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Structure predicts synaptic function of two classes of interneurons in the thoracic ganglia of *Locusta migratoria*

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Summary. The relationship between synaptic function and structure was examined for 32 spiking interneurons (13 inhibitory and 19 excitatory) in the meso- and metathoracic ganglia of the locust, *Locusta migratoria*. In no instance was the structure of an excitatory interneuron similar to that of an inhibitory interneuron. However, 12 of the 13 inhibitory interneurons shared a number of structural features, namely a ventromedially located soma, axon(s) projecting into contralateral connective(s), and a laterally bowed primary neurite. Structurally the excitatory interneurons formed a more heterogeneous group. Even so, 12 of the 19 had a combination of structural features in common, namely laterally located somata and axon(s) projecting into contralateral connective(s). The clear differences in structure of the two main groups of inhibitory and excitatory interneurons suggest that other neurons with structures similar to members of these two groups can be classified as inhibitory and excitatory, respectively. Thus we propose that structure predicts synaptic function for two distinct groups of interneurons in the thoracic ganglia of locusts.

Key words: Interneurons – Neuronal connections – Neuroanatomy – *Locusta migratoria*

Considerable progress has now been made in determining the neuronal circuitry for simple behaviors in invertebrates (Getting 1983; Miller and Selverston 1982; Wine 1984; Stretton et al. 1985; Calabrese 1979; Byrne 1983; Robertson and Pearson 1985; Pearson 1985). The interconnections among neurons in these circuits have usually been established by intracellular recording from pairs of neurons. This technique is reasonably straightforward when the neurons are large, visible and identifiable, as is the case in most of the now well-defined systems. However, because the neurons in many neuronal systems are small and numerous they cannot be visualized in living preparations. In these systems it is often very difficult to use intracellular recording to establish synaptic connections. This is particularly true for most systems in insects. Although some progress has been made towards determining the connections between identified neurons in these animals (Burrows 1982; Marquart 1985; Pearson et al. 1980; Robertson and Pearson 1983, 1985), it is clear that any approach relying solely on the use of intracellular recording is limited and will yield only a partial understanding of neuronal circuitry (Robert-

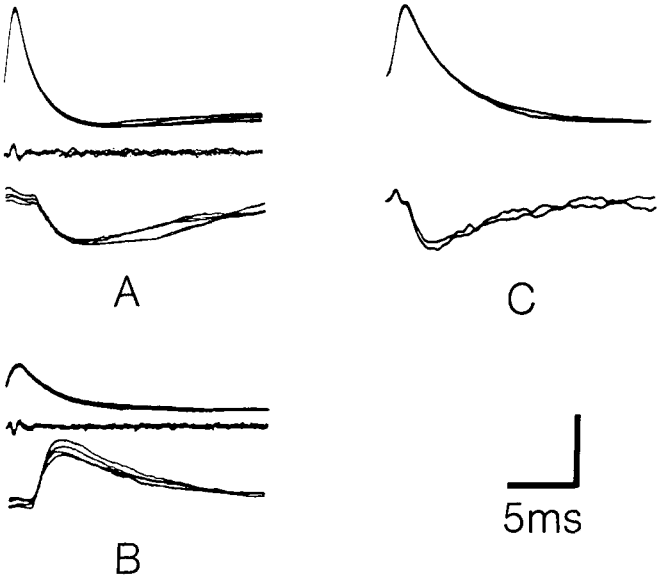

Fig. 1 A–C. Short-latency postsynaptic potentials evoked by spikes in identified interneurons. **A** Spikes in interneuron 302 (Fig. 3 right) evoke IPSPs in a flight motoneuron in the metathoracic ganglion. The IPSP latency was 2.3 ms, most of which was due to conduction time in the axon of the interneuron. This delay due to conduction was estimated from the time of occurrence of axonal spikes recorded extracellularly from the meso-metathoracic connective (middle trace). By subtracting conduction time, the estimated synaptic delay was 0.8 ms. **B** Spikes in interneuron 314 (Fig. 7A) evoke EPSPs in the fast extensor tibiae motoneuron in the metathoracic ganglion. The EPSP latency was 1.8 ms and the estimated synaptic delay, after subtracting the conduction time from the meso- to metathoracic ganglion, was less than 1 ms. The middle trace shows extracellularly recorded spikes from the axon of 314 in the meso- to metathoracic connective. **C** Spikes in interneurons 535 (Fig. 5 left) evoke IPSPs in a flexor tibiae motoneuron in the same ganglion. The small positive deflection just preceding the IPSPs is the field potential produced by the action potential in the large lateral process of the interneuron. The synaptic delay estimated from the time of the extracellular field potential to the onset of the IPSP was 0.8 ms. Vertical calibration: A and B 5 mV; C 2.5 mV

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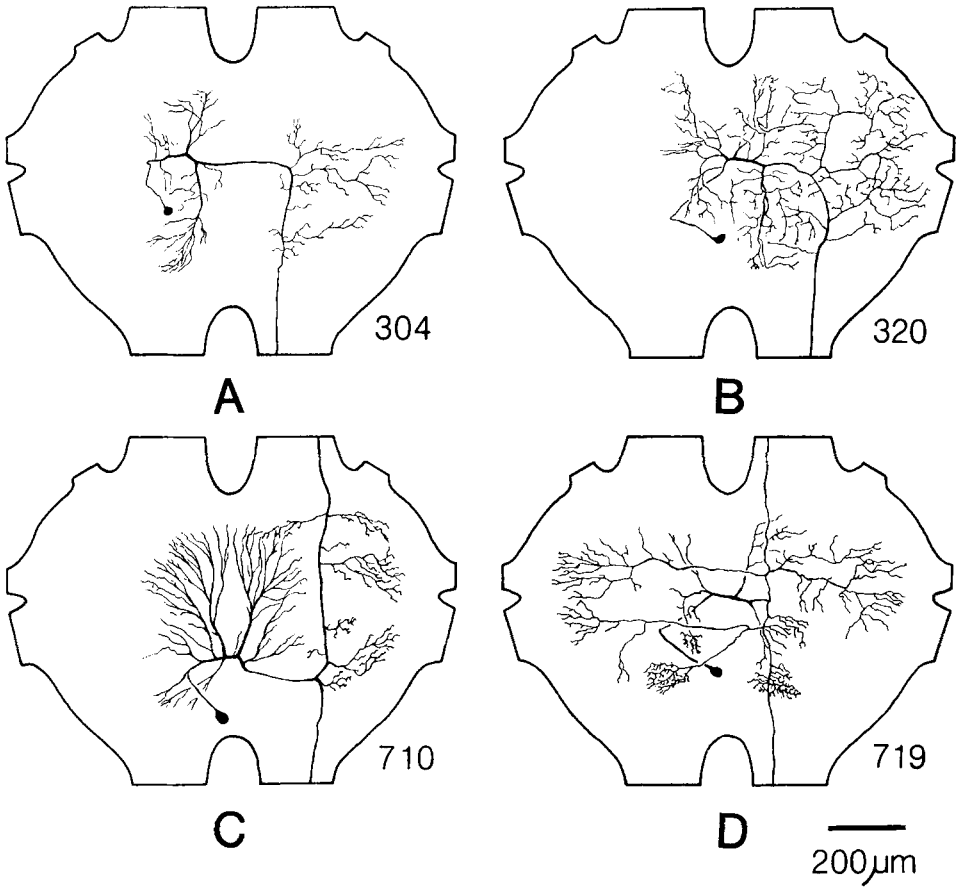

