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Arthropod apodeme tension receptors

D. L. MACMILLAN

10.1 Introduction and definitions

In common practice the terms *tension* and *stress* are used synon mously. In physiological usage, however, a *stress* receptor is a receptor which detects changes in force/unit area, irrespective whether these are produced by an external force acting upon t animal or by the animal's own musculature. The term *tensi* receptor is usually reserved for that subset of stress receptors whi respond specifically to changes in muscle tension. This tradition division is not entirely satisfactory but will be adhered to here avoid the necessity of tendering further definitions in a subje already burdened with a plethora.

The problem of determining whether a particular receptor receptor organ is a generalized stress detector, a tension detector both, arises in all phyla but is particularly noticeable in t arthropods because of the presence of a hard exoskeleton. There a numerous stress receptors embedded in the exoskeleton which can shown to respond to forces applied to the animal (Sections 1.4, 5 5.4, 8.3; Chapter 7), but because the arthropod's muscles also atta internally to the same exoskeletal structure, many of these recept are also potential tension receptors.

Some confusion also arises in determining whether a receptor is specifically, or even primarily, measuring changes in stress because this appears to be monitored by measurement of the concomitant change in strain (change in length/resting length). Thus, a strain receptor may be said to be monitoring macro-strain changes while a stress receptor monitors micro-strain changes. Because receptors do not necessarily fall exclusively into one category or the other it can prove very difficult assessing the functional sensitivity of a particular strain receptor. Some indication of the primary role is often given by the mechanical arrangement of the receptor components in relation to the surrounding skeletal and muscular elements. However, one must be extremely careful not to overlook the possibility of a secondary stress detecting role in an organ which appears to be structurally arranged as a strain detector, or vice versa.

The discussion in this chapter will be limited to those stress receptors which are found on the tendons of arthropod muscles. One of the most interesting features of these receptors is that on structure alone their nature and position virtually precludes the problems of modal definition discussed above and this supposition (confirmed by experimental data) makes them, to date, the only clear-cut examples of tension receptors in the arthropods.

10.2 Structure and distribution

It seems probable that crustacean tension receptors have been described in a variety of situations without actually being recognized as such.

Methylene blue staining techniques have been the primary tool used to study the gross morphology of the crustacean peripheral nervous system (Bullock and Horridge, 1965; Wales, Clarac, Dando and Laverack, 1970). One of the striking results of methylene blue staining, and it has been remarked on by most exponents of the technique, is the vast number of axons, dendrites and nerve cell bodies which are apparent in the connective tissue on the inner surface of the integument and on its internal expansions (e.g. Alexandrowicz, 1933, 1957). These bipolar and multipolar sensory cells have not usually been described as being associated in any particular aggregation, their axons running into integumentary nerves without first collecting into specific bundles. Occasionally, however, as in the case of the detailed descriptions of the chordotonal organs

at the mero-carpopodite and carpo-propopodite joints of *Carcin* sensory nerves of this general type have been described in associat with specific joint and apodeme areas (Whitear, 1962).

In some cases the axons of cells on the muscle apodemes coll together into nerves which only carry fibres from the apodemes a which have therefore been called apodeme sensory nerves (Fig. 10.1

In the Brachyura, the cells described in this situation exclusively bipolar and two different types have been describ Proximally, there are several (up to five) large (50 μm diamet bipolar cell bodies situated close to the apodeme, but not usua among the muscle fibres (Fig. 10.1b). The long, unbranc dendrites of these proximal sensory cells run down onto the surf of the apodemes where they may be traced for some distance bef they no longer stain clearly because of associated dense connect tissue. In the region of these cells the apodeme sensory nerve is closely associated with the apodeme and the axon from the cells r individually to join it. More distally, the apodeme sensory nerv closely apposed to the apodeme. Here cell bodies, which generally smaller than the proximal ones, are found along its leng associated with it. Their dendrites cross the apodeme in the region the muscle fibre attachments (Fig. 10.1c) (Macmillan and Dan 1972).

