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INNERVATION PATTERNS OF INHIBITORY MOTOR NEURONES IN THE THORAX OF THE LOCUST

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SUMMARY

The innervation pattern of inhibitory motor neurones of the locust has been revealed by intracellular recording from their cell bodies in the meso- and metathoracic ganglion and simultaneous recording from muscle fibres in a middle, or in a hind leg.

Three neurones in each ganglion, the common inhibitor ($CI = CI_1$), the anterior inhibitor ($AI = CI_2$), and the posterior inhibitor ($PI = CI_3$) innervate several muscles in one leg and are thus common inhibitory neurones. Metathoracic CI innervates 13 muscles in one hind leg and mesothoracic CI innervates 12 muscles in one middle leg. The muscles are all in the proximal parts of the legs and move the coxa, the trochanter and the tibia. Metathoracic AI and PI innervate four muscles in the more distal parts of one hind leg that move the tibia, the tarsus and the unguis. None of these muscles is innervated by CI. Each inhibitor innervates muscles that have different and often antagonistic actions during movements of a leg.

AI and PI receive many synaptic inputs in common and show similar patterns of spikes during imposed movements of a tibia. Tests fail, however, to reveal evidence for any electrical or synaptic coupling between them. A revised scheme of nomenclature for these inhibitory neurones is proposed.

INTRODUCTION

Motor neurones that cause inhibition of the axial or limb muscles that they innervate occur in several invertebrate phyla, but they have been most widely studied in the arthropods. In these animals, two types of inhibitory motor neurones have been recognized on the basis of their patterns of innervation. There are common inhibitors which innervate several muscles, often with distinct functions, and specific inhibitors which innervate one muscle or a small group of functionally similar muscles.

In crustaceans, common inhibitors innervate muscles in the legs and claws (Wiersma & Ripley, 1952; Hill & Lang, 1979), swimmerets (Davis, 1971) and antennae (Clarac & Vedel, 1975). In insects, common inhibitors innervate leg muscles (Pearson & Bergman, 1969; Pearson & Iles, 1971; Graham & Wendler, 1981) and neck muscles (Shepheard, 1974). The existence of neurones with wide fields of innervation makes it necessary to assess with caution the existence of specific inhibitors whose field of

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innervation has not yet been revealed fully. Even the common inhibitory neurones themselves may have wider fields of innervation than previously suspected, as is now suggested for crayfish (Cooke & Macmillan, 1983) and crab limbs (Bevengut, Simmers & Clarac, 1983). Specific inhibitors have nevertheless been reported in crustacean limbs (Wiersma, 1961), uropods (Larimer & Kennedy, 1969) and abdomen where they are shared by two or more functionally similar muscles (Kennedy & Takeda, 1965; Parnas & Atwood, 1966). They also occur in some insect spiracles (Miller, 1969), in some abdominal muscles (Tyrer, 1971; Lewis, Miller & Mills, 1973) and possibly in some flight muscles (Piek & Mantel, 1970; Ikeda & Boettiger, 1965).

More than one inhibitory neurone may innervate a single muscle fibre in insects (Iles & Pearson, 1969; Pearson & Iles, 1971) and in crustaceans they can exert both pre- and postsynaptic effects. In this way the inhibitors can modulate the force produced by the action of the excitatory motor neurones (Burns & Usherwood, 1979). In addition, their own effectiveness can be modified by activity in other neurones. The inhibitory potential produced in the extensor tibiae muscle of the locust by a common inhibitory neurone is depressed by octopamine and therefore is also likely to be depressed by activity in the dorsal unpaired median neurone to that muscle (Evans & O'Shea, 1977).

The role of these inhibitory neurones in the behaviour of the animal, however, remains difficult to rationalize (see Pearson, 1973, for review) because the problem is to understand the action of a neurone that innervates many muscles which have different functions. The approach that we have taken here is to define the patterns of innervation of two sets of three inhibitory neurones to muscles in a middle and a hind leg of a locust. In the metathoracic segment, one of these neurones is known to be a common inhibitory neurone (CI) innervating at least two muscles (Pearson & Bergman, 1969), but the other two are known only to innervate the flexor tibiae muscle (Burrows & Horridge, 1974; Heitler & Burrows, 1977). In this paper we show that all three are common inhibitory neurones.

MATERIALS AND METHODS

Experiments were performed on adult *Schistocerca gregaria* (Forskal) of both sexes taken from our crowded culture about 2–8 days after their final moult. To map the innervation patterns of the meso- and metathoracic inhibitory neurones, three different preparations, ventral, dorsal and side, were used to gain access to muscles of the thorax, and a hind or middle leg. For the ventral preparation (Hoyle & Burrows, 1973), a locust was restrained, ventral surface uppermost, and the muscles exposed by removing appropriate parts of the ventral thoracic, coxal or femoral cuticle. For the dorsal preparation, a locust was secured dorsum uppermost and was opened by a midline incision. The two sides of the body were pulled apart and the gut was removed to expose the thoracic muscles. The side preparation, in which the cuticle overlying the coxal abductor muscles was removed, was used only for access to muscles 125 and 126 (metathoracic coxal abductors) and their homologues in the mesothorax (94, 95 and 96). These muscles could also be reached in a dorsal preparation by removing the overlying muscles. Similarly, muscles 133a or 103a

(trochanteral depressors) had to be removed to record from the trochanteral levators (131, 132, and 102).

