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A strand receptor with a central cell body synapses upon spiking local interneurones in the locust

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Summary. Movements of the femoro-tibial joint of a locust hind leg are monitored by three classes of proprioceptors; a chordotonal organ (Usherwood et al. 1968), multipolar joint receptors (Coillot and Boistel 1968) and a strand receptor innervated by a single afferent with a central cell body (Bräunig 1985). All three classes are excited by imposed or voluntary extension of the tibia. The strand receptor (fe-tiSR) spikes tonically and at a frequency dependent upon the position of the joint whilst the multipolar joint receptors give overlapping information but for a more restricted range. The afferent from the strand receptor makes an excitatory connection with a spiking local interneurone in the midline group of the metathoracic ganglion. The central latency and consistency with which the EPSP follows each sensory spike suggests that the connection is direct. This interneurone also receives convergent inputs from neurones in the chordotonal organ, but not from multipolar joint receptors. Neither the strand receptor nor the multipolar joint receptors apparently synapse upon leg motor neurones that we have tested, in contrast to receptors in the chordotonal organ.

Introduction

The major propulsive force for jumping, defensive kicking and swimming by a locust are generated by rapid extensions of the tibiae of the hind legs (Brown 1967; Heitler and Burrows 1977a; Pflüger and Burrows 1978). During walking or postural adjustments, however, the same joints must be moved slowly and precisely (Burns and Usherwood 1979). Tibial extensions over a wide range of amplitudes and velocities are therefore an essential element of the locomotory repertoire of a locust and require precise monitoring by sense organs. At least three different classes of proprioceptor occur at the femoro-tibial joint of a hind leg. First, and perhaps the most important is a chordotonal organ (Usherwood et al. 1968). It contains some 30–40 sensory cells that respond to different parameters of movement, and that monitor position by signalling with a tonic discharge (Usherwood et al. 1968; Zill 1985).

Second, is a femoro-tibial strand receptor consisting of a single receptor cell with a cell body in the metathoracic ganglion (Bräunig 1985). The peripheral dendrites are embedded in a strand of connective tissue linking the body of the chordotonal organ with the apodeme of the flexor muscle. This receptor codes the angle of the femoro-tibial joint in the frequency of its tonic spikes (Bräunig 1985).

Third, are five multipolar sensory cells (hereafter called multipolar joint receptors) arranged in three groups (Coillot and Boistel 1968). The RDPL (récepteur dorso-postéro-latéral) and the RVPL (récepteur ventro-postéro-latéral) each contain two multipolar receptor cells and the RDAL (récepteur dorso-antéro-latéral) just one receptor cell. The cells of the RDPL and RDAL are sensitive to tibial extensions within the range of 80 °–160 ° (RDPL) and 125 °–160 ° (RDAL). Like the strand receptor they also code the position of the joint by tonic changes of frequency (Coillot and Boistel 1969; Coillot 1974, 1975). The two cells of the RVPL are activated by flexion movements, mainly by tension in the flexor muscle apodeme and have been called the 'lump receptor' by Heitler and Burrows (1977b) because of their location at the 'lump' of the flexor apodeme.

In addition to these specific proprioceptors,

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other receptors which may be activated by movements of the femoro-tibial joint are the tactile hairs around the joint, and campaniform sensilla that signal stress in the cuticle.

A first step in understanding how this flow of sensory information from a joint is processed is to find the first order interneurones and describe their properties. Spiking local interneurones with cell bodies clustered at the midline of the metathoracic ganglion receive inputs directly from hair afferents on a hind leg (Siegler and Burrows 1983). An individual interneurone receives inputs from arrays of receptors arranged in complex receptive fields (Burrows and Siegler 1985). These interneurones also receive inputs from receptors monitoring the passive movements of the tibial spurs that initiate reflex movements of a leg (Burrows and Pflüger 1986). Finally, these local interneurones receive direct inputs from proprioceptors such as the femoral chordotonal organ (Burrows 1987). Chordotonal afferents, however, also make direct connections with the motor neurones that are excited in the resistance reflexes initiated by the chordotonal organ.

In this paper we examine the processing of information from the femoro-tibial joint that is provided by the strand receptor and the multipolar joint receptors. We show that for the strand receptor the spiking local interneurones are essential elements.

Materials and methods

Adult female and male locusts, *Locusta migratoria* or *Schistocerca gregaria* (Forskal) were obtained from our culture in Cambridge. *Locusta* were used for all experiments on the femoro-tibial Strand Receptor (fe-tiSR)[1] because only in this species could we record its spike. Locusts were mounted ventral surface uppermost and the thorax dissected to expose the meso- and metathoracic ganglia. These were stabilized on a wax-covered steel platform and the thorax was perfused continuously with saline. The sheath overlying the ventral surface of the metathoracic ganglion was treated for 1–2 min with a 1% (wt/vol) solution of Protease (Sigma Type IV) in saline. Electrodes, made from 1.0 mm diameter glass and with resistances of 50–80 MΩ were driven across the sheath of the ganglion and into the cell bodies of motor neurones and interneurones.

