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THE ORGANIZATION OF FLIGHT MOTONEURONES IN THE MOTH, *MANDUCA SEXTA*

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SUMMARY

The morphology and the innervation of the main wing depressor muscles have been studied. The motoneurones to these muscles have dendrites ipsilateral to the muscle they innervate and located in the dorsal neuropile. With the exception of one motoneurone, to the dorsal longitudinal muscle, all motoneurone cell bodies are ipsilateral to the muscle they innervate. The morphologies of individual cobalt stained motoneurones are described. Flight motoneurones to wing depressor muscles are not electrically or chemically coupled to one another.

INTRODUCTION

Insects have relatively few neurones, often with large cell bodies, which renders them suitable for a study of the role of neurones in producing behaviour. The neural basis of flight has been studied in several insects, particularly in the locust and the dragonfly, but has received little study in moths. In *Manduca sexta*, recordings have been made from some wing muscles during tethered flight (Kammer, 1971) and the cell bodies of the five motoneurones to the mesothoracic dorsal longitudinal muscles (wing depressors in this species) have been located (Casaday & Camhi, 1976).

This paper provides the basis for further investigation of the neurones involved in flight in *Manduca sexta*. The muscles in the mesothorax are described, and their motoneurones are studied in fine detail using three main techniques: methylene blue staining to establish the innervation of the wing muscles, cobalt backfilling of wing motoneurone axons to reveal the motoneurone cell bodies, and finally intracellular injection of cobalt into physiologically characterized motoneurones to show their dendritic branching.

MATERIALS AND METHODS

Moths, *Manduca sexta* (Johannson), were reared on an artificial diet supplemented with carotene (B. Ballard, in preparation). Moths were used at least three days after eclosion to ensure complete degeneration of pupal motoneurones (Taylor & Truman, 1974).

The innervation of mesothoracic flight muscles was investigated using 'Rongalite'

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reduced methylene blue (Pantin, 1946). The solution was injected into the haemocoel, and after 30 min at 5 °C, the moth was dissected to allow the flight muscles and their innervation to be drawn.

The motoneurones innervating the flight muscles were revealed by cobalt backfilling from their axons (Sandeman & Okajima, 1973). After the cut end of the nerve from a flight muscle had been immersed for 12 h in 5 % (w/v) cobalt chloride, the ganglion was dissected out and placed in a solution of 1 % (w/v) ammonium sulphide to precipitate the sulphide. The ganglion was then fixed in 7 % formaldehyde solution (buffered to pH 7), dehydrated in a graded series of alcohols and finally cleared in methyl salicylate. The motoneurones filled in this way were photographed and drawn using a camera or a camera lucida mounted on a microscope.

For intracellular recording the moth was immobilised by keeping it at 5–6 °C for 12 h. The moth remained immobile for 4 min when taken out of the cold room and, if it was allowed to recover, showed no obvious ill effects. The pterothoracic ganglion was exposed by a dorsal midline incision in the thorax, followed by gently pinning the thorax open. The only tissue to be removed was the spina, a cuticular strut between the pro- and pterothoracic ganglia. A platform was then slid under the pterothoracic ganglion to stabilize it. The tracheal sacs overlying the ganglion were removed from the region of the ganglion where the recordings were made. The preparation was bathed in saline (Robertson, 1974). Microelectrodes had a d.c. resistance in saline of 25–30 MΩ when filled with 10 % (w/v) cobalt chloride. For identification of motoneurones, twitches seen in a muscle were correlated with spikes produced either spontaneously or in response to an imposed depolarization of a motoneurone. The wing elevator muscles, which overlie some wing depressors, were cut 2 mm from their dorsal insertion during the dissection so that contraction of all the flight muscles could be seen. Cobalt was injected from the microelectrode using 10 nA pulses of positive current, 250 ms long, once per second for 20 min, and then allowed to diffuse for a further 30 min. The ganglion was then dissected out, developed in ammonium sulphide, and dehydrated and stored in 70 % alcohol overnight. Subsequently the motoneurone was intensified with silver by the method of Bacon & Altman (1977). Descriptions of the morphologies of individual motoneurones are based on at least three complete stainings of each. Physiological recordings from a pair of identified flight motoneurones were made using microelectrodes filled with 2-M potassium acetate.

