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THE CENTRAL NERVOUS ORGANIZATION OF THE MOTOR NEURONES TO A STEERING MUSCLE IN LOCUSTS

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SUMMARY

1. The pleuroaxillary or pleuroalar muscles of the locust (M85, M114) are located in the meso- and metathoracic segments only. Each extends from the posterior face of the pleural ridge and runs dorsally and obliquely, inserting on the third axillary sclerite of the wing hinge. Each muscle consists of two distinct parts, a and b (Fig. 1).

2. Each pleuroaxillary muscle is innervated by two motor neurones which give rise to a small and a large muscle potential in electromyogram recordings (Fig. 6E). The cell body of each neurone lies posteriorly in the ganglion and the axon runs out in nerve 4 (Figs 3–6).

3. The two motor neurones of a particular muscle share many common morphological features (Figs 3–6). There is also clear segmental homology between the motor neurones supplying the meso- and metathoracic muscles (Fig. 3).

4. Serial transverse sections of the motor neurones show that their arborization is confined mainly to a dorsal region of the neuropile. Some of the collaterals encompass, and terminate in, dorsal longitudinal tracts. Branching extends far anteriorly. Posteriorly, one secondary neurite runs ventrally (Figs 7, 8). A few secondary and tertiary neurites of the metathoracic pleuroaxillary motor neurones terminate within the neuropile of the first abdominal neuromere (Figs 6, 8). Additional features which distinguish these neurones from other flight motor neurones are discussed.

INTRODUCTION

A prerequisite for a cellular study of locust flight is the identification of motor neurones innervating the wing muscles. The number and location of motor neurones supplying the power (elevator and depressor) muscles of the wings has been revealed by backfilling the motor nerves of these muscles with cobaltous chloride (Tyrer & Altman, 1974). Physiological and anatomical identification of individual motor neurones has been achieved by intracellular recording and dye filling (Bentley, 1970;

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Burrows 1973*a*; Burrows & Hoyle, 1973). Almost all of the cell bodies of these flight motor neurones occur in clusters comprising neurones with axons in the same nerve, for example a posterior-lateral cluster of neurones whose axons run in peripheral nerve root 4. Motor neurones of a single muscle lie together and their processes follow parallel courses through the neuropile (Bentley, 1970; Tyrer & Altman, 1974). The location of the soma of an individual flight motor neurone within a ganglion is consistent from animal to animal, so that maps of motor neurones become useful in guiding microelectrodes for intracellular recording.

The relationship of a stained flight motor neurone to identified neuronal tracts, commissures and sensory neuropiles (Tyrer & Gregory, 1982) can be revealed by serial sectioning. Motor neurones of the power muscles arborize in a relatively thin sheet in the most dorsal neuropile (Tyrer & Altman, 1974; Tyrer, 1983). However, in addition to the large power muscles a small pleuroalar muscle is found in each pterothoracic segment and may exert fine control over wing twisting, thus acting as a flight steering muscle (Pfau, 1976, 1977, 1983). This pleuroalar muscle inserts close to, or at, the third axillary sclerite (a component of the wing hinge) and was termed the pleuroaxillary muscle by Alicata (1962), a name adopted in this and the subsequent paper (Elson & Pflüger, 1986). In the numbering of Snodgrass (1929) the mesothoracic pleuroaxillary muscle is M85 and the metathoracic one M114. This muscle has been largely overlooked in previous studies of insect flight.

This paper describes the anatomy and innervation of the muscle, the location and structure of its two motor neurones and their arborization in the neuropile as revealed by serial sections. It also provides the anatomical basis for the subsequent paper dealing with functional aspects of the pleuroaxillary muscles (Elson & Pflüger, 1986).

MATERIALS AND METHODS

Locusts used for this investigation were *Locusta migratoria* (L.) and *Schistocerca gregaria* Forskål kept in crowded laboratory cultures at Konstanz and Cambridge. As no differences between the two species regarding the morphology of the investigated neurones were noticed, results were pooled unless otherwise stated in the text.

All muscles were numbered according to Snodgrass (1929).

Cobalt backfills

Exposing the motor nerve to the pleuroaxillary muscle (N4D4; Campbell, 1961) was achieved in one of two ways: either, the locust was opened dorsally and the tergocoxal remotors (M90/91 and M119/M120) removed, or a window was cut into the meso- and metathoracic pleura and the subalar muscle (M99 and M129) removed (see also Fig. 1). A pool of Vaseline was formed around N4D4 and, after cutting the nerve, it was filled with 3–6% hexammine cobaltic chloride (Brogan & Pitman, 1981). This allowed peripheral and central axonal backfilling in the same preparation (Pitman, Tweedle & Cohen, 1972; Mulloney, 1973). The preparation was kept for 12–48 h at about 6°C in the refrigerator. Then the pterothoracic ganglia were

exposed and the whole preparation immersed in about 1% $(NH_4)_2S$ for 10 min. The peripherally stained muscles M85 and M114 inserting on their wing base, and the central stains, consisting of the dye-filled motor neurones in the meso- and metathoracic ganglia, were subsequently silver intensified (Bacon & Altman, 1977).

The results are based on the following numbers of backfills: 48 M85 and 40 M114 in 50 *Locusta migratoria,* and 10 M85 and 15 M114 in 20 *Schistocerca gregaria*.

Intracellular cobalt fills

The motor neurones of the pleuroaxillary muscles were stained intracellularly by microelectrodes filled with 6% hexammine cobaltic chloride (resistance 60–80 MΩ) using depolarizing current pulses of 5 to 10 nA, and 500 ms duration, at 1 Hz for 15–20 min. The ganglia were then left within the animal under continuously running saline (Usherwood & Grundfest, 1965) for another 20–30 min to let the cobalt ions diffuse. The ganglia were dissected out, developed conventionally, silver intensified and drawn as whole mounts. The results are based on seven intracellular fills of M85 motor neurones in *Schistocerca gregaria* and 20 intracellular stains of M114 motor neurones in *Locusta migratoria*.

Light microscopic sections

The ganglia with the stained motor neurones were embedded in soft resin (Durcupan, Fluka-Chemie) and serial transverse sections (10–20 μm) were made. The sections were photographed, and filled motor neurones were reconstructed by *camera lucida* drawings. Tracts and neuropiles were named after Tyrer & Gregory (1982), Pflüger, Bräunig & Hustert (1981) and Siegler & Burrows (1984). Transverse sections (20 μm), stained with methylene blue, were also made from both muscles (two M85 and two M114) and from the motor nerve, N4D4, where it enters the muscle.

Electron microscopic sections

To reveal the number of axons within the motor nerve, electron microscopic (EM) sections were made from N4D4 in the meso- and metathorax (two from *Locusta migratoria* and two from *Schistocerca gregaria*). The exposed nerve was prefixed within the animal in a solution containing: 0·1 mol l^{-1} sodium cacodylate buffer, 3% glutaraldehyde and 3% formaldehyde. The nerve was dissected and fixed in 2% OsO_4 in 0·1 mol l^{-1} sodium cacodylate buffer for 2 h. After dehydrating it was embedded in Spurr's resin (Spurr, 1969).

