THE NEURONAL CONTROL OF DRAGONFLY FLIGHT

I. ANATOMY

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(Received 22 April 1977)

SUMMARY

The mechanical action and innervation of the major flight muscles of dragonflies are described. All flight muscles investigated are innervated by at least 3 motor neurones and one by as many as 15. Cell bodies of motor neurones that innervate the same muscle are clustered together, and have similar, widespread dendritic branching patterns. Motor neurones of leg muscles have greater variety in cell body size and position than the major flight motor neurones.

Striking similarities between the positions of cell bodies of motor neurones in dragonflies and the positions of homologous motor neurones in other insects raise interesting questions about the evolution of insect nervous systems.

GENERAL INTRODUCTION TO THE NEURONAL CONTROL OF DRAGONFLY FLIGHT

The flight of the locust has been much studied as an example of a patterned rhythmical behaviour that is generated entirely within the central nervous system, but comparable studies have not been made in detail for any other insect.

The dragonfly is not closely related phylogenetically to the locust. Dragonflies, unlike locusts, spend most of the active part of their adult lives in flight, engaging in complicated flight manoeuvres, and are capable of little terrestrial locomotion. Locusts probably only use flight as a means of dispersal and rapid escape.

INTRODUCTION TO PAPER I—ANATOMY

The positions of cell bodies of all the major flight motor neurones of locusts are known and the motor neurones all have extensively branching processes (Bentley, 1970; Burrows, 1973; Tyrer & Altman, 1974). The organization of flight motor neurones in dragonfly ganglia is strikingly similar to that in locusts, but the similarities probably reflect properties of arthropod nervous systems in general rather than providing clues as to how insects control their flight.

The musculature of the dragonfly thorax has been described a number of times, and the most complete and accurate account is that of Clark (1940). Neville (1960) studied the mechanical action of the wing muscles by manipulating thoraces and observing the effect on wingbeats of cutting muscles. Zawarzin's (1924) description of the
mesothoracic and fourth abdominal ganglia of dragonfly larvae has become a classical account of neuronal organization, and many of the neurones that he described in the mesothoracic ganglion are recognizable in the adult as flight motor neurones.

In this paper the structure, function and innervation of the flight musculature of dragonflies is first considered, followed by a description of the morphology and organization of the flight motor neurones. These descriptions provide the anatomical background for the following paper (Simmons, 1977) in which the physiology of the neuronal control of dragonfly flight is considered.

MATERIALS AND METHODS

Dragonflies were caught locally and kept for up to a week in a moist atmosphere at 10 °C. Most observations were made on male *Hemianax papuensis* (Burmeister), but females of this species and male *Aeshna brevistyla* (Rambur) were also used. (*A. brevistyla* ganglia usually have a darkly pigmented sheath, rendering them unsuitable for the examination of neuronal structure in whole mounts.) Both species and sexes average 65 mm in length. No differences in the flight apparatus were found between sexes or between species.

The anatomy of the nerve trunks was studied in specimens which were stained by injection of leucomethylene blue while still alive (Pantin, 1946) and in unstained specimens preserved in ethanol. Counts and dimensions of axons in various nerve trunks were determined in 1–2 μm thick toluidene blue-stained Araldite sections cut from material fixed in buffered gluteraldehyde and post-fixed with osmium tetroxide. Whole thoraces embedded in wax, sectioned longitudinally in the horizontal plane at 5 μm and stained with Mann's stain (Pantin, 1946), provided a check on axonal counts, as did methylene blue-stained and cobalt-filled nerve trunks.

To see neurone cell bodies in whole mounts live ganglia were stained with toluidene blue (Altman & Bell, 1973). Some toluidene blue-stained ganglia were embedded in wax and sectioned serially at 5 μm. Neurones in about 100 ganglia were back-filled with cobalt chloride (Sandeman & Okajima, 1973; Tyrer & Altman, 1974). Positions of the major flight motor neurone cell bodies were revealed by injecting Procion brown (H3R) or brilliant red (H3B) into them through microelectrodes with resistance 50–80 MΩ. Filling with Procion was achieved by applying a 180 V pulse across the electrode for less than 1 s. Ganglia containing injected cells were stained with toluidene blue to reveal the positions of other cell bodies.

