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Morphological Study of Flight Motor Neurons in the Cricket

S. WANG AND R.M. ROBERTSON
Department of Biology, McGill University, Montreal, Quebec, Canada H3A 1B1

ABSTRACT

The motor innervation of the major flight muscles powering the fore- and hindwings of the cricket *Teleogryllus oceanicus* was investigated. The morphology of the motor neurons was determined by filling them via their axons in the periphery with either Lucifer Yellow or cobalt chloride followed by silver intensification. Details of the location of branches of motor neurons within the ganglion were obtained by serially sectioning ganglia containing filled neurons. For each flight muscle at least two motor neurons were found. The somata of motor neurons were located in two clusters in the ganglion, the anterior lateral cluster and the posterior lateral cluster. Motor neurons in the same cluster had similar morphologies. Most of the arborizations of these motor neurons were in the dorsal neuropil with a few branches in the lateral intermediate neuropil. The morphology of flight motor neurons was compared with the morphology of leg motor neurons in consideration of the possible functional organization of the ganglion. A comparison was made between motor neurons innervating homologous muscles of the cricket and the locust to determine the extent of the difference between the flight systems of these two groups.

Key words: insects, wing muscle, neuronal structure, homology

Neuronal structure is a fundamental component of the spectrum of characteristics that establishes the identity of particular neurons. Moreover, neuronal structure can be closely related to neuronal function (Bacon and Murphey, '84; Miller and Jacobs, '84; Pearson and Robertson, '87). Morphological studies of neurons thus provide an essential basis for further physiological studies. In addition, morphological similarity of neurons is an important criterion for establishing probable homology (Croll, '87). Neurons in the flight systems of locusts and crickets show some similarities in their morphology. The morphologies of the motor neurons innervating the thoracic dorsal longitudinal muscles are extremely similar (Bentley, '70, '73) and similar flight interneurons can be found in both systems (Robertson, '87). However, dissimilarities do exist between these two systems (Robertson, '87), and since it is thought that insect flight evolved only once (Gillot, '80), it is likely that differences in the details of how the two systems are constructed will reflect adaptive differences in the two systems.

There is a great deal of information available on various aspects of the locust flight system (e.g., Hedwig and Pearson, '84; Reichert and Rowell, '86; Robertson, '86; Pearson and Wolf, '87; Wolf and Pearson, '87). In contrast, cricket flight is best documented in terms of the role of flight in phonotaxis behavior (Moiseff et al., '78; Pollack and Hoy, '81; Nolen and Hoy, '86a,b). There is some information on the flight motor pattern and on the structure of a few motoneurons innervating wing muscles (Bentley and Hoy, '70; Elepfandt, '80; Elliott, '83; Robertson, '87). However, the information about flight motor neurons is incomplete, especially for the motor neurons that drive hindwing muscles. In this article we describe the number, location, and morphologies of the motor neurons innervating different wing muscles of both the forewing and the hindwing in the cricket and compare them with the motor neurons innervating homologous muscles in the locust. This is a necessary preliminary step to a more detailed comparison of the flight systems of the two species.

MATERIALS AND METHODS

Animals

Adult crickets, *Teleogryllus oceanicus*, were obtained from a laboratory colony at McGill University. Both sexes were used. The animals were pinned ventral side down in a dissection dish. An incision was made along the dorsal

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Address reprint requests to R.M. Robertson, Department of Biology, Queen's University, Kingston, Ontario, K7L 3N6, Canada.

midline and the thorax and abdomen were opened. The gut and other tissue were removed to reveal the wing muscles and the nerve roots supplying them. The nerve to a chosen muscle was cut at the muscle and the proximal stump was placed in a small cup made with vaseline.

Staining

A possible artifact of filling neurons with cobalt through their cut axons is that neurons in the same nerve bundle can be filled en passant without having a cut end in the pool of stain (Altman and Tyrer, '80; Fredman and Jahan-Parwar, '80). However, we avoided this problem by using low concentrations of the stain and by filling for long periods at a low temperature (Hackney and Altman, '83).

The nerve stump was immersed in distilled water for 1 minute in an attempt to cause osmotic swelling of the cut end and aid entry of the dye. The distilled water was replaced with 0.4 M cobalt chloride or 3% Lucifer Yellow CH (Sigma Chemical Co., St. Louis). The preparation was stored in a refrigerator (5°C) for 12–18 hours (Cobalt) or 2–8 hours (Lucifer Yellow). After this period the vaseline cup was removed and the meso- and metathoracic ganglia were dissected out. For the cobalt-filled preparations a dark precipitate of cobalt sulfide was produced by soaking the dissected ganglia for 5 minutes in the physiological saline (Fielden, '60) saturated with hydrogen sulfide. The ganglia were fixed in 4% paraformaldehyde for 30 minutes. After dehydration in an ethanol series, the ganglia were cleared in methyl salicylate. Stained neurons were drawn in plan view.

Selected cobalt preparations were then intensified after Bacon and Altman's method ('77). This wholemount silver intensification method was slightly modified by adjusting the pH of the developer solution to 2.45 for a slower reaction. The intensified preparation was redrawn and photographed.

Selected Lucifer Yellow preparations were subsequently embedded in resin (Spurr, '67) and sectioned (20 μm thick). Serial sections were drawn and photographed.

