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THE STRUCTURE AND PHYSIOLOGY OF ABDOMINAL PROPRIOCEPTORS IN LARVAL DRAGONFLIES (ANISOPTERA)

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A pair of lateral chordotonal organs is found in abdominal segments 2 to 8 in larvae of *Anax imperator* Leach, *Aeshna cyanea* (Müll.) and *Libellula depressa* L. The ultrastructure of the chordotonal organs has been determined. Each contains three scolopidia embedded in a connective tissue strand. A single type I cilium from a bipolar neuron innervates each scolopidium and is surrounded by a scolopale cell which forms the intracellular scolopale, extracellular scolopale space and distal cap. Surrounding the distal region of the scolopidium is the attachment cell. Activity from the longitudinal and vertical stretch receptors has been recorded from an intact larva. These receptors behave antagonistically to each other during rhythmic ventilation. Electrophysiological recordings also indicate that the chordotonal organ is active during expiration. This suggests a relaxation sensitive organ, a finding which is discussed in relation to its ultrastructure.

INTRODUCTION

The presence of internal abdominal receptors in arthropods has been known for some time, but not until comparatively recently have their structure and function started to be elucidated. In insects, abdominal stretch receptors and chordotonal organs have been described in representatives of most orders (cf. FINLAYSON, 1976, for references).

Stretch receptors always have a single sensory cell, and in insects they generally occur on the dorsal side of the abdomen above the longitudinal musculature. In some orders there is a pair of longitudinal receptors in most segments; in others, including the Odonata, there is an additional vertical pair. In the larva of *Phormia* there is also a ventral receptor (OSBORNE, 1963). They vary in complexity from the longitudinal receptors of aeshnid

larvae, where the cell body has a single unbranched dendrite ending in a strand of connective tissue (ROGOSINA, 1928; FINLAYSON & LOWENSTEIN, 1958; MILL, 1965) to the muscle receptor organs of lepidopterans, where the dendrites are branched and the connective tissue strand is closely associated with a muscle fibre. The ultrastructure of dragonfly stretch receptors has not been studied, but that of the cockroach (which is somewhat more complex) and lepidopteran receptors has (OSBORNE, 1963; OSBORNE & FINLAYSON, 1965).

In most insects there is a pair of lateral segmental chordotonal organs. Some also possess another one or more pairs, which may be located mid-ventrally, ventro-laterally or dorsally. The number of sensory cells in each chordotonal organ varies from 1 to 7 (cf. ORCHARD, 1975); FINLAYSON, 1976). Aeshnid larvae have only lateral chordotonal organs and each is comprised of 3 sensory cells embedded in a strand of connective tissue (ROGOSINA, 1928; MILL, 1965).

There have been comparatively few physiological studies on the abdominal stretch receptors and chordotonal organs of insects and our knowledge of the physiology of the latter is particularly poor. The stretch receptors are tonic, but with a large phasic component, and are probably stimulated by telescoping and bending movements of the abdomen (FINLAYSON & LOWENSTEIN, 1958; LOWENSTEIN & FINLAYSON, 1960; MILL, 1963; WEEVERS, 1966). The chordotonal organs are rapidly-adapting phasic receptors which respond to vibrations of the substrate in some insects at least (FINLAYSON, 1968; KEHLER et al., 1970; ANWYL, 1972; ORCHARD, 1975). In dragonfly larvae the chordotonal organs are arranged so that they could be stimulated by the dorso-ventral ventilatory movements (FINLAYSON & LOWENSTEIN, 1958). The mid-ventral chordotonal organs of the cockroach and the ventro-lateral chordotonal organs of *Carausius* have been seen to be stimulated occasionally by inspiratory movements (KEHLER et al., 1970; ORCHARD, 1975).

MATERIAL AND METHODS

Late instar larvae of *Anax imperator* Leach, *Aeshna cyanea* (Müller) and *Libellula depressa* L. were used to study the anatomy and structure of the receptors, and the first two species were also used for the physiological investigation.