Fig. 2. Drawings of four inhibitory interneurons in the mesothoracic ganglion. The somata of all these neurons are located close to the ventral surface of the ganglion. Note that the primary neurite joining the soma to the main processes is bowed laterally

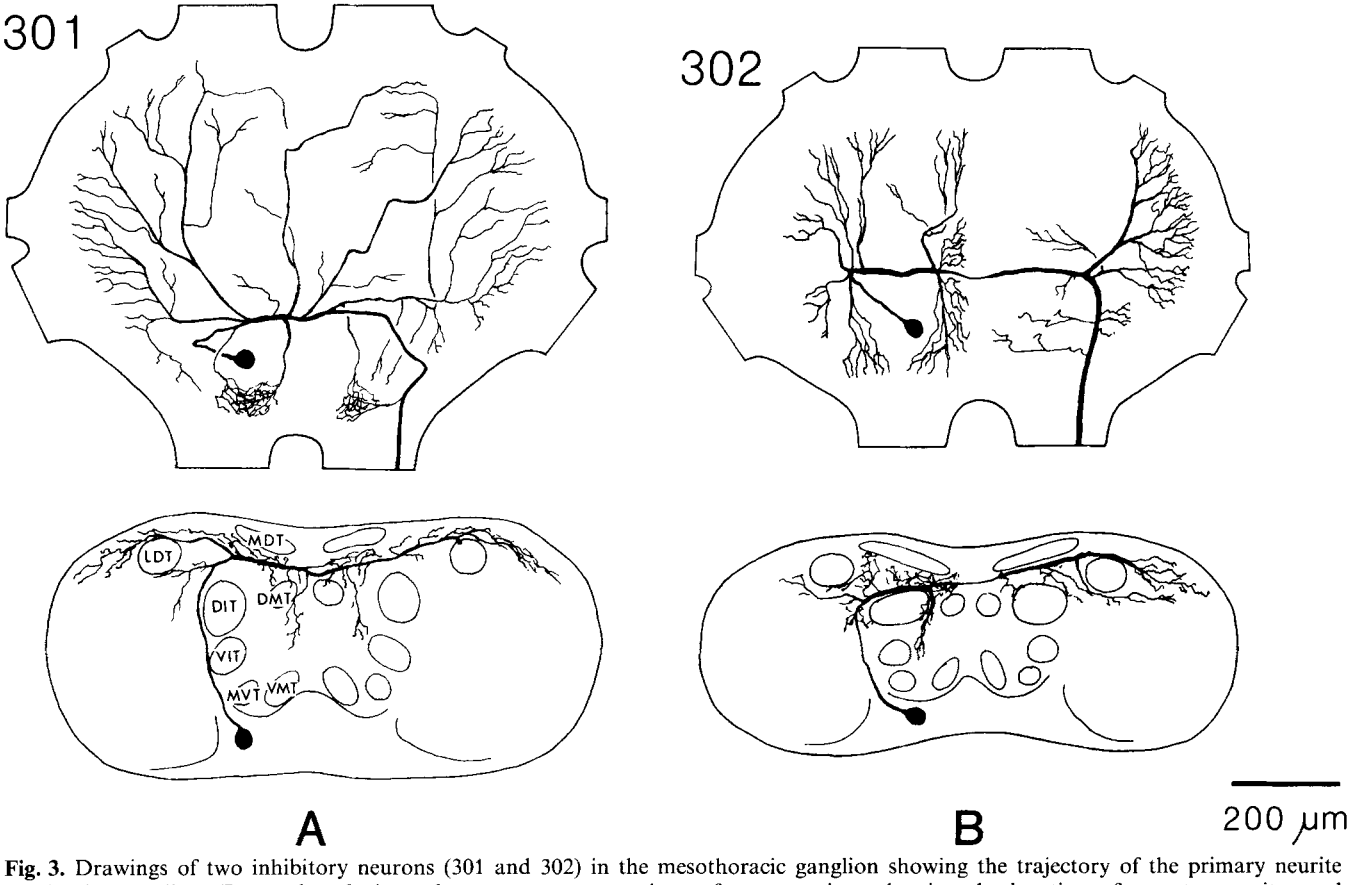

Fig. 3. Drawings of two inhibitory neurons (301 and 302) in the mesothoracic ganglion showing the trajectory of the primary neurite within the ganglion. Top – dorsal views; bottom – reconstructions of cross sections showing the location of somata, neurites and processes within the ganglion (dorsal up). In this figure and in Figs. 5 and 6 the longitudinal tracts have been labelled according to the scheme of Tyrer and Gregory (1982). The lateral bowing of the primary neurites is seen clearly in the reconstructional drawings at the bottom

Table 1. List of interneurons with known postsynaptic connections. Drawings of all the interneurons with the exception of 139 and 202 are shown in the figures of this paper

	Neuron number[a]	Behavior	Number of connections[b]	Previous description
Excitatory	110	flight	1	–
	139	hearing	1	Marquart (1985)
	201	flight	5	Robertson and Pearson (1983)
	202	flight	2	–
	206	flight	1	Robertson and Pearson (1985)
	314	jump	2	Pearson and Robertson (1981)
	503	flight	3	Robertson and Pearson (1983)
	504	flight	2	Robertson and Pearson (1983)
	505	flight	1	–
	506	flight	1	–
	514	flight	2	Robertson and Pearson (1983)
	521	flight	1	–
	529	hearing	3	Pearson et al. (1985)
	530	hearing	3	Marquart (1985)
	531	hearing	1	Pearson et al. (1985)
	537	–	1	–
	606	respiration	1	–
	701	flight	4	Robertson and Pearson (1983)
	714	hearing	3	–
Inhibitory	301	flight	3	Robertson and Pearson (1983)
	302	flight	2	Robertson and Pearson (1983)
	304	flight	2	–
	320	–	2	–
	401	flight	2	Robertson and Pearson (1983)
	501	flight	3	Robertson and Pearson (1983)
	511	flight	5	Robertson and Pearson (1983)
	513	flight	1	–
	515	flight	2	–
	520	flight	1	–
	535	jump	3	Pearson et al. (1980)
	710	jump/flight	2	–
	719	jump	1	–

[a] Numbering according to the scheme of Robertson and Pearson (1983)
[b] Number of different postsynaptic neurons which have been found to receive input from the interneuron

son and Pearson 1985). Currently the only other approach for demonstrating connections between identified neurons is electron microscopy. Electron microscopy has recently been used in insect motor systems to show direct connections between sensory afferents and identified motoneurons (Watson and Pflüger 1984; Peters et al. 1985). However, this technique has not yet provided information on the connections between identified interneurons. Because electron microscopy is very time consuming it seems unlikely that this technique will be useful for routine establishment of neuronal connections in insect motor systems. In the absence of techniques other than intracellular recording and electron microscopy, how is it possible to obtain more information on the organization and function of motor circuits in these animals?