RESULTS

Innervation pattern of forewing muscles

The flight muscles in *Manduca* may be divided into those that depress and those that elevate the wing. The muscles act either directly, by their insertion on the wing base, or indirectly, by deforming the thoracic exoskeleton which in turn moves the wing. Those that insert directly on the wing base not only move the wing vertically but also alter the angle of attack of the wing relative to the air stream (supination/pronation), and the degree to which the wing is held close to the body (promotion/remotion). The muscles of the forewing and their patterns of innervation are detailed in Table 1. Several wing muscles are themselves subdivided, into muscle blocks. In

Table 1. *The innervation pattern of the forewing muscles in* Manduca sexta

	Action (Kammer, 1971)	Name in this study	Abbreviation	Anatomical name (after Nüesch, 1953)	Innervated by nerve (N) (after Eaton, 1974)	Number of motoneurones
WING DEPRESSORS						
Direct	Depress and pronate	1st Basalar	B1	P.V.1	2bi	1
		2nd Basalar	B2	P.V.2	2bii	1
		3rd Basalar	B3	P.V.2	2bii	1
		4th Basalar	B4	P.V.3	5b	1
	Depress and remote	1st Pleuroaxillary	P1	P.D.2a & b	6	1
		2nd Pleuroaxillary	P2	P.D.2c	6	1
	Depress and supinate	Subalar	S	P.V.4 & 5	6	1
Indirect	Depress	Dorsal longitudinal	D.L.	D.L.1a–e	1c	5
		Dorsal oblique	D.O.	D.L.2	1c	–
WING ELEVATORS						
Indirect	Elevate	Elevators	D.V.	D.V.1–5	4 and 6	–
OTHERS	Unknown	Posterior dorsal	P.D.	P.D.1,3–7	2a	–

Table 1 I have divided these wing muscles into functional blocks corresponding t anatomical divisions and to innervation pattern. For example, one direct depressor, the basalar muscle, is divided into four units, each innervated by a different motoneurone.

Location of motoneurone cell bodies

In *Manduca* the mesothoracic, metathoracic and first two abdominal ganglia are fused together forming a single pterothoracic ganglion (Fig. 1). All muscles of the forewing except one are innervated by motoneurones in the mesothoracic segment of the pterothoracic ganglion (Fig. 2). With one exception the motoneurone cell bodies are all ipsilateral to the muscle they innervate. The exception is the motoneurone to the most medial and ventral bundle of fibres in the dorsal longitudinal muscle (D.L.1a.).

Cell bodies occur in an anterior and a posterior group, both on the lateral surface

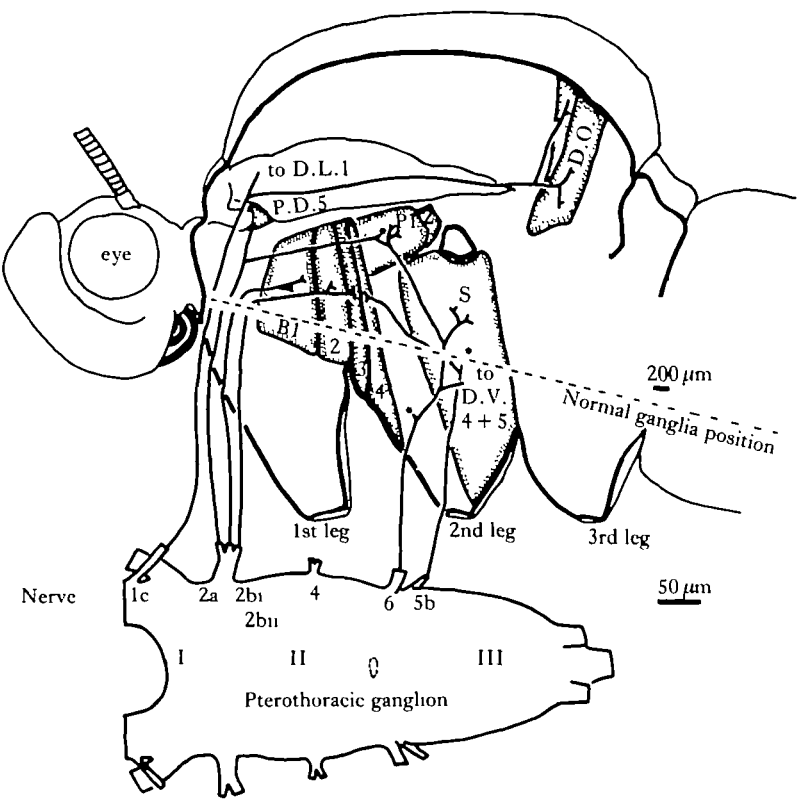


Fig. 1. Flight muscles of the mesothorax of the moth in side view (above) and their innervation (below). The right side is viewed from the midline of the moth. The dorsal longitudinal and the elevator muscles have been removed to reveal the underlying direct depressor muscles. The thoracic ganglia are viewed from above. Anterior is to the left. The abbreviations used are: B, basalar muscles; D.L., dorsal longitudinal muscles; D.O., dorsal oblique muscles; D.V., dorsoventral muscles; P, pleuroaxillary muscles; P.D., posterior dorsal muscles; S, subalar muscles. I, prothoracic segment; II, mesothoracic segment; III, metathoracic segment; *, termination unknown.