RESULTS

The peripheral location of the pleuroaxillary muscles

Each pleuroaxillary muscle is located peripherally underneath the subalar muscle (Fig. 1A, inserts B and C). A pleuroaxillary muscle originates on the posterior face of

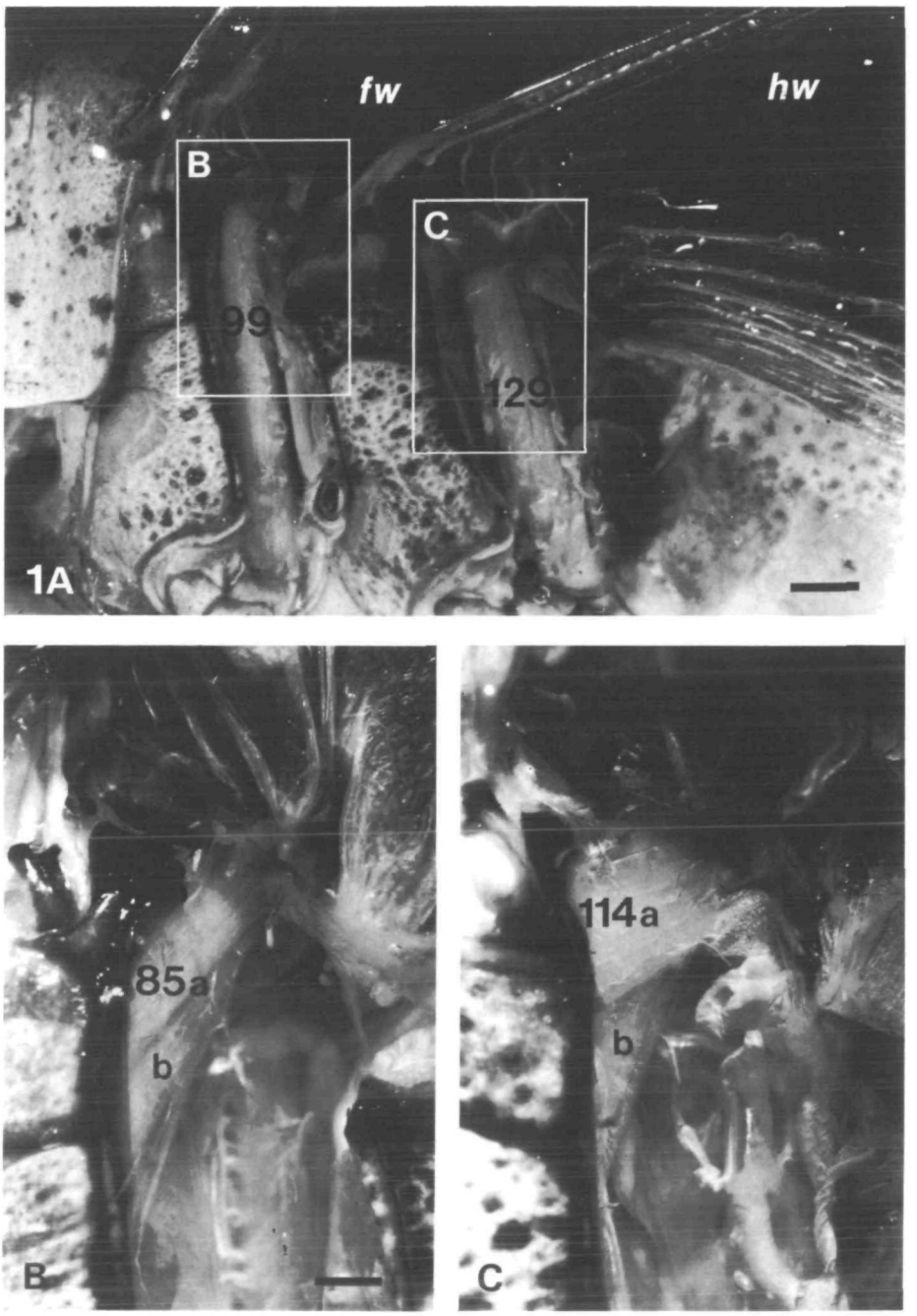

Fig. 1. External view of the left side of a *Locusta migratoria*. (A) Meso- and metathoracic epimera, as well as the base of the fore wing (*fw*) and hind wing (*hw*) are shown. Epimera are removed and the two subalar muscles (M99, insert B, and M129, insert C) are exposed. Scale bar, 1 mm. (B,C) When both subalar muscles are removed, the pleuro-axillary muscles are clearly visible (M85a,b in B and M114a,b in C). Note that in both segments each muscle consists of two parts. Scale bar, 500 μm.

the pleural ridge and runs dorsally and posteriorly to insert on the third axillary sclerite, a component of the wing hinge (Pterale 3, Pfau, 1977; Fig. 1B,C).

Both muscles are clearly divided into two parts. The upper (dorsal) part of M114 has been termed part a, the lower (ventral) part, b, by Snodgrass (1929). We have adopted this nomenclature for M85 also. These parts are clearly seen at the pleural origin (Fig. 1B,C). The length of each pleuroaxillary muscle (part a: 1–2 mm; part b: 2–3 mm) is small compared to the length of the subalar muscle, a flight power muscle (6–7 mm). In each segment, the pleuroaxillary muscles are supplied by a branch of nerve 4 of the appropriate segmental ganglion (NIVDb in Ewer, 1953, 1954*a*; and N4D4 in Campbell, 1961).

EM sections of nerve N4D4 just before it enters the muscle (Fig. 2) reveal two large axons (diameter 15 μm and 11 μm in *Schistocerca gregaria*) and a number of smaller axons (diameters between 2 and 3·5 μm). Four to five of these smaller profiles, from unidentified neurones, could always be found in *Locusta* and *Schistocerca* (Fig. 2). It is possible that these unidentified neurones belong, or once belonged, to a pleural-subalar muscle that can be seen in dissections of larvae (larval stage 4–5) and young, freshly-moulted adults, in meso- and methathoracic segments (see also Ewer 1954*b*, 1957). This muscle extends from the pleural ridge, where it inserts ventral to M85b or M114b, to the cuticle near the insertion of M90/91 or M119/120 (in Fig. 1 this point is underneath the subalar muscle). In older adults this muscle disappears, but a strand of connective tissue, often containing deposited fat, still shows the earlier course of the muscle fibres (removed in Fig. 1B,C to expose pleuroaxillary muscles more clearly). As far as we can tell this larval muscle is also supplied by N4D4 (see also Fig. 4 and Discussion).

