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Tension Receptors on the Apodemes of Muscles in the Walking Legs of the Crab, *Cancer magister*†

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1. Mechanoreceptors monitoring tension in working muscles are described in the Decapoda Crustacea.

2. The receptors are associated with apodemes of muscles in the walking leg and are well-developed in the extensor and flexor of the meropodite (Figures 1, 2).

3. The unbranched dendrites of the receptor neurones innervate the tissues surrounding the insertions of the muscle fibres (Figures 3, 4, 5(A)).

4. The receptors show spontaneous activity with the M-C joint at resting position and this activity increases when the muscle is stretched by holding the joint at a different position (Figure 7).

5. Isometric tension increase in the muscle recruits sensory units (Figures 8, 10(A)) and increases the activity of units firing (Figure 9).

6. Apodeme receptors may be an entirely distinct input channel from chordotonal organs (Figure 10(B,C)). Joint movements produced by a standard muscle stimulus against increasing loads reveal very different responses (Figure 11).

7. Attempts to determine whether chordotonal organs (CP1, Figures 5(B), 6) monitor isometric muscle tension (Figure 12) suggest possible complexities in their dynamic responses.

8. Abbreviations used in this paper are FASN flexor apodeme sensory nerve, EASN extensor apodeme sensory nerve, BASN bender apodeme sensory nerve, and OASN opener apodeme sensory nerve.

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INTRODUCTION

The mechanoreceptors which monitor the position and movement of the segments of the walking legs in the Decapoda Crustacea form one of the best known proprioceptive systems in the invertebrates (Finlayson, 1969; Wales, Clarac, Dando and Laverack, 1970) and the role of these receptors in the control of posture and locomotion is now being investigated (Evoy and Cohen, 1969; Evoy, Barnes and Spirito, 1970; Moody, 1970; Clarac, 1971).

In his original study of the structure and physiology of a chordotonal organ in the decapods, Burke (1954) reported responses from the propodite-dactylopodite (PD) receptor to isometric contraction of the closer muscle (to which the receptor is attached). In spite of the importance of the finding for studies of control mechanisms little further work has been done on this aspect of the physiology of chordotonal organs. We therefore set out to reinvestigate the responses of chordotonal organs to changes in muscle tension and some initial results are presented here. We found, however, that there was a different type of receptor associated with the apodemes of working muscles and that these receptors were very sensitive to changes in muscle tension. This report is mainly concerned with the anatomy and physiology of the apodeme receptors, particularly the well-developed examples in the meropodite. Further work on the responses of chordotonal organs to tension changes and on the functional role of apodeme receptors is in progress and will be reported later.

MATERIALS AND METHODS

Specimens of the crab *Cancer magister* Dana (5–8 inches wide across the carapace) were supplied by the Institute of Marine Biology of the University of Oregon at Charleston, Oregon. Usually the 2nd, 3rd and 4th pereiopods were taken in succession from one crab, each being autotomised immediately before use. The histological preparations were made using the methylene blue staining techniques previously described (Wales *et al.*, 1970).

For the physiological experiments the segments not under investigation were removed and the preparation was pinned out in a wax dish and covered with cold crab saline.† The joint under study was free to move although for some of the isometric experiments it was encased in periphery wax to preclude

† Composition based on an analysis of *Cancer* serum made by Charles Hunter of the Institute of Marine Biology, Charleston, Oregon, was as follows: (Salt/mM/gm. per litre); NaCl/466.00/27.29; KCl/10.80/0.81; $MgSO_4.7H_2O$/19.50/4.81; $CaCl_2.2H_2O$/12.55/1.85; $NaHCO_3.10H_2O$/3.00/0.97; 10mM TRIZMA buffer (≃ 20 ml/litre) was added to the saline to obtain a pH between 7.45 and 7.55.

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the possibility of small movements. The preparation was maintained at 12°C. After dissection the nerves were lifted into oil on bipolar platinum hook electrodes mounted on micro-manipulators. Isometric tension across the joint was recorded with an isometric transducer (Grass Model FT.03 or Medical Systems Model 2STO2) connected to the movable segment by a short inflexible metal link. Joint position was monitored with a linear movement transducer. Active joint movements resulting from motor nerve stimulation were recorded with an isotonic transducer (Medical Systems Model 2LDO1) which introduced a negligible amount of inertia into the system. Weights were added to the movable segment so that the receptor responses could be studied while the muscles lifted known loads.

RESULTS

The second pereiopod was mostly used for the anatomical studies because it is the largest of the walking legs. The descriptions refer to the second left pereiopod in order to facilitate comparisons with Whitear's study (Whitear, 1962). No substantial differences were found in the 3rd and 4th pereiopods. The cheliped and 5th pereiopod, which have different structures and functions, were not examined.

Anatomy

Meropodite-carpopodite (M-C) receptors The merus is the longest segment of the leg but is quite narrow antero-posteriorly and deep dorso-ventrally. Two major muscles, the flexor and extensor of the carpus, occupy most of the interior. The extensor inserts via an apodeme onto the dorsal part of the carpus and originates inside the anterior surface of the merus. The flexor originates inside the posterior surface of the merus and inserts via an apodeme onto the ventral part of the carpus. A small accessory flexor muscle originates at the extreme proximal end of the merus and inserts, via a long tendon which traverses almost the entire length of the merus, onto the anterior distal edge of the flexor apodeme. A small number of muscle fibres also insert onto the distal part of the accessory flexor apodeme (for details see Evoy and Cohen, 1969). The meropodite-carpopodite (M-C) joint is hinged anteriorly and posteriorly allowing almost 180° of movement in the dorso-ventral plane. The M-C joint is usually held at 80°–90° but resting positions over the whole range were observed in the living animal.

The main leg nerve and blood vessel run side by side through the mid-

ventral part of the merus between the two major muscles. The previously described propriosensory innervation of the M-C joint is complex. Two chordotonal organs lie ventrally attached to the flexor apodemes near the joint (Whitear, 1962; Bush, 1965a). The cells of the MCl chordotonal organ receptor lie in a connective tissue sheet which is attached to the ventral cuticle of the meropodite and also to the accessory flexor tendon. This receptor does not cross the joint. The cells of the MC2 chordotonal organ receptor lie in a connective tissue strand which is attached close to the anterior distal corner of the main flexor apodeme and passes over the joint to insert on the anterior wall of the carpus. There is a complex myochordotonal organ receptor lying at the proximal end of the accessory flexor muscle (Clarac, 1968; Evoy and Cohen, 1969) but it will not concern us further here. As in *Carcinus* fibres from the MC1 receptor run in a distinct nerve tract for a considerable length of the merus. Fibres from the MC2 receptor form a nerve which joins the main leg nerve very near the organ. The MC1 and MC2 nerves eventually form a single bundle as they run proximally in the posterior ventral part of the main leg nerve.

Figure 1 shows a view of the interior of the merus from the anterior aspect after removal of the anterior wall and the extensor muscle. The major part of the main flexor muscle originates on the dorsal part of the posterior wall of the merus and passes ventrally onto the apodeme. A smaller part of the muscle, which originates on the ventral part of the posterior wall, runs dorsally to the apodeme. In addition, some muscle bundles originate from the inside of the ventral edge of the merus and from the ventral part of the anterior wall of the merus. These bundles are attached to the anterior lateral edge of the apodeme. These anteriorly-attaching muscle bundles and also the accessory flexor muscle and most of its tendon have been removed in order to show clearly the arrangement of the receptor nerve. With the M-C joint at an angle of 90°, which is at the middle of its range of movement, the flexor apodeme passes medially and horizontally for about two-thirds of the length of the merus.

The flexor apodeme is thin dorso-ventrally but wide antero-posteriorly and for most of its length the width is constant but it does narrow to a point proximally. The thickness of the cuticle increases progressively towards the distal insertion and at the joint the apodeme is stout and inflexible. A thin flexible band runs down both lateral edges and this broadens to a shelf for the insertion of the lateral anterior bundles of the flexor muscle. At the distal end the apodeme is concave due to an upturn of the posterior edge and lateral thickenings of both edges. The connection of the apodeme with the carpus has a complex structure. The carpus joins first onto a U-shaped piece of cuticle and this is then attached to the flexor apodeme by a narrow membranous region. A small part of the flexor muscle attaches onto the U-shaped piece of cuticle. This type of attachment also occurs for the P-D closer muscle but the dorsally-attaching antagonist muscles in each case have more direct connections. The joints allowing lateral movements have different types of apodeme attachments. We presume that the two ventral attachments for the dorso-ventral M-C and P-D joints relate to the large amount of movement possible at these joints.