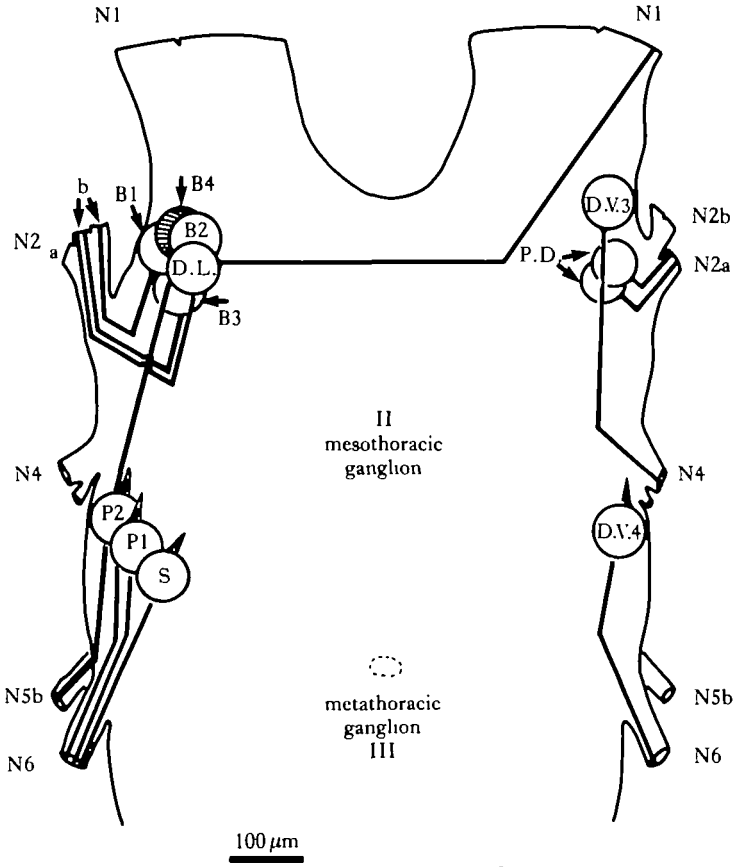


Fig. 2. Map of cell bodies of the motoneurones to mesothoracic flight muscles, names abbreviated as in Table 1. The circles represent the cell bodies, the filled or cross-hatched black lines the neurite and axon, and the unfilled black lines the length of the neurite giving rise to the dendrites. A dotted circle marks the division between meso- (II) and metathoracic (III) segments of the pterothoracic ganglion. The abbreviations used in naming the motoneurone cell bodies are as in Table 1.

of the ganglion. One group is anterior to the entry of nerve 2 and posterior to nerve 1, and the other group is at the extreme hind end of the mesothoracic ganglion just anterior to nerves 5 and 6. In unfixed material both areas are clearer than the surrounding neuropile. The motoneurones to the wing muscles have cell bodies in the range 20–50 μm in diameter. Those of the small posterior dorsal muscles (P.D.) are at the lower end of this range. The motoneurone cell bodies to the dorsal longitudinal (D.L.1a.), the four basalar units (P.V. 1–3), the small posterior dorsal muscles (P.D. 1, 3–7) and the anterior wing elevators (D.V. 1–3) are all in the anterior group, whereas those of the two pleuroaxillary (P.D. 2a–c), the subalar (P.V. 4 and 5) and the posterior two elevators (D.V. 4 and 5) are all in the posterior group. By referring to Fig. 1 it can be seen that the position of the muscle in an anterior/posterior direction is reflected in the position of its cell body. Motoneurones to anterior muscles have cell bodies in the anterior group.

General features of motoneurone fine structure

The neurite is about 10 μm wide and leaves the cell body either on its dorsal side

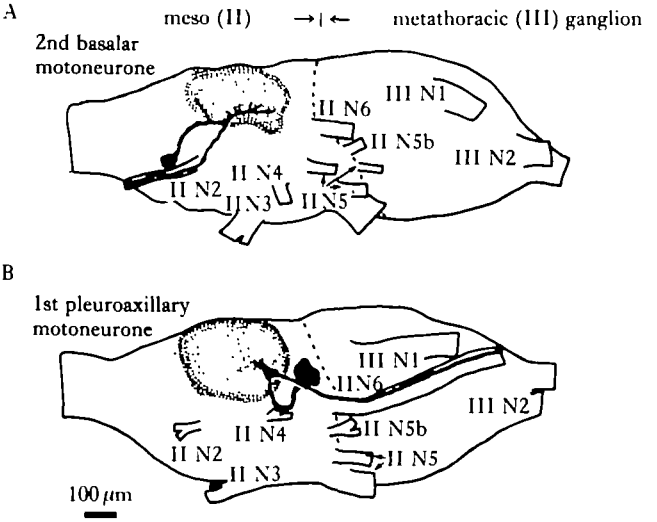


Fig. 3. Side view of the pterothoracic ganglion showing motoneurones with cell bodies in the anterior (A, 2nd basalar) and posterior (B, 1st pleuroaxillary) group. Stippled areas represent the dendritic field of the neurone. Neurones in both areas have dendrites restricted to the dorsal neuropile.

