

A SPIKING STRETCH RECEPTOR WITH CENTRAL CELL BODIES IN THE UROPOD COXOPODITE OF THE SQUAT LOBSTER *GALATHEA STRIGOSA* (CRUSTACEA, ANOMURA)

BY D. P. MAITLAND, M. S. LAVERACK AND W. J. HEITLER

*Gatty Marine Laboratory, University of St Andrews,
St Andrews, Fife KY16 8LB Scotland*

(Received 10 March 1982 – accepted 16 June 1982)

SUMMARY

1. A proprioceptor located at the base of the uropod coxopodite in the telson of *Galathea strigosa* is described. The main component of this organ is an elastic strand in which are embedded dendrites from several neurones (approximately 11) whose cell bodies are located within the 5th (last free) abdominal ganglion. A small accessory muscle runs parallel to this strand.

2. Several afferent axons innervating the receptor conduct action potentials in a phasic manner in response to stretch.

3. Information conveyed to the CNS by the receptor causes reflex modulation of the discharge in at least two motoneurones.

4. When afferent spikes from the receptor are blocked by sucrose, reflexive discharges are still recorded in response to stretching the receptor. This suggests that certain reflexes may be mediated by transmission of graded electrotonic potentials from the uropod proprioceptor to the CNS.

5. When sensory hairs on the margins of the uropods are displaced, feedback via the nerves innervating the uropods results in efferent output to the receptor complex (elastic strand and accessory muscle). The receptor also receives bouts of efferent impulses during attempted tail-flips in a restrained animal.

INTRODUCTION

In recent years, a new class of serially homologous basal joint proprioceptors has been described in the Crustacea. These are the thoracico-coxal receptors located at the base of the legs (Alexandrowicz & Whitear, 1957; Ripley, Bush & Roberts, 1968; Bush, 1981); the receptor located at the base of the swimmerets in the crayfish (Heitler, 1982); and the proprioceptor at the base of the uropods in the Anomuran *Emerita* (Paul, 1972). In contrast to the great majority of crustacean mechanoreceptor neurones which have peripheral cell bodies and transmit information by means of action potentials, these neurones have central cell bodies and communicate by means of graded electrotonic potentials. Another crustacean proprioceptor which may also be included in this list is the oval organ, located at the base of the scaphognathites, which is innervated by three sensory neurones whose somata lie within the central

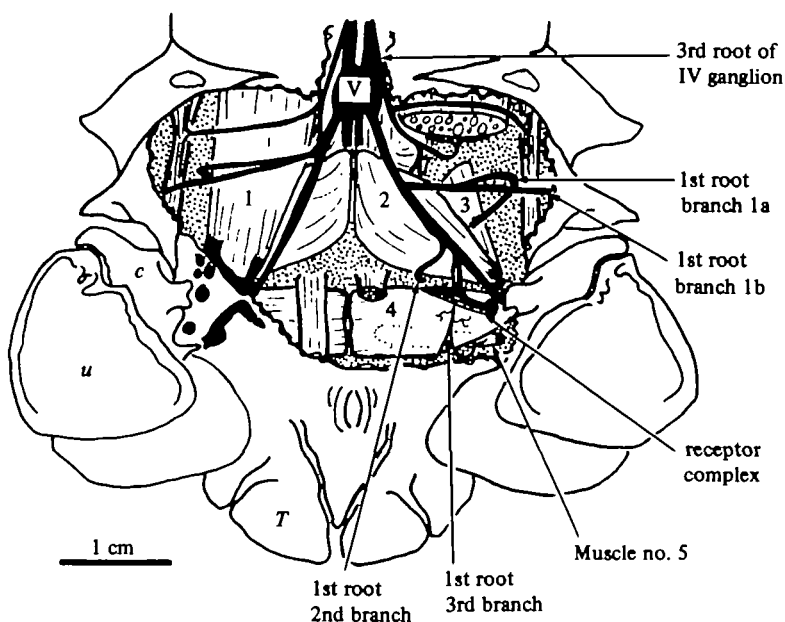


Fig. 1. A diagram of the ventral view of the terminal abdominal segments of *Galathea strigosa* with the arthrodial membrane removed. The fifth abdominal ganglion (V), muscles 1–5 of the tailfan, the uropods (u), coxopodite (c), telson (T) and receptor are labelled. See text for details. The nervous system has been relatively enlarged for clarity.

nervous system (CNS) (Pasztor, 1969, 1979). However, in contrast to those receptors mentioned earlier, the three oval organ neurones propagate electrotonic potentials and action potentials within the *same* afferent fibres (Pasztor & Bush, 1982).

In this paper we show that the receptor at the base of the uropods in the anomuran *Galathea strigosa* has an elastic strand in which are embedded several sensory neurones each with centrally located cell bodies. This receptor conducts information to the CNS by means of action potentials, and possibly also by graded electrotonic potentials.

MATERIALS AND METHODS

Innervation of the uropod proprioceptor was examined in four of the five British species of Galatheidae, *Galathea strigosa* (Linnaeus), *G. dispersa* (Bate), *G. squamifera* (Leach) and *Munida bamffica* (Pennant), using standard methylene blue staining. The uropod proprioceptor is present, and structurally similar, in all these species. Experimental studies were carried out on adult intermoult *G. strigosa*, which were obtained locally in St Andrews Bay and maintained for up to 3 months in holding tanks of circulating, aerated sea-water.

