The structure and topography of stretch receptors in representatives of seven orders of insects

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Summary

In *Ephemera* (Ephemeroptera), *Dictyopterygella* and *Isoperla* (Plecoptera), *Periplaneta* and *Blaberus* (Dictyoptera), *Forficula* (Dermaptera), and *Dytiscus* (Coleoptera) there is a pair of stretch receptors on each side in the dorsal region of most abdominal segments. Each receptor consists of a connective-tissue strand to which is attached a single sensory neuron. One member of each pair is approximately longitudinal and the other approximately vertical in orientation.

In *Sialis* (Neuroptera–Megaloptera) the longitudinal receptor consists of a muscle-fibre and a neuron; the vertical receptor consists of a neuron with one or two long processes. Connective-tissue fibres are absent from both receptors.

In *Limnophilus* and *Phryganea* (Trichoptera) there is a longitudinal receptor only. It consists of a muscle-fibre to which is attached a tube of connective tissue containing the dendrites of the sensory neuron. The caddis receptor resembles closely the lepidopteran receptor.

No abdominal stretch receptors could be found in *Rhodnius* or *Nepa* (Hemiptera–Heteroptera), and in *Schistocerca* and *Locusta* (Orthoptera) no vertical receptors could be found.

Introduction

STRETCH receptors have been described in Orthoptera (Slifer and Finlayson, 1956), Dictyoptera, Odonata, Hymenoptera, and Lepidoptera (Finlayson and Lowenstein, 1958). Physiological studies of their function were made by Finlayson and Lowenstein (1958) and Lowenstein and Finlayson (1960). The present paper describes the structure and topography of stretch receptors in Ephemeroptera, Plecoptera, Dermaptera, Neuroptera, Trichoptera, and Coleoptera and extends previous observations on the Dictyoptera (Finlayson and Lowenstein, 1958). The receptors of the Diptera will be described in a subsequent paper on the peripheral nervous system of the blowfly larva.

Methods

The morphology of the stretch receptors was studied from dissections and whole mounts, the majority of which were stained vitally with methylene blue. This was used in concentrations ranging from 0·001% to 0·5% made up in Ephrussi and Beadle's (1936) insect Ringer (NaCl, 7·5 g; KCl, 0·35 g; $CaCl_2$, 0·21 g; H_2O, 1 l). The concentration used depended on the size of the animal to be stained and on the degree of penetration into the tissues which was required. As a general rule the larger the insect, the higher is the required concentration.

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The following technique for vital staining gave the best and most consistent results. The insect was cut along the ventral mid-line to ensure that the dorsal muscles were not damaged, and pinned out flat in a metal dish partly filled with paraffin wax. The remaining inner surface of the dish was coated with a thin layer of paraffin wax to prevent the staining solution coming into contact with the metal. The dissection was flooded with methylene blue and placed in a refrigerator at 5 to 7° C for periods ranging from 6 to 18 h. The tissues were fixed in 8% ammonium molybdate made up in Ephrussi and Beadle's insect Ringer for 1 to 24 h, usually at room temperature but sometimes at 5 to 7° C. In some instances 5 to 10 drops of 2% osmic acid were added to each 10 ml of ammonium molybdate used. After fixation the preparation was washed in tap-water for 2 to 3 h. Rapid dehydration of the preparation was followed by clearing in xylene or cedar-wood oil, and either the whole preparation or isolated receptors were mounted in dammar. Counter staining with picric acid dissolved in xylene (Alexandrowicz, 1954) was employed in the study of muscular tissue where this was found to be present in the stretch receptors. Other stains used were Ehrlich's and Heidenhain's haematoxylin, and for this the material was fixed in Bouin's fluid.

In this investigation, the main purpose was to locate stretch receptors in the abdomen of insects, and so no detailed search was undertaken in the thorax. However, stretch receptors have been found in the thorax of the larva of *Dictyopterygella* (Plecoptera). Wherever possible every abdominal segment has been carefully examined in each insect. The numbers of the segments in which the receptors have been located are given for each insect, but this does not necessarily mean that receptors are absent from segments not listed.

The nomenclature adopted here for the receptors is that of Finlayson and Lowenstein (1958). Receptors that are orientated more or less longitudinally along the abdomen and are slung between the intersegmental folds, or from the posterior intersegmental fold of a segment to a point on the tergal epidermis, are termed longitudinal receptors. Receptors that are slung from a branch of the tergal nerve or dorsal muscles to the tergal epidermis are called vertical receptors.