The ventral preparation was used when intracellular recordings were to be made from neurones in thoracic ganglia. A small, wax-covered platinum platform was manoeuvred beneath the meso- and metathoracic ganglia to isolate them from movement. Before recording, the ganglia were treated with a 1% solution of protease (Sigma Type VI) for 2–3 min: care was taken to keep the protease away from the muscles. Intracellular recordings from muscle fibres and neurones were made with microelectrodes filled with 2 mol l^{-1} potassium acetate and with resistances of 30–50 MΩ. The tips of the electrodes were made more visible by dipping them in Indian ink. The preparations were perfused throughout with locust Ringer (Usherwood & Grundfest, 1965) at room temperature.

The metathoracic tibiae were moved in a controlled way with a servo-motor controlled by a microprocessor. Recordings were stored on magnetic tape for later analysis and filming. The numbering of muscles used throughout is that of Snodgrass (1929).

RESULTS

The innervation pattern of the metathoracic common inhibitor

The axon of the common inhibitory neurone (CI) branches as it emerges from the metathoracic ganglion to send axons into lateral nerves 3, 4 and 5 (Burrows, 1973). Within each of these main lateral nerves, an axon may divide again. No other leg motor neurones have this pattern of axonal branches. Therefore, this unique anatomy makes it possible to stimulate an axon of CI in one nerve and then search for muscles innervated by the other axons. Inhibitory junctional potentials (IPSPs) recorded with an intracellular microelectrode can be correlated with the stimulus pulses (Fig. 1). The nerve chosen for stimulation was the extensor nerve ($N5b_2 + N3b_2c$) within the femur, because it is known that CI innervates the extensor tibiae muscle (Pearson & Bergman, 1969), and this was readily confirmed in these experiments. Moreover, this nerve does not contain an axon of either of the other two inhibitory neurones that innervate muscles of the hind leg. These results could then be supplemented by observing the effects of the sporadic spikes that occur spontaneously in CI without imposed or voluntary movements by a hind leg. The muscles were usually explored in pairs with muscle 130 (coxal adductor), which is known to receive CI input (Hoyle, 1966), or one of the other muscles in which innervation could be readily established, as the reference member of the pair (Fig. 1B,H). This was an additional check that the stimulation was effective in evoking an antidromic spike. A failure to find CI input to a muscle fibre could then be attributed with some certainty to the failure of CI to innervate it and not to a failure of CI activation.

The metathoracic CI innervates the following 13 muscles: 120 (second coxal remotor), 121 (anterior coxal rotator), 122, 123, 124 (posterior coxal rotators), 125, 126 (coxal abductors), 130 (coxal adductor), 131, 132 (trochanteral levators), 133a, 133d (trochanteral depressors) and 135 (extensor tibiae). The type of evidence for this conclusion is shown for 10 of the muscles in Fig. 1A–H. In all these muscles the IPSPs