STRUCTURE

The larva was immersed in dragonfly ringer (FIELDEN & HUGHES, 1962) and opened along the abdominal mid-dorsal line. The alimentary tract,

tracheal system and all obscuring pleural muscles were removed to expose the chordotonal organs in a series of segments. Individual chordotonal organs were removed and examined with phase contrast or Nomarski optics, or prepared for electron microscopy. For the latter they were fixed in 2.5% glutaraldehyde (SABATINI et al., 1963) for three hours, washed in cacodylate buffer, post-fixed for one hour in 1% osmium tetroxide in veronal buffer (PALADE, 1952) and washed in veronal buffer. They were dehydrated in a series of alcohols and embedded in Epon. Transverse sections were cut with glass knives, using a Cambridge ultramicrotome. The sections were placed on carbon-coated 100 mesh copper grids and stained with uranyl acetate followed by lead citrate (REYNOLDS, 1963) for examination in an AEI EM6B electron microscope.

PHYSIOLOGY

The larva was left as intact as possible, so that normal ventilation movements could continue. It was secured dorsal side down in a wax depression by means of braces across the legs and abdomen, and arranged so that the anal appendages could be passed through a Perspex barrier into a separate compartment of the experimental bath, if required. The bath was flooded with cooled dragonfly ringer. When the Perspex barrier was used the compartment containing the anal appendages was flooded with water. The sternal cuticle was removed carefully from one side of the ventral mid-line in abdominal segment 5 or 6 to expose the underlying nerves and muscles. In some preparations the procedure was repeated on the opposite side and often necessitated extension to include abdominal segments 4 and 7. The pleuron was carefully raised to expose the primary division of the first segmental nerve into branches 1B, to the chordotonal organ, and 1C, to the stretch receptors (MILL, 1965). For the chordotonal organ preparation the first segmental nerve was cut centrally and the 1C branch was cut through. Recordings were obtained using a pair of platinum electrodes. In some preparations records were obtained from the larger 1C branch of the first segmental nerve, which contains the two axons from the dorsal stretch receptors. The expiratory motor rhythm was recorded in the same segment, either from the second nerve cut peripherally, or by making a small hole in the pleural cuticle above the respiratory dorso-ventral muscle and inserting an insulated copper-wire (0.04 mm Lewcosol) electrode into the latter to obtain a myogram. The indifferent electrode was inserted into a wing-bud. The signals were amplified using Grass P9 preamplifiers and displayed on an oscilloscope.

RESULTS

A pair of oblique chordotonal organs is present in each of the second to the eighth abdominal segments of both aeshnid and libellulid larvae (Fig. 1). The

