

THE NERVOUS CONTROL OF LIMB AUTOTOMY IN THE HERMIT CRAB *PAGURUS BERNHARDUS* (L.) AND THE ROLE OF THE CUTICULAR STRESS DETECTOR, CSD₁

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SUMMARY

Limb autotomy results from the fracture of a preformed breakage plane within the second limb segment. Fracture is produced by the contraction of the large anterior levator (AL) muscle at the same time as its synergist, the posterior levator (PL) muscle. The AL force is thus directed on to a small portion of the breakage plane; withdrawal of this plug initiates cuticular fracture. Autotomy is a response to damage inflicted on the limb. In the absence of sensory information from the second limb segment there is less activity in the units serving the PL. It is shown that stimulation of the sense organ, cuticular stress detector one, provides feedback to PL motor neurones. The feedback is an integral part of the nervous control of limb autotomy.

INTRODUCTION

Autotomy has been most frequently studied in crustacean limbs. In the Crustacea the limb is shed at the second limb segment, the basi-ischiopodite (BI), by separation along a preformed breakage plane which encircles the segment. Fracture is initiated by a powerful contraction of the anterior and larger of the two BI levator muscles (Fredericq, 1892; McVean, 1973, 1974; Moffett, 1975). This anterior levator (AL) muscle also provides the main levatory force for the limb during locomotion. For locomotion, the force generated by the muscle is spread around the dorsal rim of the BI; for autotomy, it is concentrated on to a cuticular plug which forms the only firm connexion across the breakage plane and whose withdrawal initiates cuticular fracture (McVean, 1973, 1974; Moffett, 1975; McVean & Findlay, 1976).

Force deployment of the AL depends upon the orientation of a cuticle block which is interposed between the AL tendon blade and the BI and is flexibly linked to both. A ventral projection from this tendon head abuts on to the dorsal rim of the BI (Moffett, 1975; McVean & Findlay, 1976). The abutting faces are separated when the tendon head is rotated by the contraction of the posterior levator (PL) muscle. McVean (1973, 1974) has proposed that in *Carcinus* force generated by the AL is spread when the faces are closed and concentrated when they are opened by contraction of the PL. Moffett (1975) has proposed the opposite for *Cardisoma*: that autotomy is achieved when the PL allows the faces to close. McVean & Findlay (1976) explained this difference of opinion by showing that in brachyuran crabs such

as *Carcinus* and *Maia* the posterior levator muscle is split into two anatomically and physiologically distinct entities. McVean & Findlay (1976) also showed that force concentration and thus limb autotomy result when the PL tendon rotates against the AL tendon head, separating the head from the BI, as suggested by McVean (1974).

In the anomuran *Pagurus bernhardus* the posterior levator muscle is not divided into two. The experiments described here examine the coordination of the anterior and posterior levator muscles in *Pagurus* during autotomy, and the role of cuticular stress detector one (CSD₁). The latter sense organ is situated between the insertion of the anterior levator muscle and the cuticular plug; it responds to strains imposed upon the dorsal cuticle of the BI by contraction of the AL, and evokes reflex activity in the PL (Wales, Clarac & Laverack, 1971; Clarac, Wales & Laverack, 1971; Moffett, 1975). Clarac & Wales (1970) proposed two possible actions for CSD₁ induced reflexes in *Carcinus*. Their first hypothesis, subsequently taken up by McVean (1974) and McVean & Findlay (1976), stated that the reflex activity serving the PL, observed when tension is applied by the AL, is utilized by the animal to maintain PL tendon rotation and thus AL force concentration on to the cuticular plug. The second alternative was adopted by Moffett (1975) and stated that the CSD₁-PL reflex acts to prevent accidental autotomy by spreading excess strains imposed by the AL around the BI, but is centrally inhibited by limb injury to allow autotomy to occur.

MATERIALS AND METHODS

Experiments were carried out at the Plymouth Laboratory of the Marine Biological Association (U.K.) upon fresh *Pagurus bernhardus* (L.).

Preparations. These were dissected preparations (Fig. 1) except where stated. The animal was secured, ventral surface upwards, on a Perspex plate by rubber straps across the cephalothorax and abdomen. The experimental limb, usually the third left pereopod, was held in a Palmer tendon clamp; other limbs were immobilized by elastic bands. The limb was rotated so that its anterior face was uppermost, and the BI levator musculature and innervation were exposed by dissection. The preparation was continuously perfused with cool sea water.

In the dissected preparation autotomy does not occur, but the activity of levator muscle motor neurones following stimulation of the limb can be obtained from their peripheral axons.

