THE FUSED THORACIC–ABDOMINAL GANGLION OF THE HERMIT CRAB (*PAGURUS POLLICARIS*): NEUROMUSCULAR RELATIONSHIPS IN THE THORACIC AND ABDOMINAL FLEXOR MUSCLES

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SUMMARY

1. The physiological and morphological properties of the thoracic flexor neuromuscular systems are described for the hermit crab *Pagurus pollicaris*. There are two pairs of flexor muscles in thoracic segments 3 to 5: the dorsal flexors and the ventral flexors.

2. The dorsal flexors are composed of fast fibres and are asymmetrical. On the left side the muscle branches laterally so that it has two points of insertion on the thoracic–abdominal sternite, compared with only one for the right side. The ventral flexors are composed of slow fibres.

3. The dorsal flexors are supplied by two excitatory motor axons that run in the thin nerve of the first abdominal root. The ventral flexors are innervated by at least seven excitors: two from the thin nerve of the first abdominal root, three from the thick nerve of the first abdominal root, and two from the thin nerve of the fifth thoracic root. Cobalt backfilling of the first abdominal root revealed that most cells are located on the dorsal and ventral surfaces in the centre of the thoracic–abdominal (TA) ganglion. Although most of the efferent cell bodies from the thin nerve of the fifth thoracic root are located rostrally in the midline of the TA ganglion, two or three somata can be found in the same region as cell bodies from the first abdominal root.

4. Stimulation of the giant interneurone elicits a spike in the giant flexor motor neurone and a contraction of the dorsal flexor muscles, and a spike in one of the axons in the thin nerve of the fifth thoracic root and a contraction of the ventral flexors.

5. Axons in the third abdominal root innervate the flexor muscles in the first abdominal segment. Motor axons in this root, which includes a giant flexor motor neurone, have cell bodies in the TA ganglion – not in the first abdominal ganglion.

6. Most of the motor axons in the fourth and fifth thoracic roots have cell bodies located in the fused TA ganglion. This suggests that the TA ganglion consists of a fusion of the first abdominal ganglion and the fourth and fifth thoracic ganglia.

INTRODUCTION

Some reptantian crustaceans, for example crayfish and lobsters, use their muscular abdomens to produce escape responses. Each abdominal segment contains four pairs of muscles: two flexors and two extensors. The superficial flexors and superficial extensors are made up of slowly contracting tonic fibres and are responsible for maintaining the posture of the abdomen. The deep extensors and deep flexors have a larger mass than their superficial counterparts and are composed of rapidly contracting phasic fibres (Jahromi & Atwood, 1972; Hajek, Chari, Bass & Gutmann, 1973; Lehmann & Szent-Gyorgi, 1975; Ogonowski & Lang, 1979). Activity in either the medial giant interneurone, the lateral giant neurone, or a non-giant pathway results in these fast muscles undergoing a rhythmic series of contractions to produce the tail-flip response (Krasne & Wine, 1977).

Other crustaceans have escape responses with certain features that are similar to the tail-flips of crayfish and lobsters. The hermit crab, for example, uses rapid flexions of its soft abdomen to withdraw itself back into the gastropod shell in which it lives. Withdrawal can be produced by a shadow or by touching the head or thorax, and the response is mediated by a single pair of giant interneurones. These inter-neurones are considered to be homologous to the medial giant interneurones of crayfish, since they have a similar morphology (Stephens, 1985), make rectifying electrical connections with the ipsilateral giant abdominal flexor motor neurones (Furshpan & Potter, 1959; Umbach & Lang, 1981), and have axons that run the length of the ventral nerve cord (Wiersma, 1961; Chapple, 1966b).

In the present paper I have examined the morphology and the innervation of the thoracic flexor muscles of the hermit crab. In crayfish the layout of the muscles in the thorax has been described (Pilgrim & Wiersma, 1963) and for some of these muscles the fine structure (Crabtree & Sherman, 1980) and certain physiological properties (Suzuki, 1978, 1979; Suzuki & Hisada, 1979) have been studied. These muscles have been categorized as either fast or slow, and are used to produce rotation between the thorax and the abdomen. In the fourth and fifth thoracic segments of the hermit crab there are only two pairs of flexor muscles. These muscles are innervated by motor neurones with cell bodies that are located in the fused thoracic–abdominal (TA) ganglion, and axons that run in either the first abdominal root or the thin nerve of the fifth thoracic root.

MATERIALS AND METHODS

Male and female flat clawed hermit crabs (*Pagurus pollicaris*) were collected from the waters around Woods Hole, Massachusetts. The animals were held at ambient temperature in running seawater tanks at the Marine Biological Laboriesm and were fed small pieces of squid twice weekly. Crabs were generally used for experi-mentation within 2 weeks of capture.

Electrophysiology

Electrophysiological recordings were made from two preparations. One involved isolating the suboesophageal and thoracic ganglia from the animal and pinning the

preparation to the bottom of a Sylgard-lined dish filled with saline, as previously described (Stephens, 1985). The second, semi-intact, preparation was made by pinning an animal ventral surface uppermost to the base of a large Sylgard-lined dish, and then making an incision through the cuticle along the ventral midline from the fourth thoracic segment to the mouth. The two halves of the thorax were gently separated and secured with pins. The nervous system was carefully exposed and the membrane over the last (fifth) thoracic segment was removed to expose the flexor musculature.

For both preparations fresh crab saline was constantly perfused through the preparation dish and observations were made at 16°C; the temperature was maintained (±0·25 °C) by heat exchange between the saline and a cooling coil attached to a thermostatically controlled, constant circulating bath. Axon spikes were produced by applying brief (0·1 ms duration) shocks through tungsten hook electrodes placed under the nerves, through suction electrodes into which the cut end of a nerve was drawn or (in the case of giant interneurone stimulation) through a microelectrode placed in the abdominal or the oesophageal connective (Stephens, 1985). Evoked nerve activity was recorded using suction electrodes attached to the cut roots, and excitatory junctional potentials (EJPs) were recorded through fine glass microelectrodes placed in single flexor muscle fibres. Signals were amplified, and displayed and photographed from the screen of an oscilloscope using conventional techniques.