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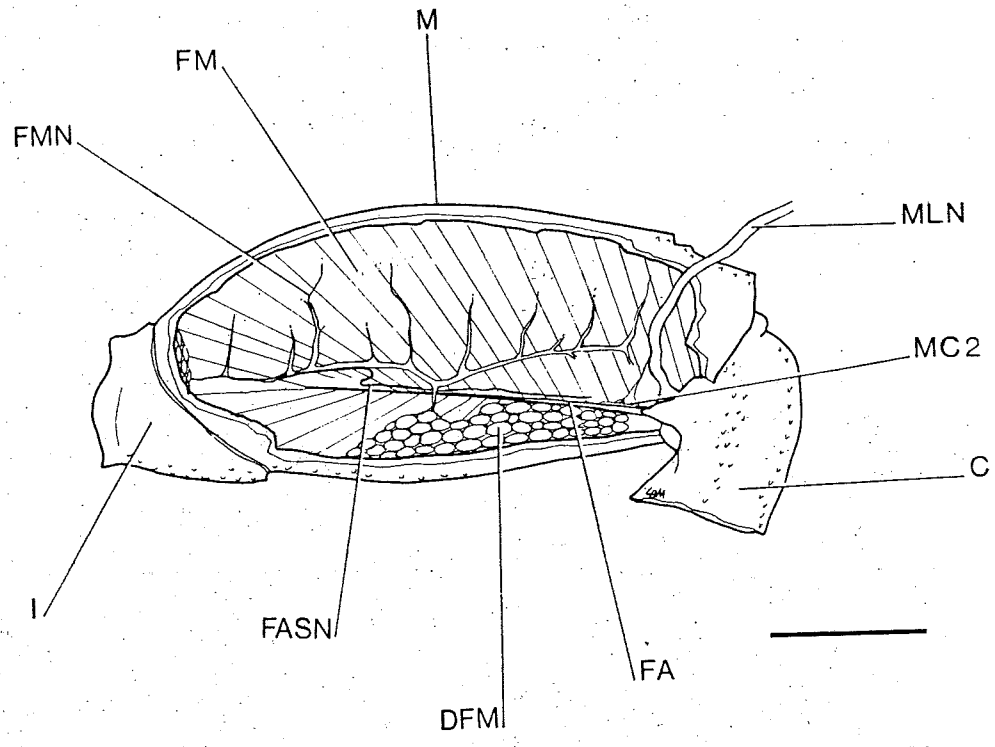

FIGURE 1 An anterior view of the meropodite to show the main flexor muscle and its associated motor and sensory nerves. This dissection is of a second left pereiopod and dorsal is uppermost in the diagram. The ischium (I) is proximal to the merus (M) and the carpus (C) is distal. The flexor apodeme (FA) can be seen running back from the M-C joint and the damaged ventral and antero-lateral muscle bundles (DFM) are located below the apodeme. The main leg nerve (MLN) has been reflected and the MC2 chordotonal organ and its associated nerve running directly to the main nerve can be seen near the M-C joint. The blood supply to the flexor muscle has been completely removed. The flexor motor nerve (FMN) and the flexor apodeme sensory nerve (FASN) run together proximally until the sensory nerve drops down onto the apodeme and then runs along it distally towards the joint (the figure has been simplified by not drawing the nerve right into the joint). The scale mark is 10 mm and further details are in the text.

The main leg nerve and the blood vessel follow the line of the apodeme in the proximal two-thirds of the merus, coursing slightly dorsal distally. In this illustration the blood vessel has been removed and the main leg nerve reflected in order to expose the flexor motor nerve (for details see Evoy and Cohen, 1969), and a second nerve containing medium and small-sized fibres. Examination of many preparations has shown that these two nerves always lie in this position between the flexor muscle and the blood vessel. The second nerve we have named the flexor apodeme sensory nerve (FASN). The flexor

motor nerve has branches which run ventrally and anteriorly to innervate the minor sections of the flexor muscle, but the sensory nerve is confined to the posterior side of the leg nerve and blood vessel. Sensory innervation of the apodeme has not been described previously and it is this innervation that we found to be monitoring muscle tension.

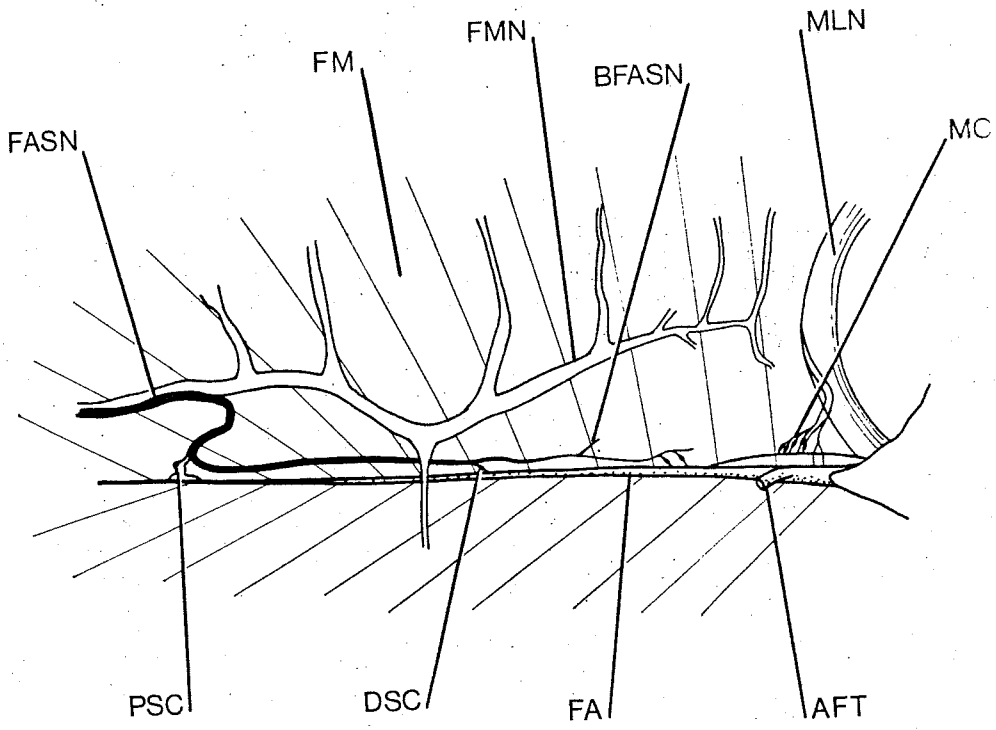

FIGURE 2 A detail of Figure 1 to show the distal part of the flexor apodeme and the flexor apodeme sensory innervation. As in Figure 1 dorsal is uppermost in this diagram. The MC2 chordotonal organ is located at the joint and its sensory nerve runs directly into the main leg nerve (MLN). The flexor apodeme (FA) passes back from the joint and the small distal stump of the accessory flexor tendon (AFT) can be seen at the distal end of the main flexor apodeme. The flexor muscle (FM) is located on both sides of the apodeme and its motor (FMN) and apodeme sensory (FASN) supply run together proximally. The sensory nerve drops down onto the apodeme and a large proximal cell (PSC) is shown in a small branch of the main nerve near the apodeme. The sensory nerve then runs along the edge of the apodeme towards the thickened distal portion. Some distal cells (DSC) are shown branching off from the sensory nerve and a major branch (BFASN) passes into the muscle on the dorsal surface of the apodeme. The figure has been simplified by showing the FASN displaced dorsally away from the surface of the apodeme and not running it directly into the joint. The scale mark is 5 mm and further details can be found in the text.

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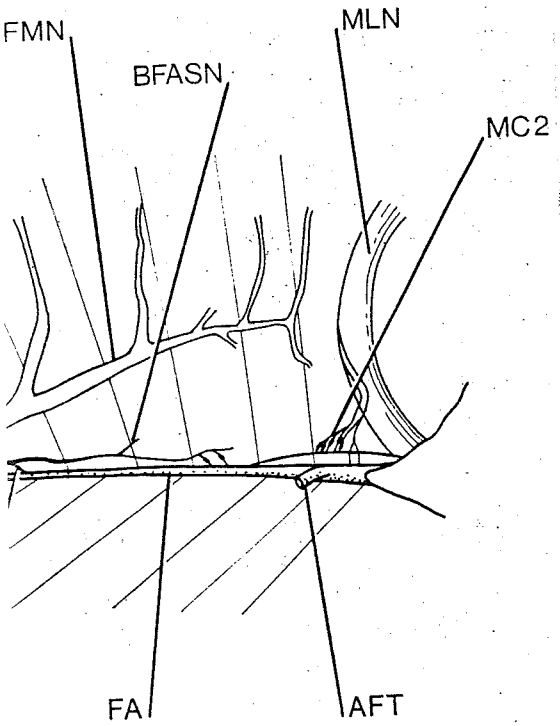

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Proximally the FASN is usually fused with the flexor motor nerve (Figure 2). It is usual to find a few small branches of the sensory nerve in this proximal region. These proximal branches typically have only one or two fibres and run towards the flexor apodeme. The fibres are the axons from large (50μm) bipolar cell bodies (proximal sensory cells, PSC) situated near the apodeme. The long unbranched dendrites of these cells run for some distance on the dorsal surface of the apodeme (Figure 4(A)). We have not found more than five such isolated proximal cell bodies in any one stained preparation.