Ephemeroptera

In the larva and adult of *Ephemera danica*, two pairs of receptors have been found above the dorsal musculature in abdominal segments 1 to 9. In structure and topography they resemble those of the Odonata (Finlayson and Lowenstein, 1958). Each receptor consists of a single sensory neuron associated with a thin strand of connective tissue. The fibres within the connective tissue are orientated longitudinally along the strand. The receptors are situated above the principal dorsal longitudinal muscle-band and are revealed when this muscle-band is pulled aside.

The longitudinal receptor extends for about one-third of the length of the segment, and is attached at one end to the posterior intersegmental fold and at the other to the tergal epidermis, at or near to the insertion of the vertical receptor. The vertical receptor is slung from a branch of the tergal nerve running above the dorsal muscles to a point on the epidermis where, as previously stated, the longitudinal receptor has its anterior attachment. In the longitudinal receptor, the neuron is situated about one-third of the way along the connective-tissue strand from its anterior end; it is bipolar and the dendron runs towards the intersegmental fold. The neuron of the vertical receptor is situated within the receptor's own attachment to the tergal epidermis and is tripolar, the two dendrites extending along the connective-tissue strand towards the tergal nerve.

Both receptors are innervated by a branch of the tergal nerve which passes between the ventral and lateral muscle-bands to supply the tergal epidermis. The vertical receptor is connected to this nerve by a short axon, but the connecting axon of the longitudinal receptor is usually much longer, and is supported by connective-tissue fibres.

The sense organ corresponding to the 'oblique receptor' in the dragonfly larva (Finlayson and Lowenstein, 1958) has been found in *Ephemera* to be a chordotonal organ having three scolopidia. It runs forwards and obliquely from a point on the epidermis just posterior to the intersegmental fold to attach to the epidermis of the sternite, about half-way along the segment. It is also accompanied by other smaller chordotonal organs having one or more scolopidia. Recently, Mill (1960) has pointed out that the oblique receptor in the dragonfly is also a chordotonal organ with three scolopidia.

Plecoptera

The description of the anatomy of the plecopteran receptors is based on those which occur in *Dictyopterygella recta. Isoperla grammatica* has been examined less intensively as it is very much smaller, but its receptors appear to be similar in structure to those of *Dictyopterygella.* In both species only the larvae have been examined.

Two pairs of receptors were found in abdominal segments 1 to 8. Each pair of receptors is located above the third dorsal muscle-band counting from the dorsal mid-line. Each receptor consists of a bipolar neuron associated with a strand of connective tissue (fig. 1).

The longitudinal receptor runs obliquely across the segment and is attached at each end to the intersegmental fold. It is also attached to the dorsal surface of the third muscle-band which makes it difficult to isolate without damage. The bipolar neuron is encapsulated within the connective-tissue strand close to the posterior end, and its distal process runs along the strand towards the posterior intersegmental fold. The axon passes anteriorly along the connective-tissue strand for some way before leaving it to join a branch of the tergal nerve which passes upwards between the third and fourth dorsal muscle-bands to the tergal epidermis. Connective-tissue fibres in the strand surround the neuron and its processes. Near the ends of the strand they fan out to make the attachments with the intersegmental folds.

The connective-tissue strand of the vertical receptor is anchored at one end to the tergal epidermis and at the other to the main tergal nerve where it passes below the second and third dorsal muscle-bands. As usual the connective-tissue fibres splay out at the ends of the strand. The cell-body of the neuron is usually located on the epidermis some distance away from the attachment of the connective-tissue strand (fig. 1, B). The distal process runs

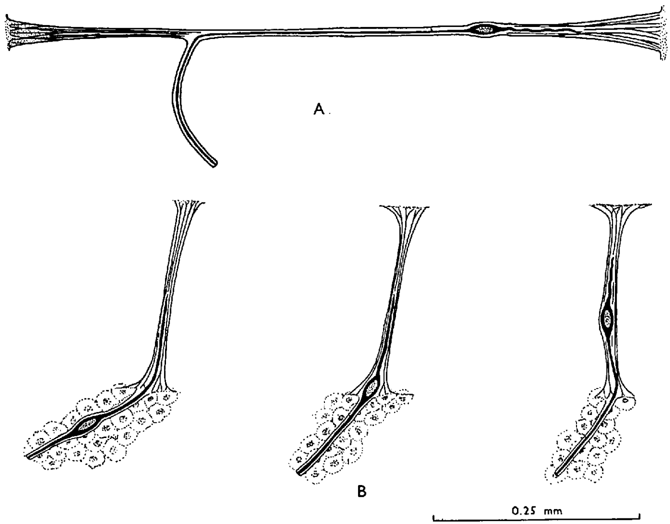

FIG. 1. A, longitudinal stretch receptor of *Dictyopterygella* (Plecoptera). B, diagram to show the variation in position of the neuron in the vertical stretch receptor of *Dictyopterygella*.

along the surface of the epidermis, enters the strand of connective tissue, and runs along inside it towards the tergal nerve. Sometimes the cell-body may be situated within the attachment of the strand to the epidermis. In one case the cell-body was stationed about half-way along the strand of connective tissue.

