J. exp. Biol. **154**, 179–200 (1990)
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PHYSIOLOGY AND STRUCTURE OF THREE NEW UROPOD PROPRIOCEPTORS IN THE CRAYFISH *PROCAMBARUS CLARKII*

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Accepted 25 June 1990

Summary

Three new chordotonal organs are described: APCO for the abdominal–protopodite joint, PExCO for the protopodite–exopodite joint and PEnCO for the protopodite–endopodite joint of the crayfish uropod. The PEnCO is a distinct strand chordotonal organ, while the APCO and PExCO are webbed structures arising from peripheral nerve roots 2 and 3 of the terminal abdominal ganglion, in which some of their somata are located ('root cells').

Physiological experiments showed that the organs monitor position and movement at all three joints. Position monitoring is limited to open angles of the exopodite and extended angles of the protopodite (no limits on endopodite position sensitivity). Distinct hysteresis is shown by most position-sensitive units.

The abdomen–protopodite joint is monitored through four orders of velocity magnitude, while the exopodite and endopodite, which are involved in tailfan flare, are primarily monitored at high movement velocities. Large, phasic units in all three chordotonal organs (COs) can monitor continuous, high-velocity movement with little adaptation.

These results are discussed in relation to known motor control mechanisms for crayfish uropods during swimming, walking, escape and righting behaviours.

Introduction

The uropods are the terminal appendages of the tailfan of crustaceans and lie on either side of the medial telson. Each uropod is biramous, consisting of a basal

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Key words: crayfish, chordotonal organs, uropod, proprioceptors, *Procambarus clarkii*.

protopodite (arising from the abdomen) bearing a blade-like endopodite and exopodite. The uropods are used in many types of behaviour, including equilibrium reflexes, such as righting and steering, as well as in a variety of postures and active behaviours, including defence and escape swimming (Larimer and Kennedy, 1969; Bowerman and Larimer, 1974*a*,*b*; Takahata *et al.* 1981; Newland and Neil, 1987; Newland, 1989).

The neuronal control of the uropods has been studied in detail, since it represents a relatively simple motor system that is, however, complex enough to produce asymmetrical as well as symmetrical postures. Larimer and Kennedy (1969) and Bowerman and Larimer (1974*a*,*b*) showed that the uropods participate in a variety of behaviours that can be driven by the stimulation of command fibres in the connectives. Some of these behaviours include the reflexive steering and righting responses that are controlled by descending interneurones with inputs from the vestibular organs, the statocysts (Takahata and Hisada, 1982). These interneurones make direct connections with uropod motor neurones and, in addition, make connections with the uropod motor neurones *via* non-spiking interneurones (Nagayama *et al.* 1984); Takahata and Hisada, 1986). Other studies have shown that non-spiking and spiking interneurones in the sixth abdominal ganglion act as premotor and sensory integration sites in uropod motor pathways, including some for behaviour other than the steering and righting reflexes (Reichert *et al.* 1982; Sigvart *et al.* 1982; Nagayama and Hisada, 1985).

Experiments in which the nerve roots of the sixth abdominal ganglion were cut have shown that the neuronal control systems for steering and righting behaviour do not require proprioceptive feedback from the uropods (Larimer and Kennedy, 1969; Takahata *et al.* 1985). Perhaps for this reason investigations of uropod proprioceptor structure and function (in a range of behaviours) have largely been neglected. A single type of stretch receptor has been reported in the anomuran decapods. This consists of an elastic strand and accessory muscle complex spanning the telson–uropod articulation at the base of the uropods. The primary sensory neurones have centrally located somata in the terminal abdominal ganglion. In *Emerita analoga* the neurones signal stretch of the telson–uropod joint with graded electrotonic potentials (Paul, 1972), while in *Galathea strigosa* they fire spikes, as well as producing electronic potentials (Maitland *et al.* 1982). In *Homarus gammarus* the receptor fires spikes when stretched (Laverack, 1989). The treading-water behaviour of *Emerita analoga* was shown by Paul (1976) to be dependent on feedback from this receptor; in *Galathea strigosa* the receptor mediates efferent reflex activity of two motor neurones and of the receptor muscle itself (Maitland *et al.* 1982). One further undefined phasic–tonic receptor that detects movement of the telson is apparently located in the region of the crayfish anus (Barth, 1964).

In this report we show that each of the three joints of the crayfish uropod possesses previously undescribed proprioceptors, and that these sense organs are capable of signalling position, velocity and direction of movement of each uropod segment.

Materials and methods

The uropods were initially surveyed by immersing partially dissected preparations in van Harreveld's saline to which 6 drops of 1% acidified Methylene Blue (Pantin, 1964) were added per 100 ml. After 4–7 h (at 5 °C) the axons, somata and scolopidia in the stretch receptor organs were stained. The organs were further dissected as required. However, for receptors that had bipolar neurones within the peripheral nerve trunks (see Results), the best stains developed after 10–24 h in a solution of 3 drops of Methylene Blue per 100 ml of saline. All preparations were illuminated with fibre optic lighting and drawn using a Wild M5 binocular microscope with *camera lucida*. Thirty-four preparations were stained.

Physiological studies were carried out on 29 additional preparations. An isolated abdomen–tailfan preparation was pinned out on a wax-bottomed dish and covered with van Harreveld's saline. Individual uropod segments were moved in the plane of their articulation by a solenoid connected to a function generator which delivered sinusoidal, triangular or trapezoidal waveforms. The solenoid probe terminated in a sharpened pin which was inserted through the cuticle of the segment under study; this provided a direct-drive, artefact-free movement. The remainder of the uropod was immobilized with pins. Angles of normal joint movement were measured visually against a small protractor fixed behind the moving segment.

Extracellular nerve recordings were made with suction or oil-hook electrodes (Wilkins and Wolfe, 1974) leading to conventional a.c. preamplifiers, while uropod movements were monitored with a selenium photocell. Both signals were stored on a TEAC R-410 tape recorder for subsequent photography and analysis. The nerve roots were always cut proximal to the receptor to eliminate efferent signals and, in most cases, cut distal to the receptor to eliminate non-receptor distal afferent signals.

Results

Receptor anatomy

Stretch receptor organs were found in close proximity to each of the three major joints of the uropod: the abdomen–protopodite (AP) joint, the protopodite–endopodite (PEn) joint and the protopodite–exopodite (PEx) joint (Fig. 1). All three organs appear to be chordotonal organs (COs) because, in at least one Methylene Blue stain of each, scolopidia were observed at the dendritic endings of the sensory neurones. The organs are named according to the joint that they span: APCO, PEnCO and PExCO.

PEnCO is a strand CO, in which an elastic strand of connective tissue containing sensory neurones stretches across the joint. APCO and PExCO each consists of a web of connective tissue extending from a major nerve root to the hypodermis of the appropriate uropod segment. This latter type is unusual since bipolar sensory neurones occur along its nerve root as well as in the web itself. All the COs are

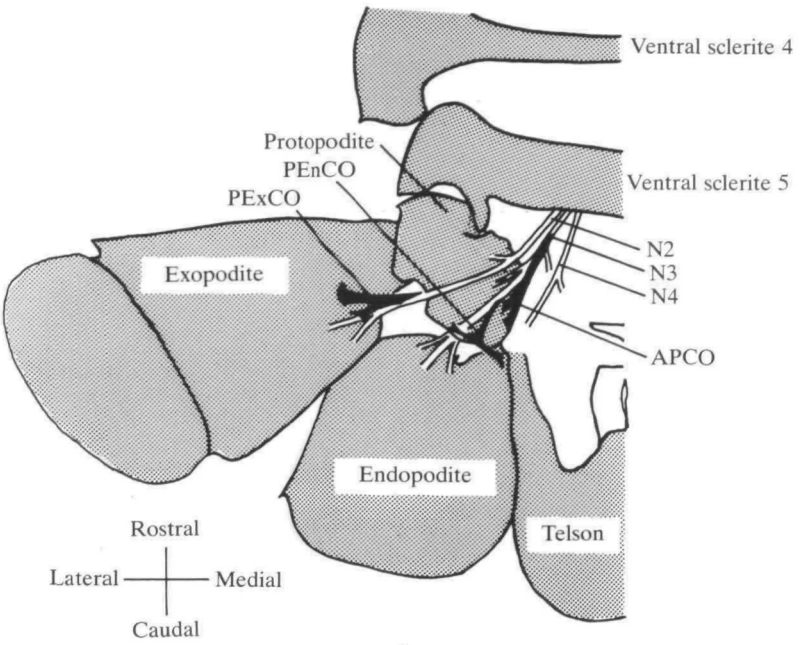

Fig. 1. Ventral view of the right half of the tailfan of *Procambarus clarkii* showing the uropods, telson and three chordotonal organ proprioceptors (APCO, PExCO, PEnCO). The ventral sclerites of the fourth and fifth abdominal segments are shown. Sixth abdominal ganglion roots are labelled N2, N3 and N4.

innervated by nerve roots 2 or 3 of the sixth abdominal ganglion, as described below.