Distally the flexor motor nerve runs dorsal to the apodeme but just proximal to the region where the lateral muscle bundles attach, the FASN drops ventrally onto the edge of the apodeme. The sensory nerve then runs along the edge of the apodeme towards the M-C joint. More cells are found on this edge and the dendrites course across the apodeme surface or along the edge. The FASN always has several branches which pass onto the dorsal surface of the apodeme and one of these branches is usually larger than the rest. Very few, if any, fibres pass to the ventral surface of the apodeme. To trace the sensory nerve branches onto the dorsal surface of the apodeme it is necessary to remove the dorsal muscle fibres.

Good staining of the branches of the FASN on the dorsal surface of the distal part of the apodeme is difficult to achieve. The part of the nerve which runs straight down the edge of the apodeme can be traced fairly easily to the region of the origin of the MC2 strand (Figures 1, 2) but the branches going into the muscle are often removed with the muscle fibres. The best results were obtained by leaving the preparation in a pale methylene blue solution for some time. While the nerve fibres are staining the muscle attachments deteriorate a little so that the muscle fibres can be removed with less damage to the fine sensory nerve branches. The concentration of methylene blue was then increased so that the nerves would stain rapidly. Figure 3 is a low power view of one example. Typically the major branch of the FASN ran distally and posteriorly over the dorsal surface of the apodeme to the extreme posterior distal edge (opposite the insertion of MC2). Bipolar cell bodies are found in association with the branch along its entire length. Clearly some of the distal sensory neurones (DSC) on the apodeme (Figure 4(B,C)) are as large as the isolated proximal cells (Figure 4(A)) but most are smaller (SSC) (Figure 4(C,D,E)). We presume that we are only staining a small proportion of the sensory cells as the apodeme sensory nerves obviously carry many fibres (Figure 4(C)) and the conditions for stain penetration are poor, particularly for small cells on the surfaces of the apodemes.

Some of the fibres of the FASN run into the region of the M-C joint both from the extension of the main nerve along the apodeme edge and from the branches running over the dorsal surface. Not many larger-sized cell bodies were found in the branches to the joint region but some small cells were

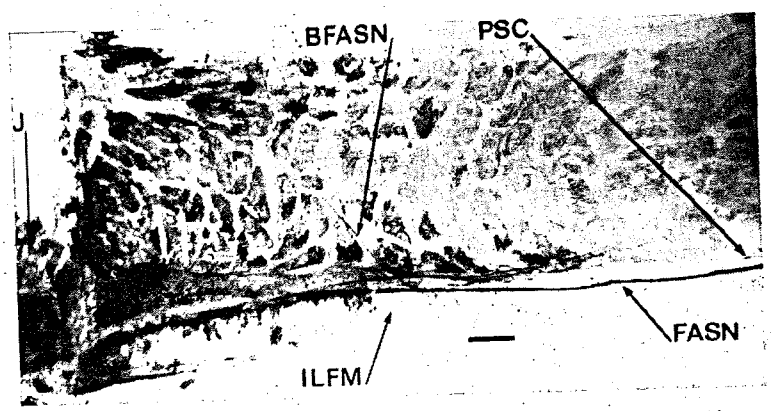
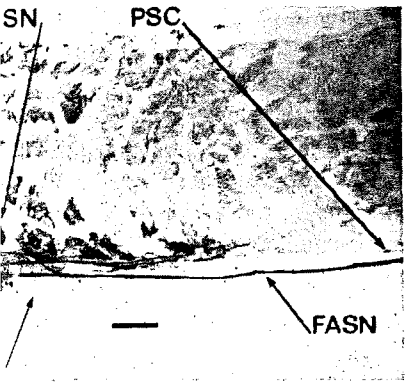


FIGURE 3 A low power view of the dorsal surface of a flexor apodeme. The posterior (i.e. lateral edge) of the apodeme is uppermost in the photomicrograph. The thinner more proximal part is not shown. The soft tissue of the M-C joint (J) has been preserved at the anterior distal edge of the apodeme but has been removed posteriorly. The flexor apodeme sensory nerve (FASN) is seen (after staining with methylene blue) on the anterior (medial) proximal edge of the apodeme just after it has dropped down from the motor nerve. A proximal large cell (PSC) can be seen innervating the apodeme before the main nerve reaches the shelf where the lateral flexor muscle bundles insert in life (ILFM). The sensory nerve can then be followed as it courses towards the M-C joint and one of the branches to the dorsal apodeme surface is also visible (BFASN). The branch passes between the insertions of the flexor muscle bundles towards the posterior distal corner of the apodeme. Scale mark is 0.8 mm; further details are in the text.

normally stained in the soft tissue of the joint (Figure 5(A)). Few, if any, fibres from the FASN pass distal to the U-shaped cuticular connection. Additionally, as mentioned by Whitear, some branches of the MC2 sensory nerve pass into the tissue at the distal end of the apodeme and not into the connective tissue strand. Some cell bodies were also found in these chordotonal organ nerve branches. Once again we believe that we were seeing only a small proportion of the small cells in the joint region.

On the extensor muscle apodeme there is an extensor apodeme sensory nerve (EASN) running with the motor nerve in the proximal part of the merus. Both nerves lie between the leg nerve, and blood vessel and the extensor muscle. As for the FASN, large isolated cells are found proximally before the EASN joins the posterior edge of the apodeme. The extensor apodeme sensory cells innervate the ventral surface of the extensor apodeme and, because there are fewer muscle bundles inserting distally, the cells on the apodeme are easier to stain than those on the flexor apodeme. Normally the major branch onto the apodeme surface does not go through the muscle but swings around its distal edge into the distal anterior corner of the apodeme. Some of the fibres from this branch go into the joint region but the cell bodies



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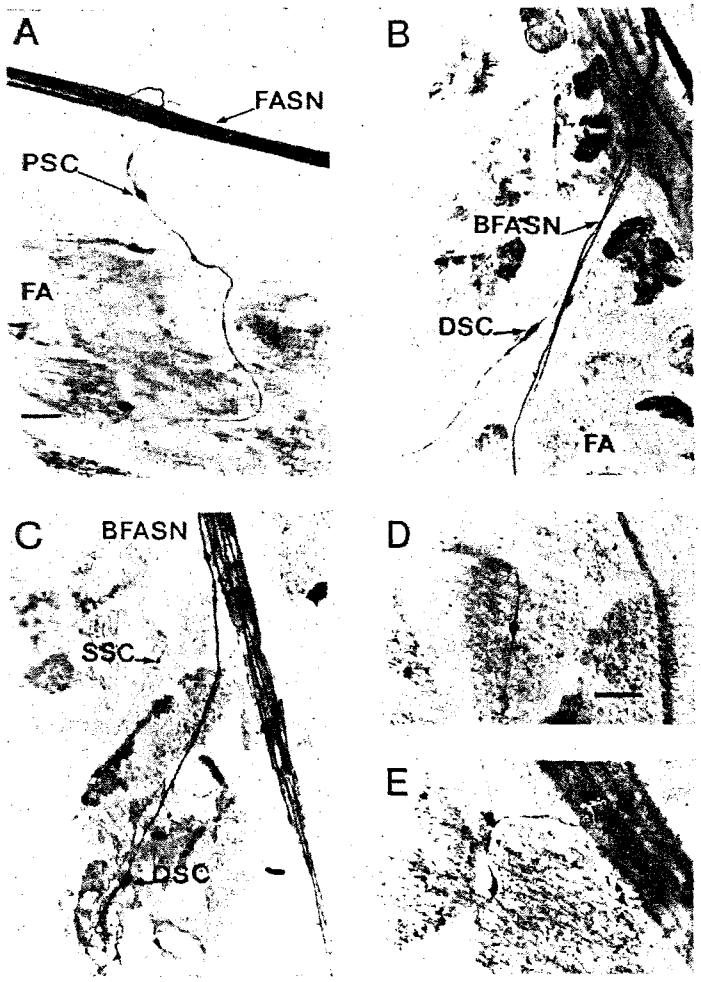


FIGURE 4(A–E) Photomicrographs of methylene blue-stained preparations of flexor apodeme sensory cells. (A) A large proximal cell (PSC) is shown leaving the main flexor apodeme sensory nerve (FASN). The dendrite of the cell courses for some distance on the surface of the flexor apodeme (FA). (B) This is a detail from Figure 3. It shows the branch of the sensory nerve (BFASN) passing from the main nerve onto the dorsal surface of the apodeme (FA). A large distal neurone cell body (DSC) is located in a sub-branch and the dendrite of this cell again courses for some distance on the surface of the apodeme. (C) This shows a branch of the flexor apodeme sensory nerve (BFASN) from another preparation. The branch obviously carries many nerve fibres and a sub-branch containing a large sensory cell (DSC) is again evident. The dendrite from this cell recurves and runs back along the surface of the apodeme. Note also the much smaller cell body (SSC) nearer the major branch of the sensory nerve. (D) The small sensory cell body of Figure 4C is shown at higher magnification. (E) A high power view of a small sensory cell from a different preparation. Scale mark is 200μm for A-C and 100μm for D and E.