Nomenclature

The muscles and nerve roots were numbered after Furukawa et al. ('83):

muscle 89a	mesothoracic anterior tergocoxal
muscle 90	mesothoracic posterior tergocoxal
muscle 98	mesothoracic 2nd basalar
muscle 99	mesothoracic subalar
muscle 103a	mesothoracic tergotrochanteral
muscle 112a	metathoracic dorsal longitudinal
muscle 118a	metathoracic anterior tergocoxal
muscle 119	metathoracic posterior tergocoxal
muscle 127	metathoracic 1st basalar
muscle 128	metathoracic 2nd basalar
muscle 129	metathoracic subalar
muscle 133a	metathoracic tergotrochanteral

The naming of tracts and commissures within the ganglia follows Wohlers and Huber ('85) and Tyrer and Gregory ('82):

aRT	anterior part of ring tract
aVAC	anterior region of ventral association center
DC	dorsal commissure
DIT	dorsal median tract
DMT	dorsal median tract
iLVT	inner lateral ventral tract
LDT	lateral dorsal tract
LVT	lateral ventral tract
MDT	median dorsal tract
MVT	median ventral tract
oLVT	outer lateral ventral tract
VAC	ventral association center
VIT	ventral intermediate tract
VLT	ventral lateral tract
VMT	ventral median tract

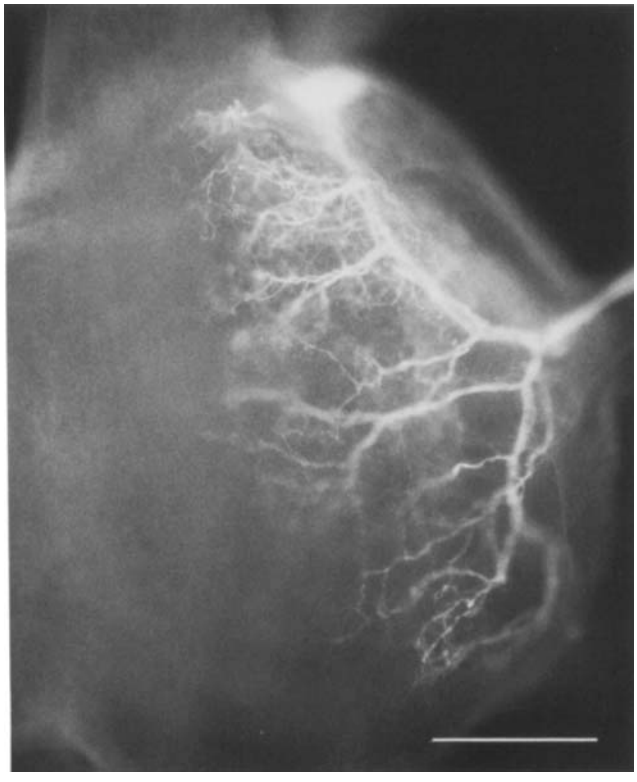


Fig. 1. Photomicrograph of motor neurons in the right mesothoracic hemiganglion that innervate muscle 98. The motor neurons have been filled with the fluorescent dye Lucifer Yellow. Note 2 parallel neuropil segments and paired branching in the neuropil. The brightness of the fluorescence makes it difficult to discern 2 somata. Scale bar: 100 μm.

RESULTS

The following results were obtained from 107 preparations. Intensified cobalt fills were more detailed than the Lucifer Yellow fills, although the latter were clearer, allowing individual processes to be traced. The general morphology of the motor neurons described below was not dependent on the dye used to fill the neurons, and the results therefore do not specify which particular dye was used. Different preparations of the same motor neurons showed some minor variation in their morphologies. This variation was primarily restricted to the fine branching in the neuropil. Soma location, primary branching, secondary branching, extent of dendritic branching, and course of the axon were constant enough to enable generalized drawings of the motoneurons to be made. Figure 1 presents a photomicrograph of the motor neurons innervating muscle 98 as an example of the sort of preparation from which the drawings were made.

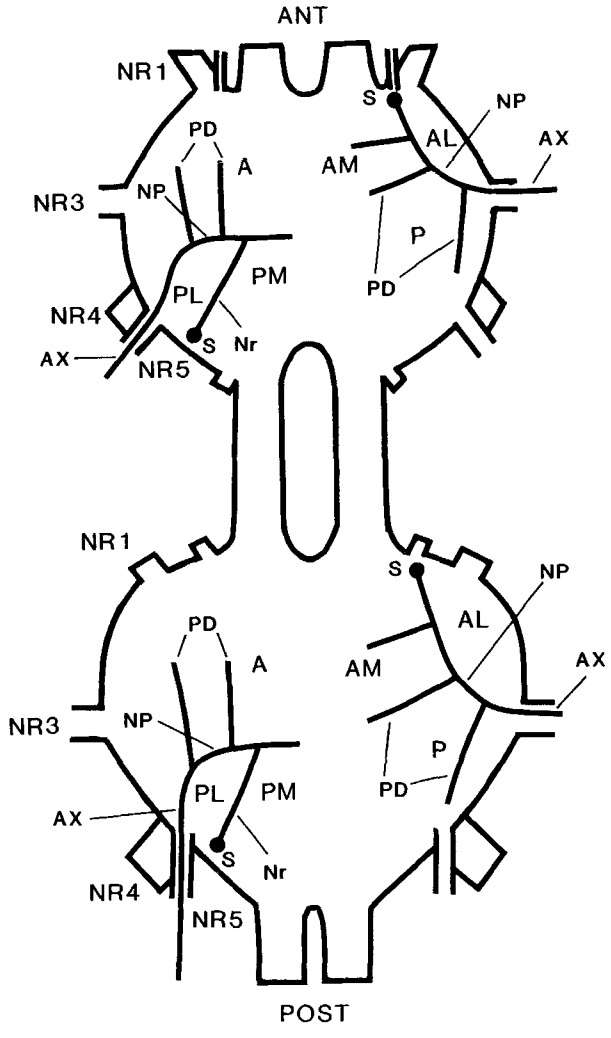


Fig. 2. Schematic diagram of 4 idealized motor neurons in the meso- and metathoracic ganglia to demonstrate the general location of the somata (S) and dendritic distribution. A, anterior field; AM, anterior medial field; AL, anterior lateral field; AX, axon; NP, neuropil segment; NR, nerve root; Nr, neurite; P, posterior field; PM, posterior medial field; PD, primary dendrite; PL, posterior lateral field.