Abdominal–protopodite organ (APCO)

This organ consists of two branched webs of hyaline connective tissue which emerge from the sheath of root 3, proximal to the entry of the nerve into the protopodite (Figs 1 and 2A). The webs spread and attach to the hypodermis on the medio-ventral aspect of the protopodite (arrows, Fig. 2A). A minor web branch often attaches to root 2 and/or the productor muscle (*pro* in Fig. 2A).

A maximum of 19 bipolar neurones per organ (mean±S.D.=13±3, N=16) were stained, of which 5±2 occurred on root 3, just beneath the nerve sheath. These latter neurones may not necessarily be homologous with those of the web, since, in at least one preparation, a bipolar root cell (asterisk in Fig. 2B) had a distal process (presumably a dendrite) that bifurcated, sending one branch out to a root 3 motor nerve and the other distally past the APCO. It was clear, however, that the neurones within the web possessed scolopidia and formed the main chordotonal organ innervation.

Protopodite–exopodite organ (PExCO)

This webbed organ arises from root 2 and sends a major, tough hyaline strand of

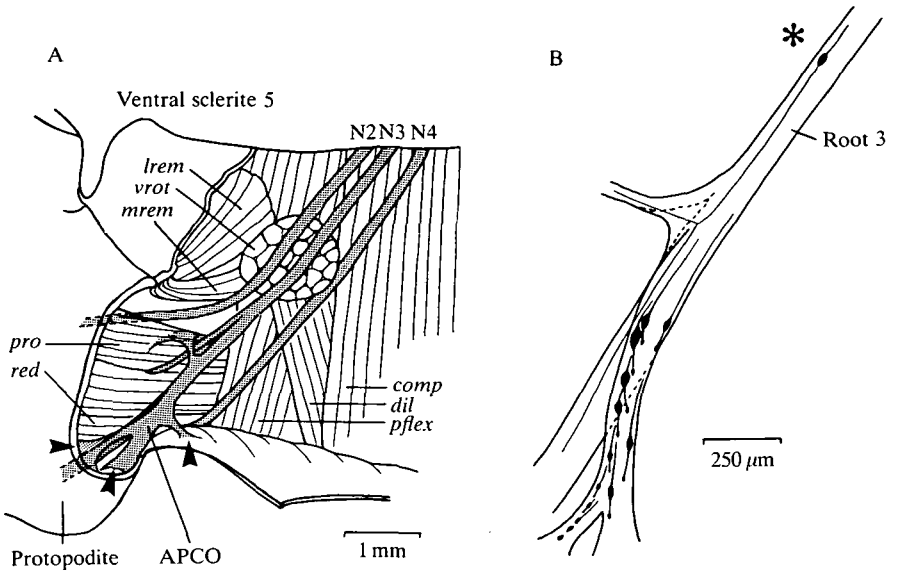

Fig. 2. (A) Ventral view of the abdominal–protopodite chordotonal organ (APCO), shown arising from root 3 and attaching to the ventral inner surface of the protopodite *via* web-like strands (arrowheads). (B) Enlarged view of a Methylene-Blue-stained preparation showing individual sensory neurones with scolopidia endings on the dendrites. The root cell (asterisk) is exceptional because its distal process bifurcated and extended past APCO. *lrem*, lateral remotor; *vrot*, ventral rotator; *mrem*, medial remotor; *comp*, anal compressor; *dil*, anal dilator; *pflex*, posterior telson flexor, *pro*, productor; *red*, reductor.

elastic tissue to the ventro-medial corner of the exopodite, adjacent to the insertion of the exopodite productor muscle (Figs 1, 3A). Other minor branches of elastic tissue extend more laterally to the ventral hypodermis.

A maximum of eight sensory neurones per organ (mean±S.E.=5±1) was observed in nine preparations. Of these 3±1 were root cells. An additional cluster of 9–16 very small neurones was often associated with the distal attachment of PExCO (arrowhead, Fig. 3B). These cells sent dendrites along the hypodermis to the region of arthrodial membrane at the protopodite–exopodite joint, but did not appear to possess scolopidia. Therefore, they do not appear to be joint stretch receptors.

Protopodite–endopodite organ (PEnCO)

This strand chordotonal organ consists of an elastic strand of connective tissue which spans the protopodite–endopodite joint and receives innervation from a small branch of root 3 in the protopodite (see Fig. 1). The strand arises from the arthrodial membrane on the distal rim of the protopodite and connects to the proximal, medial corner of the endopodite (Fig. 4A). The sensory neurones,

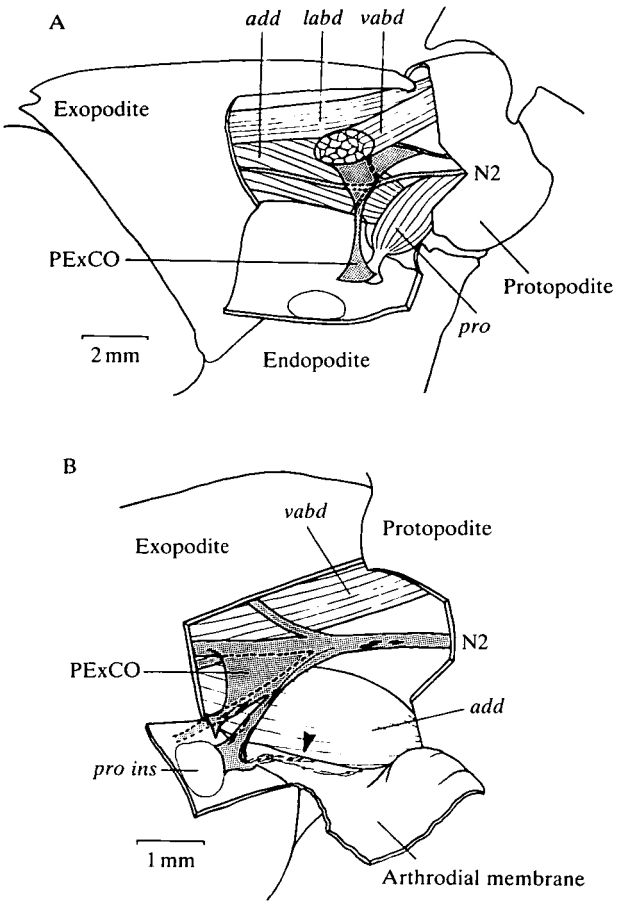

Fig. 3. Ventral view of the protopodite–exopodite chordotonal organ (PExCO). (A) The location of the organ was revealed by reflecting the ventral medial surface of the exopodite and detaching the ventral exopodite abductor muscle (*vabd*). Note attachment point of the strong elastic strand next to the insertion of the exopodite productor muscle (*pro*). PExCO is distorted in this view. (B) Enlarged view of a different dissection of PExCO showing its natural webbed shape arising from root 2. Root cells and web cells were stained with Methylene Blue, as was the cluster of very small sensory neurones (arrowhead), which do not appear to be part of PExCO. The productor muscle has been removed to show clearly the elastic strand attachment adjacent to its insertion (*pro ins*). *add*, exopodite adductor muscle; *labd*, lateral exopodite abductor muscle.

somata and scolopidia lie either in the web-like expansion of tissue, where the sensory nerve joins the elastic strand, or on the strand itself (Fig. 4B).