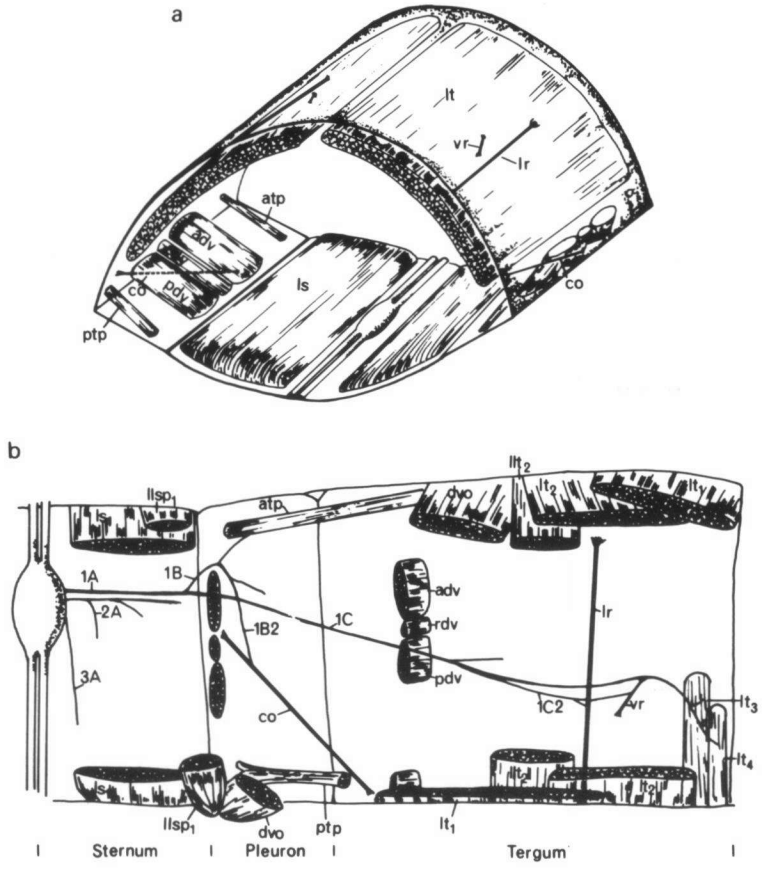


Fig. 1. Diagrams of an aeshnid larva fifth abdominal segment to show the positions of the proprioceptors: (a) A whole abdominal segment viewed obliquely from the rear; — (b) The right half of an abdominal segment. Obscuring muscles have been removed. Muscles: *adv*, anterior dorso-ventral; — *atp*, anterior tergo-pleural; — *dvo*, dorso-ventral oblique; — *ls*, longitudinal sternals; — ls_1, primary longitudinal sternal; — $llsp_1$, lateral primary longitudinal sternopleural; — *lt*, longitudinal tergals; — $lt_{1..4}$, primary, secondary, tertiary and quaternary longitudinal tergal; — llt_2, lateral secondary longitudinal tergal; — *pdv*, posterior dorso-ventral; — *ptp*, posterior tergo-pleural; — *rdv*, respiratory dorso-ventral. — Nerves: *1A-3A*, nerve roots. Proprioceptors: *co*, chordotonal organ; — *lr*, longitudinal stretch receptor; — *vr*, vertical stretch receptor. (b, after MILL, 1965).

anterior end of each chordotonal organ is attached to the pleuron, half-way along the segment just lateral to the attachment of the respiratory and anterior dorso-ventral muscles. The receptor strand runs posteriorly and obliquely to insert on the tergum, adjacent to the intersegmental membrane (PILL, 1978; cf. FINLAYSON & LOWENSTEIN, 1958). Each organ contains three bipolar sensory cell bodies and three associated scolopales lying in the anterior half of the strand matrix. The axons run into the first segmental nerve (via nerve 1B2 in aeshnid larvae - MILL, 1965).

STRUCTURE

Using phase microscopy or Nomarski optics, three spindle-shaped scolopidia can be seen embedded anteriorly in the strand. In *Aeshna* all three are more or less aligned; in *Anax* two occur more proximally than the third (Fig. 2); in *Libellula* they are all staggered.

The strand in the scolopidial region has a diameter of 10-20 μm. The scolopidia are embedded in an area rich in loosely arranged extracellular connective tissue, and discrete patches of electron dense amorphous material occur around the periphery of the strand. Other than the scolopidia and accessory cells, cellular components are noticeably absent (Fig. 2).

A single scolopidium is shown diagrammatically in Figure 3. Each sensory cell bears a tapering dendrite which contains a ciliary root (Fig. 4a). Distally,

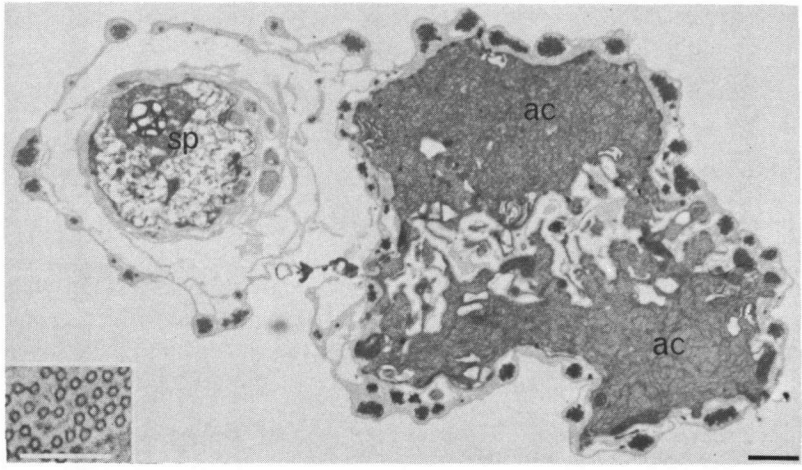


Fig. 2. Transverse section (electron micrograph) of *Anax* chordotonal organ strand, showing the large attachment cells (*ac*) of two of the scolopidia and the scolopidium (*sp*) of the third. Scale bar represents 1 μm. Insert shows details of the microtubules and their connections in an attachment cell. Scale bar represents 0.2 μm.