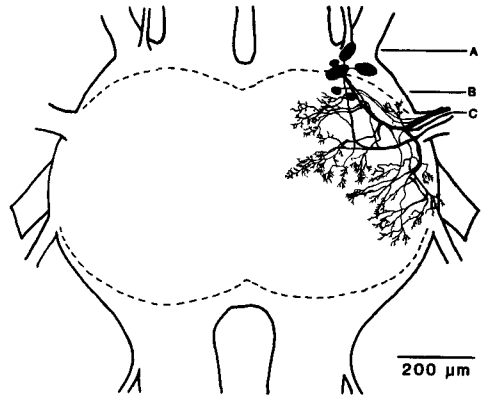
The somata of motor neurons innervating wing muscles were located in both the meso- and metathoracic ganglia in two main clusters ipsilateral to the muscle they innervated (the anterior lateral cluster and the posterior lateral cluster). Figure 2 is a diagram illustrating the location, morphology, and dendritic extent of four idealized motor neurons in the meso- and metathoracic ganglia. The terminology referring to neuronal structure was adopted from Tyrer and Altman ('74) (Fig. 2). Motor neurons in the same cluster had similar morphology. For the neurons in the anterior lateral cluster, we used the path of the neuropil segment as a marker to aid description of the dendritic field. From the dorsal view, the field anterior to the laterally oriented neuropil segment at nerve root 3 was designated the anterior field. This field was subdivided into the anterior medial field and the anterior lateral field by the anteroposteriorly oriented portion of the neuropil segment. The field posterior to the laterally oriented portion of the neuropil segment was called the posterior field. For the neurons in the posterior lateral cluster, the dendritic field was divided in a similar way. The field anterior to the laterally oriented portion of the neuropil segment near nerve root 4 was the anterior field. The area below this was designated the posterior field, which was subdivided into posterior lateral field and posterior medial field by the pathway of the neurite as seen in plan view (Fig. 2).

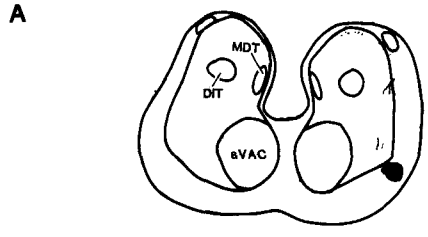
Motor neurons innervating mesothoracic flight muscles

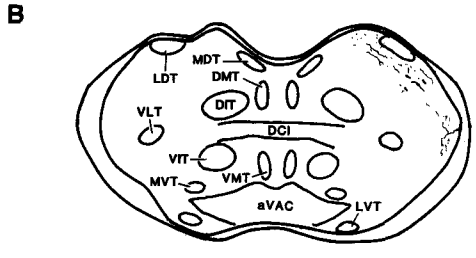
Elevators. Muscle 89a is innervated by 3 large motor neurons (N = 19) and several smaller motor neurons (Fig. 3). The somata of the large neurons have diameters of 40–60 μm and are located in the anterior lateral cluster of the mesothoracic ganglion between the pro-meso connective and nerve root 1. The axons (diameter 4–6 μm) travel via branch 1 or nerve root 3 to innervate the muscle. The somata are located ventrally in the cortex of the ganglion and send neurites toward the dorsal surface (Fig. 3A). Each neuropil segment has two large primary dendrites (diameter 3–5 μm) in the anterior medial field and one primary dendrite in the posterior field. All the dendrites are dorsally located, between the lateral dorsal tract (LDT) and median dorsal tract (MDT) and surrounding the LDT (Fig. 3B,C). There are some small branches in the anterior lateral field, but no large dendrite is found in this field. Among these 3 motor neurons, 2 have neuropil segments that have the same pathway and are more laterally located than the neuropil segment of the third motor neuron. The third motor neuron has an L-shaped neuropil segment that allows this neuron to be distinguished from the other motor neurons innervating muscle 98. This muscle is also innervated by several (from 1 to 3) smaller neurons with diameters of the somata less than 20 μm (Fig. 3). Their axons travel more laterally than those of the large motor neurons. Due to the fine dimensions of the axons, they were not filled in every preparation and their arborization was often obscured by the dendrites from the large motor neurons.

In some preparations intensification revealed small axons that bifurcate into both nerve roots 3 and 5. However, due to the very small diameter of these axons they were not filled in every preparation and we were unable to locate the somata of these neurons. Similar axons could be found when filling from the nerves innervating muscles 90, 99, 118a, and 128. In all these instances detailed information on the course, provenance, and branching of the axons was not obtained. It is likely that they are the axons of dorsal unpaired median (DUM) or common inhibitor neurons (see, e.g., Kutsch and Schneider, '87).

Muscle 90 is innervated by 5 motor neurons (N = 14) (Fig. 4). The somata of 4 of them are located in the posterior lateral cluster and the fifth is located anteriorly near the nerve root 3 in the mesothoracic ganglion. All the somata are ventrally located. The axons travel in the second branch of nerve root 5 to innervate the muscle. Three of the four posterior somata have diameters of 40–65 μm and the fourth soma is smaller, with a diameter of 20–30 μm. Each of the 4 posterior somata sends a neurite dorsally, anteriorly and medially. When this neurite reaches the level of nerve root 4, it turns laterally into the neuropil segment. The neuropil segment has one primary dendrite (diameter 2–3 μm) directed toward the midline and two large primary dendrites (diameter 3–5 μm) in the anterior field. There are several medium-sized dendrites (diameter 1–2 μm) in the anterior field and they are oriented anteriorly and medially. The two large primary dendrites bifurcate to form several secondary dendrites. These dendrites extend anteriorly to the







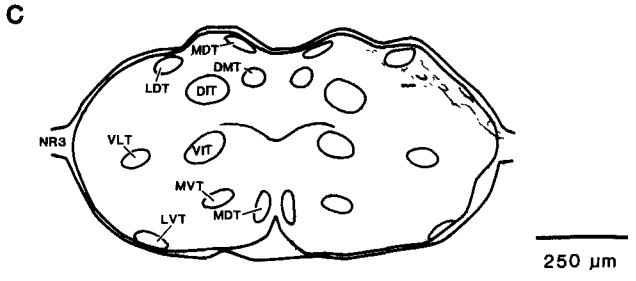


Fig. 3. Structure of motor neurons innervating forewing elevator 89a. Note that 2 of the large motor neurons have similar morphology, whereas the third is more medially located and has an L-shaped neuropil segment. On the plan view of the ganglion in this and subsequent figures, the dashed line indicates the approximate limit of the neuropil and the letters indicate the position of each of the transverse sections that are drawn. The somata are ventrally located in the cortex of the ganglion and each sends a neurite to the dorsal surface (A). The neuropil segment runs under LDT and the arborization is around LDT (B,C). There are some branches in the most lateral part of the ganglion that are more ventrally located (B). See Materials and Methods for explanation of abbreviations.