In the nine organs examined, the maximum number of bipolar neurones recorded was 12±2 (mean±S.D.); usually these included 10 large neurones, plus two very small ones embedded in the medial (distal) end of the band (arrowhead in Fig. 4B). Two additional axons (asterisk in Fig. 4B) were often seen passing

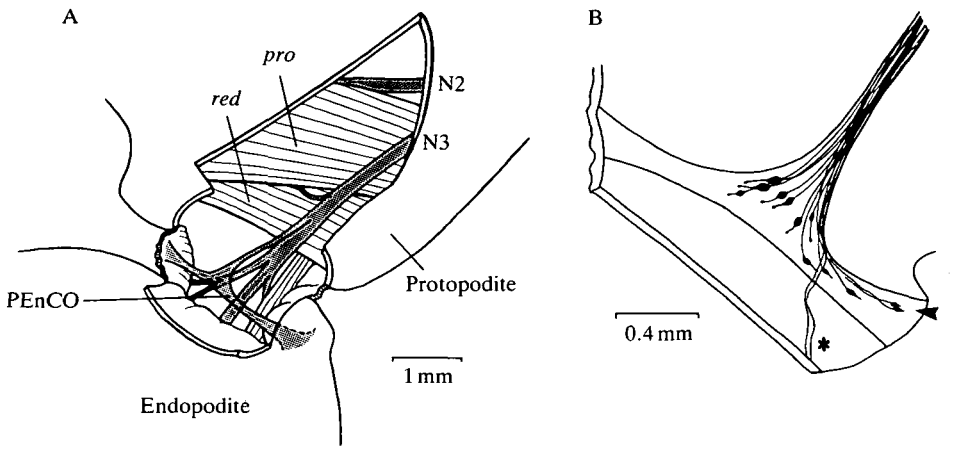

Fig. 4. Ventral view of the protopodite–endopodite strand chordotonal organ (PEnCO). (A) Location of the organ seen spanning the joint, but with its proximal (left) end displaced from the protopodite margin by pulling the arthrodial membrane to enhance viewing. The nerve of PEnCO branches from root 3. (B) Enlargement of Methylene-Blue-stained organ showing the 12 sensory cells (including two very small distal ones: arrowhead) and a pair of axons (asterisk) which extend past the organ into the endopodite hypodermis. *pro*, productor; *red*, reductor.

through the PEnCO near the lateral (proximal) edge of the web, and continuing on to the protopodite hypodermis.

Physiology of chordotonal organs

Abdominal–protopodite chordotonal organ

Since the abdominal–protopodite joint can be moved in both the vertical and horizontal planes (see Fig. 5G), sensitivity to each plane of movement was tested separately. Whole-nerve responses to sinusoidal movement of the protopodite at 10, 1.0 and 0.1 Hz in the vertical plane are shown in Fig. 5A–C, while responses to horizontal movements at the same frequencies are shown in Fig. 5D–F. Some units responded to movements in both planes, while others were sensitive to either vertical or horizontal movements, but not to both. The following two examples demonstrate units sensitive to both planes of movement. At 10 Hz the largest units (dotted) fired on both vertical extension and horizontal opening (upward movements of the lower trace, Fig. 5A,D). At 1 Hz a medium unit (dotted) fired on vertical flexion (Fig. 5B) and on horizontal opening and closing (Fig. 5E).

The rows of dots (rasters) in Fig. 6 represent firing patterns of neurones during horizontal and vertical protopodite movement. Only medium- and large-sized units were directionally sensitive in the APCO, as illustrated by the upper two rasters in Fig. 6 (two neurones that fire on closing only) and in the large spikes of Fig. 5D (two neurones that fire both on opening and on closing). Most of the smaller units did not show directional sensitivity (Fig. 6, lower rasters, and small spikes in Fig. 5C,F), but fired only in a certain range of angles, regardless of the

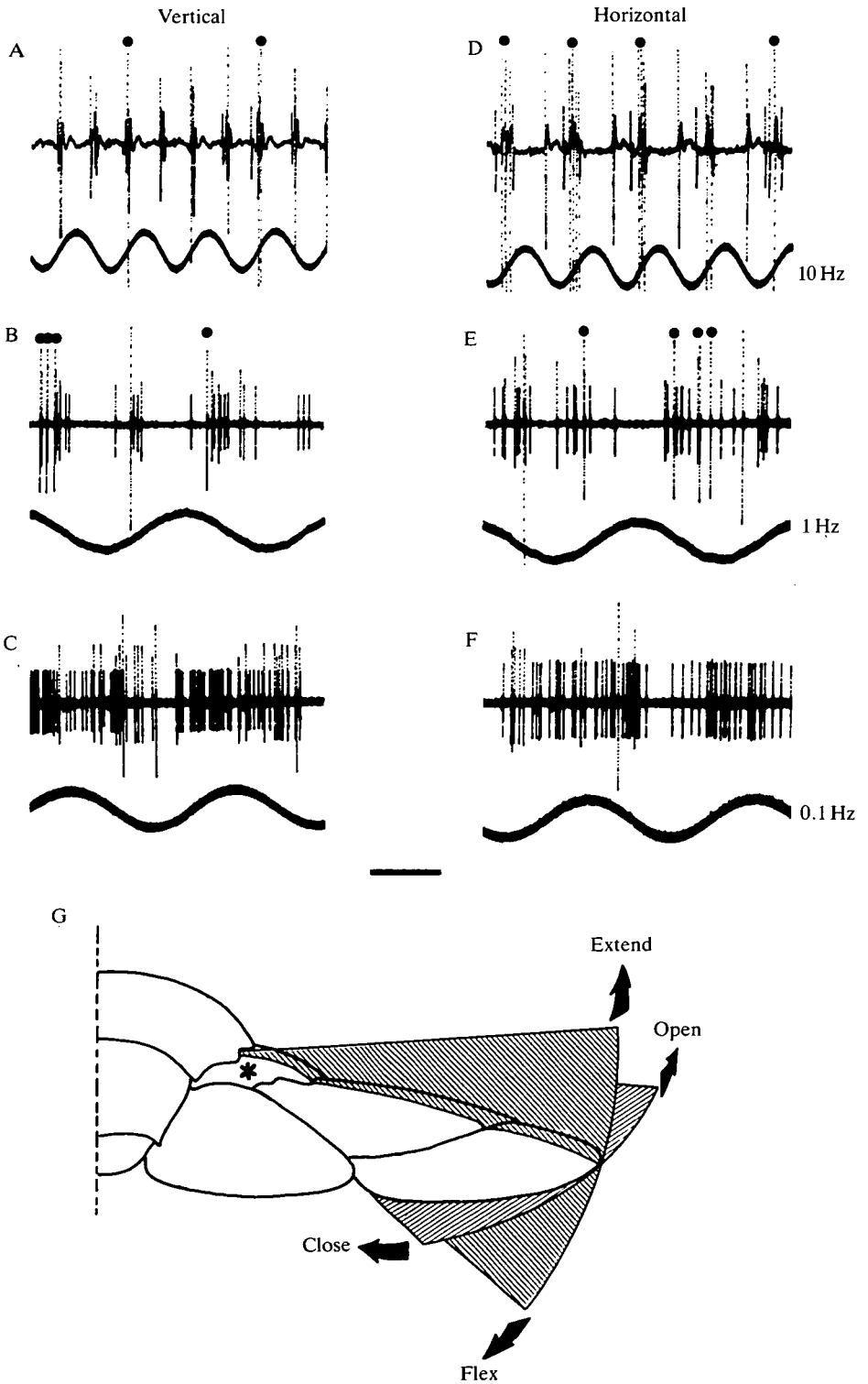
Vertical
Horizontal
A
D
10 Hz
B
E
1 Hz
C
F
0.1 Hz
G
Extend
Open
Close
Flex

Fig. 5

Fig. 5. Recordings of APCO responses (upper traces) to sinusoidal movement (lower traces) of the protopodite (asterisk in G) in either the vertical plane (A–C) or the horizontal plane (D–F) at 10, 1 and 0.1 Hz. Units that responded to both planes of movement are marked with dots. (G) The horizontal and vertical planes of protopodite stimulation (dorso-posterior view). Scale bar, 100 ms (A,D), 400 ms (B,E) and 4s (C,F).