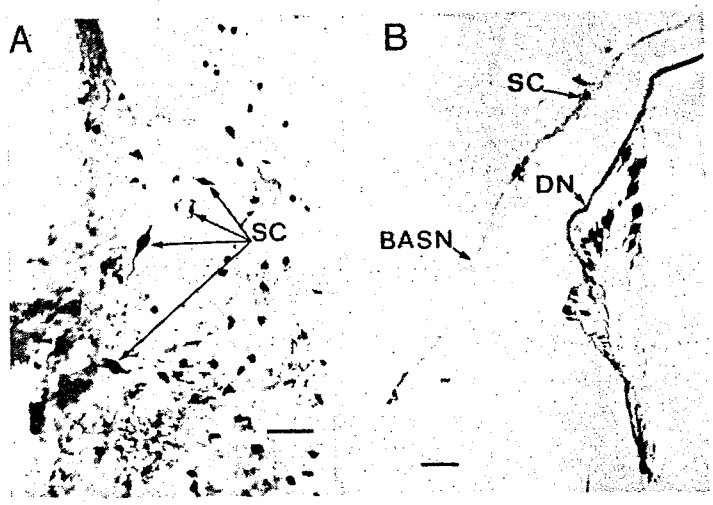


FIGURE 5(A, B) Photomicrographs of methylene blue-stained preparations of other sensory cells. (A) Distal sensory cells (SC) associated with the flexor apodeme sensory nerve situated in the soft tissue of the M-C joint just distal to the anterior distal corner of the flexor apodeme. (B) The CP1 chordotonal organ with the dorsal nerve (DN) to the small cell group and the more dorsal nerve to the bender apodeme (BASN). A cell body (SC) is stained in the proximal part of this nerve. Scale mark for A is 100μm and for B is 200μm. Further details are in the text.

are mostly on the apodeme. In good extensor apodeme preparations 30-plus neurone cell bodies could be stained regularly.

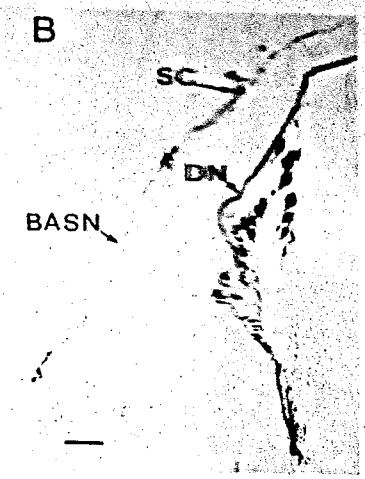
We have not seen a clear-cut example of a dendrite from the apodeme sensory nerves ending on a muscle. We think it probable that the endings are all in the tissue overlying the apodeme or in the connective tissue in the joint region.

Carpopodite-propodite (C-P) and propodite-dactylopodite (P-D) receptors

The apodemes of the muscles across the joints distal to the M-C joint were also examined for sensory innervation.

An apodeme receptor of the type described for the flexor and extensor muscle apodemes was found on the apodeme of the opener muscle of the P-D joint. The opener apodeme sensory nerve (OASN) normally runs with the motor nerve to the opener muscle but exceptions have been found in which it ran alone as a direct branch from the main leg nerve. No large proximal isolated cells were found but near the joint the OASN separates from the opener motor nerve and passes onto the edge of the apodeme. Most of the sensory cell bodies were found on the distal and ventral part of the apodeme. Several large-sized bipolar cells and a larger number of smaller cells stained in each preparation.

Although no apodeme sensory nerve was found associated with the P-D



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propodite-dactylopodite (P-D) receptors

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pe described for the flexor and extensor he apodeme of the opener muscle of the ensory nerve (OASN) normally runs with le but exceptions have been found in which m the main leg nerve. No large proximal the joint the OASN separates from the to the edge of the apodeme. Most of the he distal and ventral part of the apodeme. d a larger number of smaller cells stained

nerve was found associated with the P-D

closer nerve a small nerve, noted also by Whitear in *Carcinus*, runs from the apodeme to join the P-D chordotonal organ nerve. This apodeme nerve was traced onto the apodeme and at least one medium-sized bipolar cell was regularly stained in the nerve, suggesting that it has a similar function to the other apodeme sensory nerves.

The CP1 chordotonal organ is very similar to that described by Whitear (1962) for *Carcinus* but in this species a small nerve passes from the chordotonal organ nerve onto the bender apodeme (Figure 6). A number of medium-sized bipolar cells were regularly found in the connective tissue around the

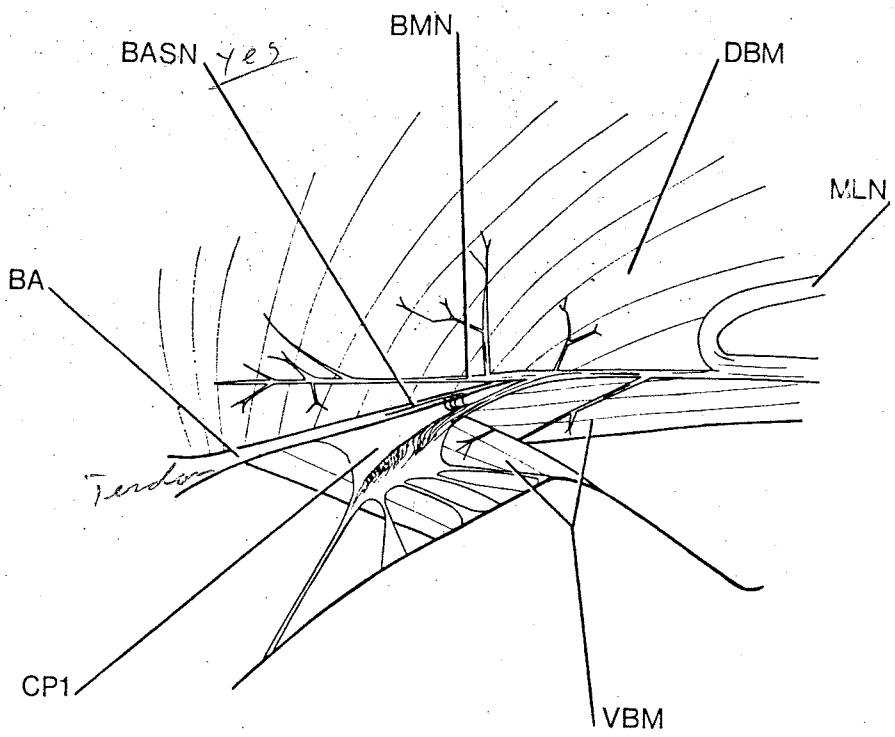

FIGURE 6 A posterior view of the carpopodite in the region of the CP1 organ. In the diagram dorsal is uppermost and the proximal segments of the limb lie to the right. The stretcher muscle has been removed and the main leg nerve (MLN) and some damaged bender muscle fibres have been reflected proximally. The bender apodeme (BA) is shown distally and the bender apodeme sensory nerve (BASN) can be seen proximally running on the apodeme for a short distance. Some of the dorsal and ventral parts of the bender muscle can be seen (DBM, VBM) with the bender motor nerve (BMN) which innervates them. Note the complex connective tissue suspension of the chordotonal organ (CP1). The scale mark is 2 mm and further details can be found in the text.

insertion of CP1 and their dendrites passed onto the apodeme in this region. The axons from these cells and from others further along the apodeme form only a very short, free, distal loop of nerve (bender apodeme sensory nerve, BASN) before fusing with the separate axons of the small cells of the chordotonal organ (dorsal chordotonal nerve, DN), quite close to their cell bodies (Figures 5(B),6). The bender apodeme sensory nerve and the CP1 chordotonal organ nerve are thus very closely associated right from their origins, making experiments to distinguish their physiological function very difficult. The BASN passes distally along the edge of the apodeme towards the joint but is difficult to follow because it becomes deeply embedded in connective tissue as it approaches the joint. In CP2 we found branches of the chordotonal organ nerve which pass onto the apodeme as in Whitear's (1962) description of *Carcinus*. In addition we found recurrent branches from the main leg nerve which run to the stretcher apodeme and to the C-P joint region. It is probable that these have the same function as the other apodeme sensory nerves.

Physiology

Apodeme receptors We found no major differences between the properties of the extensor and flexor apodeme sensory organs. We did not, however, conduct a detailed sampling of fibre types so that the spectrum of fibre type and sensitivity may not be the same.

In our preparations the apodeme sensory nerves discharged at all times. The level of this ongoing activity was variable from preparation to preparation but in any one preparation changes could be detected with large changes in joint position. When there was no load on the joint it usually adopted a resting position between 80° and 90° and a load had to be applied to the joint to hold it flexed or extended from this rest position. Figure 7 (A,B,C) shows the output of the FASN in the resting position and in response to two loads which extend the M-C joint to 135° and 165° respectively. As described in the Anatomy Section it was necessary to damage some of the muscle fibres and peripheral motor nerve branches in order to approach the apodeme sensory (AS) nerves. It was quite common for damaged muscle fibres to twitch for some time and so develop some tension on the apodeme. This tension development could have been responsible for the observed background activity. In order to determine whether a background discharge arose from the AS nerve of an undisturbed muscle we recorded from the nerves in a more proximal segment so that the meropodite and carpopodite remained intact. A resting discharge was still obtained and correct identification of the nerves subsequently confirmed by post-staining with methylene blue.