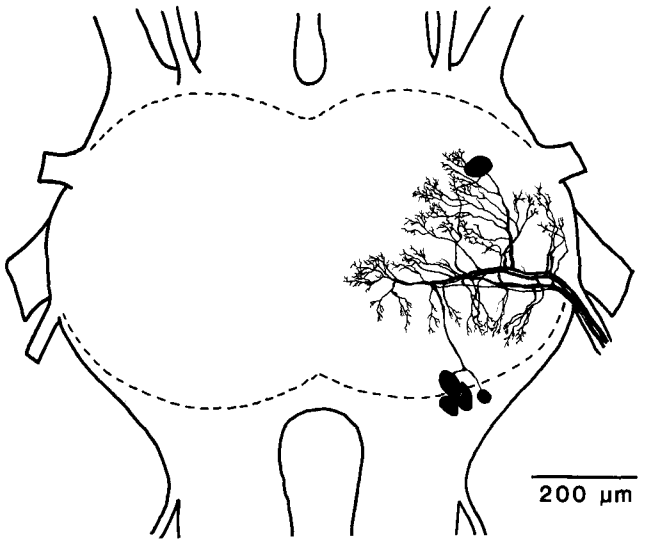


Fig. 4. Structure of motor neurons innervating forewing elevator 90. The 4 posterior motor neurons have similar morphology and extensive branching in the anterior field. The fifth motor neuron is in the anterior field near nerve root 3. The branching pattern of this neuron is not clear due to the extent of overlap of the branches of the 4 posterior motor neurons.

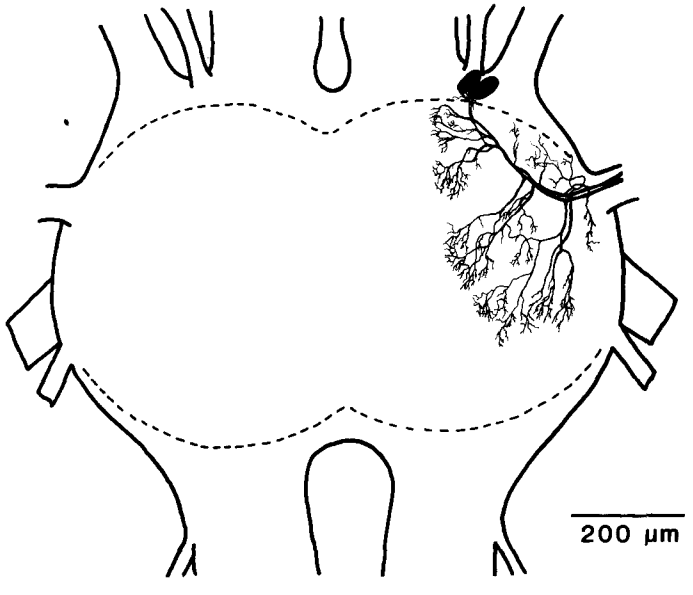


Fig. 5. Structure of motor neurons innervating forewing depressor 98. There are 2 motor neurons innervating this muscle. The somata are ventrally located in the anterior lateral cluster. The dendritic arborizations are similar to those of the motor neurons innervating muscle 89a.

level of nerve root 3 as well as medially. There are 2–3 medium-sized dendrites (diameter 2 µm) in the posterior lateral field and they bifurcate to form secondary dendrites that bifurcate again to give rise to several small dendrites. The fifth motor neuron sends a very fine neurite dorsoposteriorly. After the point where the neurite reaches the neuropil segment, it follows the path of the other 4 neurons to innervate the muscle. This neuron has at least 1 primary dendrite in the anterior lateral field and 2 in the posterior lateral field. Because of the overlapping neuropil segments of these 5 neurons, it was not easy to determine the medial projection of this neuron.

Depressors. Muscle 98 is innervated by 2 motor neurons (N = 9) (Fig. 5). The somata (diameter 40–60 µm) of these motor neurons are located in the anterior lateral cluster near nerve root 1 of the mesothoracic ganglion. The axons

