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SHORT COMMUNICATION

REVERSAL OF AN INTERSEGMENTAL REFLEX ELICITED BY A MUSCLE RECEPTOR ORGAN

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One of the most common reflexes observed in invertebrates is the resistance reflex, in which a proprioceptor at a given joint excites the motor neurones innervating the muscles controlling the joint so as to resist imposed movement (Bush, 1962, 1963, 1965; Barnes, Spirito & Evoy, 1972). As well as these intrasegmental reflexes, proprioceptive reflexes in which sensory information is used to control muscles at joints other than the one spanned by a given proprioceptor have been reported (Ayers & Davis, 1977; Clarac, Vedel & Bush, 1978). These intersegmental reflexes may also control the state of excitation of other receptors (Moody, 1970; Clarac *et al.* 1978). Resistance reflexes and intersegmental reflexes are presumed to have a role in postural maintenance and load compensation (*op. cit.*; for review see Mill, 1976). However, resistance reflexes can be suppressed during locomotion (Barnes *et al.* 1972) and intersegmental reflexes may be modified during walking (Ayers & Davis, 1977). In addition, we have recently shown that a resistance reflex elicited by the thoracic-coxal muscle receptor organ (TCMRO) in the crab can be reversed to become a positive feedback assistance reflex (DiCaprio & Clarac, 1981). In this report we demonstrate that an intersegmental reflex activation of the basipodite levator and depressor motor neurones mediated by the TCMRO can also be reversed with respect to movement of the thoracic-coxal (TC) joint.

All experiments were performed at room temperature (18 °C) on the fifth leg of the shore crab, *Carcinus maenas*. The nerves innervating the TC remotor and promotor and the coxal-basal (CB) levator and depressor muscles of the leg were cut and their activity monitored with suction electrodes. All other nerves in the leg, with the exception of the TCMRO afferents, were cut. Care was taken to ensure that the elastic levator and depressor receptors (Alexandrowicz & Whitear, 1957) were severed close to their origins in the thorax. Passive movements of the coxa were made with an electromechanical puller via a mechanical linkage to a pin glued to the coxa.

Passive movement of the TC joint normally elicits a resistance reflex activation of remotor and promotor neurones and an intersegmental reflex in the CB levator and depressor neurones (Fig. 1). When a resistance reflex is evoked in promotor and remotor neurones, the activation of levator and depressor motor neurones is always in phase with the promotor discharge, i.e., on remotion of the joint. Although the reflex activation of levator and depressor neurones occurs on remotion of the joint,

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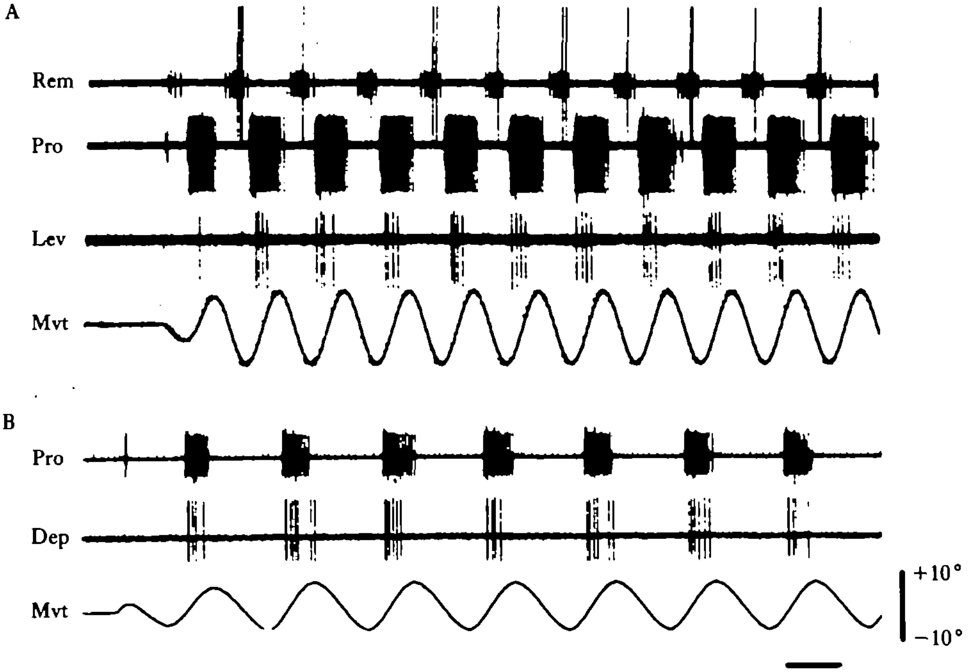

Fig. 1. Resistance and intersegmental reflexes evoked by passive TC joint movement. (A) Top three traces are extracellular recordings from the nerves innervating the coxal remotor (Rem), coxal promotor (Pro) and basipodite anterior levator muscles (Lev). The bottom trace (Mvt) is a record of TC joint angle, taken from the input signal of the movement transducer, with an angle of zero degrees indicating the midpoint of normal TC joint movement. Remotion of the joint corresponds to an upward deflection of this trace. (B) Extracellular recordings from coxal promotor and basipodite depressor nerves (Dep) during imposed TC joint movement. Time scale: (A) 1 s; (B) 400 ms.