Backfilling

Isolated preparations of the suboesophageal and thoracic ganglia were made as described above, and pinned to the Sylgard-lined base of a small Petri dish. A petroleum jelly well was constructed close to where the root left the TA ganglion or the abdominal connective, so that the root passed through the wall and into the well. The saline in the well was replaced with deionized water for 90s and then a 300 mmol l^{-1} solution of cobalt chloride or a mixture of cobalt chloride and nickel chloride (Hackney & Altman, 1983); the dish was covered and incubated at 4°C overnight. Preparations were bathed for 10–20 min in crab saline containing a few drops of rubeanic acid dissolved in ethanol. The tissue was fixed for 2h in 4% formalin, dehydrated in a graded series of alcohols, and cleared in methyl salicylate. Wholemount preparations were observed and photographed through a dissection microscope.

Sarcomere length measurements

Sarcomere length measurements were made from the flexor muscles in the fourth and fifth thoracic segments of hermit crabs using an established technique (O'Connor, Stephens & Leferovich, 1982). A hermit crab was pinned out with its ventral surface uppermost and with its tail extended, and a semi-intact preparation was made as described above. To prevent muscle contraction, and therefore measurement error, the preparation was soaked for 60 min in a large volume (>400 ml) of crab saline in which the calcium ions had been replaced with magnesium. The preparation was fixed in alcoholic Bouin's solution for 2 days and the

flexor muscles were removed and transferred to 80 % alcohol. Individual muscle fibres were carefully teased apart in a drop of 80 % ethanol on a glass slide, and examined under a compound microscope fitted with Nomarski optics. The length of five successive sarcomeres was measured using a calibrated filar ocular micrometer. Three measurements were made for each muscle fibre and an average length value for a single sarcomere was calculated.

RESULTS

Anatomy

In the hermit crab the cuticle on the ventral surface of the first three thoracic segments is fused. In the fourth and fifth thoracic segments, however, sternites extend across the ventral surface and are separated from one another by a soft arthrodial membrane. The presence of this membrane may increase the flexibility of these segments and may be an adaptation for living in the whorls of gastropod shells. Since the appendages on these segments are vestigial and are not used for walking, it seems unlikely that this increased flexibility would affect the animal's locomotion.

Fig. 1 is a *camera lucida* drawing of thoracic segments 3 to 5 and the first abdominal segment, and shows the nervous system and the layout of the two pairs of flexor muscles in this region. On each side, the dorsal flexor muscle inserts on to the cuticle caudal to the third thoracic appendage. The muscle extends caudally and inserts close to the midline at a level with the sternite between the first and second abdominal segments (Fig. 1). Interestingly, this muscle exhibits asymmetry, since on the left side the muscle gives off a branch which crosses the midline and inserts onto the thoracic–abdominal sternite on the right side. Sarcomere length measurements made from fibres removed from the dorsal flexor muscles gave mean values of 3·7 and 3·8 μm (S.D. ± 0·37 and 0·36; for 40 fibres from each side) for the left and right side, respectively; similar measurements made from fibres removed from the left dorsal flexor 'branch' were not significantly different ($P > 0.05$, Student's t-test). Measurements were made using fibres removed from different areas of each muscle, and no regional variation in sarcomere length was observed. The sarcomere length values indicate that the dorsal flexor muscles are composed of fast or phasic fibres (Atwood, 1973).

A pair of muscles is located ventral to the dorsal flexor muscles. The ventral flexor muscle on each side inserts on to the lateral portion of the sternite of the fourth thoracic appendage and runs caudally and medially to insert on the thoracic–abdominal sternite (Fig. 1). Fibres removed from different regions of the left and right ventral flexor muscles had mean sarcomere lengths of 11·05 μm (S.D. ± 1·6 left, 1·4 right; for 40 fibres from each side); no regional variation of sarcomere length was observed within the muscles. These sarcomere length values indicate that the ventral flexor muscles are composed of slow or tonic fibres (Atwood, 1973).