Often in the analysis of insect motor systems we know the physiological properties of identified neurons (e.g., their discharge patterns during behavior and their responses to sensory stimuli) but we lack knowledge of their connections or synaptic function. Nevertheless, knowledge of structure and physiological properties of an interneuron in relation to the structure and properties of other identified neurons makes it possible to suggest plausible schemes concerning its connections with other neurons. To facilitate the development of these schemes it would be useful to have a simple method for specifying the postsynaptic action of interneurons. This would eliminate some possible interconnections. For example, if we know that a particular interneuron is inhibitory then it could not be connected to neurons that do not receive inhibitory input at the time that it is active.

One method that has been used to establish the synaptic function of neurons has been to examine the ultrastructure of the synaptic connections. Depending on the fixative, certain features of the vesicles, and the pre- and postsynaptic thickenings have been correlated with synaptic function in mammalian and invertebrate nervous systems (Tisdale and Nakajima 1976). Another approach for some classes of neurons has been to use immunological methods to identify the transmitter. This can only be used for neurons that release transmitters such as GABA that always produce the same synaptic action (Jones and Hendry 1986). In our studies on neurons in the thoracic ganglia of locusts we have been interested in establishing whether there is any relationship between the overall morphology of a neuron and its synaptic function. To date we have identified more than 100 intersegmental interneurons in the meso- and metathoracic ganglia of the locust, *Locusta migratoria*, and determined the synaptic action of 32 of these neurons. We have been able to classify neurons into a limited number of morphological types and, for those neurons for which

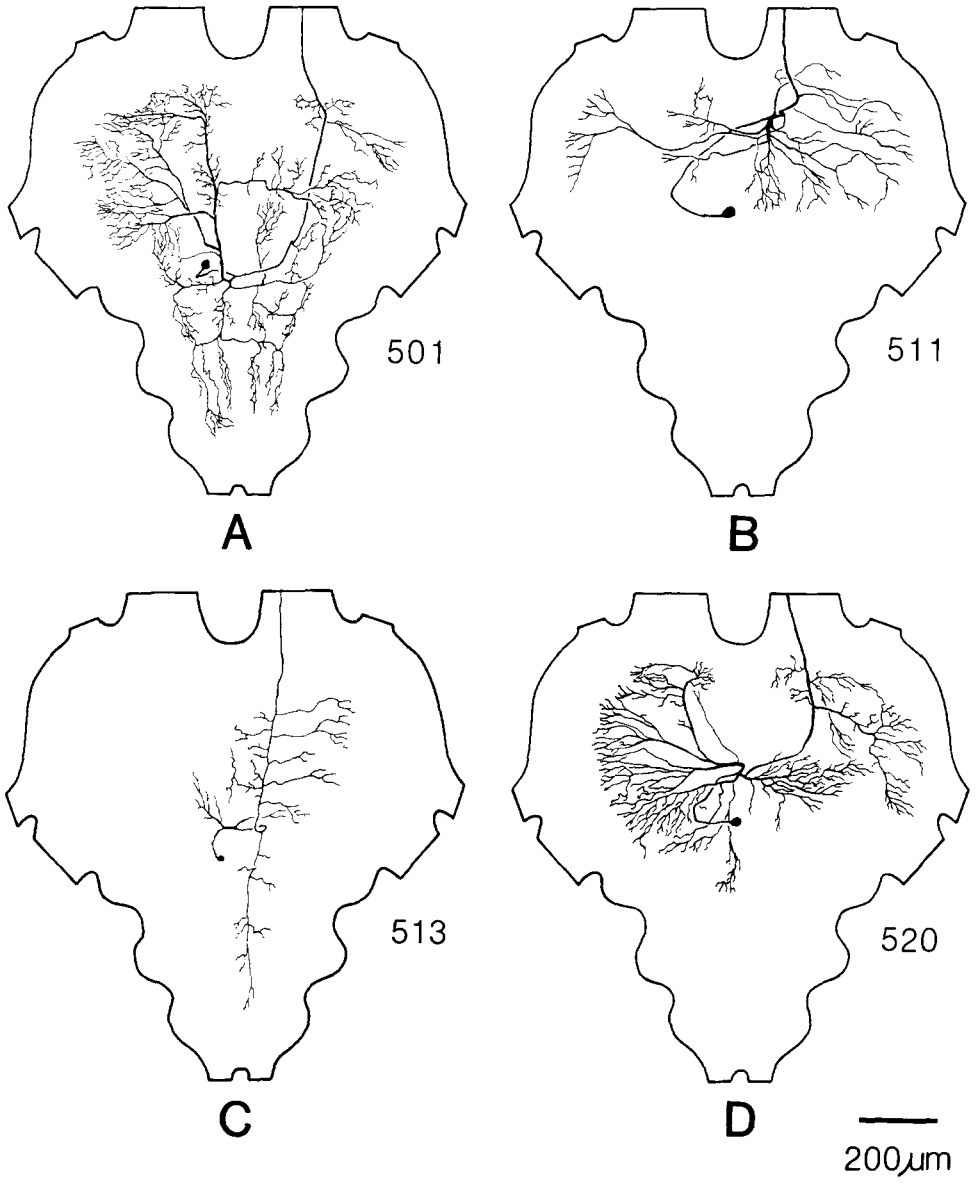

Fig. 4. Drawings of four inhibitory interneurons in the metathoracic ganglion. The somata of all these interneurons are located close to the ventral surface of the ganglion

synaptic function is known, we have found that the members of one morphological type are inhibitory and those of another morphological type an excitatory. Thus we conclude that the structure of neurons can be used for establishing the synaptic function of at least two types of neurons in thoracic ganglia of this species.

Materials and methods

Data presented in this report were accumulated in the course of investigations in the neuronal mechanisms controlling jumping (Pearson et al. 1980; Pearson and Robertson 1981), flight (Robertson and Pearson 1983), respiration and hearing in the locust, *Locusta migratoria*. By simultaneously recording from an interneuron and either another interneuron or a motoneuron (see Pearson et al. 1980, for experimental procedure) we have identified some of the connections made by 30 intersegmental interneurons and 2 local neurons.