The abdomen of each animal was isolated from the cephalothorax and pinned out rigidly, ventral side up in a sculptured paraffin mould. The ventral cuticular membrane was removed from the 6th abdominal segment, exposing the muscles inserting on the uropod coxopodite and their nerve supply from the 5th (last free) abdominal ganglion (the first abdominal ganglion is fused to the thoracic CNS: Pike, 1947). The

Tergites located alongside the uropod coxopodite, to which muscles 1, 2 and 3 (Fig. 1) are attached, were isolated and the muscles removed, thus exposing the proprioceptor. Three drops of 1% methylene blue added to 100 ml lobster saline (Mulloney & Selverston, 1974) and left overnight at 5 °C gave satisfactory staining. Stained material was fixed in chilled 8% ammonium molybdate for 12 h, dehydrated and cleared for permanent mounting.

Peripheral and central projections of nerves innervating the receptor were stained with cobalt chloride. The cut ends were dipped in 0.4 M cobalt chloride and wick-filled for 24 h. The sulphide salt was precipitated by ammonium sulphide. For preparation of whole-mounts, the tissue was fixed in 4% buffered formaldehyde, dehydrated in alcohol, and cleared in methyl salicylate. For the preparation of thin sections for light microscopy, the tissue was fixed in phosphate buffered 2% osmium tetroxide, dehydrated in acetone, and embedded in Araldite: 2 µm sections were cut and stained with toluidine blue.

For physiological recordings the receptor was exposed as described above. The receptor complex (elastic strand and accessory muscle) is attached to a tergite on the ventral surface alongside the uropod coxopodite. This tergite was isolated and gripped in a pair of forceps mounted on an electromechanical transducer (Ling Dynamic Systems Ltd), driven by sinusoidal, ramp and square waveform currents. When recording the spiking characteristics of the receptor the 1st root of the 5th abdominal ganglion was severed and a polyethylene suction electrode was placed on the distal (peripheral) cut end. Identical responses were recorded whether the cut was made distally, so as to isolate the receptor nerve alone, or more proximally, close to the ganglion, thus including various other nerve axons. The latter technique was generally employed.

The experiment which revealed a possible non-spiking component employed the sucrose gap technique. A Vaseline well on a Parafilm base was constructed across the 1st root between the receptor and the 5th abdominal ganglion. A 0.568 M solution of sucrose served as a block to action potentials travelling up and down the root, but allowed the propagation of electrotonic potentials. Solutions of sucrose and saline could be flushed and replenished at will.

Function of muscles was investigated by stimulating them with brief trains of current pulses, delivered via a pair of platinum electrodes embedded in the muscle tissue.

RESULTS

Each of the species studied possesses a well-developed conventional tail fan which is normally held flexed beneath the cephalothorax. To escape or swim, the abdomen is extended and flexed in a series of rapid tail flips which propel the animal backwards. The stretch receptors which monitor the position of the uropods are located at the base of the uropod coxopodites.

Anatomy

The following description applies to *Galathea strigosa*.

Muscles

The muscles surrounding the uropod coxopodite proprioceptor have been numbered 1–5 for reference (Fig. 1).

Muscle no. 1 is a uropod–telson flexor muscle. It is inserted ventrally on a tergite located alongside the anterior rim of the uropod coxopodite, and it arises from the posterior side of a partial sternal rib at the junction between segment 5 and 6. This muscle rotates the coxopodite around its medio-lateral axis, flexing the uropods forwards, and transmitting tension to flex the telson. This muscle works in conjunction with the flexor musculature that spans the length of the abdomen, and is innervated by a branch of the 3rd root from the 4th abdominal ganglion. In two other anomurans, *Emerita* and *Blepharipoda*, the ventromedial muscle (VM) would appear to be homologous to muscle no. 1 in *Galathea* (Paul, 1981), while in crayfish the ventral rotator muscle is the homologue (Schmidt, 1915; Larimer & Kennedy, 1969).

Muscle no. 2 is an abdominal oblique muscle with its insertion on the ventral anterior margin of the uropod coxopodite. It was found to function primarily as a coxopodite flexor muscle with some adduction, causing the coxopodite to roll forwards around its medio-lateral axis while swinging inwards. Muscle no. 2 is also innervated by a branch of the 3rd root from the 4th abdominal ganglion. The crayfish homologue would appear to be the anterior oblique muscle (Larimer & Kennedy, 1969).

Muscle no. 3 lies directly beneath muscle no. 2, and originates on the anterior, medial dorsal surface of the 6th abdominal segment and inserts ventrally on the same tergite as muscle no. 2. It is innervated by branch 1(a) from the 1st root of the 5th abdominal ganglion. It causes stronger adduction of the coxopodite than muscle no. 2, but weaker flexion. Working in conjunction with each other, muscles 2 and 3 effectively cup the tail fan. In crayfish the medial remotor muscle would appear to be homologous to muscle no. 3. In *Emerita* and *Blepharipoda* the medial muscles (MR) are homologous to muscles 2 and 3 in *Galathea*.