A brief examination of the thorax in *Dictyopterygella* revealed the presence of longitudinal receptors in the meso- and metathorax. The connective-tissue strands, however, differ in their topographical arrangement from the abdominal longitudinal receptors. Posteriorly each receptor is anchored to the intersegmental fold, but anteriorly it is attached to the dorsal epidermis, about half to three-quarters of the way across the segment. The neuron is again located close to the posterior end of the strand. The vertical receptors could not be found.

Dermaptera

In the adult *Forficula auricularia* two pairs of receptors have been located in abdominal segments 1 to 8. Each pair is situated above the main dorsal muscle-band (fig. 2).

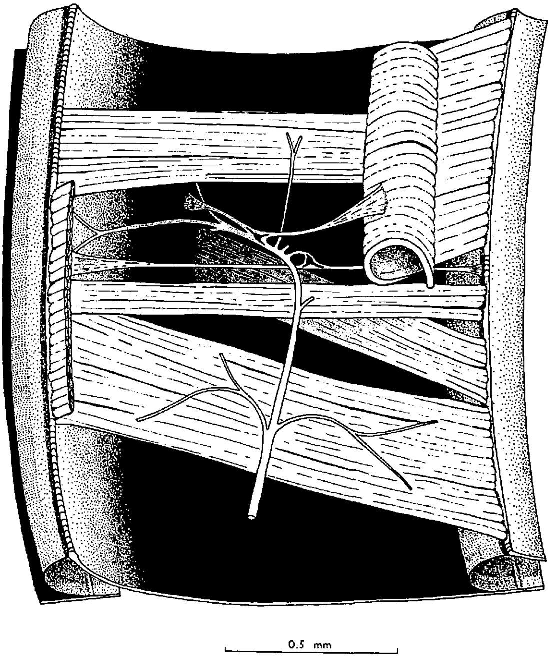

FIG. 2. Right side of the second abdominal segment of *Forficula* (Dermaptera) with various muscles cut or removed to reveal the two stretch receptors.

The longitudinal receptor is slung between the intersegmental folds, and consists of a multipolar neuron associated with a strand of connective tissue, which is slung between the intersegmental folds. Usually the neuron is situated alongside the strand nearer to the posterior than to the anterior end, and its dendrites enter the strand and run in both directions along it (fig. 3). The axon joins a branch of the tergal nerve which passes up through the dorsal longitudinal muscle-band to innervate the tergal epidermis. Fine connective-tissue fibres connect the receptor to adjacent muscle-fibres and to this nerve-branch.

The connective-tissue strand of the vertical receptor is anchored at one end to the dorsal oblique muscle (fig. 2), runs alongside the nerve-branch which innervates the tergal epidermis, and is attached at its other end to the tergal epidermis. The cell-body of the sensory neuron is situated within the adjacent nerve-branch (fig. 3). It may have a single thick distal process which passes out of this nerve-branch and enters the connective-tissue strand where

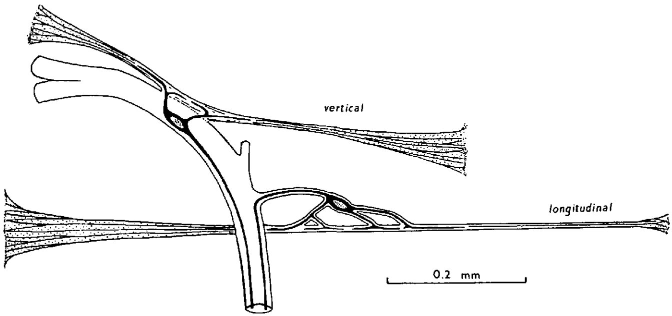

FIG. 3. Schematic drawing of the longitudinal and vertical receptors from *Forficula* (Dermaptera). On this scale the full length of the longitudinal receptor cannot be shown. It is approximately 1·5 mm long.

it subdivides and ramifies among the connective-tissue fibres, or two or more dendrites may leave the cell-body to enter the connective-tissue strand (fig. 3).