The structure of the interneurons was determined by intracellular injection of Lucifer yellow (minus 5nA for 5 min). Ganglia were fixed in 4% paraformaldehyde for 1/2 h, then dehydrated and cleared in methyl salicylate. The identity of individual interneurons was established by viewing whole-mounts of cleared ganglia. To establish the location of the processes of the interneurons relative to identified tracts within the ganglia (Tyrer and Gregory 1982) the cleared ganglia were returned to absolute alcohol, embedded in Spurr's resin, and serially sectioned (15 µm thick sections). Sections were stained with an equal parts mixture (1 g/100 ml) of azure B and methylene blue, and viewed either under epifluorescence or with transmitted white light. The ganglionic tracts and the fluorescent processes of the stained neuron were drawn for each section with the aid of a drawing tube. Alignment of drawings from adjacent sections allowed us to reconstruct the pathways taken by processes of stained neurons within the ganglion.

The criteria used for classifying an interneuron as inhibitory or excitatory were: (1) that each spike in the inter-

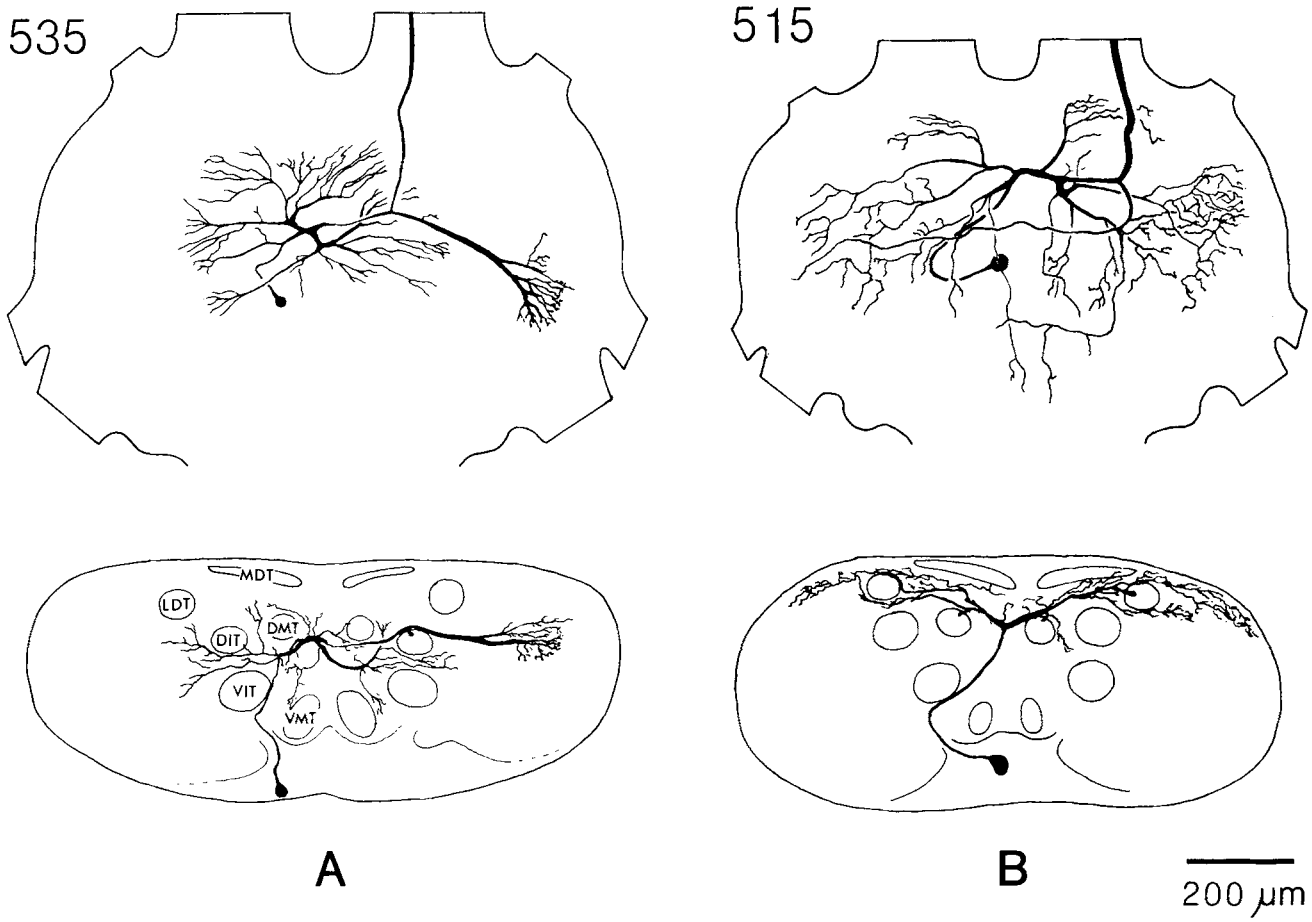

Fig. 5. Drawings of two inhibitory interneurons (535 and 515) in the metathoracic ganglion showing the trajectory of the primary neurite within the ganglion. Top – dorsal views; bottom – reconstructions of cross sections showing the location of the somata, neurites and processes within the ganglion (dorsal up)

neuron evoked a postsynaptic potential (PSP) in another neuron with a short constant latency (Fig. 1), which, after subtracting the conduction time of the action potential, indicated a synaptic delay of less than 1 ms, and (2) that the axonal processes of the interneuron overlapped the processes of the neuron in which it evoked the PSPs (see Pearson et al. 1980 for an example). The possibility that these postsynaptic potentials were produced via an interposed interneuron is unlikely because a latency of less than 1 ms in a disynaptic pathway implies at least one of the synapses is an electrical junction. To date no electrical synapses have been found between thoracic interneurons in the locust, nor have gap junctions been observed in electron micrographs of interneurons (Watson and Burrows 1982, 1983). The only reported instance of electrical coupling of thoracic neurons in the rare occurrence of coupling between supernumerary motoneurons (Siegler 1982).

Results

We have determined the synaptic action of 32 interneurons in the meso- and metathoracic ganglia of *L. migratoria*. Table 1 lists these interneurons and classifies them as excitatory or inhibitory. The numbering of the interneurons is that proposed by Robertson and Pearson (1983). Drawings of the structure of 30 of these interneurons are shown in Figs. 2–9. Although we refer to a single morphological type with a single name, we know that many of these interneurons are not unique. For example, there are at least two 201 neurons; also neurons 401, 503 and 504 are repeated serially in the metathoracic and first three abdominal ganglia (Robertson and Pearson 1983). So far none of our data indicate that neurons with similar morphology and similar discharge patterns have different synaptic functions, i.e., every 201 neuron for which connections have been determined has been excitatory, and all segmental homologues of the neurons 401, 503 and 504 have the same synaptic function. Thus all individuals within a single group have the same synaptic function. At the beginning of this analysis one concern was whether the interneurons could be strictly classified as either excitatory or inhibitory. For those interneurons known to form direct connections with two or more neurons (20 out of 32) (Table 1), none produced different short-latency synaptic actions on different neurons. Thus classifying interneurons as either excitatory or inhibitory appears sound at present.