Muscle no. 4 is a coxopodite adductor muscle. It has a large head anchored dorsally close to the midline of the posterior 6th abdominal segment. The coxopodite is flexed ventrally in a plane exactly normal to the longitudinal axis of the animal. It is innervated via branch 3 of the 1st root from the 5th abdominal ganglion. The homologue in *Emerita* and *Blepharipoda* is the dorso medial muscle (DM).

Muscle no. 5 is a coxopodite adductor muscle which appears to be accessory to muscle no. 4. In *Emerita* and *Blepharipoda* the homologue is the lateral muscle (LA). Muscle no. 5 inserts on a very small tergite in the ventral arthrodivial membrane on the posterior lateral margin of the uropod coxopodite and arises from the anterior dorsal surface of the telson, close to the midline. It runs nearly parallel to muscle 4, and is innervated via the 3rd branch of the 1st root from the 5th abdominal ganglion. Its main function seems to be to control the posterior region of the coxopodite.

In contrast to muscles 1–4, which are all fast (or phasic) muscles with short sarcomeres 2–5 μm in length, muscle 5 is a slow (or tonic) muscle with long sarcomeres 8–10 μm in length. It responds with slow contractions to constant-frequency stimulation and fails to respond to single shocks.

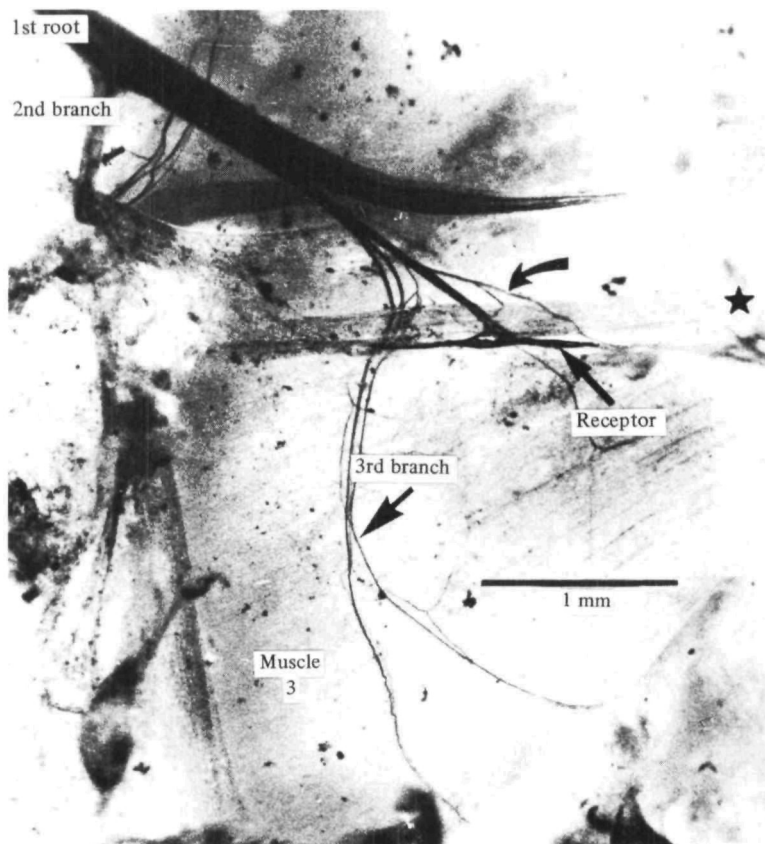


Fig. 2. A methylene-blue stain of the receptor and associated structures in *G. strigosa*. The star shows the posterior insertion on a tergite close to the coxopodite. The curved arrow shows a nerve, possibly a single axon, which innervates both the receptor and accessory muscle.