RESULTS

Neuromuscular morphology

Each wing of a dragonfly is moved by five muscles that contract in a dorso-ventral direction (Fig. 1; Table 1). The action of the muscles was confirmed by stimulating each one with electrical shocks. Elevation and depression occur about a pivot. The depressor muscles dvm₃ and pm₁ attach directly to the wing distal to the pivot; the main elevator muscle, dvm₁, acts via the scutum on the proximal part of the wing; and the smaller elevator muscles, dvm₆ and dvm₇, attach directly to the wing proximal to the pivot. Important for producing lift and propulsion throughout a wingbeat are...
Neuronal control of dragonfly flight. I

Fig. 1. The five major muscles that move the right forewing of a dragonfly, viewed from the anterior: dvm₄, a minor depressor muscle, is also shown. The dorsal tendons of muscles are labelled. Except for dvm₁ and dvm₂, each muscle inserts into a sclerotized cap which is attached to the thorax by a flexible membrane. dvm₂ has a heavily sclerotized dorsal cap fused to the scutum and dvm₇ has a transparent dorsal tendon. The most important articulations of the wing are: two pivots, one of which is shown here, lying in a line between the points of attachment of the depressor muscles and the elevator muscles; and a line of weakness between the humeral and axillary complexes. Wing veins: C, costa; Sc, subcosta; R & M, radius and media (fused); CuP, cubitus; 1 A, first anal.

wing supination and pronation, and wing promotion and remotion (e.g. Pringle, 1957). Supination is achieved largely by a rapid separation of the axillary and humeral complexes caused by contraction of the elevator muscle dvm₄ (Neville, 1960). Pronation is achieved by contraction of the large depressor muscle dvm₃, but is opposed by the much smaller depressor muscles pm₁ and pm₃. The degree of pronation or of supination is therefore directly controlled by muscles. Promotion of a wing occurs passively during depression, and remotion occurs passively during elevation, although remotion is reinforced by dvm₄ through its action on the axillary and humeral complexes.

The axes of the wing base muscles (dlm, pm₁, pm₂, pm₃) are parallel to the thorax. Apparently they alter the form of the wingbeats by altering the geometrical relation between different sclerites in the wing base.
Table 1. Muscles of the dragonfly thorax

(A) Wing elevators

Major

\(dv_{m1} (= \text{first tergosternal})\)

\(dv_{m4} (= \text{anterior coxoalar})\) – main action is to supinate the wing. Also responsible for active remotion.

\(dv_{m6} (= \text{posterior coxoalar})\)

Minor

\(dv_{m2} (= \text{second tergosternal})\) – very small fan-shaped muscle situated on the anterior border of \(dv_{m4}\)

(B) Wing depressors

Major

\(pm_{1} (= \text{first subalar depressor})\)

Minor

\(dv_{m5} (= \text{first basalar})\) – small muscle situated adjacent to \(dv_{m8}\)

\(pm_{5} (= \text{second subalar depressor})\) – also supinates the wing

\(pm_{9} (= \text{third subalar depressor})\) – a minute, watery muscle with a dorsal tendon of pure resilin (Weis-Fogh, 1960)

Supinates the wing.

(C) Wing base muscles

\(dim\)

\(pm_{14}; pm_{16}\)

\(pm_{8}\)

(D) Muscles that raise the abdomen

\(III vlm_{1}\)

\(III ism_{1}\)

(E) Leg muscles

\(dv_{m4}\)

\(pm_{7}\)

Abbreviations. The abbreviations used in this paper are taken from Clark (1940).

II mesothoracic

III metathoracic

dvm dorso-ventral muscle

pm pleural muscle

vlm ventral longitudinal muscle

dim dorsal longitudinal muscle

ism intersegmental muscle

The innervation pattern of the flight muscles

Fig. 2 and Table 2 summarize the innervation pattern of the flight muscles. Nerves leaving each ganglion are numbered 1–3, from anterior to posterior. Major branches are labelled with capital letters.

The first abdominal ganglion is completely fused with the metathoracic ganglion, except for a small hole. A large nerve trunk from the first abdominal ganglion innervates III vlm\(_1\) and III ism.

Anatomical relations between thoracic nerves, muscles and skeleton are shown in Figs. 3–5. Ganglia are enclosed in a chitinous box formed by the floor of the thorax and the heavily sclerotized endoskeleton (Fig. 1). Nerves fit snugly into spaces between cuticular struts that form the sides of this box.