Dictyoptera

Finlayson and Lowenstein (1958) only describe a longitudinal receptor in *Periplaneta americana*, but their figure 1 shows the connective-tissue strand of the vertical receptor. As is shown in that figure the vertical and longitudinal receptors are joined together by a strand of connective tissue. The topography of the receptors of *Periplaneta* is shown in fig. 4. The arrangement in *Blaberus craniifer* is similar. Both the longitudinal and vertical receptors have been found in abdominal segments 1 to 7. They are located above the fourth and fifth dorsal muscle-bands, counted from the dorsal mid-line. Each receptor consists of a multipolar neuron embedded within a strand of connective tissue. The longitudinal and vertical receptors in *Blaberus*, however, are not joined to one another by a strand of connective tissue (fig. 5).

The longitudinal receptor is attached posteriorly to the intersegmental fold and anteriorly to a point on the tergal epidermis about a third of the way along the segment. Connective-tissue fibres also anchor the receptor anteriorly to the branch of the tergal nerve which runs above the dorsal muscles to innervate the tergal epidermis. The axons from both receptors join this nerve-branch. The neuron is situated about half-way along the strand (fig. 5), and the dendrites run along the strand as far as its attachment

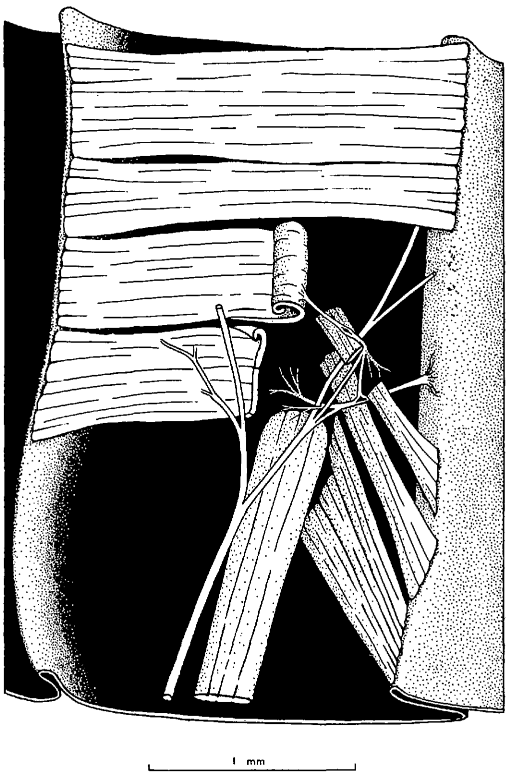

FIG. 4. Right side of the third abdominal segment of *Periplaneta* (Dictyoptera) showing longitudinal and vertical stretch receptors.

to the intersegmental fold. In *Blaberus* a dendrite sometimes leaves the cell-body and divides into two short branches, one of which runs posteriorly along the strand as do the rest of the dendrites, whereas the other runs anteriorly alongside the axon.

The vertical receptor is anchored at one end to the tergal epidermis, close to the anterior attachment of the longitudinal receptor, and at the other end either to the dorsal surface of the fourth muscle-band or to a motor-branch of the tergal nerve which runs above this muscle. The neuron is situated close to the attachment of the connective-tissue strand to the tergal epidermis, and its dendrites run in both directions along the strand (fig. 5).

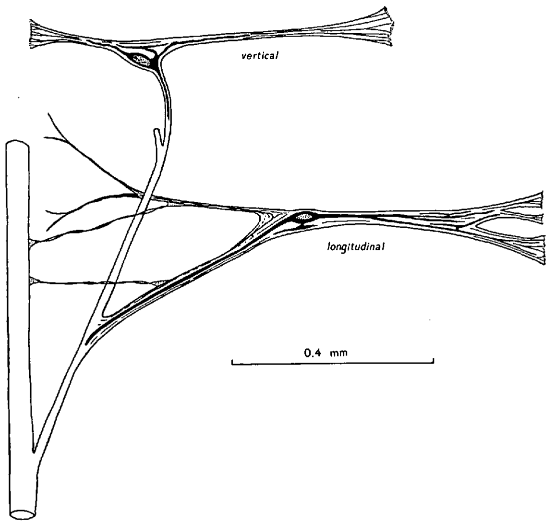

FIG. 5. Diagram to show the structure of the longitudinal and vertical receptors from *Blaberus* (Dictyoptera).