When the M-C joint was fixed and the motor nerves to either of the muscles

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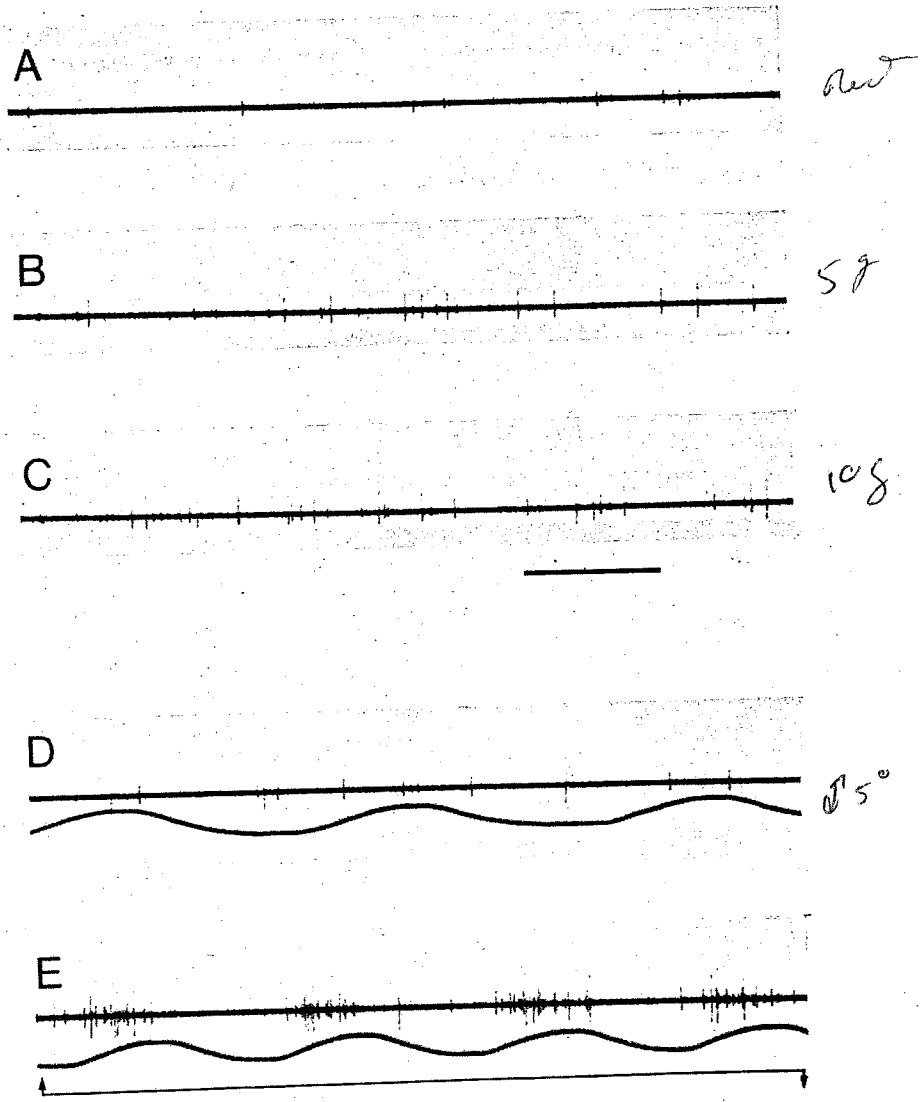


FIGURE 7(A–E) (A) Response in the FASN in the resting position of slightly less than 90°; (B) with a load of 5 gm which extends the joint to approximately 135°; (C) with a load of 10 gm which extends the joint to 165°; (D) The response in the FASN to a movement of 5° is shown when there is no tone in the flexor muscle and (E) when the flexor motor nerve is stimulated (indicated by the arrows) at a frequency of approximately 55/sec. Time calibration 0.5 sec.

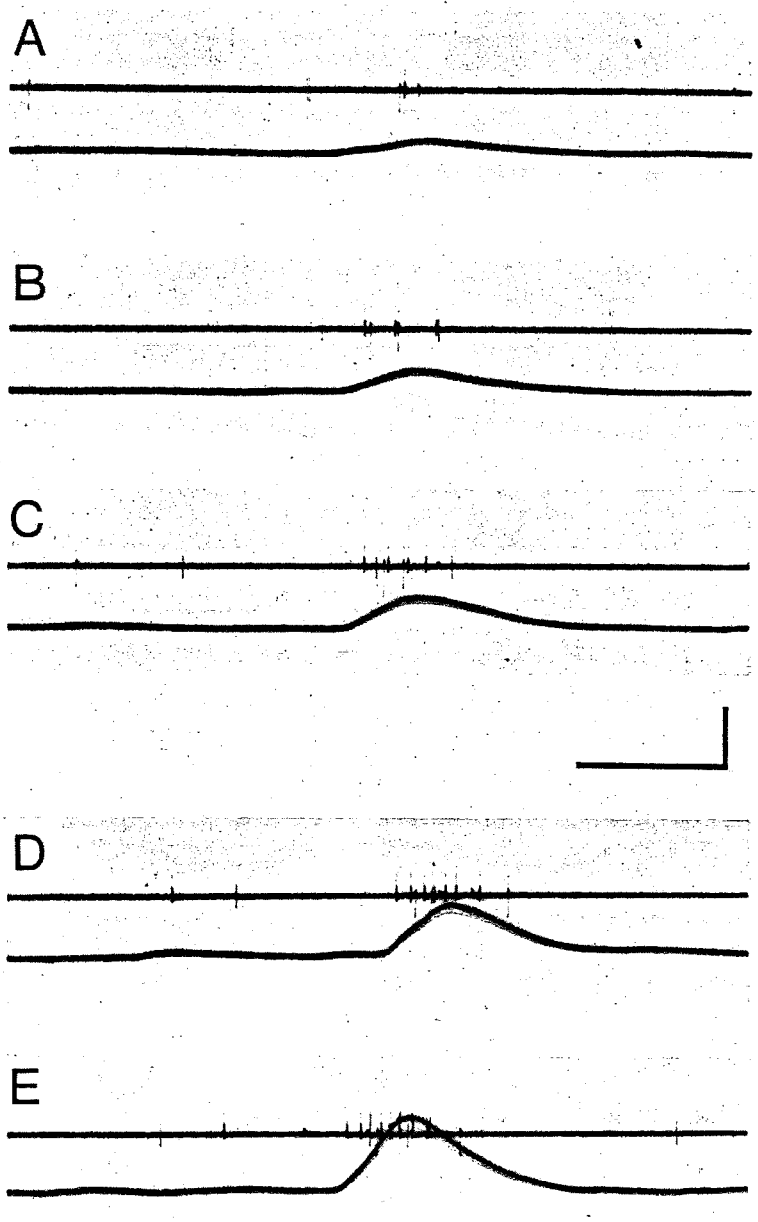
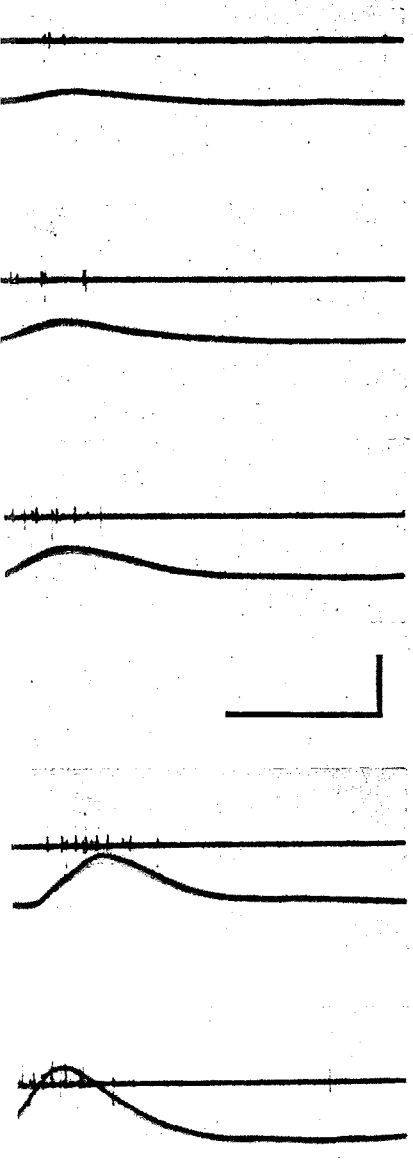


FIGURE 8(A–E) The response in the EASN to stimulation of the extensor motor supply at frequencies of (A) 10/sec; (B) 20/sec; (C) 30/sec; (D) 40/sec; (E) 50/sec. The lower trace shows isometric tension developed in each case. Time calibration 0.5 sec; tension calibration 20 gm.