Location of motor neurone somata and overall branching pattern

Fig. 3 shows a mesothoracic (Fig. 3A,C) and metathoracic (Fig. 3B) ganglion in which the nerve innervating the pleuroaxillary muscles had been filled with cobaltous chloride. In each ganglion the cell bodies of two large motor neurones (diameter about 65 μm and 75 μm) lie posteriorly on the ventral edge of the ganglion, a feature which corresponds well with the position of somata of other flight motor neurones leaving the ganglion through nerve 4 (Bentley, 1970; Tyrer & Altman, 1974). A side view of the mesothoracic (Fig. 3C) and metathoracic ganglion (not shown in Fig. 3) shows that the branching of these motor neurones occurs mainly in the dorsal part of the ganglion, except for a few small branches given off by the primary neurite soon after emerging from the cell body. This can be seen more clearly in sections of these ganglia (Figs 7, 8). The pattern of branches (secondary neurites) which arise from the primary neurite is characteristic for these neurones. All four motor neurones show a striking similarity of overall branching pattern (Fig. 3A,B). In each of the neurones the secondary neurites arise from the primary neurite at similar locations and the neurites of the two motor neurones to a given muscle run parallel for considerable distances through the neuropile, sometimes twisting around one another (see also Fig. 7B,C). A difference from other flight motor neurones is that the pleuroaxillary motor neurones possess only few conspicuous secondary neurites;

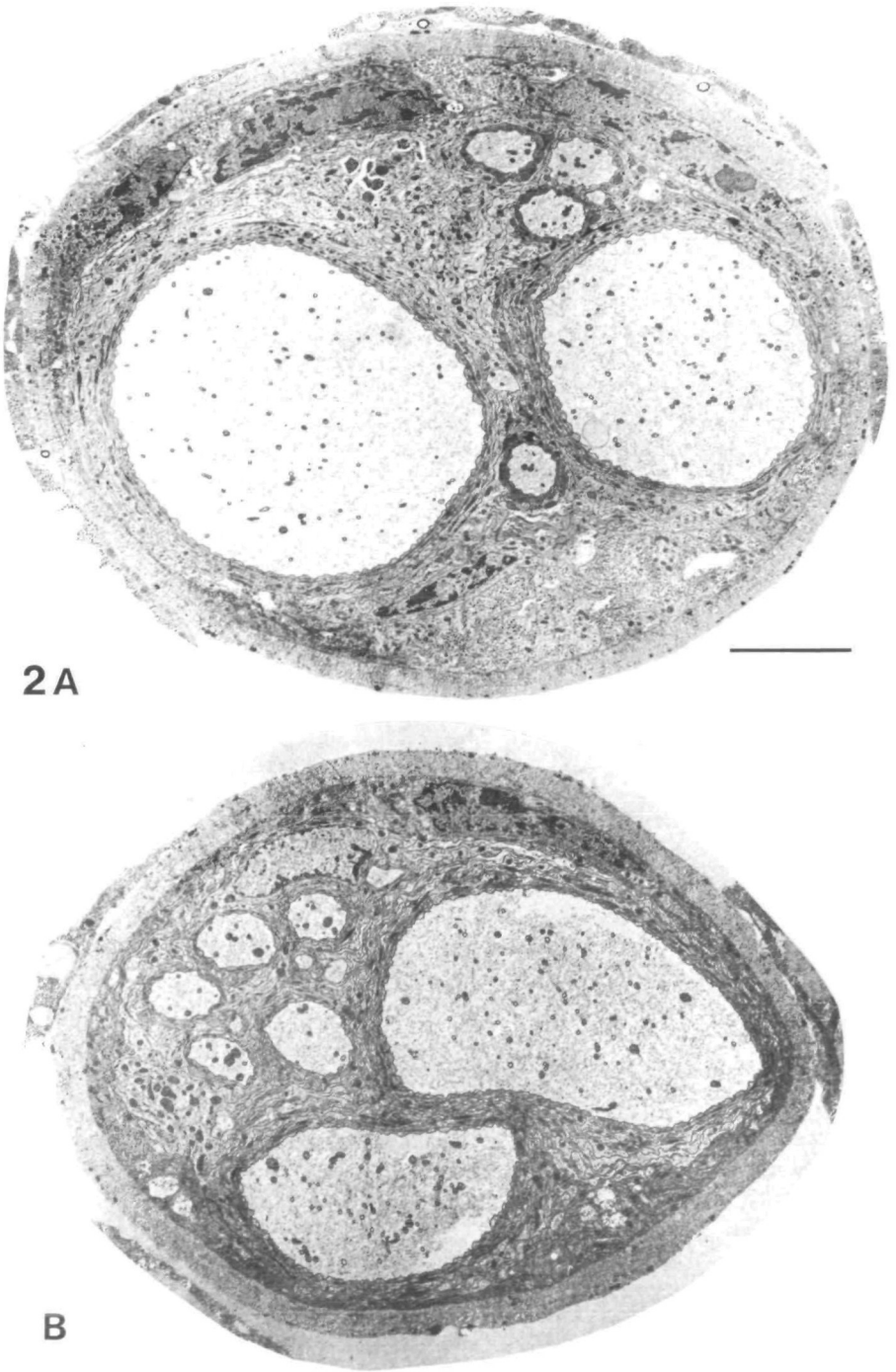

Fig. 2. Electron microscopic cross sections through the mesothoracic N4D4 at its entrance into M85. (A) *Schistocerca gregaria,* (B) *Locusta migratoria.* Scale bar, 5 μm.

these prominent branches taper and divide to form profuse fine branches (tertiary and higher order neurites) that occupy specific distinctive areas of neuropile. In contrast, other flight motor neurones have many more, thinner secondary neurites,