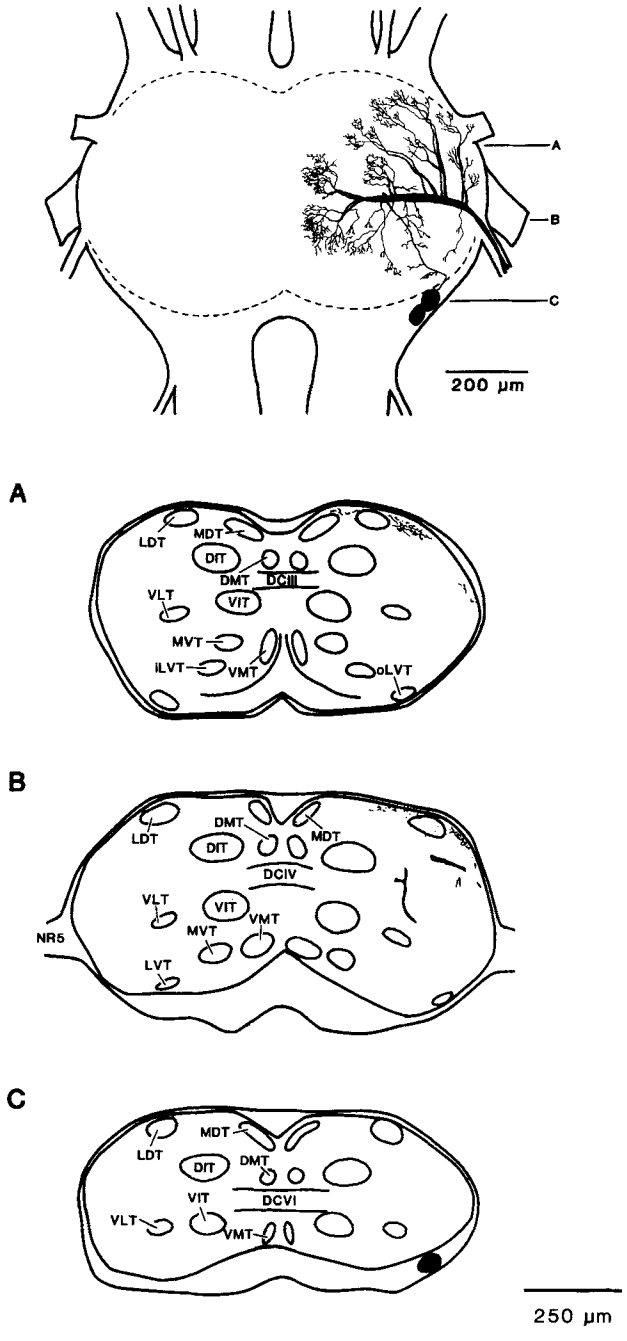


Fig. 6. Structure of the motor neurons innervating forewing depressor 99. There are 2 motor neuronal somata in the posterior lateral cluster. The general structure is similar to the 4 posterior motor neurons innervating muscle 90. Transverse serial sections reveal that most of the arborizations are in the dorsal neuropil around LDT and some extend to MDT (**A,B**). There are some branches in the intermediate neuropil and these are mostly laterally located (**A**). The neuropil segment runs under LDT (**B**).

innervate the muscle via nerve root 3 branch 2. The positions of the somata are similar to the positions of the somata of the motor neurons that innervate muscle 89a. It was therefore not possible to distinguish the motor neurons innervating these 2 different muscles simply on the basis of soma position. The basic neuronal structure is very similar to the structure of motor neurons that innervate muscle 89a. Each motor neuron has 2 large primary dendrites (diameter 3–5 μm) in the anterior medial field and 1 large dendrite in the posterior field. The branches of these dendrites are found around LDT (not shown). Within the anterior lateral field there are several small dendrites. These dendrites are more ventrally located and reach the intermediate neuropil.

Muscle 99 is innervated by two motor neurons (N = 7) (Fig. 6). The motor neuron somata (diameter 40–60 μm) are in the posterior lateral cluster similar to the somata of the posterior motor neurons innervating muscle 90. The axons travel via branch 2 of nerve root 5 to innervate the muscle. Each ventrally located soma sends a neurite dorsally, anteriorly and medially. The neuropil segment runs laterally, ventral to LDT (Fig. 6B) and sends 1 primary dendrite to the medial field. This bifurcates to form 2 secondary dendrites. The presence of these 2 secondary dendrites made it possible to distinguish the motor neurons innervating muscle 99 from the motor neurons innervating muscle 90. There are 3 primary dendrites in the anterior field. They extend anteriorly anterior to the level of nerve root 3. The dendrites are all dorsally located surrounding LDT. Only the most laterally located dendrites branch in the intermediate neuropil. There are very few smaller dendrites in the posterior lateral field.

Motor neurons innervating metathoracic flight muscles

Elevators. Muscle 118a is innervated by 3 large motor neurons (N = 22) and a variable number of smaller neurons, all of which are located in the anterior lateral cluster of the metathoracic ganglion (Fig. 7). The axons travel to the muscle via branch 1 of nerve root 3. The somata of the large motor neurons (diameter 60–75 μm) are located ventrally in the cortex of the ganglion and each soma sends a neurite toward the dorsal neuropil. The neuropil segment gives off 2 primary dendrites (diameter 4–6 μm) toward the medial field. There is 1 primary dendrite in the posterior field. The anterior lateral field is occupied by several smaller dendrites and there is no large primary dendrite in this field. The several small dendrites in this field have branches in the intermediate neuropil (Fig. 7B). Dendrites within the medial field do not cross the midline but can be detected in the initial portion of the meso-meta connective. The more anteriorly located dendrites extend farther medially than the more posteriorly located dendrites. In the most anterior part of the ganglion, the small branches reach MDT, whereas in the posterior part of the ganglion the branches are restricted to the area around LDT (Fig. 7A,B,C). The dendrites in the posterior field extend to the level of nerve root 4. Several small neurons (diameter less than 30 μm) were also found to innervate this muscle. However, due to the fine dimensions of their axons, they were not filled in every preparation and the number filled in a single preparation was variable (from 1 to 4). Their branching patterns were obscured by the dendrites of large motor neurons preventing a more detailed morphological description.

Muscle 119 is innervated by 3 motor neurons (N = 13) (Fig. 8). The somata (diameter 60–70 μm) of these motor neurons are located in the posterior lateral cluster. The axons leave the ganglion via branch 2 of nerve root 5 to innervate the muscle. The somata are ventrally located and each soma sends a neurite dorsally, anteriorly, and medially. For each neuron there are 2 large primary dendrites (diameter 4–6 μm) in the anterior field and their fine