Extracellular recordings of the spikes from the fe-tiSR were made from a branch (N5b1c) of the main leg nerve (N5) in the proximal femur. To verify that one of the constituent axons in this nerve belongs to the fe-tiSR, and to reveal its central projections, the nerve was backfilled by placing it in a pool of 3% cobalt chloride (wt/vol) in situ. Five days were allowed for diffusion before the cobalt stain was developed and intensified with silver. Drawings were then made of whole mounts of ganglia with the aid of a drawing tube. Spikes of the multipolar joint receptors (RDPL and RDAL) (Coillot and Boistel 1968, 1969) were recorded from the lateral nerve (a lateral, posterior branch of N5; Heitler and Burrows 1977) in the femur. Movements of the tibia were imposed either by hand or in controlled waveforms by a mechanical actuator driven by a microprocessor.

Recordings of spiking local interneurones were made from their cell bodies at the ventral midline of the metathoracic ganglion. The interneurones were identified by their receptive fields limited to one hind leg and by the position of their somata (see Siegler and Burrows (1983) and Burrows (1985) for further details of the identification procedure). Recordings of motor neurones were also made from their somata. They were identified by the movement that was elicited when they were made to spike with current injected through the recording microelectrode.

All recordings were stored on FM magnetic tape for later display on a Gould ES1000 recorder or on an XY plotter linked to a digital oscilloscope.

Results

Anatomy

The axon of the fe-tiSR travels within nerve N5b1c in the femur of a hind leg, joints N3b5 in the coxa and finally enters the metathoracic ganglion through N3b (Bräunig 1985). Cobalt backfills of N5b1c reveal the cell body of the fe-tiSR lying anteriorly in the metathoracic ganglion (Fig. 1A) within a cluster of similarly sized cell bodies of other strand receptors and close to the cell body of the slow extensor tibiae motor neurone. The axon of fe-tiSR gives off one group of branches in lateral neuropil, a second more medially and a third more anteriorly. The pattern of central branches is thus similar to those of coxal strand receptors (Bräunig 1982). The only other axons in N5b1c are from tactile hairs along the ventrolateral ridge of the proximal half of the femur. The hair afferents enter the metathoracic ganglion through N5 and form a distinct projection to ventral regions of neuropile (Fig. 1B) where other hair afferents also project (Pflüger 1980; Pflüger et al. 1981).

Sensory responses

Extension of the tibia excites fe-tiSR and some of the joint receptors (Fig. 2). With the tibia held at 100 ° about the femur, the fe-tiSR spikes tonically but the multipolar joint receptors are silent. Repetitive movements excite both types of receptor phasically (Fig. 2A) as does a maintained shift to a

[1] This strand receptor was named fetiSR (fe = femur, ti = tibia, SR = Strand Receptor by Bräunig (1985), but a similar acronym, FETi, has been given to a leg motor neurone (Hoyle and Burrows 1973) (F = fast, E = extensor, Ti = tibia). To lessen confusion created by the same acronym (albeit in upper and lower case letters) representing two different structures, whilst maintaining current usage, we suggest that the acronym for the strand receptor be hyphenated: fe-tiSR