Nerves always bifurcate as they enter muscles and commonly run along tracheal
Neuronal control of dragonfly flight. I

Fig. 2. Plan of the innervation of flight muscles and sensory organs in the dragonfly thorax. Not drawn to scale. The pattern of nerve 1 is shown for the mesothorax, and of nerves 2 and 3 and the median nerve for the metathorax. Only minor differences exist between nerve patterns in the two segments. See also Figs. 3–5 and Table 2.

2A, 3A innervate legs

Table 3 shows the number and diameters of axons that innervate each major flight muscle. No axon was seen to branch and innervate more than one muscle. Each elevator muscle is innervated by axons of the same diameter (Figs. 6c, e, g). Among the depressor muscles, pm1 is innervated by axons of different diameter — two being 12–15 μm in diameter, and two being about 9 μm in diameter (Fig. 6f). The depressor muscle dvm3 receives many more axons than other muscles: 15 in each of two metathoraces examined, and 13 in another (Fig. 6b). At least 10 axons enter dvm3 in
Fig. 3. Dragonfly thorax bisected longitudinally: view of the right side showing muscles, ganglia and nerves. Sclerotized cuticle is stippled. III dlm is very small and has been removed. The only nerves visible are: II and III N1D, which innervate dlm and wing base sensory structures; part of III median nerve; and the nerve innervating III ism. The cuticular tunnel that encloses posterior connectives is left intact. Abbreviations: see Tables 1 and 2 for muscles and nerves; abd., abdominal; sp., spiracle.

Fig. 4. Innervation of the right side of the dragonfly thorax. II and III dvm3 and dvm4 have been removed, and articular structures in the wing bases and ventral regions have been omitted for clarity. In the mesothorax, details of nerve 1 and the median nerve are shown. In the metathorax nerves 2 and 3 are shown. Both segments are very similar. Note the variation in dorsal attachments of muscles. Most have sclerotized caps, but pm3 attaches to a resilin tendon. The apodeme of dvm7 is transparent and the apodeme of pm4 and a branch of N2C can be seen through it.
Table 2. Destinations and routes of thoracic nerves

<table>
<thead>
<tr>
<th>Nerve</th>
<th>Origin</th>
<th>Route</th>
<th>Destination</th>
</tr>
</thead>
<tbody>
<tr>
<td>1A</td>
<td>Near the ganglion</td>
<td>Anterior-dorsally</td>
<td>vlm</td>
</tr>
<tr>
<td>1B</td>
<td>N1 branches into N1B, N1C and N1D less than 1 mm from the ganglion</td>
<td>Laterally around the posterior border to the lateral border of dvm, which it enters median to the spiracle of the next anterior segment</td>
<td>(1) dvm, (2) dvm, (3) Mesothorax only: a small branch travels anteriorly.</td>
</tr>
<tr>
<td>1C</td>
<td>—</td>
<td>Along the lateral border of dvm, dorsally to the wing base.</td>
<td>(1) Chordotonal organ at origin of radius and media wing vein. (2) Fine branch to each wing vein innervates hairs. To slit-shaped organs on dorsal and ventral surfaces of radius &amp; media wing vein, and tough spines ventrally on subcostal wing vein.</td>
</tr>
<tr>
<td>1D</td>
<td>—</td>
<td>Along the median border of dvm1 to the thorax roof</td>
<td>(1) dlm (2) In the thorax roof dorsal to pm4 hairs and a chordotonal organ. (3) Posterior part of wing base.</td>
</tr>
<tr>
<td>2A</td>
<td>Near the ganglion</td>
<td>Ventro-laterally</td>
<td>Leg. One fine branch joins branch from N3A.</td>
</tr>
<tr>
<td>2B</td>
<td>N2 passes through a notch in the ventral attachment of dvm1 and immediately branches into NaB and NaC</td>
<td>Enters dvm1</td>
<td>(1) dvm1 (2) dvm1 (3) Small branch to the region of the next anterior spiracle. (4) dvm4, innervated from axons that travel up NaB inside dvm1.</td>
</tr>
<tr>
<td>2C</td>
<td>—</td>
<td>Dorsally, laterally and posteriorly to the anterior border of dvm6. Branch a travels dorsally along the anterior border of dvm6</td>
<td>(1) dvm6 (2) (a) pm4 (3) Joins branch of N3B; innervates pm4 (4) Fine fibres enter connective tissue surrounding dvm6 and dvm1. Methylene blue stains all bodies in this tissue.</td>
</tr>
<tr>
<td>3A</td>
<td>Near the ganglion</td>
<td>To the leg</td>
<td>Leg</td>
</tr>
<tr>
<td>3 except 3A</td>
<td></td>
<td>Mesothorax: dorso-laterally Metathorax: posterior along the endocuticular box that encloses the ganglion</td>
<td></td>
</tr>
<tr>
<td>3B</td>
<td>N3 branches into N3A and N3B at the posterior border of dvm7</td>
<td>Enters dvm7 at its posterior border. One branch travels dorsally</td>
<td>(1) dvm7 (2) Joins branch of NaC and innervates pm4.</td>
</tr>
<tr>
<td>3C</td>
<td>Around the posterior border of pm4 to enter pm1 and pm3</td>
<td></td>
<td>(1) pm4 (2) pm1 (3) pm3 (4) Small branches join the median nerve.</td>
</tr>
<tr>
<td>Median</td>
<td>Dorsal surface of ganglion, posterior to centre.</td>
<td>Branches into 2 on exit from ganglion. Each branch travels laterally and dorsally</td>
<td>Spirocal - closer muscle and other structure (Maybe heart).</td>
</tr>
</tbody>
</table>