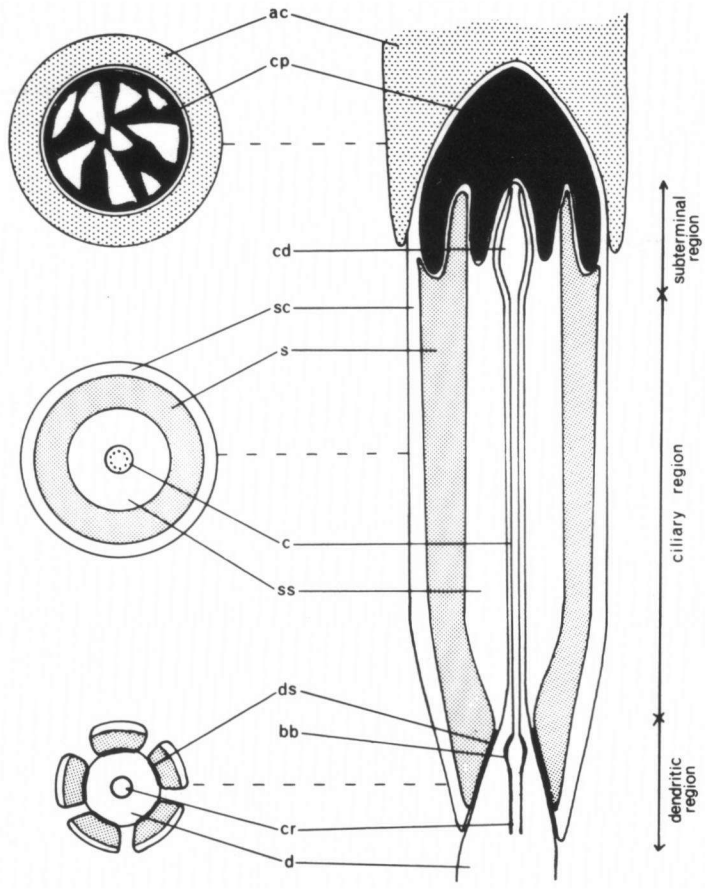
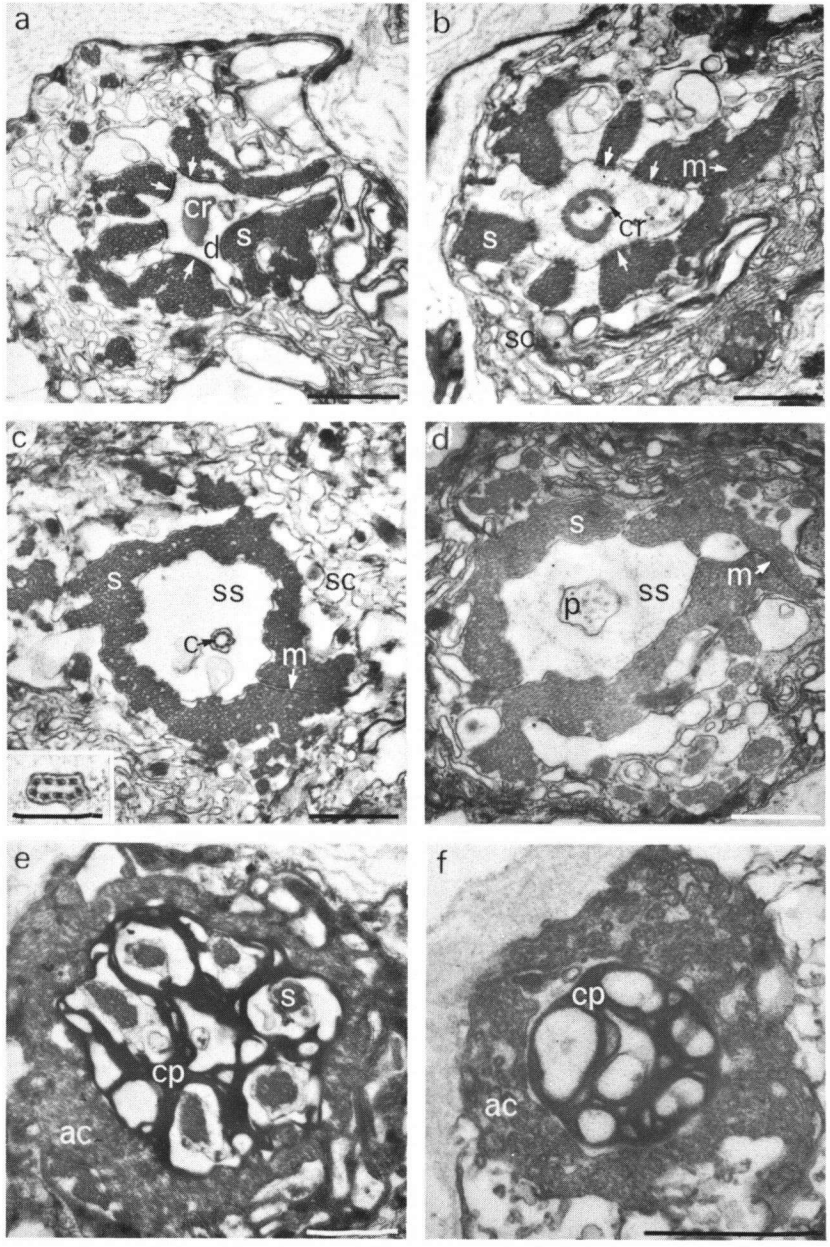