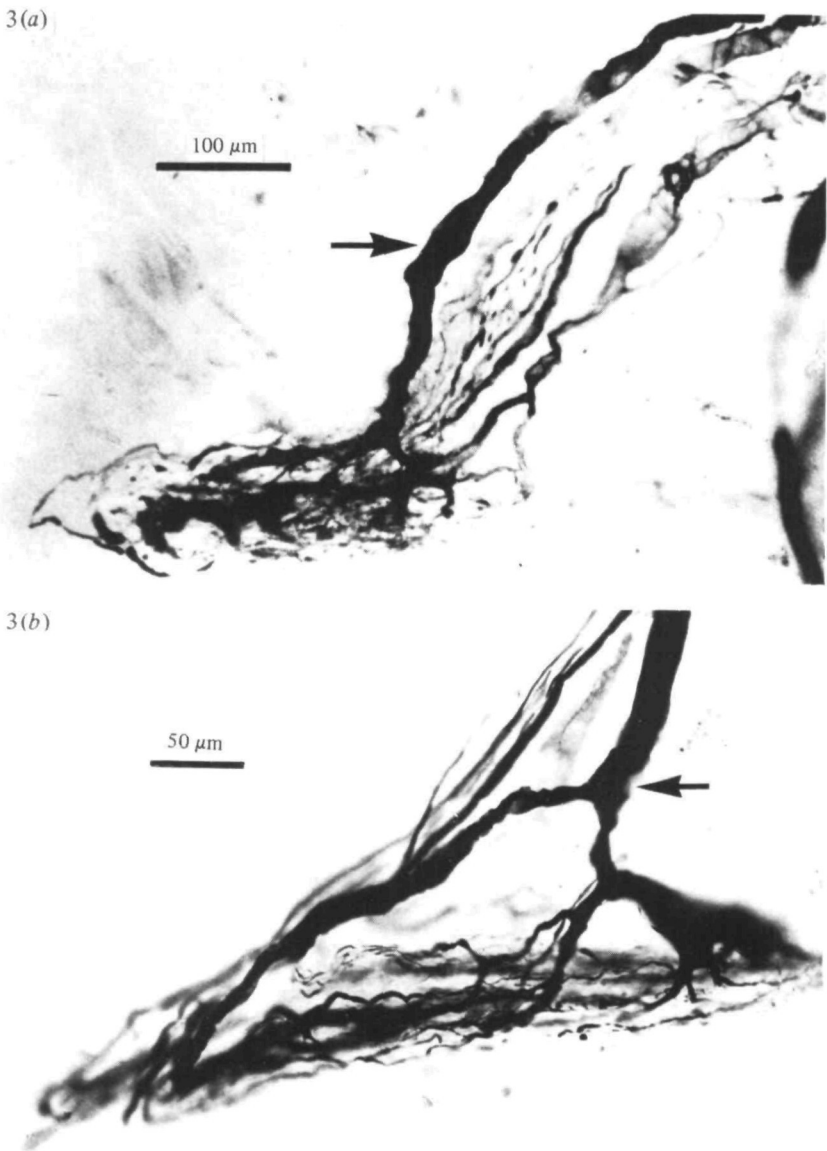
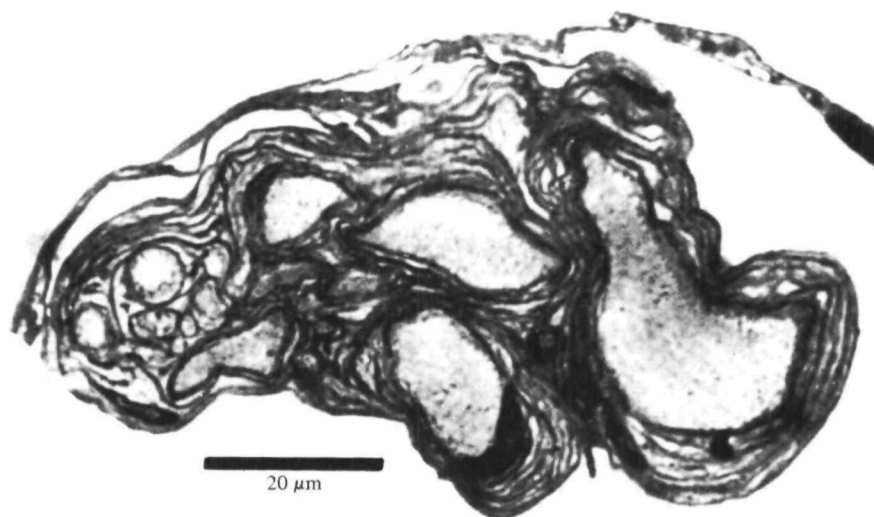


Fig. 3. Two examples of cobalt sulphide stains showing the innervation of the receptor. One of the axons consistently stains more intensely than the others (arrows) (from *G. strigosa*).



4

Fig. 4. Cross-section ($2\ \mu\text{m}$) taken immediately proximal to the elastic strand of the nerve innervating the receptor alone, stained with toluidine blue. This contains the afferent axons innervating the elastic strand, and may also contain efferent innervation of the receptor complex (elastic strand and accessory muscle) (from *G. strigosa*).

Receptor complex

The receptor complex was similar in all the species of Galatheidæ examined and consisted of an elastic strand, an accessory muscle, and their combined innervation. It lies sandwiched between the uropod-telson flexor muscle (no. 1) (lying ventral to the receptor) and the coxopodite adductor muscle (no. 4) (lying dorsal to the receptor) (Fig. 1). The receptive component of the complex is an elastic strand which stretches from its posterior lateral insertion on a small calcified tergite, adjacent to the medio-ventral rim of the uropod coxopodite, to an anterior medial insertion point on the anterior mid-dorsal hinge in the middle of the 6th abdominal segment, a distance of 2–3 mm in animals with a carapace length of 4–5 cm.

The orientation of the receptor is such that promotion and/or abduction of the coxopodite stretches the receptor, while remotion and/or adduction relaxes it. Parallel to, and, in many cases, sandwiching, the elastic strand are a pair of small muscle bundles, each 100–150 μm in diameter, which have insertion points common to those of the elastic strand (Fig. 2). This receptor accessory muscle has long sarcomeres (8–10 μm in length) and is presumably a slow (or tonic) muscle.