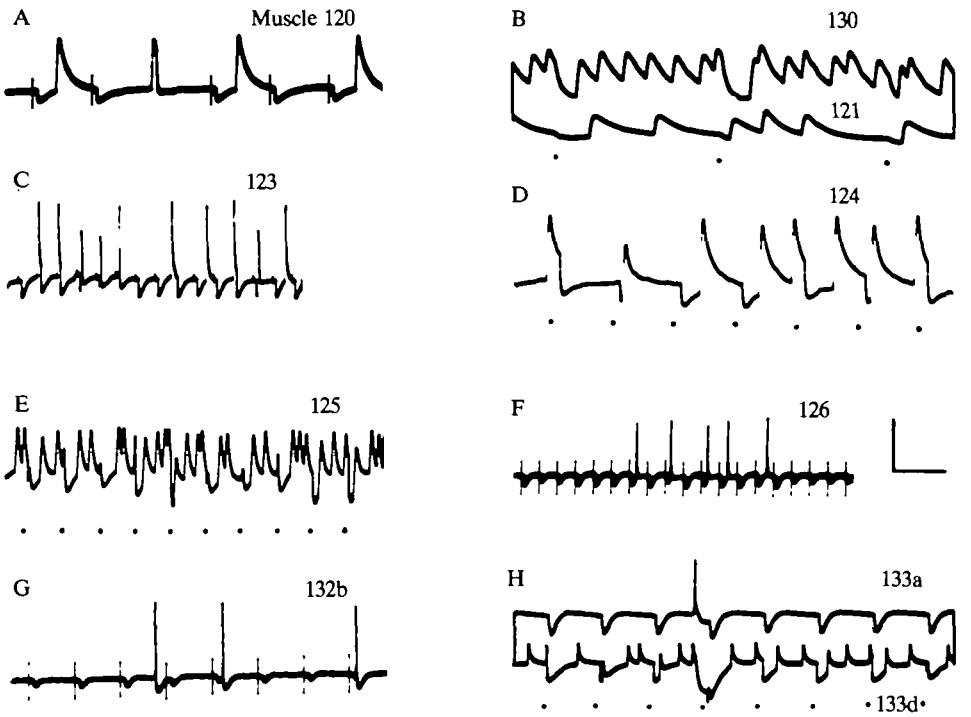

Fig. 1. Intracellular recordings from muscles innervated by the metathoracic common inhibitory neurone (CI). An axon of CI in the nerve to the extensor tibiae muscle within the femur is stimulated antidromically. Where the stimulus artefacts are not readily visible, stimuli are indicated by a dot. In B and H simultaneous recordings are made from two muscles. Calibration: voltage (A, B upper trace, D) 17 mV; (C) 10 mV; (E,G,H lower trace) 12·5 mV; (B lower trace) 33 mV; (F,H upper trace) 25 mV; time (A,C,E,G,H) 200 ms; (B) 50 ms; (D) 100 ms; (F) 400 ms.

would follow antidromic stimulation of an axon of CI at frequencies of at least 50 Hz. The field of innervation of CI is confined to muscles that move the proximal joints of a hind leg, the coxa, the trochanter and the tibia. Muscles moving the distal joints, the tarsus and the unguis, are not innervated. To determine which axon of CI innervates a particular muscle the nerve supply was traced by injecting locusts with reduced methylene blue. The nerve suspected of providing CI input to a particular muscle was then cut whilst recording from that muscle and antidromically stimulating the CI from the extensor nerve in the femur. The pattern of innervation is shown in Fig. 2.

No CI input was found, despite extensive searching, in muscles 113 (tergosternal), 118 (coxal promoter), 119 (first coxal remotor), 127 and 128 (pronator-extensors of the hindwing), 129 (depressor-extensor of the hindwing) or in 133b and c (bifunctional muscles which act as trochanteral depressors and hindwing elevators). There is a remote possibility that failure to find CI input to these muscles may have been due to failure of the CI spike in one of its axons.

The distribution and proportion of fibres receiving CI input differs in the various muscles. For example, in muscle 120 the innervated fibres are confined to a posterior