* Simmons (in preparation).
Fig. 5. Dragonfly thorax seen from the ventral side looking dorsally. In the left half of the diagram legs have been removed at their bases, some cuticular struts have been cut, and muscles of muscles of coxal regions, except most of II and III pm, have been removed. Dragonflies were dissected to this extent for the physiological experiments described in the following paper (Simmons, 1977). The right half of the diagram shows a further stage-in dissection. All the ventral cuticle and most ventral muscle attachments have been removed, as well as vlm. Note that the tough attachments for the major elevators, dvmI (dvmI tdn.) lie immediately dorsal to the ganglia.

Table 3. Numbers and sizes of axons supplying muscles

<table>
<thead>
<tr>
<th>Muscle</th>
<th>No. of axons</th>
<th>Diameter (μm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Depressors</td>
<td></td>
<td></td>
</tr>
<tr>
<td>dvmI</td>
<td>10-15 (see text)</td>
<td>8-12</td>
</tr>
<tr>
<td>pmI</td>
<td>4</td>
<td>9-12.5</td>
</tr>
<tr>
<td>Elevators</td>
<td></td>
<td></td>
</tr>
<tr>
<td>dvmI</td>
<td>3</td>
<td>12-14</td>
</tr>
<tr>
<td>dvmII</td>
<td>3</td>
<td>12-14</td>
</tr>
<tr>
<td>dvmIII</td>
<td>5</td>
<td>12-14</td>
</tr>
<tr>
<td>Spiracle closers</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>Minor depressors</td>
<td></td>
<td></td>
</tr>
<tr>
<td>dvmIV</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>pmI</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>pmII</td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

the mesothorax (Fig. 6a). Axons that innervate dvmI have diameters ranging from about 7 to 14 μm (Figs. 6a, b).

Within most major muscles a single major nerve trunk travels in a dorso-ventral direction. In dvmI there are two such trunks: one in the medial part of the muscle and one in the lateral part. Within each muscle fine bundles of axons branch from the major trunk throughout its length (Fig. 6d). The exact number of axons in fine bundles of dvmI could not be determined but in the other fine bundles there was the same number of axons as in the major trunk (Figs. 6c, g).
Fig. 6. Histology of nerves supplying major muscles. All except (d) are 2 μm plastic-embedded sections stained with toluidene blue and osmium. (a) II N1B before a fine sensory branch leaves it—small axons on the left side. (b) III N1B as it enters dvm1. (c) the main nerve trunk (MT) and a fine branch (FB) of it inside dvm1—both contain three axons. (d) the major nerve trunk and fine branches from it in dvm4. Axons stained with methylene blue. (e) III N3 splits into two groups of axons within dvm4. Three axons travel dorsally to join a branch of N11 2C and innervate pm4; five axons innervate dvm4. (f) the main nerve trunk innervating III pm1. (g) the main nerve trunk and a branch from it innervating III dvm1. Scale: (a, b) 35 μm; (c) 25 μm; (e) 65 μm; (f) 40 μm; (g) 50 μm.

