

AN ANALYSIS OF THE TYPES OF SENSORY UNIT PRESENT IN THE PD PROPRIOCEPTOR OF DECAPOD CRUSTACEANS

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INTRODUCTION

The responses of sensory units in the limb proprioceptors of decapod crustaceans have received a great deal of attention since the first report of sensory activity in crustacean legs (Barnes, 1930, 1931). The activity of each leg joint is monitored by one or more chordotonal organs, each comprising a group of sensory cells associated with a strand or sheet of 'elastic' tissue (Burke, 1954; Whitear, 1962; Mill & Lowe, 1971). Burke (1954) studied the receptor, which spans the propodite-dactylopodite joint – the PD organ – in *Carcinus maenas* and found that movement of this joint initiated phasic responses, while resting discharges were maintained when the joint was held in the extended* or flexed† positions. Wiersma & Boettiger (1959) extended this study and showed that the PD organ consists of three types of sensory units – movement, position and intermediate. The movement units only respond during either flexion or extension of the joint, whilst position units respond towards the flexed or extended extremes of the movement arc with a discharge whose frequency is dependent on the position within the sensitive range. The discharge of intermediate units is determined by movement and position to varying degrees. Similar responses have been recorded in the PD organs of *Maia*, *Palinurus* and *Homarus* (Wiersma, 1959), *Callinectes* (Mendelsohn, 1963) and *Cancer magister* (Hartmann & Boettiger, 1967), except that in *Homarus* flexed position units were scarce (Wiersma, 1959).

It was further shown by Wiersma & Boettiger (1959) that in the PD organ of *Carcinus* the sensory cells could be divided into a proximal group with large bodies, which are the movement (and intermediate)-sensitive units, and a distal group with small cell bodies, which are the position-sensitive units; this basic grouping was confirmed by Hartmann & Boettiger (1967) in *Cancer*. In *Cancer* the elongation (flexion)-sensitive movement cells (ESMC) insert into the anterior surface of the strand and are particularly numerous at the proximal end of the movement group, while the relaxation (extension)-sensitive movement cells (RSMC) are inserted into the dorsal surface and are more abundant at the distal end of the movement group (Hartmann & Boettiger, 1967).

Interest has been shown in the factors which determine the firing pattern of units in these organs. There are basically two classes of movement-sensitive units. On the one hand there are those which are virtually unaffected by either rate of movement

* Extended = open = organ relaxed.

† Flexed = closed = organ elongated (stretched).

(velocity) or position in the movement arc. These do show some sensitivity to velocity, especially near threshold, but a saturation frequency is attained at fairly low velocities, and so they approximate to pure movement fibres. Also at threshold extension units tend to be less sensitive towards the fully flexed position and vice versa (Wiersma & Boettiger, 1959).

At the other extreme are those units whose frequency continues to increase with increase in velocity over a considerable range of the latter; also, the firing of these cells is affected by position in the movement arc. In most instances the extension units are more sensitive towards the extended position and flexion units towards the flexed position. However, some units do show the reverse. The range over which different units fire varies from the whole arc of movement to a restricted zone at one of the extremes. Furthermore, the range of an individual unit may depend on the velocity of movement (Wiersma & Boettiger, 1959; Boettiger & Hartman, 1968). These units all show 'differential sensitivity' or 'dynamic position sensitivity'.

In the PD organ of *Cancer magister* the first type (movement units) is located medially in the movement-sensitive cell group, whilst the second type occurs in the proximal and distal parts of this group (Boettiger & Hartman, 1968). Furthermore, Boettiger & Hartman (1968) showed that the proximal units have their greatest sensitivity in flexed positions whilst the distal units have their greatest sensitivity in extended positions; this is irrespective of whether the units are flexion-sensitive or extension-sensitive.

Chordotonal organs monitoring other leg joints have also been studied physiologically (e.g. Wiersma, 1959; Cohen, 1963; Bush, 1965*a, b*; Clarac, 1968) and shown to contain the three main types of unit described by Wiersma & Boettiger (1959), except that in two of them, CP₂ and MC₂, elongation-sensitive units are possibly absent; Bush (1965*a, b*) also described velocity-sensitive units in MC₂ and CB. Cohen (1963) presents evidence that in MCO₂ the differentially sensitive units have a more restricted range and thus show 'range fractionation' rather than differential sensitivity.

The proprioceptive information provided by these chordotonal organs gives rise to reflexes which tend to resist passively applied movements (Bush, 1962, 1963). Such reflexes are probably important in the control of joint movements during walking (Evoy, Barnes & Spirito, 1970) and may also be involved in controlling posture. Detailed knowledge of the afferent information involved in such feedback loops is essential.

The results described in this paper are the initial stages of a study aimed at quantifying the stimulus-response relationships in these chordotonal organs.

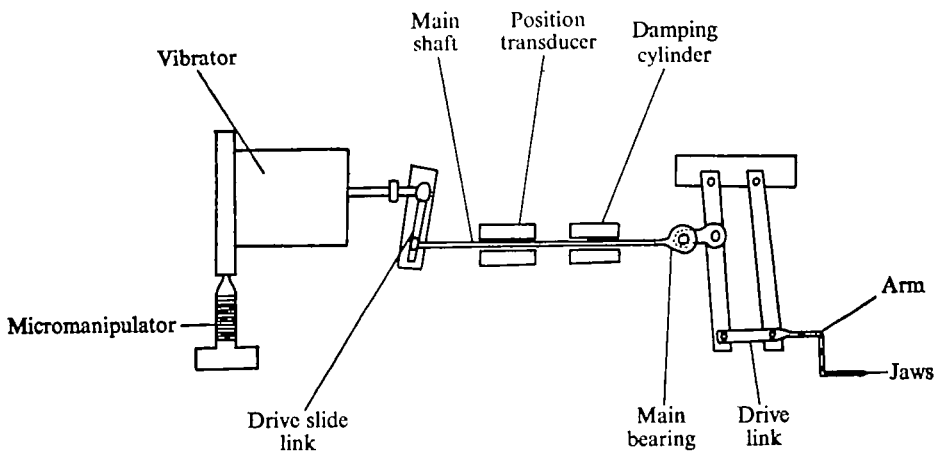
MATERIALS AND METHODS

Representatives of three infra-orders of the Decapoda-Pleocyemata were investigated. These were *Cancer pagurus* and *Maia squinado* (Brachyura), *Eupagurus bernhardus* (Anomura) and *Nephrops norvegicus* and *Homarus gammarus* (Astacidea).

In each case the leg was removed close to the autotomy plane and a window was cut in the anterior surface of the propodite. The preparation was immersed in sea water, the PD organ and associated nerves were carefully exposed and the organ was separated from its distal insertion on the cuticle of the dactylopropodite. The dactylopropodite

was then removed and the preparation was arranged so that the distal end of the organ could be clamped in the jaws of the stimulating apparatus.

The stimulating apparatus (Text-fig. 1) consisted of a vibrator (Advance type VI) driven from a variable voltage source. Movement was transmitted through a drive slide-link to the main shaft which passed through an Electromechanisms (DCLVDT) position transducer and a damping cylinder to its linkage with the main head of the apparatus. At the bottom of this head was the drive link into which was screwed an interchangeable light-weight arm ending in the jaws which held the distal end of the organ. The throw of this arm could be altered from about 1 or 2 μm up to 10 mm by



Text-fig. 1. Schematic diagram to show the arrangement of the apparatus used for elongating and relaxing the chordotonal organ.

adjusting the height of the vibrator arm in the sliding link; this was achieved by a micrometer adjusting screw operating on the vibrator bed. To ensure stretch and release of the organ in the correct plane the whole apparatus could be tilted by up to 10 degrees.