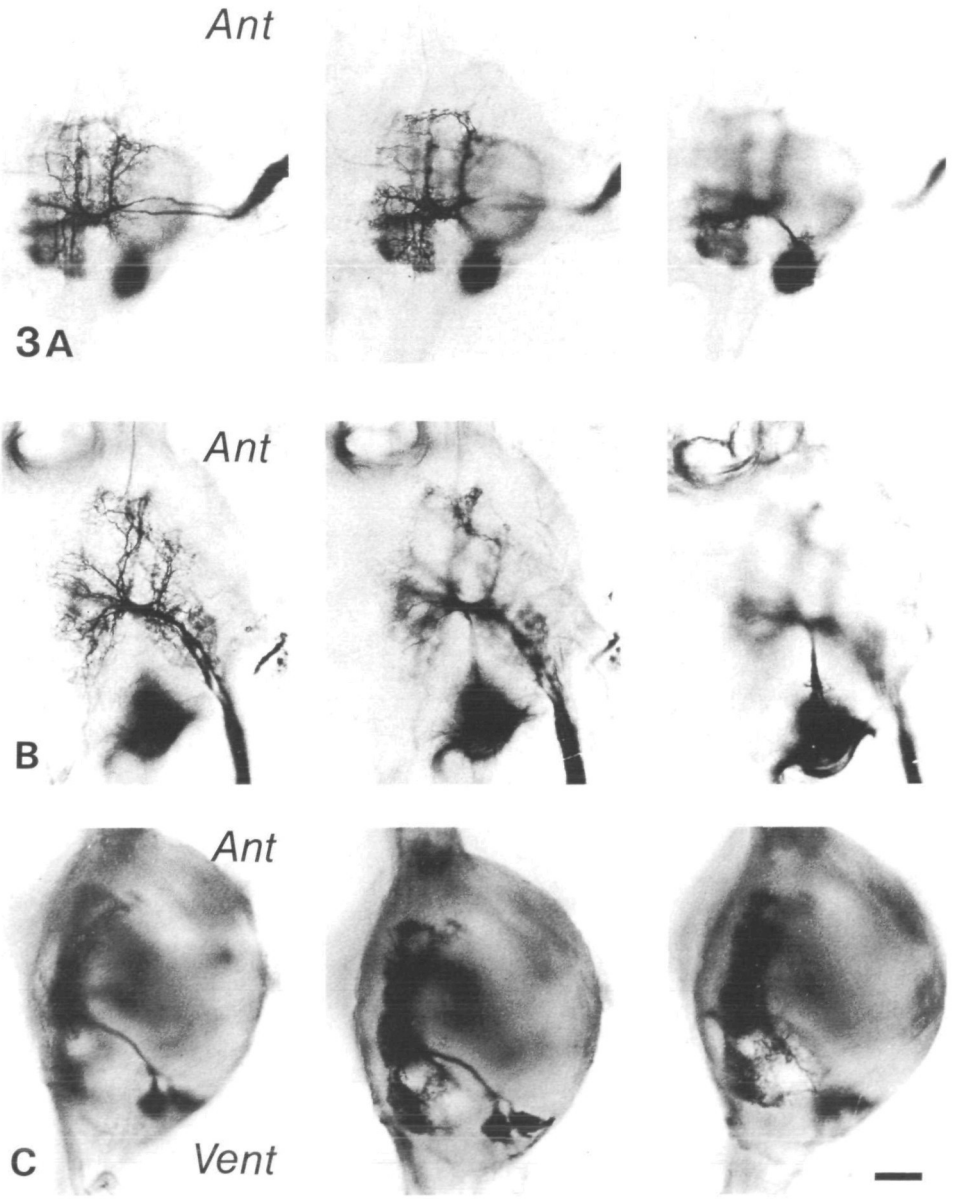

Fig. 3. Central cobalt backfill of a mesothoracic (A,C) and metathoracic (B) N4D4 showing both motor neurones of M85 (A,C) and M114 (B). (A) and (B) focus series from dorsal (left) to ventral (right) of a mesothoracic (A) and metathoracic (B) ganglion. (C) A side view of a mesothoracic ganglion with both M85 motor neurones stained, focusing from lateral (left) to median (right). Scale bar, 100 μm. Ant, anterior; Vent, ventral.

and form a uniform sheet of fine branching in the dorsal neuropile (Tyrer & Altman, 1974).

In 10 out of the 35 backfills of N4D4 of the metathoracic ganglion, several additional small cell bodies (diameters between 10 and 20 μm) were observed (Fig. 4, arrow). These cell bodies lay in the same cluster as the two large motor neurones of M114. Although the axons belonging to these small cell bodies could be seen in nerve 4, their processes within the ganglion were largely masked by those of the two large motor neurones. Their primary neurites were visible for only a short distance before they joined the primary neurite path of the two large cells. From three specimens in which the large motor neurones were not as densely stained as usual, it was found that the processes of the small neurones followed a course similar to that of the large motor neurones.

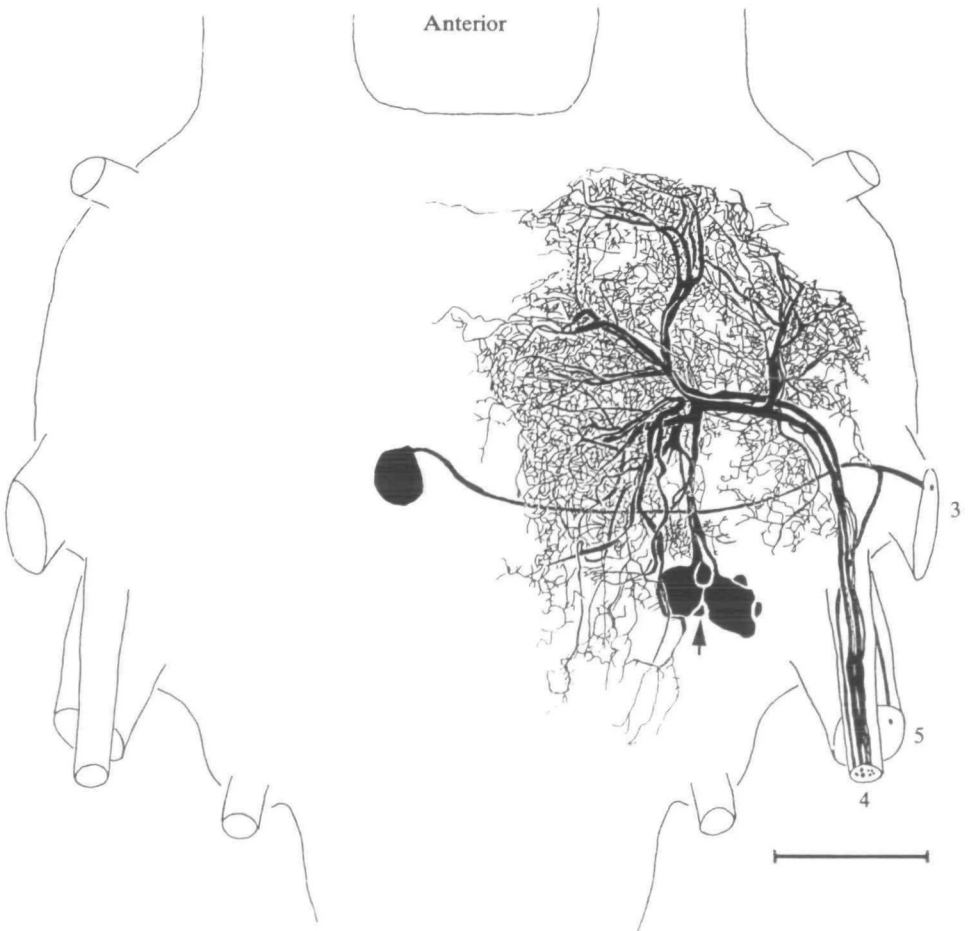

Fig. 4. A *camera lucida* drawing of the metathoracic ganglion showing the neurones which stain when N4D4 was cobalt backfilled. Arrow, see text. Scale bar, 200 μm. 3–5, number of peripheral nerves.

A median cell body (diameter approx. 70 μm) was observed, weakly stained, in 10 of the preparations of M114 (e.g. Fig. 4). The axon of this cell was observed to form collaterals which left the ganglion through peripheral nerves 3, 4 and 5. These morphological features suggest that it is the common inhibitor neurone (CI, Burrows, 1973*b*). In eight additional preparations out of a total of 58 preparations of M85 one axon was stained which ran in nerves 3, 4 and 5, again suggesting innervation by CI.

Detailed branching pattern of the two pleuroaxillary motor neurones of one segment

This was revealed by individual staining by intracellular injection of cobalt. Best recordings were usually obtained from neuropilar processes. The motor neurones could be distinguished by the size of the muscle potential that they evoked (see Fig. 6E): one motor neurone gave rise to a large muscle potential (large unit), the other to a smaller one (small unit). The two motor neurones in Fig. 5 were identified as those of a small (Fig. 5A) and large (Fig. 5B) unit of M85.