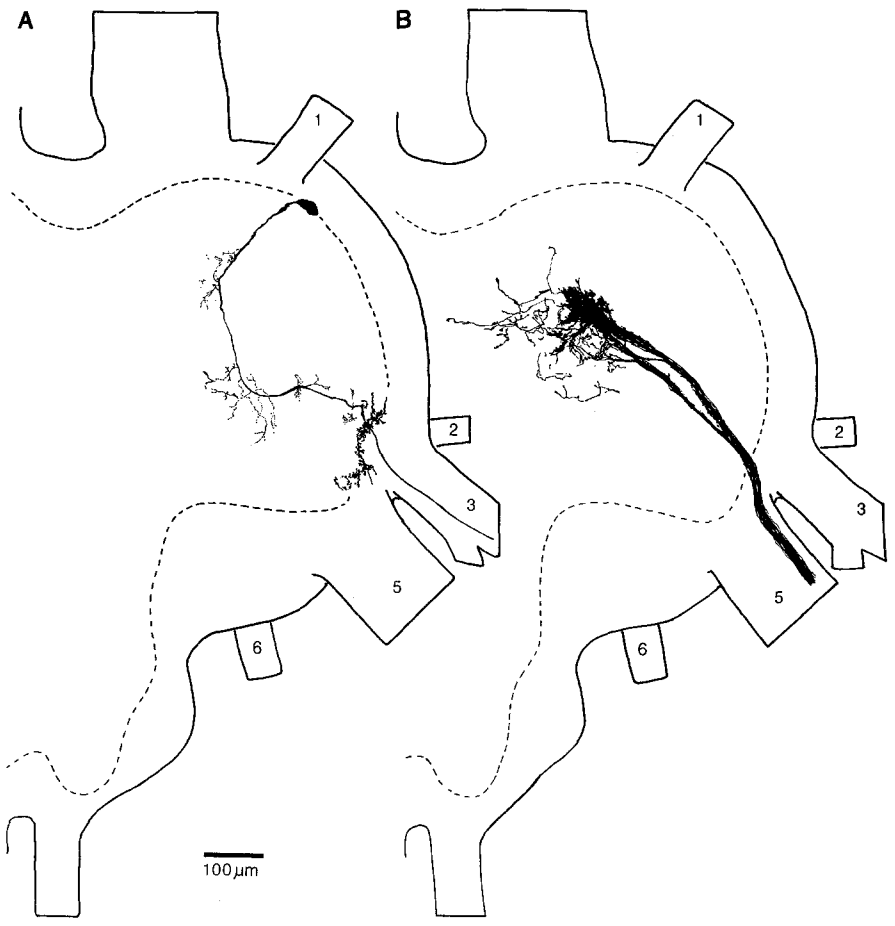

Fig. 1A, B. Drawings of the central projections of sensory neurones with axons in N5b1c in the femur.
A Central cell body and arborizations of fe-tiSR. Its axon leaves the ganglion in nerve 3.
B Ventral projections of sensory neurones from hairs on the femur. These axons enter the ganglion in nerve 5 and have a compact ventral array of branches. Their somata are in the periphery. Drawings are dorsal views of the right half of the metathoracic ganglion. Lateral nerves 1–3, 5 and 6 are numbered, others are omitted. Dashed line indicates the approximate boundary of the neuropil

new more extended position (Fig. 2B). The frequency of the tonic discharge of both types of receptor depends on the amplitude of the extension movement and adapts little whilst the new imposed position is held (Fig. 2C). Both receptors also signal active movements of the femoro-tibial joint. For example, a burst of spikes in the fast extensor tibiae motor neurone causes a rapid extension of the tibia which is signalled by a high frequency burst of spikes in fe-tiSR that slowly subsides as the tibia returns toward its previously flexed position (Fig. 2D).

Connections with a local interneurone

A spiking local interneurone in the midline group codes the position of the tibia about the femur by the frequency of its spikes (Burrows 1985). If this interneurone and the fe-tiSR are recorded simultaneously whilst the tibia is extended from 100 °, the frequency of spikes in both increases (Fig. 3A). If the interneurone is hyperpolarized to abolish its tonic spikes an underlying pattern of EPSPs is revealed (Fig. 3B). Extension of the tibia now results in a rapid depolarization of the interneurone that precedes the increased frequency of receptor spikes. This implies that receptors other than the fe-tiSR are excited by the movement and are contributing to the response of the interneurone. The inhibition at the start and end of each movement must have a similar explanation. A movement of the tibia to a more extended position which is maintained for several seconds results in a sustained increase in the frequency of fe-tiSR spikes, whilst the frequency of spikes in the interneurone shows a transient increase followed by an adaptation to a lower but sustained level (Fig. 3C).

A direct connection between fe-tiSR and this interneurone is nevertheless apparent on closer inspection (Fig. 4). Superimposed sweeps of an oscilloscope triggered by sensory spikes show that an EPSP follows each spike with a consistent latency (Fig. 4A). Many of the EPSPs lead directly to a spike in the interneurone. Signal averaging shows even more clearly the relationship between sensory spikes and EPSPs in the interneurone (Fig. 4B–D). The regularity of the tonic sensory spikes at a maintained position of the femoro-tibial joint