Inhibitory interneurons. Drawings of 13 inhibitory interneurons are shown in Figs. 2–6. To date all the inhibitory

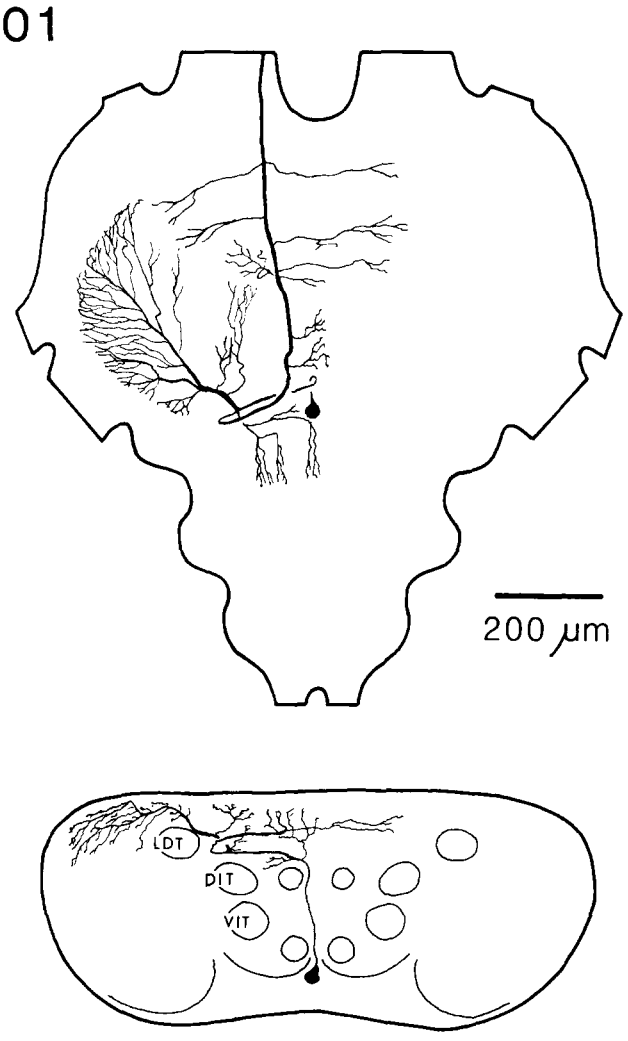

Fig. 6. Drawing of the only inhibitory interneuron (401) found to have a structure distinctly different from all other inhibitory interneurons (Figs. 2 to 5). Top – dorsal view; bottom – reconstruction from cross sections showing the soma located close to the ventral surface (dorsal up) and the primary neurite entering the neuropile in the middle of the ganglion (compare with Figs. 3 and 5)

interneurons that we have identified are intersegmental (sending at least one axon from the ganglion containing their somata) and all but one have axon(s) lying contralateral to the soma. The striking feature of the 12 inhibitory interneurons with their axon(s) contralateral to their soma is that all share other structural features that distinguish them from all excitatory interneurons identified to date. The first is that their somata are located ventromedially within the ganglion, and the second is that their primary neurites connecting the soma to the main processes have a laterally bowed appearance when viewed from the dorsal surface (Figs. 2–5). The lateral bowing of the primary neurite is the result of the neurite entering the neuropile at a site located about 150 µm from the midline (Figs. 3–5). This site of entry is more lateral than the location of the somata of these neurons. Tyrer and Gregory (1982) in their description of the organization of the thoracic ganglia did not label this site of entry, although it is shown clearly in their Figs. 2F and 8F. The trajectory of the primary neurites of the inhibitory interneurons through the ganglia varied from neuron to neuron. In some cases it was medial to the ventral intermediate tract (Fig. 5) whereas in others it was located lateral to both the ventral and dorsal intermediate tracts. There was no strict correlation between the trajectory of the primary neurite and the location of the main processes. For example, some neurons with most of their processes located near the dorsal surface of the ganglion had primary neurite located lateral to the dorsal intermediate tract (Fig. 3A, B), whereas others had their primary neurite situated medial to the ventral and dorsal intermediate tracts (Fig. 5B).

The only inhibitory neuron that we have identified with an overall structure distinctly different from that of the interneurons shown in Figs. 2–5 is interneuron 401 (Fig. 6) in which the axon was ipsilateral to its soma and the primary neurite lacked the characteristic bowed appearance of the other inhibitory interneurons. Interneuron 401, however, had its soma located ventrally on the midline of the ganglion. In this regard it was similar to the other 12 inhibitory interneurons.

Excitatory interneurons. In overall structure, the 19 excitatory interneurons could be classified into five groups. The first and most common group, 12 out of 19 neurons, had somata located posterolaterally within the ganglion and contralateral to their axon(s) (Figs. 7–8). A second group consisted of 3 interneurons with ventromedially located somata and axons lying ipsilateral to the somata (Fig. 9A, B). The third includes a single interneuron with an axon located ipsilateral to its soma and the soma lying laterally within the ganglion (Fig. 9D). The fourth was a pair of interneurons (one local, not shown, and one intersegmental with a contralateral axon) with somata in the anterior region of the metathoracic ganglion (Fig. 9E). These neurons have previously been described by other authors (Römer and Marquart 1984). The final group consisted of a single local interneuron with a posterolaterally located soma and processes extending into both sides of the mesothoracic ganglion (Fig. 9C).

Inspection of the structure of all of these excitatory interneurons shows that not one of them had a morphology similar to an inhibitory interneuron. In particular, none of the excitatory interneurons with somata contralateral to their axons had a ventromedially located soma and a primary neurite with a bowed appearance when viewed from the dorsal surface. It should be noted, however, that some of the excitatory interneurons did have ventromedially located somata (Fig. 9A, B).