The elastic strand is innervated via the 3rd branch of the 1st root from the 5th abdominal ganglion. This branch also carries motor nerves to the accessory muscle and surrounding musculature of the uropods and uropod coxopodite. One of the motor nerves innervating the elastic strand also innervates the accessory muscle (Fig. 2). In some preparations an axon has been observed which branches to innervate the receptor accessory muscle and the accessory coxopodite adductor muscle (no. 5). Wick-fillings with cobalt down the nerve which supplies the receptor, reveals a complex innervation of the elastic strand (Fig. 3). Three large axons (one of which consistently stains more intensely than the other two) 20–30 μm in diameter, and approximately eight smaller axons < 15 μm in diameter, arrive at the elastic strand approximately midway along it. These neurones divide into a network of dendritic arborizations some of which travel a short distance ($\approx 200 \mu\text{m}$) towards the anterior insertion of the strand, before they loop back upon themselves, while the remainder follow the strand towards its posterior ventral insertion on the uropod coxopodite ($\approx 1000 \mu\text{m}$) (Fig. 3a). None of the neurones innervating the receptor has a cell body in the periphery.

Cross-sections of the nerve immediately proximal to the elastic strand reveal at least 11 axon profiles (Fig. 4). The larger axons are ensheathed in several layers of glial cells. Central wickfills of this nerve usually reveal 11 cell bodies 10–40 μm in diameter arranged in tandem in the posterior lateral margin of the 5th abdominal ganglion (Fig. 5). In the example shown in Fig. 5, three of the cell bodies are located in the head of the 1st root. The occurrence of cell bodies within the proximal regions of ganglionic roots is relatively common elsewhere in *Galathea*. The dendritic region of the 11 neurones is spread out over a considerable distance ($\approx 800 \mu\text{m}$) along the root, and there appear to be three specific regions which have more extensive neuropil than the rest. In general these neurones show the characteristic restricted dendritic arborizations which seems to be a common feature of sensory neurones possessing central cell bodies in invertebrates (Paul, 1972; Bush, 1976; Bräunig & Hustert, 1980; Bitler, 1982).

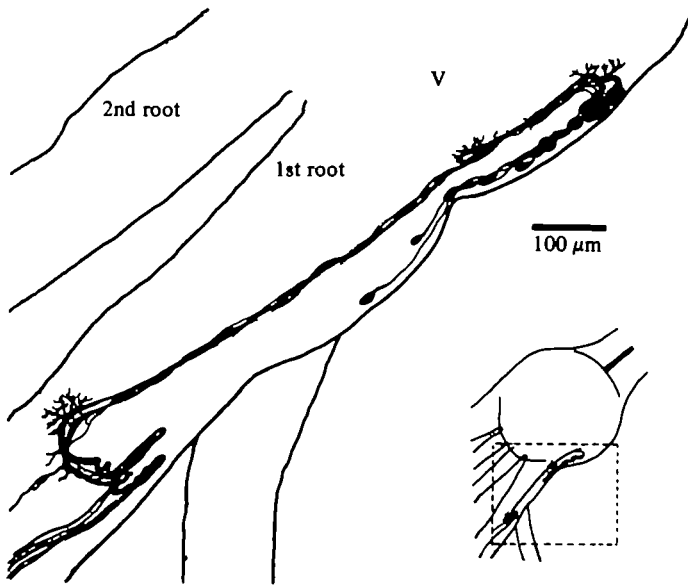


Fig. 5. Cobalt stain introduced into the receptor nerve of *G. strigosa* cut immediately proximal to the elastic strand showing the central anatomy of the receptor innervation. The inset shows the position within the whole ganglion. See text for details.

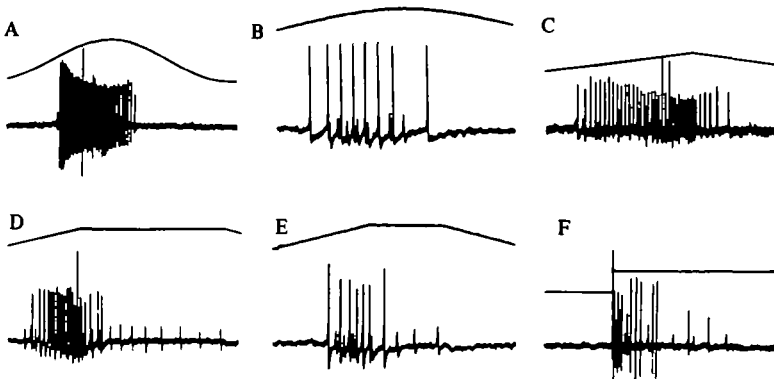


Fig. 6. Afferent units recorded from the receptor of *G. stringosa* isolated from the central nervous system by cutting the first root. The drive applied to the electromechanical transducer (upper trace, stretch upwards) and the sensory response (lower trace) are shown for various forms of stretch. Records are shown from four preparations: A + B, C, D + E, F. Note trace A is a similar waveform to B, but at higher stretch and slower time base. Similarly D and E. Total stretch A, D and F, 0.75 mm; B, E and C, 0.5 mm. Duration of record; A, D and F, 1 s; C, 250 ms; B and E, 500 ms.