Fig. 3. Longitudinal diagram of a scolopidium: *ac*, attachment cell; — *bb*, basal body; — *c*, cilium; — *cd*, ciliary dilation; — *cp*, cap; — *cr*, ciliary root; — *d*, dendrite; — *ds*, desmosome; — *s*, scolopale; — *sc*, scolopale cell; — *ss*, scolopale space.

the ciliary root increases in girth and becomes a hollow cylinder (Fig. 4b) just below the basal body. The basal body gives rise to a cilium with an axoneme containing a 9 + 0 arrangement of filaments (Fig. 4c), evenly spaced around the periphery. Each filament is composed of two microtubules, one of which

Fig. 4. Transverse sections (electron micrographs) of *Anax* scolopidium: (a-b) Dendritic region; — (c) Ciliary region (Insert shows details of the structure of the axoneme), — (d-e) Subterminal region, — (f) Distal region: the cap (*cp*) is reduced and surrounded by an enlarged attachment cell (*ac*). *c*, cilium; — *cp*, cap; — *cr*, ciliary root; — *d*, dendrite; — *m*, mesaxon; — *p*, paracilium; — *s*, scolopale; — *sc*, scolopale cell; — *ss*, scolopale space; — arrows, desmosomes. (Scale bar represents 1 μm, except for insert where it represents 0.5 μm.)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is a solid rod and bears a pair of arms (Fig. 4c - insert). The cilium passes through a large extracellular 'scolopale space' (0.9-2.1 μm in diameter) (Fig. 4c, d). In the subterminal region of the cilium there is a ciliary dilation which contains some fibrous material and the filaments appear as nine solid T-shaped structures attached to the cell membrane. Following the dilation there is a short paraciliary region, in *Anax* at least (Fig. 4d), where the arrangement of the microtubules becomes disorganized.