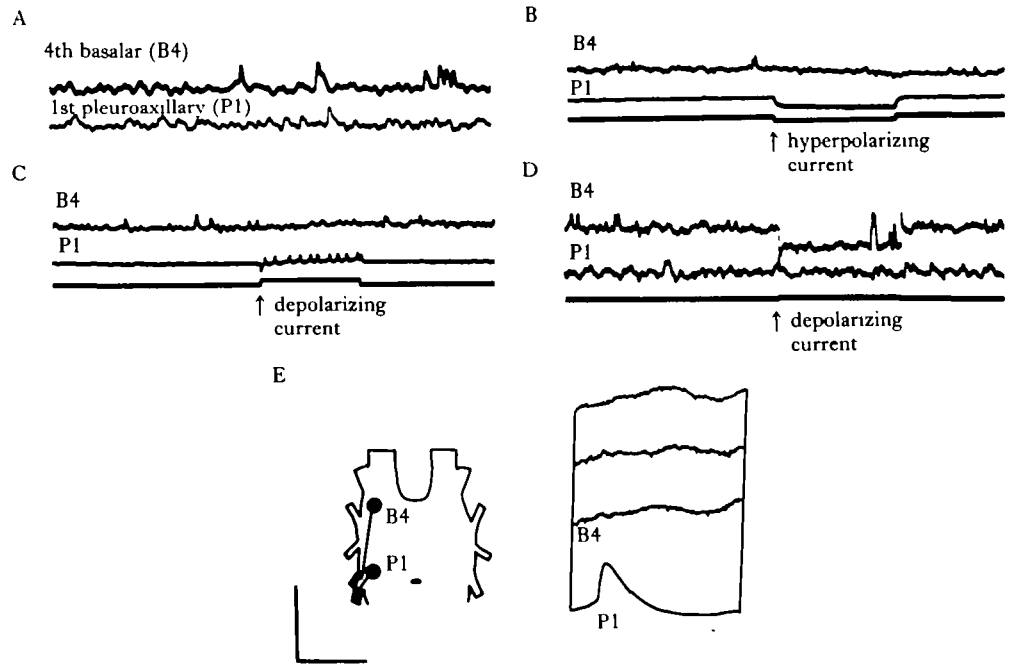


Fig. 4. Intracellular recording from a pair of depressor motoneurones. A–D, Top trace, fourth basalar motoneurone; lower trace, first pleuroaxillary motoneurone; bottom trace, current monitor. E, Signal average triggered from a spike in the basalar neurone. Each trace represents 64 sweeps. The upper three traces show the membrane potential in the pleuroaxillary motoneurone following a spike in the basalar motoneurone, bottom trace. Calibrations: A, Vertical, 5 mV for upper and lower traces. Horizontal, 0·2 s. B and C, Vertical, 10 mV upper, 105 mV lower, 150 nA bottom. Horizontal, 0·4 s. D, Vertical, 10 mV upper and lower, 300 nA bottom. Horizontal, 0·4 s. E, Vertical, 23 mV upper three traces, 20 mV bottom. Horizontal, 23 ms. The inset shows the position of the two motoneurones.

the cell body is in the anterior group or on the ventral if it is in the posterior group. The cell bodies are more ventral in the anterior compared with the posterior group. Once it has emerged from the cell body the neurite is devoid of branches for 100 μm. After this it expands and branches, giving off large dendrites up to 10 μm in diameter. These further divide giving rise to a dense mat of branches restricted always to the dorsal part of the ganglion and almost entirely ipsilateral to the muscle that the neurone innervates (Figs 3, 4). The neurite narrows to 5 μm as it enters the tract of motoneurones which later leave the ganglion via the same nerve (Fig. 4; 1st pleuroaxillary, P1 and subalar, S). Once in the nerve, the diameter of the axon of the motoneurone increases to a maximum of 10 μm before dividing up to innervate its flight muscle.

Aspects of motoneurone physiology

All the wing depressor motoneurones studied were fast motoneurones, each action potential producing a twitch in the muscle. Several of those to the wing elevators produced a clear contraction only upon repeated firing of the motoneurone. In no case did recordings made from the cell bodies of wing motoneurones show overshooting action potentials, indicating that there is a passive invasion of the soma by a spike produced elsewhere. If a motoneurone was to be stained, it was impaled in its cell body as stain migrates most easily away from the cell body into the rest of the neurone. Recordings were also made from the neuropilar section of the motoneurones. Recordings from the axon showed large overshooting action potentials and very little synaptic activity whereas recordings from the dendritic tree showed synaptic potentials of up to 6 mV and a more attenuated spike. Flight motoneurones receive a constant barrage of post synaptic potentials (PSPs) from which individual PSPs can be discerned (Fig. 4A). Simultaneous recordings from two wing depressor motoneurones, the 4th basalar and the 1st pleuroaxillary, show that there are very few PSPs which are obviously common to both neurones (Fig. 4A). In particular there are some large PSPs, arrowed in Fig. 4A, which were recorded in the 4th basalar motoneurone but not in the 1st pleuroaxillary. Passing depolarizing current into either motoneurone does not alter the membrane potential of the other (Fig. 4B, C and D) nor does a spike in one of them (Fig. 4E). Despite considerable morphological overlap in the extent of their dendritic fields (Figs 3, 5) there is no evidence for common presynaptic input or any apparent electrical or chemical coupling between these neurones. This conforms to the pattern seen in locust (Burrows, 1973, 1977) and the dragonfly (Simmons, 1977*b*) where there were no direct connections between flight motoneurones.