The nerves located in this region are the fourth and fifth thoracic roots and the first abdominal root (Fig. 1). The fourth thoracic root is composed of two nerves, both of which run close to the insertion of the dorsal flexor muscles and into the fourth
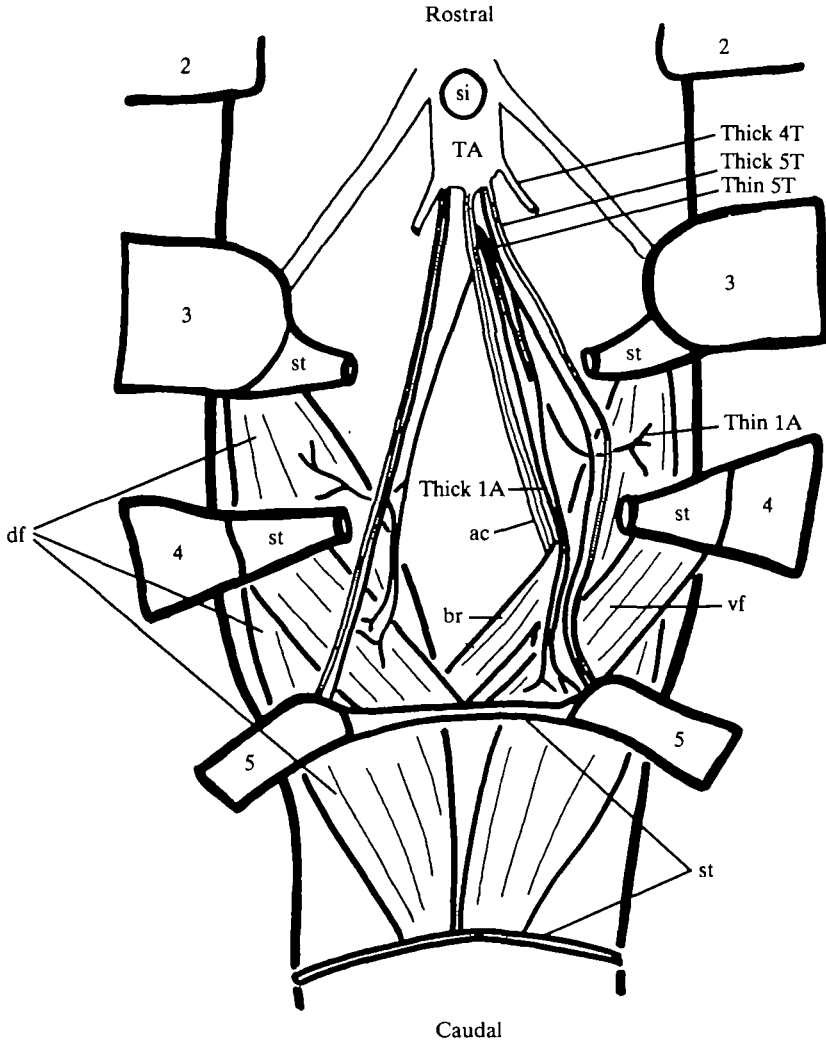
Fig. 1. A *camera lucida* drawing of a methylene blue-stained preparation, viewed from the ventral surface, to show the layout of the nerves and flexor muscles in thoracic segments 3 to 5 and the first abdominal segment of the hermit crab; the abdominal flexor muscles in the first segment have been dissected away. The numbers represent the thoracic appendages attached to the sternites (st), which have been cut in thoracic segments 3 and 4. The abbreviations for the nerves are as in the text; ac, abdominal connectives; br, branch of the dorsal flexors on the left side; df, dorsal flexor muscles; si, sinus; vf, ventral flexor muscles. Scale bar, 5 mm.

(vestigial) thoracic appendage. The fifth thoracic root is also composed of two nerves, one thick and one thin. The thick fifth thoracic nerve travels caudally from the TA ganglion, over the surface of the ventral flexor muscle and into the fifth thoracic limb; electrical stimulation of this nerve elicited movement of the vestigial limb. The thin fifth thoracic (5T) root also travels caudally and branches. In some preparations the root branches as it leaves the ganglion, in some others the nerve

branches at the level of the dorsal flexor muscles, whereas in most other preparations the branch occurs between these two extremes. One branch enters the limb, while the other travels medially, joins the abdominal roots and has axons that innervate the ventral flexor muscle – see later section.

The abdominal connectives travel caudally from the TA ganglion and give off a pair of roots. Since these roots innervate the flexor muscles they have been referred to as third roots (Umbach & Lang, 1981; Stephens, 1985), presumably to maintain a degree of consistency with the literature on the crayfish abdomen. In the present paper these roots will be called the first abdominal (1A) roots, because I have found that the third pair of roots to leave the abdominal connectives (just caudal to the first abdominal ganglion) contain motor axons that innervate the flexor muscles in the first abdominal segment – see later section.

The 1A roots are dimorphic. Although there is great variation between animals, the root on the left side always emerges rostral to the root on the right. On the right side, the root emerges and then usually branches just before reaching the dorsal flexor muscle. However, on the left side the root emerges as two nerves or as a single nerve that branches within 5 mm of emergence to form two nerves of different diameters. The two nerves of the left 1A root travel close to the abdominal connective. The thin 1A nerve travels laterally to the dorsal flexor muscle, while the thick 1A nerve runs alongside the thin 5T nerve to the ventral flexor muscle.

Innervation

The present investigation concentrates on the left side because the 1A roots on the left side are longer. The nerves were cut, drawn into suction electrodes, and the tip of each electrode was moved to a location away from the other nerves. In this way, when the nerve was stimulated the chance of current spreading to stimulate motor axons in other nerves was minimized. The shorter nerves on the right side made this procedure more difficult and in many cases current spread evoked activity in other nerves.

Suction electrode recordings from the thin 5T, thin 1A and thick 1A roots revealed spontaneous activity in all three roots (Fig. 2A). In semi-intact preparations, spontaneous nervous activity (recorded *en passant* from intact nerves) was correlated with EJPs in the ventral flexor muscle (Fig. 2B); no spontaneous EJP activity was ever recorded from the dorsal flexor muscle. The application of carefully graded stimulus shocks to the different roots revealed that the ventral flexor muscle is innervated by at least two axons in the thin 5T nerve (Fig. 2C), three axons in the thick 1A nerve (Fig. 2D) and two axons in the thin 1A nerve (Fig. 2E).

The dorsal flexor muscle, by contrast, is supplied by motor axons in only the thin 1A nerve. There is no shared innervation from axons in this nerve between the dorsal and ventral flexor muscles (Fig. 2E). However, simultaneous recordings from the main body of the left dorsal flexor muscle and the 'branch' (Fig. 1) showed that these two regions are innervated by the same motor axons (Fig. 3A). Determining the number of thin 1A axons that supply the dorsal muscle was complicated by the observation that the axon with the lowest stimulus threshold usually produced a large

amplitude EJP and a muscle twitch, which displaced the microelectrode. However, in some preparations two thin 1A axons were seen to innervate the dorsal flexor muscle (Fig. 3A).