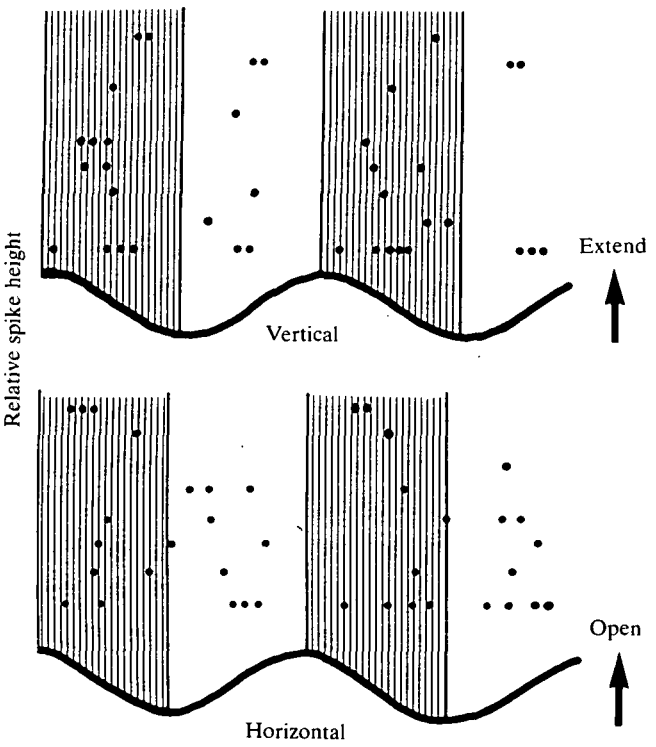

Fig. 6. Firing patterns (dot rasters) of individual APCO units during sinusoidal movements in the vertical (upper) and horizontal (lower) planes. Rasters from 10 Hz and 1 Hz are superimposed, to show the presence or absence of directional sensitivity. Shading of half-cycle duration assists this distinction. Relative size of unit spikes increases with distance above movement trace.

direction of imposed movement. This is characteristic of phasic–tonic units, and is discussed later. The plots of Fig. 6 show responses at 1 and 10 Hz.

When tested for velocity-sensitivity with horizontal ramps, many units showed a peak response at $20°s^{-1}$, although three (which were large units) had peak sensitivities at $200°s^{-1}$ (Fig. 7A). The APCO showed very little response to the lowest-velocity horizontal ramp ($0.2°s^{-1}$). Vertical movement velocity receptors responded at all velocities tested. Eight units showed increased firing with increased velocity, up to the maximum tested ($200°s^{-1}$, Fig. 7B). These units

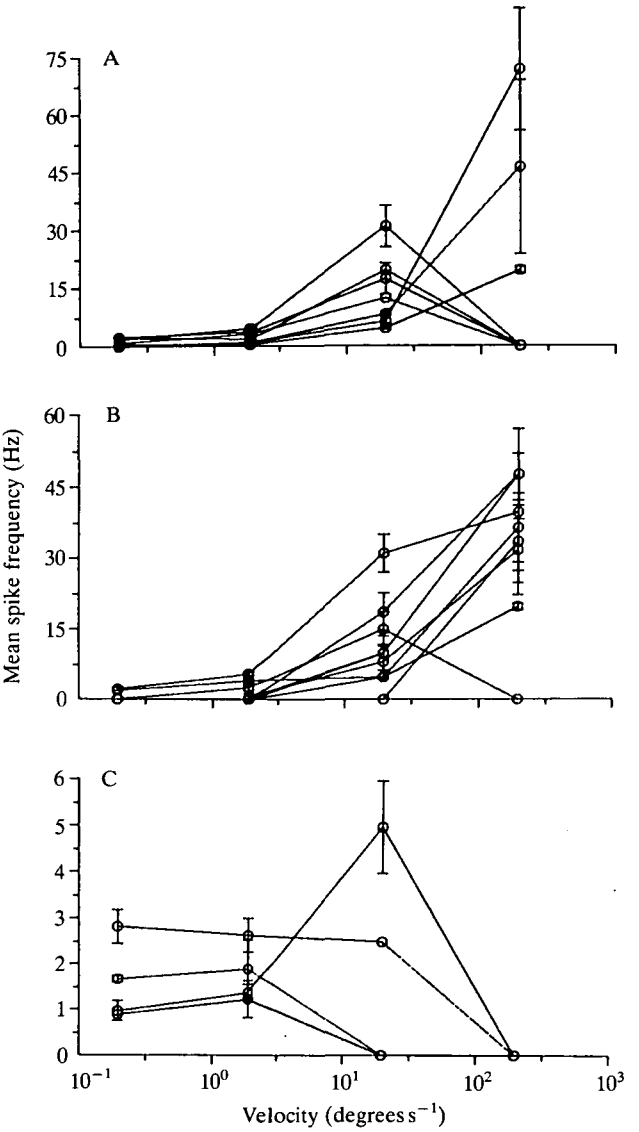

Fig. 7. Velocity-sensitivity of APCO units to ramp movements of the protopodite in the horizontal (A) and vertical (B,C) planes. Mean (±standard deviation, N=2–7 samples at each velocity tested) firing frequencies (spikes s^{-1}) are plotted for velocities of 0.2, 2.0, 20 and 200° s^{-1} for 20° horizontal and 17° vertical movements. The units in A and in B primarily responded to high velocities while those in C primarily responded to low velocities, with low firing frequencies. Note the clear range fractionation of units in B and C.

showed little response at 2° s^{-1} and the greatest increase between 20 and 200° s^{-1} Four additional units showed low velocity-sensitivity (Fig. 7C), with peaks at 0.2, 2.0 or 20° s^{-1} and no response above 2.0 or 20° s^{-1}. Therefore, range fractionation

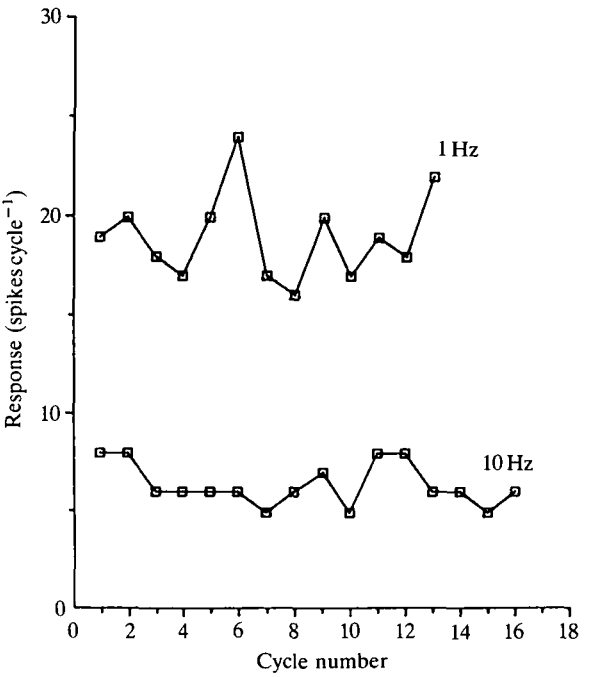

Fig. 8. Test for adaptation of APCO to repeated sinusoidal 20° movement (horizontal) of the protopodite at 1 and 10 Hz. The data are from a whole-nerve recording.

occurred over the full range of velocities tested for vertical movement, but only for the higher two velocities of horizontal movements.

Adaptation of phasic units to continuous sinusoidal movement in the horizontal plane was tested at 1 and 10 Hz and is plotted as the number of spikes per cycle *versus* cycle number (Fig. 8). No adaptation occurred over 13 cycles at 1 Hz, while only slight adaptation occurred at 10 Hz over 16 cycles.