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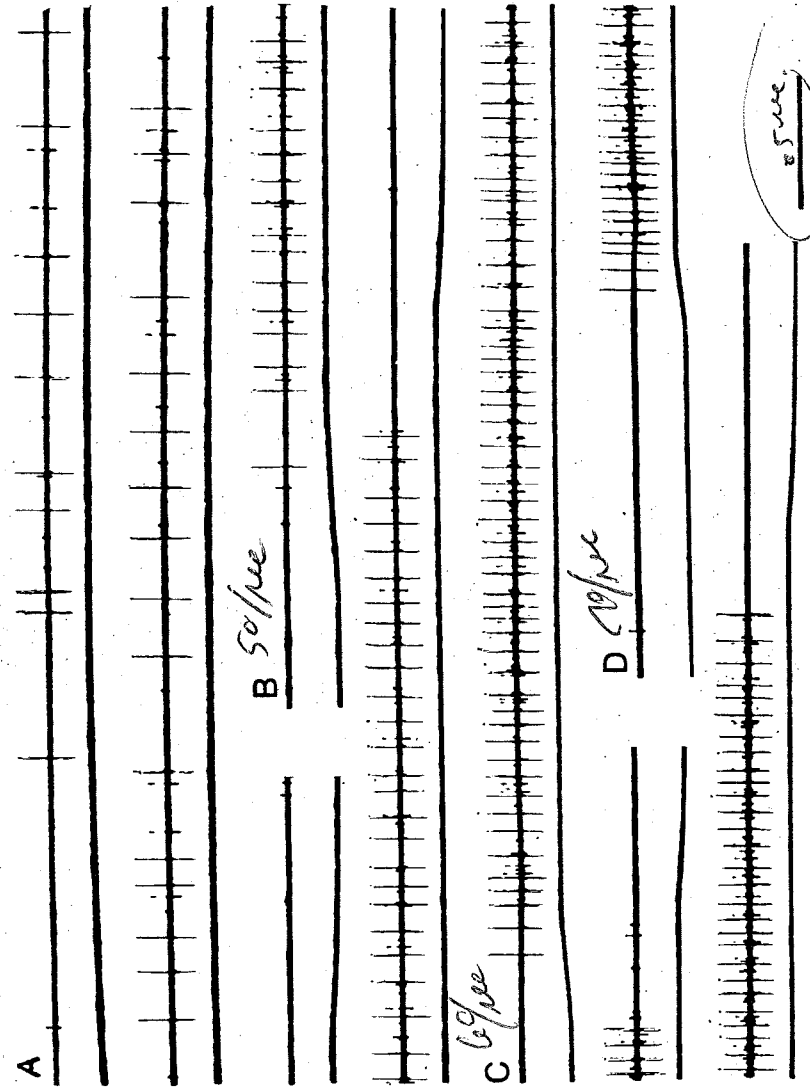


FIGURE 9(A-D) Response in a tensed slip of the FASN to stimulation of the motor supply to the flexor motor nerve at frequencies of (A) 40/sec; (B) 50/sec; (C) 60/sec; (D) 70/sec. The lower trace allows tonelike tension development but is not calibrated as the transducer was allowed to strike a stop so that the tension trace would be more uniform. Time calibration 0.5 sec.

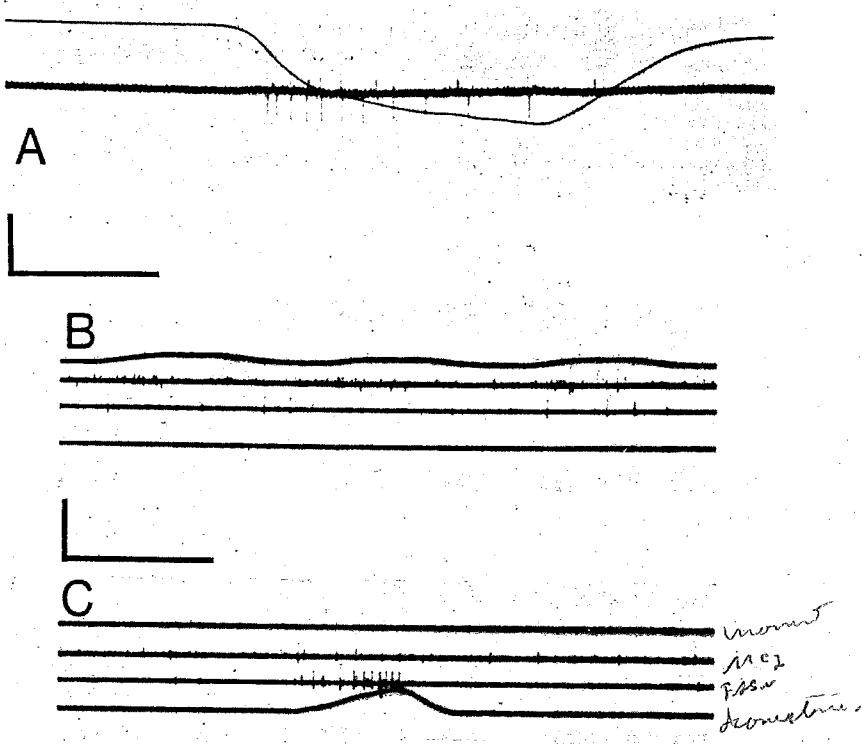
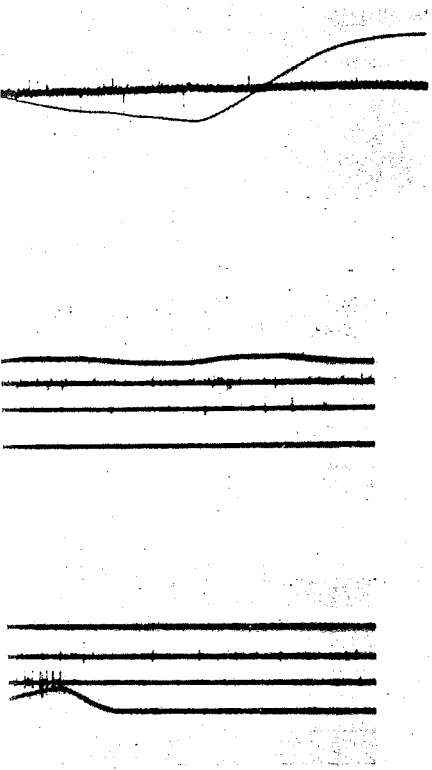


FIGURE 10(A–C) (A) Single unit from the FASN which shows response to tension onset and adapts if the tension is maintained. Time calibration 0.5 sec; tension calibration 15 gm. The four records in both (B) and (C) show from top to bottom, movement, the response in MC2, the response in the FASN and isometric tension development in the flexor muscle. Time calibration 0.5 sec; movement calibration 5°; tension calibration 3 gm.

stimulated, a discharge was seen in the AS nerve from the apodeme of the contracting muscle. Figure 8 shows the response in the EASN to increasing isometric tension development by the extensor muscle and shows that with increasing tension the number of fibres responding also increases. If this experiment is repeated with a teased slip of the FASN containing only a few fibres it can be seen (Figure 9) that with increasing tension not only is there a recruitment of fibres but also the frequency of discharge of some single units increases. The large unit shown here gives a tonic response which reflects the increasing tension. We also found units which respond to tension onset and then adapt to a lower rate of discharge (Figure 10(A)), but did not find units which increased their firing rate in response to a fall in tension. We did not attempt an analysis of the range of single fibre responses and units responding in other ways may be present, particularly among the smaller diameter fibres.