Morphology of individual motoneurones

The following is a description of the morphology of individual identified flight motoneurones, each of which shares the basic features outlined previously but also possesses features which are individual. The motoneurone to dorsal longitudinal muscle fibres in the most medial and ventral bundle (D.L. 1a) has a 35 μm diameter cell body in the anterior group, contralateral to the muscle it innervates. There are no dendritic branches on the same side of the ganglion as the cell body. They all occur on the side ipsilateral to the muscle that the motoneurone innervates (Fig. 6). The dentritic field does not extend across the midline of the ganglion, and most processes come off the main

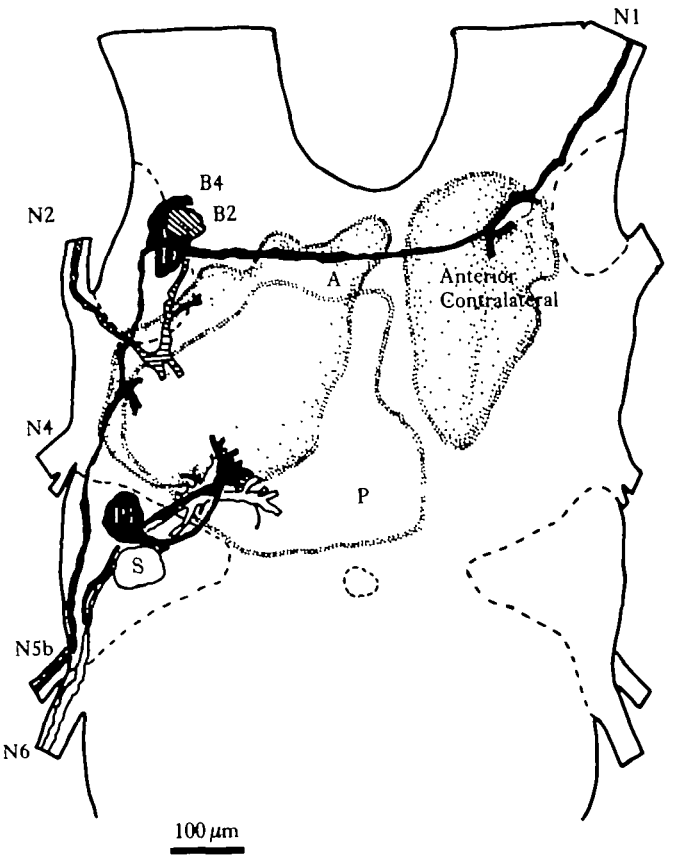


Fig. 5. Dendritic fields of motoneurones in either the anterior or posterior groups. A, dendritic field of the 2nd and 4th basalar, of the anterior group; C, dendritic field of the dorsal longitudinal (D.L. 1a) of the anterior group; P, dendritic fields of the subalar and 1st pleuroaxillary of the posterior group. The abbreviations used in naming the motoneurones are as in Table 1.

neurite or a single long process which extends posteriorly within the dorsal neuropile. The 2nd and 4th basalar motoneurones (Fig. 7) also have cell bodies in the anterior group, but their processes are ipsilateral to both their cell body and the muscle they innervate. They both have cell bodies 40 μm in diameter. In the neurone innervating the 4th basalar muscle the larger processes from the neurite start less than 50 μm beyond the cell body and continue for 200 μm as the neurite travels in one plane from anterior to posterior. In the 2nd basalar motoneurone, however, the neurite is devoid of processes for 100 μm as it arches dorsally as well as posteriorly. The three major processes arise from the neurite over a more restricted anterior–posterior distance than in the 4th basalar, but in side view of the same neurone (Fig. 3A) it can be seen that the neurite arches dorsally with the processes coming off at the top of the arch. This makes measurements in the anterior–posterior axis alone deceptive. Unlike the 4th basalar motoneurone the dendrites of the 2nd basalar cross over the midline of the ganglion. The processes of both neurones follow the contours of the dorsal region of the neuropile. The axon of the 2nd basalar leaves the ganglion via nerve 2, branch bii, whereas that of the 4th basalar leaves in the more posterior nerve 5b. In overall