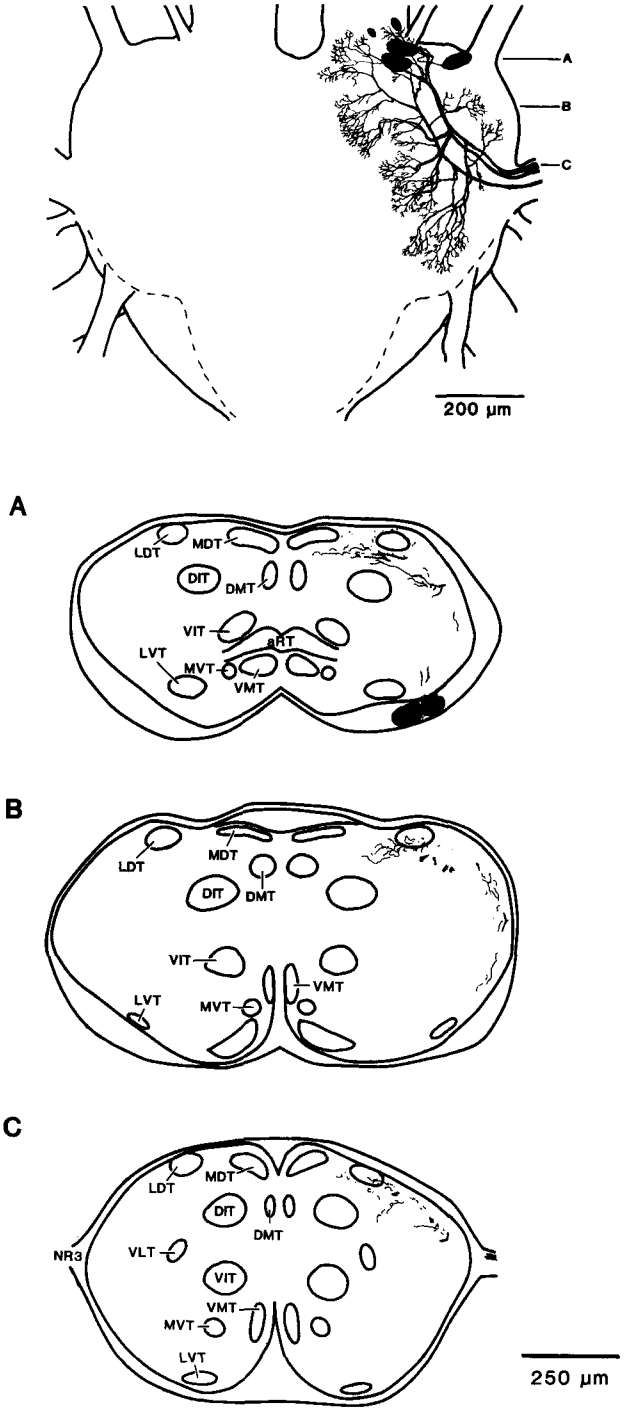


Fig. 7. Structure of motor neurons innervating hindwing elevator muscle 118a. There are 3 motor neuron somata (60–75 µm) and several (1–4) small neurons (diameter less than 30 µm) in the anterior lateral cluster. Transverse serial sections show that the somata lie in the ventral cortex of the ganglion and send neurites to the dorsal surface (A). The neuropil segments run under LDT (B). In the most lateral field of the ganglion there are some branches in the intermediate neuropil (A,B).

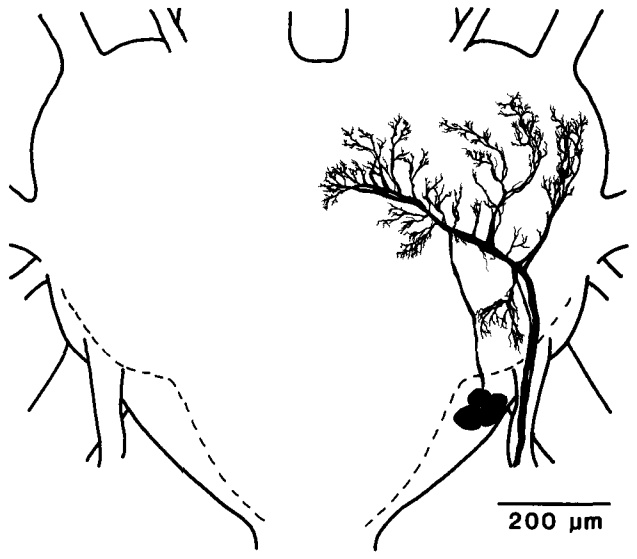


Fig. 8. Structure of the motor neurons innervating hindwing elevator 119. Three large motor neurons (60–70 µm) are in the posterior lateral cluster. The motor neuron somata are in the ventral cortex of the ganglion, whereas the arborizations are in the dorsal neuropil with extensive branching in the anterior region of the ganglion.

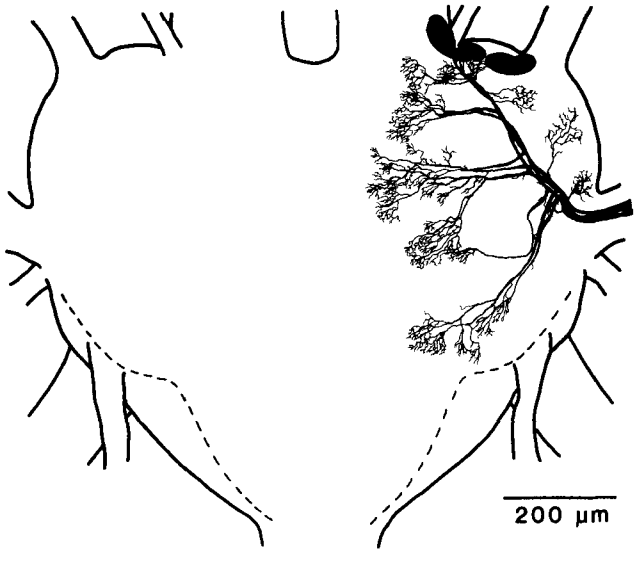


Fig. 9. Structure of the motor neurons innervating hindwing depressor 128. Three large motor neuron somata (60–80 µm) are located in the anterior lateral cluster. The general structure of each is similar to that of the motor neurons innervating muscle 118a with the exception of the anterior large dendrites near the soma and extending to the MDT, which is seen in motor neurons to 118a. The arborizations are in the dorsal neuropil and there are some branches in the lateral intermediate neuropil.

branches extend as far anteriorly as the level between nerve root 1 and 3. One primary dendrite extends toward the midline and bifurcates several times to produce many fine branches. None of these fine branches crosses the midline. There is only 1 medium-sized dendrite (diameter 2–3 µm) in the posterior lateral field and this extends posteriorly to the level of the middle of nerve root 4.