Position-sensitive units were tested by giving ramp-and-hold stimuli in vertical and horizontal directions. Only one or two vertical-position-sensitive units were ever recorded in any preparation. These were phasic–tonic units (e.g. smallest spike, Fig. 9) which fired a burst of spikes with each flexion or extension ramp (upwards on bottom trace), as well as firing more strongly at each succeeding position approaching full extension. An almost linear relationship between spike frequency and position was demonstrated (Fig. 10A, different preparation) as the protopodite was moved from full flexion to full extension and back. Horizontal-position-sensitive units showed range fractionation over the entire 14–16° range of movement (Fig. 10B–F). Three of nine units analyzed were phasic–tonic and directionally sensitive (two fired during opening ramps while one fired during closing). The remaining six showed no movement sensitivity. These purely tonic horizontal position units showed marked hysteresis, the nature of which depended on the particular neurone: those with maximum firing frequencies at closed angles (Fig. 10B,C) fired most strongly at any particular angle if that angle was

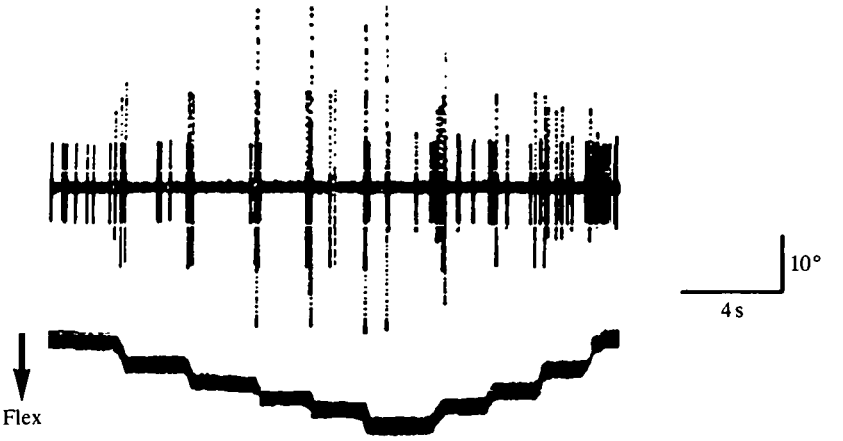

Fig. 9. Ramp-and-hold movement (lower trace) of the protopodite in the vertical plane to demonstrate APCO position-sensitive firing of the smallest unit (upper trace) towards extreme extension (upwards). This unit also responded phasically to movements in either direction.

approached from a more closed angle. The opposite was true for neurones with maximum firing frequencies at open angles. At some angles neurones either failed to fire or fired at up to 1 Hz depending on the direction of approach (Fig. 10E).

Protopodite–exopodite chordotonal organ

Although this organ had the fewest sensory neurones, it nevertheless showed velocity and position sensitivity. Ramp-and-hold 12° movements revealed: (a) that the largest units have high velocity thresholds (Fig. 11A); (b) that the medium units are position-sensitive and fire tonically (Fig. 11C); and (c) that the smallest units are direction- and velocity-sensitive (Fig. 11B,C). A detailed analysis of single-unit directional sensitivity is shown in Fig. 12A, in which each raster represents the firing pattern of a single unit during trapezoidal 20° movement at $20°s^{-1}$. The three smallest units (lower three rasters) respond to closing (R1), opening (R2) and both directions (R3), while the larger tonic units (upper rasters) fire mostly in the static open position.

The velocity sensitivity of six single units is plotted in Fig. 12B for velocities from 2 to $2000°s^{-1}$. Three high-frequency units are plotted together in Fig. 12Bi, while the remaining three low-frequency units are plotted together in Fig. 12Bii. The peak responses for all units except one occur at $200–2000°s^{-1}$ (approximately 1–10 Hz of sinusoidal movement). The single exception had a peak response at $20°s^{-1}$ (Fig. 12Bii) and fired at a low frequency.

Adaptation to continuous sinusoidal stimulation was analyzed in two neurones: a large unit sensitive to high velocity, and a small unit that responded to closing only (Fig. 12C). The small (*a*) unit adapted to 66% of its initial firing rate within 15 cycles at 1 Hz, while at 10 Hz it fired weakly and was completely adapted by the seventh cycle. The high-threshold unit (*b*) did not fire at 1 Hz, and at 10 Hz it

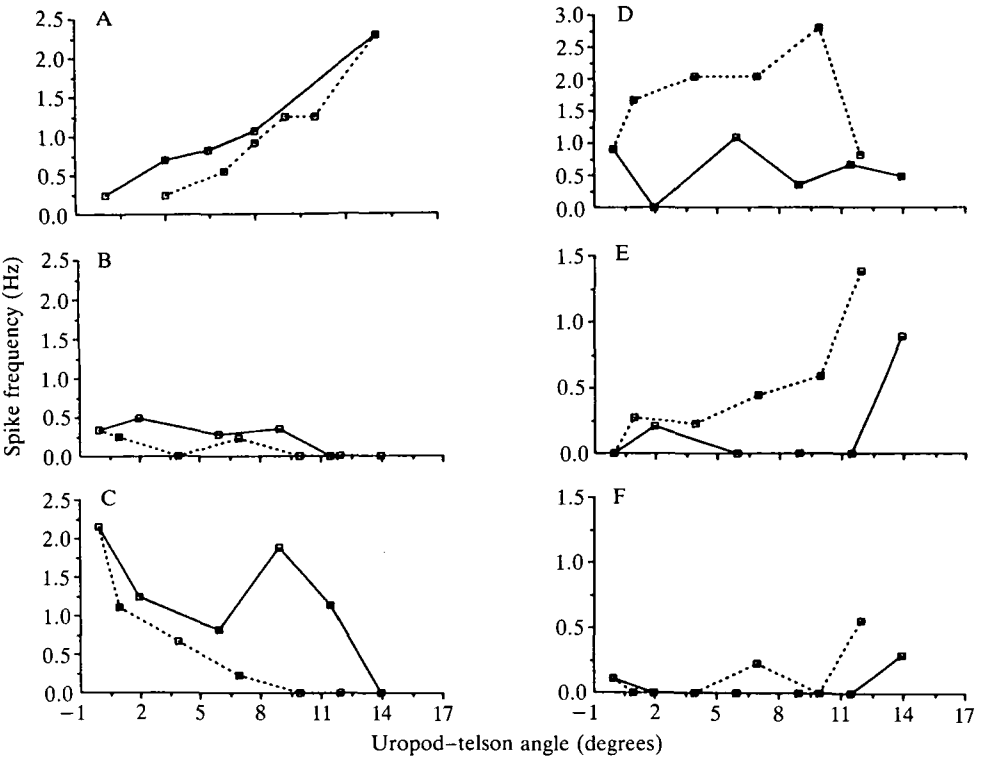

Fig. 10. Position-sensitivity of APCO units. The protopodite was set at different positions (uropod–telson angle) in the 12° vertical range of movement (A) or 14° horizontal range (B–F). Dashed lines represent progressive settings toward flexion (vertical) or closing (horizontal) of the protopodite, while solid lines represent progressive settings in the opposite directions.

dropped from an initial firing rate of 4 spikes cycle^{-1} to a plateau of 2 spikes cycle^{-1} by the fifth cycle, with occasional spike failure thereafter. It continued to fire at this low rate for many cycles.

PExCO neurones showed maximum position sensitivity at or nearly at the fully opened position of the exopodite (i.e. 14, 17 and 20°), and were silent or fired weakly over the rest of the range (Fig. 12D). These units also showed a strong hysteresis in response, determined by the direction from which any given setting was approached. Two of the units fired most strongly during the opening sequence of position settings (the opposite hysteresis pattern was noted for APCO neurones).

