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Tension Receptor Reflexes in the Walking Legs of the Crab *Cancer pagurus*

THE decapod crustaceans have many advantages for the study of the neuronal mechanisms controlling simple behaviour[1–3]. Numerous authors have investigated the functions of the walking legs, but models of the control mechanisms have been presented in terms of central programmes and reflexes related simply to the positions and movements of the joints[4,5]; little attention has been paid to the control of tension in the chief working muscles. It has been shown, however, that the tension of some of these muscles is monitored by sense organs[6]. We present here some initial findings on the reflexes produced by input from these tension receptors and the integration of such reflexes in the intact animal.

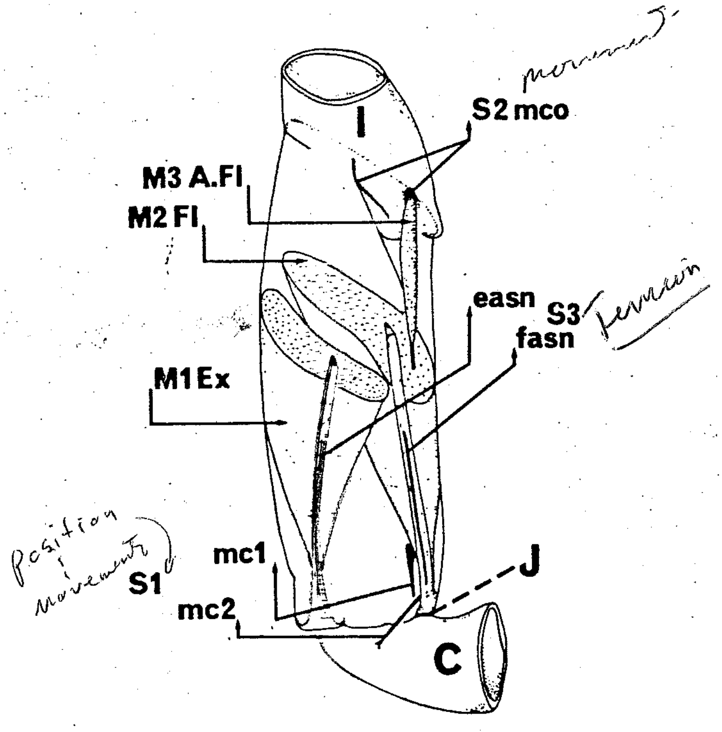

Fig. 1 The organization of the muscle (M1–3) and sensory (S1–3) systems controlling the M–C joint (J) of the first right walking leg. All the structures lie in the merus which is seen from the anterior surface lying between the ischium (I) proximally and the carpus (C) distally. The extensor (M1 Ex) lies on the anterior side of the segment and attaches to the carpus dorsally. It is innervated by two excitatory neurones and one inhibitory motor neurone. The flexor (M2 Fl) lies on the posterior side of the segment and attaches ventrally to the carpus. It is innervated by four excitatory neurones and one inhibitory motor neurone. Further, a small accessory flexor muscle (M3 A.Fl) attaches by way of a tendon to the distal end of the flexor apodeme. The simple chordotonal organs (S1 mc1, mc2) lie ventrally near the joint and are attached to the flexor muscles. For clarity the distal part of the accessory flexor muscle and the sub-groups of the myochordotonal organ (S2 mco) are not shown.

The investigation was carried out on the merus carpus (M–C) joint of *Cancer pagurus*. The organization of this joint (Fig. 1) is very similar to that of *Cancer magister*[7]. It allows almost 180° of movement in the dorso-ventral plane and is controlled by two major muscles which lie in the merus. Three types of sense organ are known at M–C. The simple chordotonal (S1) organs monitor joint position and movement, and generate resistance reflexes which oppose imposed (passive) joint movements[8]. It is curious therefore, that these reflexes should operate during walking to oppose ongoing (active) movements. In the propus-dactylus joint resistance reflexes do not occur during undisturbed walking on even surfaces (that is, wh possibility of imposed load variations from cycle to cyc been eliminated), but the mechanism governing this inhib is unknown[4]. At M–C it is thought that in such circumst the resistance reflexes operate only at extreme joint posi The complex myochordotonal organ (S2) monitors joint ments but it can also be set, without joint movement, by o to the accessory flexor muscle from the CNS. During ment the receptor generates subsidiary resistance reflexe principal role, however, is thought to be in a complex reflexes which stabilize joint resting position[5].