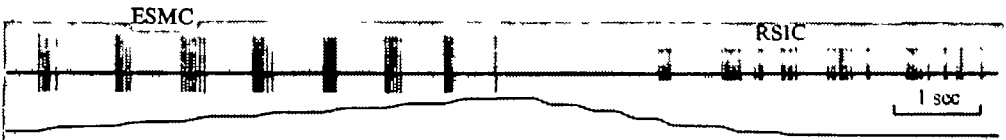
In initial experiments the vibrator was driven from a stabilized d.c. voltage supply (Farnell Instruments L30/2), whose output was regulated by hand. In later experiments, where precise waveforms were required, an Advance SG88 function generator with interchangeable function disks was used to produce single functions.

Small bundles of the PD nerve were obtained by longitudinal splitting. Recordings were made from these using a single platinum wire electrode, with the indifferent electrode in the preparation bath. Signals were amplified by a Tektronic 122 pre-amplifier before display on one beam of a Tektronix 502A or 565 oscilloscope. The other beam was used to display the output from the position transducer. Permanent records were obtained with a Grass C4 camera. Alternatively, signals from the pre-amplifier and transducer were stored on magnetic tape (Thermionic T4000) for computer processing. Details of this latter system will be published in a separate paper.

RESULTS

As was indicated in the introduction, the sensory cells can be divided into three types in terms of their responses to applied movements of the strand (Wiersma & Boettiger, 1959).

Unidirectional movement cells are entirely phasic, responding only during change in length of the strand. Some respond only to elongation or stretch of the strand (elongation-sensitive movement cells or ESMC (Boettiger & Hartmann, 1968)); others respond only to relaxation of the strand (relaxation-sensitive movement cells or RSMC). These units are always large. *Position cells* may be entirely tonic, but some



Text-fig. 2. Recording of an ESMC and a RSIC from *Eupagurus* (upper trace). Elongation is indicated by upward movement of the lower trace, relaxation by downward movement.

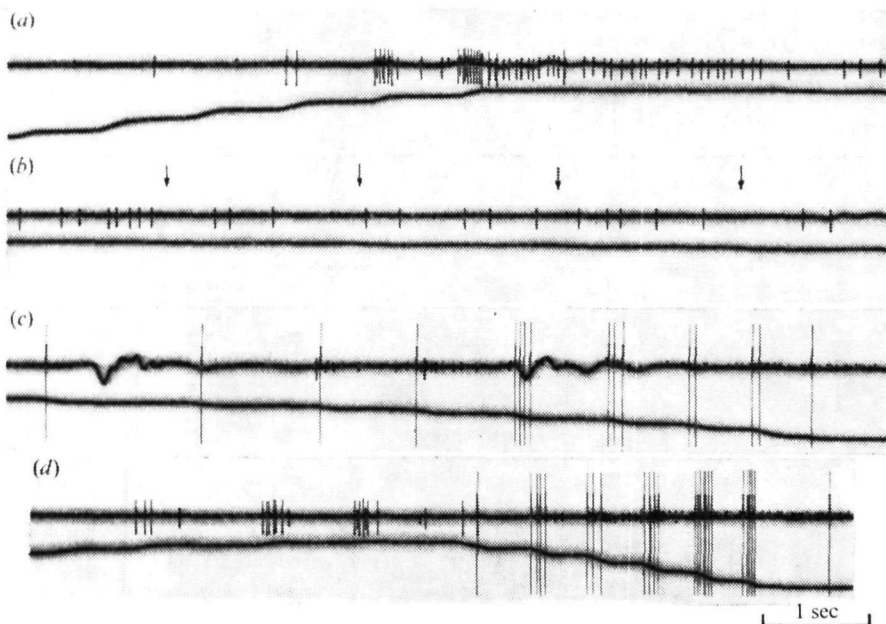
possess a small phasic component. Again there are two categories: those which fire maximally when the strand is in the fully elongated state (elongation-sensitive position cells or ESPC) and those which fire maximally when the strand is in the fully relaxed state (relaxation-sensitive position cells or RSPC). They are all small units. Finally there are *intermediate cells*, so named because they have a marked phasic as well as a tonic component and these are generally large units. They will be divided into elongation-sensitive intermediate cells (ESIC) and relaxation-sensitive intermediate cells (RSIC) on the basis of the direction of movement which produces their phasic response; this is because there is not always a direct relationship between the phasic and tonic components.

(1) *Unidirectional movement cells*. Some movement units respond over most or all of the range of movement (movement arc) with apparently equal sensitivity throughout. An example of an ESMC of this type from *Eupagurus* is shown in Text-fig. 2. Although the rates of movement were not accurately controlled in this experiment they were low (0.6–0.7 mm/sec) and the variation was sufficiently small to indicate that, within these velocity limits, there was equal sensitivity over the whole range. A similar unit, this time an RSMC from *Homarus* is shown in Pl 1, fig. 1. There is some indication here of decreased sensitivity as the relaxed position is approached.

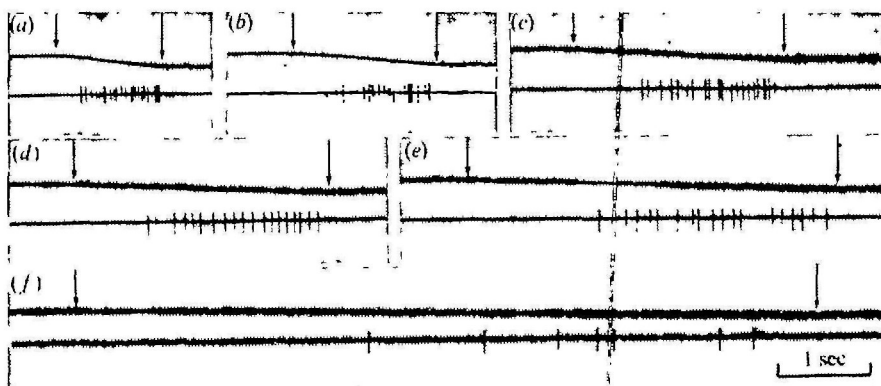
In contrast, other units at low velocities respond over only part of the movement range, as shown by the RSMC from *Eupagurus* illustrated in Pl 1, fig. 2. This particular unit only fires when the strand is in the relaxed part of its range. (In Pl. 1, fig. 2d, e the initial length of the strand is slightly less than in Pl. 1, fig. 2b, c.) In Text-fig. 3 the properties of two similar units (one ESMC and one RSMC) from *Homarus* are illustrated. The ESMC shows no response to elongation in the relaxed part of the range, but responds with increasing sensitivity as the fully elongated position is approached. The RSMC responds over most of the range, except for the extreme elongated region; it shows increased sensitivity in the relaxed half of the range at the higher rates of movement shown in Text-fig. 3d (1.5–1.7 mm/sec) (i.e.

differential sensitivity) and comparison of this with Text-fig. 3c (0.5–0.7 mm/sec) demonstrates the velocity-sensitive nature of this unit. There is, in fact, a very wide range of units of this type, and selected examples from *Cancer* will now be described in some detail to illustrate this.