Protopodite–endopodite chordotonal organ

The 12 neurones of the strand chordotonal organ, PEnCO, monitor position, velocity, direction and probably acceleration of endopodite movement. Whole-nerve recordings during sinusoidal movements at 1.0 and 0.1 Hz (Fig. 13B,C) showed that the strongest firing occurred while the endopodite passed through the

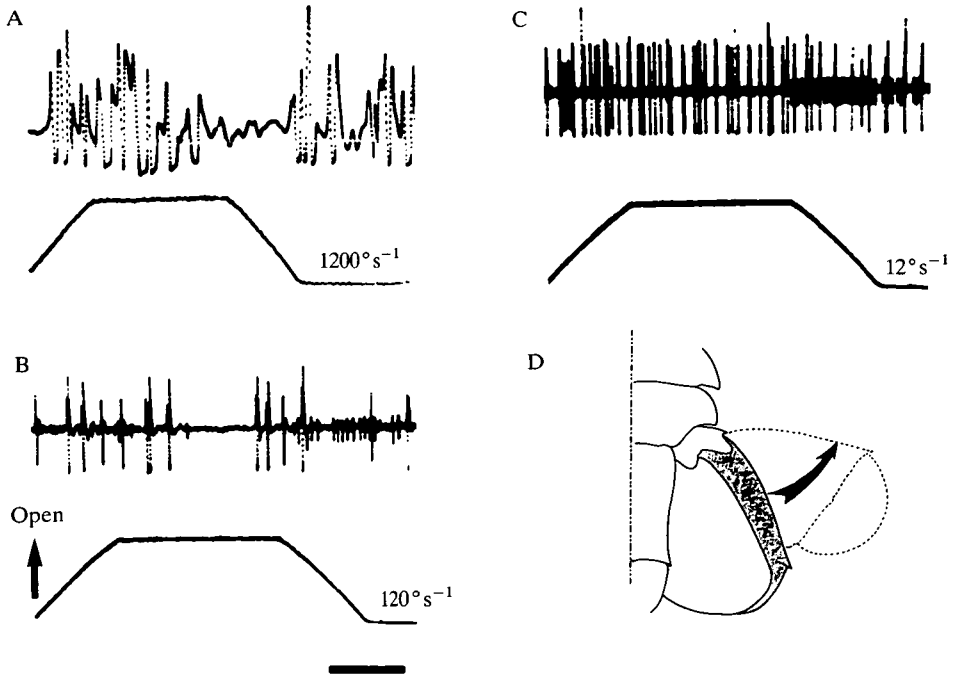

Fig. 11. Responses (upper traces) of the protopodite–exopodite chordotonal organ (PExCO) to 12° trapezoidal movements of the exopodite (lower traces) at 1200, 120 and 12°s^{-1} (A–C, respectively). (D) The plane of stimulation of the exopodite (dorsal view). Scale bar, 10 ms (A), 100 ms (B) and 1 s (C).

open end of its displacement range (between approximately 9 and 18°). During stimulation at 10 Hz, the PEnCO fired most strongly during closing movements (Fig. 13A). This record also shows that a very sudden closing movement superimposed on the sinusoidal pattern evoked a brief discharge of at least one large, high-threshold unit.

When stimulated at 1 Hz, the four smallest neurones (Fig. 14, lower rasters) are phasic and directionally sensitive (primarily to closing), while the larger neurones

Fig. 12. Response properties of the PExCO. (A) Dot raster plots of single-unit responses to 20° trapezoidal exopodite movement (opening upwards), showing presence or absence of directional sensitivity. Relative size of unit spikes increases with distance above movement monitor trace. Shading indicates periods of movement. The three lowest rasters, R1–R3, are discussed in the text. (B) Velocity-sensitivity of phasic units to horizontal 20° ramp movements of the exopodite. Firing frequencies (mean±standard deviation, N=2–7) of six units are plotted for velocities of 2, 20, 200 and 2000°s^{-1}. Note differences in ordinate scales for the two plots and range fractionation. (C) Adapatation of two units (*a* and *b*) to continuous sinusoidal stimulation at 1 and 10 Hz. (D) Position-sensitivity for three units. Mean (±standard deviation, N=2–7) firing frequencies are shown as the exopodite was set at different uropod–telson angles in the 20° range of horizontal movement. Dashed lines represent progressive settings towards the closed position, while solid lines represent progressive settings towards the open position.

do not show directionality and represent a combination of phasic and phasic–tonic cells which fire during both opening and closing (Fig. 14).

Phasic units were analyzed for velocity-sensitivity with ramp movements varying from 2.4 to 720° s^{-1} (Fig. 15A, arbitrarily divided into two plots for clarity). As with the other chordotonal organs, the majority of phasic units responded most strongly to high velocities and showed little response at low velocities. All units except three had peak responses at 240–720° s^{-1}. The three exceptions (Fig. 15Ai) showed peak responses at 24° s^{-1} (equivalent to 1 Hz triangular movement). The units showing peaks at the highest velocities were large, high-threshold neurones, and may represent acceleration receptors. They gave no responses below 240° s^{-1}.

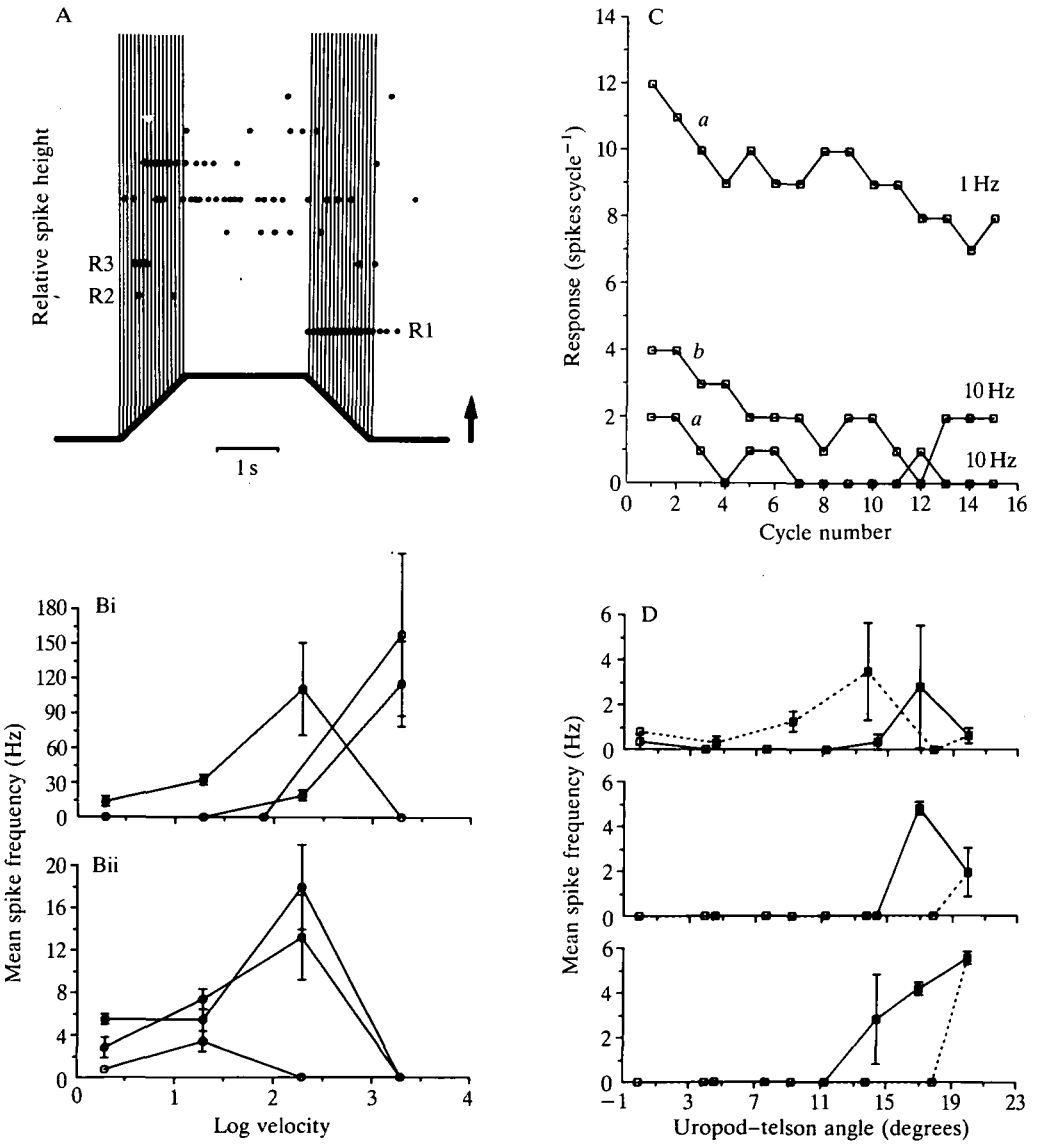

Fig. 12

Thus, the PEnCO has rather limited range fractionation and is primarily a high-velocity stretch receptor.