The sensory apparatus of each bipolar sensory neuron is surrounded by a scolopale cell, which contains an electron dense structure, the 'scolopale', which is first distinguished, in the ciliary root region, as five electron dense rods around the inner circumference of the scolopale cell (Fig. 4a, b). In this region desmosomes occur between the dendrite and the scolopale cell (Fig. 4a, b). Distally, the scolopale rods widen and coalesce in *Anax* (Fig. 4c) and *Aeshna*, but remain partially distinct in *Libellula*; while the scolopale cell increases in diameter to enclose the large scolopale space (Fig. 4c, d). An amorphous matrix appears to be present in the scolopale space and the cilium is connected to the scolopale cell by extracellular material (Fig. 4d). In Fig. 4b-d the mesaxon, where the scolopale cell has encircled the sensory apparatus and become adhered to itself, is seen clearly. In both *Aeshna* and *Libellula* the scolopale occupies almost the whole of the scolopale cell, whereas in *Anax* (Fig. 4c) it is less extensive, but there are additional patches of scolopale material dispersed throughout the cell. In the subterminal region of the cilium, the scolopale becomes less extensive and separates into rods again (Fig. 4e).

Distal to the cilium, scolopale space and scolopale cell is a cone-shaped extracellular structure, the cap (Fig. 4e, f), which is probably secreted by the scolopale cell. In all three species, the cap is of similar diameter and appears as a uniform, electron-dense, amorphous material containing lacunae. Proximally it interdigitates with the scolopale cell, while distally it tapers and inserts into the attachment cell, which extends distally (Figs. 2; 4e, f) and has an intricate internal membrane enclosing numerous longitudinally-orientated microtubules interconnected by cytoplasmic bridges (Fig. 2 - insert). In *Libellula* the attachment cell contains mitochondria at its proximal end, and desmosomes are occasionally found between the scolopale and attachment cells. Distal to the caps the attachment cells of the three scolopidia dominate transverse sections of the chordotonal organ strand (Fig. 2).

PHYSIOLOGY

Recordings from the nerve containing the axons from the stretch receptors showed either one or two comparatively large units, each firing at a fairly regular frequency; when two were present they tended to fire at

Fig. 5. Activity in the two stretch receptors recorded from nerve 1C.

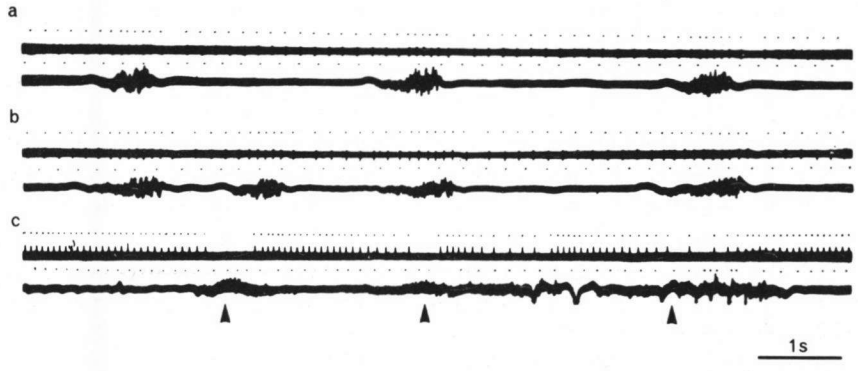

Fig. 6. Abdominal stretch receptor activity during (a-b) rhythmic ventilation, and — (c) longitudinal pulling of the abdomen (indicated by arrows). The lower traces are myograms from a respiratory (expiratory) dorsoventral muscle. Dots are inserted for clarity to indicate the firing of the two stretch receptors.

rather different frequencies, as noted by MILL (1963). Figure 5 illustrates a smaller unit firing at a faster frequency (2.0 s^{-1}) than the larger one (1.6 s^{-1}). The phase relationship between them thus changes steadily. Tactile stimulation had no effect on their frequency, but activated a number of smaller units. On one occasion, when the myograms indicated that rhythmic ventilation was fairly deep (cf. below), modulation of the activity of both units was observed during the expiratory phase. Thus, in Figure 6 the large unit increases in frequency at the onset of expiration while, at the onset of inspiration, there is a rapid decrease in its frequency to a level below the resting discharge, which latter is resumed and maintained throughout inspiration. The smaller unit shows a slight decrease in frequency towards the end of expiration and increases again at the start of inspiration. The effect of the longitudinal elongation of the segment in this preparation is shown in Figure 6, where the larger unit is inhibited.