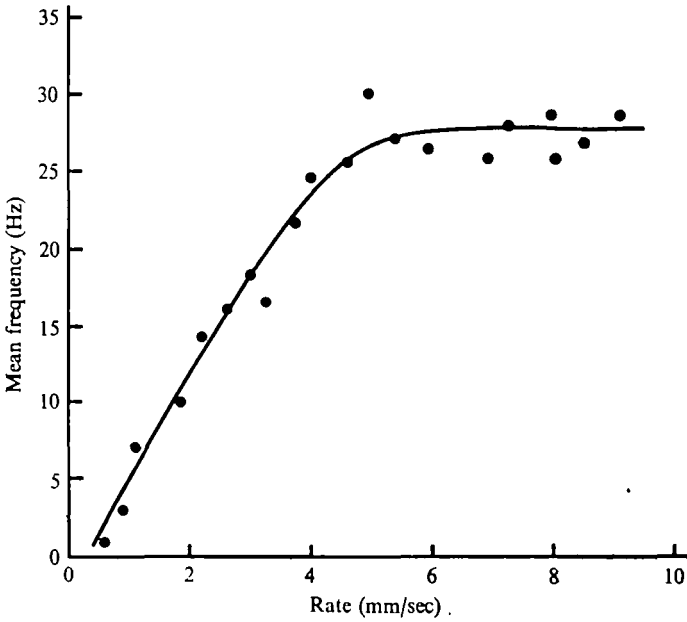
The first example (Text-figs. 4–6) is an ESMC which shows increasing sensitivity as the fully elongated position is approached. Changes in velocity of stretch produce several effects on this unit. At 0.65 mm/sec (Text-fig. 4f) the average response frequency is low (0.7 Hz) and the unit fires over about half of the movement range. As



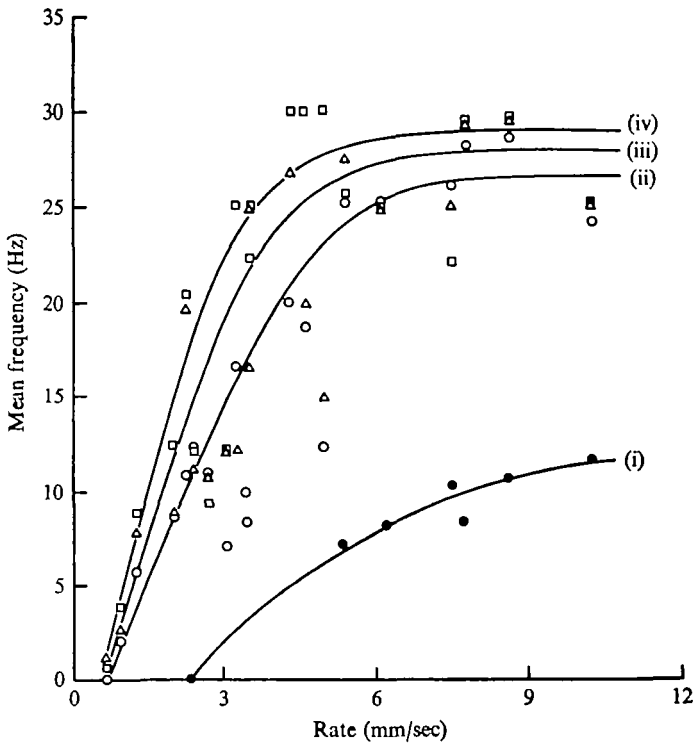
Text-fig. 3. Recording of unidirectional movement cells and position cells from *Homarus* (upper trace). Lower trace indicates elongation (upwards) and relaxation (downwards) of the strand. Arrows indicate small relaxation movements. Records a–c are continuous. In (d) the rates of relaxation are greater than in (c).



Text-fig. 4. Recording of an ESMC from *Cancer*. The lower trace indicates elongation (downwards) of the receptor strand. The extent of the stimulus is indicated by the arrows.

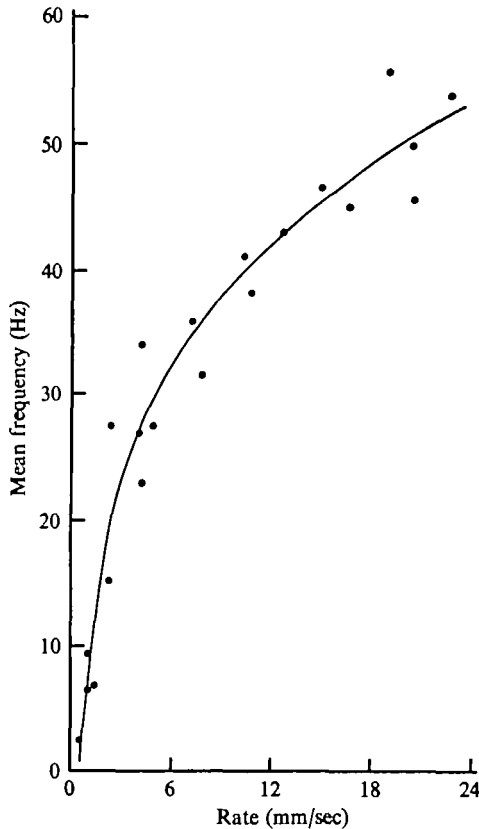


Text-fig. 5. Graph demonstrating the relationship between mean frequency and rate of stretch for the ESMC illustrated in Text-fig. 4.



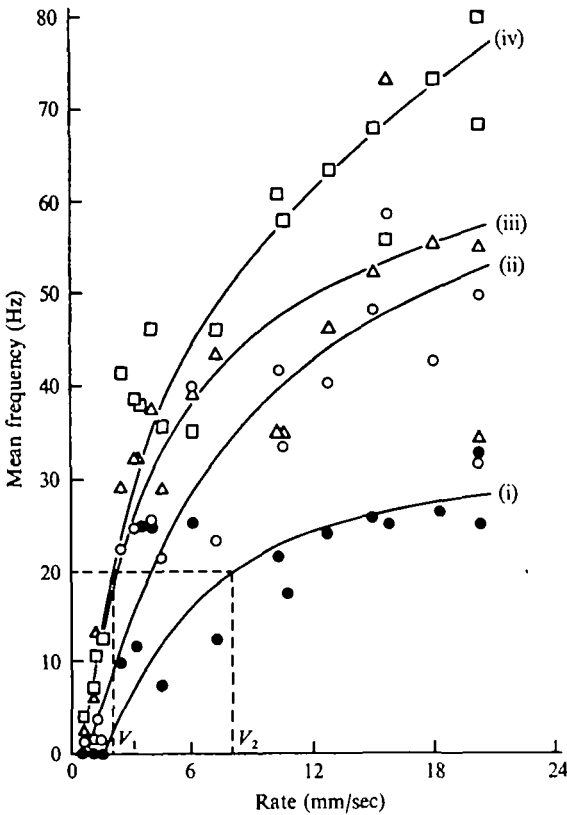
Text-fig. 6. Graph showing the relationship between mean frequency and rate of stretch for different parts of the range of the ESMC illustrated in Text-fig. 4. Curves i-iv are for the first-fourth quarters of the range respectively.

The velocity is increased it starts to fire progressively closer to the relaxed end of the range, and the average response frequency increases linearly until, at about 5 mm/sec, saturation frequency is reached (Text-fig. 5). For this unit saturation frequency is 24–28 Hz. Furthermore, the instantaneous frequency at any given position in the sensitive range increases with increase in velocity. If the range is divided into four equal parts and the average frequency in each part is plotted separately against velocity of stretch then it can be seen that for each of the last three quarters of the range the relationship between frequency and velocity of stretch is similar; only in the first quarter is there a marked difference (Text-fig. 6).