Recording techniques. Extracellular myograms from the BI levator muscles were obtained with paired 50 μm diameter steel wire electrodes, Trimel coated except for the tip (Johnson Matthey Metals Ltd, London). They were placed on the relevant muscles through pin holes drilled in the coxa. Intracellular recordings from posterior levator muscle fibres were obtained with 5–15 M Ω glass microelectrodes filled with 3 M-KCl. During intracellular recordings the preparation was perfused with cool sea water. Nerve recordings were obtained with suction electrodes. Signals were amplified and displayed conventionally.

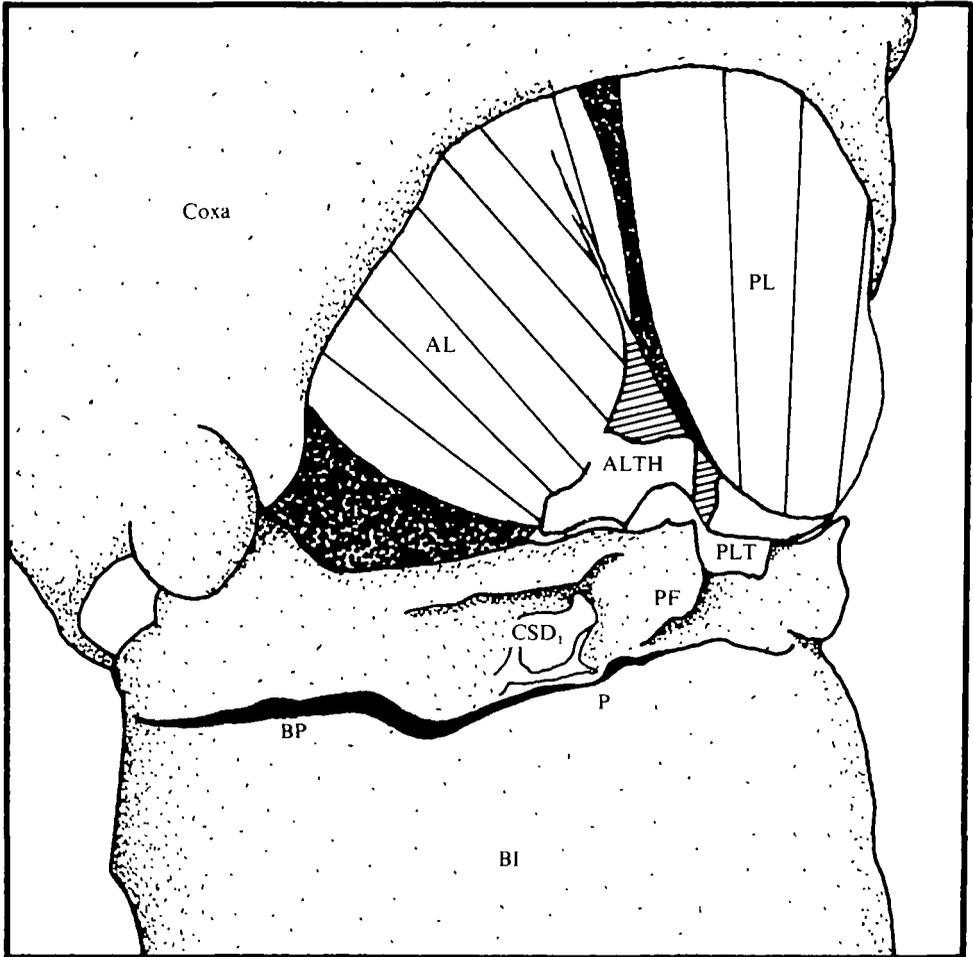


Fig. 2. The breakage plane region of the third left pereiopod of *Pagurus bernhardus*. A drawing of the anterior-dorsal face of the proximal region of the BI, showing the cuticular plug spanning the preformed breakage plane, with the levator muscles, their tendons and insertions. ALTH, Cuticle block forming the anterior levator muscle tendon head; P, cuticular plug spanning the breakage plane; PF, Paul's Furrow; PLT, posterior levator muscle tendon. Other labels as Fig. 1.

projection has no connexion with the breakage plane (Fig. 3). McVean & Findlay (1976) described the same structure in *Carcinus* and suggested that it functions as an energy store, being deformed when the AL contracts isometrically. Between the AL tendon head and the BI, in the anterior region of the AL insertion, are found ventral projections as in *Cardisoma* (Moffett, 1975) (Fig. 3). Forces transmitted through these projections do not act upon the cuticular plug, as suggested by Moffett (1975) for *Cardisoma*, but are transmitted into the cuticular projection (Fig. 3a). In *Carcinus* the forces are absorbed by deformation of the cuticular ridge (McVean & Findlay, 1976). The posterior portion of the AL insertion is the cuticular plug whose withdrawal initiates fracture of the breakage plane (Fig. 3).