simultaneous activity in these neurones only occurred in a small number of trials ($< 10\%$). This simultaneous activity was most commonly evoked when the animal was active, as indicated by spontaneous firing of any of the nerves, or by movements of the other leg stumps. The most commonly observed pattern was a reciprocity between levator and depressor activity, where one group of neurones was active while the other was silent. All of these reflex patterns were abolished by cutting the TCMRO and all could be reproduced by manually pulling the cut TCMRO with forceps.

Although activation of levator and depressor neurones was most commonly elicited by remotion of the TC joint, the pattern of levator and depressor activation may spontaneously alter in response to imposed TC joint movement. These changes in levator and depressor activity were usually associated with spontaneous tonic firing of promotor neurones, or when an assistance reflex was evoked in promotor and remotor neurones. The most common response which was observed during periods of assistance reflex activity of promotor neurones was a complete cessation of levator and depressor activity. In some cases, levator and depressor neurones were active tonically at rates of 20–40 impulses/s with no discernable modulation resulting from TC joint movement.

The most pronounced alteration of the levator/depressor intersegmental refle occurred when these neurones continued to fire in bursts in response to TC joi

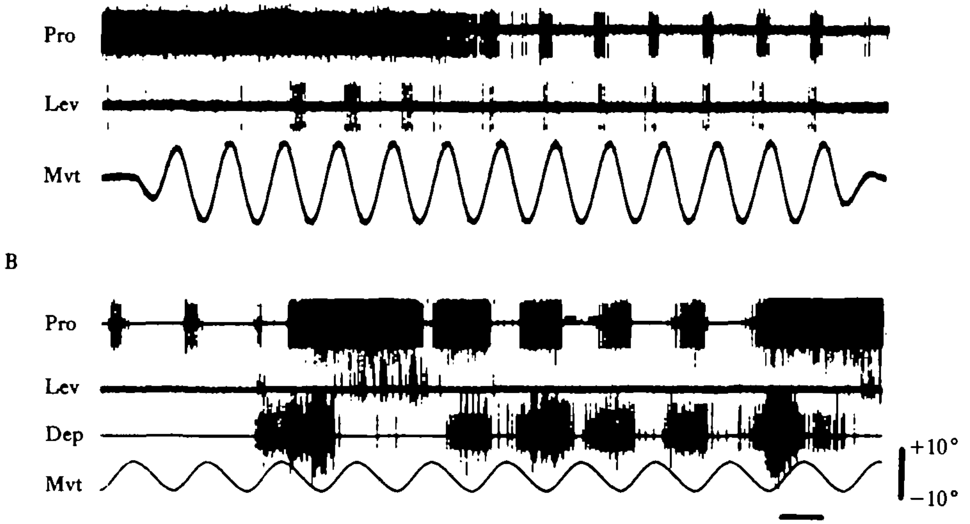

Fig. 2. Alteration of levator and depressor motor neurone discharge. (A) Levator bursts occur on promotion of the TC joint during a period of tonic promotor neurone discharge. When a resistance reflex firing pattern resumes in promotor neurones the levator firing is then evoked by remotion of the joint. (B) Reversal of depressor motor neurone firing occurs when passive TC joint movement evokes an assistance reflex in promotor neurones. Time scale: (A) 1 s; (B) 400 ms.

movement, but these bursts shifted phase with respect to the imposed movement, and occurred on promotion of the joint (Fig. 2). Promotion-evoked levator bursts were correlated with unmodulated high frequency firing of promotor neurones (Fig. 2A), while promotion-evoked depressor bursts were associated with assistance reflex activity in promotor neurones (Fig. 2B).

The functional significance of these different levator/depressor reflexes is not immediately obvious. A postural maintenance role could be ascribed to the promotor-levator linkage when resistance reflexes are elicited at the TC joint. For example, if the animal were disturbed and the TC joint remoted, the resultant promotion and levation would step the leg forward in order to support the animal. The alteration of the TCMRO mediated reflex to levator and depressor motor neurones does not appear to have a clearly defined behavioural role. The 'normal' intersegmental reflex pattern, where levator and depressor neurones are active on remotion of the TC joint, may be completely abolished or these neurones may reverse their firing pattern with respect to TC joint movement (Fig. 2). As the fifth leg of the crab is used in two different locomotor functions, lateral walking and swimming, a study of the motor patterns of these activities may suggest a role for the different levator/depressor intersegmental reflex patterns evoked by the TCMRO.

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REFERENCES

EXANDROWICZ, J. S. & WHITEAR, M. (1957). Receptor elements in the coxal region of decapoda crustacea. *J. mar. biol. Ass. U.K.* **36**, 603–628.