P. SIMMONS

(Facing p. 130)
Fig. 7. Large cell bodies in thoracic ganglia, stained with toluidene blue. (a) Metathoracic ganglion, view of the ventral surface. (b–d) 5 μm wax sections of another metathoracic ganglion, planes of section as indicated. In (c) the motor neurones of spiracle closer muscles can be seen; they act as convenient landmarks. (e) Another metathoracic ganglion, rotated so that the most lateral anterior cell bodies may be seen. (f) Mesothoracic ganglion. (g) Prothoracic ganglion.

P. SIMMONS
Cellular material surrounding branching points of nerves contains cell bodies that stain with methylene blue, and probably has a secretory or sensory function (Orchard & Finlayson, 1976).

**General features of motor neurone organization**

Most motor neurone cell bodies lie on the ventral surface of ganglia, but several are lateral or almost dorsal. Their general arrangement can be seen clearly in ganglia stained with toluidene blue (Fig. 7).

Cell bodies of motor neurones that innervate the same muscle lie very close to each other, and homologous motor neurone cell bodies occupy similar positions in the meso- and metathoracic ganglia. Fig. 8 summarizes cell body positions for all major flight motor neurones. Cell bodies of motor neurones that innervate different muscles are often of similar size and their possible positions overlap, so that it is not always possible to identify a particular toluidene-blue-stained cell body with absolute certainty. This is particularly true for motor neurones of the elevator muscles dvm₁ and dvm₆. It is also difficult to back-fill motor neurones of only one of these muscles...
in a single preparation because the nerve that innervates dvm\textsubscript{6} branches from nerve 2 just as it enters dvm\textsubscript{1}. Positions of cell bodies of dvm\textsubscript{1} and dvm\textsubscript{4} were confirmed by injecting them with Procion dye through microelectrodes; dvm\textsubscript{1} motor neurones generally have cell bodies that are anterior and medial to those of dvm\textsubscript{6}.

Dendritic processes of flight motor neurones are largely confined to the dorsal regions of the ganglia (Fig. 9). Proximal to the region where the axon of a motor neurone begins there is usually a swollen region from which originate major dendritic processes and a narrow process which connects the cell body to the rest of the motor neurone. In preparations where it was not badly distended with stain this region was 10 to 15 \( \mu \text{m} \) wide, slightly wider than the axon. Axons of motor neurones that innervate the same muscle originate close to each other, and sometimes twist around each other before they leave the ganglion (particularly axons of dvm\textsubscript{3} – Fig. 12). Third- and fourth-order dendritic processes, about 1 \( \mu \text{m} \) wide, branch from the larger processes. The largest processes of flight motor neurones that have axons in the same nerve run parallel to each other. Beading was commonly seen along the finest branches, and swelling often occurred at branch points.

All major flight-motor neurones have dendritic processes that extend over much of the side of the ganglion ipsilateral to the axon and all have a few processes that cross the midline of the ganglion. Processes from controlateral homologues cross each other but stain was never seen to have passed from one motor neurone to another. Passage of stain into other small cell bodies, possibly of interneurones (Strausfeld & Obermayer, 1976) or glial cells did occasionally occur. Some idea of variability in branching pattern between homologous motor neurones from ganglia of different animals can be seen by comparing the dvm\textsubscript{1} motor neurone in Fig. 11 and the pm\textsubscript{1} motor neurone in Fig. 12 with those in Fig. 9.
Fig. 10. Features of flight motor neurone structure. (a) Depressor motor neurone, pm₁, and elevator motor neurone, dvm₃, are stained in the mesothoracic ganglion. Cell bodies are not in the plane of focus. (b) Many dvm₃ motor neurones are stained in this metathoracic ganglion, as well as one dvm₁ motor neurone. View on to the ventral surface. (c) Mesothoracic elevator dvm₂ motor neurones on one side stained. Dorsal view. (d) Detail showing the mid-region of a metathoracic ganglion in which depressor, pm₁, motor neurones and elevator, dvm₁, motor neurones were stained on one side, and dvm₃ motor neurones were stained on the other. Major branches of pm₁ run parallel to each other; fine branches from all neurones cross the midline. Scale bars: 100 \( \mu \)m.