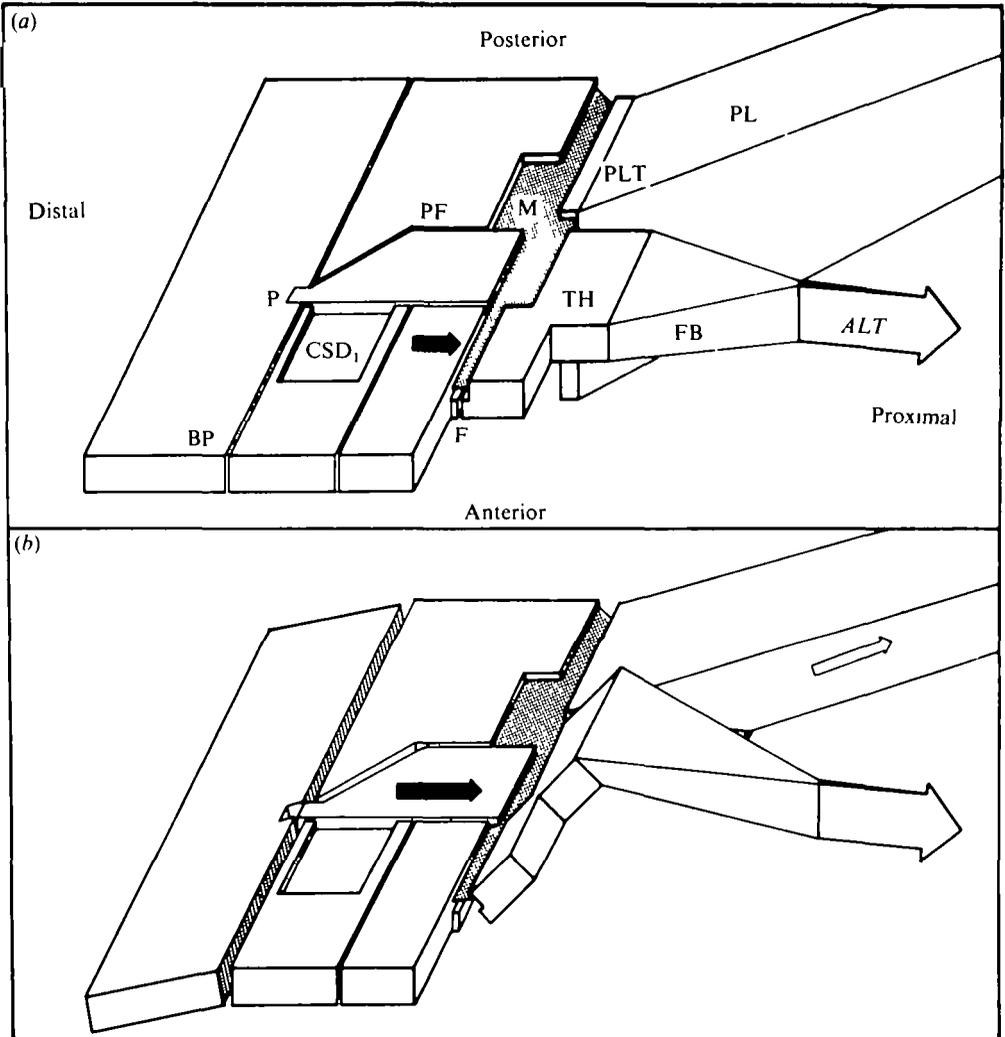


Fig. 3. A diagrammatic representation of the dorsal rim of the basi-ischiopodite of *Pagurus*, showing cuticular structure, levator muscles and tendons, and their interactions during locomotion and autotomy.

(a) During normal locomotion the anterior levator muscle would shorten as the BI levates about the coxa-BI articulation and little strain would be imposed upon the dorsal BI cuticle. If the limb met an external resistance, contraction of the anterior levator may approach an isometric state, and in such circumstances tension would be exerted by the anterior levator on to the dorsal rim of the BI via the closed abutting faces (F) into the cuticle ridge region of the dorsal BI (solid arrow). The large open arrow indicates contraction.

