POSTURAL REFLEXES COORDINATING WALKING LEGS IN A ROCK LOBSTER

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It is well established that a proprioceptive organ in the walking legs of decapod crustacea is able to influence not only the muscle of the joint where it is situated but also most of the other muscles of the same leg. Resistance reflexes elicited by several chordotonal organs have been described (Bush, 1962, 1965), and it has been demonstrated that one of them (the CB chordotonal organ) evokes a response in the main muscles of the same leg when it is passively stretched (or relaxed) (Clarac, Vedel & Bush, 1978). In addition to proximo-distal reflexes, such as CB proprioceptive action, disto-proximal controls also have been described. For example, an imposed mero-carpus (M-C) movement influences the discharge of the motoneurones which command the muscles of the thoracico-coxal (T-C) or of the coxo-basal (C-B) joint (Ayers & Davis, 1977; Vedel & Clarac, 1979). When the reflexes are initiated by imposed joint movements, not only the chordotonal organs but also other kinds of receptors are stimulated. These include cuticular receptors such as the stress detector (C.S.D.), muscle receptor such as the thoracico-coxal muscle receptor (TCMRO), the myochordotonal organ (MCO) or the apodeme tension receptors (see Clarac, 1977). A very complex picture emerges from these proprioceptive interactions. Nevertheless most of the previous coupling described concern reflexes within a leg; very little information has been published on the coordination between legs. Only two short results have been presented; Evoy & Cohen (1969) demonstrated that a passive movement of the mero-carpus joint of leg 2 evokes a slight response in the leg 1 flexor muscle of the crab and Ayers & Davis (1977) found that in *Homarus* a passive movement of both T-C and C-B joints of leg 3 evokes a reflex response in the posterior levator of the homolateral leg 2. The present paper reports an experimental study of inter-leg reflexes in the walking legs of the rock lobster.

Experiments were carried out on the rock lobster *Jasus lalandii*. The animal was placed on its side and held by rubber bands in a perspex dish. Mechanical stimulation of the different walking legs was provided by a micromanipulator and the resulting imposed leg movements were recorded with a miniature angle transducer (Marelli & Hsiao, 1976). The first leg joint associated with the thorax (T.C joint) was studied in all experiments. This joint is controlled by a single promotor and two remotor muscles, all situated within the thorax. Motor unit activity was recorded as electromyograms using teflon-coated silver wire insulated except at the tip (diam. = 125 μm).

Passive remotion of the T-C joint in leg 3 evokes a resistance reflex in the same leg joint : the promotor neurones are excited while the remotor neurones are inhibited.
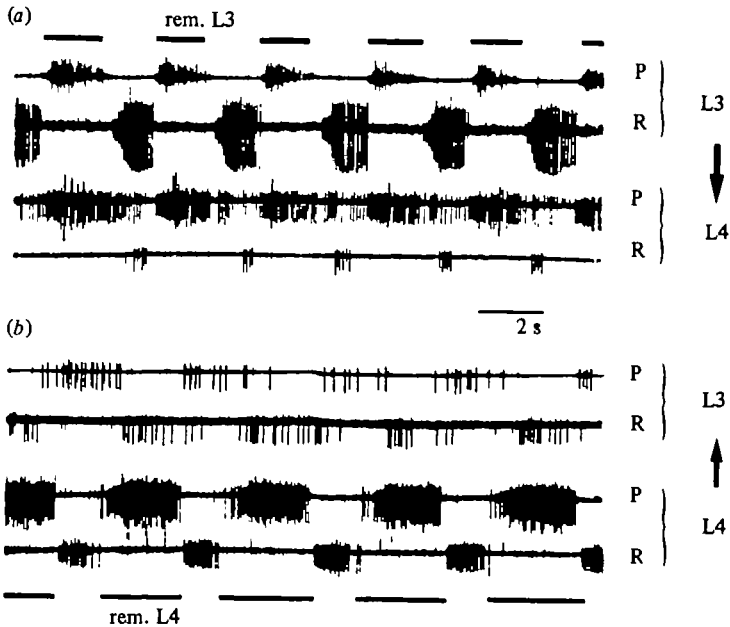
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Fig. 1. Intra- and interleg reflexes of promotor (P) and remotor (R) muscles of legs 3 and 4 with T-C joint movements of leg 3 (L3) or leg 4 (L4). (a) Descending reflex: imposed passive movement of the T-C joint of leg 3 (remotion indicated by bars – rem L3) induces resistance reflexes in leg 3 and interleg reflexes in promotor and remotor muscles of leg 4. (b) Ascending reflex: imposed passive movement of the T-C joint of leg 4 (rem L4: remotion of the leg 4 indicated by bars) induces resistance reflexes in leg 4 and interleg reflexes in promotor and remotor muscles of leg 3.