P. SIMMONS

(Facing p. 132)
Neuronal control of dragonfly flight. I

III dvm

II dvm

III dvm

II dvm

100 μm

Fig. 11. Elevator motor neurones in meso- and metathoracic ganglia. Only major dendritic branches shown.

Major flight motor neurones

Elevator motor neurones

Of the motor neurone cell bodies, the largest in the ganglia are dvm₁ (Figs. 9, 10(c), (d), 11) and dvm₆ (Figs. 10(a), 11); usually they are 60–65 μm across in toluidene-blue preparations. The dendritic processes of dvm₁ and dvm₆ motor neurones are similar in shape and the axons of the dvm₆ motor neurones originate slightly posterior to those of the dvm₁ motor neurones. Characteristically one large process runs posteriorly and another laterally towards the ganglion midline, but this pattern was not always clearly seen because one process usually swelled more than the other.

The five cell bodies of dvm₇ motor neurones (Fig. 11) are not clustered as closely as those of other motor neurones that innervate a common muscle. They are posterior
Fig. 12. Depressor motor neurones in meso- and metathoracic ganglia. Several III dvm₃ motor neurone cell bodies are shown, and the major neuropilar segment of two of them.

to nerve 3, near and medial to the pm₁ cell bodies (see later). Too few dvm₇ motor neurones were filled to draw conclusions about the shape of their dendritic processes, but they usually resembled those of the depressor motor neurones, pm₁, which also have their axons in nerve 3.

**Depressor motor neurones**

Motor neurones of dvm₃ (Figs. 10b, 12) have cell bodies that are contralateral to the major part of their dendritic process, axon and muscle. They are situated on the edges of the ganglia, anterior to nerve 1. Twelve, 40–45 μm across, were filled in a single metathoracic ganglion. Some of these may have innervated dvm₄ because I did not succeed in distinguishing dvm₄ from dvm₃ motor neurones. The major process traverses the ganglion from the axon to the midline, where the narrow process joined to the cell body originates. Other secondary processes branch from the major transverse process and extend posteriorly and slightly medially or laterally.

Four pm₁ motor neurones (Figs. 9, 10(a), (d), 12) were filled in some preparations, and had cell bodies 50–60 μm in diameter. They are closely packed on the edges of their ganglion, posterior to nerve 3. One major process extends from each towards the midline and another towards the anterior of the ganglion.
Neuronal control of dragonfly flight. I

Fig. 13. Non-flight motor neurones in the metathoracic ganglion. (a) One spiracular motor neurone; its dendritic processes show considerable overlap with its contralateral partner, which is not shown. Axons branch into both median nerves. The cell body is swollen considerably. (b) Consensus of three fills of nerve 3A, which innervates the leg.

Remaining motor neurones that were studied

**Median nerve**

The motor neurones of the closer muscles of the spiracles, and a number of other neurones, were filled from the median nerves. All of these neurones have axons that branch as they leave the ganglion, one branch travelling along each nerve. Spiracle motor neurones, which are easily recognizable in preparations stained with toluidene blue (Fig. 7), have cell bodies 40–50 μm in diameter and between the levels of nerves 2 and 3 in each thoracic ganglion. By comparing Figs. 9, 11 and 12 with Fig. 13 it can be seen that the shape of spiracle motor neurone dendritic processes is distinct from that of flight motor neurones. Processes from left and right spiracle motor neurones overlap extensively, but I have seen no evidence of direct contact between them.

In each thoracic ganglion three cell bodies less than 5 μm in diameter, in a lateral position near nerve 2 and clearly joined to axons, were often filled from a median nerve. Near the cell bodies of the spiracle motor neurones a number of small cell bodies, not clearly joined to axons, were also filled.

**Nerve 1D**

This nerve innervates dlm. The axons turn sharply on entering a ganglion and travel anteriorly along the ipsilateral connective to the next ganglion. Four cell bodies of II dlm are situated in the posterior part of the prothoracic ganglion.