Stimulation of the giant interneurone (GI) in the left oesophageal connective evoked activity in the ipsilateral giant flexor motor neurone (Umbach & Lang, 1981). This explains how GI stimulation produces an EJP and a twitch in the ipsilateral dorsal muscle, but not how an EJP and a twitch are produced in the ipsilateral ventral muscle (Fig. 3B). Cutting the thin 1A nerve abolished the response in the dorsal flexor muscles. The response in the ventral flexors was unaffected by cutting the thick 1A nerve but was abolished by cutting the thin 5T root. In the isolated ganglion preparation, GI stimulation provoked a spike in the thin 5T nerve (Fig. 3C). These data suggest that the GI makes a connection with an ipsilateral motor neurone which has its axon in the thin 5T nerve and innervates the ventral muscle.

In fresh, semi-intact preparations stimulation of the GI axon in either oesophageal connective produced activity in the left and right giant flexor motor neurone (GFMN) and in the dorsal flexor muscles on both sides (Fig. 3D). Cutting the oesophageal connective (and therefore the GI axon) rostral to the point of stimulation did not abolish the bilateral response, indicating that the crossover of
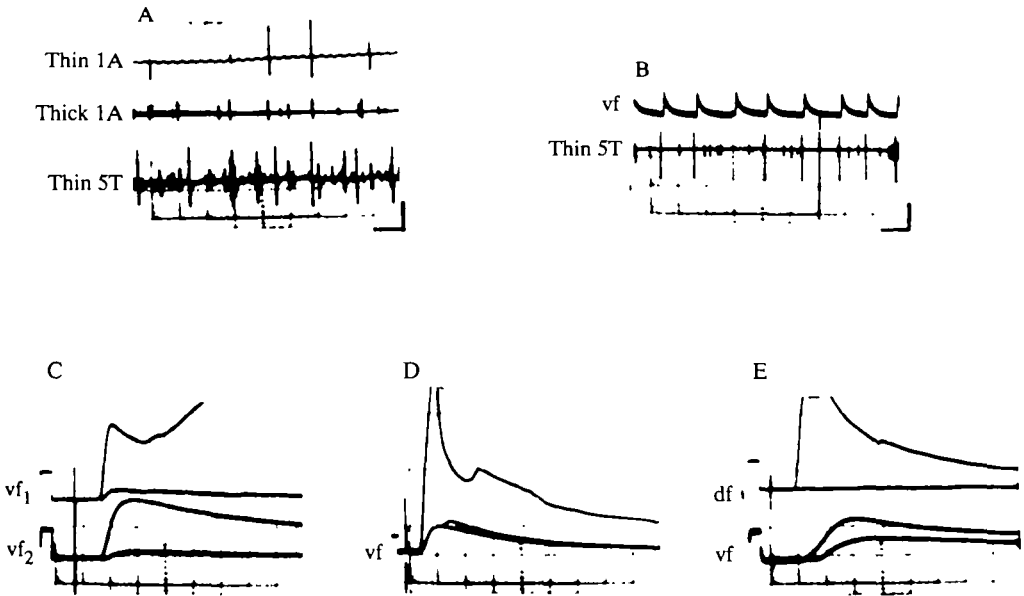

Fig. 2. Innervation of the left ventral flexor muscle. Spontaneous nervous activity (A) could be correlated with activity in the muscle (B). Careful grading of the intensity of the stimulus applied to the cut ends of nerves produced different classes of EJPs in the muscles (C–E), presumably by stimulating different motor axons at different stimulus intensities. The thin 5T nerve (C) and the thick 1A nerve (D) have at least two and three axons (respectively) innervating the ventral flexor muscle. The thin 1A nerve has at least two axons to the ventral flexor (vf) and one axon to the dorsal flexor (df) (E). Calibration 500 μV (extracellular), 5 mV (intracellular), 100 ms (A,B), 5 ms (C–E).
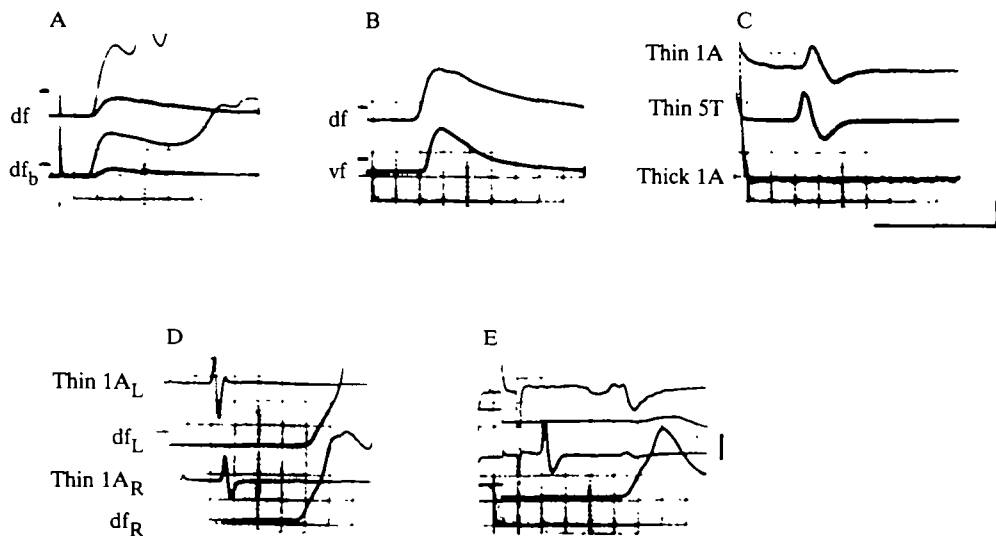
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Fig. 3. Innervation of the left dorsal flexor muscle (df). Careful grading of the stimulus intensity applied to the left thin 1A nerve showed that it contains at least two axons that innervate the dorsal flexor muscle, and that the innervation is shared with the branch (b) (A). Stimulation of the left GI axon produced activity in the left dorsal and ventral (vf) flexor muscles (B) and activity in the thin 1A and thin 5T nerves (C). A spike in the right GI axon evoked activity in the thin 1A nerves and the dorsal flexor muscles on the left (L) and right (R) side (D), but the response to the left side fatigued during repetitive stimulation (E). Scale bar, 5 mV (intracellular), 500 μV (extracellular), 5 ms.

information to the contralateral side was not *via* the brain (Stephens, 1985). Repeated GI stimulation resulted in an irreversible fatigue of the contralateral GFMN response (Fig. 3E). Data presented in the following paper indicate that this response is produced by a chemical synapse from the GI to the contralateral GFMN (Stephens, 1986).