A survey of the distribution of apodeme tension receptors has been carried out. They occur on most of the peripheral leg muscle a variety of brachyurans examined. Methylene blue staining of apodemes in the legs of anomurans, astacideans and palinu reveals fine fibres and occasional bipolar cells but thus far it has been possible to determine where, or even whether, the axons fr these cells run together to form specific apodeme sensory ne (Unpublished results in collaboration with L. H. Field and F. Clar. It is clear, however, that the anatomical situation in these gro must be different from that in the brachyurans where the nerves large and obvious. Descriptions of cells in the apodeme region some of the muscles in *Squilla* suggest possible tension receptor ag gations but this also remains to be investigated (Alexandrowicz, 1957

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The only other clear example of apodeme sensory receptors i *Limulus* (Xiphosura) where they are found in association with flexor muscles responsible for tailspine movement. As in Brachyura, the apodeme sensory nerves are also composed of ax from two different cell types. Multipolar cells up to 110 μm in

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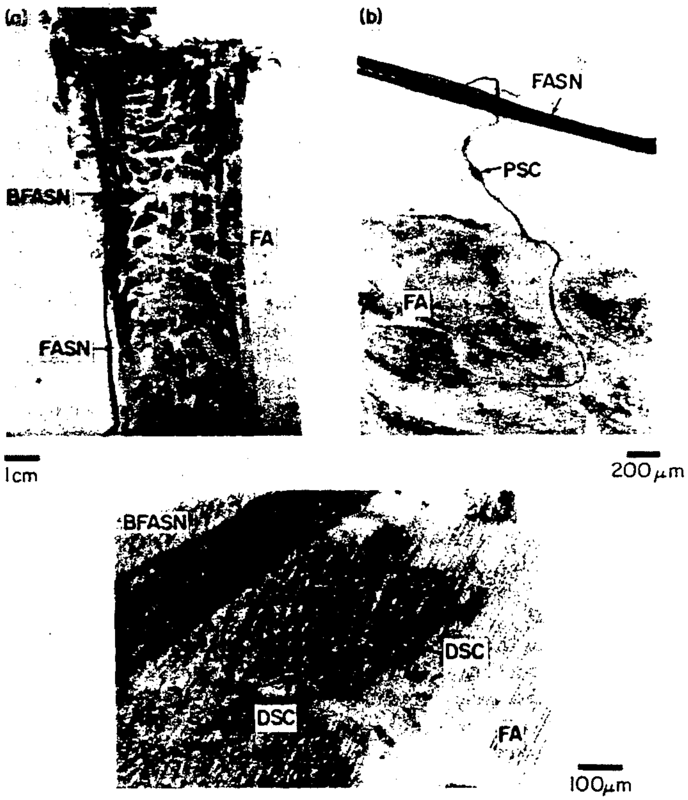

Fig. 10.1 (a) Photomicrograph of the distal part of the flexor of the crab *Cancer magister* where it is attached to the carpopodite at the mero-carpopodite joint. The medial edge of the apodeme is to the left and the distal end, which attaches to the carpopodite, to the top. The muscle fibres of the flexor muscle were gently removed to show the flexor apodeme (FA) and the flexor apodeme sensory nerve (FASN) running along the edge of the apodeme. Branches of the apodeme nerve can be seen running onto the surface of the muscle in the region where the muscle fibres insert.

(b) An example of a large proximal sensory cell (PSC) the axon of which joins the flexor apodeme sensory nerve (FASN) prior to its close association with the edge of the flexor apodeme (FA) and sends its dendrite onto the apodeme.

(c) Examples of the smaller, more numerous distal sensory cells (DSC) which are situated on the apodeme among the muscle fibre insertions. All prepartions are stained with methylene blue. (After Macmillan and Dando, 1972.)

are found around the point where the muscle fibres insert into th apodemes, or within the body of the muscle itself. The dendrites o these cells show extensive arborization around the muscle insertions where they appear to enter the connective tissue layer. There are als smaller (20 μm) cells, which are thought to be less numerous although this impression may be given because they stain less readily These cells are bipolar and are found embedded in the connectiv tissue around the shafts of the apodemes (Eagles and Hartman 1975). Similar receptors embedded in the connective tissue of tendon in the legs of *Limulus* have also been described but thes appear to be involved in detecting the movement of the trochant (Barber and Hayes, 1964).