Hemiptera

Both the adult and larva of *Nepa cinerea* and of *Rhodnius prolixus* were examined in an attempt to find stretch receptors. None were found.

Neuroptera (Megaloptera)

Two pairs of stretch receptors have been found in the larva of *Sialis lutaria*, in abdominal segments 1 to 7. They are located above the third dorsal muscle-band counting from the dorsal mid-line (fig. 6). The longitudinal receptor has been found in the adult.

The longitudinal receptor is slung between the intersegmental folds. It usually pursues an oblique course, but sometimes follows an exact longitudinal path.

The vertical receptor is slung between a branch of the tergal nerve innervating the dorsal epidermis and two smaller longitudinal muscles above the main second and third dorsal muscle-bands (fig. 6). This same nerve which innervates the epidermis also provides sensory and motor innervation for the receptors.

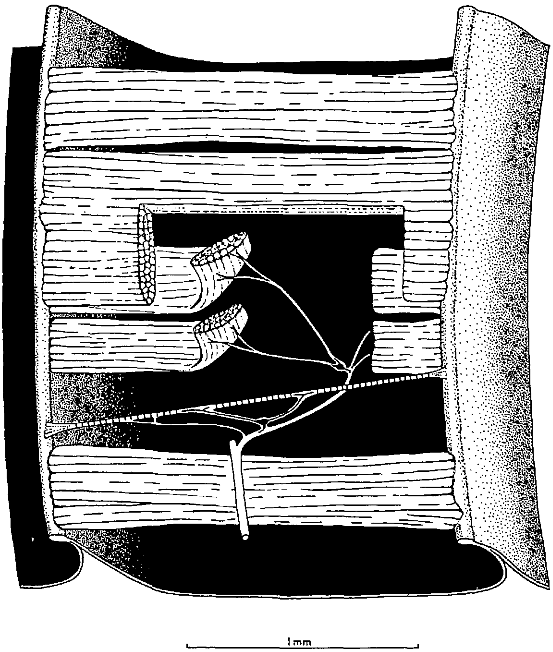

FIG. 6. Right side of the fifth abdominal segment of the larva of *Sialis* (Neuroptera) with the third dorsal muscle-band removed to show the location of the receptors. Motor and sensory innervation are shown.

The longitudinal receptor consists of a single multipolar neuron associated with an isolated muscle-fibre. This fibre sometimes divides into two branches near its attachments to the intersegmental folds, as shown in fig. 7. The muscle-fibre usually receives a single motor branch, containing two axons, which joins it near to the point of entry of one of the sensory branches. From this point the motor axons run in both directions along the muscle-fibre. The cell-body of the neuron is usually situated very near to the nerve, but may be located inside the nerve itself. From the cell-body the dendrites normally run in two or occasionally four extensions of the neural sheath to the muscle-fibre, where they ramify amongst the myofibrils. No connective-tissue fibres were seen in association with the dendritic terminations. The muscle-fibre is distinctly striated.

The vertical receptor is extremely simple in structure, consisting of a neuron anchored to the nerve which supplies its innervation, in a manner similar to the neuron of the longitudinal receptor. The cell may have two distal processes, or a single process only which bifurcates some distance away from the cell. In both cases the dendrites run in extensions of the neural

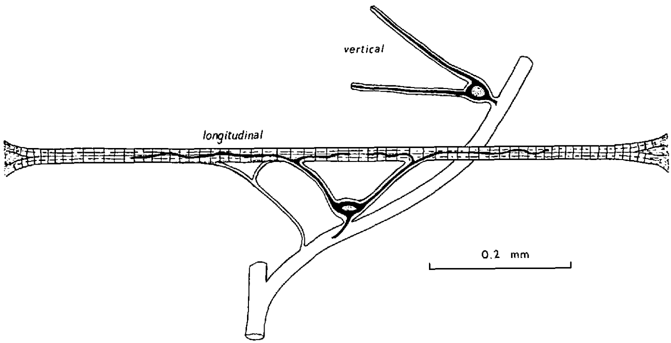

FIG. 7. Schematic drawing to show the structure and innervation of the longitudinal and vertical stretch receptors in *Sialis* (Neuroptera).

sheath and pass ventrally and obliquely to attach, as stated above, to two smaller dorsal muscles. Again no connective-tissue fibres were evident in the receptor.