Backfilling

Backfilling the thick 4T and the thick 5T roots showed that axons in these nerves have their cell bodies confined to the TA ganglion (Fig. 4A,C). The thin 4T nerve enters the nervous system in the short connective, located on either side of the sinus, and has axons with cell bodies located in the TA and in the next rostral thoracic ganglion (Fig. 4D). The thin 5T root has cell bodies that are confined to the TA ganglion, although it does send axons rostrally through the thoracic ganglia (Fig. 4B). Most of the cell bodies are located in the midline on the dorsal and ventral surfaces, towards the rostral end of the ganglion (Figs 4B, 5E). However, some somata on the ventral surface are situated more caudally, and still others are located laterally in the TA ganglion.

The branching of the left 1A root so close to the TA ganglion into two easily distinguishable nerves made it possible to backfill each nerve selectively. Backfilling the thick 1A nerve showed that the cell bodies are located on the dorsal or ventral regions in the central midline region of the ganglion (Fig. 5A,B). The mean number
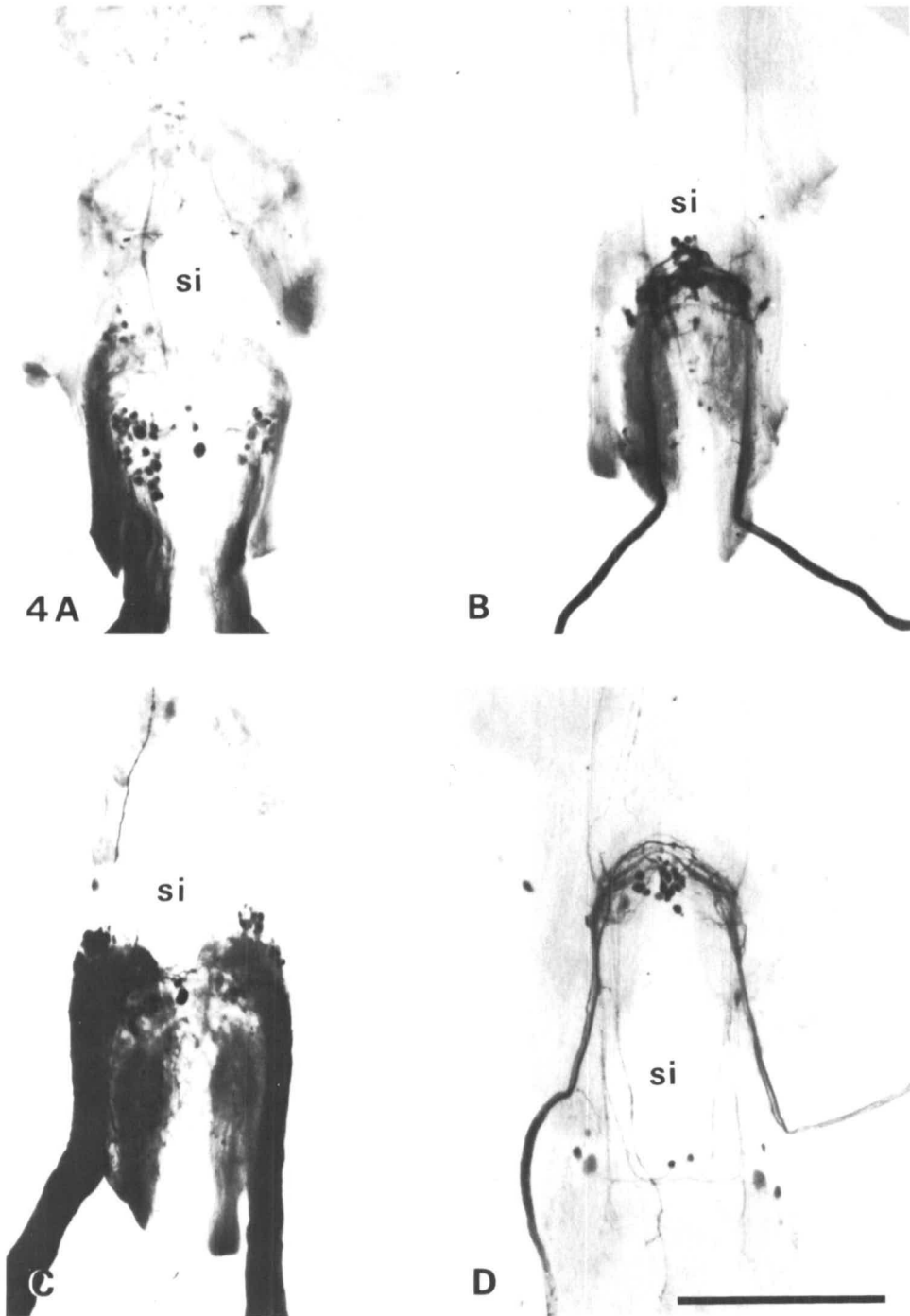
Fig. 4. Views of TA ganglia in which the thick 5T (A), the thin 5T (B), the thick 4T (C) and the thin 4T (D) on both sides were backfilled with cobalt ions. si, the sinus between the TA and the third thoracic ganglion. Scale bar, 1 mm (A–C); 700 μm (D).

