Comp. Biochem. Physiol. Vol. 68A, pp. 331 to 335
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# THE RELATIONSHIP BETWEEN MUSCLE TENSION AND OUTPUT IN A CRUSTACEAN MEROPODITE-CARPOPODITE CHORDOTONAL ORGAN (MC1)

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(*Received* 18 *July* 1980)

**Abstract**—1. The MC1 chordotonal organs of *Jasus novaehollandiae* and *Trizopagurus strigimanus* have a close and extensive association with the tendon of the flexor muscle of the pereiopod.

2. Contraction of the flexor muscle in the absence of joint movement causes a number of units in the MC1 nerve to respond to both increasing and decreasing tension.

3. Some small units in the MC1 nerve provide an analog of muscle tension.

4. The movement responses of some units of the MC1 organ are modified by tension—some responses are augmented, others reduced or abolished.

## INTRODUCTION

There is evidence, from loading experiments in whole animals, that crabs (Brachyura), hermit crabs (Anomura) and lobsters (Macrura) detect and respond to changes in muscle tension (Clarac & Beaubaton, 1969; Field, 1976; Macmillan, 1975; Macmillan *et al.*, 1976). 'In series' tension receptors have been described on the muscle apodemes of the limbs of Brachyurans (Macmillan & Dando, 1972) but, in spite of reports of searches by workers in several laboratories (Clarac & Vedel, 1975; Field, 1974, 1976; Macmillan, 1976), similar organs have not been found in Anomurans or Macrurans. In the absence of obvious 'in series' receptors in these two decapod tribes, consideration must be given to the postulate that receptors which have been shown to mediate other proprioceptive modalities may also be involved in monitoring muscle tension. Chordotonal organs, for example, which have been shown to monitor joint movement and position, are often associated with muscle apodemes and could possibly monitor muscle tension. Clarac & Vedel (1971, 1975) described a small response from the MC1 chordotonal organ of *Palinurus vulgaris* (Macrura) during isometric contraction of an associated muscle but concluded that the response could not be important for monitoring muscle tension.

In the work reported here we used the hermit crab *Trizopagurus strigimanus* and the rock lobster *Jasus novaehollandiae*, both of which have a close and extensive association between the MC1 chordotonal organ and the tendon of the flexor muscle, to examine the relationship between flexor muscle tension and the output of the chordotontal organ.

## MATERIALS AND METHODS

The animals for this study were collected using SCUBA and held until used in closed-circulation seawater systems at the University of Melbourne and the University of Canterbury. Specimens of the rock lobster *J. novaehollandiae* were collected from coastal waters adjacent to both Melbourne and Christchurch. Specimens of the hermit crab *T. strigimanus* were collected from Port Phillip and Western Port, Victoria, and held at the University of Melbourne.

Usually the 2nd, 3rd and 4th pereiopods were taken in succession from one animal, each being autotomized immediately before use. Anatomical studies were made using methylene blue staining techniques (Wales *et al.*, 1970). For physiological experiments, pereiopods were pinned out in a wax dish: the crab preparations in filtered seawater and the rock lobster preparations in Maynard's saline (Maynard & Walton, 1975). Preparations were maintained at 12°C with a thermo-couple plate (Cambion Thermionic Corp.). Tension developed by the muscles was recorded by an isometric force transducer (Grass Instrument Co., Model FT03) attached to a hinged arm which could be firmly fixed or freely swinging. Movements of the joint under study, whether externally imposed or generated by contraction of the muscles, were monitored with a light beam and photo-cell. The photo-cell was calibrated in position for each experiment. Imposed movements were applied to the preparations by means of a manually operated mechanical lever system. Some recordings were made from preparations with the joint embedded in periphery wax to prevent slight movements or vibrations. Recording and stimulation of nervous activity was done with either silver hook electrodes or suction electrodes connected to conventional electrophysiological stimulating and recording apparatus. Recordings were made either from whole nerves or from teased slips of nerve; the latter recordings allowed us to examine the responses of small groups of units or single units. The experimental situation described above is summarized in Fig. 1.