(b) The posterior levator muscle tendon hangs perpendicularly in the limb and muscle fibres originating dorsally in the coxa insert only on to the proximal face of the tendon, so that muscle contraction results in the rotation of the tendon blade around its attachment to the BI (small open arrow). Rotation of PL tendon causes rotation of the AL tendon head and opening of the abutting faces. Thus force exerted by AL contraction would be directed on to the wedge of cuticle bordered anteriorly by the soft membrane overlying CSD₁, posteriorly by Paul's Furrow, and distally by the plug which forms the connection across the breakage plane (P). The concentration of AL force on to this plug (solid arrow) causes a shearing along Paul's Furrow and the withdrawal of the plug to initiate fracture of the whole breakage plane.

ALT, Anterior levator tendon (the muscle fibres have been removed for clarity); F, abutting faces situated ventrally between the AL tendon head and the cuticle ridge in the dorsal rim of the BI; FB, flexible band of cuticle between AL tendon head and AL tendon which allows rotation of the tendon head without disruption of the mechanical advantage of AL muscle fibre contraction; M, articulation membrane attaching levator muscle tendons to the BI; PLT, posterior levator tendon. Other labels as Fig. 1.

Fig. 3 shows how the posterior levator muscle can influence the forces exerted upon the dorsal rim of the BI by contraction of the AL.

Autotomy

The natural stimulus for autotomy is probably limb damage caused by crushing. The most effective stimulus in dissected preparations is to cut the main limb nerves peripheral to the BI, causing a violent and sustained firing of axons within them.

In intact restrained animals, myograms recorded from the BI levators during autotomy caused by crushing the limb reveal that both levators fire in response to limb injury and that both are firing up to the moment of autotomy (Fig. 4*a*). The recruitment of the PL contrasts with the inhibition recorded for *Cardisoma* by Moffett (1975). In the present study, the PL was shown to be active not only by the myograms but also by the visual observation that the PL tendon rotated. It was usually impossible to distinguish different types of activity in the myograms. However, in the first section of Fig. 4(*a*) it is possible to differentiate the two units which supply the PL (Fig. 7).

Recording the injury responses of the motor neurones serving the BI levators in dissected preparations revealed a different picture (Fig. 4*b*). The suppression of firing in PL units after the initial stimulation caused by injury was unexpected following the muscle's maintained response to injury shown in Fig. 4(*a*). Further experiments showed this response to be a centrally determined programme initiated by peripheral injury, being observed when either AL nerve or AL tendon was severed and peripheral feedback from any sense organs situated in the BI prevented. This would explain why it was not observed in the intact animal.

Sensory reflexes

Two sense organs are found in association with the dorsal rim of the BI: the coxa-BI chordotonal organ (CB), and the more proximal of the two cuticular stress detectors (CSD₁).

The CB chordotonal organ spans the coxa-BI articulation, originating in the dorsal coxa and inserting on the dorsal rim of the BI between the insertions of the two levator muscles (Fig. 1). It responds to the movement, velocity, and position of the BI relative to the coxa (Bush, 1965*a*) and elicits resistance reflex responses from motor neurones serving the BI musculature (Bush, 1962, 1965*b*). In the dissected preparation of *Pagurus*, one unit serving the PL usually fires tonically (Fig. 5*a*). When the CB strand is stretched, a resistance reflex response is elicited from one or sometimes two units in the AL nerve, while the PL tonic unit increases its firing frequency (Fig. 5*a*).

The window of soft membrane to which is attached the strand bearing the sensory somata of CSD₁ is situated between the insertion of the anterior levator and the cuticular plug connexion across the breakage plane (Figs. 2, 3). The response from CSD₁ varies according to the strain imposed upon the dorsal rim of the BI by contraction of the anterior levator (Clarac *et al.* 1971; Moffett, 1975). Discrete distortion of the soft membrane with a probe (Clarac *et al.* 1971) stimulates CSD₁ and also evokes reflex activity of a new unit in the PL (Fig. 5*b, c*). The tonic unit is usually inhibited, but occasionally may be reflexly excited alongside the new unit.

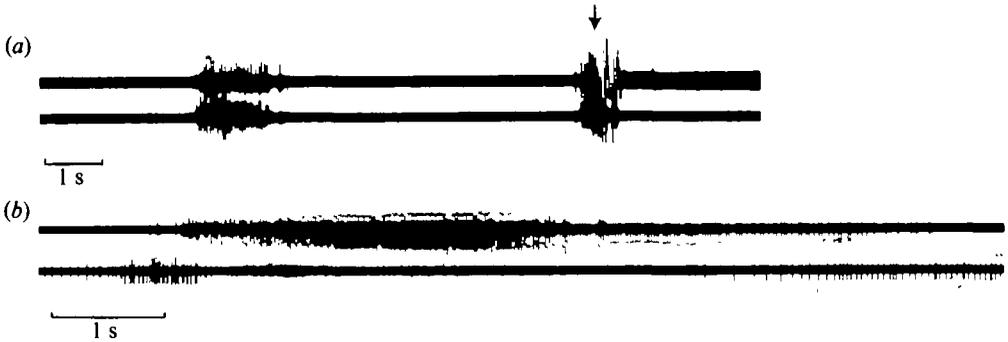


Fig. 4. Motor unit responses to limb injury.