It seems unlikely that apodeme tension receptors are limited t these two groups or to the limited situations described so far. It therefore probable that there will be further descriptions of tensio receptors of the type already known. It is also probable that tensio afference is of general functional importance in other arthropo motor systems so that receptors which are functionally analogou but structurally different may also occur.

10.3 Physiology

In both *Cancer* and *Limulus* it is possible to record from inta apodeme sensory nerves while manipulating the homonymous muscl in a variety of ways. It is also possible, by teasing the nerves, t record the acitivity of single units.

In *Cancer*, recordings from an apodeme sensory nerve durin isometric contraction of the muscle which it innervates (by stim lation of the motor nerve) shows that as tension increases there is a increase in both the number of units responding and also in th frequency of the response of some individual units (Fig. 10.2a Because they respond to muscle tension, these units also respond t imposed movements of the joints if these produce a concomita change in muscle tension but not if there is no tension change (Fi 10.2b). Tonic units which increase their rate of firing with increase tension and phasotonic units which respond to tension onset increment with a phasic component and then adapt slowly are bot found, but units which respond phasically to falling tension have n been described (Macmillan and Dando, 1972).

In *Limulus* there are units which respond either to stretching or to relaxing of the muscles in the absence of motor nerve stimulation but it is not yet clear whether these units are responding to muscle tension or muscle length changes, i.e. whether they also respond to an isometric contraction and whether their response to passive movement is due to residual muscle tension. These units appear to be phasic only and the rate of discharge is increased by increasing the velocity of the movement. There are also phasotonic units which are silent during movements imposed on a resting muscle but acti during muscular contraction. These units also respond to impos movements in the presence of muscle tension (Eagles and Hartm. 1975).

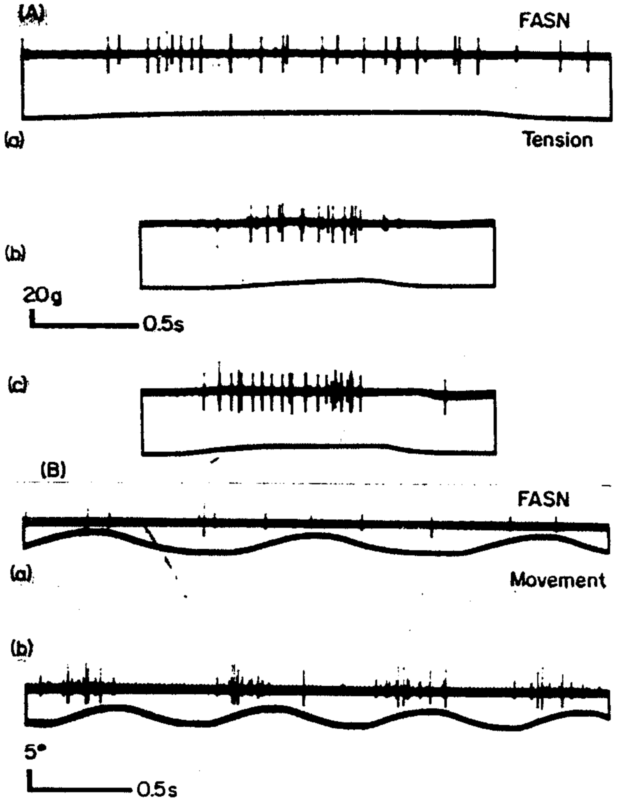

Fig. 10.2 (A) Examples of the response elicited in the flexor apodeme sens nerve of *Cancer magister* to a series of isometric contractions of the flexor mu produced by stimulating the flexor motor nerve. The strength of contractions (lower trace in each pair of records) was graded by increasing frequency of the stimulation (a) 20; (b) 25; (c) 30 pulses per s. Both the nun of units responding and the response frequency of individual units, w increased by increasing tension.