**Nerve 2**

Back-fills of this nerve to stain dvm, and dvm, motor neurones often stained a number of smaller cell bodies as well. Nerve 2 innervates dvm, dvm, pm, (see under nerve 3C) and pm, and these smaller cell bodies are likely to belong to motor neurones of these muscles. Most of these smaller cell bodies lie near and posterior to dvm, cell bodies.
Fig. 14. Central projections of metathoracic wing base sense organs. Fibres travel up the medial part of the ipsilateral connective to the mesothoracic ganglion, where one of them is shown in side view.

**Nerve 3A**

Leg motor neurones have cell bodies that are scattered in position and variable in size with none as large as those of the major flight motor neurones (Fig. 13). Many leg motor neurones have cell bodies in anterior parts of the ganglia, in contrast to pm₁ and dvm₁, which are flight motor neurones of nerve 3. Dendritic processes of leg motor neurones are not as extensive as those of flight motor neurones, and none has been seen to cross the midline of a ganglion.

**Nerve 3B**

Often more than the five cell bodies of motor neurones that innervate dvm₁ are filled from nerve 3 B. Some of these are median and lie near the spiracle motor neurone cell bodies. Some fills of nerve 2C also stain cell bodies in this region which probably belong to pm₄ motor neurones.

**Nerve 3C**

Nerve 3C innervates pm₉ and pm₃ as well as pm₁. Up to seven cell bodies were filled from this nerve, all of them in one posterio-lateral region of the ganglion.

**First abdominal ganglion**

The cell bodies of motor neurones to III ism are 40 μm in diameter and contralateral to their axons.

**Central projections of sense organs of the wings**

Cobalt back-fills from nerves 1C and 1D, which innervate sensory organs of the wing base, were attempted only five times. Sufficient lengths of these nerves for filling are difficult to dissect. Bundles of fibres run towards the midline of the ganglion and
then parallel to the midline in anterior and posterior directions (Fig. 14). Short branches project from the fibres, and I have seen none that cross the midline of the ganglion. Sensory processes from the mesothoracic ganglion run through the ipsilateral connectives into the pro- and metathoracic ganglia and sensory processes from the metathoracic ganglion have been traced into the pro-meso-thoracic and metathoracic–abdominal connectives.

**DISCUSSION**

*Dragonfly motor neurones and flight*

Each of the major flight muscles of dragonflies must act as a single functional unit because all the axons that innervate a particular muscle have similar distributions within it. Motor neurones that innervate the same muscle cannot be distinguished by the sizes or positions of their cell bodies, or by the overall branching pattern of their dendritic processes, and all the major flight motor neurones appear to produce fast twitches in muscles (Simmons, 1977). If there are differences between the motor neurones that innervate a particular muscle – which is to be expected if dragonflies make full use of opportunities to regulate the power output from muscles – they must reside largely in the central connections of the motor neurones.

One dragonfly muscle, dvm₃, is innervated by an unusually high number of motor neurones, almost as many as the total that innervate all other major flight muscles. A possible interpretation is that dvm₃ plays the main part in the abrupt acceleration often exhibited by freely flying dragonflies. This muscle depresses a wing, particularly the leading edge, an action required for acceleration.

*Comparison of the organization of flight motor neurones in dragonflies and in locusts*

In both locusts and dragonflies fast motor neurones that innervate the same flight muscle tend to have cell bodies of similar size clustered together and very similar dendritic branching patterns (Bentley, 1970; Burrows, 1973; Tyrer & Altman, 1974). Flight muscles of dragonflies are generally innervated by more motor neurones than are flight muscles of locusts; a characteristic which may be related to the greater control required by dragonflies for aerial manoeuvres. There are important differences in the mechanical action of the power-providing flight muscles in the two types of insect. In locusts the largest depressor muscle is the dorsal longitudinal muscle, which does not attach to the wing base but exerts force on the wings indirectly; in dragonflies almost all flight muscles pull almost directly on the wing bases. Also, wing supination in locusts is a passive event during the up-stroke (Wilson & Weis-Fogh, 1962) whereas in dragonflies it is actively controlled by the small elevator muscle dvm₄ (Neville, 1960).