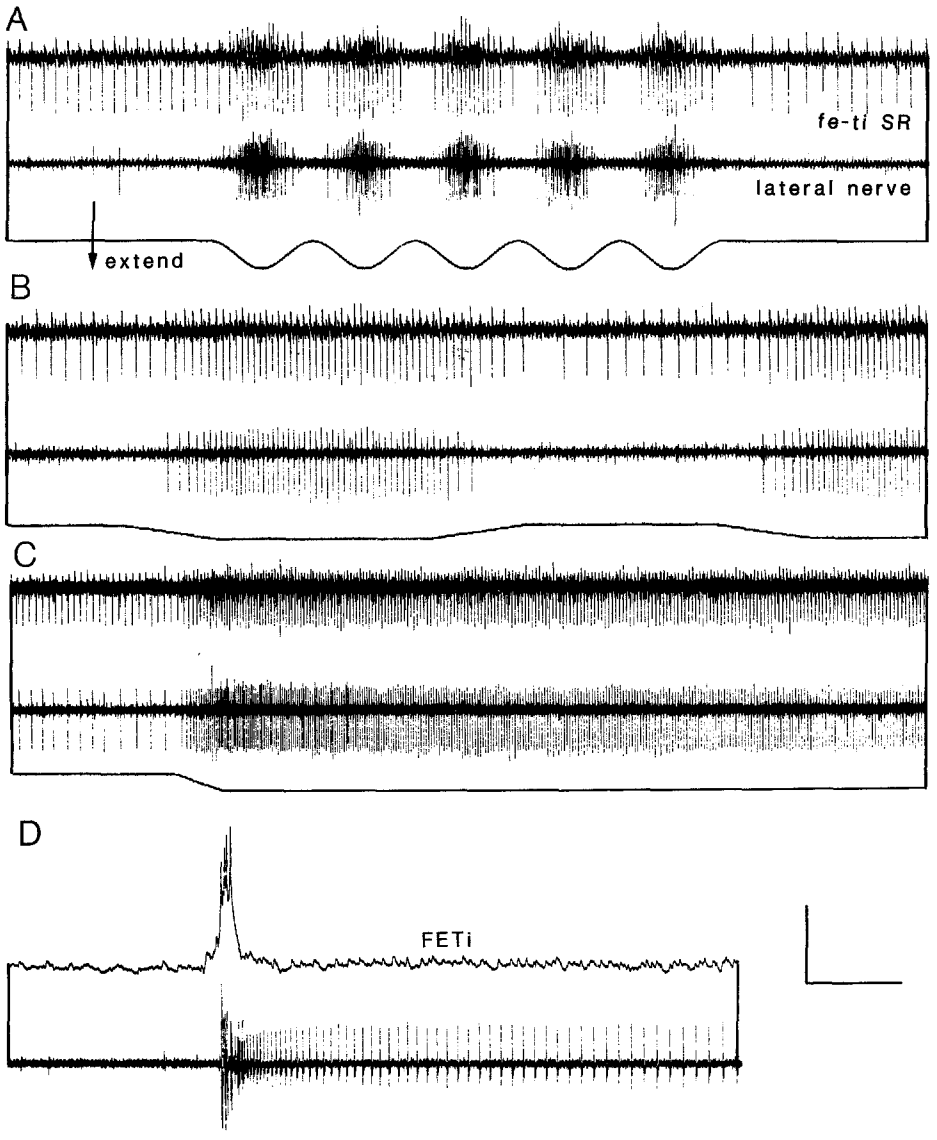

Fig. 2A–D. Extension of the tibia excites both the fe-tiSR and joint receptors with axons in the lateral nerve. All imposed movements in this and subsequent figures start from a femoro-tibial angle of 100 °.
A At this position the fe-tiSR spikes tonically but the multipolar joint receptors are silent. Each sine-wave extension excites both types of receptor.
B A ramp and hold movement evokes a maintained increase in the frequency of fe-tiSR spikes and a steady discharge of spikes in the multipolar joint receptors.
C A larger amplitude movement evokes higher frequencies of spikes in both types of receptors which do not adapt whilst the tibia is held in an extended position. In this example obtained following a series of imposed movements, a joint receptor is tonically active at the starting joint position.
D An active movement of the tibia caused by a burst of spikes in the fast extensor tibiae (*FETi*) motor neurone (which are visible as the first large potentials in the nerve recording) is signalled by a burst of spikes in fe-tiSR. The frequency declines as the tibia slowly returns to its previously flexed position. Calibration: vertical 90 °, 10 mV; horizontal **A, B, D** 500 ms, **C** 1 s

means that in an average using a slow time base a sequence of spikes is captured, each of which is followed by an EPSP (Fig. 4B). On a faster time base, the consistency of the EPSP can be seen in four successive averages, each of 256 sensory spikes (Fig. 4C). All these recordings reveal that a delay of 25 ms exists between the sensory spike recorded approximately 12 mm from the metathoracic ganglion and the EPSP in the interneurone.

To establish the central latency of this pathway requires that the conduction velocity of the sensory spike be known. This is difficult to measure because of the tortuous path taken by the receptor axon and its small diameter. The best method to estimate the time taken for the sensory spike to reach the ganglion was to record from nerve 3b just as it entered the metathoracic ganglion, and to reveal the sensory spike here by signal averaging triggered from the second, distal recording site on N5b1c (Fig. 4D). Measurements of the separation between the electrodes and the more accurately measured delay of the spike indicate conduction velocities of approximately 0.5 $m \cdot s^{-1}$. The delay between the two recording sites is 24 ms, so that the central delay, which includes the time for conduction of the spike to synaptic sites and for synaptic transmission is approximately 1 ms. The consistent relationship between sensory spikes and EPSPs, and the short central latency are physiological indicators that the connection between the fe-tiSR afferent and the interneurone is probably direct.

The response properties of this local interneurone are not fully explained by the connections from fe-tiSR. The rapid depolarization at the onset of a movement has indicated inputs from other