(B) Activity recorded in the flexor apodeme sensory nerve of *Cancer mag* (upper trace in each pair of records) in response to an imposed sinuso movement of the carpopodite. The movement (lower trace in each pai records) was not effective in eliciting an apodeme nerve response if the fl muscle was completely slack. (a) When the resting tension of the muscle augmented by continuous stimulation of the flexor motor nerve at 55 pu per s. (b) the tension on the muscle was increased by lengthening the mu (upward deflection of movement trace) so that the apodeme sensory n responded.

In neither *Limulus* nor *Cancer* was a detailed analysis of sin fibre responses made, and units responding in other ways may w be present. The important findings to date are that in both cas muscle tension appears to be the adequate stimulus and further th the apodeme receptor is capable of providing continuous informati on the phasic and tonic state of the tension in the muscle which innervates.

10.4 Relationship between tension receptors and chordotonal organs

The relationship between tension receptors and chordotonal org occurs on two levels: anatomical and functional.

10.4.1 Anatomical

All the apodeme sensory nerves studied in brachyuran limbs h been found in close association with another nerve almost to point where they run onto the muscle apodeme (Fig. 10.3). T nerve is always the same for each muscle; either the motor nerve the same muscle or the nerve of the chordotonal organ associa

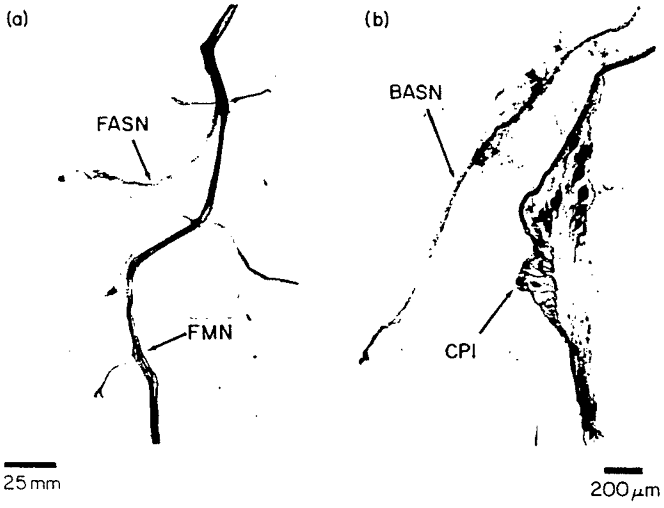

Fig. 10.3 Examples from *Cancer magister* legs of the close associations between apodeme sensory nerves and the nerves to nearby structures.

(a) The flexor apodeme sensory nerve (FASN) is closely associated with the flexor motor nerve (FMN) to the point where the apodeme nerve runs onto the apodeme and the motor nerve branches to supply the flexor muscle.

(b) The bender apodeme sensory nerve (BASN) is closely associated with the nerve to the CP1 chordotonal organ to the point where the apodeme nerve runs onto the apodeme and the chordotonal organ nerve enters the receptor strand.

with that muscle and joint. In *Limulus* the sensory nerve runs in a bundle with the corresponding motor nerve.

The association between the apodeme sensory nerves and the other nerves gives rise to several problems in interpretation, particularly of previous results concerning chordotonal organ reflexes. For example, in the case of the mero-carpopodite joint of *Cancer magister* where recordings have been made from both intact and sectioned motor nerves to study the reflex motor activity elicited by chordotonal organs the question arises as to whether the motor nerve alone or the motor nerve plus the apodeme sensory nerve was severed (Evoy and Cohen, 1969). This could be expected to have some bearing on the experimental conclusions. Similarly, in the case of chordotonal organ ablation and its effects upon motor patterning and movement (Evoy and Cohen, 1971) the question of whether some of the tension receptor afference was destroyed along with the chordotonal input makes interpretation of the results very difficult.