Depressors. Muscle 128 is innervated by 3 motor neurons (N = 15) located in the anterior lateral cluster of the metathoracic ganglion (Fig. 9). The axons leave the ganglion by branch 2 of nerve root 3 to innervate the muscle. The somata (diameter 60–80 µm) are ventrally located and each soma sends a neurite dorsoposteriorly. Each neuron has 2 large primary dendrites (diameter 3–5 µm) in the

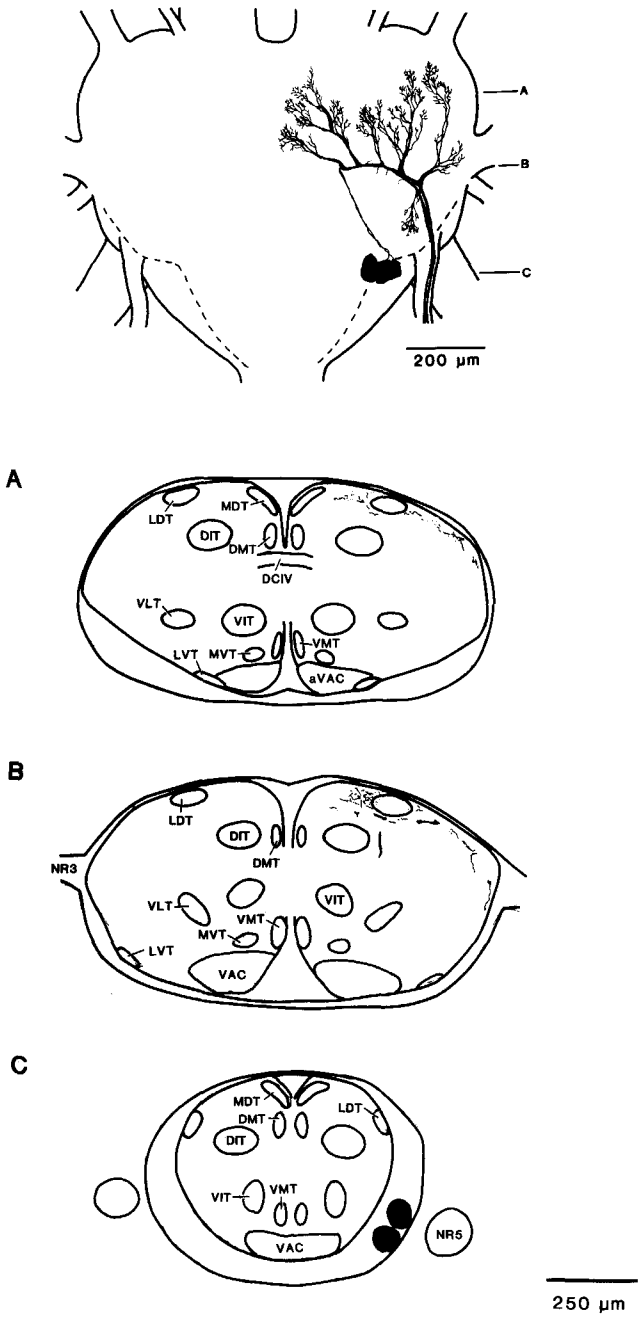


Fig. 10. Structure of the motor neurons innervating hindwing depressor 129. The two large motor neuron somata (60–75 μm) are in the posterior lateral cluster. Transverse serial sections show that the somata are in the ventral cortex of the ganglion (C). The neuropil segments run ventral to LDT (B). The dendritic arborizations are in the dorsal neuropil, around the LDT (A,B) with some branches extending as far as MDT. The branches in the intermediate neuropil are all laterally located (A,B).

anterior medial field. The dendrite more posteriorly located extends farther medially but does not cross the midline. There is only 1 primary dendrite in the posterior field. This dendrite extends posteriorly and medially and reaches the level of nerve root 5. There are several small branches in the anterior lateral field and some of them penetrate into the intermediate neuropil (not shown). However, there are no large primary dendrites in this area. A criterion to distinguish the motor neurons innervating muscle 128 from those innervating 118a is that the latter (118a) has large primary dendrites in the anterior portion of the ganglion with dendrites extending more medially (to MDT, Fig. 7A) than other primary dendrites, whereas the former (128) has smaller primary dendrites in the anterior part of the ganglion and the dendrites that extend farthest medially are posteriorly located.

Muscle 129 is innervated by 2 motor neurons (N = 8) (Fig. 10). The motor neuron somata (diameter 60–75 μm) are located ventrally in the posterior lateral cluster of the metathoracic ganglion. The axons leave the ganglion by branch 2 of nerve root 5 to innervate the muscle. Each neurite extends dorsally, anteriorly, and medially. The neuropil segment runs laterally just ventral to the LDT (Fig. 10B). Each neuron has 3 large primary dendrites (diameter 3–5 μm) in the anterior field. The 2 laterally located dendrites extend anteriorly as far as the level of nerve root 1. The most lateral has branches in the intermediate neuropil (Fig. 10A,B). The third dendrite is oriented both anteriorly and medially. One dendrite extends toward the midline and its branches reach the MDT but do not cross the midline. There are only small branches in the posterior lateral field and these are ventrally located.

DISCUSSION

In this study we describe the number and morphology of motor neurons innervating the major wing muscles in the cricket. Wing elevator muscles were found to be innervated by more motor neurons than the wing depressors. The motor neurons were located in 2 clusters in the ganglion—the anterior lateral cluster and the posterior lateral cluster. Motor neuronal location was correlated with the position of the muscle innervated in that motor neurons in the anterior lateral cluster innervate anteriorly located muscles, whereas motor neurons in the posterior lateral cluster innervate posteriorly located muscles.

Motor neurons innervating antagonistic flight muscles were found in the same cluster and their axons travelled via the same nerve root (but not necessarily the same branch) to innervate the muscles. These motor neurons had similar morphologies. However, there are some differences that can help to distinguish them. Elepfandt ('80) reported that motor neurons innervating muscle 90 can be distinguished from those innervating muscle 99 by the location of their entrance into the nerve root. Motor neurons innervating muscle 99 enter the nerve at the caudal edge and the motor neurons innervating muscle 90 enter the nerve at the frontal edge. However, we found this not to be a reliable method of distinguishing these motor neurons. In this study they could be distinguished by the observation that the motor neurons innervating muscle 99 (Fig. 6) had two large secondary dendrites running toward the midline, whereas the motor neurons innervating muscle 90 (Fig. 4) had less extensive branching toward the midline. Motor neurons innervating antagonistic muscle 89a and muscle 98 could not be distinguished with the exception of the L-shaped motor neuron of muscle 89a. In the metathoracic ganglion, motor neurons innervating muscle 118a could be distinguished from motor neurons innervating muscle 128 by the presence of a large dendrite at the anterior part of the ganglion near the soma. Motor neurons innervating muscle 119 and 129 could be distinguished by the observation that motor neurons to muscle 129 have more extensive dendritic branching in the anterior field.

