Comp. Biochem. Physiol. Vol. 72A, No. 3, pp. 579 to 58[illegible]. 1982
Printed in Great Britain.

0300-9629/82 [illegible]

THE RELATIONSHIP BETWEEN MUSCLE TENSION AND OUTPUT IN A CRUSTACEAN MEROPODITE–~~CARPOPODITE~~ CHORDOTONAL ORGAN (MC2)

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(*Received* 26 *October* 1981)

Abstract—1. The MC2 chordotonal organ of *Jasus novaehollandiae* has a limited association with the tendon of the flexor muscle of the pereiopod.

2. Isometric contraction of the flexor muscle evokes activity in a number of units in the MC2 nerve. Some units respond only during the contraction and relaxation phases, others during maintained tension.

3. Tension in the flexor muscle modifies the response of the MC2 chordotonal organ to a given movement.

4. The problem of how tension is monitored in muscles which are not associated with chordotonal organs is discussed.

INTRODUCTION

Evidence from loading experiments in whole animals suggests that Brachyuran, Anomuran and Macruran Decapods can detect and respond to changes in muscle tension (Clarac & Beaubaton, 1969; Field, 1976; Macmillan, 1975; Macmillan *et al.*, 1976). The structure and function of "in series" tension receptors has been described in several Brachyurans (Macmillan & Dando, 1972; Parsons, 1980, 1981) but this type of receptor does not appear to be present in the Anomurans and Macrurans where a search has been made for it (Clarac & Vedel, 1975; Field, 1974, 1976; Macmillan, 1976).

In a recent examination of the response characteristics of the MC1 chorodotonal organ in an Anomuran and a Macruran, we showed that MC1 will respond to isometric tension development by the flexor muscle (Macmillan *et al.*, 1981). In both the cases examined in that report there is an extensive and close association between the sheet-like chordotonal organ and the flexor muscle. The findings suggested a way in which these animals could detect tension changes in the muscle.

Many chordotonal organs, such as the MC2 organ, have a much more limited association with the muscle. In this report we examine the response chafacteristics of one such organ to determine whether it too is capable of responding to isometric tension.

MATERIALS AND METHODS

The animals used in this study were collected using SCUBA and held in closed-circulation seawater systems at the University of Melbourne and the University of Canterbury. Specimens of the rock lobster *Jasus novaehollandiae* were collected from coastal waters adjacent to both Melbourne and Christchurch.

The animals were induced to autotomise one limb at a time, only the 2nd, 3rd and 4th pereiopods being used. The disposition of the nerves was examined using methylene blue stain (Wales *et al.*, 1970). For physiological experiments, the pereiopod was pinned out in a wax dish and covered with Maynard's saline (Maynard & Walton, 1975). The preparations were maintained at 12°C with a thermoelectric battery (Cambion Thermionic Corp.). Muscle tension was recorded with an isometric force transducer (Grass Inst. Co., FT03) attached to a hinged arm which could be firmly fixed or allowed to swing free. The change in angle of the M–C joint was monitored by interrupting a light beam falling on a photocell. The photocell system was calibrated in place before each experiment. Externally imposed movements were applied to the carpus by means of a manually operated lever system. Recording and stimulation of nerual activity was done with either silver hook electrodes or polyethylene suction electrodes connected to a conventional electrophysiological system. Records of the results were made by photographing the oscilloscope image. By recording from whole nerves and teased slips of nerve we were able to examine the response of the entire nerve or that of only small numbers of units. The experimental situation is summarised in Fig. 1.