Both neurones are very similar in overall morphology. The motor neurones are characterized by prominent secondary neurites which run longitudinally and anteriorly (labelled *a–c* in Fig. 5). The neurone of Fig. 5A has three such neurites, whereas the neurone of Fig. 5B has only two of them (*a* and *c*) that are conspicuous, although the third (*b*) is present but much shorter. Some of the prominent secondary neurites turn medially, to follow the anterior edge of the neuropile (Fig. 5A, *a* and *b*; Fig. 5B, *a*). Both motor neurones are also characterized by two layers of posterior-medial branches (Fig. 5, *d* and *e*) that arise at the transition between the primary neurite and its expanded part, the neuropilar segment. These form an intricate fan of fine branches. An unusual feature of these neurones as compared to other flight motor neurones is the possession of a distinct branch (*f* in Fig. 5) which arises from the primary neurite close to the cell body. Its fine branches mingle with the posterior-medial branching. The other difference by which we could always distinguish the motor neurones of M85 from each other in our fills was the presence of a branch (Fig. 5B, arrowhead) running anteriorly and medially from the longitudinal neurite (*a*).

Fig. 6 shows *camera lucida* drawings of the two motor neurones of M114 in which only the main branches have been drawn (except Fig. 6A, which shows the finest terminal branches of one of the two neurones). The motor neurone producing the small muscle potential is shown in Fig. 6A,B and that causing the large muscle potential in Fig. 6C,D. An example of the difference in size of the extracellularly recorded muscle potential is shown in Fig. 6E, in which an intracellular record of the motor neurone producing the large muscle potential is also shown. A distinctive feature is the clear transition between the primary neurite which leaves the soma, and its expanded part, the neuropilar segment, from which all the secondary neurites arise, in contrast to other flight motor neurones (Tyrer & Altman, 1974). A comparison of the meso- and metathoracic motor neurones shows again that they share many common features. These include the two layers of posterior medial (*d* and *e* in Fig. 6B,C), as well as anterior branches (*a–c* in Fig. 6B,C) that run longitudinally and turn medially (only *a* and *c* in Fig. 6B,C) at the edge of the neuropile. The two motor

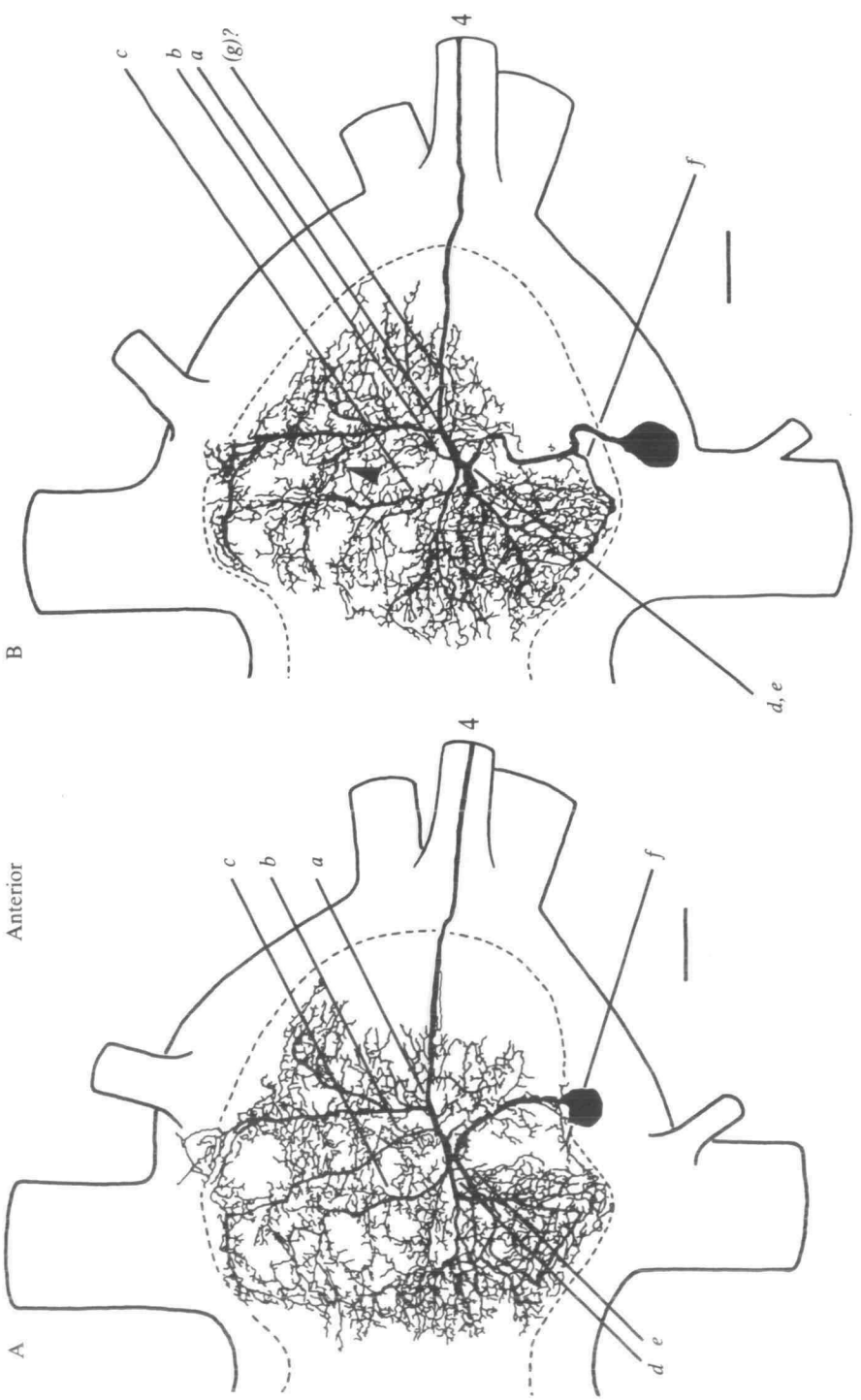

Fig. 5. *Camera lucida* drawings of M85 motor neurones stained by intracellular injection of cobalt. (A) Motor neurone of small unit. (B) Motor neurone of large unit. Arrowhead refers to the neurite which distinguishes between motor neurones. Different neurites are labelled *a–f*. Scale bar, 100 μm.