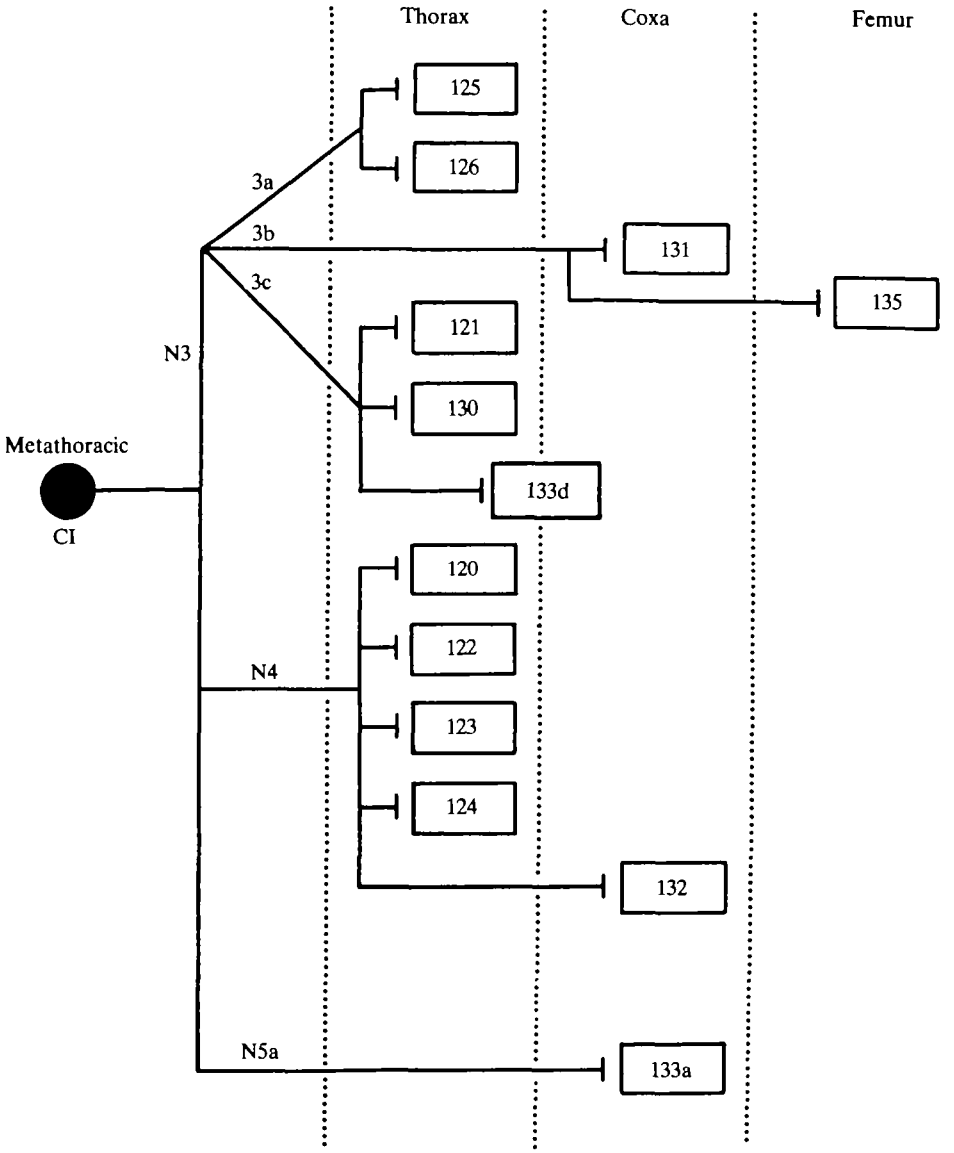

Fig. 2. Diagram of the innervation pattern of the metathoracic CI. Muscles that move the coxa, trochanter and femur are innervated by axons in nerves 3, 4 and 5.

region close to the apodeme (Fig. 1A). In muscle 123 the input is restricted to the more ventral part of the muscle (Fig. 1C). Recordings from this muscle were made in a dorsal preparation in which muscle 130 lies immediately ventral, so that it is possible that the electrode may have entered muscle 130. Cutting nerve 3c, which contains the CI axon to muscle 130, did not abolish the input to muscle 123. By contrast, in muscle 121 the distribution of CI innervation is more widespread.

The amplitude of an IPSP evoked by CI varies in different fibres of one muscle and in different muscles. IPSPs as large as 15 mV were recorded, although the majority

were less than 10 mV. No relationship between a particular muscle and the size of an IPSP was apparent. Occasionally depolarizing IPSPs were recorded, but usually from old preparations. The effect of the IPSP on an EPSP also varies; an EPSP could be reduced to as little as 10 % of its normal value, but again the variation within a muscle could be as large as the variation between muscles. One generalization that can be made, however, is that every fibre receiving CI input also receives an input from a tonic excitatory motor neurone.

The innervation pattern of the mesothoracic common inhibitor

The innervation pattern of mesothoracic CI was mapped using the same technique as for the metathoracic CI. Its axon in the extensor nerve in the mesothoracic femur