RESULTS

Anatomy

The general anatomy of the proprioceptive sense organs in the Macruran pereiopod and their relationships to the other elements of the legs have been described in some detail elsewhere (Wales *et al.*, 1970). The arrangement in the rock lobster *J. novaehollandiae* does not differ significantly from that description and so will not be dealt with again here. It is important, for interpreting the work described here, however, to understand the disposition of the MC2 chordotonal organ. The connective tissue strand of the MC2 organ in the animal examined here is not a flat sheet like the MC1 organ (Macmillan *et al.*, 1981). It

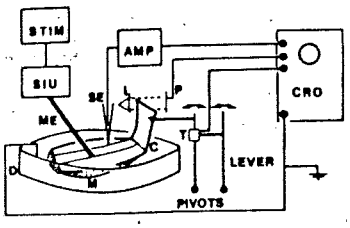

Fig. 1. Diagram showing the arrangement used for physiological experiments. The merus (M) and carpus (C) of the pereiopod were pinned out in the dish (D). The carpus was attached to an isometric transducer (T) which was itself attached to a lever system that permitted controlled movement of the merocarpal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

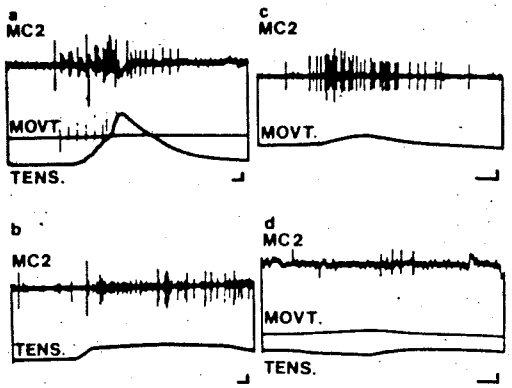

Fig. 3. (a) Brief isometric contraction of the flexor muscle produced by stimulation of the flexor motor nerve evokes activity in the MC2N. Stimulus parameters: 2.6 V, 30 Hz, 0.1 msec. (b) A maintained isometric contraction of the flexor muscle produced by stimulation of the flexor motor nerve evokes both phasic and maintained responses in the MC2N. Stimulus parameters: 2.6 V, 40 Hz, 0.1 msec. (c) Brief contraction of the flexor muscle against a strong spring produced by stimulation of the FMN. This arrangement resulted in a high level of tension (TENS.) coupled with a small change in the size of the merocarpal angle (MOVT.) and significant evoked activity in the MC2N. (d) A movement matched to that obtained in (c) above but with no tension development results in only a small amount of MC2N activity. Calibration: Movement—occurs around the rest position of the limb and mark represents 2°; tension—15 g; time—100 msec.

is a very thin, cylindrical strand which originates on the dorsal edge of the extreme, distal end of the flexor apodeme, crosses the merocarpal joint, and inserts on the dorsal wall at the proximal end of the carpus. The nerve from the MC2 organ joins the main leg nerve almost immediately after leaving the strand and can be found on the lower, medial aspect of the main leg nerve as it runs through the merus.

Physiology

We examined the overall responses of the MC2 chordotonal organ to externally imposed movement in the absence of muscle tension but no attempt was made to compare signal composition at the single unit level. We found large phasic units that respond to extension of the carpus, and some smaller tonic units that appear to signal a maintained extension (Fig. 2(a)). We also found phasic units responding to flexion (Fig. 2(b)). These results do not agree with those reported previously from other decapods (Mill, 1976) or with our own observations on the MC2 organ of the Anomuran *Trizopagurus* (unpublished results). This is the first report of an MC2 organ that responds to both stretch and relaxation.

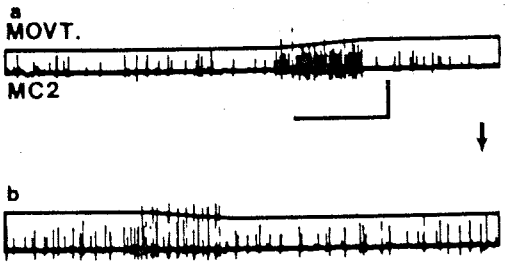

Fig. 2. Response from the MC2 nerve (MC2N) to externally imposed changes in merocarpal angle (MOVT.) in the absence of tension (TENS.) in the flexor muscle. (a) Flexion of the carpus which stretches the MC2 strand evokes a response in MC2N. (b) Extension of the carpus which relaxes the MC2 strand evokes a response in MC2N. Calibration: Movement—downward movement indicates flexion; calibration bar represents 10°; the most extended position shown represents a merocarpal angle of 97° which is around the middle of the range; time—250 msec.