A passive promotion evokes the opposite reaction. If the two homologous muscles of the homolateral leg 4 are simultaneously recorded, an identical reflex response is observed; leg 4 remotor neurones are stimulated with leg 3 remotor neurones and leg 4 promotor neurones are excited with leg 3 promotor fibres (Fig. 1a). The response in leg 4 is less powerful than the leg 3 response but it is sufficient to evoke a movement of the joint.

With leg 3 fixed, a passive movement of the T-C joint of leg 4 elicits a resistance reflex in leg 4 and an interleg reflex in leg 3. Leg 3 remotor neurones discharge in phase with leg 4 promotor neurones and leg 3 promotor neurones discharge in phase with leg 4 remotor units (Fig. 1b).

The interleg reflexes can be obtained from each walking leg. The reflexes elicited by each of them influence not only the neighbouring appendages but also all other homolateral legs; for example, a leg 2 remotion evokes a promotor discharge of legs 3, 4 and 5 and a remotion of leg 5 evokes a remotor discharge of legs 4, 3 and 2. There is nevertheless a gradient in the strength of the response, which diminishes with the distance from the leg stimulated. Thus two oppositely directed reflexes can occur from each T-C leg joint. One follows a rostro-caudal direction; the other is caudo-rostral in orientation.

To study more carefully these opposite actions, the activities of leg 3 and leg 4 T-C muscles were recorded electromyographically during a passive T-C movement of
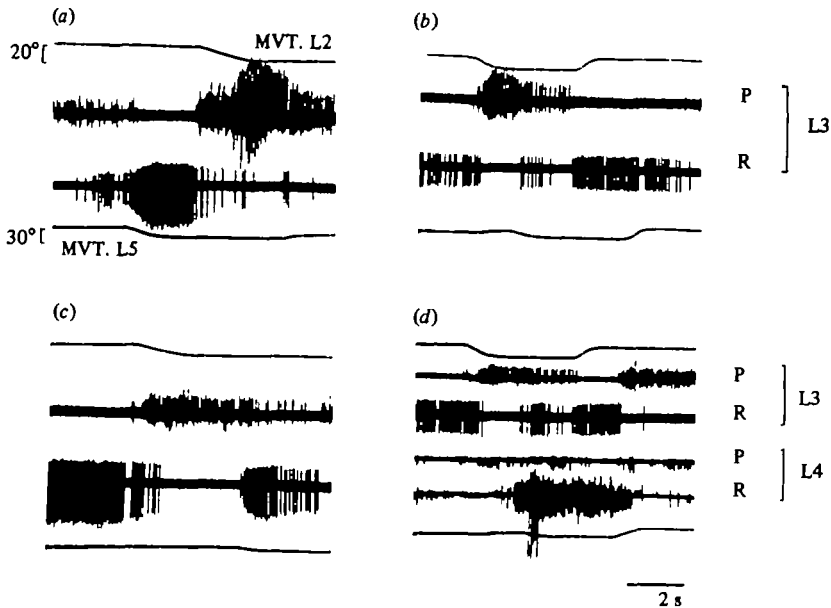
Fig. 2. Ascending and descending reflex actions on the promotor (P) and remotor (R) muscles of leg 3 (L3) and leg 4 (L4). Several combinations of stimulation demonstrate the opposite influences on these muscles of leg 2 (top traces) and leg 5 (bottom traces) T-C joint position and movement (remotion downwards). (*a–c*) Effects of imposed passive movement of the T-C joint of leg 2 (L2) and leg 5 (L5) on the T-C joint muscles of leg 3. A leg 2 remotion excites the promotor units while a leg 5 remotion excites the remotor units. (*d*) The effects of imposed remotion and promotion of leg 2 and of leg 5 on the T-C joint muscles of leg 3 and leg 4.