Physiology

(1) *Spike transmission.* Actively propagated action potentials were recorded by suction electrodes on the cut 1st root of the 5th abdominal ganglion in response to various forms of stretch of the elastic strand. A length increase of about 20% from a relaxed state is sufficient to cause several units to fire with phasic or phasico-tonic

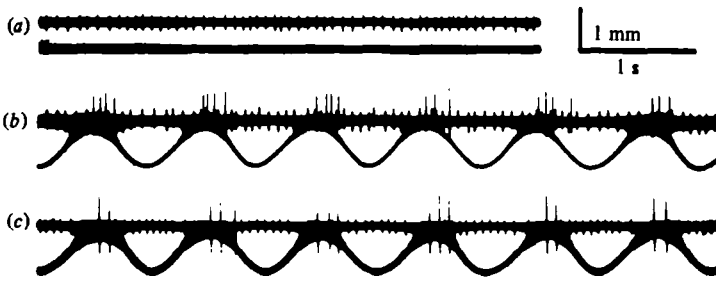


Fig. 7. Reflex efferent units (upper trace) recorded from branch 3 of the first root, innervating muscles 4 and 5, in response to stretching the receptor (monitor lower trace, increased stretch upwards). (a) Tonic activity with the receptor relaxed. (b) Recruitment of a large phasic unit. The small tonic unit shows a slight increase in frequency at peak stretch. (c) Later in the same experiment, recruitment of the phasic unit with concurrent inhibition of the tonic unit (from *G. strigosa*).

response characteristics (Fig. 6). These afferent units can be recorded after all nerves other than those innervating the elastic strand have been cut, but a more intact preparation was usually used, since no difference could be detected. There is no 'off' response on relaxation of the receptor.

(2) *Reflexes*. Stretching the receptor causes reflex modulation of the discharge of at least two motoneurons. The frequency of one motoneuron is always increased by stretch, while that of the other is sometimes increased and sometimes decreased (Fig. 7). This reflex reversal (Bässler, 1976), can take place within the course of a single experiment, but its significance is unknown. The motoneurons have axons in branch 3 of the 1st root, which innervates the coxopodite adductor muscles nos. 4 and 5. Contractions of these muscles counteract forces that elongate the proprioceptor.

(3) *Non-spiking transmission*. The apparent homology between this spiking proprioceptor and the non-spiking proprioceptor in *Emerita* (Paul, 1972) led us to investigate possible non-spiking modes of transmission. Reflexes evoked by stretching the proprioceptor were recorded by hook electrodes placed on the 1st root close to the ganglion. These electrodes also recorded spikes propagated from the receptor to the ganglion (Fig. 8a). A sucrose gap was then placed on the 1st root distal to the electrodes but proximal to the receptor. This blocked afferent spikes (including those from the receptor), and thus all spikes recorded in this situation arose from centrally mediated activity. Stretching the receptor modulated this central activity, indicating that a reflex arc was still present (Fig. 8b). Cutting the 1st root proximal to the electrodes (thus abolishing centrally mediated activity) induced a vast discharge, followed by a small response which completely disappeared after two or three cycles. It seems likely that this was a transitory injury effect. No further spikes were recorded, indicating that the sucrose gap had effectively blocked afferent spikes (Fig. 8c, d). On replacing the sucrose with saline, afferent discharge resumed (Fig. 8e).

These results suggest that certain reflex discharges in response to stretching the uropod proprioceptor are maintained even after blocking spikes from the receptor. It seems reasonable to propose that these reflexes are mediated by transmission of non-spiking information from the uropod proprioceptor to the CNS.

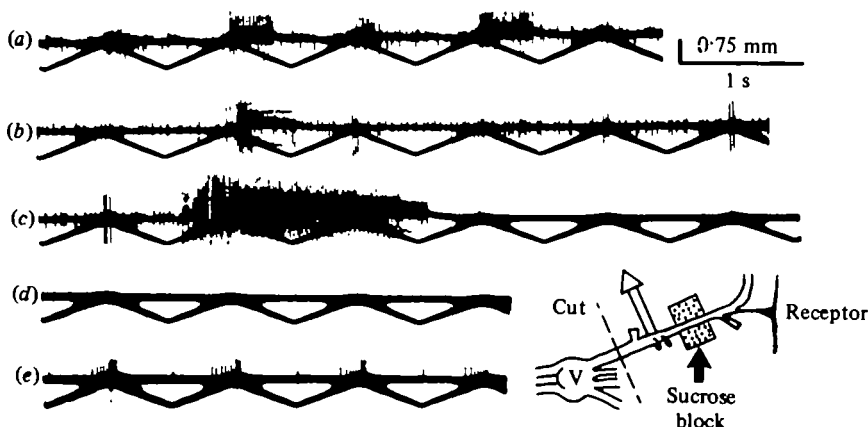


Fig. 8. Evidence for a non-spiking component in the receptor response. (a) Recordings from the first root close to the ganglion (upper trace) show efferent reflex activity in response to stretching the receptor (monitor, lower trace, increased stretch upwards). Afferent spikes similar to trace (e) are present but barely visible at this gain. (b) A sucrose gap across the nerve distal to the electrode blocks afferent spikes (as in trace (d)) but the efferent spikes remain. Only the 1st branch of the 1st root is proximal to the sucrose block, and this has been cut. Both the 2nd roots and the contralateral 1st root have also been cut. (c) Cutting the 1st root proximal to the electrode causes an injury discharge and (d) abolishes further spikes. (e) Afferent activity is once more recorded when the sucrose is replaced with saline after about 5 min. The inset shows the experimental arrangement. See text for details. Results shown are from a single experiment, but similar results were obtained from at least 5 preparations (from *G. strigosa*).