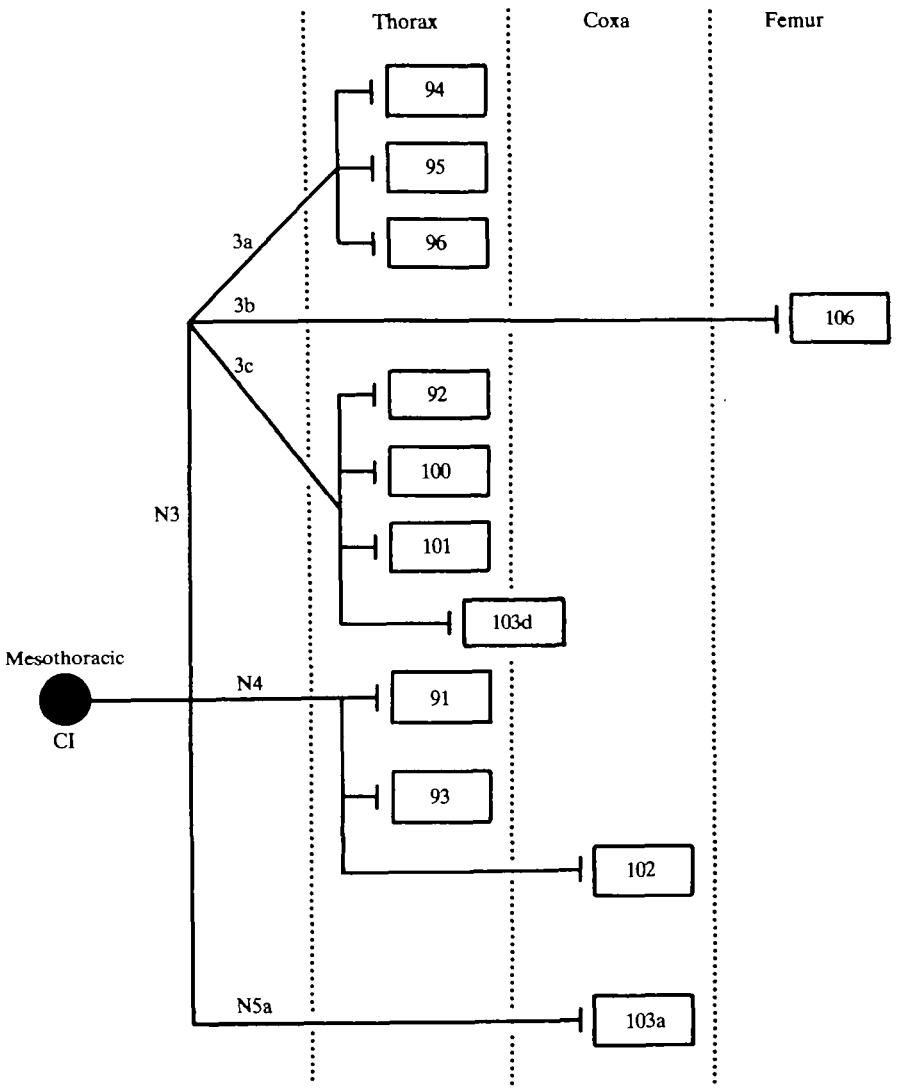

Fig. 3. Diagram of the innervation pattern of the mesothoracic CI. Note the similarity to that of the metathoracic CI.

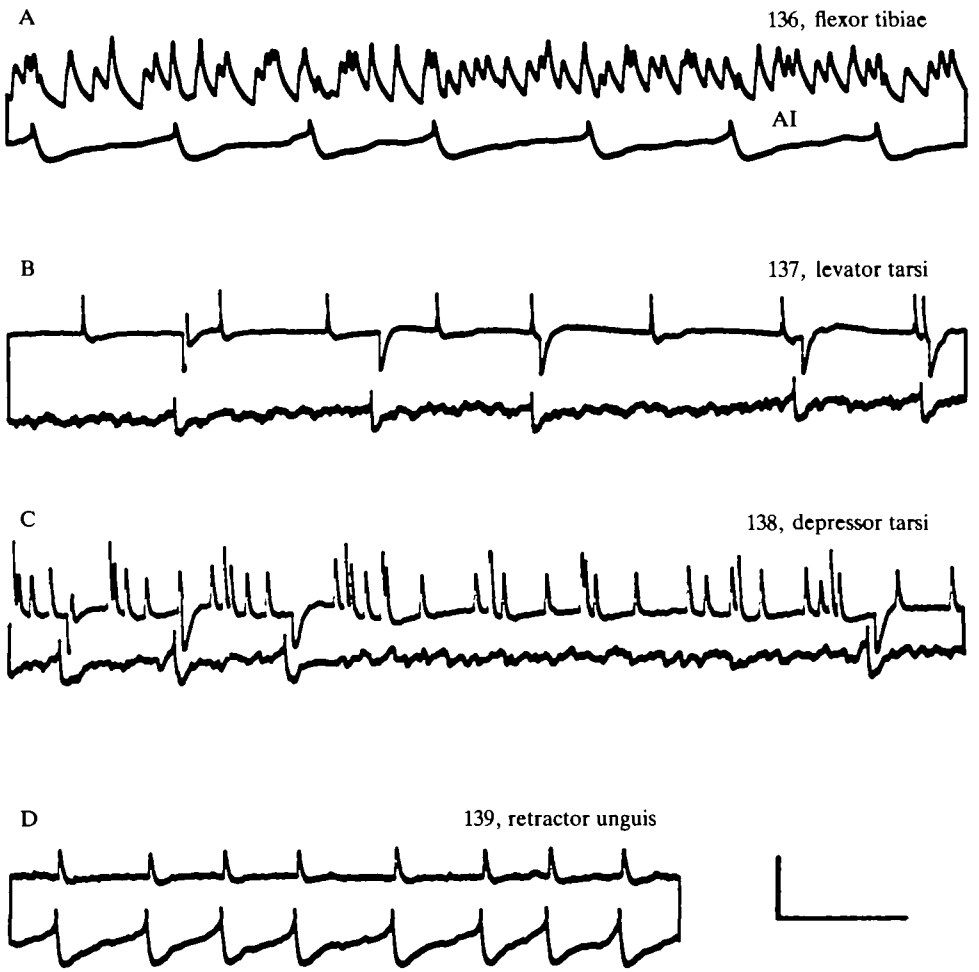

Fig. 4. Intracellular recordings from muscles innervated by the metathoracic anterior inhibitory neurone (AI). The recordings are made simultaneously from the soma of AI and from a fibre in the muscle indicated in (A–D). The spikes in AI occur spontaneously or after the application of depolarizing current through the recording microelectrode. Depolarizing potentials are recorded in the retractor unguis in the example shown (D). Calibration: voltage AI, (A) 10 mV; (B–D) 5 mV; muscle fibre (A,C) 10 mV; (B) 25 mV; (D) 5 mV; time (A) 200 ms; (B–D) 400 ms.

was stimulated antidromically, as it is known to innervate the extensor tibiae muscle (Burns & Usherwood, 1979). Alternatively, paired recordings were made from the muscle to be tested and from a muscle which had been shown to have CI input by the previous method. The CI was then excited by stroking the ipsilateral mesothoracic tarsus with a fine paint brush.