Trichoptera

In the Trichoptera stretch receptors have been located in the larva and pupa of *Limnophilus flavicornis* and *Phryganea grandis*. They are situated above the third dorsal muscle-band, counting from the dorsal mid-line, in segments 1 to 8 of the abdomen. Sensory and motor innervation for the receptor is provided by a branch of the tergal nerve which passes up between the third and fourth dorsal muscle-bands.

Each receptor consists of a muscle-fibre, along one side of which runs a tubular sheath of connective-tissue fibres, the fibre tract (fig. 8). This tract is attached at each end to the intersegmental fold. The muscle-fibre is also attached posteriorly to the intersegmental fold, but near the anterior end of the receptor it disappears, leaving only the fibre tract to make the attachment to the intersegmental fold. The muscle-fibre is weakly striated. In the region where the muscle disappears is situated a multipolar neuron (fig. 8), the axon of which joins the tergal nerve. The dendritic processes run in 2 to 4 extensions of the neural sheath and enter the fibre tract. It is almost certain that the dendrites extend to the extremities of the fibre tract. The branch of the tergal nerve that supplies the sensory innervation runs alongside the fibre tract anteriorly from the neuron and passes on to the intersegmental fold, giving off in its course two branches to the cuticle. A large nucleus is situated within the neural sheath just anterior to the neuron. It is about $20\,\mu \times 15\,\mu$ and is probably homologous with the larger of the two giant nuclei of the lepidopteran receptor (Finlayson and Lowenstein, 1958). A smaller nucleus associated with the fibre tract is probably the counterpart of the smaller of

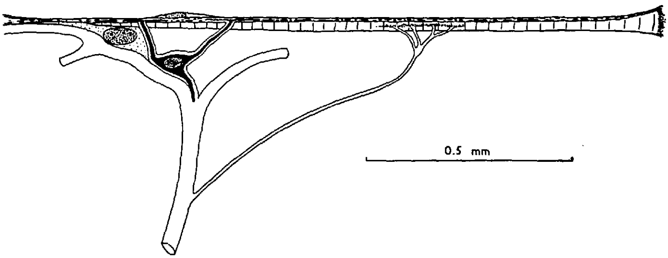

FIG. 8. Diagram of a stretch receptor of *Phryganea* (Trichoptera) showing its structure and innervation.

the two giant nuclei found in the Lepidoptera. Similar nuclei occur in the sheaths of peripheral nerves, but the nuclei in the receptor always occupy the same positions whereas those in the nerve-sheaths vary in their location. The whole organ is covered by a sheath of connective tissue.

Coleoptera

Stretch receptors have been found in adult *Dytiscus marginalis*, *D. circumcinctus*, *D. circumflexus*, and *D. dimidiatus*.

Two pairs of receptors have been found in abdominal segments 2 to 7 above the dorsal musculature in all the species examined. In all species the receptors are identical.

In *Dytiscus* the longitudinal receptor runs from the posterior intersegmental fold, obliquely and upwards, for about one-third of the length of the segment to a point of attachment on the tergal epidermis (fig. 9). The vertical receptor is slung from a branch of the tergal nerve running below the dorsal muscles to the epidermis of the tergum near to the base of the posterior intersegmental fold. As the dorsal muscles vary in each segment, the position of the receptors cannot be stated with reference to a particular muscle-band. The topography of the receptors in fig. 9 applies to the fifth abdominal segment.

Each receptor consists of a multipolar neuron in association with a strand of connective tissue. The cell-bodies are encapsulated within a continuation of the neural sheath. Both the strands and capsules are nucleated. The dendrites in the longitudinal receptor run mainly towards the intersegmental fold (fig. 10). In the vertical receptor, the majority of the dendrites run along the strand of connective tissue towards the tergal nerve (fig. 10). The axons from the neurons join a major branch of the tergal nerve which runs above the dorsal musculature to innervate the tergal epidermis. The attach-

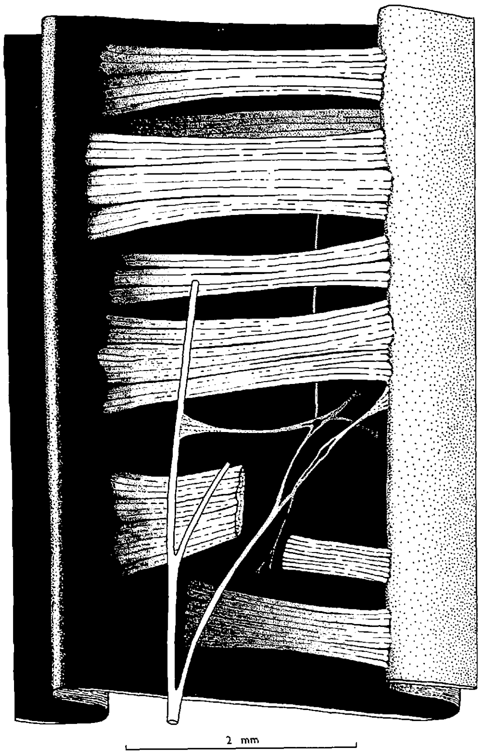

FIG. 9. Right side of the fifth abdominal segment of *Dytiscus* (Coleoptera) with various muscles cut or removed to reveal the stretch receptors.