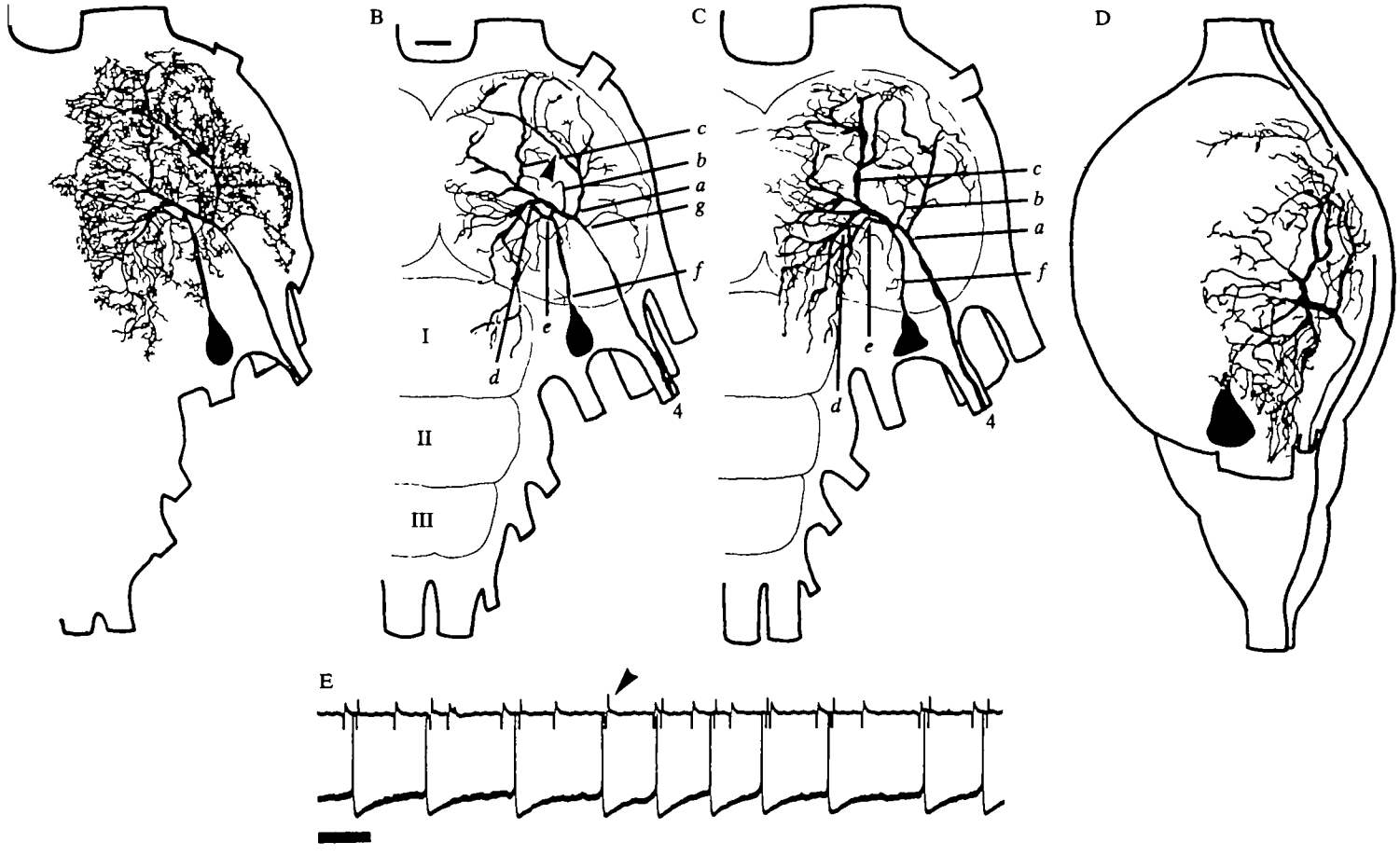

Fig. 6. *Camera lucida* drawing of M114 motor neurones stained intracellularly. (A) and (B) Motor neurone of small unit; in B only main branches (primary, secondary and conspicuous tertiary neurites) are shown. Arrowhead, see text. (C) and (D) Motor neurone of large unit; D shows a side view. Only main branches are drawn. (E) An electromyogram of the metathoracic pleuroaxillary muscle (upper trace) and an intracellular record from the motor neurone causing the large muscle potential (lower trace) is shown. Arrowhead shows summation of amplitudes of both units due to simultaneous firing. Scale bar, 100 μm (A–D), 100 ms (E). Different neurites are labelled *a–g*.

neurones of M114 differ from each other in several respects. (i) The motor neurone of the small unit (Fig. 6B) possesses one branch (Fig. 6B, arrowhead) running antero-medially from the secondary neurite (*a*) which is missing or not prominent in the other motor neurone (Fig. 6C). Also there is a fourth secondary neurite (*g* in Fig. 6B) which is missing in the motor neurone of the large unit. (ii) The motor neurone of the large unit has more conspicuous branches from the secondary neurites (see branches of *c*, *d* and *e* in Fig. 6C,B). (iii) More branches extend into the first abdominal neuromere from the motor neurone of the large unit than from that of the small unit (Fig. 6B). In contrast to the mesothoracic pleuroaxillary motor neurones, those of the metathorax lack a prominent branch close to the soma (*f* in Fig. 5). Only a very short branch occurs at this point (*f* in Fig. 6B,C).

Arborizations of pleuroaxillary motor neurones in the neuropile

The distribution of branches within the neuropile was revealed by transverse sections. In a backfill of the nerve innervating M85 (Fig. 7) the main branches of the two motor neurones could be distinguished easily as one of them was more darkly stained (black and shaded in Fig. 7). Most of the branching of the primary neurite is confined to a very dorsal area of the ganglion bounded laterally by the dorsal lateral edge of the neuropile, medially by the MDT (median dorsal tract) and ventrally by the DMT (dorsal median tract) and the DIT (dorsal intermediate tract). Many of the fine branches enter the dorsal tracts, mainly MDT, DMT, DIT, and to a lesser extent also LDT (lateral dorsal tract), in which they terminate (Fig. 7A–C). In the most anterior region, fine branches terminate in the region of the incoming root of nerve 1, which contains all the sensory neurones of the wing and wing hinge (not shown in Fig. 7, but cf. Fig. 8, section 1). In the most posterior region a prominent branch (cf. Fig. 5, *d* and *e*) runs ventrally and terminates in the neuropile around the VIT (ventral intermediate tract), MVT (median ventral tract) (which it also penetrates) and VMT (ventral median tract). The most posterior branches are shown in Fig. 7D. One very dorsal branch (arising from neurite *c*, cf. Fig. 4) crosses the longitudinal midline and runs into the contralateral half for about 40 μm (Fig. 7B, cf. also Fig. 4). Otherwise the branching is entirely ipsilateral. As mentioned before, secondary neurites originate from the primary neurite at similar locations and are often twisted around each other (Fig. 7A,C).

Sections of the motor neurone of the large units of M114 are shown in Fig. 8A, that of the small unit in Fig. 8B. There are many features similar to those of M85 neurones (cf. Fig. 7). Extensive branching occurs, mainly in a very dorsal area bounded by the MDT, DMT, DIT and LDT (Fig. 8, sections 2 and 3). Laterally, fine branches follow the edge of the neuropile to an intermediate level which corresponds to a plane drawn through VIT (Fig. 8, section 2). Many fine branches terminate in the same dorsal tracts (MDT, DMT, DIT and LDT, Fig. 8, sections 2 and 3). As in the mesothoracic ganglion the most anterior dorsal branches terminate near the incoming axons of the nerve 1 root (section 1 in Fig. 8). Similarly, one secondary neurite runs ventrally and terminates in a neuropilar area surrounded by VIT, MVT and VMT. However, it was not seen to penetrate MVT (Fig. 8,