The mesothoracic CI innervates the following 12 muscles: 91 (second coxal remotor), 92 (anterior coxal rotator), 93 (posterior coxal rotator), 94, 95, 96 (coxal abductors), 100, 101 (coxal adductors), 102 (trochanteral levator), 103a, 103d (trochanteral depressors) and 106 (extensor tibiae) (Fig. 3). CI input was not found

in muscles 89 (coxal promotor), 90 (first coxal remotor), 103c (trochanteral levator) and 104 (femoral reductor, a muscle that is absent in the metathorax).

The innervation pattern of the metathoracic anterior and posterior inhibitors

The innervation pattern of these neurones was mapped by recording intracellularly from their somata in the metathoracic ganglion and, at the same time, exploring muscles in a hind leg with an intracellular electrode to look for IPSPs which corresponded 1:1 with the spikes (Fig. 4). The neurones were identified by the position of their somata in the ganglion and by their shape after injection of cobalt (A. H. D. Watson, M. Burrows & J. P. Hale, in preparation). The low frequency of spikes in these neurones could be increased by injecting depolarizing current into their cell bodies.

Both these inhibitors innervate the same four muscles which move the more distal segments of a hind leg, the femur, the tarsus and the unguis; 136 (flexor tibiae), 137 (tarsal levator), 138 (tarsal depressor) and 139 (retractor unguis) (Figs 4A–D, 5). Both neurones have a single axon that emerges from the metathoracic ganglion in nerve 5B (Fig. 5). Their axons do not divide to form branches in nerves 3B, 4 or 5A so that it is unlikely that they innervate any of the coxal or trochanteral muscles. Indeed, no IPSPs were recorded in these muscles which correlated with spikes in either the anterior (AI) or posterior (PI) inhibitors. Sometimes depolarizing potentials occurred in a muscle fibre whenever a spike of an inhibitory neurone was recorded in its soma (e.g. Fig. 4D). In other locusts the same arrangement of electrodes recorded conventional IPSPs. It is assumed that the depolarizing potentials are reversed IPSPs.

Reflex excitation of metathoracic inhibitors

AI and PI are both excited during imposed movements of the tibia about the femur. To discover whether the neurones are driven by common synaptic inputs during these responses, intracellular recordings were made simultaneously from AI and PI (Fig. 6). Each neurone was identified by the position of its cell body and by correlating spikes recorded from its cell body with IPSPs in the ipsilateral flexor tibiae muscle. In the absence of any imposed movements both neurones spike sporadically and at different times. Many of their synaptic inputs are common (Fig. 6A). Extension of the ipsilateral metathoracic tibia, starting from a femoro-tibial angle of 90°, causes an

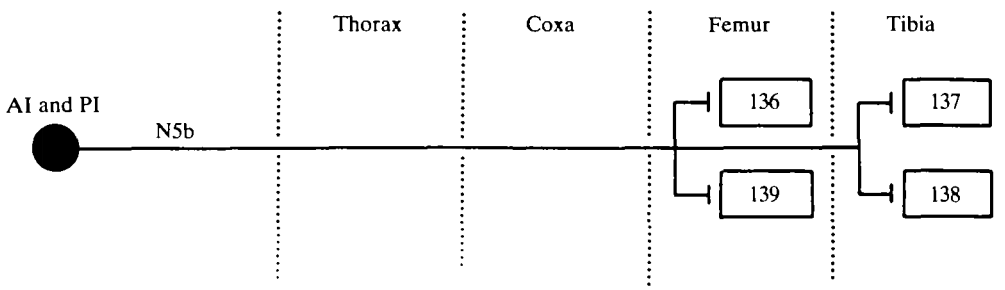

Fig. 5. Diagram of the innervation pattern of the metathoracic AI and PI. Muscles that move the tibia, tarsus and unguis are innervated.