The adaptation to continuous sinusoidal stimulation varied among the three

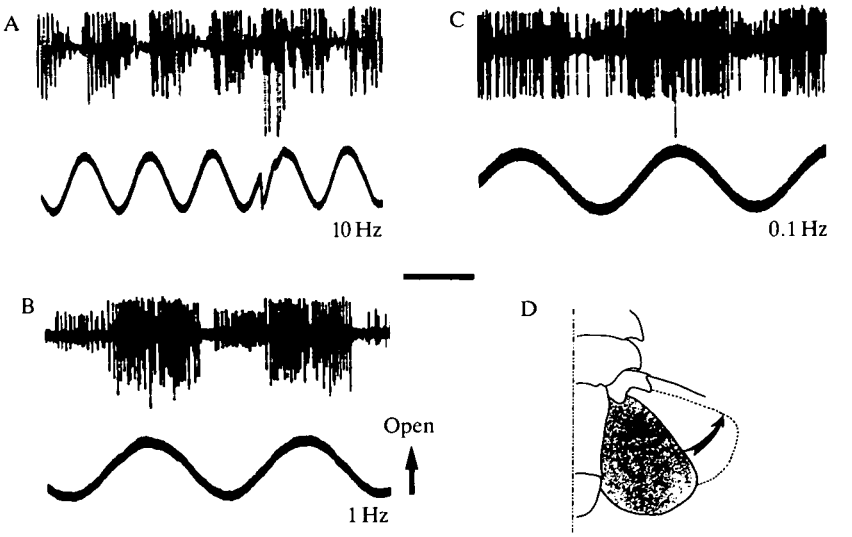

Fig. 13. Responses (upper traces) of the protopodite–endopodite chordotonal organ (PEnCO) to endopodite 12° sinusoidal movement at 10, 1 and 0.1 Hz (A, B and C, respectively). Horizontal opening is upwards in lower traces. A superimposed rapid closing of the endopodite in the fourth stimulus cycle in A evokes a burst of spikes in a high-threshold unit. (D) The plane of imposed movement of the endopodite (dorsal view). Scale bar, 100 ms (A), 400 ms (B) and 4 s (C).

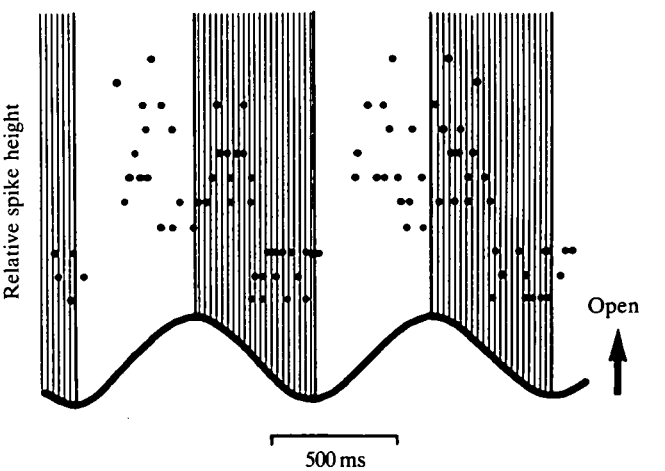

Fig. 14. Directional sensitivity of PEnCO units shown as a dot raster plot of firing patterns during 12° sinusoidal endopodite movement (bottom) at 1 Hz. Relative size of spikes increases with distance above movement trace. Shading indicates endopodite closing.

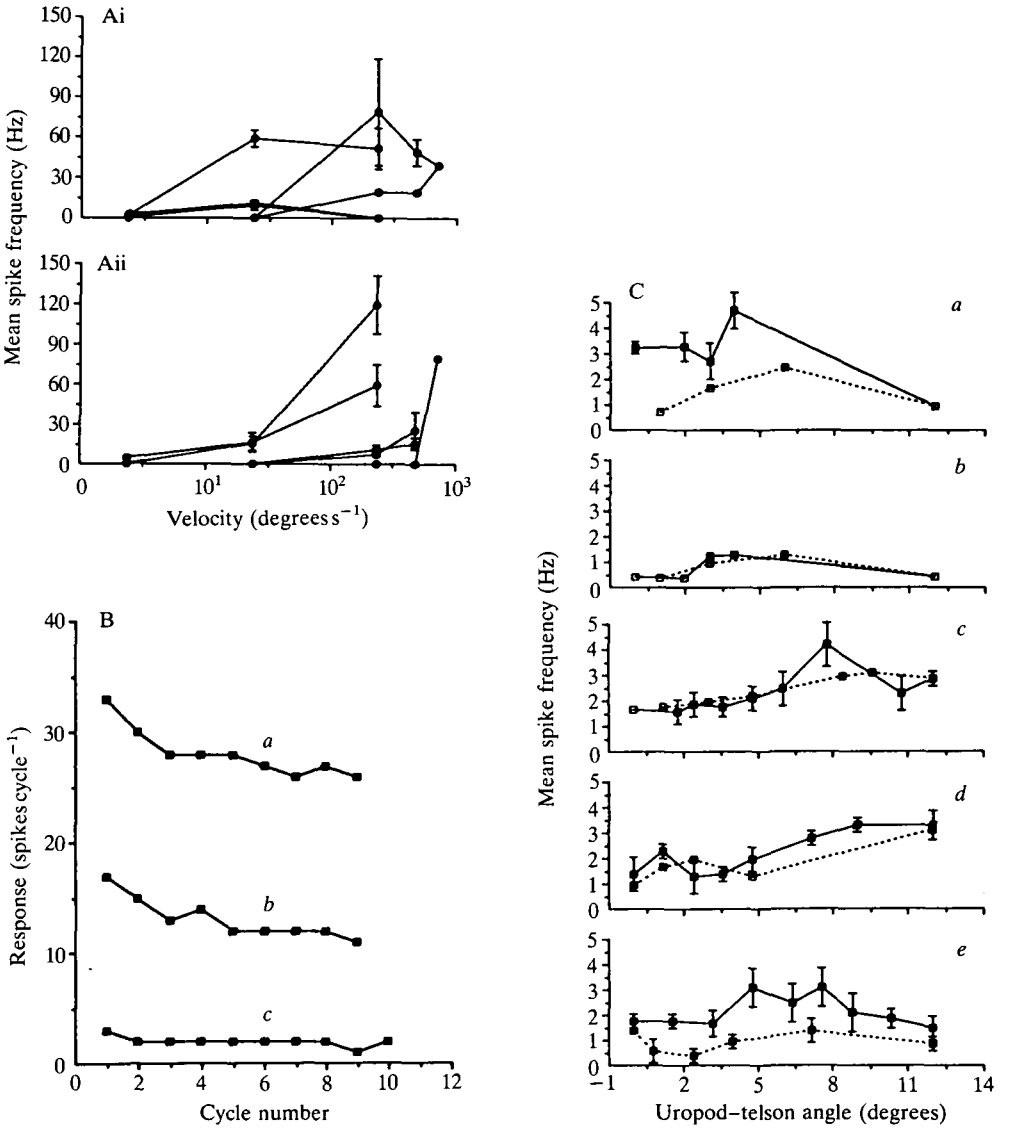

Fig. 15. Response properties of PEnCO. (A) Velocity sensitivity of phasic units to horizontal ramp movements of the endopodite. Firing frequencies (mean±standard deviation, N=2–7) are plotted for velocities of 2.4, 24, 240, 480 and 720° s^{-1}; units are displayed on two plots to enhance clarity. (B) Adaptation of three units (*a–c*) to continuous sinusoidal stimulation. Units *a* and *b* were stimulated at 1 Hz, while unit *c* was stimulated at 30 Hz (and did not respond at 1 Hz). (C) Position-sensitivity is shown for five units (*a–e*). Firing frequency (mean±standard deviation, N=2–7) is shown as the endopodite was set at different positions (uropod–telson angle) in the 12° range of horizontal movement. Dashed lines represent progressive settings towards the closed position, while solid lines represent progressive settings towards the open position.

phasic units analysed (Fig. 15B). Curve *a* was from a medium-sized unit which adapted to 78 % of its initial firing rate within 8 cycles at a stimulation frequency of 1 Hz. At the same frequency a small unit, curve *b*, adapted to 64 % of its initial firing rate over the same period. However, the rate of adaption was faster for the medium unit, which had a generally higher firing rate. Curve *c* was from a large, high-threshold unit stimulated at 30 Hz. Its response dropped rapidly from 3 to 2 spikes $cycle^{-1}$ and remained steady over many cycles in this and other experiments.