## RESULTS

### *Anatomy*

The general anatomy of the proprioceptive sense organs in the meropodite of the macruran pereiopod and their relationships to the leg nerves and muscles have been described elsewhere (Wales *et al.*, 1970). Some variations peculiar to *J. novaehollandiae* have also been described (Oakley & Macmillan, 1980). The

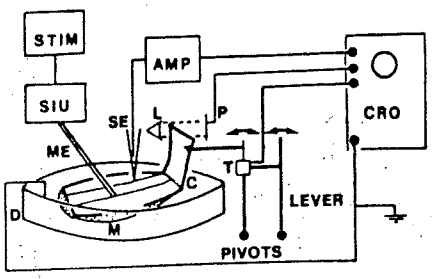



Fig. 1. Diagram showing the arrangement used for physiological experiments. The merus (M) and carpus (C) of the pereiopod are pinned out in the dish (D). The carpus is attached to an isometric transducer (T) which is itself attached to a lever system which permits controlled movement of the merocarpal joint. The movements of the carpus are monitored with a light source (L) and photocell (P). The motor nerve is stimulated with motor electrodes (ME) connected to a stimulator (STIM) through a stimulus isolation unit (SIU). The activity in the sensory nerve is recorded with a suction electrode (SE) and amplified (AMP). The movement, force and sensory nerve signals are displayed on an oscilloscope (CRO).

attachments and relationships of the MC1 chordotonal organ in *Trizopagurus* are essentially similar to those described for *Jasus*. The structural relationships necessary for understanding the present work are summarized below and in Fig. 2.

The MC1 chordotonal organ comprises a sheet of connective tissue with embedded bipolar sensory cells. The connective tissue sheet lies in the distal part of the merus and has an extensive connection with the tendon of the flexor muscle and a smaller attachment

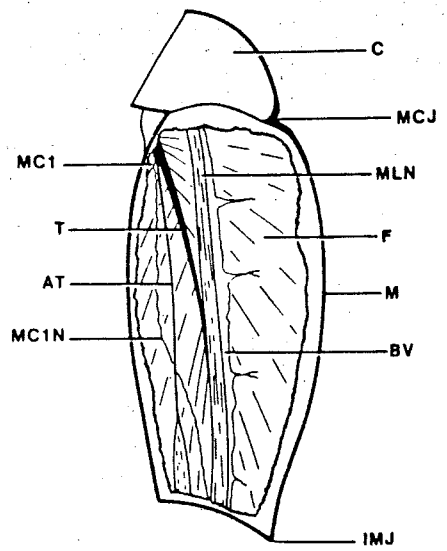



Fig. 2. Diagram showing anterior view of the merus and part of the carpus of the pereiopod of *Trizopagurus*. Part of the anterior wall of the merus, together with the extensor muscle which attaches to it, has been removed to expose the underlying structures. The structures are labelled as follows: C—carpus; MCJ—merocarpal joint; MLN—main leg nerve; F—flexor muscle; M—merus; BV—blood vessel; IMJ—ischiomeral joint; MC1—MC1 chordotonal organ; T—tendon of flexor muscle; AT—tendon of accessory flexor muscle; MC1N—nerve from MC1 chordotonal organ.

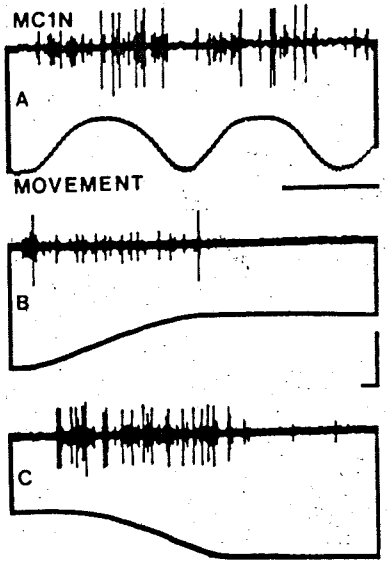



Fig. 3. Response from the MC1 nerve (MC1N) of *Trizopagurus* to externally imposed changes in merocarpal angle (movement) in the absence of tension in the flexor muscle. (A) Response to sinusoidal movement. Flexion indicated by upwards movement of trace. (B–C) Response to ramp movements. Calibration: Movement—10° angle; the most extended position shown represents a merocarpal angle of 97° which is around the middle of the range; time—250 msec.