Discussion

In this analysis we have examined the relationship between the structure of identified thoracic interneurons in *Locusta migratoria* and their synaptic function, i.e., whether they are excitatory or inhibitory. The striking result is that all interneurons with one distinct structure (Figs. 2–5) are inhibitory, whereas all interneurons with another distinct structure (Figs. 7–8) are excitatory. In every instance in which we determined the synaptic function of an inter-

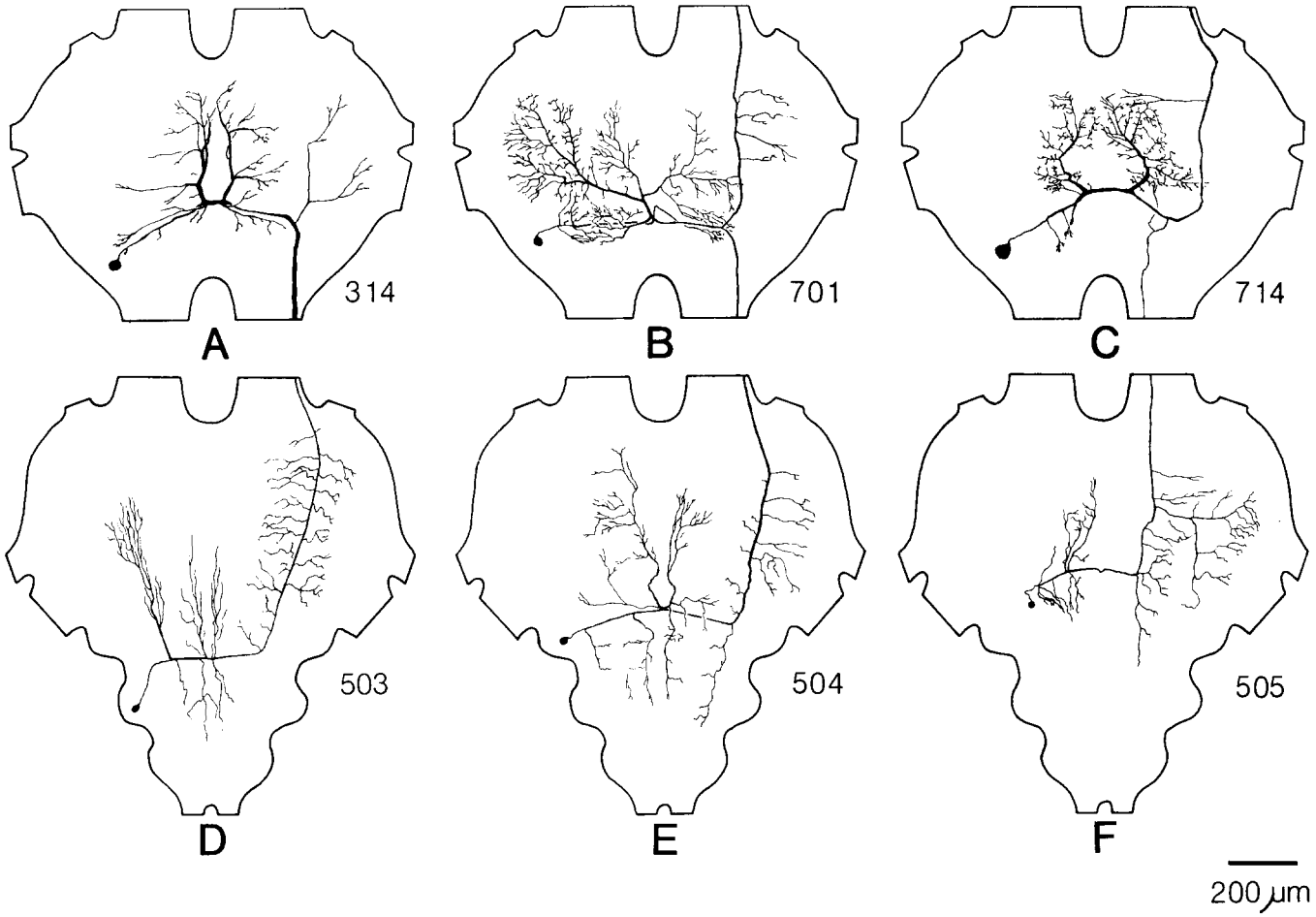

Fig. 7A–F. Drawings of three excitatory interneurons in the mesothoracic ganglion (**A** to **C**) and three excitatory interneurons in the metathoracic ganglion (**D** to **F**). The somata of neurons shown in **A** to **E** are located laterally within the ganglion, and the soma of the neuron shown in **F** is located close to the dorsal surface

neuron with its soma located ventrally near the midline and with axon(s) projecting contralaterally (n = 12), we found the interneuron to be inhibitory. On the other hand interneurons with somata located laterally in the posterodorsal region of the ganglion and axon(s) projecting contralaterally ($n = 12$) were found to be excitatory. The obvious question is: Are all neurons in the thoracic ganglia with one or the other of these two structures inhibitory or excitatory, respectively? In the absence of contrary evidence we assume that they are and propose that the synaptic function of these two morphologically distinct classes of neurons can be predicted from structure alone. Our confidence in this proposal stems from the fact that we began predicting the synaptic function of these two classes of interneurons when we had determined the connections of only 4 inhibitory and 5 excitatory interneurons. Subsequently, all our findings have been consistent with our predictions.

It is important to note that we are not proposing that all inhibitory neurons have one particular structure and that all excitatory neurons have another structure. Clearly this is not true. For instance, one inhibitory interneuron (Fig. 6) has a different structure from all the others that we examined; also there are at least four additional morphological types of excitatory interneurons (Fig. 9). It would be of some interest, however, to know whether or not these other structures will prove to predict synaptic function. Until the numbers within each of these other classes are considerably greater we cannot answer this question. Nonetheless, it should be noted that in no instance have we found an excitatory and an inhibitory interneuron to have a similar structure.

An interesting question is whether any differences in structure are related to specific behavioral roles of the interneurons within each class. Unfortunately specific behavioural roles for the majority of the interneurons described in this article have not been determined, although most can be classified according to whether they are involved in flight, jumping, respiration or hearing (Table 1). We do know that some features of structure are related to the behavior in which the neurons is involved. For example, flight interneurons have many secondary processes located preferentially in the dorsal neuropile regions of the thoracic ganglia, and auditory interneurons in the metathoracic ganglion have processes projecting into the anterior auditory neuropile of the ganglion. However, the structural features that we have examined in this investigation, i.e., soma locations and trajectories of the main processes, do not appear to be related to behavior. One particularly clear example