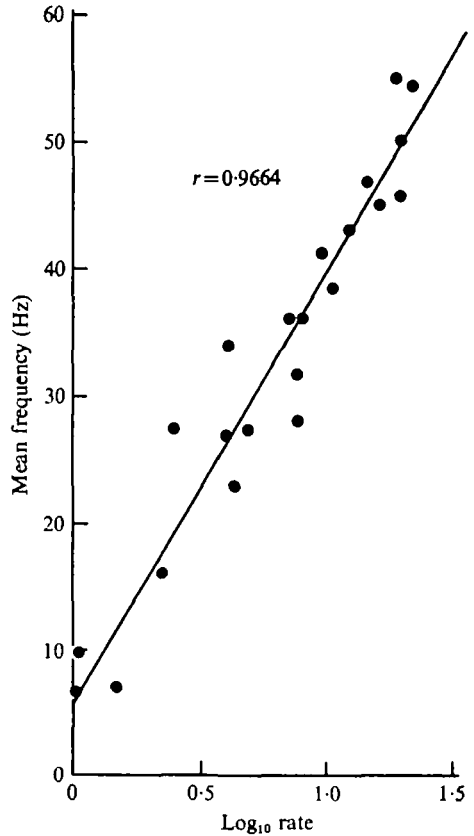
Text-fig. 7. Graph showing the relationship between mean frequency and rate of stretch for an ESMC which is velocity sensitive.

The ESMC shown in Text-figs. 7–9 also displays differential sensitivity but, unlike the above unit, its frequency does not increase linearly with increase in velocity of stretch; rather, the rate of increase steadily decreases. However, even at the highest velocity used (24 mm/sec) saturation was not reached, and this lack of saturation of the unit, even at high stretch velocities, is reflected in the average frequency plots for individual sectors of the range (Text-fig. 8) which show that the differential sensitivity is maintained throughout most of the range. Over this 'unsaturated' part of the range there is a linear relationship between the mean response frequency and the logarithm of the velocity of stretch (Text-fig. 9), and the regression line for this



Text-fig. 8. The relationship between mean frequency and rate of stretch for the four quarters (i-iv) for the unit in Text-fig. 7.

Text-fig. 9. The relation between mean frequency and the logarithm of the rate of stretch for the unit in Text-fig. 7. r is the correlation coefficient of the regression line for frequency on log rate.



graph has a correlation coefficient of 0.9664. One feature which this unit has in common with the previous one is that the instantaneous frequency at any given position in the range increases with increase in velocity of stretch.

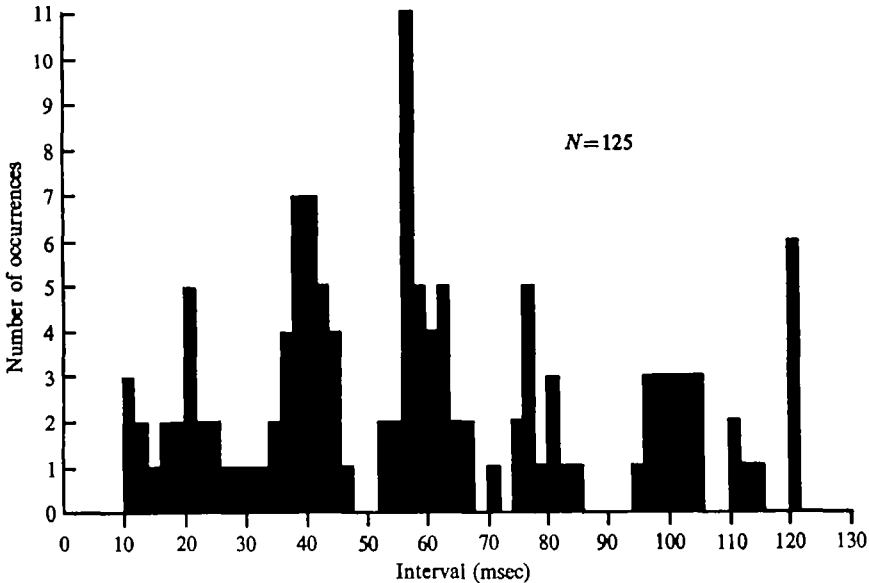
The occurrence of 'doublets' in the firing pattern of these movement units is widespread, even at velocities of stretch below that required for saturation (Text-fig. 4). One RSMC was analysed by an interval histogram programme, and the results showed that there was a basic minimum period in the region of 20 msec with the longer periods tending towards exact multiples of this figure. Firing patterns for this unit at different velocities of stretch are shown in Text-fig. 10 (see Wiersma *et al.* 1970).

(2) *Position cells*. In these units the rate of firing is determined by the length of the strand. Usually sensitivity is limited to one end of the range, so that the fibre only responds towards the fully elongated or relaxed extremes (ESPC and RSPC from *Eupagurus* (Pl. 1, fig. 2) and *Homarus* (Pl. 2, fig. 1)).

In addition the response frequency at any one position usually depends on whether the strand was elongated or relaxed to that level, in other words the response is

asymmetric (Pl. 2, fig. 1, RSPC). However, some units are more or less symmetrical in their response (Pl. 2, fig. 1, ESPC).

A detailed study was made of the asymmetric RSPC from *Eupagurus* shown in Text-fig. 11. The organ was progressively elongated from the fully relaxed position and held at different lengths for 2-7 sec. When the fully elongated extreme was reached the strand was progressively relaxed to different lengths. Text-fig. 11 d-e shows the same unit on a faster time scale. This unit shows a slight phasic component



Text-fig. 10. Pulse-interval histogram of the movement unit shown in Text-fig. 4. Note the increased number around 20 msec and at multiples of this.

which is excitatory on relaxation and inhibitory on elongation. The adapted frequency at each length was plotted. (Text-fig. 12.) It can readily be seen that the frequency is dependent not only on position but also on the direction of movement by which that position is achieved, being greater on relaxation than on elongation. Over a large part of the range the adapted frequency is almost linear with length, but as the relaxed extreme is approached the rate of increase in frequency declines so that in the fully relaxed position the frequency is about 19 Hz.

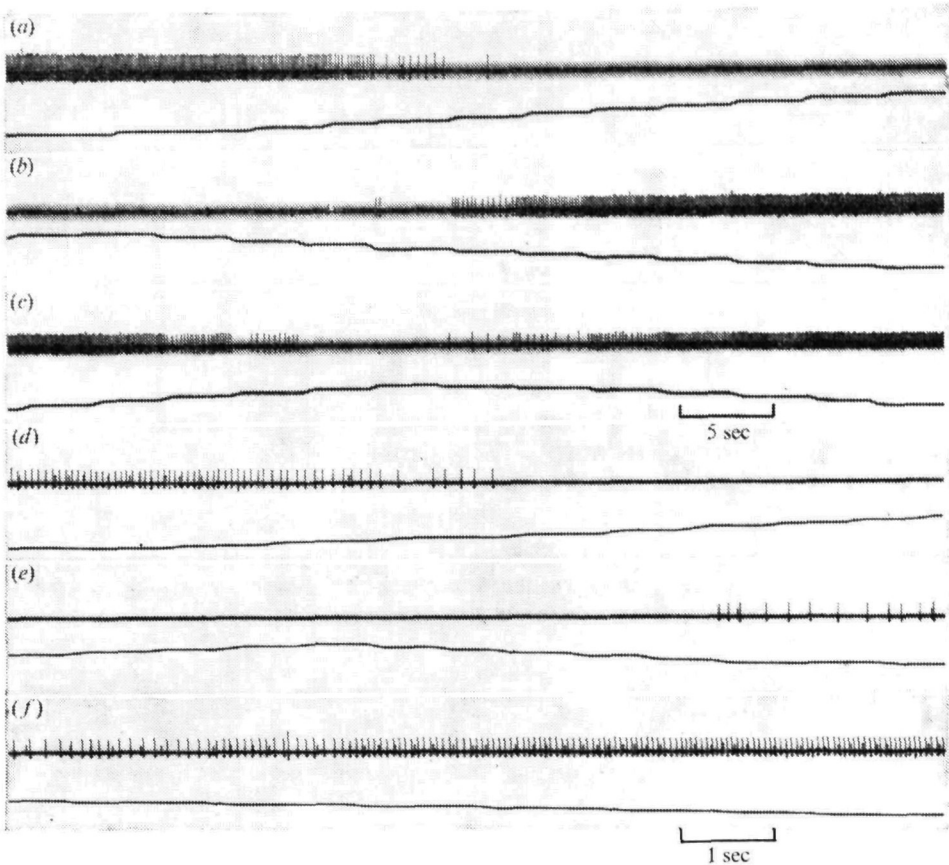
A similar RSPC, this time from *Homarus*, is shown in Text-fig. 13. It differs from the previous unit in that the maximum tonic frequency is only about 12 Hz, and this is achieved on relaxation at a strand length where, on elongation, the unit is silent.