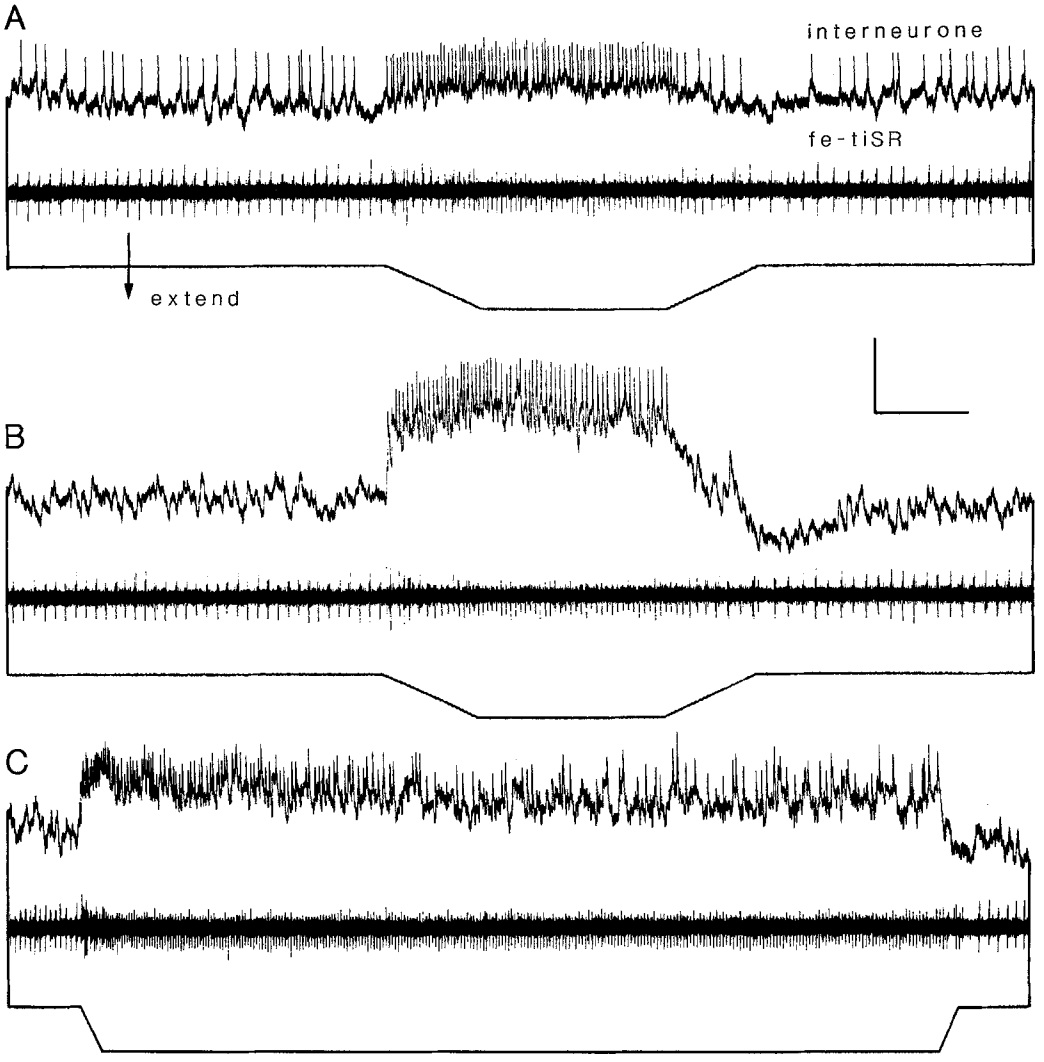

Fig. 3A–C. Effects of imposed tibial movements on a spiking local interneurone. **A** With the tibia held at an angle of 100 ° about the femur, both the interneurone and the fe-tiSR spike tonically. Extension of the tibia increases the frequency of spikes in both. **B** The interneurone is hyperpolarized with a steady current to reveal underlying synaptic potentials. Extension evokes a rapid depolarization that is still sufficient to evoke a maintained increase in the spikes of the interneurone. **C** An extension that is maintained for 10 s. The spikes in the interneurone transiently rise to a high frequency but then adapt to a maintained, if irregular and lower frequency. Calibration: vertical 90 °, 4 mV; horizontal **A, B** 500 ms, **C** 1 s

receptors, and indeed this interneurone has been shown to receive inputs from afferents in the femoral chordotonal organ sensitive to extension (Burrows 1986). There is thus convergence of proprioceptive signals from different classes of receptor onto this interneurone.

Lack of connections with motor neurones

In addition to synapsing upon spiking local interneurones afferents from the metathoracic femoral chordotonal organ synapse directly onto motor neurones (Burrows 1986). To test whether this is also true for the fe-tiSR, intracellular recordings were made from many motor neurones innervating muscles that move the tibia and tarsus (Fig. 5). Extension of the tibia evokes resistance reflexes in tibial motor neurones and compensatory reflexes in tarsal motor neurones. The fast (FETi) and the slow (SETi) extensor tibiae are hyperpolarized (Fig. 5A), the levator tarsi motor neurone receives a distinct input of IPSPs (Fig. 5A), whilst a flexor motor neurone and common inhibitor CI_2 are excited (Fig. 5C, D). The responses in all the motor neurones often begin before a change in the frequency of fe-tiSR can be detected, indicating that other afferents must be contributing to these effects. Signal averages triggered from the fe-tiSR