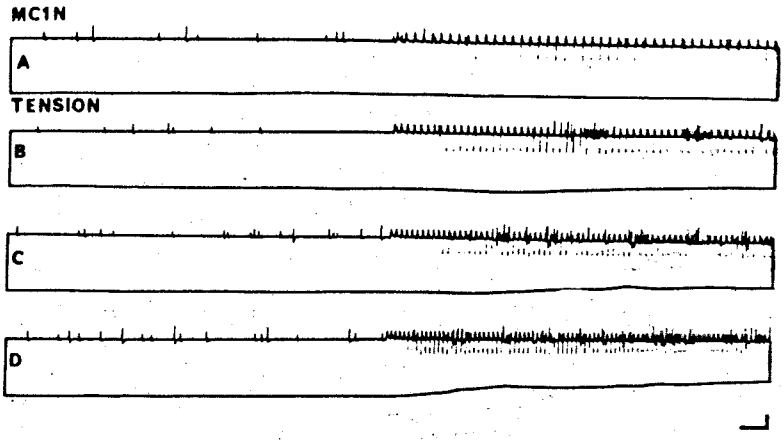
to the accessory flexor tendon at the point where it merges with the flexor tendon. The sheet also has extensive connections with the inner, ventral wall of the merus; it does not cross the merocarpal joint. In *Jasus*, the nerve from the organ lies ventrally in the merus and joins with the main leg nerve just distal to the ischio-meral joint. In *Trizopagurus* the nerve crosses the accessory flexor tendon posteriorly and runs parallel and ventral to the main leg nerve throughout the length of the merus.

Methylene blue staining revealed no discrete nerves associated with the apodemes of the flexor or accessory flexor muscles of either species.

*Physiology*

We examined the basic proprioceptive responses of the MC1 chordotonal organ to externally imposed movements in the absence of muscle tension in both *Trizopagurus* and *Jasus*. There were no gross differences between the responses in the two species, but no attempt was made to compare signal composition at


Fig. 4. Response from the MC1 nerve (MC1N) of *Trizopagurus* to isometric contraction of the flexor muscle. Merocarpal joint was fixed in wax to prevent small vibrations. Lower trace shows movement and time of stimulation of the flexor motor nerve which produced a strong twitch of the flexor muscle. Calibration: Time—250 msec.



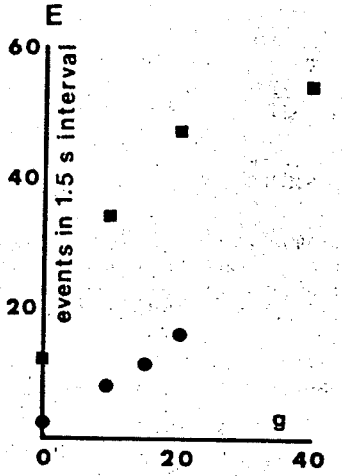




Fig. 5. (A–D) Response of a few units from a teased slip of the MC1 nerve of *Trizopagurus* to graded isometric contractions of the flexor muscle. Upper trace shows the response in the nerve slip. The lower trace shows the signal from the isometric force transducer. (A) Stimulation of the flexor motor nerve with pulses of 10 V, 0.1 msec duration at a frequency of 30/sec produces no contraction. (B–D) Other parameters as in (A) but frequency of B—40/sec, C—50/sec, D—60/sec. Calibration: Tension—40 g; time—100 msec. (E) Plot of number of action potentials occurring in a teased slip of the MC1 nerve at different isometric tension levels. Squares represent a count made on the preparation shown in (A–D) where there are at least three different units responding. Circles show the activity of a single unit in another preparation.

the single unit level. The MC1 organs have some small diameter tonically active fibres which presumably measure joint angle, and some larger, phasic units which respond to flexion and extension at the MC joint (Fig. 3). The results agree with those previously reported from other decapods (Mill, 1976).

Recordings made from the whole MC1 nerve of both *Trizopagurus* and *Jasus* showed that many units in these chordotonal organs respond during isometric contraction of the flexor muscle. To eliminate the possibility that such responses could be due to small vibrations of the joint some of these experiments were conducted with the MC joint embedded in periphery wax. Figure 4 shows a response recorded from this type of preparation in *Trizopagurus*. In this case a high level of stimulus was applied to the flexor motor nerve so that a rapid and powerful flexor contraction was produced. Most activity was seen during the contraction but a response during relaxation was also seen.

By sampling teased slips of the MC1 nerve we were able to record from a few units at a time. One type of small unit revealed by this technique appeared to increase its firing frequency with increasing strength of contraction (Fig. 5A–D). When whole muscle tension was plotted against the mean firing frequency of these units it was found that their firing frequency was a function of muscle tension (Fig. 5E). The small units shown in Fig. 5A were typical of this type of unit in that we were unable to activate them by movement or steady position in any part of the range of the joint in the absence of muscle tension.