Stretches of constant velocity have been applied to an RSPC from *Cancer* when a steady decline in the instantaneous frequency can be seen as elongation proceeds.

The units just described are typical of most position cells. However, a single unit from *Cancer* was found which responded maximally in the centre of the range rather than at one of the extremes. It had a small phasic component which was excitatory on relaxation and inhibitory on elongation (Pl. 2, fig. 2).

(3) *Intermediate cells*. These are generally large units with a tonic and a marked phasic component.

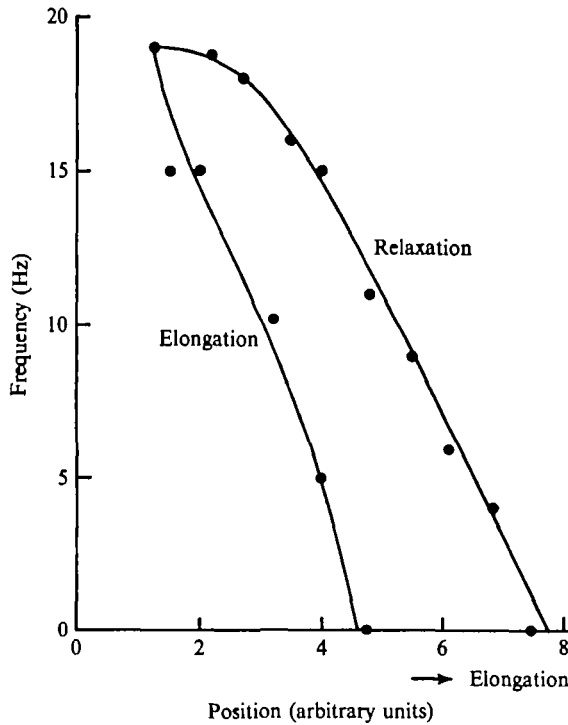
In some cases there is a direct relationship between the phasic and tonic components. Thus the ESIC from *Homarus* shown in Pl. 2, fig. 3, produces a burst of activity when the strand is elongated, and its sensitivity increases as the elongated extreme is approached. In relaxed positions the unit continues to fire at a low frequency but, as it is progressively elongated, the firing rate tends to increase, reaching 25–35 Hz at the most elongated positions shown. Relaxation of the strand causes inhibition of both components. Another intermediate cell, an ESIC from *Eupagurus*, is



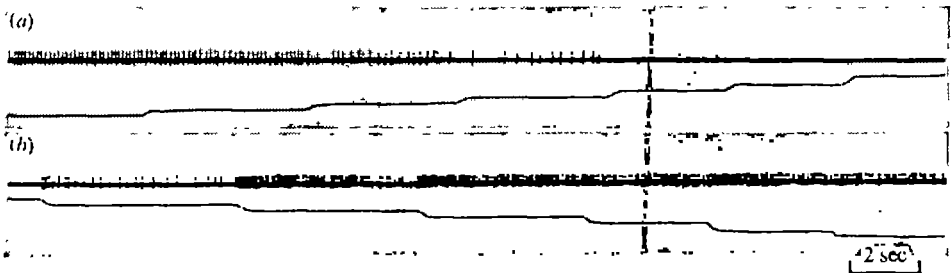
Text-fig. 11. Recording of an asymmetric RSPC from *Eupagurus*. The lower trace shows elongation (upwards) and relaxation (downwards) of the receptor strand. Records *a-c* are continuous, as also are records *d-e*, which show the same unit on a faster time scale.

shown in Pl. 1, fig. 2. This unit responded with a rapid burst of impulses when the strand was elongated and seemed to be of equal sensitivity throughout the range. Adaptation of the burst was slow; towards the elongated end of the range the unit continued to fire for about 2 sec, while towards the relaxed end this 'tonic' component was of longer duration. Relaxation of the strand caused inhibition of the unit.

In other units the relationship between phasic and tonic components seems to be more tenuous. In *Nephrops*, for example, a unit (RISC) was found which fired tonically at a fairly low frequency in the elongated part of the range. However, elongation itself



Text-fig. 12. Graph demonstrating the relationship between the adapted firing frequency of the unit illustrated in Text-fig. 11 and the position within the movement range. The arrows on the curve show the direction of movement used, relaxation to the left, elongation to the right. Note the hysteresis effect which this produces.

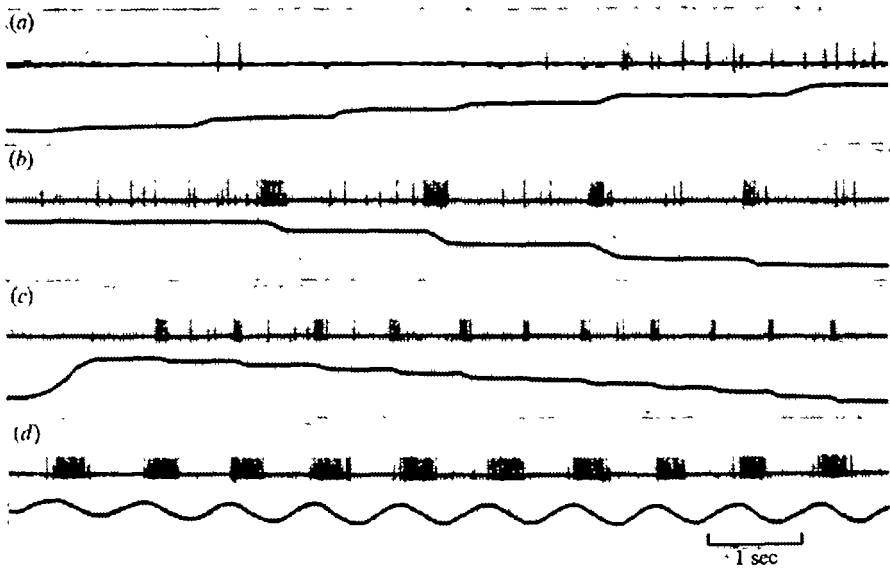


Text-fig. 13. Recording of an asymmetric RSPC from *Homarus*. The lower trace shows elongation (upwards) and relaxation (downwards). *a* and *b* are continuous.

caused inhibition, while relaxation produced a phasic burst of activity (Text-fig. 14). Similarly, an RSIC from *Homarus* is shown in Pl. 2, fig. 4 which fires at a fairly low tonic rate over the whole range (possibly slightly faster at the elongated end). As in the previous unit elongation is inhibitory, whilst relaxation is excitatory. As the velocity of stretch increases the phasic bursts contain fewer impulses at a higher frequency. In both of these units the phasic burst is followed by a silent period lasting up to about 500 msec.

Another RSIC is shown in Text-fig. 2. This unit from *Eupagurus* has a phasic response to relaxation in the relaxed half of the range, and close to the relaxed extreme it remains active when held at a steady length.