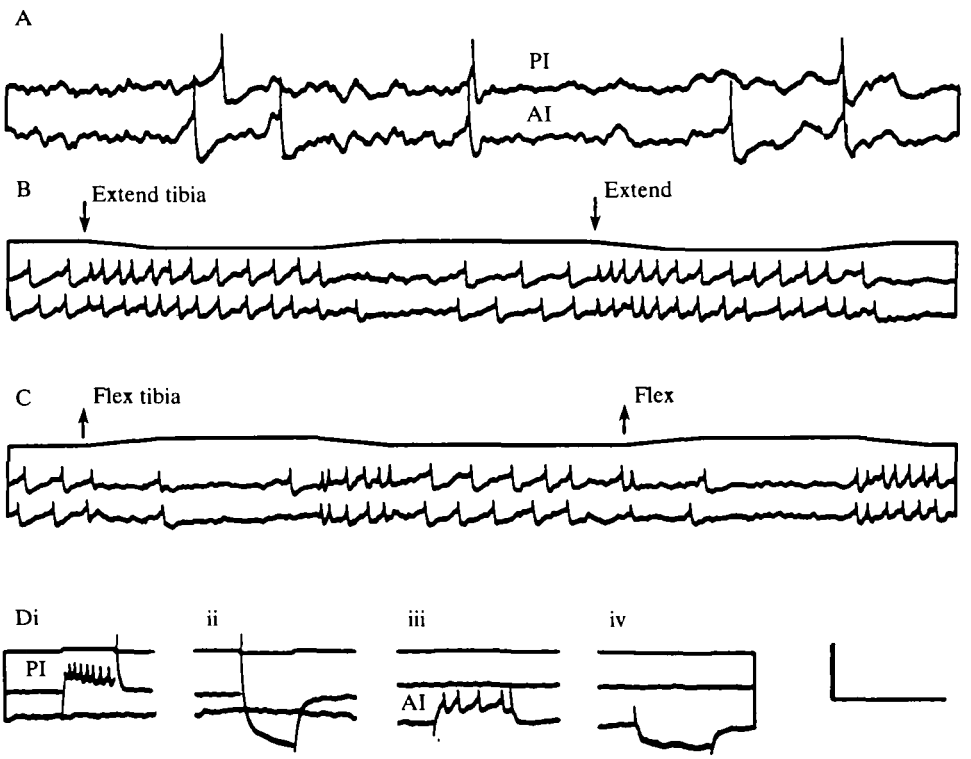

Fig. 6. Common synaptic potentials and reflex responses in AI and PI. Intracellular recordings are made simultaneously from the somata of the two neurones. (A) Spontaneous activity in which many of the synaptic potentials are common to both neurones. (B) The tibia is extended (arrows) about the femur from an initial femoro-tibial angle of 90° to 130°. Both neurones are excited, but their spikes are not synchronous. (C) The tibia is flexed (arrows) from 90°–50°. The spikes in both neurones decrease in frequency. (D) Tests for electrical coupling. Depolarizing (i,iii) and hyperpolarizing (ii,iv) current is injected into PI and then into AI. Upper traces, current; middle traces, PI; lower traces, AI. No coupling is revealed. Calibration: voltage (A) 4 mV; (B–D) 16 mV; current 30 nA; time (A) 200 ms; (B–D) 400 ms.

increase in the frequency of EPSPs and spikes in both AI and PI (Fig. 6B). By contrast, flexion of the tibia causes a decrease in the frequency of spikes in both neurones (Fig. 6C). Flexion or extension of the contralateral metathoracic tibia does not reliably affect the frequency of spikes in either neurone. Depolarizing current injected into PI to evoke spikes has no effect on the membrane potential of AI (Fig. 6Di). Hyperpolarizing current injected into PI is also without effect on AI (Fig. 6Dii). Similarly, current of either polarity injected into AI has no effect on PI (Fig. 6Diii, iv). These tests and the independent occurrence of the spikes during voluntary or imposed movements indicate that the two neurones are not coupled synaptically or by electrotonic junctions.

Other metathoracic inhibitory motor neurones

Other inhibitory motor neurones with cell bodies in the metathoracic ganglion innervate axial musculature through axons in nerve 6 or nerve 1. Intracellular recordings from muscles 117 (sixth ventral longitudinal), 141 (abdominal dorsal

longitudinal) and 143 (median internal ventral muscle) showed that they receive inhibitory innervation from nerve 6. One of these inhibitors to muscle 143 has been described (Yang & Burrows, 1983). Muscle 116 (fifth ventral longitudinal) also receives inhibitory input from metathoracic nerve 1A so the cell bodies may be in the meso- or metathoracic ganglion. Paired recordings have failed to provide evidence that the inhibitors are common to these muscles, although they do have a tendency to spike at the same time. This result does not necessarily mean that these inhibitors are specific ones, but probably indicates that all their target muscles have yet to be revealed.

DISCUSSION

Common inhibitory neurones

The three inhibitory neurones which innervate muscles in the hind or in the middle legs are all common inhibitory neurones. These neurones have been named in two different ways. CI was so named because it was shown to innervate two muscles (Pearson & Bergmann, 1969). AI and PI were named according to the position of their cell bodies in the metathoracic ganglion (AI anterior, PI posterior) (Burrows & Horridge, 1974). There was then no evidence to indicate whether these two neurones were specific or common inhibitors, so that names that implied nothing about the distribution of their terminals in the muscles were deemed appropriate. Now that they are also established as common inhibitory neurones it would seem sensible to name all inhibitors according to the same scheme. Our proposal therefore is that CI be called CI_1, AI to be called CI_2 and PI to be called CI_3. This scheme would then allow the other inhibitory neurones that we know to exist in the metathoracic ganglion (see also Yang & Burrows, 1983) to be incorporated by an appropriate subscript.