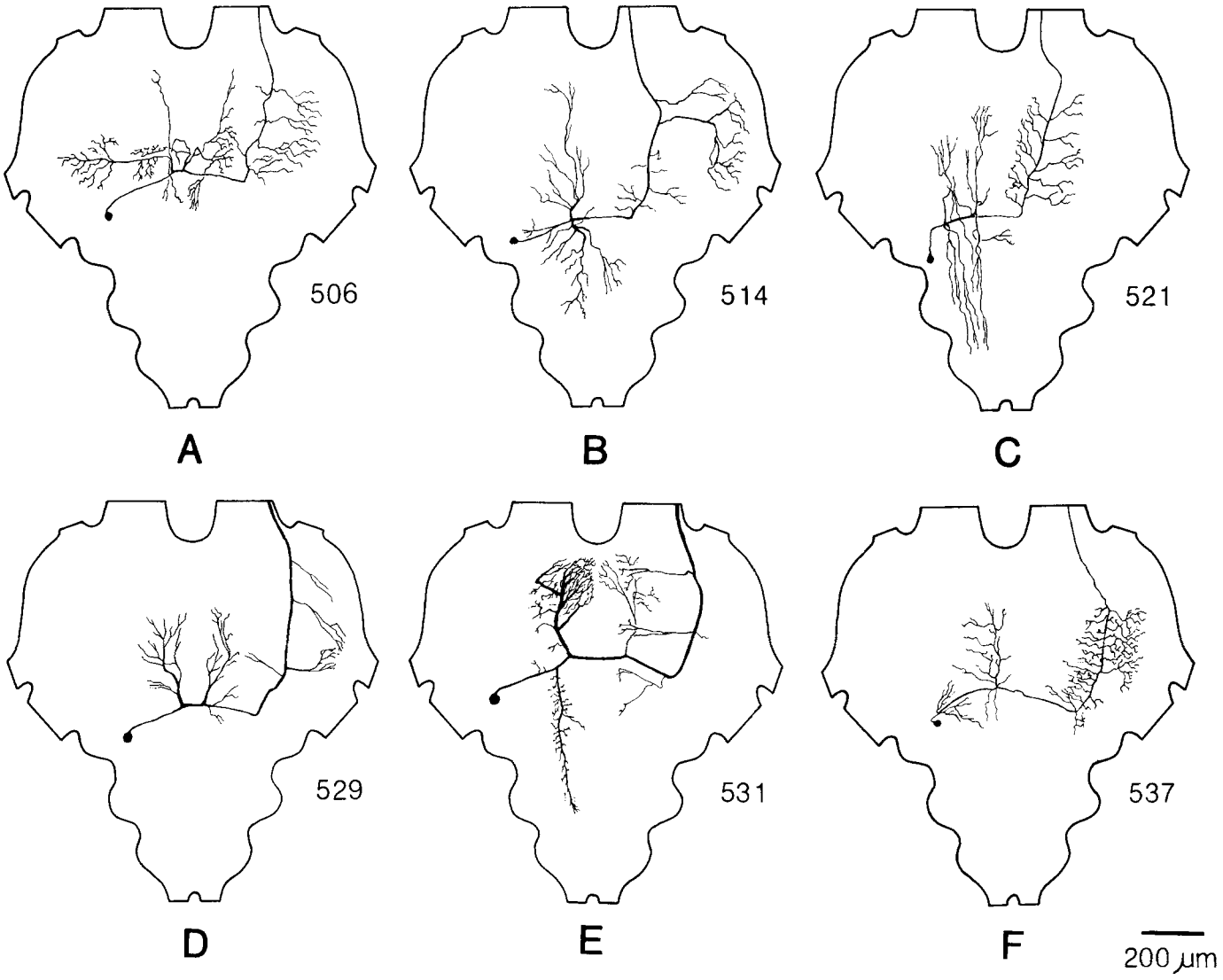

Fig. 8A–F. Drawings of six excitatory interneurons in the metathoracic ganglion. The somata of the interneurons shown in **A, D, E** and **F** are located close to the dorsal surface of the ganglion

is the similarity of these features in interneurons 314 (Fig. 7A) and 714 (Fig. 7C). Although these two neurons are involved in completely different behaviors (314 in hearing and 714 in jumping) their soma have similar soma locations and their transverse processes are located in the same commissure. This similarity in structure is a consequence of two neurons with a common developmental lineage, arising from the division of the second ganglion mother cell of neuroblast 7-4 (Raper et al. 1982).

Another interesting aspect of our analysis of the structure of inhibitory interneurons is that the somata of all of these interneurons were located close to the midline on the ventral surface of the thoracic ganglia (Fig. 10, right). By contrast, the somata of all but three of the excitatory interneurons were located in the lateral and dorsal regions of the ganglia (Fig. 10, left). The ventromedial location of the somata of the inhibitory interneurons corresponds to the location of the somata of all other spiking inhibitory neurons so far described in thoracic ganglia of locusts, namely an intersegmental interneuron in the respiratory system (Burrows 1983), a group of spiking local interneurons (Siegler and Burrows 1984), and all inhibitory motoneurons (Burrows 1973). The question is whether inhibitory neurons exist with somata situated outside the ventromedial region of the ganglia. An indication that they may is that immunocytochemical studies of thoracic ganglia have shown numerous laterally located somata containing the transmitter GABA (G. Bicker, personal communication). Currently it is assumed that GABA is only an inhibitory transmitter in insect nervous systems. Another indication is that in a related species, the cricket, one inhibitory interneuron in the auditory system has its soma located laterally within the prothoracic ganglion (Selverston et al. 1985). Even if some inhibitory neurons in the locust have somata outside the ventromedial regions of the thoracic ganglia, the data so far indicate that the majority of somata of inhibitory neurons are localized in the ventromedial region. A similar conclusion was reached in a study of the position of somata