The position-sensitive units showed range fractionation over most of the range of endopodite displacement (Fig. 15C). For five units, which fired tonically at the positions tested, peak responses occurred at 4°, 4–6°, 5–8° and 9–12°. Hysteresis in the response curves was marked for two of the units (*a* and *e*): the sequence of steps towards the fully opened position gave stronger responses than the closing sequence, as noted for position-sensitive tonic units in PExCO. The tonic firing frequencies of the other three neurones were low (usually less than 5 Hz).

Discussion

Three previously undescribed proprioceptors in the tailfan of *P. clarkii* are shown to monitor position, movement velocity and direction of movement of the three joints in the uropods of the crayfish. Although the strand chordotonal organ, PEnCO, is typical of those found in crustacean legs, antennae and maxillipeds (Mill, 1976), the other two organs are highly unusual because of their attachment to nerve roots of the terminal abdominal ganglion, and because of the presence of sensory somata in these roots. The presence of bipolar sensory neurone somata in peripheral nerves is unusual in Crustacea. The centrally associated somata of a spiking stretch receptor in the telson of *Galathea strigosa* occur at the base of root 1 of the terminal ganglion (Maitland *et al.* 1982). A spiking stretch receptor in the abdominal nerve cord of the crayfish (Kennedy *et al.* 1966) is sensitive to cord distension during extreme extension of the abdomen and uropods. However, it is not known whether the receptor soma is in the cord or in a ganglion. The best-documented case is the presence of several cuticular mechanoreceptor somata in nerve roots 1 and 2 of crayfish abdominal ganglia (Pabst and Kennedy, 1967). These bipolar and tripolar neurones occur within a few millimetres of each ganglion and apparently are not associated with any chordotonal organs. The long, branched dendrites have broad receptive fields in the soft ventral cuticle of the abdomen, where the dendritic terminals bear distal expansions. The uropod root cells of the present study generally appear to innervate the CO connective tissue webs, but in one case the distal process of a root cell of APCO extended past the CO and bifurcated into a motor branch of root 3. Since this cell was clearly not part of the CO, it, and possibly others in the uropods, could have been a cuticular mechanoreceptor (although bipolar somata have not been reported previously in root 3 of the abdominal ganglia). In insect peripheral nerves, a few neurosecretory

Table 1. *Summary of the physiological properties (rows) of the three uropod chordotonal organs with regard to position and movement of the three uropod segments (columns)*

	Protopodite (APCO)	Exopodite (PExCO)	Endopodite (PEnCO)
Maximal position sensitivity	Vertical: extension Horizontal: full range	Open	Full range
Directional sensitivity	Vertical: flexion and extension Horizontal: open and close	Open and close	Mostly close
Hysteresis	Inverse – both directions	Maximal on opening	Maximal on opening
Maximal velocity sensitivity	Vertical: full range Horizontal: 20–200° s^{-1}	200–2000° s^{-1}	240–720° s^{-1}
Adaptation to continuous movement	Slight at 10 Hz (large units)	To 50 % at 10 Hz (large units)	Slight at 30 Hz (large units)

and mechanosensory somata are found in two dipteran genera and one phasmid species (Finlayson and Osbourne, 1968; Finlayson, 1976).

The results from this study and those on the telson stretch receptor (Paul, 1972; Maitland *et al.* 1982; Laverack, 1989) indicate that the uropods are almost as richly innervated by proprioceptors as are the other major appendages of crustaceans, which have one or two enteroreceptors (chordotonal organs, myochordotonal organs or non-spiking coxal receptors) per joint, as well as apodeme tension receptors in certain muscles. It is clear from previous deafferentation studies, however, that the uropod proprioceptors are not involved in the equilibrium righting and steering reflexes mediated by statocysts and leg proprioceptors (Hisada and Neil, 1985). They must, therefore, be involved in proprioceptive feedback control of the uropods during voluntary behaviour. Bowerman and Larimer (1974*a*,*b*) described a number of command interneurones in the crayfish which activated the uropods as part of specific behavioural drives. They demonstrated 14 command units that produced phasic behaviour such as swimming, escape, forward walking and backward walking. At least 20 other units activated tonic postures involving the uropods. These behaviours included abdominal extension, turning, abdominal flexion, general promotion, bilateral cheliped lifting plus abdominal extension (as in the defence posture) and bilateral cheliped lifting plus abdominal flexion. It may be postulated that these descending drives provide the neuronal frames of reference in which uropod proprioceptive feedback operates.

The physiology of the chordotonal organs indicates that, although they can monitor position and movement parameters of all uropod joints, there are constraints on how effectively such parameters are measured. This is shown in Table 1, which summarizes the properties of the three COs.

Position monitoring is limited to open angles of the exopodite and extended angles of the protopodite, but includes the full range of endopodite positions. The maximum discharge of the position-sensitive units is obtained if open positions have been reached by opening movements in both the exopodite and the endopodite. Thus, there is enhanced sensitivity to flared positions of the crayfish tailfan. It is of interest to note that many of the command-driven postures reported by Bowerman and Larimer (1974*a*,*b*) involved flaring the exopodites and endopodites to open positions. These movements are often accompanied by abdominal extension, as seen in the lateral merus defence posture. Forward walking is another behaviour that is accompanied by uropod flaring and abdominal extension and, in this case, the degree of exopodite–endopodite opening is often variable and finely tuned, depending upon the walking rate and substratum conditions (L. H. Field personal observation). We have noted that, in general, crayfish in an aquarium tend to maintain the uropods in an open or semi-open position most of the time, whether resting or moving. However, in a habitat with water currents, the uropods would become very important in maintaining a hydrodynamically streamlined profile. Newland *et al.* (1988*b*) and Maude and Williams (1983) have studied orientation behaviour of the Norwegian lobster *Nephrops norvegicus* and eight species of freshwater crayfish, respectively. Although the behaviour of these crustaceans differs in some respects (crayfish exhibit both upstream and downstream orientation, while lobsters only orient downstream), it is clear that in both genera the uropods are deployed in a flared, partially flexed posture which decreases hydrodynamic drag from either direction. All the above observations fit well with the tonic position sensitivities found for the uropod COs.

Table 1 indicates that sensitivity to movement of the exopodite and endopodite joints, but not of the protopodite joint, is restricted. Thus, the joint that controls the entire uropod attitude relative to the abdomen is monitored through four orders of magnitude of velocity in the vertical plane, but the exopodites and endopodites, which adjust the degrees of tailfan flare, are primarily monitored at high velocities. In addition, it should be noted that the large phasic units of all three COs are capable of monitoring continuous cyclic uropod movement at 10–30 Hz with little adaptation. Two important points arise from these observations. First, the utilisation of the uropods in the vertical plane of movement is important in behaviour such as water-current orientation (Newland, 1988*b*) and one would expect proprioceptive feedback to monitor perturbations in any set posture, particularly in the dynamic resistance to water flow of the above example. Second, the rapid tail flips in escape and swimming behaviour could be effectively monitored by phasic units in all three uropod joints, because the frequency responses for adaptation exceed measured tail-flip frequencies [e.g. *Nephrops* (2.6±0.1 Hz, Newland *et al.* 1988*a*) and *Procambarus* (7–14 Hz, from data in Wine and Krasne, 1972)]. In addition, position proprioceptive feedback from the COs could enhance the rapid opening movements of the uropods which occur during the powerful flexion stroke of the tail flip. Resistance reflexes might utilise

negative feedback to prevent excessive opening of the tailfan during abdominal flexion. Similarly, during re-extension of the abdomen following the power-stroke of the swimming cycle, the uropods are held in a closed position to minimise drag (Webb, 1979). The properties of the chordotonal organs are such that they could detect drag-induced opening of the uropods towards the end of extension and generate appropriate resistance reflexes to streamline posture. The above ideas could provide guidelines for investigations of central projections and reflex pathways mediated by uropod chordotonal organs.

PLN was supported by a fellowship from the Japan Society for the Promotion of Science.

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