Ramps of constant velocity of stretch were applied to an ESIC from *Cancer*. It responded phasically to elongation, except at the relaxed end of the range, and also had a low-frequency tonic response towards the elongated extreme. The stretch velocities used were low, and under these conditions the phasic component was in the region of 10 Hz, with a tonic firing rate at the elongated extreme somewhat less than this.



Text-fig. 14. Recording of an RSIC from *Nephrops*. The lower trace indicates elongation (upwards) and relaxation (downwards). Note in (d) the similarity of this unit to a pure movement unit when the receptor strand is alternately elongated and relaxed at a frequency of about 1 Hz. *a* and *b* are continuous.

DISCUSSION

It has been confirmed that the PD organ in the periopods of the Brachyura, Astacuridea and Anomura contains unidirectional movement units, position units and intermediate units (Wiersma, 1959; Wiersma & Boettiger, 1959). Particular attention has been paid in this current study to those factors which determine the firing patterns, and some of the resulting implications will now be discussed.

Three factors may affect the discharge frequency of movement units: (i) the sensitivity of the fibre, (ii) the rate of movement (velocity) and (iii) the position within the sensitive range at which movement occurs (differential sensitivity). These interact to varying degrees in different units, thus giving rise to a wide range of fibre types.

At one extreme are those highly sensitive units (type 1) which respond at very low velocities and attain a saturation frequency at a low velocity. This type has been described by Wiersma & Boettiger (1959) and Hartmann & Boettiger (1968) and most closely approaches a unit designed to indicate movement as such. Only at low velocities

can it provide information on velocity and position within the movement arc. Units of this type probably led Burke (1954) to consider this organ as a vibration detector.

Next are those units which show velocity sensitivity over a range of velocities before saturation occurs (type 2). Some of these show differential sensitivity at all velocities below saturation only (type 2*a*); others have different saturation frequencies in different parts of the range, so preserving differential sensitivity at all velocities (type 2*c*); and yet others are intermediate, showing a differential sensitivity which, above saturation, is maintained over only a part of the range (type 2*b*). Sensitivity may increase towards either extreme position irrespective of whether the unit is elongation-sensitive (ESMC) or relaxation-sensitive (RSMC) (Wiersma & Boettiger, 1959; Boettiger & Hartmann, 1968). However, in this study ESMC and RSMC with increased sensitivity towards the fully elongated and relaxed extremes respectively were the more common. Type 2 units have the capability, to varying degrees, to signal velocity and position within the movement arc.

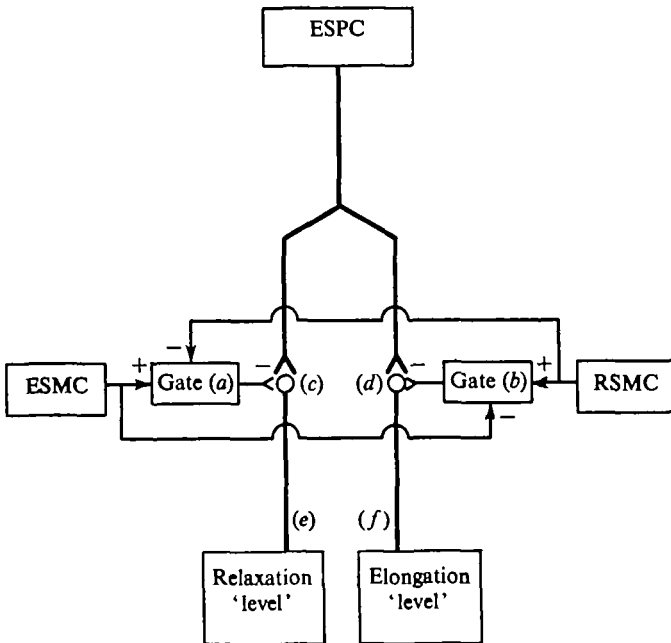
Finally there are units (type 3) which are comparatively insensitive and show velocity sensitivity over a wide range, with saturation occurring only at extremely high velocities which are probably well outside the biological range. Differential sensitivity is maintained at all velocities. These units can potentially provide information on velocity and position within the movement arc over a wide range.

It is immediately apparent that the information on velocity and position within the movement arc provided by units of types 2 and 3 is of a much more complex nature than a simple frequency relationship; and the firing pattern is of the utmost importance. Indeed, under many conditions it is extremely doubtful whether these units can provide the central nervous system with any meaningful information other than that movement is occurring. For example, if we take a unit of type 3, (Text-fig. 8) its firing frequency over the least sensitive part of its range at velocity V_2 is the same as its frequency over the most sensitive part at a lower velocity (V_1). However, if movement occurs over the full arc the overall frequency at V_2 will be greater than at V_1 , the duration of firing will be less and the pattern will thus probably differ.

It is still not certain whether the apparent complex information content of these units is interpreted by central neurones. If such information is required by the central nervous system it may have to be derived by a complex integration of activity in several separate sensory channels – parallel computing (Wiersma, 1962). It is hoped that the current study of transfer functions of the different types of unit will indicate the precise information content which each carries.

If movement units were to be found which fired only over a small part of the movement arc they would not be subject to this interaction and could carry information on velocity. Furthermore, if a number of such units were present, each covering a different part of the range (i.e. true range fractionation) then the central nervous system would also receive information on position within the arc. The movement units of MCO₂ are like this, at least at low velocities of movement (Cohen, 1963, 1965), but further work at higher velocities may reveal a similar situation to that in the PD organ. Such primary velocity-sensitive, position-labelled units may be necessary in MCO₂ in view of the fine control of movement and positions with which this receptor is involved (Evoy & Cohen, 1969).

Position units also present a problem. Their discharge is generally asymmetrical. That is to say, an ESPC has a higher firing frequency at any given level within its sensitive range when the strand has been elongated, rather than released, to that level; the reverse is the case for RSPCs. Thus two positions are represented by a single frequency. A possible way of compensating for this centrally is by directing the information into one of two different channels, depending on the direction of movement. This could be achieved either by using movement sensitive cells (Text-fig. 15) or the phasic component of the relevant position cell. In Text-fig. 15 activation of an



Text-fig. 15. Schematic diagram to illustrate how the asymmetry of an elongation sensitive position cell (ESPC) may be resolved by utilising information from movement-sensitive cells (RSMC and ESMC). Details are given in the text.

ESMC (by elongation) opens gate (a) and thus causes inhibition of transmission at (c), and ensures that gate (b) is closed. Thus the information in the ESPC travels down channel (f) only. Conversely, relaxation will stimulate the RSMC to open gate (b), close gate (a) and block transmission at (d), so that information only travels down channel (e). Instead of directing the information into one of two channels the ESMC and RSMC could work through gates to inhibit and enhance respectively the input from the ESPC, in other words to act in a compensatory role. However, this would be less satisfactory because the degree of asymmetry varies throughout the sensitive range.

It thus appears that the sensory units of the PD organ do not provide detailed, accurate information in a simple form concerning position and velocity; rather, this can only be derived by fairly complex central integration. The results indicate that the overall afferent input to the central nervous system increases considerably as the

joint approaches either extreme – this applies to both movement and positional information – and it may be that this general trend, rather than the precise details of the afferent signals, may be the significant input to the central nervous system. Cohen (1963) came to a similar conclusion in considering the afferent information from the crustacean statocyst. However, the problem cannot be resolved until we know in some detail what the afferent input is used for.