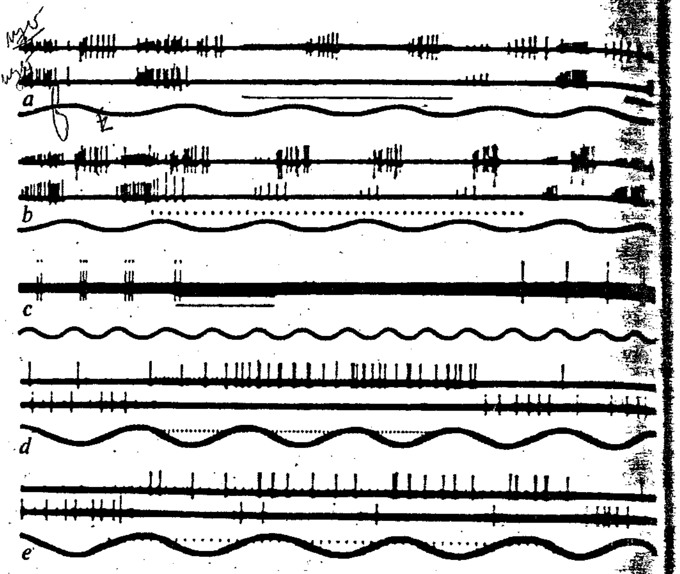

Fig. 2 Effects of stimulations of apodeme sensory nerves on resistance reflex motor activity. All stimulations were series of pulses of length 0.5 ms at low stimulus strengths. Each set of traces is described from top to bottom. *a*, Flexor plus extensor myogram, extensor myogram, stimulus of 50 pulses s^{-1} (line) movement of merus–carpus joint with flexion, an upward deflexion and extension downwards; *b*, as in *a*, but stimulus 5 pulses s^{-1}; *c*, extensor motor nerve, stimulation at 20 pulses s^{-1}, joint movement with flexion downwards; *d*, extensor myogram, flexor myogram, joint movement with extension upwards, stimulation at 20 pulses s^{-1}; *e*, as in *d*, but 10 pulses s^{-1}. Time mark is 1 s in *a* to *c* and 0.5 s in *d* to *e*.

The tension receptors (S3) are associated with the extensor and main flexor apodemes. The sensory fibres run with the respective motor nerves proximally but separate distally to form distinct apodeme sensory nerves. Each apodeme sensory nerve carries numerous axons from bipolar cells whose dendrites run on the surface of the apodemes. Little activity was recorded in either sensory nerve when the joint was moved passively with low tension in the relevant major muscles. When the joint was fixed and the motor supply to a muscle stimulated, sensory responses were recorded from its apodeme sensory nerve at tensions well within the normal range observed in intact animals. All the units sampled responded with an increase in activity to increasing tension but other responses could be present in small neurones[6].

In our experiments crabs were placed in a clamp with a platform on which the merus of the first right walking leg was fixed with the anterior surface exposed for dissection (the levator muscle apodeme of the leg was cut to prevent autotomy). Myograms were recorded from both major muscles with implanted insulated copper wire electrodes, and after a simple dissection, platinum wire electrodes were used to stimulate the extensor apodeme sensory nerve and to record from branches of the extensor motor nerve. Alternatively, by dissecting further into the meropodite the platinum wire electrodes could be used to stimulate the flexor apodeme sensory nerve and to record from branches of both flexor and extensor motor nerves.

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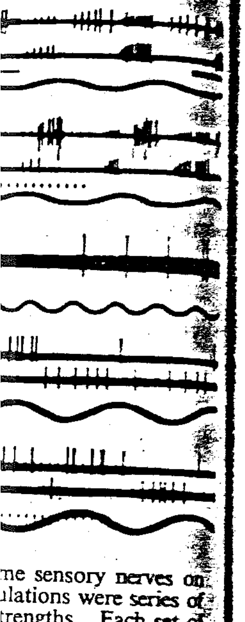

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Movements of the carpus were made with a potentiometer-monitored micromanipulator. Conventional methods of stimulation, amplification, display and photography were used.