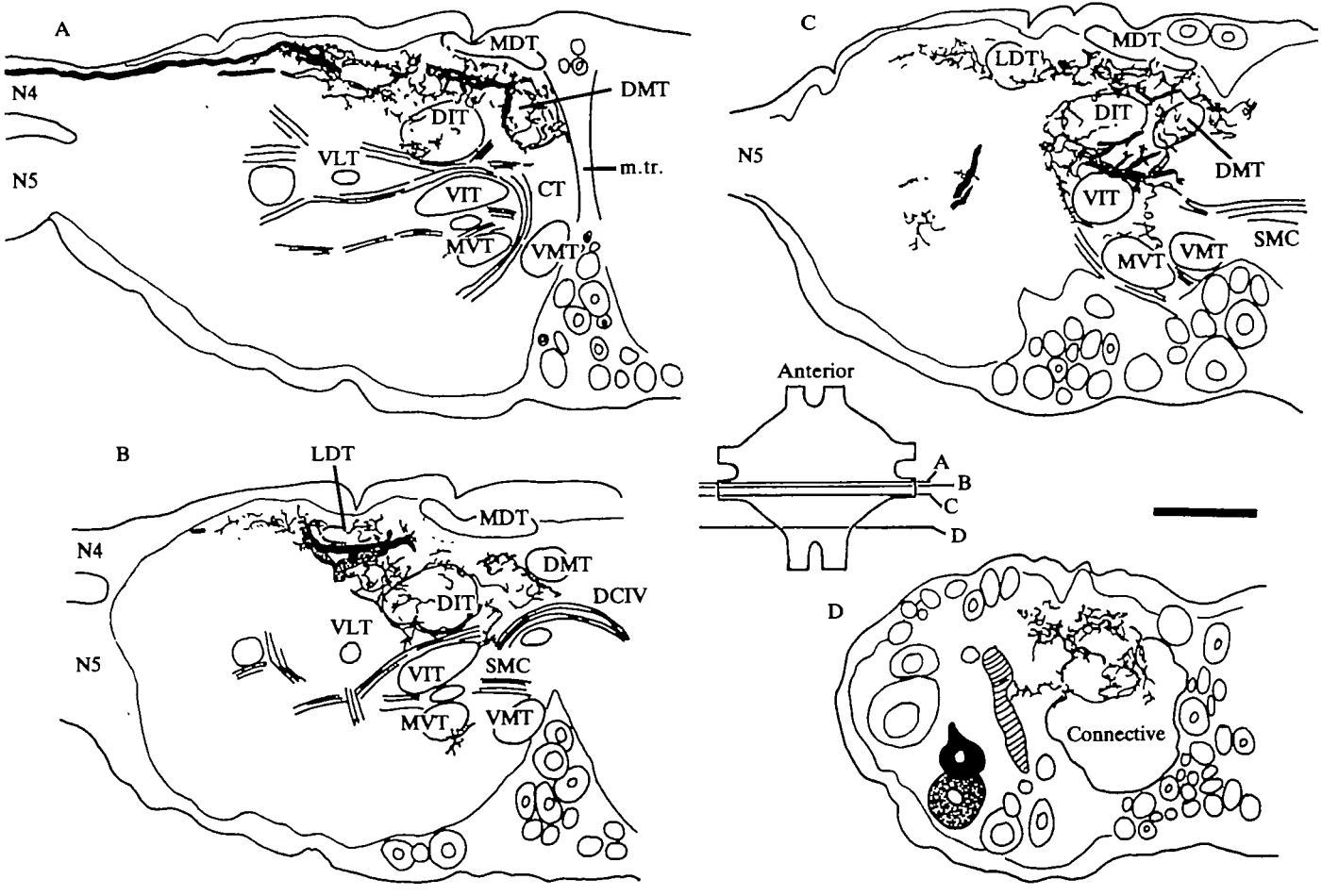

Fig. 7. Transverse sections (20 μm) of a mesothoracic ganglion, in which both motor neurones of M85 have been stained. Abbreviations (also valid for Fig. 8, if used in both figures): tracts: CT, C-tract; DIT, dorsal intermediate tract; DMT, dorsal median tract; LDT, lateral dorsal tract; MDT, median dorsal tract; MVT, median ventral tract; VIT, ventral intermediate tract; VMT, ventral median tract; VLT, ventral lateral tract. Commissures and nerve roots: DCI–VI, dorsal commissures I–VI: SMC, supramedian commissure. Nerves: N4 and 5 correspond to the peripheral nerves. m.tr., midline trachea. Scale bar, 100 μm. Insert shows level of sections.

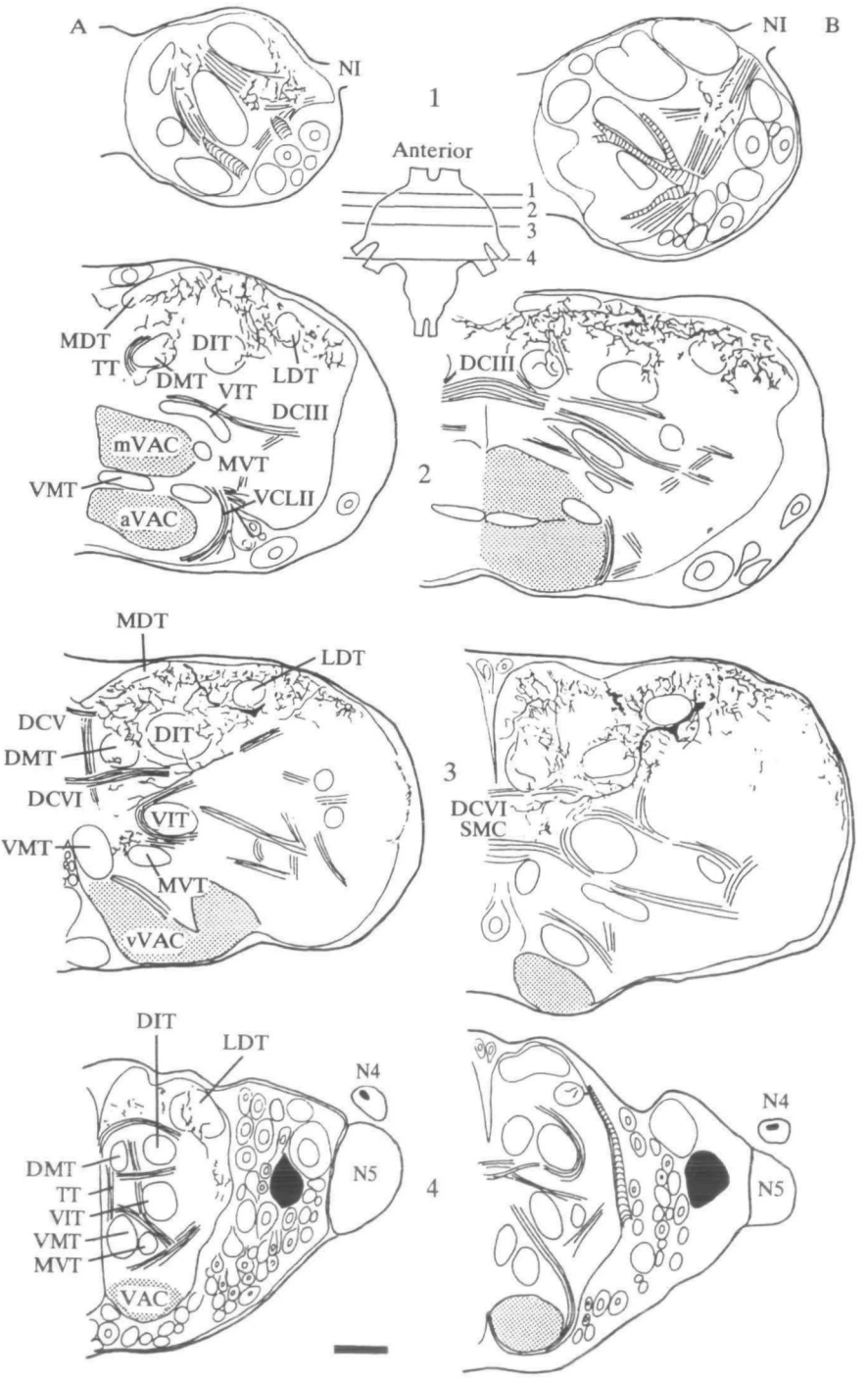

Fig. 8. Transverse sections (10 μm) of both M114 motor neurones: Sections in column A are small unit, sections in column B are large unit. Section 4 is at the level of the first abdominal neuromere. For abbreviations see Fig. 7 and TT, T-tract; VAC, ventral association centre; mVAC, median VAC (Bräunig, Hustert & Pflüger, 1981); vVAC, ventralmost VAC; nerves N1, N4, N5, peripheral nerves. Scale bar, 100 μm. Insert shows level of sections.