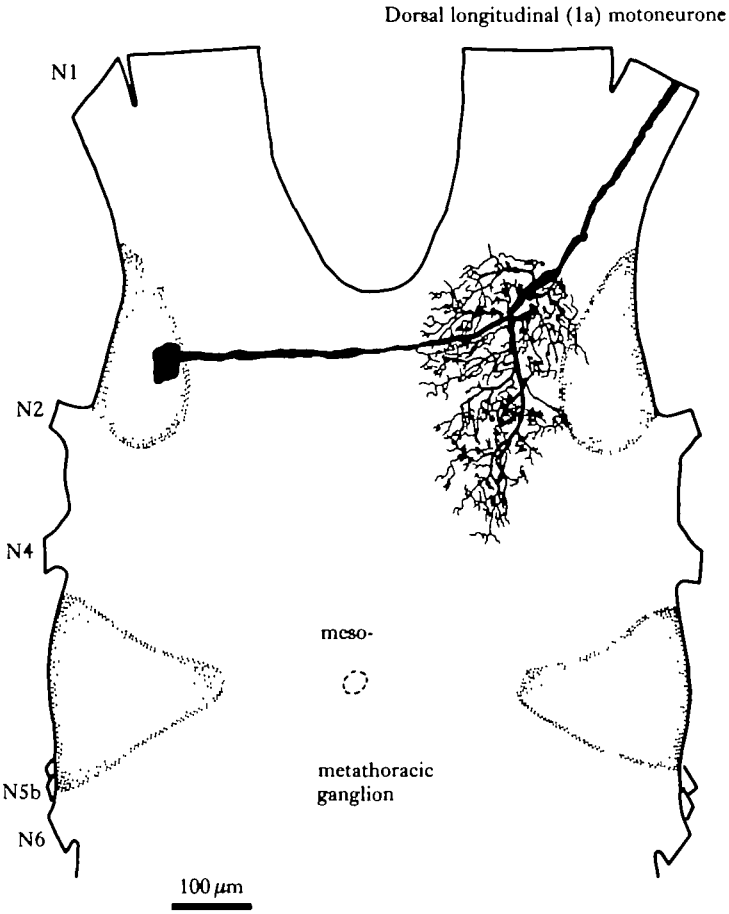
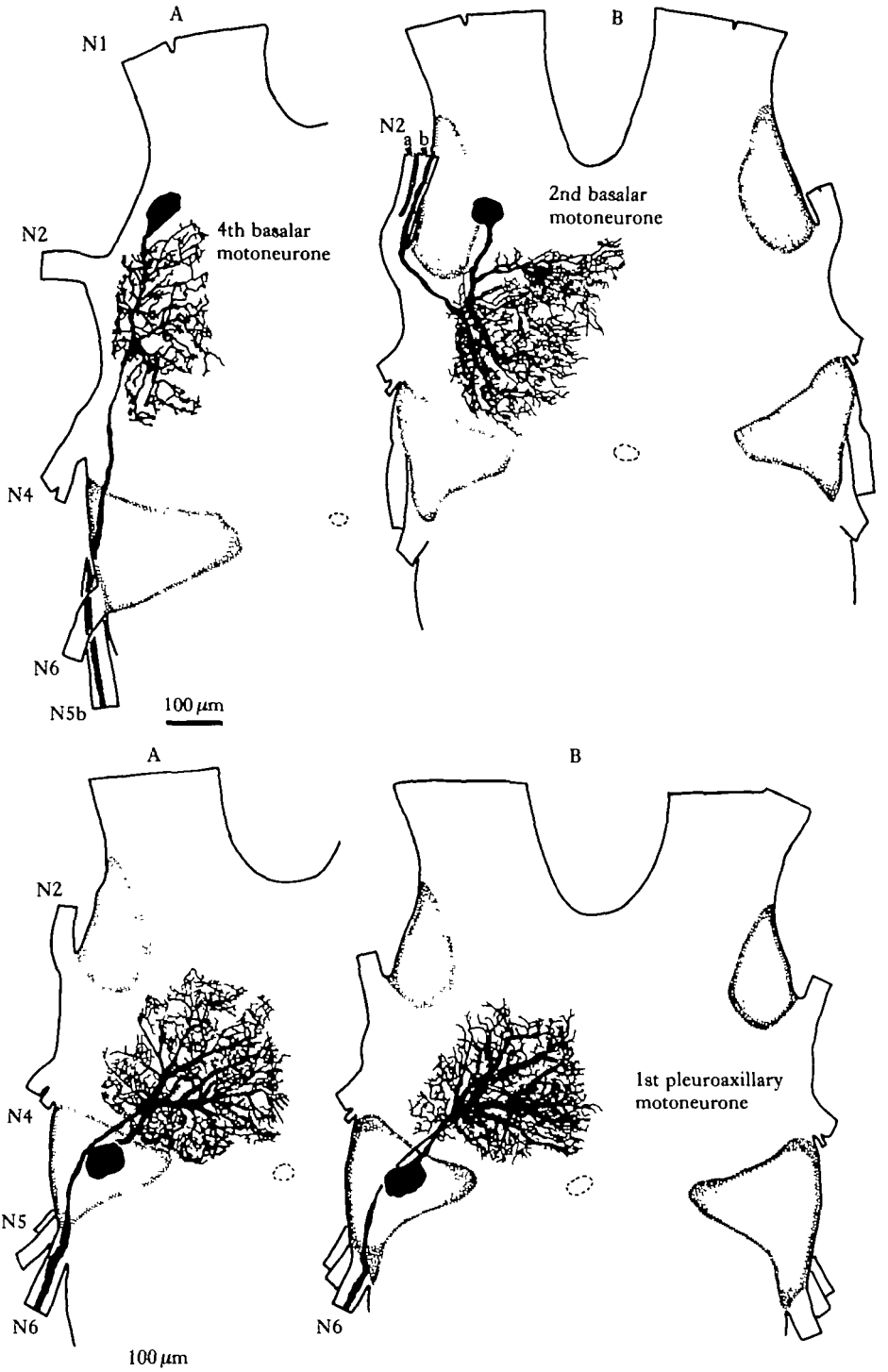