The chordotonal organ proved to be a difficult receptor from which to obtain information and activity was not recorded very often. Nevertheless, groups of spikes were recorded from nerve 1B (which contains the three axons

from the chordotonal organ), the pattern of which was unrelated to the rhythmic ventilatory movements of the resting larva (Fig. 7). However, during more vigorous, deep ventilation, which is generally observed for example immediately before and after jet-propulsive swimming in unrestrained larvae (MILL & PICKARD, 1975) sensory impulses organized into groups in phase with ventilation were occasionally recorded (Fig. 8). This deeper ventilation is typified in myograms from the respiratory (expiratory) dorsoventral muscles by potentials of fairly uniform high frequency with the absence of the slow build up in frequency observed in normal rhythmic ventilation in a resting larva (MILL & HUGHES, 1966; MILL & PICKARD, 1975). There is probably also some longitudinal contraction of the abdomen. The main period of activity was during expiration, but there was also an after-discharge which extended well into the inspiratory period.

It seems highly likely that the sensory activity illustrated in Figures 7 and 8 was from the chordotonal organ, since the only other receptors innervated by the nerve branch which was being recorded from are tactile receptors, and care was taken to avoid tactile stimulation as far as possible. If this is the case then the sensory cells of the chordotonal organ show an increase in firing frequency when the receptor strand is relaxed, since the strand is relaxed during expiration (FINLAYSON & LOWENSTEIN, 1958).

Fig. 7. Bursts of activity in nerve 1B, probably from the chordotonal organ.

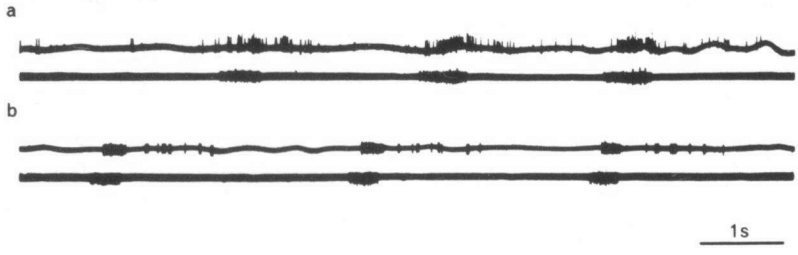

Fig. 8. Probable abdominal chordotonal organ activity (upper trace) during rhythmic (probably fairly deep) ventilation. The myograms on the lower trace are from the respiratory (expiratory) dorso-ventral muscle and indicate expiration.

DISCUSSION

The chordotonal organs each contain three sensory cells and three scolopales, i.e. the dendrites are unpaired. This is also the case in the ventrolateral chordotonal organs of *Carausius* which have two sensory cells and two scolopales (ORCHARD, 1975). In this respect at least, these receptors are like the chordotonal organs of the tympanal organs (e.g. GRAY 1960; HOWSE, 1968; GHIRADELLA, 1971; FRIEDMAN, 1972; YOUNG, 1973; MICHEL, 1974) and unlike many of the limb joint chordotonal organs, which have a mixture of single and paired dendrites, or are composed entirely of paired dendrites (e.g. WHITEAR, 1960, 1962; YOUNG, 1970; MILL & LOWE, 1971, 1973; MOULINS & CLARAC, 1972; LOWE et al., 1973; WIESE & SCHMIDT, 1974).

ROGOSINA (1928) first described the position of an oblique abdominal receptor (so named by FINLAYSON & LOWENSTEIN, 1958). Later, MILL (1965) described the strand as a chordotonal organ. Light and electron microscope evidence presented in this study have confirmed this. In addition to their location in each of abdominal segments 4-8 in aeshnid larvae (MILL, 1965), a pair has been observed in both segment 2 and segment 3 (PILL, 1978). Also a similar segmental complement has been described for *Libellula*. However, abdominal chordotonal organs appear to be absent in aeshnid adults (MILL & HULME, unpublished observations).