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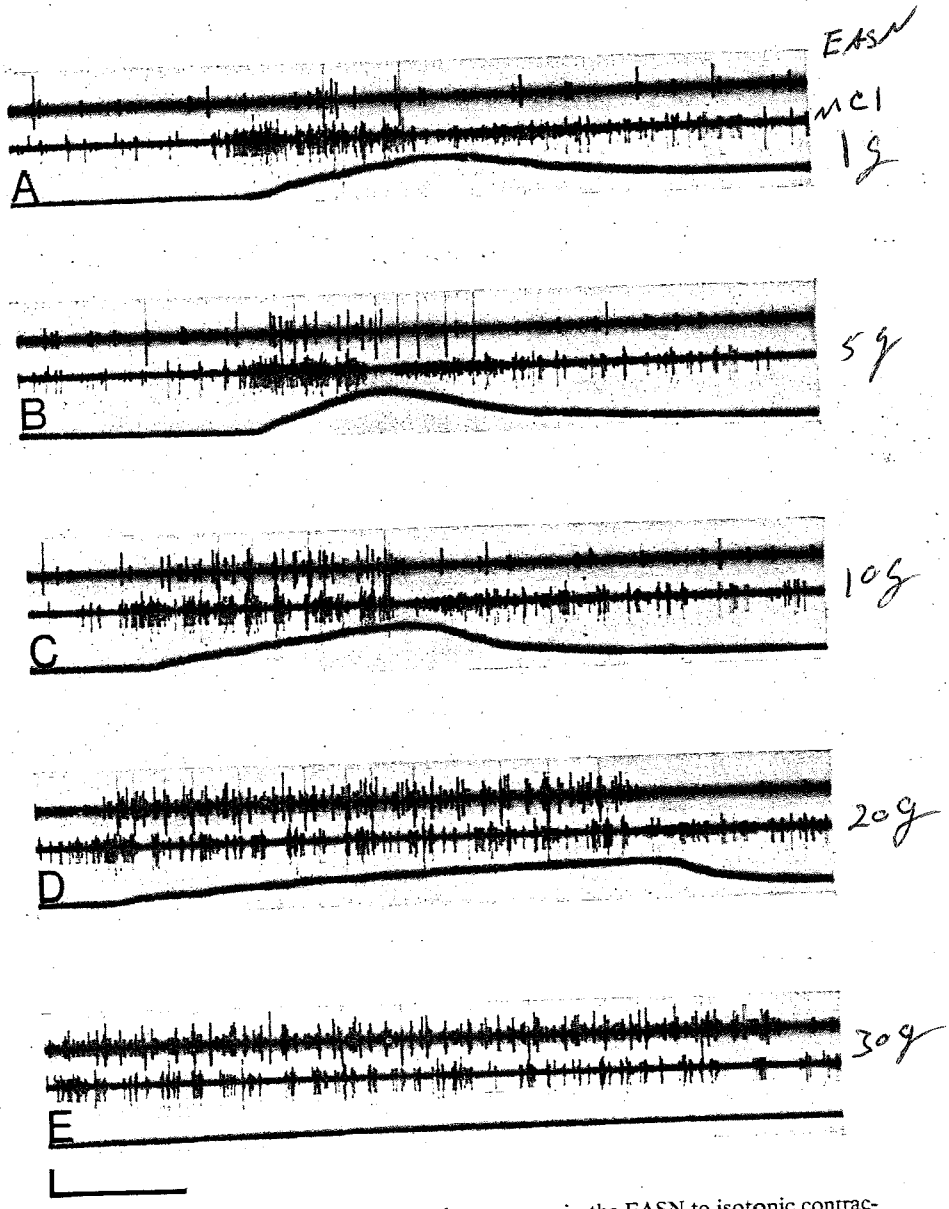

FIGURE 11(A–E) The upper trace shows the response in the EASN to isotonic contraction of the extensor muscle when a standard stimulation of 30/sec is applied to the extensor motor nerve supply. The second trace shows the response in MC1 and the third the degree of shortening in the muscle with loads of (A) 1 gm; (B) 5 gm; (C) 10 gm; (D) 20 gm; (E) 30 gm. Time calibration 0.5 sec; movement calibration 10°.

Small movements at the M-C joint (5°–10°) did not normally evoke a detectable change in the discharge of the EASN or FASN nerves, unless the applied movement was very rapid or there was an abnormal level of muscle tone due to muscle fibre or nerve fibre damage (Figure 7(D)). When the motor nerve to one of the muscles was stimulated so that its tone increased, and a similar movement was applied to the joint the AS nerve from the stimulated muscle responded to the movement (Figure 7(E)). It is interesting that under these conditions the AS nerve response was very similar to the response in a chordotonal organ nerve to joint movement. This result and the close anatomical proximity of some of the AS nerves and chordotonal organ nerves suggests that the two receptor responses could have been confused in the past.

In order to observe the response of an AS nerve while the muscle with which it is associated moves a joint, the motor nerve to the extensor muscle was stimulated and a series of loads was applied to the carpus. Figure 11 shows the response in the EASN and MC1 as the extensor muscle shortened against increasing loads. The response in the EASN can be seen to be increasing as the tension on the apodeme increases and this is quite different from the phasic and tonic components of the MC1 response to the movement. Some measure of the sensitivity of the apodeme receptors is seen in Figure 11(A) where a load of 1 gm causes a discharge in the AS nerve and responses were seen in many AS nerves to similarly low isometric tensions. To test whether the tensions we were recording from the apodemes fell within the physiological range we weighed a medium-sized crab in sea water. The animals are almost neutrally buoyant so that a 400 gm crab would have quite low tensions to sustain in each leg in a normal resting posture. We took the crab, immobilised the merus and attached a series of weights to the carpus in the same position that we used for the isolated preparations. On stroking the merus we elicited complete M-C flexion against loads up to 600 gm. The larger crabs would certainly be capable of moving greater loads and we believe that in our isolated preparations we were observing tensions in the lower part of the range that an animal might normally encounter.

Chordotonal organs and tension Since many chordotonal organs attach to apodemes the question still remains as to whether these organs can detect tension changes. It has been shown that the contraction of the main flexor and extensor muscles significantly modifies the output from MC1 in response to movement (Clarac and Vedel, 1971). We found, during the experiments in which we fixed segments to isometric tension transducers, that the chordotonal organs are so highly sensitive to movement and vibration that it was virtually impossible to immobilise the joint sufficiently to be sure that any discharge occurring upon muscle contraction was not caused by very small movements and distortion of the joints. With a

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segment connected to the isometric transducer, it was possible to show a response in the apodeme receptor without a detectable response in the chordotonal organ associated with the apodeme, only for very low tensions (Figure 10(B,C)). We found that we could sometimes obtain a similar discharge in a chordotonal organ not attached to the apodeme of the stimulated muscle and this confirmed our opinion that at least some of the observed discharge was caused by joint movement or vibration of the preparation. Because of this problem all experiments involving the response of the chordotonal organs to isometric tension development were conducted with the joint involved entirely encased in periphery wax.

MC1 and MC2 have attachments to the apodemes of the accessory flexor muscle and the flexor muscle respectively. These insertions are close to the point where the two apodemes insert into the carpopodite. With the M-C joint fixed in mid-range, its normal resting position, no response was obtained in either MC1 or MC2 to isometric contraction produced by stimulation of the flexor or extensor motor nerves. We did not study the effect of different joint angles on this result or the effect of stimulating the individual excitatory and inhibitory axons to these muscles differentially. Both could, however influence the result. The effect of contraction of the small accessory flexor muscles was not studied either.

CP1 is a sheet-like chordotonal organ with a very extensive connection with the bender apodeme. The anatomical arrangement of its apodeme association and the configuration of its bipolar cells (Figures 5(B),6) suggested that it might be better placed to detect isometric tension development than any of the other chordotonal organs we investigated. The bender muscle has both dorsal and ventral fibres inserting into its apodeme and it was difficult to open the anterior surface of the carpus without damaging some of the motor nerves or muscle bundles of the bender muscle, particularly those lying ventrally. In addition, the BASN runs through connective tissue which is involved in the connection of CP1 with the bender apodeme and then runs with the CP1 nerve. When the BASN was cut or teased away from the CP1 nerve to eliminate its response the suspension of CP1 was almost certainly altered. Although we often obtained a response from CP1 with stimulation of the bender motor nerve, particularly a phasic response to turning the stimulus on and off (Figure 12(A)), results obtained with all these complications were very variable and certainly open to question as normal responses. To control for changes in the suspension of CP1 we left the carpus intact and teased the main leg nerve as it passes through the merus. By teasing nerve bundles containing nerves to the carpus we attempted to obtain the CP1 nerve alone and to stimulate the bender motor nerve. Each preparation was dissected after the experiment and post-stained with methylene blue to determine what elements had been involved in the stimulus-recording sequences.

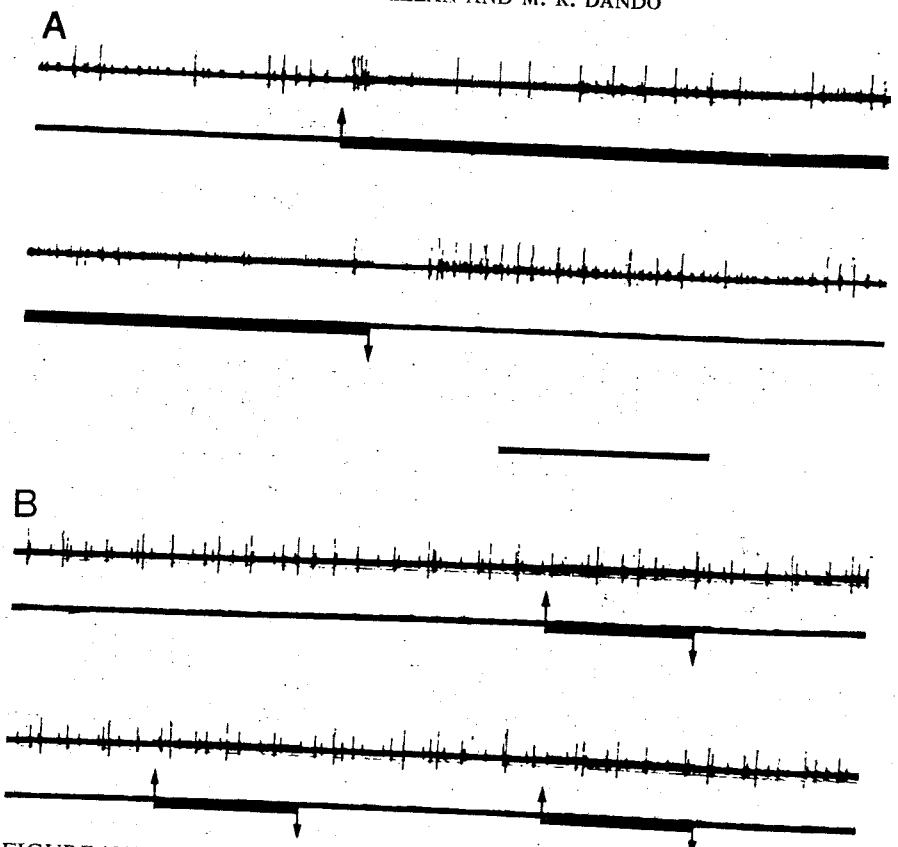

FIGURE 12(A–B) Responses from CP1 chordotonal organ evoked by stimulation of the bender motor supply. (A) A response recorded in the carpus with the posterior surface and the stretcher muscle removed. (B) A response recorded in the preceding segment with the carpus intact. Time calibration 0.5 sec. Periods of motor nerve stimulation indicated by the arrows.