(a) Extracellular recordings from the BI levator muscles during an ineffectual and an effective attempt to evoke autotomy by crushing the limb. After the moment of autotomy (arrowed) the electrodes in the posterior levator were removed by the dorsal rotation of the retained BI stump. Note that during both responses, the posterior levator (upper trace) is active in addition to the anterior levator (lower trace).

(b) Centrally determined responses of BI levator motor neurones to injury of the peripheral limb (arrowed). Anterior levator units (upper trace) respond with a sustained burst of firing. In the posterior levator nerve (lower trace), on the other hand, both units, after a short burst, are silenced until the background frequency of the tonic unit returns as ALN's burst fades. A small unit appears to fire throughout the silent period in PLN, which probably results from artifactual crosstalk with electrical activity in the anterior levator muscle.

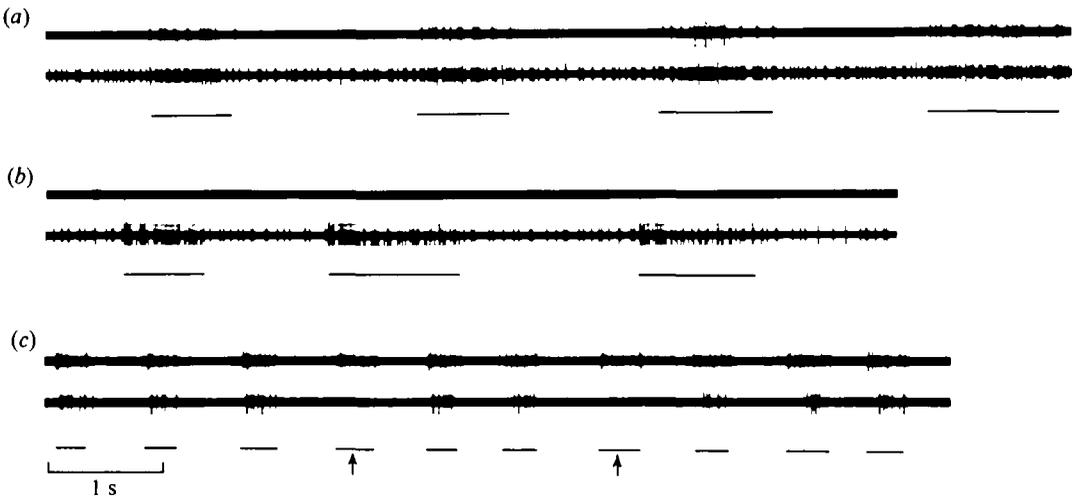


Fig. 5. Sensory reflexes evoked in levator motor units. Recordings in pairs: upper trace, AL nerve; lower trace, PL nerve. Bars represent period of stimulation.

(a) Manually stretching the strand of the chordotonal organ CB elicits the resistance reflex responses described by Bush (1962). A unit is already firing at a low tonic rate in the PL nerve and increases its firing frequency on stretching CB.

(b) Manually stimulating the CSD₁ membrane with a probe elicits firing in a new unit in the posterior levator nerve. No response is recorded in the anterior levator nerve. Same preparation as (a).

(c) In a preparation lacking the tonic unit in the posterior levator, the other unit responsive to CSD₁ stimulation can be seen in isolation, with simultaneous recording from the CSD₁ afferent nerve. On a number of occasions (arrowed) what appear to be adequate stimulations of CSD₁ (see text) fail to elicit a reflex response from the unit in the PL nerve.

In the anterior levator, no response to CSD₁ stimulation can be recorded (Fig. 5*b*) but responses can be recorded to stretching CB (Fig. 5*a*). The new unit in the PL, together with the response of the whole CSD₁ nerve resulting from manual pressure applied to the soft membrane, is illustrated in Fig. 5*c*, in a preparation lacking the tonic unit. Clarac *et al.* (1971) noted that different CSD₁ units fired when different parts of the membrane were strained. In Fig. 5*c*) it can be seen that while stimulation of the dorsal margin of the membrane adjacent to the cuticular plug activates CSD₁ units and initiates the reflex response in the PL nerve, ventral stimulation does not initiate the reflex although it does activate CSD₁ units.