The evolutionary origin of the Odonata is unknown (Corbet, Longfield & Moore, 1960), so the evolutionary origin of differences in the flight musculature of dragonflies and locusts is unknown. All the major flight muscles in dragonflies have been homologized with muscles in locusts, apparently only on the basis of their general position (Clark, 1940). Homologies can be extended to the positions of the cell bodies of the motor neurones that innervate these muscles, as illustrated in Fig. 15. The only significant disparity, concerning the second basalar muscle (dvm₄ in dragonflies; muscle 98 in the locust mesothorax) may be related to two factors. First, this muscle is
Fig. 15. Positions of major mesothoracic flight muscles of locusts and dragonflies compared. For clarity the number of motor neurones innervating each muscle is indicated following the name of the muscle, and only one motor neurone to each muscle is drawn. In all cases, except possibly for the posterior coxalar muscle in dragonflies, cell bodies of motor neurones of the same muscle are clustered closely together. Before the name of each muscle its number (for locusts) or abbreviation (for dragonflies) is given. The map for the locust is based on Bentley (1970) and Tyrer & Altman (1974).

by far the largest muscle in dragonflies, and is innervated by at least ten motor neurones, whereas it is not exceptionally large in locusts and is innervated by only two motor neurones (Wilson & Weis-Fogh, 1962). Second, in dragonflies it is innervated through nerve 1, but in locusts it is innervated through nerve 3 — the significance of this is discussed in the next section.
The organization of motor neurones in insect ganglia in general

Some strikingly constant features of the way motor neurones are organized in ganglia of insects, and perhaps of arthropods in general, are beginning to emerge. The clearest of these concern positions of cell bodies of motor neurones that have axons in nerve 1, but generalizations about differences between the innervation of different types of muscle are also possible.

In the contrast to flight motor neurones, the leg motor neurones of locusts (Burrows & Hoyle, 1973) and dragonflies have cell bodies that are diverse in size and position, which is probably correlated with their greater diversity in function. In locusts, movements made by legs are versatile compared with the more stereotyped movements of the wings, to cope with variations in load due, for instance, to unevenness in the substrate. Dragonflies use their legs to grasp perches and prey; actions requiring fine control of muscle contraction rather than fast twitches.

All motor neurones which have cell bodies contralateral to their axons have axons in nerve 1 or, in fused ganglia, in nerves that can be homologized with it. This is true for one motor neurone that innervates each thoracic dorsal longitudinal muscle in locusts (Tyrer & Altman, 1974) and cicadas (Simmons, unpublished observation), for locust abdominal ganglia (Lewis, Miller & Mills, 1973), moth abdominal ganglia (Taylor & Truman, 1974) and dragonfly abdominal ganglia (Zawarzin, 1924; Mill, 1964; Simmons, unpublished observations). The motor neurones of dvm₃ in the dragonfly thorax emphasize the point in that they are so numerous (Fig. 11). No nerve other than nerve 1 has been found to contain motor neurones with axons contralateral to their cell bodies, and this tendency extends also to other arthropods, as indicated by recent work on *Limulus* (Levy, Nystrom & Nadelhaft, 1975) and crayfish (Wine, Mittenthal & Kennedy, 1974).

Another constant feature of the organization of motor neurones in insects is the innervation of the dorsal longitudinal muscle. Four cell bodies of motor neurones that innervate this muscle in insects as diverse as locusts (Neville, 1963; Bentley, 1970; Tyrer & Altman, 1974), cicadas (Simmons & Young, unpublished) and dragonflies, are situated in the next anterior ganglion. In locusts and cicadas the axons travel up the recurrent nerve, but this is absent in dragonflies and the axons enter a ganglion by nerve 1 and then travel anteriorly by the ipsilateral connective. As the recurrent nerve has been found in most insect orders the feature is probably common to them all. The dorsal longitudinal muscle is of prime importance in locusts and cicadas in providing power in flight, but in dragonflies it is minute by comparison, particularly in the metathorax, although its points of attachment are similar. No explanation can be offered as to why such a small muscle is innervated by five motor neurones, but possibly the muscle is a vestige from an ancestral flying insect in which it was large.

There may be constant features of neuronal organization throughout the insects. Evolution of muscular function may well be primarily a matter of change of functional central connections. Study of the motor neurone organization in further insect types can be expected to lead to generalizations about the evolution of nervous systems.
I thank Professor G. A. Horridge for initiating this work and for guidance in performing it. Dr E. E. Ball provided helpful advice during the work, and he and Drs S. Shaw and D. Dvorak criticized the manuscript during various stages of preparation.

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