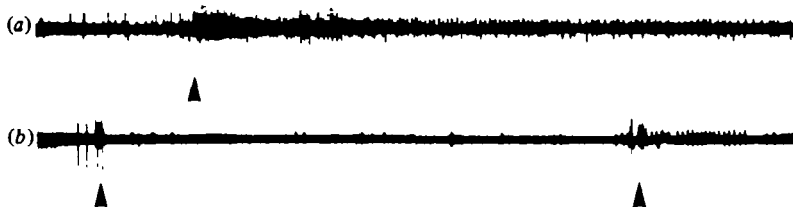


Fig. 9. Efferent activity recorded in the cut nerve innervating the receptor complex. (a) Touching the uropod hairs (arrow). (b) Spontaneous activity during two restrained tail-flips (arrows). Total duration of each trace: 6 s (from *G. strigosa*).

(4) *Efferent innervation of the receptor.* As well as conveying afferent information to the CNS, the receptor complex also receives efferent impulses from it. Efferent input to the receptor can be recorded in response to tactile stimulation of the ipsilateral uropod (Fig. 9a); this response is abolished by cutting the nerve carrying sensory information from the uropod hairs. The receptor also receives bursts of efferent impulses during attempted tail-flips in a restrained animal (Fig. 9b). The function of the efferent information to the proprioceptor is unknown, but the receptor muscle has occasionally been observed to contract in response to tactile stimulation of the uropods, and during restrained tail-flips.

DISCUSSION

The uropod proprioceptor described here is a member of a group of special Decapod crustacean sense organs that are almost certainly homologous, and whose primary sensory neurones possess cell bodies located within the central nervous system (CNS). This group includes the coxal receptors, *Emerita* uropod proprioceptor, the oval organ, and the swimmeret receptor in crayfish. The oval organ propagates both graded and action potentials in response to stretch, while the others all propagate graded electrotonic potentials.

The uropod proprioceptor in *Galathea strigosa* is located within the telson, spanning the thoracic-coxal joint. It is composed of an elastic strand in which are embedded dendritic arborizations of about 11 monopolar neurones whose cell bodies are located within the 5th (last free) abdominal ganglion. No cell bodies are present within the receptor complex itself. At least one of the nerves innervating the elastic strand also innervates the adjacent accessory muscle, and is thus probably efferent, but its function is unclear at present.

At rest *Galathea* holds its tail in a flexed position beneath the cephalothorax. The first part of the tail-flip cycle is abdomen extension (equivalent to the return-stroke in lobsters and crayfish). During this phase the uropods are folded, presenting minimal resistance to movement, and the receptor is relaxed. At the end of the return-stroke, however, the uropods are flicked open causing the proprioceptor to be suddenly stretched. During the power-stroke the uropods remain spread and the coxa rotates forwards to maintain maximal surface area perpendicular to the movement vector.

An approximation to the stimulus resulting from the sudden opening of the uropods can be achieved experimentally by stretching the receptor rapidly with a ramp pulse. The afferent spiking response of receptor units to this stimulus is phasic, and lacks an 'off' (or relaxation) response. It is likely that the phasic group of units recorded during stretch are responsible for signalling the initial dynamic phase when the uropods are opened. Later they may monitor any change in length of the receptor during the power-stroke, when the uropods remain spread and it is important to maintain an optimum angle of attack to the water in order to develop maximum thrust. Efferent input to the receptor has been recorded in response to tactile stimulation of uropod hairs. These hairs are displaced by the resistive forces of the water during the tail-flip, and may thus cause efferent input to the receptor. The function of this input is not known.

When afferent spikes are blocked by a sucrose gap, reflexes in response to stretching the receptor are still observed. This implies that some of the information conducted from the receptor to the CNS takes the form of graded electrotonic potentials. It is not known whether the same neurones conduct both graded electrotonic potentials and action potentials (as in the oval organ: Pasztor & Bush, 1982) or whether the different modes of conduction occur in different neurones. At present the exact destination of the reflexes is unknown. They are not identical to those observed without the block, but this is not surprising since the spiking afferents from the receptor, and unrelated tonic spiking afferents from the periphery, have been eliminated.

In order to overcome the inherent problems of faithfully relaying information via

graded potentials over long distances (1 cm or more in *Galathea*, as much as 2 cm in *Munida bamffica*), without suffering heavy conduction losses, the axons involved commonly have large diameters, high length and time constants and a high specific membrane resistance. At the periphery non-spiking axons in *Emerita* are 45–50 μm in diameter (Paul, 1972), in crayfish these are 50–60 μm (Heitler, 1982) and 40–70 μm in *Carcinus* (Bush, 1981). Of the 11 neurones innervating the receptor in *Galathea* three have larger diameters than the rest (20–30 μm) and thus become obvious candidates for non-spiking conduction; however, in the barnacle lateral ocellus sensory axons 5–20 μm in diameter conduct electrotonically over distances of up to 11 mm (Shaw, 1972), and hence the smaller diameter neurones cannot be ruled out.