One is to produce resistance reflexes (Bush, 1962). These occur as a result of passive, rather than active, movement of the joint. During normal walking resistance reflexes occur if movements of the PD joint are passively applied during active joint movement, and they are greater when the applied movement is in the opposite direction to that in which the joint is actively moving (Evoy *et al.* 1970). It appears that the sequence of joint movements involved in normal walking is controlled by a central programme, which produces a specific sequence of activity in each of the limb muscles. If the intended movement is altered peripherally a reflex resisting this alteration is evoked. Thus the input from the PD organ must in some way be ‘compared’ with the input ‘expected’ from it by the central programme and any deviation produces the appropriate reflex. This is similar to an ‘efference copy’ situation (von Holst, 1954). Even so there is no indication at present that this requires any more than a rather general afferent input from the receptor. In a resting animal resistance reflexes probably help to maintain the *status quo* by correcting any passively applied movements.

Since the amount of sensory information provided increases as the extremes of joint movement are approached, it may be expected that the resistance reflexes would similarly increase in magnitude, and so help to prevent the extremes from being reached and hence to avoid straining of the joints.

SUMMARY

1. The PD organs of various decapod crustaceans were stimulated by elongation and relaxation of the strand, and single-unit recordings were made from the different types of sensory unit.

2. The sensory units can all be placed in one or other of three categories: unidirectional movement cells, position cells and intermediate cells.

3. Unidirectional movement cells are large, phasic units which respond either to elongation or relaxation of the strand. Some are pure movement-sensitive units, which reach saturation at very low movement velocities and fire over most or all of the range of movement. Other units show velocity sensitivity and differential range sensitivity in varying degrees.

4. Position cells are small tonic units and are usually maximally sensitive at one end of the range of movement. Their firing pattern is asymmetric in that the frequency of impulses is dependent on the direction of movement by which a given position is achieved.

5. Intermediate cells have large phasic and tonic components which may or may not show a direct relationship to each other.

6. The importance of the detailed information produced by the PD organ is discussed and suggestions made as to how it could be utilized by the central nervous system.

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REFERENCES

- BARNES, T. C. (1930). Sensory impulses in crustacean nerve. *J. Physiol.* **69**, 32-33.
- BARNES, T. C. (1931). Responses in the isolated limbs of crustacea and associated nervous discharges. *Am. J. Physiol.* **99**, 321-31.
- BOETTIGER, E. G. & HARTMANN, H. B. (1968). Excitation of the receptor cells of the crustacean PD organ. *Symp. Neurobiol. Invertebrates*. pp. 381-90.
- BURKE, W. (1954). An organ for proprioception and vibration sense in *Carcinus maenas*. *J. exp. Biol.* **31**, 127-37.
- BUSH, B. H. M. (1962). Peripheral reflex inhibition in the claw of the crab *Carcinus maenas*. *J. exp. Biol.* **39**, 71-88.
- BUSH, B. M. H. (1963). A comparative study of certain limb reflexes in decapod crustaceans. *Comp. Biochem. Physiol.* **10**, 273-90.
- BUSH, B. M. H. (1965*a*). Proprioception by chordotonal organs in the mero-carpopodite and carpopodite joints of *Carcinus maenas* legs. *Comp. Biochem. Physiol.* **14**, 185-99.
- BUSH, B. M. H. (1965*b*). Proprioception by the coxo-basal chordotonal organ, CB, in legs of the crab, *Carcinus maenas*. *J. exp. Biol.* **42**, 285-97.
- CLARAC, F. (1968). Proprioception by the ischio-meropodite region in legs of the crab *Carcinus mediterraneus*. *Z. vergl. Physiol.* **61**, 224-45.
- COHEN, M. J. (1963). The crustacean myochordotonal organ as a proprioceptive system. *Comp. Biochem. Physiol.* **8**, 223-43.
- COHEN, M. J. (1965). The dual role of sensory systems: detection and setting central excitability. *Cold Spring Harb. Symp. quant. Biol.* **30**, 587-99.
- EVROY, W. H., BARNES, W. J. P. & SPIRITO, C. P. (1970). Interactions between central commands and reflexes in crab walking legs. *Am. Zool.* **10**, 202.
- EVROY, W. H. & COHEN, M. J. (1969). Sensory and motor interaction in the locomotor reflexes of crabs. *J. exp. Biol.* **51**, 151-69.
- HARTMANN, H. B. & BOETTIGER, E. G. (1967). The functional organization of the propus-dactylus organ in *Cancer irroratus* Say. *Comp. Biochem. Physiol.* **22**, 651-63.
- VON HOLST, E. (1954). Relations between the central nervous system and the peripheral organs. *Br. J. Anim. Behav.* **2**, 89-94.
- MENDELSON, M. (1963). Some factors in the activation of crab movement receptors. *J. exp. Biol.* **40**, 157-69.
- MILL, P. J. & LOWE, D. A. (1971). Transduction processes of movement and position sensitive cells in a crustacean limb proprioceptor. *Nature, Lond.* **229**, 206-8.
- WHITTEAR, M. (1962). The fine structure of crustacean proprioceptors. I. The chordotonal organs in the legs of the shore crab, *Carcinus maenas*. *Phil. Trans. R. Soc. Lond. B* **245**, 291-325.
- WIERSMA, C. A. G. (1959). Movement receptors in decapod crustacea. *J. mar. biol. Ass. U.K.* **38**, 143-52.
- WIERSMA, C. A. G. (1962). The organization of the arthropod central nervous system. *Am. Zool.* **2**, 67-78.
- WIERSMA, C. A. G. & BOETTIGER, E. G. (1959). Unidirectional movement fibres from a proprioceptive organ of the crab *Carcinus maenas*. *J. exp. Biol.* **36**, 102-112.
- WIERSMA, C. A. G., VAN DER MARK, F. & FIORE, L. (1970). On the firing patterns of the 'movement' receptors of the elastic organs of the crab, *Carcinus*. *Comp. Biochem. Physiol.* **34**, 833-40.