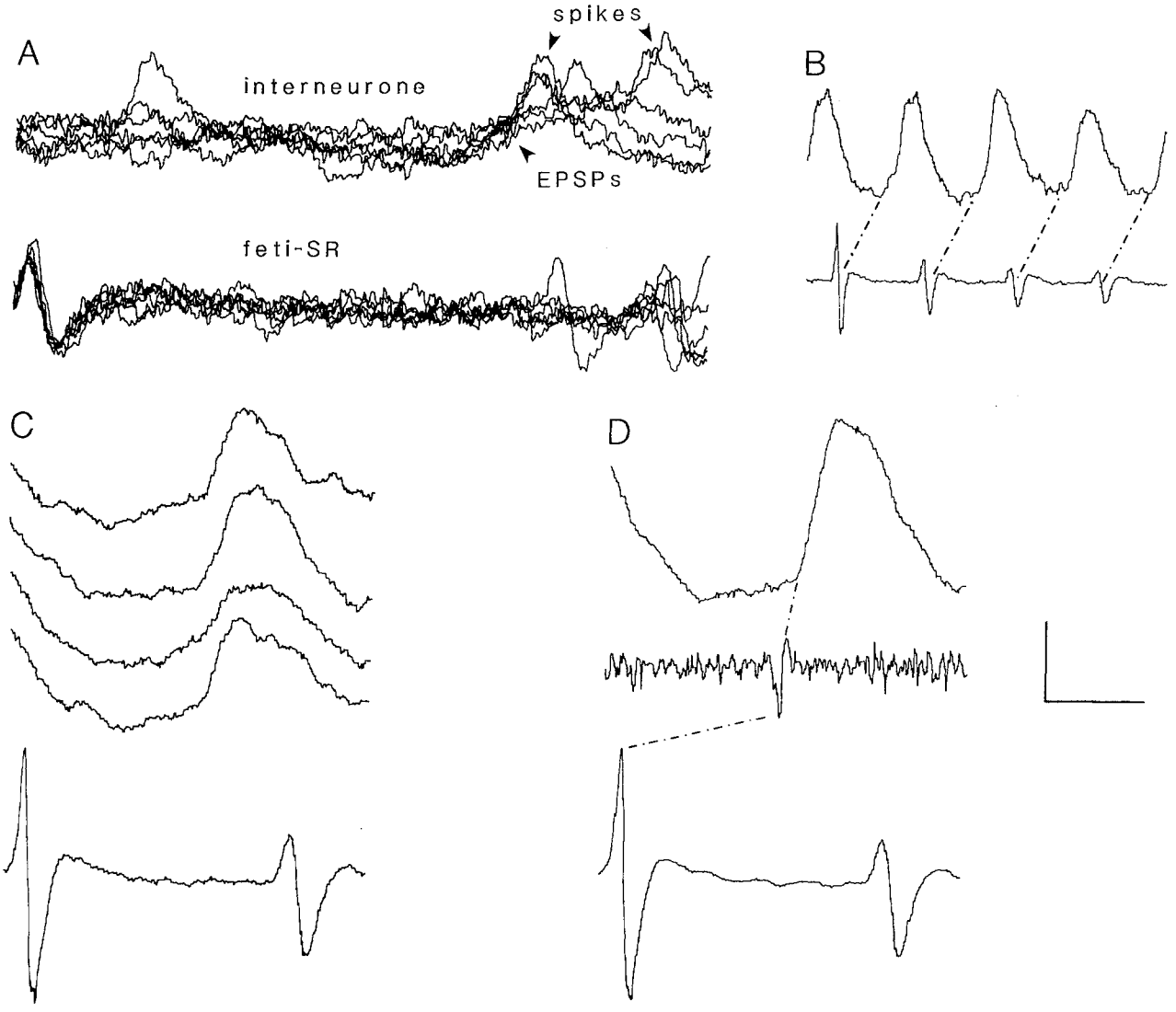

Fig. 4A–D. Connections between fe-tiSR and the spiking local interneurone shown in Fig. 3. **A** Several superimposed sweeps of an oscilloscope triggered by sensory spikes each show linked EPSPs (arrow) in the interneurone that evoke spikes. **B–D** Signal averages of synaptic events in the interneurone triggered by a tonic sequence of sensory spikes that occur at a femoro-tibial angle of 100 °. **B** A slow time base triggered for 128 sweeps by the first spike in the record. The regularity of the sensory spikes means that the averaged record contains three further spikes of progressively broader and smaller size. Each spike is followed by an EPSP in the interneurone (dashed line). **C** A faster time base during which two sensory spikes occur (bottom trace). The 4 upper traces, each representing 256 sweeps, show a consistent EPSP in the interneurone. **D** The same time base showing an average of 1024 occurrences of the sensory spike. The middle trace shows the sensory spike recorded from N3b close to the ganglion. The dashed line links the fe-tiSR spike recorded in the tibia (bottom trace) to the spike in N3b (middle trace) to the EPSP in the interneurone (top trace). Calibration: vertical 3 mV (applies only to **A**); horizontal **A** 6 ms, **B** 42 ms, **C, D** 14 ms

spikes revealed no linked potentials in any of these motor neurones that were either excited or inhibited. We have also recorded from at least six other motor neurones of the flexor tibiae muscle and four of the motor neurones of the depressor tarsi muscle and the retractor unguis. None of their potentials could be linked to the sensory spikes of the strand receptor. The possibility still remains, however, of a direct connection with motor neurones that have yet to be tested.

Processing of information from the multipolar joint receptors

To test whether afferents from multipolar joint receptors also synapse upon spiking local interneurones, recordings of their sensory spikes were made from the lateral nerve (Fig. 6). Extension of the tibia evokes a correlated increase in the frequency of spikes in the receptors and in a local spiking interneurone with the same properties as the one