Recordings from the MC2N during isometric contraction of the flexor muscle show that large, phasic units respond, particularly during the relaxation phase following contraction (Fig. 3(a)). We also found smaller units that respond tonically during periods of maintained isometric tension (Fig. 3(b)).

We were particularly interested in whether the chordotonal organ produced different responses to a given movement when it was accompanied by different levels of tension in the flexor muscle. Figure 3(c) shows the response recorded in the MC2 nerve when the flexor muscle contracted against a strong spring. In this situation, tension development was high but only a small movement occurred. We produced movements of the same amplitude in the absence of significant muscle tension both by moving the joint passively and also by stimulating the FMN at a very low level while permitting a contraction against no load. The MC2 responses produced by these two methods were identical and an example is shown in Fig. 3(d). The comparison of the MC2 response obtained in the presence (Fig. 3(c)) and absence (Fig. 3(d)) of flexor muscle tension showed that there are several notable differences. Some units in the MC2 nerve responded when tension increase and movement occurred together but not to movement alone. Other units, responded to both passive extension and to the relaxation following a high-tension flexor contraction, but the relaxation response was always larger.

DISCUSSION

It is clear from the results reported here that the MC2 chordotonal organ responds to isometric contractions of the flexor muscle. It is not clear, however, whether there is a signal coding unambiguously for tension. The response of the MC2 to isometric tension in the flexor includes at least three categories: response during contraction, response during maintained tension and response during relaxation.

The MC2 organ of *Jasus* responds to both extension and flexion at the M–C joint which relax and stretch the chordotonal organ strand respectively. It is therefore perhaps not surprising to find that the organ also responds to both increasing and decreasing tension in the flexor muscle. Indeed, our experiments indicate that some of the same units respond to strand relaxation whether it is produced by movement or by muscle tension. The response is augmented by tension which suggests that tension has a modulating effect on the movement units but not that the relaxation units are themselves coding for tension. It appears that the only units likely to be able to code unambiguously for tension are the small units that are active during sustained, steady isometric tension. A detailed single fibre analysis will be necessary to determine whether they do so unambiguously or whether they too are movement units which are also capable of responding to tension.

Our previously reported result showing that the MC1 organ can code for flexor tension (Macmillan *et al.*, 1981) was not perhaps surprising given the close and extensive association between the MC1 organ and the flexor apodeme. An interaction between flexor tension and the MC2 organ was much less expected. The connection between MC2 and the flexor apodeme is not only limited, but also, the strand of MC2 runs from the end of the apodeme and more or less in line with its long axis: not a particularly effective mechanical arrangement for producing significant strand distortion in response to the small changes in length produced by tension in the flexor muscle.

We were stimulated to make this investigation because although the animals appear to be capable of detecting tension development in the limb muscles, there is no evidence of specific tension receptors. The results presented here, together with those reported previously (Macmillan *et al.*, 1981) establish that both chordotonal organs can detect isometric tension development in the flexor muscle and that tension in the flexor muscle modifies some of the movement responses of the chordotonal organs. If the chordotonal organs are the only channels available to these animals for the passing of information on limb muscle tension we are left with a difficulty: some of the limb muscles, the extensor for example, have no association with a chordotonal organ. We must therefore conclude either that the animal monitors tension in only some muscles or that there are still undescribed tension receptors in the limbs.

Acknowledgements—Support for this work was provided by an ARGC grant to DLM; a University of Canterbury Research Committee Travel Grant to LHF; and a Victorian Education Department Studentship to JKO. We wish to thank Chris Porter for valuable suggestions on the manuscript.

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