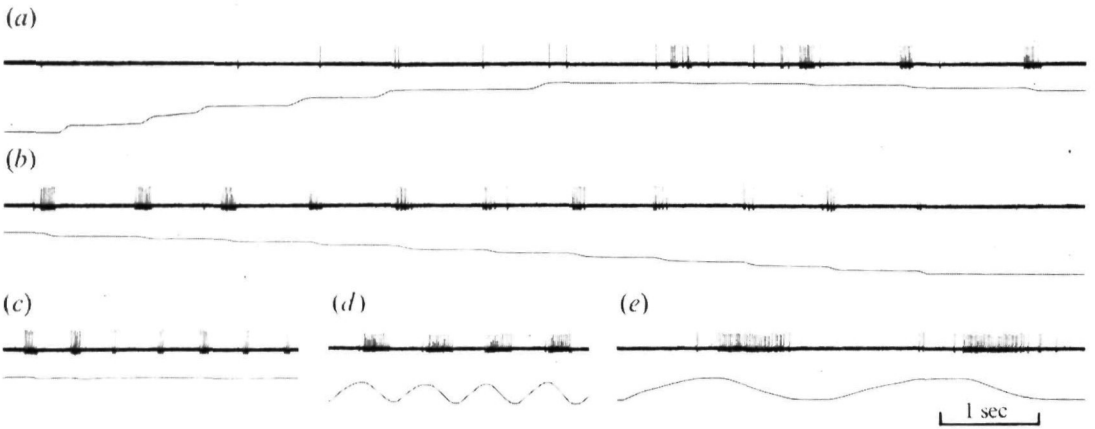


Fig. 1

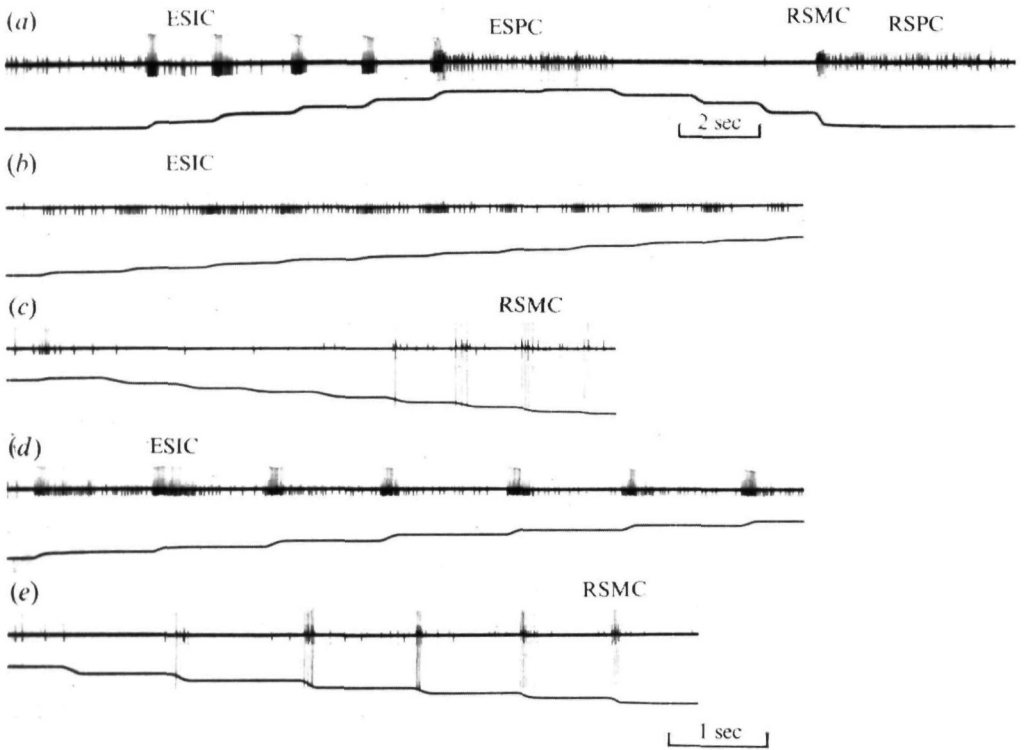


Fig. 2

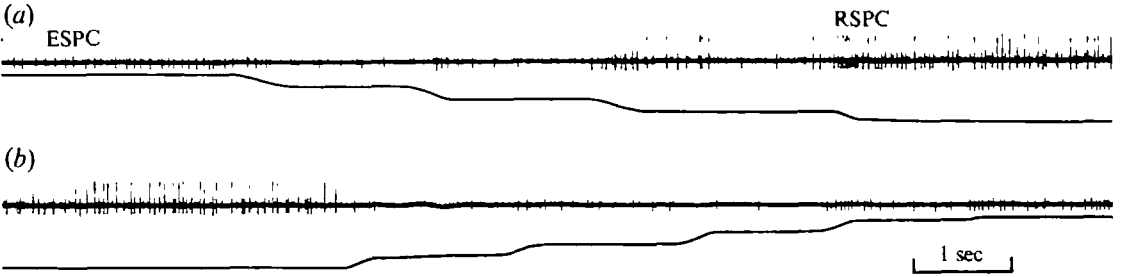


Fig. 1

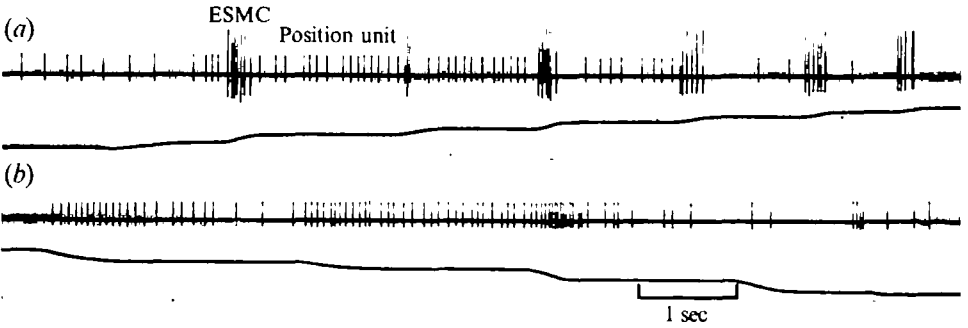


Fig. 2

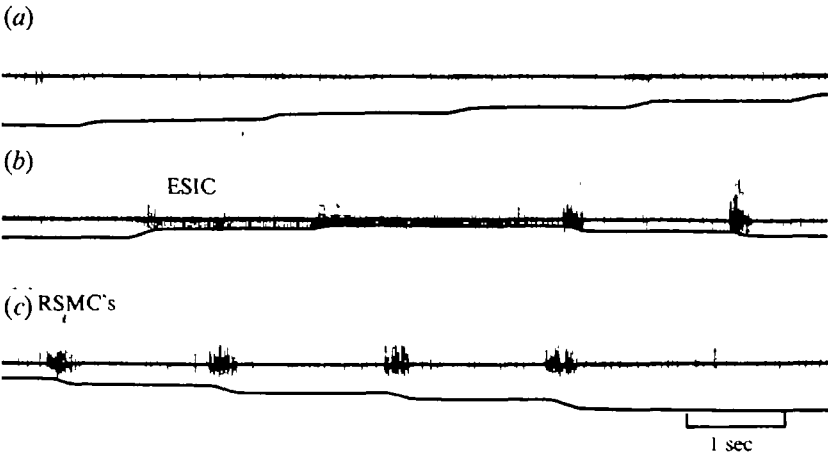


Fig. 3

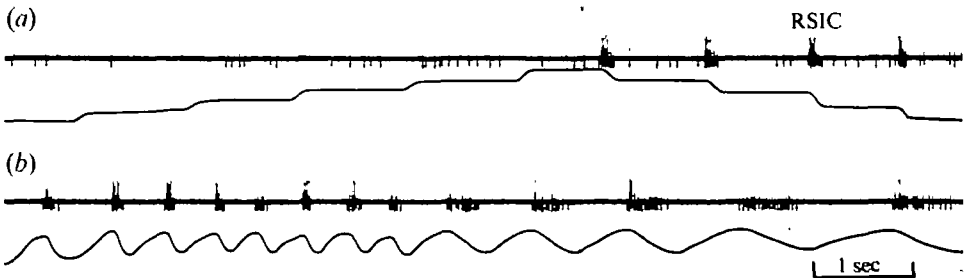


Fig. 4

EXPLANATION OF PLATES

PLATE 1

In each case the upper trace is a record from a sensory unit(s) while the lower trace indicates elongation (upwards) and relaxation (downwards) of the receptor strand.

Fig. 1. A pure movement RSMC from *Homarus*. *a* and *b* are continuous. This unit is extremely sensitive (*c*).

Fig. 2. Various units from *Eupagurus*. The very large unit is an RSMC which only fires over part of the range, the medium unit is an ESIC, and there are several smaller position units (both ESPC and RSPC). *b* and *c* are continuous, as also are *d* and *e*.

PLATE 2

In each case the upper trace is a record from a sensory unit(s) while the lower trace indicates elongation (upwards) and relaxation (downwards) of the receptor strand.

Fig. 1. Position-sensitive units (ESPC and RSPC) from *Homarus*. *a* and *b* are continuous.

Fig. 2. A position cell which is maximally sensitive in the middle of the range and an ESMC from *Cancer*. *a* and *b* are continuous.

Fig. 3. An ESIC and several RSMCs from *Homarus*. Records *a-c* are continuous.

Fig. 4. An RSIC from *Homarus*. Note how this unit approximates to a movement unit when the strand is elongated and relaxed relatively slowly, even below 1 Hz. This is presumably because of the inhibitory effect produced during elongation.