of cells stained by backfilling the thick 1A nerve was 10·2 (range 10–11; $N = 18$). However, the number in each region varied dramatically between preparations. The mean number of cells was 4·8 for the dorsal group and 4·9 for the ventral group
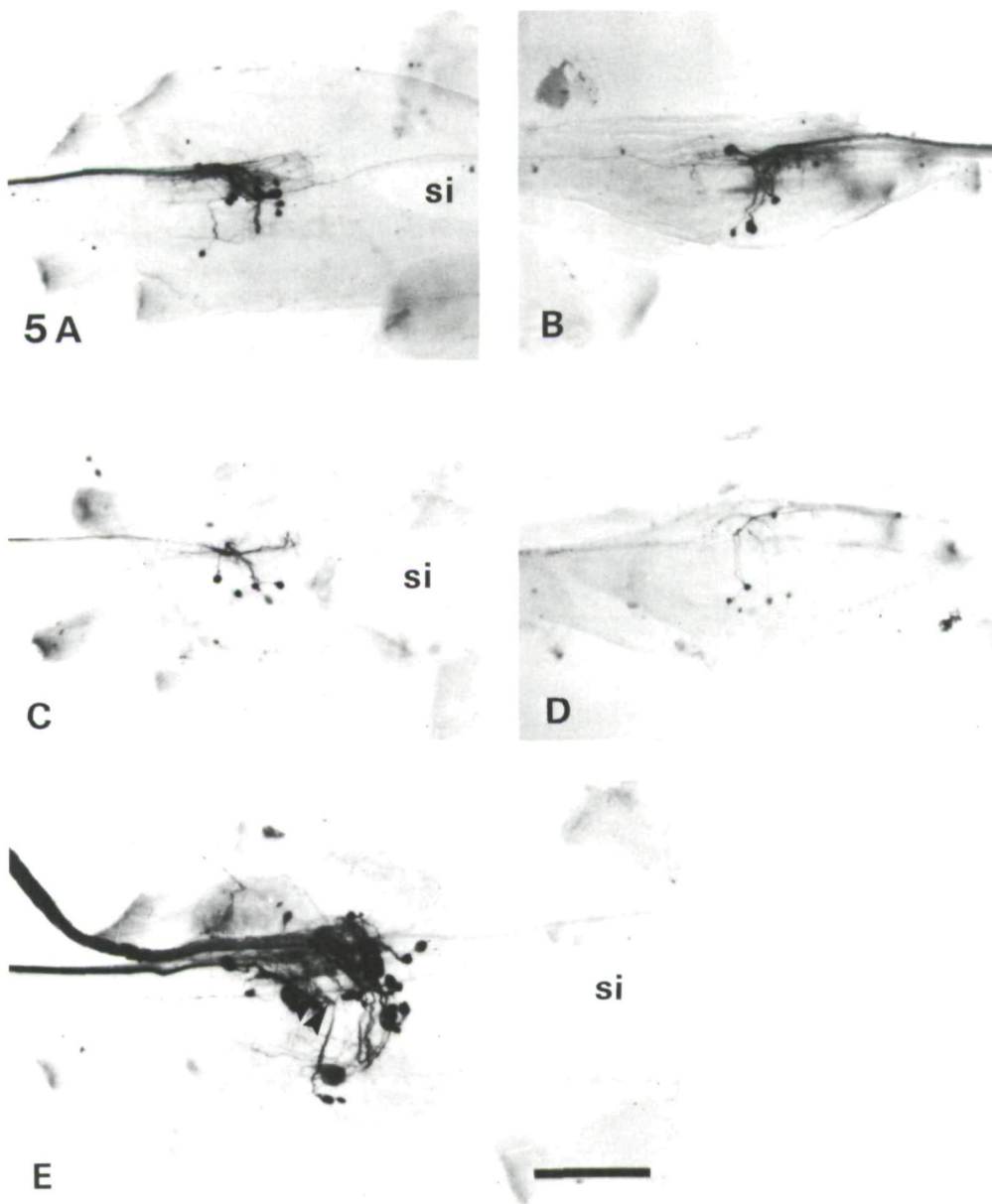

Fig. 5. Dorsal (A,C,E) and side (B,D) views of TA ganglia in which the thick 1A (A,B), the thin 1A (C,D) and the 1A and thin 5T roots (E) on the left side were backfilled with cobalt. In all cases the stained axons enter the TA ganglia caudally in the abdominal connectives and on the dorsal surface. Arrows indicate somata from the thin 5T root located with 1A root cell bodies. Scale bar, 500 μm (A–D), 250 μm (E). si, sinus between the TA and the third thoracic ganglion.

(the number of cells in each group ranged between three and seven in different preparations).

Backfilling the thin 1A nerve stained five or six cells ($\bar{x} = 5\cdot5$; $N = 16$). One or two cells were found on the dorsal surface: one cell was always located in the central midline of the ganglion, while, in six preparations, one cell was located caudally and laterally (Fig. 5C,D). The remaining cells ($\bar{x} = 4\cdot3$; range 3–5) were located ventrally in the midline of the TA ganglion. Axons from both the thick and thin 1A nerves extend rostrally on both sides through the thoracic ganglia (Fig. 5A,D). This was confirmed by matching activity recorded from the cut 1A roots with spontaneous activity recorded with microelectrodes from single axons in the short connective on either side of the sinus.

The use of cobalt and a mixture of cobalt and nickel allowed the differential staining of cell bodies in two roots. When this was done for the thin 5T root and the 1A roots it was found that in many preparations (nine) two or three axons in the thin 5T root had cell bodies in the same region as those from the 1A root (Fig. 5E).