Stimulation of the extensor apodeme sensory nerve at very low voltage (that is, activation of only large receptor neurones) effectively inhibited any spontaneous extensor motor activity. Extensor motor activity produced by evoking resistance reflexes (initial part, Fig. 2*a*) was also inhibited by stimulation of the extensor sensory nerve. Total inhibition was always obtained at 50 pulses s^{-1} (Fig. 2*a*), but the inhibition could be reduced by lowering the stimulus frequency (Fig. 2*b*). After a stimulus, inhibition could persist for many seconds (Fig. 2*c*). The effects on the antagonistic flexor motor neurones were more varied. In some examples there was little change in flexor activity during stimulation of the extensor sensory nerve (Fig. 2*a*, *b*) but more often an excitation was observed. We suspect that other factors (for example, the flexor apodeme sensory input) are involved in the antagonistic motor response. Stimulation of the flexor apodeme sensory nerve during passive movements of the carpus produced effects symmetrical to those observed for the extensor sensory nerve. At low stimulus strengths inhibition of the flexor motor activity was obtained (Fig. 2*d*) and this effect could be modulated by changes in stimulus frequency (Fig. 2*e*). Again, more variable results were obtained for the antagonistic (extensor) motor neurones but most often an excitation was observed (Fig. 2*d*, *e*). No significant changes in any of the responses to low stimulus strength activation of the apodeme sensory nerves were observed after destroying the myochordotonal organ receptor system by removal of the accessory flexor muscle.

Stimulation of either apodeme sensory nerve at much higher stimulus strengths produced, after a short latency, a strong discharge in both extensor and flexor motor neurones. In all experiments the identities of the stimulated and recorded nerves were subsequently verified by staining with methylene blue. Additionally, a series of control experiments confirmed that the results were obtained from apodeme sensory input to the CNS.

The crab M–C joint has now been shown to have three different types of sensory receptor, each of which can be divided into at least two distinct sense organs. In view of this complexity findings of no malfunction after ablation of single sense organs in such situations do not necessarily mean that the ablated receptor has no function in the intact animal[9,10]. The widespread occurrence of tension receptors in the decapods[6], and the possibility of hysteresis in the responses of crustacean muscles to motor output[11], also mean that for this group the regulation of muscle tension can no longer be ignored in models of neuronal control mechanisms governing simple behaviour.

The fact that the apodeme sensory input, which is dependent on muscle tension, can profoundly modify the resistance reflexes due to the chordotonal organs, may explain the inhibition of resistance reflexes during undisturbed walking on even surfaces, although an entirely central inhibition would seem to be a more economical mechanism. We suggest, however, that during normal walking on uneven surfaces the crab is as likely to encounter resistance to active movements as imposed (passive) joint movements. Thus reflexes generated by tension receptors (when an active movement is prevented) could be just as important as resistance reflexes in the intact animal. Tension receptor reflexes are clearly of some importance in cockroach walking[12].

The demonstration of a negative feedback loop from sense organs in series with the meropodite working muscles suggests that the apodeme receptors are analogous to vertebrate Golgi tendon organs. We would be cautious of a direct analogy because the effects of higher stimulus strength activation of the sensory nerves suggest that the apodeme sense organs also contain elements which evoke strong excitatory reflex output to the innervated muscle. More sophisticated experiments will be required to determine the nature of any such positive feedback elements. The same holds for the more complex effects tha we have observed for the antagonistic muscles in these exper ments. Our findings nevertheless show that the sensory arra at the crab M–C joint is more comparable to the vertebrate system than was previously thought, and thus probably more useful for the study of general principles.

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Trend towards Earlier Menarche in London, Oslo, Copenhagen, the Netherlands and Hungary

Brundtland and Walløe[1] have reported that the trend ward earlier maturation in children, as evidenced by age menarche, has stopped, at least for the present. Usi probit estimates in a *status quo* inquiry they gave the mea ages as 13.27 yr in 1952 and 13.24 in 1970. Both results we based on large samples of Oslo schoolgirls.

Here I report a similar finding in London schoolgirls. a large-scale survey[2] made in 1959 in randomly select London schools the mean, estimated by probits, was 13.05 0.02 yr. A survey made between November 1966 ar February 1967 (unpublished data), using a similar samp gives a mean of 13.02 ± 0.03 yr. This figure relates on to those girls (approximately 7,000) between the ages of and 16 whom the health visitor questioners had noted as "European" as opposed to "non-European". Because there were fewer non-Europeans in 1958 than in 1966 this may make the two samples more comparable. Inclusion of non-European girls, however, alters the value only trivially.

The previously well marked trend, therefore, seems to have stopped in London and Oslo. This is not (? yet) the case in all parts of Europe. Two other studies, comparable in both numbers and method with those cited, show that in Holland between 1955 and 1965 the mean age decreased from 13.6 yr to 13.4 yr, and in West Hungary[4] between 1960 and 1965 it