section 3). A characteristic feature of M114 motor neurones is branches that run posteriorly and terminate within the dorsal neuropile of the first abdominal neuromere (section 4 in Fig. 8). In sections of both metathoracic motor neurones a single thin branch crossed the midline dorsally, extending about 50 μm into the contralateral neuropile (section 2 in Fig. 8). All other branches terminate within the ipsilateral half of the ganglion.

DISCUSSION

Innervation of pleuroaxillary muscles

The pleuroaxillary muscle in both the meso- and metathoracic segments consists of two parts (A and B, cf. Fig. 1). A similar division into two or more bundles occurs in at least two power flight muscles (Neville, 1963, dorsal longitudinal flight muscle; Kutsch & Usherwood, 1970, subalar muscle). Two large axons innervate a pleuroaxillary muscle and these are ascribed to the two large motor neurones with posterior cell bodies. These motor neurones resemble other flight motor neurones in that their somata lie together and occur in the same cluster as other motor neurones which exit the ganglion in nerve 4. Similarly, their primary neurites and main branches run together in the neuropile. In a subsequent paper (Elson & Pflüger, 1986) we show that each muscle part is supplied by only one motor neurone. It is not known which of the two motor neurones innervates which part. This could only be decided in paired intracellular recordings from muscle fibres and motor neurones. The only distinction that was made in the course of recording was in the size of the muscle potential in the electromyogram (e.g. Fig. 6E; cf. Heukamp, 1984). This may depend largely on the location of the electrode wires in the two muscle parts. Therefore discrepancies in the size of the muscle potential may not reflect true differences in the properties of the motor neurones. This might account for the occurrence of the antero-medial branches in the 'large' unit of M85, but in the 'small' unit of M114. We assume that in the case of the wing mechanism each pleuroaxillary motor neurone of the meso- or metathorax with homologous morphological features probably exerts the same functions.

Backfills of the nerve (N4D4) which supplies these muscles sometimes stain a midline cell which is probably the common inhibitor (CI, cf. Fig. 4). The innervation of the pleuroaxillary muscle by CI may be variable or non-functional as this cell cannot always be stained in N4D4 (P. Bräunig, personal communication) and intracellular recordings from single muscle fibres do not show inhibitory junction potentials (Elson & Pflüger, 1986). This might result from developmental changes in the region of the pleuroaxillary muscles during the larva–adult transition (see below). The function of innervation by a peripheral inhibitor of leg muscles (CI) remains obscure.

Several small axons were always seen in cross sections of N4D4. These are unlikely to arise from peripheral sensory neurones, as none were ever stained in peripheral backfills. Therefore we assume that the small axons belong to the small central cell bodies filled in addition to the large motor neurones (cf. Fig. 4). The same motor

nerve, N4D4, contains axons innervating adjacent larval muscles (Ewer, 1954*b*, 1957). These additional muscles may form a third part of the pleuroaxillary muscle (cf. adult crickets, in which M85 consists of three parts, Elliot, 1983) or may include the pleuro-subalar muscle described by Ewer (1954*b*). The motor neurones which supply these larval muscles are unknown, but they may survive in young adults as the observed small neurones. Dense core vesicles in some of them (Fig. 2) may suggest a possible neurosecretory function for them in an adult locust.

Morphology of motor neurones

The two motor neurones which supply a single pleuroaxillary muscle are remarkably similar in the course of the primary neurite and their pattern of secondary neurites. The motor neurones can be distinguished only by the absence or presence of branches running anteriorly and medially (Figs 5, 6). The pattern of higher order neurites is more variable. Such a similarity between motor neurones of the same muscle is found in other flight motor neurones (Burrows, 1973*a*; Tyrer & Altman, 1974; Elepfandt, 1980; Elliott, 1983). The meso- and metathoracic pleuroaxillary motor neurones have many features in common, showing extensive serial homology (also a feature of other flight motor neurones, cf. Tyrer & Altman, 1974; Hedwig & Pearson, 1984).

Nevertheless, pleuroaxillary motor neurones differ from those of other flight muscles in several respects. The metathoracic neurones possess posterior branches which extend into the first abdominal neuromere. In contrast all other hindwing flight motor neurones are confined wholely to the metathoracic neuromere. It is interesting to note that several premotor interneurones originate and branch in the first abdominal neuromere (Robertson & Pearson, 1983). The mesothoracic neurones possess a prominent branch arising from the primary one close to the soma, a feature not observed in other flight motor neurones, which possess branches at the same point that are thinner and much shorter (cf. Burrows, 1973*a*; Tyrer & Altman, 1974). This branch in the pleuroaxillary neurones arborizes in the same posterior region as other branches. However, it is not clear why any input should be conveyed to the primary neurite so far from the presumed zone of spike initiation (near the origin of the axon, as in other arthropod motor neurones). Like other flight motor neurones, the main branching area lies within the ipsilateral half of the ganglion, but one neurite runs a short distance into the contralateral half, a feature again undescribed in other flight motor neurones. As the contralateral branch was not seen in all fills it may result from a lack of close developmental constraints there.

The motor neurones of M85 and M114 produce an arborization of fine branches that occupies predominantly dorsal neuropile. Many branches occur just below the dorsal edge of the neuropile and above a plane drawn through the DIT. In this respect there is again a close comparison with other flight motor neurones (Tyrer & Altman, 1974; Tyrer, 1983). This raises the possibility that pleuroaxillary and power muscle motor neurones may share some premotor elements, such as the wing-hinge stretch receptor neurone, which branches in dorso-medial and dorso-lateral areas and connects directly to depressor motor neurones (Burrows, 1975; Altman

& Tyrer, 1977), and premotor interneurones (Robertson & Pearson, 1983). Some prominent branching is more ventral. The significance of this is unclear without more knowledge of the functional organization of the neuropile. Some of the arborization is associated with identified regions of the ganglion core. Thus pleuro-axillary motor neurones send branches far anterior to mingle with the axons of the nerve 1 root. In addition fine branches associate with or penetrate into dorsal longitudinal tracts containing wing sensilla (Tyrer & Altman, 1974; Kien & Altman, 1979; Bräunig, Pflüger & Hustert, 1983) and interneurones transmitting information from the head receptors (Bacon & Tyrer, 1978). There is therefore the possibility of anatomical overlap with these receptors (cf. Tyrer, 1983). However, anatomical overlap is no indication of the existence of direct connectivity.

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