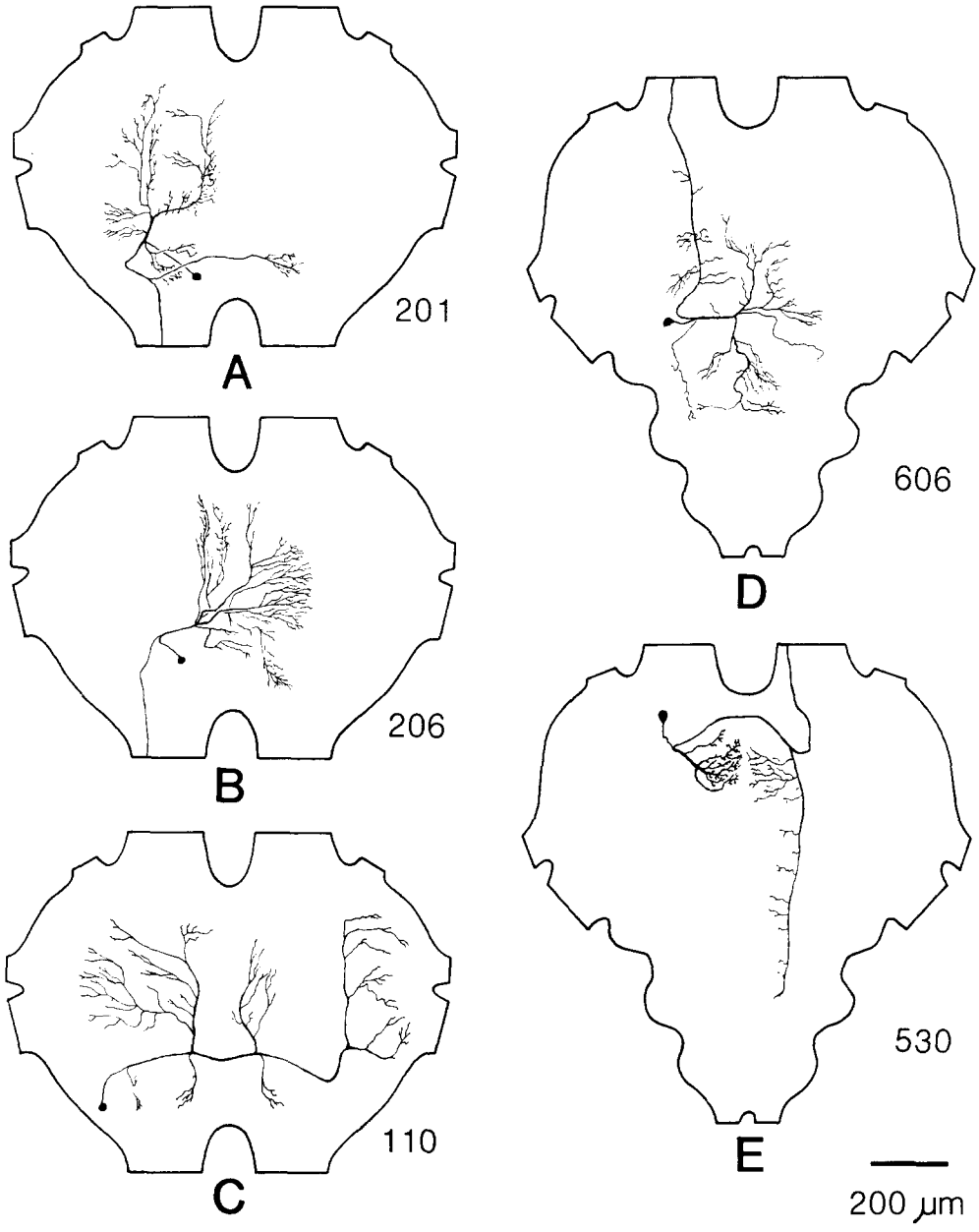

Fig. 9 A–E. Drawings of excitatory interneurons in the mesothoracic, **A–C**, and metathoracic, **D, E** ganglia with structures distinctly different from those excitatory interneurons shown in Figs. 7 and 8. **A** and **B** These two neurons have their somata located near the ventral surface of the ganglion and each sends a single axon out the ipsilateral meso-metathoracic connective. **C** A local interneuron with a laterally located soma. **D** This neuron has a ventrally located soma and an ipsilateral ascending axon. **E** This neuron has its soma located near the ventral surface in the anterior region of the ganglion

of inhibitory motoneurons in the lobster in which somata of inhibitory neurons are localized in the ventromedial regions of the abdominal ganglia (Otsuka et al. 1967).

Apart from providing a useful procedure for specifying the synaptic function of certain interneurons, our analysis has raised some fundamental questions. For example, why is there a correlation between structure and synaptic function, and why are the somata of spiking inhibitory and excitatory interneurons generally located in different regions of each ganglion? No firm answers to these questions can be given at present but from our knowledge of the ontogeny of identified neurons in thoracic ganglia in locusts we assume that they involve phenomena related to developmental origin of the different types of interneurons. All dorsal unpaired medial (DUM) neurons, for example, have bifurcating primary neurites and dorsally located somata. These shared structural features are a consequence of development of DUM neurons from a single medially located neuroblast (Goodman and Spitzer 1979). Similarly, a laterally located neuroblast gives rise to a group of neurons with somata that cluster in the dorsolateral region of each ganglion and with primary neurites, as far as has been determined, of the same initial form (Raper et al. 1982). These observations suggest the testable hypothesis that excitatory and inhibitory interneurons of the type with which we have been mainly concerned in this analysis (spiking and intersegmental) originate from different neuroblasts during the course of development.

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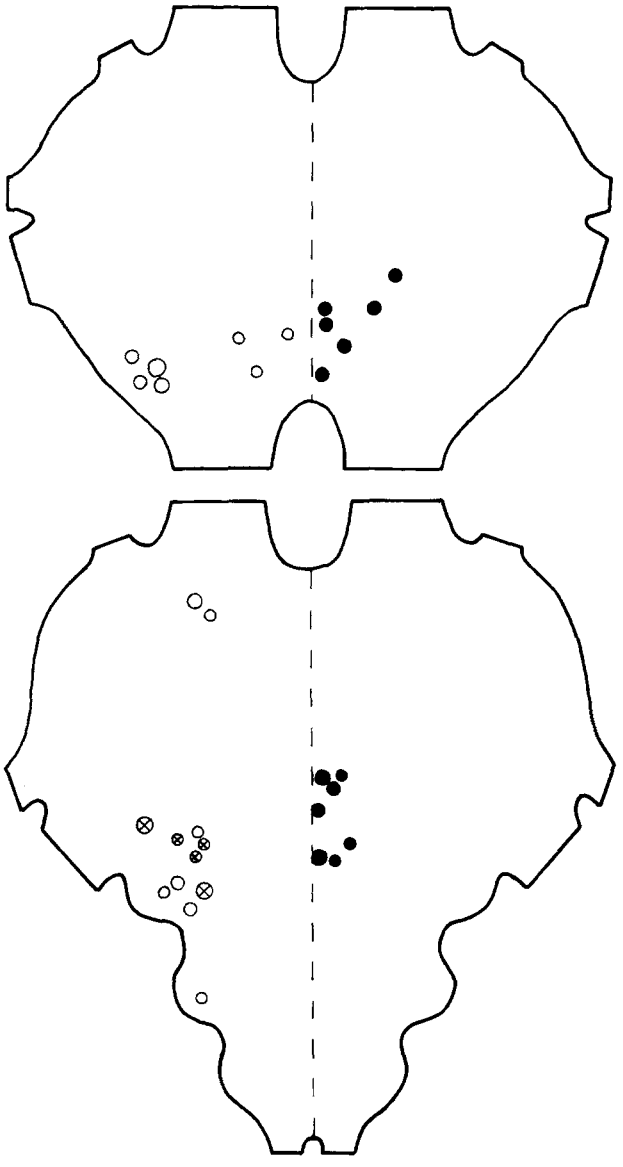

Fig. 10. Location of the somata of the 32 interneurons examined in this study in the mesothoracic (top) and the metathoracic (bottom) ganglia. The somata of the inhibitory interneurons are shown as filled circles on the right and the somata of the excitatory interneurons are shown as open circles on the left. The crossed circles represent somata of excitatory neurons located on the dorsal surface of the metathoracic ganglion

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