Fig. 6. Dorsal view of an intracellularly filled dorsal longitudinal motoneurone. The cell body is on the contralateral side of the ganglion to the muscle innervated. In Figs 5–9 the stippled areas represent areas of cell bodies, the dotted circle represents the depression marking the division between meso- and metathoracic ganglia.

branching pattern the 1st and 3rd basalar motoneurones (not illustrated) look very similar to the 2nd basalar.

The 1st pleuroaxillary motoneurone (Fig. 8) looks quite different from the other motoneurones. The cell body is around 40 μm in diameter, and is located in the dorsal area of the posterior group (Figs 3B, 8). The neurite emerges on the ventral side of the cell body and loops ventrally making a ventrally and anteriorly directed U bend. The dendritic branches emerge from a 20–30 μm region at the far arm of the U (Figs 3B, 8). The primary processes are large relative to those of other moth flight motoneurones and can be up to 13 μm in diameter. The overall pattern of these larger branches looks very similar in different fills of the 1st pleuroaxillary motoneurone (compare Fig. 8A and B). The axon emerges dorsally and narrows to 4–5 μm as it enters the tract of neurones which leave via nerve 6.

The axon of the subalar motoneurone also enters this tract. Fig. 5 shows a drawing of the two neurones from a single preparation, to demonstrate the close association of their processes. The cell body is around 40 μm in diameter and can lie in slightly


A
N1
N2
4th basalar
motoneurone
N4
N6
N5b
100 μm
B
N2
a
b
2nd basalar
motoneurone
A
N2
N4
N5
N6
100 μm
B
1st pleuroaxillary
motoneurone
N6

Figs. 7 & 8

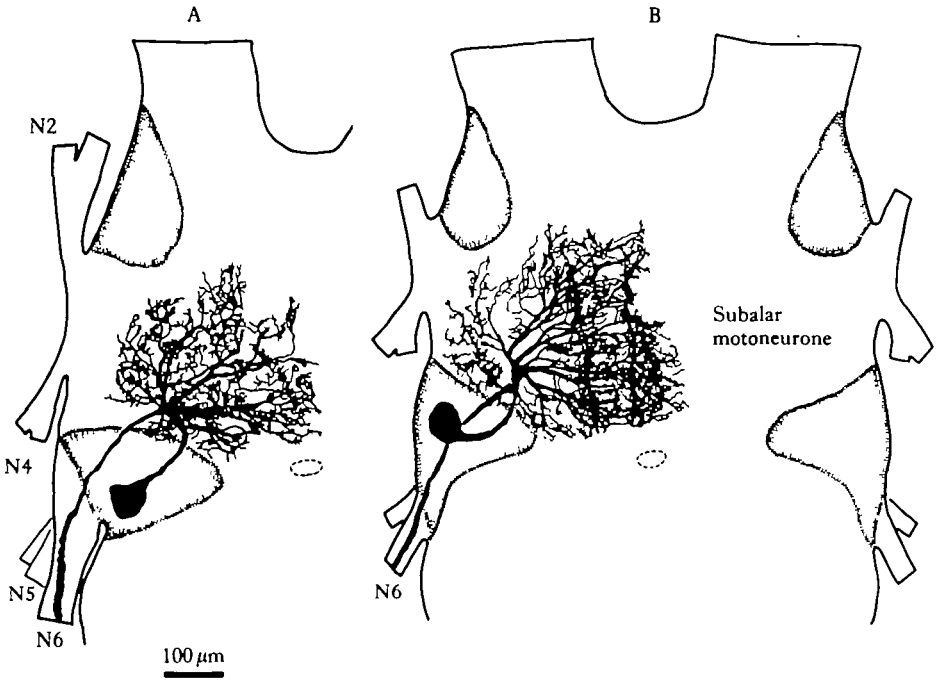


Fig. 9. A and B, Dorsal views of two intracellularly filled motoneurones to the subalar muscles in two different moths.

different positions in the ganglion (Fig. 9). The neurite emerges from the central side of the cell body and makes the same loop described from the 1st pleuroaxillary motoneurone. The processes are thinner than in the 1st pleuroaxillary motoneurone and in Fig. 9B there is a clear channel where the main tract of interganglionic interneurones have their axons.

