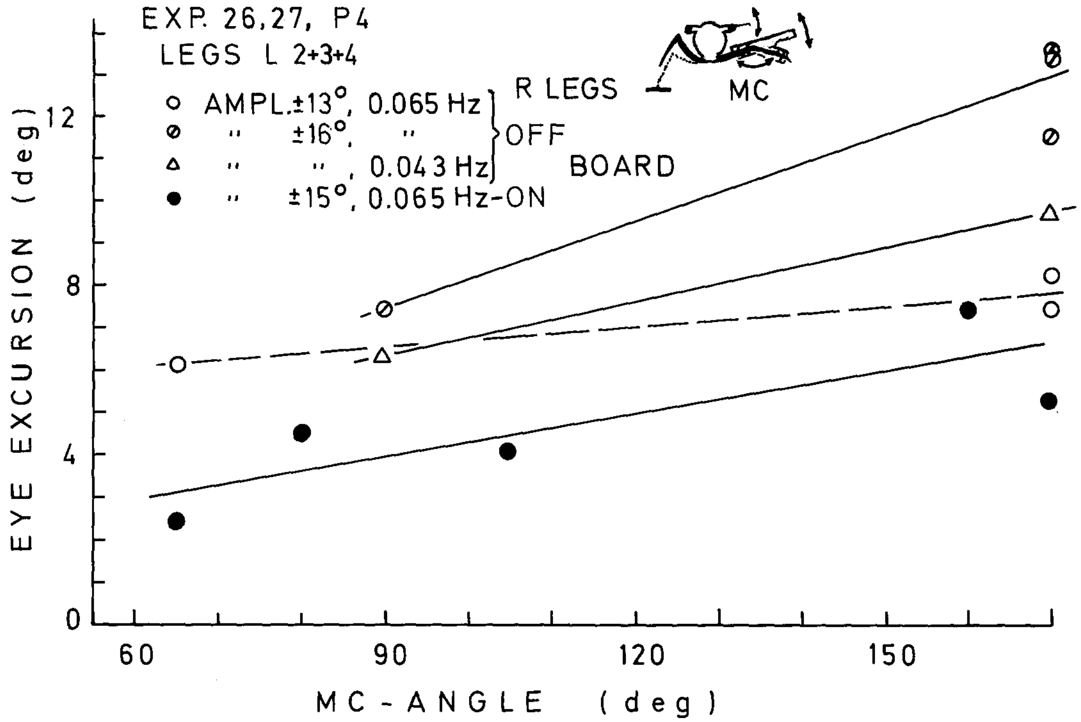

Fig. 2. Eyestalk response to oscillatory movement of left meri of legs 2, 3, 4 at various fixed positions of M-C joint. Open circles refer to experiments with right legs strung up, filled circles to those with right legs touching stationary substrate. Note that eye responses are reduced in the latter case (due to interaction of both sides; cf. Schöne and Neil, 1977)