The effect on the reflexes may well prove to be of minor importance, in which event, the results, together with the conclusions based upon them would remain unaltered. Nevertheless, the knowledge of the close and sustained anatomical association between apodeme receptor nerves and these other nerves demands a careful reassessment of all previous work dealing with resistance reflex physiology as well as caution when planning future experiments.

10.4.2 Functional

It is quite clear from simultaneous recordings from chordotonal organs and tension receptors that in some situations their responses to the same movement are quite different and that they are coding different sensory information (Fig. 10.4). There are, however, still questions concerning the division of stress and strain detecting functions between the two types of organ.

Most chordotonal organs are attached to a variable degree to a muscle apodeme. In his study of the structure and physiology of the chordotonal organ at the pro-dactylopodite joint in the walking legs of *Carcinus* Burke (1954) reported responses from what he assumed to be the receptor itself as a result of isometric contractions of the closer muscle, to the tendon of which the receptor is attached. Clarac and Vedel (1971) demonstrated that, in some cases, tension changes in muscles can modify the response to movement of the chordotonal organs with which they are associated. Thus the chordotonal organ response to a given movement applied to a passive limb may be significantly different from its response to the same movement produced by its own muscles. This finding raised the possibility that chordotonal organs might respond to isometric muscle contraction. Macmillan and Dando (1972) tested this hypothesis for three chordotonal organs, the proximal ends of which are inserted on muscle tendons and found that at least under some limited conditions it was possible for the muscles to contract isometrically without the chordotonal organ responding. In other cases they appear to respond. However, some of the phasic units in chordotonal

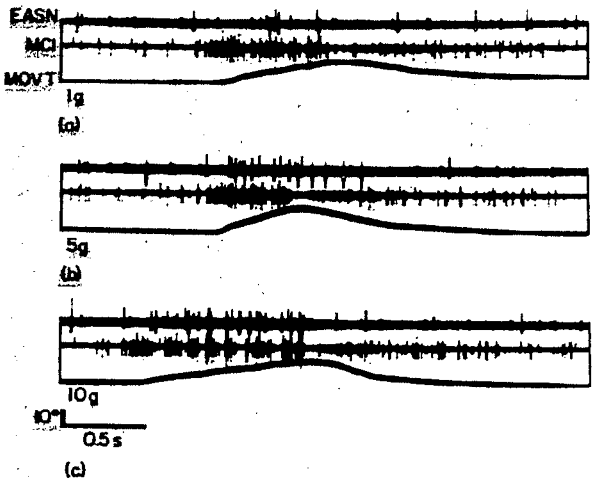

Fig. 10.4 Example of the way in which a chordotonal organ (MC1) and the tension receptor associated with the carpopodite extensor muscle (EASN) of *Cancer magister* can code different sensory information elicited by the same movement. The upper and middle traces in each record show, respectively, the response in the extensor apodeme sensory nerve and the response of MC1 to an isotonic contraction of the extensor muscle. The bottom trace shows the movement of the carpopodite (extension, upwards). The extensor motor nerve was stimulated at 30 pulses per s and the differential response in the two types of receptor demonstrated by allowing the muscle to shorten against different loads of (a) 1 gm; (b) 5 gm; (c) 10 gm. (After Macmillan and Dando, 1972.)

organs are sensitive to very small amplitude vibrations (Chapter 6) and it is exceedingly difficult to ensure that all responses resulting from such vibrations are excluded, and indeed such responses may be of special significance to the animal (Chapter 6). Clarac and Vedel (1975) repeated this type of experiment in the walking legs of *Palinurus* but were unable to eliminate a small residual response to isometric contraction no matter how firmly they fixed the preparation. They argue that the response is so slight that it is probably experimental artifact and unlikely to be of great physiological significance. Nevertheless, they show a residual response to isometric contraction which has 'on' and 'off' phasic components and a low

frequency maintained tonic discharge, so the matter still requi further resolution.