Reflex responses elicited by AL tension and cuticular fracture

As outlined previously, contraction of the anterior levator and therefore limb autotomy are prevented in the dissected preparation. The effects of isometric contraction of the AL sufficient to cause cuticular fracture and limb separation were therefore mimicked manually, allowing the responses of levator motor neurones to peripheral feedback to be examined in isolation from the central programme response to injury. In these experiments the CB chordotonal organ was ablated as it has been shown in a number of crustaceans that the sensory reflexes stimulated by isometric tension in the AL do not arise from the CB organ but from CSD₁ (Clarac & Wales, 1970; Clarac *et al.* 1971; Moffett, 1975; McVean & Findlay, 1976).

The application of mild tension to the AL tendon caused an increase in the firing frequency of the tonic unit serving the PL (Fig. 6*a*). Increasing tension further increased firing frequency of the tonic unit and the second unit in the PL nerve was recruited (Fig. 6*b*). Eventually the cuticle fractured.

The first stage of cuticular separation is the fracture of the connexion across the breakage plane (Figs. 2, 3*b*), which releases tension from CSD₁, and accounts for the cessation of motor neurone response in the PL nerve immediately before complete separation and for the post-autotomy barrage caused by tearing of nerve trunks crossing the breakage plane (Moffett, 1975; McVean & Findlay, 1976). For *Cardisoma*, Moffett (1975) reported similar responses from the PL, with parallel and simultaneous responses from the anterior levator. In *Pagurus* no such responses were recorded in the AL but there was a short burst on the release of tension from CSD₁ at cuticular fracture (Fig. 6*b*). The responses shown in Fig. 6(*a, b*) illustrate how the PL's curtailed response to injury (Fig. 4*b*) can be prolonged by a feedback loop operated by injury-induced contraction of the AL (Fig. 4*b*).

The basic hypothesis underlying this investigation is that autotomy is caused by the concentration of force developed by the isometric contraction of the AL on to the plug spanning the breakage plane and that this concentration results from the rotation of the PL tendon altering the orientation of the AL tendon head (Figs. 3, 4, 6*a, b*; McVean & Findlay, 1976). It was noted earlier (Fig. 5*c*) that manual stimulation of the CSD₁ membrane adjacent to the plug stimulates the reflex loop on to the PL. The concentration of force on to the plug should thus operate this reflex more easily than when the same force is spread around the dorsal rim of the BI. In essence, the CSD₁-PL reflex should have a lower mechanical threshold when the abutting faces between the AL tendon head and the rim of the BI are separated by rotation of PL tendon than when they are closed. The results from an experiment designed to test

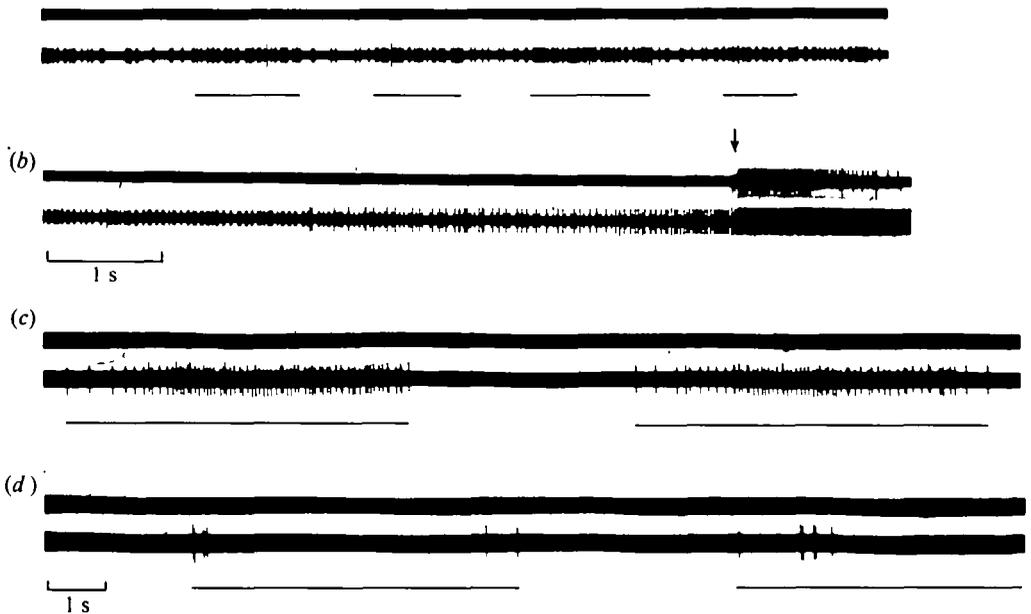


Fig. 6. Motor responses resulting from tension applied to the AL tendon and cuticular fracture around the breakage plane. Recordings in pairs: upper trace, AL nerve; lower trace, PL nerve. Bars represent period of stimulation.