ment of the vertical receptor to the epidermis is strengthened by branches from this nerve which run alongside it. Connective-tissue fibres from the receptors ramify over the nerve-branch supplying their innervation, and some fibres connect the two receptors together. Other fibres anchor the receptors to adjacent muscles and tracheae.

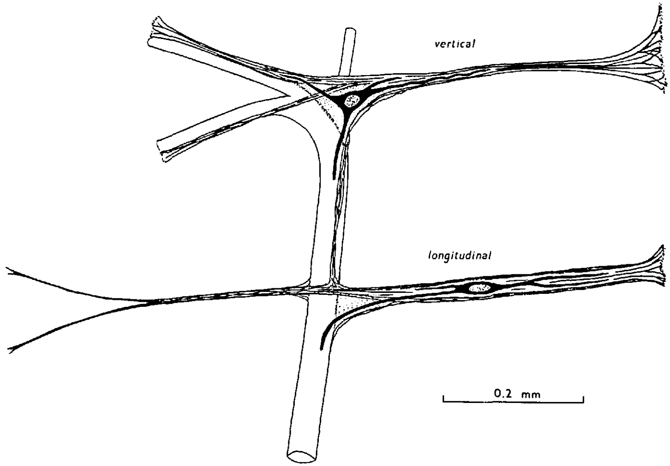

FIG. 10. Schematic drawing of the longitudinal and vertical stretch receptors of *Dytiscus* (Coleoptera).

Discussion

In the Ephemeroptera, Odonata, Dictyoptera, and Coleoptera the longitudinal receptor is attached posteriorly to the intersegmental fold, and anteriorly to the tergal epidermis. The vertical receptor is slung from a point of attachment on the tergal epidermis to a branch of the tergal nerve or to the dorsal longitudinal muscles. All these receptors consist of a single sensory neuron whose dendrites ramify inside a strand of connective tissue. In the Plecoptera and Dermaptera both the vertical and longitudinal receptors again consist of a neuron associated with a strand of connective tissue, but in this case the longitudinal receptor is suspended between the intersegmental folds. The topographical arrangement of the above receptors suggests that they are antagonistic in their response to segmental contractions, i.e. when the longitudinal receptor is stretched the vertical receptor is simultaneously relaxed and vice versa (Finlayson and Lowenstein, 1958).

In the Hymenoptera (Finlayson and Lowenstein, 1958) the longitudinal receptor is also slung between the intersegmental folds. The connective-tissue fibres, however, are organized to form a tube inside which run the dendrites from the sensory neuron. In this order of insects the vertical receptor appears to be absent.

In the Acrididae (Slifer and Finlayson, 1956) the vertical receptor also appears to be missing. (We have searched for a vertical receptor in *Locusta* and *Schistocerca*, but without success.) The longitudinal receptor has become intimately associated with the dorsal musculature, the neuron and its connective-tissue strand being found attached to the edge of a dorsal longitudinal muscle.

In the Lepidoptera (Finlayson and Lowenstein, 1958) and Trichoptera each receptor consists of an isolated muscle-fibre bearing the connective tissue and neuron. The muscle-fibre has its own separate motor innervation. The lepidopteran receptor has two giant nuclei situated close to the sensory neuron. Similar nuclei have been found in the trichopteran receptor. The connective-tissue fibres are arranged in the form of a tube which runs down one side of the muscle-fibre. Inside this tube run the dendrites from the neuron. Again the vertical receptor appears to be absent.

The neuropteran longitudinal receptor also consists of a single muscle-fibre with separate motor innervation, but connective-tissue fibres are absent and the dendrites from the neuron ramify among the myofibrils. In this case a vertical receptor is present, but as in the longitudinal receptor no connective-tissue fibres could be found. It is strange that the connective-tissue fibres which are always associated with the dendritic terminations in all other insects investigated should be missing in the Neuroptera.