Non-spiking transmission has an advantage in that it provides a more smoothly graded output signal than can be achieved by the same number of spiking units (Pearson, 1976). A disadvantage of the non-spiking stretch receptors, however, is that their long time constant (e.g. 100–200 ms in crab coxal receptors: Mirolli, 1979a) reduces the high frequency response of the conducting fibre. In non-spiking receptors described previously this characteristic has not been limiting since the receptors all occur at the bases of limbs which are not used in high frequency movements. In *Galathea*, however, the receptors monitor the movement of the uropods which are rapidly opened in the tail-flip escape response. Non-spiking transmission may not be adequate to monitor this rapid movement. By combining spiking afferent neurones together with non-spiking afferents, any differences in one system can be made up by the other. Thus the spiking component is well suited to signalling the rapid dynamic phase, when the uropods are flicked open at the end of abdomen extension, while the non-spiking component could mediate exact stretch reflexes to the muscles controlling posture during periods of inactivity, and in co-ordinating the uropods during the power-stroke. In this context it is perhaps significant that the homologous proprioceptor in *Emerita* is entirely non-spiking, and *Emerita* does not perform the rapid tail-flips characteristic of *Galathea*.

This work was supported in part by S.R.C. Grant no. GR/B/42763 to Dr W. J. Heitler.

REFERENCES

- ALEXANDROWICZ, J. S. & WHITEAR, M. (1957). Receptor elements in the coxal region of Decapod crustacea. *J. mar. biol. Ass. U.K.* **36**, 603–628.
- BÄSSLER, U. (1976). Reversal of a reflex to a single motoneuron in the stick insect *Carausius morosus*. *Biol. Cybernetics*, **24**, 47–49.
- BRAUNIG, P. and REINHOLD, H. (1980). Proprioceptors with central cell bodies in insects. *Nature Lond.* **283**, 768–770.
- BUSH, B. M. H. (1976). Non-impulsive thoracic-coxal receptors in crustaceans. In *Structure and Function of Proprioceptors in the Invertebrates* (ed. P. J. Mill), pp. 115–51. London: Chapman & Hall.
- BUSH, B. M. H. (1981). Non-impulsive stretch receptors in crustaceans. In *Neurons without Impulses* (ed. A. Roberts and B. M. H. Bush), Seminar Series, no. 6, pp. 147–176. Cambridge University Press.
- HEITLER, W. J. (1982). Non-spiking stretch-receptors in the crayfish swimmeret system. *J. exp. Biol.* **96**, 355–366.
- LARIMER, J. L. and KENNEDY, D. (1969). Innervation patterns of fast and slow muscle in the uropods of Crayfish. *J. exp. Biol.* **51**, 119–133.
- MIRROLI, M. (1979a). The electrical properties of a crustacean sensory dendrite. *J. exp. Biol.* **78**, 1–27.
- MULLONEY, B. & SELVERSTON, A. I. (1974). Organization of the stomatogastric ganglion of the spiny lobster. I. Neurones driving the lateral teeth. *J. comp. Physiol.* **91**, 1–32.

- PASZTOR, V. M. (1969). The neurophysiology of respiration in decapod crustacea. II. The sensory system. *Can. J. Zool.* 435-441.
- PASZTOR, V. M. (1979). The ultrastructure of the oval organ: a mechanoreceptor in the second maxilla of Decapod crustacea. *Zoomorphologie* 193, 171-191.
- PASZTOR, V. M. & BUSH, B. M. H. (1982). Impulse-coded and analog signalling in single mechanoreceptor neurons. *Science, N.Y.* 215, 1635-1637.
- PAUL, D. H. (1972). Decremental conduction over 'giant' afferent processes in the arthropod. *Science N.Y.* 176, 680-682.
- PAUL, D. H. (1981). Homologies between neuromuscular systems serving different functions in two decapods of different families. *J. exp. Biol.* 94, 169-187.
- PEARSON, K. G. (1976). Nerve cells without action potentials. In *Simpler Networks and Behaviour* (ed. J. C. Fentress), pp. 99-110. Sutherland, Massachusetts: Sinauer Associates.
- PIKE, R. B. (1947). *Galathea*. L.M.B.C., memoirs XXIV. Liverpool University Press.
- RIPLEY, S. H., BUSH, B. M. H. & ROBERTS, A. (1968). Crab muscle receptor which responds without impulses. *Nature, Lond.* 218, 1170-1.
- SCHMIDT, W. (1915). Die Muskulatur von *Astacus fluviatilis* (*Potamobius astacus* L.): ein Beitrag zur Morphologie der Decapoden. *Z. wiss. Zool.* 113, 165-251.
- SHAW, S. R. (1972). Decremental conduction of the visual signal in barnacle lateral eye. *J. Physiol., Lond.* 220, 145-175.