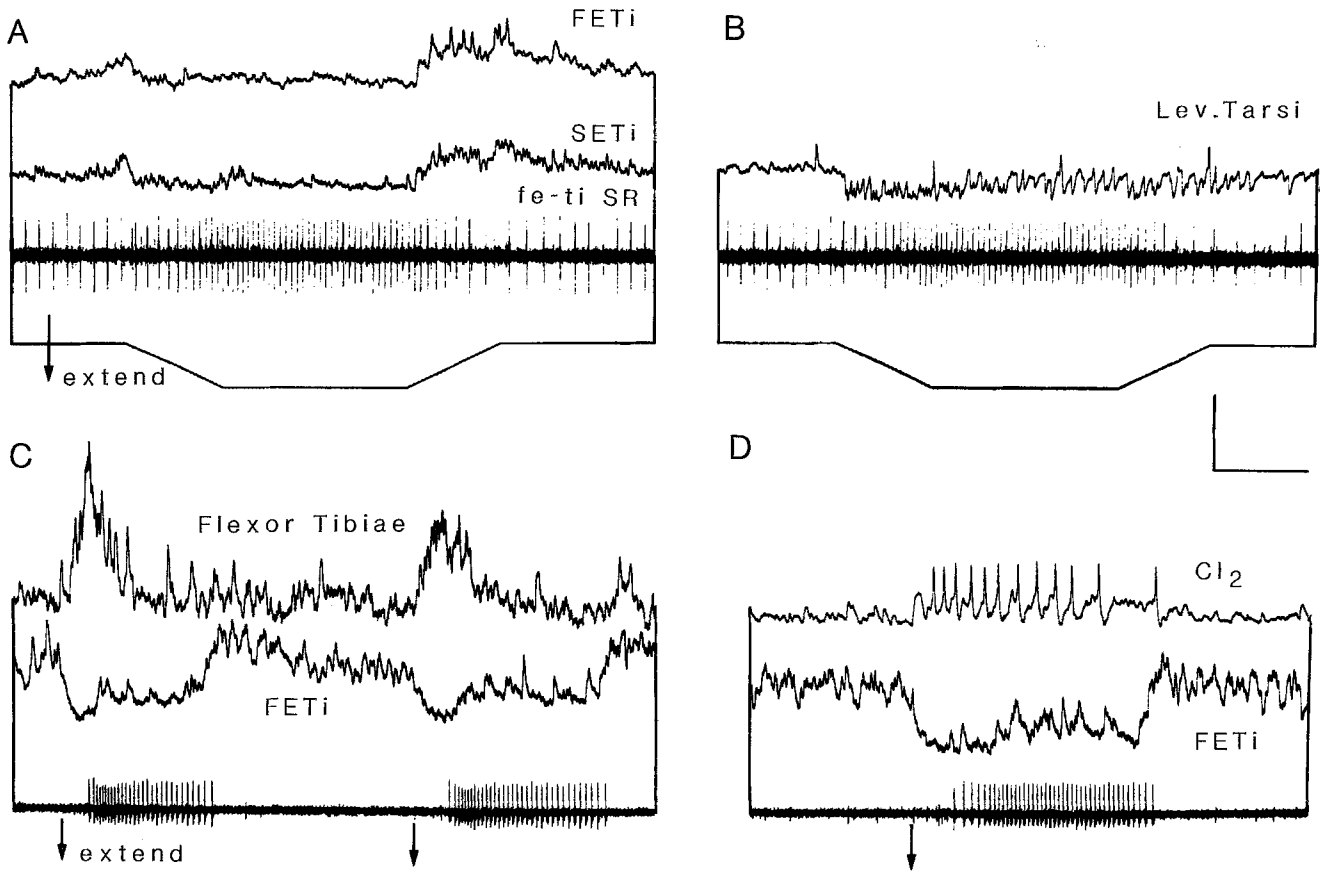

Fig. 5A–D. The fe-tiSR apparently does not connect with leg motor neurones. The tibia was extended whilst extracellular recordings were made from the fe-tiSR and intracellular recordings from the somata of pairs of motor neurones. The recordings in **A, B** are from one locust, those in **C, D** from another. **A** Extending the tibia excites the strand receptor and evokes a hyperpolarization of the slow (SETi) and the fast (FETi) extensor tibiae motor neurones. **B** The levator tarsi is also hyperpolarized during an imposed extension. **C** A flexor tibiae motor neurone is excited at the same time that FETi is hyperpolarized. **D** A common inhibitory motor neurone (CI_2) spikes whilst the FETi is hyperpolarized during an imposed extension. Movement of the tibia is monitored on the third traces in **A, B**, and in **C, D** the start of extension is indicated by arrows. Calibration: vertical 90 ° and 10 mV except FETi in **C, D** which is 4 mV; horizontal 500 ms

previously described (Fig. 6A). The depolarization in the interneurone precedes the increase in frequency of receptor spikes, but otherwise the responses are parallel. Hyperpolarizing the interneurone emphasises its greater sensitivity to extension when the movement begins from a femoro-tibial angle of 100 ° (Fig. 6B). Large EPSPs in the interneurone occur after the movement has stopped but are not correlated with the continuing spikes in the receptors, an observation that is confirmed by signal averages (Fig. 6C).

A second spiking local interneurone with a phasic response to extension was also tested for possible connections in the same way, but none were found (Fig. 6D). Inputs from fe-tiSR were also not found so that the depolarization and spikes that result from extension must derive from receptors such as the femoral chordotonal organ.

The same selection of motor neurones as for fe-tiSR were also tested for inputs from the multipolar joint receptors, but none was found. For example, the depolarizing potentials in FETi that follow the initial hyperpolarization and which are superimposed upon a maintained hyperpolarization are apparently not caused by the spikes of the multipolar joint receptors (Fig. 6A, B). These observations therefore confirm and extend those of Heitler and Burrows (1977b).