Finlayson and Lowenstein (1958) describe how the receptors may be arranged in an evolutionary series from neurons associated with the body-wall to those associated with connective-tissue strands, whose topographical arrangement is such that they respond to specific abdominal movements. The connective-tissue strands with their neurons eventually come to lie alongside a dorsal muscle-band, as in the Acrididae, and finally comes the separation of an isolated muscle-fibre plus its connective-tissue fibres and neuron from the dorsal musculature. To this series can now be added the neuropteran longitudinal receptor consisting of a neuron associated solely with a muscle-fibre.

Morphological evidence for this hypothesis of the evolution of insect receptors from neurons innervating the body-wall is provided by the ephemeropteran and plecopteran receptors. In the Ephemeroptera the neuron of the vertical receptor is situated within the receptor's own attachment to the tergal epidermis, while in the Plecoptera the cell-body of the neuron in most cases occupies a position on the tergal epidermis some distance away from the connective-tissue strand. It appears therefore that the vertical receptor was derived from a sensory neuron innervating the tergal epidermis. Regarding the origin of the longitudinal receptor it can be seen in the Ephemeroptera, Odonata, and Plecoptera that the neuron is situated very close to the receptor's posterior attachment to the intersegmental fold, and moreover, the dendrites run only towards this intersegmental fold. In the Dictyoptera the dendrites have actually been traced as far as the intersegmental fold. Thus it may well be that the longitudinal receptor has been derived from a sensory neuron whose original function was to monitor flexure of the posterior intersegmental fold.

Higher up in the evolutionary series the neuron occupies a position near the centre of the strand. The dendrites in this case run in both directions along the strand, and thus ramify over a larger area. A similar arrangement is found in some vertical receptors, e.g. in the Dermaptera, Dictyoptera, and Coleoptera. Among the Endopterygota the Hymenoptera, Trichoptera, and Lepidoptera appear to have only a longitudinal receptor, but the Coleoptera and Neuroptera possess both longitudinal and vertical receptors. In those insects which possess only the longitudinal receptor, the dendrites ramify over the entire length of the organ and thus are distributed over a very large area. This arrangement of the sensory dendrites may increase the sensitivity of a receptor to stretch. Moreover, the muscular component present in neuropteran, lepidopteran, and trichopteran receptors very likely improves the efficiency of the receptor, as the range over which the receptor functions could be constantly varied by the appropriate reflex adjustment of receptor length. In all insects that are known to possess longitudinal and vertical receptors (with the exception of the Neuroptera) the dendrites do not ramify over the whole length of the connective-tissue strand. Therefore they may not be so efficient in monitoring segmental movements as are receptors which have dendrites distributed over their entire length. Thus instead of being antagonistic in their response to segmental movements (Finlayson and Lowenstein, 1958), the longitudinal and vertical receptors may function over different ranges. The neuropteran vertical receptor is very simple in structure. There is no accessory component of connective tissue or muscle; only the sensory neuron is present. It is possible that the vertical receptor in the Neuroptera is a degenerate form and is the last vestige of the vertical receptor. The apparent loss of the vertical receptor in the Hymenoptera, Trichoptera, and Lepidoptera may thus be a consequence of the improved efficiency of the longitudinal receptor. No receptors were found in *Rhodnius* or *Nepa* (Hemiptera). In the heteropteran bugs little abdominal movement is possible as the abdominal musculature is much reduced. The need for a proprioceptor is therefore less, and the receptors may have been lost. Similarly, Pilgrim (1960) could not find any stretch receptors in the abdomen of the crab, *Cancer magister*. He suggested that their absence is correlated with the reduced form of the abdomen which does not function in locomotion.

The abdominal stretch receptors in insects undoubtedly aid in the control of abdominal posture and in various abdominal movements, e.g. respiratory movements, copulation and oviposition in the adults, swimming and spinning, &c., in the larval forms.

The stretch receptors in the Crustacea (Alexandrowicz, 1951 to 1956; Florey and Florey, 1955), Lepidoptera, Trichoptera, and Neuroptera show certain similarities to the vertebrate muscle-spindle. They have specialized muscle-fibres with separate motor innervation, and as Finlayson and Lowenstein (1958) suggest, the giant nuclei in the lepidopteran and trichopteran receptors and possibly the nucleated capsules surrounding the neurons may be analogous with the nuclear bag of the muscle-spindle. The contractile regions of the receptors probably have the same function of reflex adjustment of receptor length as occurs in the intrafusal muscle-fibres of vertebrates.

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