TABLE 1. Comparison of the Number of Motor Neurons Innervating Homologous Wing Muscles of Crickets and Locusts[a]

	MESO					META						
	Elevators			Depressors		Elevators			Depressors			
	89a	103a	90	98	99	118a	133a	119	127	128	129	112a
Cricket	3[b]	4[b,c]	5	2	2	3[b]	3[c]	3	1[c]	3	2	5
Locust	2	3	3	2	2	1	NA	3	1	1	2	5

[a]Data for the locust taken from Bentley ('70), Tyrer and Altman ('74), Burrows ('76), and Kutsch and Schneider ('87). Data for the cricket taken from this work and Bentley ('73, for muscle 112a).
[b]The muscle is additionally innervated by an undetermined number of small motor neurons.
[c]The number is from preliminary observations not otherwise described in this work.
NA = not available.

The motor neurons innervating serially homologous muscles in the meso- and metathoracic segments appeared to have similar morphologies, although their numbers could be different; e.g., 2 motor neurons innervate muscle 98 (in the mesothoracic ganglion), whereas 3 motor neurons innervate muscle 128 (in the metathoracic ganglion), the serial homolog. Two major differences in their morphologies were found. The first is that the motor neurons innervating muscle 89a and muscle 98 had no branches in the MDT, whereas their metathoracic homologous partners, the motor neurons innervating muscle 118a and muscle 128, had branches that clearly reached that tract. The second difference pertains to muscle 90. This muscle had the unique characteristic of being innervated by a large number of motor neurons including the fifth motor neuron soma found near nerve root 3. No other flight motor neurons with the same morphology could be found in this location. The unique morphology of this motor neuron compared with that of the 4 other motor neurons innervating muscle 90 suggests that this motor neuron has a developmental origin different from that of the other 4 neurons. It is known that initially the neuronal population is repeated in every ganglion and that segmentally homologous neuron clusters are derived from neuroblasts arranged in homologous positions (Miyamoto and Shimozawa, '83). It is interesting that muscle 119, the homolog of muscle 90 in the metathoracic segment, does not have a neuron homologous to the fifth motor neuron found innervating muscle 90. It is possible that this neuron is important in the control of stridulation, which is a behavior performed exclusively by the forewing. However, it has been suggested by Elepfandt ('80) that this neuron may be active only during walking and not during flight or stridulation. His reasons are that the soma of this motor neuron lies in a region of leg motor neuron somata, and that a fourth motor unit can be recorded in muscle 90 during walking, but not during flying or singing. Two points can be made about this speculation. First, the somata of leg motor neurons in the anterior region of the ganglion are dorsally located for prothoracic legs (Laurent and Richard, '86) and not ventrally located as is the fifth motor neuron of muscle 90. Second, there is no evidence that the fourth motor unit recorded from muscle 90 during walking results from activity of this particular motor neuron. More data are needed before the normal function of this motor neuron can be established.

All the muscles described in this article are bifunctional or trifunctional. They are active during flight and walking, and the forewing muscles are additionally active during stridulation. Muscles that are antagonistic during flight can be synergistic during walking. Comparing the structure of bifunctional motor neurons with that of motor neurons that are concerned only with the control of leg movements may help in understanding the functional organization of the ganglion. Leg motor neurons are known to have arborizations in the dorsal and intermediate neuropil regions with particularly extensive branching in the lateral field of the intermediate neuropil (Wilson et al., '82; Laurent and Richard, '86). For the flight motor neurons described here, the arborization is mainly restricted to the dorsal neuropil and the few branches reaching the intermediate neuropil are laterally located. It is likely that the branches in the lateral intermediate neuropil serve as a functional input site during walking. Branches in the dorsal neuropil may primarily be concerned with integration of flight-related activity but could also play a role during walking. The small somata we found when filling the axons innervating muscle 89a and 118a are similar in size and location to the Y-shaped leg motor neurons (Laurent and Richard, '86), suggesting that they may be operational during walking.

The most obvious difference between flight motor neurons of the cricket and those of the locust is in the number innervating homologous muscles. The differences are summarized in Table 1. Generally speaking, the number of motor neurons innervating elevator muscles of these 2 systems are more divergent than the numbers innervating the depressors. It is not clear yet what the functional importance of these differences in number may be, but there are two obvious possibilities. First, the forewings of crickets have an important function other than flight, namely stridulation. The extra motor neurons found in the cricket mesothoracic ganglion might indicate the results of adaptation to perform this task. Second, locust flight and cricket flight are not identical. Cricket forewings exhibit a much reduced wingbeat amplitude compared with that of locust forewings during flight, but they may have a more important role as stabilizers or in the control of steering. Flight interneurons in the cricket have many differences with those in the locust and it has been suggested that the operation of the flight systems of the 2 species are significantly different (Robertson, '87). Our finding of the divergent number of motor neurons in the 2 systems is consistent with this suggestion. Nevertheless, the morphology of motor neurons to homologous muscles in the 2 species is rather similar, and this supports the speculation that homologous motor neurons in species with the same behavioral repertoire would have the same major branching pattern (Altman, '80; Kutsch and Schneider, '87).

Finally, it is useful to speculate on the source of the input to these flight motor neurons. Several flight interneurons have been identified (Robertson, '87) and the branching pattern of the flight motor neurons described here would overlap the branches of these flight interneurons. Whether there are direct connections between these interneurons and the motor neurons remains to be determined. The flight motor pattern of the cricket can be altered by auditory

input (Pollack and Hoy, '81; Robertson, '87; Wang and Robertson, '88) and the terminations of the auditory receptors are restricted to the prothoracic ganglion (Wohlers and Huber, '85). If pattern changes are due to auditory input at the motor neuronal level rather than the interneuronal level, then the motor neurons in the meso- and metathoracic ganglion could receive the auditory information only via descending auditory interneurons from the higher ganglia. According to the morphology of the motor neurons, it is likely that these motor neurons would receive auditory input from descending auditory interneurons travelling via LDT and MDT. Several descending auditory interneurons that travel through these tracts have been described by Atkins and Pollack ('87), and these are candidates for providing auditory input to the flight motor neurons.

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