Cursory observations showed that the neuromuscular relationships for the flexor muscles on the right side are similar to those on the left.

The third abdominal root

The third abdominal (3A) root leaves the abdominal connective in the first abdominal segment, rostral to the first abdominal ganglion; convention dictates that since one abdominal ganglion is fused with thoracic ganglia to form the TA ganglion, the remaining five abdominal ganglia are numbered 1 to 5 (Chapple, 1966*a*). The 3A root travels laterally to the flexor muscles in the first abdominal segment, which lie ventral to the dorsal thoracic flexor muscles. Brief electrical shocks applied to the GI evoked a spike in the ipsilateral 3A root (Fig. 6A) and a contraction of the fast flexor muscles in the first abdominal segment. Stimulation of the 3A root produced EJP activity and contractions of the ventral and dorsal flexor muscles (Fig. 6B,C).

Backfilling of the motor axons in the 3A root usually produced poor fills, probably due to the distance between the root and the TA ganglion (>3 cm). However, in some preparations cell bodies were stained. In one preparation, eight somata were filled in the caudal region of the TA ganglion (Fig. 6D); no dye-filled cells were observed in the first abdominal ganglion.

DISCUSSION

Although axons in the thick 4T, the thick 5T and the thin 5T roots extend into the thoracic ganglia, their cell bodies are restricted to the TA ganglion (Figs 4, 5). The thin 4T root, however, enters the nervous system in the short connective, which is located on either side of the sinus, and has cell bodies in the TA and the third thoracic ganglia (Fig. 4D). Thus it appears that, with the exception of the small number of thin 4T axons, all of the axons in the fourth and fifth roots have their cell bodies in the TA ganglion. In the absence of a distinct fourth thoracic ganglion
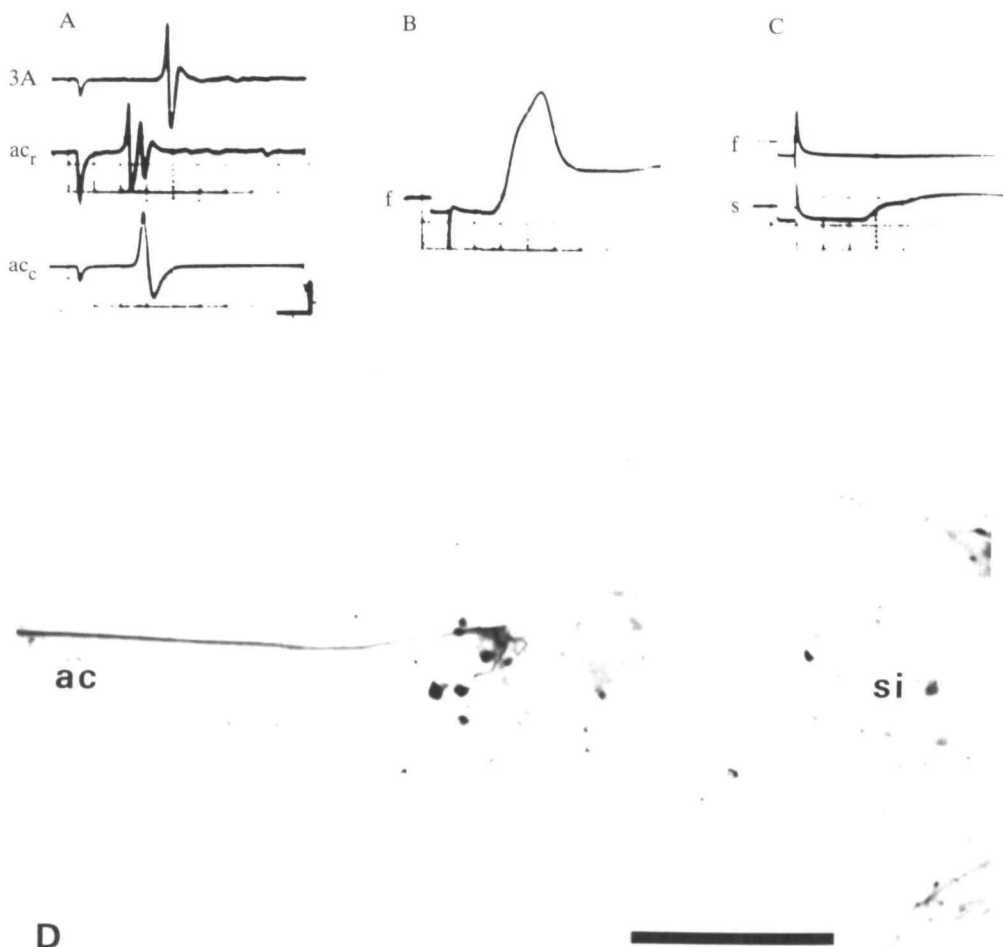
Fig. 6. Stimulation of the left GI in the oesophageal connective produced activity in a motor neurone whose axon travels in the abdominal connective and in the 3A root. Activity can be recorded in the abdominal connective (ac) rostral (r) to the root, but not caudally (c) to it (A). Stimulation of the root provoked activity in the fast (f) and slow (s) flexor muscles in the first abdominal segment (B,C). Backfilling of the left 3A root stained cell bodies in the caudal region of the TA ganglion (D). si, sinus. Calibration 500 μV (A), 5 mV (B,C), 2 ms (A), 5 ms (B,C); 500 μm (D).

in the hermit crab central nervous system (CNS), the fused TA ganglion must be considered to be composed of the first abdominal and the fourth and fifth thoracic ganglia.