Braunig (1983) has recently described the innervation pattern of the metathoracic CI_1 in the locust, by recording its spikes in the various nerve branches that innervate known leg muscles. He found innervation to all the muscles described by us and in addition showed a consistent input to muscle 115 (pleurosternal), and in one locust he found an input to muscle 114 (pleuroalar, hindwing flexor). These small differences can probably be explained by the different methods used. Kutsch & Usherwood (1970) showed that muscle 90 in the mesothorax and its homologue, 120, in the metathorax both received inhibitory innervation. These inputs are here shown to be provided by CI_1 in the meso- and metathorax respectively. Siegler (1982) has also confirmed that two inhibitory neurones innervate the levator tarsi muscle. These are here identified as CI_2 and CI_3. The cockroach also has three common inhibitory neurones to the muscles of its hind legs (Pearson & Iles, 1971; Pearson & Fourtner, 1973). Like the locust, one has a more widespread field of innervation than the other two and has axons in more than one of the lateral nerves.

Role of inhibitory neurones in posture and locomotion

The difficulty in understanding the role of common inhibitors in the control of movement has always been in explaining why they should innervate muscles which must be active at different times. This paper has not addressed directly the issue of their functional role, but it has provided constraints for ideas about function by

demonstrating their wide fields of innervation.

CI_1 was known to innervate two muscles but now it is shown to innervate at least 13 that move a hind leg and at least 12 that move a middle leg. Its field of innervation is confined to muscles moving the coxa, the trochanter and the tibia, in other words the more proximal parts of a leg. It innervates antagonistic muscles that levate or depress the trochanter, muscles that rotate the coxa anteriorly and posteriorly and muscles that abduct and adduct the coxa, and a muscle that extends the tibia.

When a locust is motionless CI_1 spikes only sporadically. During walking, however, it spikes toward the end of the retraction, and the frequency of its spikes increases with the speed of locomotion (Burns & Usherwood, 1979). If its role is to accelerate the relaxation of force between the rhythmic contractions of the many muscles it innervates, then an improved performance by one muscle might well be counterbalanced by a degraded performance of another. Moreover, the many movements performed by a leg are achieved by participation of the same muscles in different combinations. The rigidity of action imposed by innervation from a common motor neurone would seem inappropriate for the required flexibility.

CI_2 and CI_3 have a more restricted field of innervation in the more distal parts of a leg. They both innervate the flexor tibiae muscle, and muscles which move the tarsus and the unguis. None of these muscles is innervated by CI_1. All three inhibitors, however, innervate muscles in the femur which move the tibia. The extensor tibiae is innervated by CI_1 and the flexor by both CI_2 and CI_3. For these two muscles at least there is the possibility that the separate action of the inhibitors could promote their more rapid relaxation between the rhythmic contractions they might undergo during walking. There is, however, little information on the action of CI_2 and CI_3 in movement. During imposed movements of a tibia, both receive a similar pattern of synaptic potentials, many of which are common, and have similar patterns of spikes. During walking, nothing is known of the activity of these neurones. During kicking, both are excited at the same time as the excitatory motor neurones to the flexor tibiae muscle are inhibited (Heitler & Burrows, 1977). The concurrent excitation of inhibitory neurones and inhibition of excitatory ones should lead to a rapid fall in force in the flexor muscle and allow the tibia to extend quickly. The effects on the muscles which move the tarsus must now be considered because they are also innervated by these same common inhibitors. When the kick is to occur and thrust must be applied to the offending object or to the ground, these muscles will receive an inhibitory input.

These attempts to suggest a role for the inhibitors are based on two assumptions; first that the inhibitor innervates all fibres in a particular muscle, and second that all fibres in a muscle have the same mechanical, electrical and biochemical properties. These assumptions are false. First, the extensive sampling with microelectrodes that has furnished the patterns of innervation shows that not all fibres in a muscle are innervated by the inhibitors. Some muscles have only small and restricted regions innervated by an inhibitor. For example, in the metathoracic extensor tibiae only 10% of the fibres are innervated by CI_1 (Usherwood & Grundfest, 1965). All the muscle fibres that are innervated by the various inhibitors are, however, also supplied by tonically active (slow) excitatory motor neurones (extensor tibiae muscle, Usherwood & Grundfest, 1965; other muscles this paper). Second, the diversity of types of fibres within an arthropod muscle is a well established fact (see Hoyle, 1983 for

review). The function of an inhibitor may thus reside in its ability to abolish or promote the relaxation of force only in those fibres that are particularly slow at contracting and relaxing, or which show catch-like properties (Usherwood, 1967; Usherwood & Runion, 1970). Such fibres would be ideal for the maintenance of posture or for slow adjustments of posture, but their slow responses would impede rapid movements during walking or jumping. Their exclusion from rapid movements could be achieved by the inhibitors, whose pattern of spikes would not need to be linked precisely to the underlying rhythm of the movement. In addition, the effectiveness of inhibitory action may be modified by the local release of chemicals from the terminals of particular dorsal unpaired median neurones.

What has emerged from this study is the realization that the sphere of influence of the inhibitory neurones is large. By comparison all the excitatory motor neurones to a leg innervate but a single muscle. This work has emphasized the need to correlate the patterns of innervation with the properties of the individual muscle fibres. It has also highlighted the inadequacies of descriptions of the action of the inhibitors and of most of the excitatory motor neurones to muscles which move proximal parts of a leg. These descriptions, though likely to be difficult to obtain, should now become a priority.

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