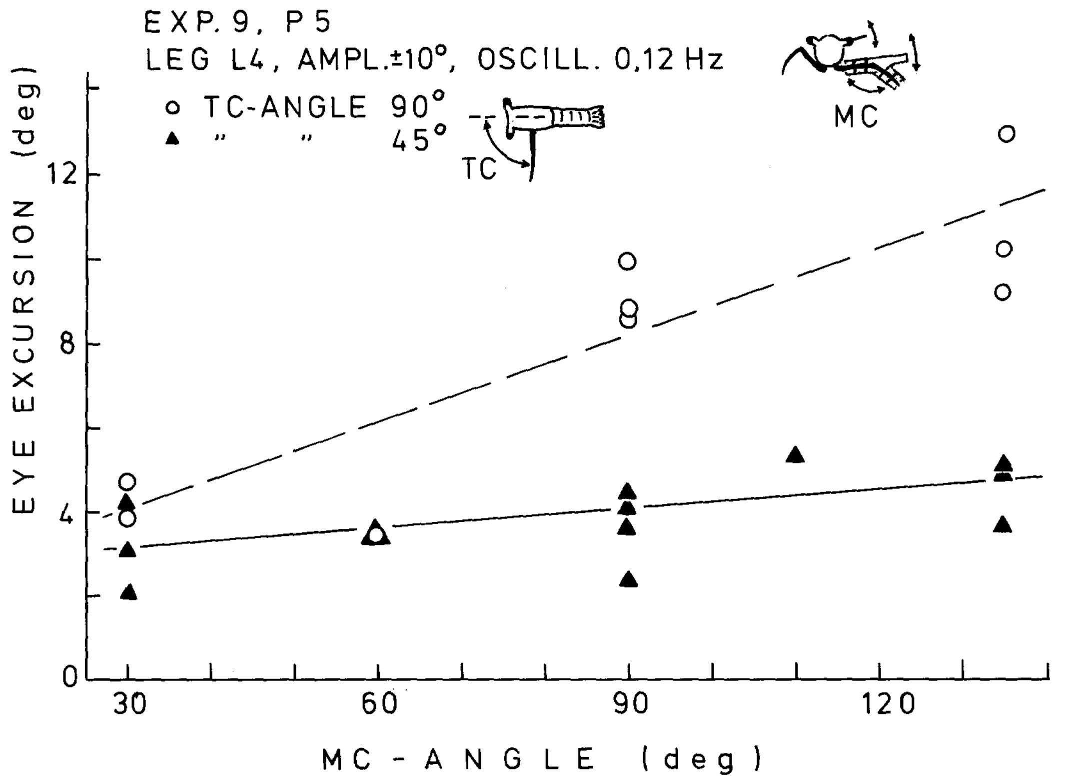

Fig. 3. Eye response to oscillatory movement of left merus (leg 4) at various fixed M-C angles, and at two settings of T-C angle (cf. left inset figure representing a dorsal view)

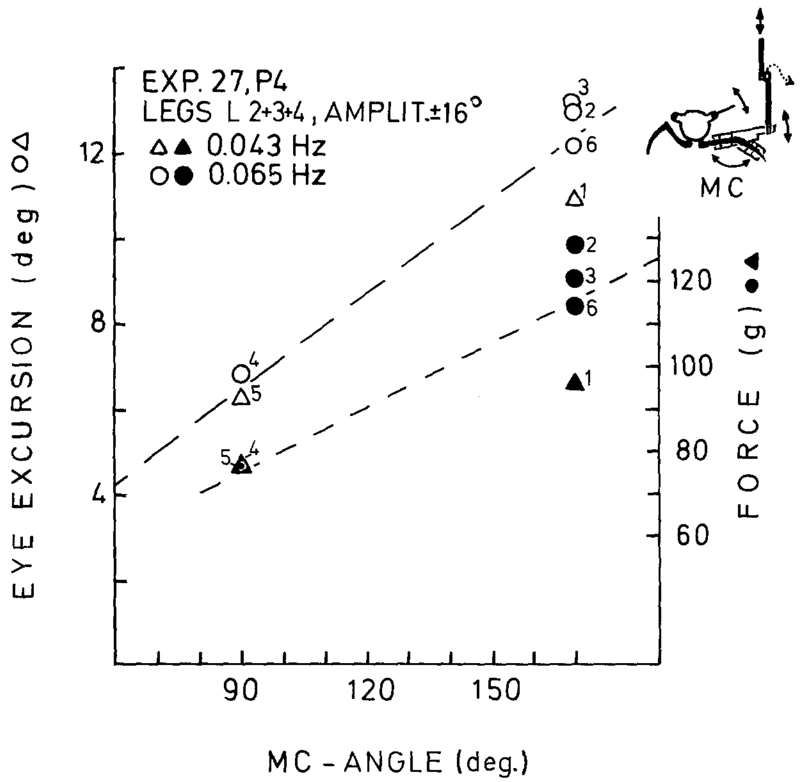

Fig. 4. Eyestalk response (open symbols) and force response (filled symbols) to oscillatory movement of left legs 2, 3, 4 at various fixed M-C angles. Eye response and force response have been recorded simultaneously, they refer to the same experiments; numbers denote sequence of measurements

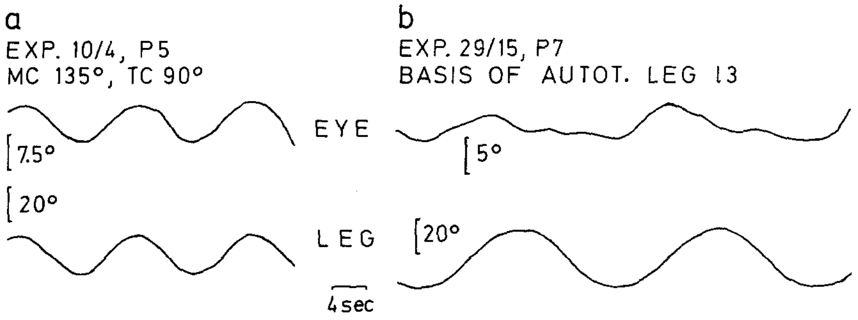

Fig. 5a and b. Eye response to oscillatory movement (a) of a single leg and (b) of the base of an autotomized leg; the basis was provided with a prothesis stick

constructed which fitted neatly over the merus and carpus leg segments of 1 or 3 legs. A fixable joint made it possible to set the carpus at any position in its normal angular range. An extension from the cradle was connected to the drive transmission into which a strain gauge (Grass force displacement transducer FT 0.3 C) was inserted.