The layout of the thoracic flexor muscles is simpler in the hermit crab (Fig. 1) than in the crayfish (Pilgrim & Wiersma, 1963). However, in the hermit crab the dorsal flexor muscles are asymmetrical since there is an extra branch of muscle on the left side (Fig. 1). This 'branch' appears to be part of the main muscle since it shares the same attachment at the rostral end, it is composed of fibres with similar contractile properties and it is innervated by the same motor axons (Fig. 3A). It would be interesting to speculate as to the selective advantage of this muscle arrangement, the

most obvious possibility being to produce a stronger contraction of the abdomen, which is curled to the right.

In the crayfish thorax, the number of axons that innervate the fast and slow flexor muscles is similar to that described for their abdominal counterparts (Kennedy & Takeda, 1965a,b), with the exception that one of the tonic flexors has two inhibitors (Suzuki, 1978, 1979). In the hermit crab, however, the innervation of the flexor muscles is different. Two motor axons in the 1A nerve innervate the dorsal flexor and produce rapid twitches of the muscle (Fig. 3A); one of these axons is the giant flexor motor neurone (GFMN) (Fig. 3D). No other motor axons appear to innervate this muscle. This is in contrast to the crayfish fast flexor muscle which is supplied by at least nine efferents in the abdomen (Mittenthal & Wine, 1978) and six efferents in the thorax (Suzuki, 1978).

The thin 1A nerve also sends two excitors to the slow ventral flexor muscles (Fig. 2C). However, backfilling of this nerve revealed that five or six thin 1A axons have their cell bodies in the TA ganglion. Therefore, there are one or two motor neurones whose function cannot be accounted for. It is possible that these axons innervate the fast dorsal muscle, but were not noticed because of the low stimulus threshold for one motor axon (probably the GFMN) that produced a large amplitude EJP and a rapid muscle twitch (Fig. 3). If this is the case, there would be a total of three or four motor axons to the dorsal muscle – still a much smaller number than in the crayfish and lobster deep flexor muscles (Kennedy & Takeda, 1965a; Suzuki, 1978; Parnas & Atwood, 1966).

The slow, ventral flexor muscle on the left side is supplied by at least seven excitatory motor neurones – there is no evidence for any inhibitory innervation. This number is larger than the number of excitors to the slow flexor muscles in the crayfish abdomen (Kennedy & Takeda, 1965b) or the thorax (Suzuki, 1979). The thick 1A nerve has at least three excitors to the slow ventral flexor muscle (Fig. 2D). Backfilling of this nerve stained about 10 somata (Fig. 5A,B); the function of the other seven efferents is yet to be established. The slow ventral flexor muscle is also supplied by at least two axons that leave the TA ganglion in the thin 5T root. It is interesting that backfilling showed that two or three efferents have their cell bodies in the same region as somata from the first abdominal roots (Fig. 5E). This provokes the idea of a grouping of functionally similar neurones within the CNS.

In crayfish the motor neurones that innervate the flexor muscles are located in three specific areas in the abdominal ganglia: anterior, medial and posterior (Mittenthal & Wine, 1978). A corresponding distribution has been found in the fourth abdominal ganglion of hermit crabs (Marrelli, 1975). Medial and posterior (caudal) cell clusters are present in the TA ganglion (Fig. 5), but the absence of anteriorly placed somata may be explained either by loss or by incorporation into the central cluster during the fusing of the thoracic and abdominal ganglia to form the TA ganglion.

In crayfish, the superficial abdominal flexor muscles are composed of slow fibres (Jahromi & Atwood, 1972; Ogonowski & Lang, 1979) and are innervated by motor neurones that exhibit spontaneous activity (Kennedy & Takeda, 1965b). Similarly,

the ventral thoracic flexor muscles are composed of fibres with long sarcomeres and are innervated by motor axons that show spontaneous activity (Fig. 2A,B). Although these data suggest that the ventral flexor muscle is slow, other results argue against this suggestion. In other slow crustacean muscles, motor neurone stimulation produces small amplitude EJPs that undergo facilitation and summation to produce a slow muscle contraction (Kennedy & Takeda, 1965b; Atwood, 1973). In the ventral muscle, however, there is at least one efferent that can produce a spike (Fig. 2D) and a muscle twitch.

In the hermit crab a GI spike produces a twitch contraction of the dorsal (fast) and the ventral (slow) flexor muscles (Fig. 3B). There is an electrical synapse between the GI and the GFMN, which innervates the ipsilateral dorsal flexors (Umbach & Lang, 1981; Stephens, 1986). Extracellular recordings (Fig. 3B) and lesion experiments indicate that the GI also makes a functional connection with a ventral flexor muscle efferent which has its axon in the thin 5T root. Finally, a GI spike elicits activity in the contralateral GFMN (Fig. 3D) *via* a chemical synapse (Stephens, 1986) and also evokes activity in a second contralateral motor neurone whose target is not known (Stephens, 1985). Therefore, a spike in one GI produces a contraction of the deep and the ventral flexors on the ipsilateral side and a contraction of, at least, the deep flexors on the contralateral side. This is in contrast to observations made in crayfish, where giant axon stimulation excites the fast neuromuscular systems but inhibits the slow (Kuwada & Wine, 1979). However, it must be remembered that the hermit crab escape response is not used for swimming but for withdrawal into a shell. Under these circumstances, it is not necessary to produce a prolonged sequence of tail flips. In fact, it seems reasonable that both fast and slow muscles should contract during the escape response of the hermit crab so that the crab can not only rapidly withdraw into the shell but can also utilize the tension built up in the slow muscle to maintain its withdrawn position. Similar observations have been made during escape in other animals. For example, in the scallop a synchronous contraction of both portions of the adductor muscle results in the fast muscle rapidly closing the shells and the slow muscle producing sufficient tension to prevent re-opening by a predator (Mellon, 1969; Stephens, 1978).

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