DISCUSSION

The wing muscles of moths were first named upon morphological criteria (Nüesch, 1953), and this approach has been used to name muscles of *Manduca sexta* (Eaton, 1971, 1974). Kammer (1971) has reassessed the naming of the three direct depressor muscles, the basalar (P.V. 1–3) the pleuroaxillary (P.D. 2a–c) and the subalar (P.V. 4 and 5), on the evidence of electromyogram recordings. The criteria I have used for subdividing these muscles into their constituent blocks are functional ones, that is, anatomical divisions supported by innervation pattern. The present study provides support for Kammer's division of the basalar into four units rather than three, since four motoneurones were found, each innervating a distinct muscle block. Similarly this study shows that in the pleuroaxillary muscle all the medial fibres (P.D. 2a and b) are innervated by a single motoneurone and would therefore contract as one unit,

Fig. 7. Dorsal view of the intracellularly filled motoneurone to the fourth basalar muscle. B. Dorsal view of the intracellularly filled motoneurone to the second basalar muscle.

Fig. 8. A and B, Dorsal views of two intracellularly filled motoneurones to the first pleuroaxillary muscles of two different moths.

whereas the more medial fibre bundle (P.D. 2c) is innervated separately by a single motoneurone. This would give two instead of three functional units to the muscle. Lastly the subalar muscle also has at least one motoneurone which innervates both morphological units. The use of morphological criteria to establish innervation patterns in *Manduca sexta* (Eaton, 1974), could not show which nerves contain motoneurones to the pleuroaxillary or the subalar muscles, as both are innervated by a fusion of nerves 2a and 6. The present study demonstrated that all the axons of the motoneurones innervate the pleuroaxillary muscle via nerve 6.

The positions of the cell bodies to many of the flight motoneurones, and in particular those of the direct flight muscles, have been revealed in this study. One of the most striking constancies in the organisation of insect ganglia is the position of the cell bodies of motoneurones with axons in nerve 1. In the thoracic ganglia of the locust (Bentley, 1970; Tyrer & Altman, 1974), the cricket (Bentley, 1973), the dragonfly (Simmons, 1977*b*) and the moth (Casaday & Camhi, 1976; Rind, this paper), and in the abdominal ganglia of the locust (Lewis, Miller & Mills, 1973), the cicada (Simmons, 1977*c*), the cockroach (Komatsu, 1980), the moth (Taylor & Truman, 1974; Truman & Reiss, 1976), and dragonfly (Zawarzin, 1924), at least one motoneurone with its axon in nerve 1 has a cell body on the contralateral side of the ganglion. This tendency also extends to other arthropods as indicated by work on *Limulus* (Levy *et al.* 1975) and crayfish (Wine, Mittenthal & Kennedy, 1974).

In the locust, moth, cricket and cicada, mesothoracic nerve 1 innervates the powerful dorsal–longitudinal depressor muscle (locust, Tyrer & Altman, 1974; moth, Casaday & Camhi, 1976; cricket, Bentley, 1973; and cicada, P. J. Simmons personal communication). This muscle is innervated by five motoneurones, four of which have their cell bodies on the ipsilateral side of the next anterior ganglion (locust, Tyrer & Altman, 1974; moth, Casaday & Camhi, 1976, Y. Obara, in preparation). The fifth dorsal longitudinal muscle motoneurone has its cell body on the contralateral side of the ganglion. In the locust and the moth this motoneurone innervates the most medial and ventral muscle block of the dorsal longitudinal muscle.

As in other adult insects, the position of the cell body and the shape of the motoneurone to a particular flight muscle, once it is known, can be used as a guide to indicate where this neurone may be found again in another specimen. There is, however, some variation in the branching pattern between motoneurones to the same flight muscle in different moths, for example, the 1st pleuroaxillary in Fig. 6. The variation is most noticeable in the pattern of fine terminal branches.

All the neurones shown in Figs 5–9 have been identified by first noting which muscle they innervate. In general, motoneurones to different fibre bundles of the same muscle look similar. The motoneurones to the 1st, 2nd and 3rd basalar muscles, or to the 1st and 2nd pleuroaxillary muscles cannot be distinguished from one another morphologically. One exception to this is shown by the fourth basalar (Figs 5, 7) and another by the dorsal longitudinal motoneurone to the most medial, ventral fibre unit. These fibre units may have been added at a later stage to an already existing group of units and may reflect the composite nature of these particular muscle blocks.

This study has provided a useful working guide to the position of flight motoneurone cell bodies, dendrites and axons and has further extended our knowledge of the organization of flight motoneurones in the insect. The investigation has

concentrated upon innervation of the direct depressor muscles, since these muscles are particularly important for finely controlled movements during flight (Kammer, 1971). It sets the stage for further investigation into both the activity of the flight motoneurones during flight, and how this activity can be modulated by the type of stimuli a flying moth would perceive.

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