One possibility in this context is that a spectrum of degrees separation of the stress detecting function from the chordoton organ may be found. In some forms the tension and moveme functions may be combined, albeit less efficiently, in the ch dotonal organ whereas in other forms there may be comple separation of the two modalities into separate organs. Although th possibility is only speculative at this time it bears serious co sideration because of the residual isometric tension response chordotonal organs and the lack of obvious tension receptor nerv in the Palinura (Clarac and Vedel, 1975); in contrast to the lack o residual isometric response and presence of obvious tension recept in the Brachyura (Macmillan and Dando, 1972). This hypothesis al agrees with considerations concerning the internalization a subsequent elaboration of receptors (Alexandrowicz, 197 (Chapter 1).

10.5 Analogies with vertebrates

As more functional elements corresponding with those of t vertebrate limb motor control system are found in such phylogenetically different group as the arthropods, it becom increasingly interesting to speculate on the possibility of analogo functional interactions at the systems level between the vario elements: central motor command, movement afference, tensi afference and so on. A particularly good example is the situation the mero-carpopodite joint of the crab (Fig. 10.5) which presents useful analog of the typical situation in the limb musculature of t vertebrate because each of the elements is separately amenable electrical recording and stimulation in partially dissected anima Thus the 'kinesthetic' afferents from the joint capsule of vertebrat are represented by chordotonal organs giving phasic and tor information on limb position and movement (Chapter 6). The musc spindle function is represented in a very limited fashion by t myochordotonal organ complex which is in parallel with the worki muscles of the leg and has its own receptor muscle and efferent ner supply. The muscle specific tension receptor provides an analog f the Golgi tendon organ (Dando and Macmillan, 1973). Although t kind of systems analogy might appear to be too speculative, it will apparent from its use in examining the functional role of tensi

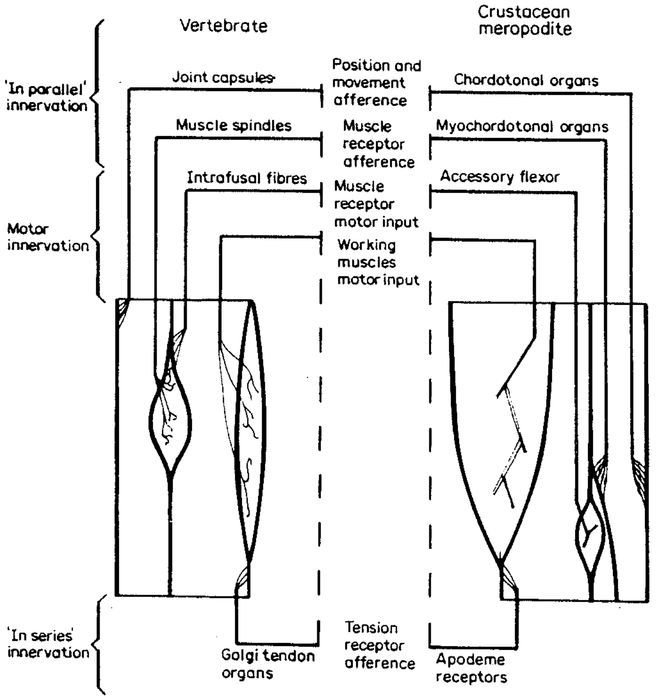

Fig. 10.5 More and more of the functional types of receptors associated with the typical vertebrate muscle and joint system have been discovered in the crustacea. In some cases the functional parallel is quite striking and the two systems may be usefully compared in order to pose questions concerning the roles of the different elements. This figure compares the typical sensory-motor system of the vertebrate limb with that found at the meropodite-carpopodite joint of many crustaceans.

receptors (Section 10.6) that it has already proved a useful guide and raised some interesting questions for the study of Golgi tendon organ function.