To examine the relationship between movement and position sensitive units and tension, we recorded responses to sinusoidal movements in the presence and absence of muscle tension. We found a variety of responses. Some units which were not responding to a movement became active with muscle tension (Fig. 6A). Other units which were responding to an imposed movement showed an augmented response during the plateau and relaxation phases of muscle contraction but not during the onset of contraction (Fig. 6B). Still other units were silenced during the onset of contraction but their response was

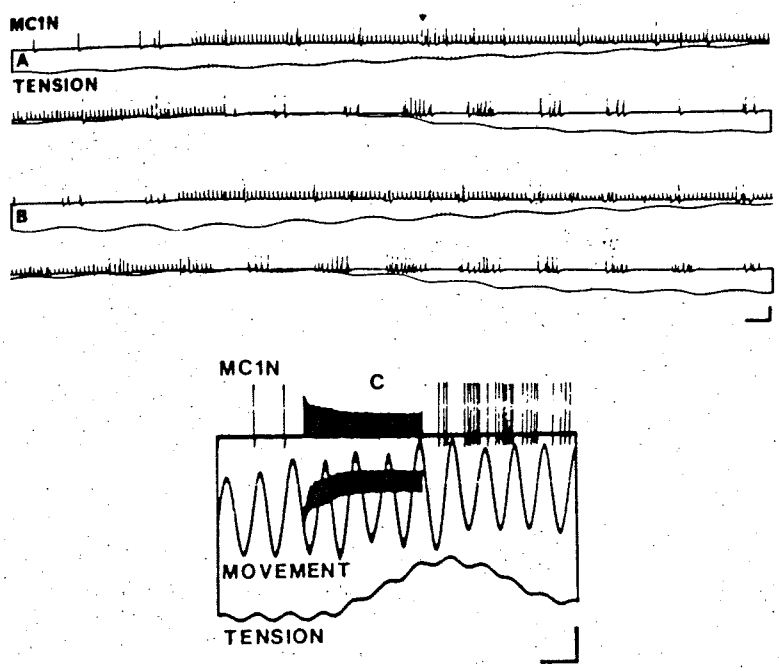



Fig. 6. Effect of tension on the ongoing proprioceptive activity in the MC1 chordotonal organ nerve of *Trizopagurus*. (A–B) Upper trace shows response in MC1 nerve to oscillating movement of constant amplitude and frequency. Lower trace shows tension recorded by isometric transducer. Unit marked with triangle in A starts to respond to movement only when tension increases. Note units in (B) which increase firing during plateau and relaxation stages of tension. Calibration: Time—100 msec. Tension—40 g. (C) Unit in the MC1N which is silenced by tension increase but increases activity during relaxation. Calibration: Time—0.5 sec; Tension—20 g; Movement 2°.

augmented during the plateau and relaxation stages (Fig. 6C).

The results obtained from the MC1 nerve of *Jasus* were similar to those shown for *Trizopagurus* in all the properties mentioned.

## DISCUSSION

Our results show that the units of the chordotonal organ have the capability of coding tension information. Because Clarac & Vedel (1975) only obtained very small responses to tension changes they concluded that chordotonal organs could not monitor tension. This discrepancy may result from species differences, although *Jasus* and *Palinurus* are morphologically similar. Another possibility is that we used greater levels of muscle contraction. It is not possible to compare our results on this basis as their paper does not include any tension calibrations.

We have demonstrated that some units which convey proprioceptive information may have their proprioceptive responses modified by tension changes in the muscles with which they are associated: the response to a given movement is in some units augmented by tension and in others reduced or abolished. Both contraction and relaxation of the muscle may affect the response of these proprioceptive units.

We also found smaller units which signal the level of tension in the associated muscle but do not appear to provide proprioceptive information in the absence of tension. A detailed fibre by fibre analysis will be necessary to establish whether or not the latter units form a completely separate tension-only set, or whether in certain circumstances they may also be proprioceptive and hence form a subset of tension-sensitive proprioceptor units.

Our demonstration that the chordotonal organ can monitor tension changes in the associated muscle raises the important question of whether or not the animal uses this information. The answer to this can only be established by experiments which determine whether any of the limb movements are load-regulated rather than proprioceptively regulated. The finding that some proprioceptive units are modified by tension raises the intriguing possibility that the gain of the proprioceptive afference onto the subsequent motorneuron or interneuron stages may be adjusted at the periphery by the effect of tension on the receptor.

Our results appear to support the hypothesis proposed by Alexandrowicz (1972) and developed by Laverack (1976). This hypothesis suggests that crustacean proprioceptors are derived from external hair-plates which have been internalized by the process of evolution.