Thus the counterforcing response of the legs to the imposed stimulus could be continuously monitored. Eye movements were measured using a miniature angle transducing device (Marrelli and Hsiao, 1976) and recorded on a chart recorder (Philips Oscilloscript).

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

Results

Eye Responses

For a constant amplitude of movement of the C-B joint, changes in the static angular setting of the M-C joint have a systematic effect on the evoked eyestalk movement (Fig. 2). Larger responses occur when the M-C joint is extended than when it is flexed.

In addition to this influence of the relations between leg segments another aspect of leg-to-body geometry is also of importance. The setting of the T-C angle was changed, so that the leg moved out of the transverse plane of the body into a plane directed 45° to the front. This systematically reduced the eyestalk response over the whole range of M-C settings (Fig. 3).

Force Responses

A new aspect concerns the counterforce produced by the moved leg itself (Fig. 4) (cf. Neil et al., 1978). The settings of the M-C angles modulate the force of the legs involved. For the same angular movement of the leg with respect to body (at C-B joint) the counterforce generated by the basal muscles is larger when the M-C joint is open (170°) than when it is closed (90°).

Autotomized Leg

Although MC-joint is of influence, the CB-joint nevertheless works in the absence of the input from the distal segments. This was demonstrated by applying sinusoidal movements to a prothesis firmly cemented to the stump of an autotomized leg (i.e. to the basis-segment) (Fig. 5). The reaction is of the same order of magnitude as that of the experiments with single legs.

Discussion

The results demonstrate that inputs from proprioceptors at the M-C and T-C joints interact with the signal from the C-B joint receptors as multiplying factors. The relationship between the results and the "distributed reflexes" recently described in crustacean legs (Clarac et al., 1978; Ayers and Davis, 1977) remains at present unclear. The observed effects on leg force output (Fig. 4) may indeed reflect such intersegmental reflexes. Our results on the eye response imply, however, that receptors at one joint can influence the output effect of receptors at another joint, an interaction which falls outside our current concept of distributed reflexes (Bush et al., 1978).

For an understanding of the functional significance of our results, the geometry of the leg-to-body relations must be taken into account. The M-C joint permits movement in a vertical plane, so that flexion and extension about the joint cause the leg to stand at different distances from the body long axis. The M-C setting is thus an important parameter determining the angular displacement of the C-B joint caused by substrate tilt. The leg articulates horizontally about T-C joint and thus a movement here both changes the standing distance from the body midline, and in addition moves the plane of action of the distal leg segments relative to the transverse body plane.

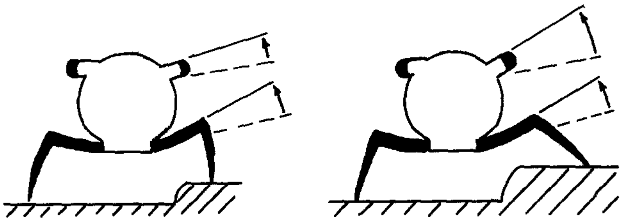

Fig. 6. Scheme of experimental situation as transferred to natural conditions. Note that same merus lift releases small eye response, when leg touches small step at close distance (M-C flexed) and larger eye response when leg touches higher step at larger distance (M-C extended)

The following explanation is in accordance with these geometrical relations and our experimental findings. If we suppose that the eye movements compensate for the shift of the (visual) surroundings as caused by the substrate-to-body movements, then our results imply that leg movements with an open MC-angle correspond to a greater shift of the surrounding than those with a more closed one. Such a situation is demonstrated in Figure 6. The same merus lift is produced by a low step at a small distance from body (i.e. flexed MC-angle) and by a higher step of a larger distance (extended M-C joint). The latter situation corresponds to a larger change of surroundings and thus should lead, and does, to a larger eyestalk reaction than the first one. A similar line of argument fits the observed effects of changing the T-C joint angle.

Thus our findings indicate that the geometrical relations of the legs with respect to body affect the compensatory eye movement. The question, however, if in addition the individual legs act differently also because of specific intrinsic weighting factors is still open.

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