The proximal appearance of the scolopale as several rods, each in close association with the dendrite via desmosomes, is in accord with work on some other chordotonal organs in insects (e.g. GRAY, 1960; YOUNG, 1970, 1975). In the anisopteran larvae investigated in the current study there are five scolopale rods as in the labellar chordotonal organ of the mosquito, *Culiseta inornata* (PAPPAS & LARSEN, 1976). In some organs the rods remain throughout the length of the scolopale, e.g. the antennal organ of *Drosophila* (UGA & KUWABARA, 1965) and the locust tympanal organ (GRAY, 1960), partially fuse, e.g. the tibio-tarsal organ of *Periplaneta* (YOUNG, 1970) and the abdominal chordotonal organ of the larva of *Libellula* (this paper), or fuse to produce a cylinder surrounding the ciliary segment, e.g. the subgenual and 'intermediate' organs of *Gryllus assimilis* (FRIEDMAN, 1972), the tarsopretarsal organ of the larva of *Anax imperator* (MILL & PILL, 1981) and the abdominal chordotonal organs of larval *Anax* and *Aeshna* (this paper). Distally the rods become separate again, although GRAY (1960) reported additional branching of them in the locust tympanal organ.

A single cilium extends distally from the ciliary root to form the proximal ciliary shaft of YOUNG (1970). As in other scolopidia the 9 + 0 cilium configuration is seen (GRAY, 1960; YOUNG, 1970, 1973, 1975; MORAN et al., 1975; PAPPAS & LARSEN, 1976). Distally, the cilium dilates and the

microtubules become disorganized. This ciliary dilation is also present in, for example, the locust tympanal organ (GRAY, 1960). In this region the dense rod and arms are absent, as has also been described by YOUNG (1970) and MORAN et al. (1975). The arrangement of the centriolar derivative is similar to that described by GRAY (1960) for the locust tympanal organ, and has more recently been termed type I (MOULINS, 1976).

MILL (1963) confirmed that the fairly regular, spontaneously firing sensory units in the first segmental nerve are from the stretch receptors, and that when both are observed together their firing frequencies are low. FINLAYSON & LOWENSTEIN (1958) demonstrated that these receptors are excited by stretch of the receptor strand. They proposed that they are affected during jet-propulsive swimming and by lateral bending of the abdomen. The former is achieved by an enhanced expiratory movement involving both lifting of the sterna and marked longitudinal contraction of the abdomen, and Finlayson & Lowenstein suggested that the longitudinal and vertical receptors are relaxed and stretched respectively by such longitudinal contraction, the reverse occurring during longitudinal extension of the abdomen. They further proposed that the longitudinal receptor at least is not affected during rhythmic ventilation, since no change in abdominal length occurs. However, as well as confirming the antagonistic responses of the two receptors, the results from the preparation illustrated in Figure 6 indicate that there can be some modulation of stretch receptor activity during fairly deep ventilation. From the results shown in Figure 6c the large unit is apparently the vertical receptor, as it is inhibited by longitudinal extension of the abdomen. Since its frequency is increased by expiration it follows that there was probably some slight elongation of the segment during this phase of ventilation. Possibly there is a greater increase in the internal abdominal pressure during deep ventilation as compared to resting ventilation; this could cause such an elongation.

It seems clear that the chordotonal organ is relaxed during expiration (FINLAYSON & LOWENSTEIN, 1958) and that it is excited during this phase of rhythmic ventilation (Fig. 8). MILL & LOWE (1973) showed a clear correlation between elongation and relaxation movement sensitive sensory cells and the structure of the receptor strand in which their scolopales are embedded for the PD chordotonal organ of *Cancer pagurus*. In the PD organ the scolopales of the elongation sensitive movement cells are surrounded mainly by strand cells, including the probable homologue of an attachment cell, whereas the scolopales of the relaxation sensitive movement cells are surrounded mainly by collagen fibres and only come into contact with the strand cells to a limited extent. In the dragonfly abdominal chordotonal organ, there are few strand cells, apart from an attachment cell, and the absence of a firm anchorage to the strand matrix via strand cells may be

indicative of its relaxation sensitivity. A study of the mechanism of transduction is required to solve this problem.

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