leg 2 or of leg 5. Leg 3 promotor units are stimulated by a passive remotion of leg 2 and reduced by a leg 5 remotion. A leg 5 remotion evokes a stronger response in the leg 3 remotor when leg 2 is promoted (Fig. 2*a*) than when leg 2 is remoted (Fig. 2*b*). The leg 3 remotor burst is stopped by a leg 2 remotion and a leg 3 promotor burst is decreased by a leg 5 remotion (Fig. 2*c*). Several combinations of stimulation confirms the interaction between the opposite reflexes (Fig. 2*d*) when the T-C joint muscles of legs 3 and 4 are recorded. The interleg reflex response consists of not only a static component but also a dynamic one (see Fig. 2*d*). This reflex has been obtained with the lobster in a wide variety of orientations. Similar interleg coupling is recorded whether the animal is ventral side up or ventral side down; it has also been recorded with the rock lobster in a normal postural position in an aquarium.

It may be concluded that the remotor/promotor discharge in a walking leg is closely controlled by the position as well as by the movement of all homolateral legs. The data presented here suggest that these reflexes may be of great importance in postural control for the maintenance of an efficient load distribution between legs. When a rock lobster is standing up in a rest position, the legs are disposed around the thorax in a fan-like manner. This is due to both anatomical and physiological features; the organization of the exoskeleton is such that the T-C joint is more and more transversely orientated from leg 1 to leg 5, and the position of the leg in the T-C angular range is progressively less promoted from leg 1 to leg 5. Thus leg 1 is roughly

in parallel with the antero-posterior axis of the body and leg 5 is about perpendicular
to the same axis. The mechanism of interleg coordination can be explained by an
opposite gradient in the strength of the two opposing reflexes: a passive remotion of
a front leg makes that leg and the neighbouring ones return to a promoted position,
while a passive remotion of a back leg evokes in the adjacent 4th limb a remotor
excitation. These controls serve to maintain the limb orientation seen in the resting
animal. The role of these reflexes during dynamic behaviour is less clear. Because
some passive resistance reflexes could be switched into assistance reflexes (DiCaprio
& Clarac, 1980), it can be hypothesized that the reflex coordination described here
could be changed into other coordinating couplings during the locomotory process.

The sense organs signalling static as well as dynamic proprioceptive information
of the T-C joint are numerous. The most well known is a muscle receptor organ, the
TCMRO (Bush, 1977). A T-C movement stimulates also some innervated elastic
strands (Alexandrowicz, 1967), several bipolar cells close to Alexandrowicz's X cells
(Bevengut and Clarac, in prep.) and some external innervated hairs which make
contact with the carapace. Lastly it is obvious that the interleg reflex is facilitated by
non-specific information coming from the other joints. Nevertheless it can be shown
that the T-C joint alone evokes this reflex, because an autotomized leg elicits it also.

This report illustrates the importance of the T-C joint in interleg coordination in
a *Palinurus*. Preliminary investigations demonstrate that this T-C reflex also exists
in the crab *Carcinus* and in *Homarus*. In the past we were not able to show any
relationships between the C-B or M-C joints in different legs. The response obtained
by Evoy & Cohen (1969) between 2 M-C joints could be explained by the peculiar
body organization of the brachyurans; the lateral orientation of the animal in walking
could be linked with this specific reflex coordination.

Similar functional connections in the proximal part of the walking legs have been
shown in insects (Wilson, 1965), but the receptors involved have not been identified.
Homolateral proprioceptive pathways seem to be important in Crustacea, while
contralateral relationships appear much more labile and have not yet been established.

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