The more primitive decapods have prominent external CAP receptors which have recently been shown to be proprioceptive (Oakley & Macmillan, 1980). The brachyurans on the other hand have none. CAP organs are always found in close association with an internal chordotonal organ. The putative advantage of internalization is that the proprioceptive signal is no longer likely to be contaminated by non-proprioceptive, external stimuli. The results reported here indicate that by associating with a tendon, an internalized proprioceptor may extend the range of

modalities monitored by signalling tension. Macmillan & Dando (1972) reported tendon receptors in brachyurans which provide an exclusive channel for tension information. They also reported that they were unable to find tension sensitivity in brachyuran chordotonal organs. If these pieces of information are considered together, two evolutionary trends appear to be occurring along with internalization. The first is an increase in the modalities monitored and the second is separation of modalities into exclusive channels.

The chordotonal organ that we have examined has an extensive association with the muscle. Some other chordotonal organs (e.g. CP1) also have extensive muscle connections and could be expected to give a similar result. Many chordotonal organs have much more limited associations with muscles (e.g. MC2) and whether such organs can also monitor tension remains to be investigated.

*Acknowledgements*—Support for this work was provided by an ARGC grant to D.L.M., and a University of Canterbury Research Committee travel grant to L.H.F. J.K.O. was supported by a Victorian Education Department Studentship.

## REFERENCES

ALEXANDROWICZ J. S. (1972) The comparative anatomy of leg proprioceptors in some decapod crustacea. *J. mar. biol. Ass. U.K.* **52**, 605–634.

CLARAC F. & BEAUBATON D. (1969) Perturbations réversibles des programmes locomoteurs induites par blocage articulaire chez le crabe *Carcinus. Comptes Rendus* **163**, 2646–2649.

CLARAC F. & VEDEL J. P. (1971) Etude des relations fonctionnelles entre le muscle fléchisseur accessoire et les organes sensoriels chordotonaux et myochordotonaux des appendices locomoteurs de la langouste *Palinurus vulgaris. Z. vergl. Physiol.* **72**, 386–410.

CLARAC F. & VEDEL J. P. (1975) Proprioception by chordotonal and myochordotonal organs in the walking legs of the rock lobster *Palinurus vulgaris. Mar. Behav. Physiol.* **3**, 157–165.

FIELD L. H. (1974) Sensory and reflex physiology underlying cheliped flexion behaviour in hermit crabs. *J. comp. Physiol. A* **92**, 397–414.

FIELD L. H. (1976) Effects of proprioceptive disruption on motor program for cheliped flexion behaviour in hermit crabs. *J. comp. Physiol. A* **105**, 313–338.

LAVERACK M. S. (1976) External proprioceptors. In *Structure and Function of Proprioceptors in the Invertebrates* (Edited by MILL P. J.), pp. 1–63. Chapman & Hall, London.

MACMILLAN D. L. (1975) A physiological analysis of walking in the American lobster, *Homarus americanus. Phil. Trans. R. Soc. B* **270**, 1–59.

MACMILLAN D. L. (1976) Arthropod apodeme tension receptors. In *Structure and Function of Proprioceptors in the Invertebrates* (Edited by MILL, P. J.), pp. 427–442. Chapman & Hall, London.

MACMILLAN D. L. & DANDO M. R. (1972) Tension receptors on the apodemes of muscles in the walking legs of the crab, *Cancer magister. Mar. Behav. Physiol.* **1**, 185–208.

MACMILLAN D. L., WALES W. & LAVERACK M. S. (1976) Mandibular movements and their control in *Homarus gammarus*—3. Effects of load changes. *J. comp. Physiol. A* **106**, 207–222.

MAYNARD D. M. & WALTON K. D. (1975) Effects of maintained depolarisation of presynaptic neurons on inhibitory transmission in lobster neuropil. *J. comp. Physiol. A* **97**, 215–243.

MILL P. J. (1976) Chordotonal organs of crustacean appendages. In *Structure and Function of Proprioceptors in the Invertebrates* (Edited by MILL P. J.), pp. 243–298. Chapman & Hall, London.

OAKLEY J. K. & MACMILLAN D. L. (1980) The morphology and physiology of CAP organs in *Jasus novaehollandiae* (Crustacea, Decapoda, Reptantia, Macrura). *Mar. Behav. Physiol.* In press.

WALES W., CLARAC F., DANDO M. R. & LAVERACK M. S. (1970) Innervation of the receptors present at the various joints of the pereiopods and third maxilliped of *Homarus gammarus* (L.) and other Macruran Decapods (Crustaacea). *Z. vergl. Physiol.* **68**, 345–384.