One interesting finding in *Limulus* (Eagles and Hartman, 1975) is that due to the mechanical arrangement of muscle fibres and apodemes the distribution of tension about the apodeme may change

in different positions and with it the tension receptor response. This suggests a complex tension receptor response which may depend on the direction of apodeme movement and the combination of motor units firing. Although this was not found in a true functional situation in *Cancer*, Macmillan and Dando (1972) demonstrated that a similar system could operate there. This deserves further investigation because of the evidence for a complex vertebrate tendon organ response. Here there is evidence that the mechanical arrangement of the receptor cells along the tendon together with the motor innervation of the muscle fibres that insert into different parts of the tendon can produce a differential Golgi tendon organ response which is dependent on the motor combination producing the muscle contraction (Stuart, Mosher, Gerlach and Reinking, 1972).

10.6 Functional role of tension receptors

It has been known for some time that Golgi tendon organs produc autogenic inhibition, i.e. the receptor input inhibits the motoneuron which activate the homonymous muscle (Granit, 1950). Initia experiments to test for the same effect in *Cancer* produced equivoca results (Macmillan and Dando, 1972; Dando and Macmillan, 1973 which will be discussed below, although Clarac and Dando (1973 found an interesting and related result in *Cancer pagurus*. The found that the resistance reflex responses to the carpopodite flexo and extensor muscles produced by imposed sinusoidal movement o the mero-carpopodite joint (Section 6.8) could be inhibited b stimulation of the tension receptors; the inhibition being restricte to the motoneurons of the homonymous muscle in each case. Whil this is clearly not the same as the autogenic inhibition described i the vertebrates, demonstration of a negative feedback loop fro sense organs in series with a muscle suggests similarities in role.

The investigation of the relationship between the inputs an reflexes from the various receptors is being carried further and whil the picture is far from clear several interesting possibilities ar emerging. Estimations of central delay times for the resistance refle to the flexor muscle at the mero-carpopodite joint of *Cancer pagur* together with conduction velocity measurements in both cho dotonal organ and tension receptor nerves indicate that tendon orga afference does not interact with the early part of the resistanc reflex. This suggests that the role of the tendon organ reflex in th passive animal is to damp the resistance reflex thus effectively preventing oscillatory interactions between flexor and extensor reflexes. When the animal is active, the situation is less clear and in at least some experimental situations it is possible to produce positive feedback onto the homonymous muscle which can be eliminated by sectioning the tension receptor nerve (Macmillan and Laverack, 1975).

It is suggested that this result could be explained by a central switching of the tension afference during certain active movements and there is some evidence that central switching is involved in turning resistance reflexes off during centrally generated motor activity (Spirito, Evoy and Barnes, 1972; Barnes, Spirito and Evoy, 1972) (Chapter 6). The finding that the different receptor inputs may be organized very differently according to the dynamic state of the animal or its chosen activity makes the analysis of their role considerably more difficult. This type of re-balancing of afferent input by central commands is also likely to be important in the adjustment of the output of the system in response to changing environmental requirements. For example, in the case of tension receptors one might expect the input to be involved in the changes in motor patterning seen when a system is loaded (Macmillan, 1974; Macmillan, Wales and Laverack, 1975; Pearson, 1972; Wales, Macmillan and Laverack, 1975a, b).

Acknowledgements

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11

The structure an
function of
proprioceptors in
soft-bodied
invertebrates

D. A. DORSETT

11.1 Introduction

In considering the role of proprioception in the sensory ph of soft-bodied invertebrates, two points must be borne in mi first is that in passing from the coelenterates to the annel molluscs, we are looking at some of the earliest stages evolution and organization of the nervous system and m ourselves at what stage does a true proprioceptive sens Secondly, the structural basis of the body plan in these phyla different from those which possess an internal or an skeleton, so that precise monitoring of the relationship of so of the body relative to another may be neither meaning necessary for the execution of the normal biological activiti organism. The evidence now available suggests that the seque muscular activity necessary for the somewhat limited beh repertoire of these simple animals is obtained by integratio synaptic level within the nervous system, resulting in prog behaviour which can proceed largely independently of sensory feedback.

In the coelenterates, the shape of the body is determine mesogloea, which forms a semi-solid, elastic substrate agains the muscles of the epidermal and gastrodermal layers may c