(a) Mild tension applied to AL tendon elicits an increase in firing frequency of the tonic unit in the PL nerve.

(b) As the tension is increased the fast unit responsive to prodding CSD₁ is recruited in the PL nerve. At cuticular fracture the tension on CSD₁ is relaxed, hence the sudden cessation of firing in the PL nerve with a short burst from the AL nerve (arrowed) (Moffett, 1975).

(a), (b) From the same preparation as Fig. 5 (a, b).

(c, d) Known tensions were applied to the AL tendon by hanging weights on to the tendon blade. (c) 250 g applied to the AL tendon with the abutting faces between AL tendon head and the BI open elicits distinct firing in the posterior levator nerve for the duration of the stimulus. (d) 250 g applied with the abutting faces closed elicits only a few potentials. These results are discussed in the text.

this hypothesis can be seen in Fig. 6(c, d), which show that when the same tension is applied to the AL tendon, the CSD₁-PL reflex produces more rapid firing in the PL nerve when the faces are separated (Fig. 6c) than when they are together (Fig. 6d). More rapid firing can be obtained when the abutting faces are together, but a much greater tension has to be applied.

Functional differentiation of the posterior levator muscle

Posterior levator muscle activity has been recorded during locomotion in *Brachyura* (Clarac & Wales, 1970; Clarac & Coulmance, 1971). Moffett (1975) puts this forward as evidence that the PL tendon rotates during normal locomotion in *Cardisoma*. McVean & Findlay (1976) have shown that the part of the posterior levator which rotates in *Carcinus* is only activated just prior to autotomy, while a small levatory section of PL is active at other times. The action of the latter is likely to aid limb elevation by spreading load around the dorsal rim of the BI.

McVean & Findlay (1976) have shown that activation of the PL tonic unit in

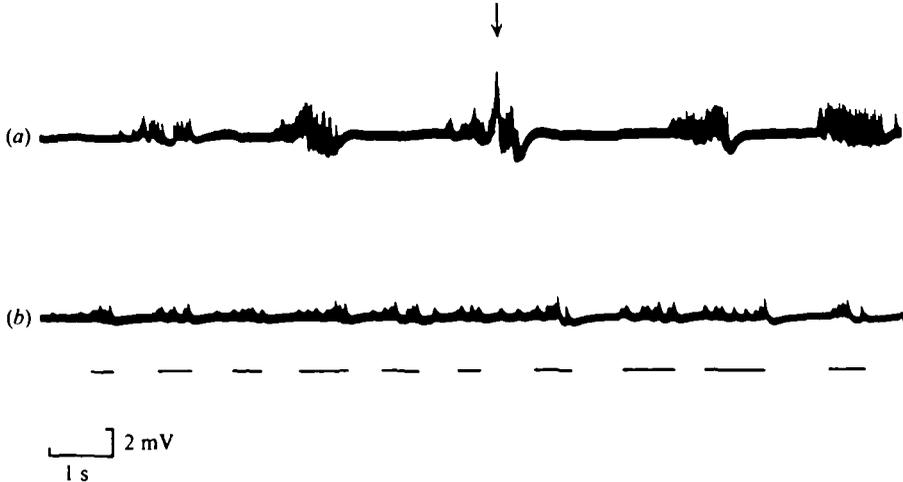


Fig. 7. Intracellular recordings from the PL muscle. (a) Large eip's resulting from manual stimulation of CSD_1 ; movement of the base line during the third burst is an artifact due to tendon movement. (b) Small eip's result from the tonic unit show facilitation when CB is stretched (bars).

Pagurus does not influence the orientation of the PL tendon, while recruitment of the new unit by CSD_1 stimulation results in tendon rotation. The hypothesis was advanced that the more dorsally situated PL fibres would be activated by the tonic unit, aiding limb levation and resisting tendon rotation, whereas the more ventrally situated fibres, with their greater mechanical advantage for rotation, would be innervated by the fast unit.

The above hypothesis was tested by recording intracellularly from ventral, medial and dorsal fibres within the PL while alternately stimulating the CB organ to recruit the tonic unit, and CSD_1 to recruit the fast unit (Fig. 7). Three categories of fibres were found but these were distributed throughout the muscle: slow fibres responded with small eip's to the tonic unit, fast fibres responded with large eip's to the fast unit, and intermediate fibres (Atwood, 1963; Sherman, Fournier & Drewes, 1976) responded to both units. Similar experiments have also failed to reveal any anatomical segregation of electrophysiologically different types of fibre in lobster claw (Govind & Lang, 1974), and the claws of *Cancer* and *Macropipus* (Warner & Jones, 1976).