In addition, the stimulus was applied again after the carpus was opened to determine whether the bender muscle was contracting strongly. In two cases we were successful in obtaining the CP1 nerve without any BASN fibres and in these two cases we did not obtain a response from CP1 to isometric bender muscle contraction (Figure 12(B)).

DISCUSSION

Apodeme Receptors

One of the central concerns of investigations into locomotory behaviour in arthropods is to determine the relative importance of peripheral feedback

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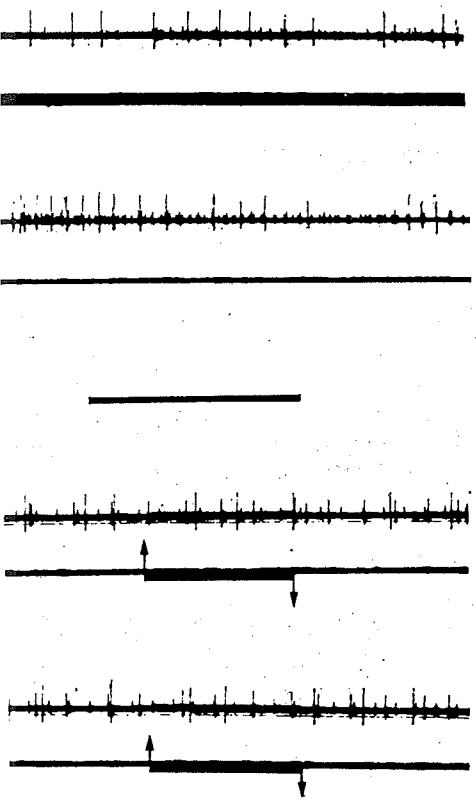

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and central programming (Wilson, 1961, 1965; Davis, 1969a,b,c; Clarac and Wales, 1970). If the animal is not receiving tension information a good measure of the afferent information being received by the animal can be obtained relatively simply. Knowledge of the position and movement responses of the chordotonal organs is combined with a record of limb position and movement during the behaviour. At the same time, if the muscle innervation is known, a measure of central activity can be obtained with simultaneous myogram recordings. In such a situation it was assumed that for the crab to obtain information about resistance to muscle contraction some sort of comparison between the efferent motor directions and the afferent position-movement response would have to be made. The experimenter could manipulate the afferent input by manipulating leg position movement and receptors in a variety of ways (Clarac and Beaubaton, 1969; Clarac, 1971) and use any compensatory response in the motor output to interpret the relative importance of the peripheral information to the production of the efferent pattern being studied. The tension receptors we describe in this report appear to have the capability of giving the crab complete and continuous information about the state of tension in its muscles whether imposed from without or caused by motor input to the muscles. Because of our new awareness of this information available to the crab our concept of the type of central integrations that the crab uses to manipulate its limbs against varying peripheral resistance must also change. With the discovery of the wider range of sensory information the situation approaches that encountered in the vertebrates. For the investigator, interpretation of changes in output due to manipulation of position-movement afference becomes much more complex because consideration must be given to the tension afference which will also interact with the motor output being studied. While the new finding certainly makes the system more complex to study it could yield findings about the control of locomotion which have a more general application. In addition, the peripheral part of the system at least is still more amenable to manipulation in a decapod than it is in a vertebrate.

The close association of the apodeme sensory nerves with either the motor or the chordotonal nerves makes interpretation of some previous results more difficult. Evoy and Cohen (1968) for example, describe responses to movements of the M-C joint in the main flexor and extensor efferent nerves with both chordotonal and myochordotonal systems intact. They found that flexion of the joint from the rest position evoked a phasic burst in the extensor efferent with depression of activity in the flexor afferent. Extension of the joint caused the opposite result. Since they describe the efferent recordings being made from 'the branches to the appropriate muscle . . . separated from the main leg nerve, cut distally and placed on platinum wire electrodes', the question arises as to whether the EASN, which runs with the extensor motor

nerve, or the FASN, which runs with the flexor motor nerve, were cut. If the apodeme sensory nerves were cut the results can be correctly attributed to the chordotonal and myochordotonal organs and the effect of the apodeme receptors should be examined separately. If, however, the apodeme sensory nerves remained intact then they too might have been involved in feedback onto the muscles. We have evidence that the apodeme sensory nerve discharge does feedback at least onto the muscle originating the sensory discharge (unpublished results).

The close association of the bender and stretcher apodeme sensory nerves with the CP1 and CP2 nerves respectively could also explain some of the variation obtained in studies involving these chordotonal organs. Bush (1965a) in some of his experiments, detached the chordotonal organs from their attachments and stretched the isolated strands. Results obtained in this manner would almost certainly preclude involvement of the apodeme sensory nerves. In other experiments he used movement of intact joints to activate the receptors and described the variability and difficulty involved in demonstrating some tonic position responses, especially with the joint towards the extremes of its range. The apodeme sensory nerves could certainly produce this kind of result. In experiments on the role of these chordotonal organs in limb reflexes (Bush, 1965b) the tension receptors were again eliminated from the major findings by stretching the chordotonal organs independently of joint movement. Some of the most erratic responses, however, were found with fast movements of the intact joint and in such a situation the apodeme responses would probably be involved (Figure 7(E)).

We have found nerves along the apodemes of limb muscles in other genera of decapods (e.g. *Homarus*, *Portunus*) examined and it seems likely that these will give physiological responses similar to those seen in *Cancer*. It is probable that tension receptors will be found to be a general phenomenon in the decapod crustacea.

Chordotonal Organs

Clarac and Vedel (1971) demonstrated that, at least in some cases, tension changes in muscles can modify the response to movement of the chordotonal organs which attach to their apodemes. The emergence of the concept of a passive chordotonal organ response differing from the dynamic response is obviously extremely important not only to the study of the organs themselves but also to behaviour involving them. Our investigation of the possibility that chordotonal organs in this situation might respond even to isometric muscle contraction is a special case of this same principle. While investigating the possible reasons for the great variability found in our results we became

aware of further complexities which might be involved in the dynamic response.

We found that, at least under some limited conditions, it is possible for a muscle to contract isometrically without a response from its attached chordotonal organ. Some of the difficulties we encountered in obtaining this result and the necessary precautions were as follows. First, the extreme sensitivity of the chordotonal organs to small movements and distortions of the joint and also to external vibration (especially the sheet type of organ) makes it difficult to obtain consistent results. We have found that small alterations to the suspension of an organ can produce a result in some cases. It could be argued that simply opening one side of a segment will alter the relationship of the muscles, vessels and chordotonal organs sufficiently to alter the response to movement or vibration. It is difficult under these circumstances to determine which is a real response and which is an experimental artifact. Second, we found that in cases where we obtained a response from CP1 to a standard stimulus to the whole bender motor supply the response could be altered by cutting small branches of the motor nerves close to the muscle. In some of these cases the movement of the bender apodeme was quite noticeably changed. This is a completely artificial situation but it suggests one which could be of importance in the intact animal. In these experiments we were stimulating the whole motor supply to a muscle and it has been demonstrated that crustacean muscles are not necessarily homogeneous in fibre structure and neither is the distribution of the innervating motor neurones (Atwood, 1967). It is therefore possible that variations in the frequency and firing combinations within the motor and inhibitor supply to a muscle will slightly change the way in which the apodeme moves during contraction. Such changes could determine whether or not the chordotonal organ would respond or not and how it would respond. It is also not possible to consider this contingency without introducing the additional effect of joint position since the way in which the muscles move the apodeme is not independent of joint position.

It is apparent that the isolated chordotonal organ response to externally imposed movement may be the simplest case only and that the dynamic responses may be quite different. The possibility of modification at the receptor level requires detailed investigation because of the important consequences this would have for behavioural analysis.

Acknowledgement

We would like to thank Dr. D. M. Maynard for his generous advice throughout this investigation.

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