The role of CSD_1 in autotomy

If CSD_1 is involved in the maintenance of PL tendon rotation on injury, as suggested above, its ablation should lead to a foreshortening of the muscle's response to injury in an otherwise intact animal; only the short-term activity resulting from the central programme should be observed. This prediction was confirmed (Fig. 8a).

The hypothesis proposed for autotomy also requires that the CSD_1 -PL reflex induced by tension in the AL can override the centrally determined response to injury. Peripherally originated reflexes have been shown to be overridden or inhibited during centrally determined motor programmes (Barnes, Spirito & Evoy, 1972; Field, 1974), and Moffett (1975) suggested that the CSD_1 -PL reflex is centrally inhibited in *Cardisoma* when the limb is injured. However, Fig. 8(b) shows that

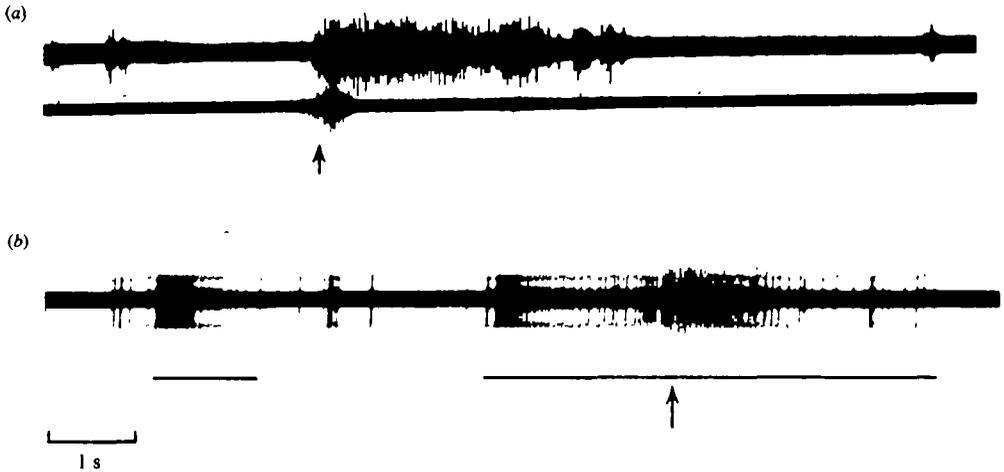


Fig. 8. (a) Extracellular myograms recorded from the BI levator muscles during the application of an injury stimulus (arrowed) when CSD_1 has been ablated. The anterior levator (upper trace) responds with a sustained burst of firing. But compare the foreshortened response from the posterior levator muscle (lower trace) with the unsuccessful injury response in Fig. 4(a). (b) Recording from PL nerve during the application of sustained manual stimulus to CSD_1 (bar) during which an injury stimulus is presented (arrowed). Firing of the CSD_1 induced unit is maintained, with no silent period typical of the centrally determined response to injury (Fig. 4b).

These results are discussed in the text.

when an injury stimulus is applied to the limb in *Pagurus* while the CSD_1 -PL reflex is active, firing of the fast PL unit is maintained; the reflex overrides any central inhibition initiated by injury.

Experiments have shown that autotomy can still occur if the PL insertion is cut, and also that if CSD_1 and the posterior levator are removed, normal locomotion is apparently unimpaired. We believe that the specialization of the BI cuticle, the levator muscles and sensory feedback serve to reduce the chance of accidental autotomy during normal activity.

Cuticular stress detector one may not solely be concerned with a reflex loop from the anterior levator to posterior levator. Clarac (1976) provides evidence that in *Carcinus* stimulation of CSD_1 with a probe elicits or facilitates responses from accessory flexor motor neurones, and also implicates physiological connexions with other peripheral muscles. It was noted earlier (Fig. 5c) that activity in CSD_1 units need not stimulate PL motor neurones. The responses we have been discussing in relation to autotomy all result from the high levels of isometric tension in the anterior levator which are required to elicit reflex responses from PL. These could be the upper end of a spectrum of stimulus strengths to which CSD_1 is normally subjected. Strains imposed upon the limb cuticle by posture and movement could just as effectively be represented by CSD_1 in a more general sense without PL activation, as well as operating under the extreme situation of cuticular strain imposed by isometric contraction of the anterior levator muscle.

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