Discussion

The role of local interneurones

Sensory signals from the large number of receptors on a leg converge onto a set of spiking local interneurones with cell bodies at the midline of a seg-

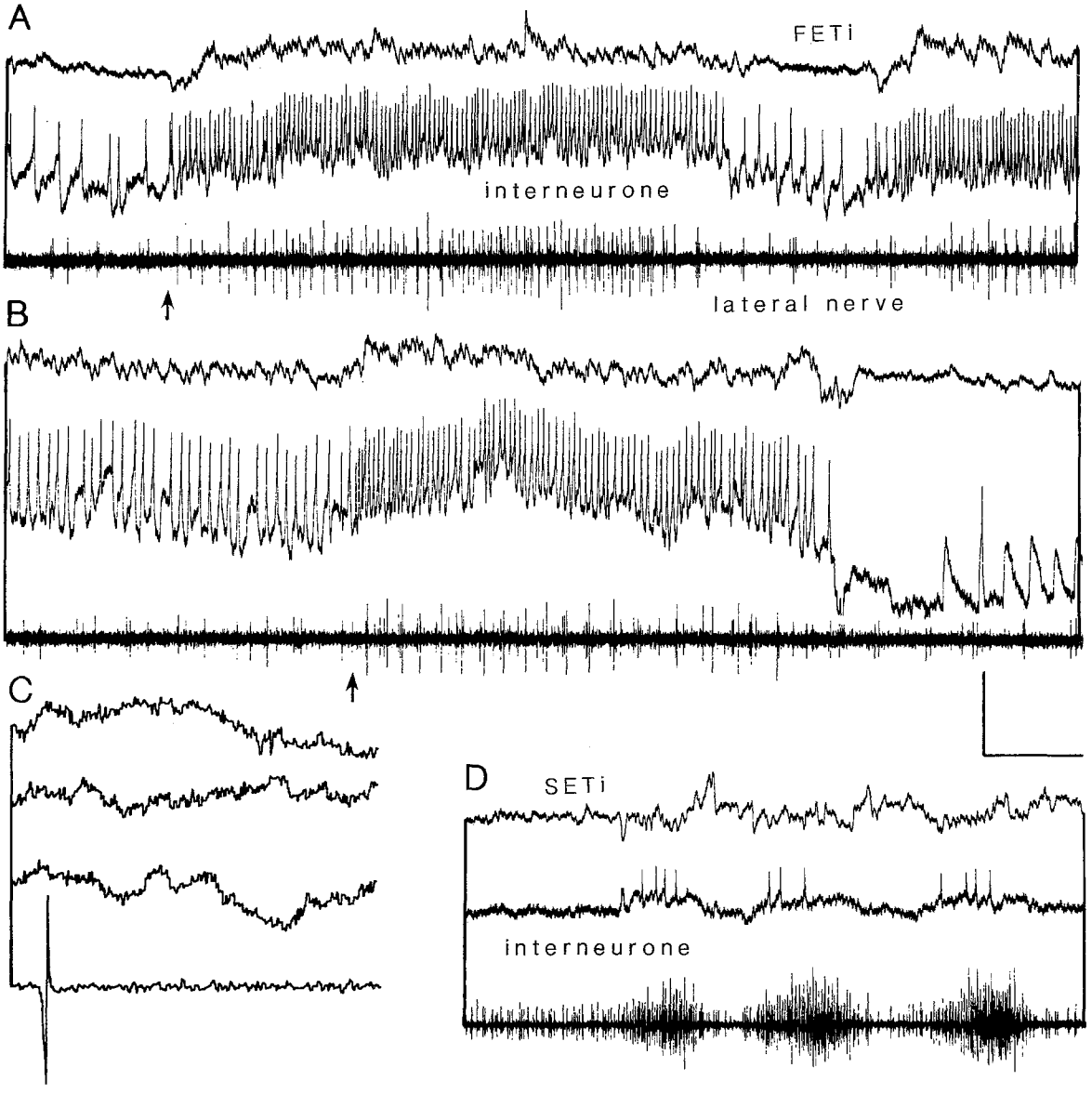

Fig. 6A–D. Joint receptors are without effect on the interneurone excited by fe-tiSR. **A** An imposed extension (arrow) of the tibia evokes a sustained increase in the frequency of spikes in the interneurone that begins before an increase in the frequency of the sensory spikes. The FETi recorded at the same time shows a sequence of depolarizing synaptic potentials after an initial hyperpolarization. **B** The interneurone is hyperpolarized by a steady current. During an imposed movement (arrow) its frequency of spikes rises abruptly in contrast to the small increase in the receptor spikes. There is no correlation between the large EPSPs in the interneurone and the sensory spikes at the end of the movement. **C** Signal averages show no potential in the interneurone linked to the sensory spike. Each of the three sweeps represents the occurrence of 256 sensory spikes. **D** A second interneurone with a phasic response to imposed tibial extension again does not receive a direct input from the multipolar joint receptors or from fe-tiSR. A recording from SETi is on the first trace. Recordings from *Schistocerca*. Calibration: vertical **A, B, D** 4 mV; horizontal **A, B, D** 500 ms, **C** 28 ms

mental ganglion. These local interneurones receive direct excitatory inputs from exteroreceptors such as hairs and campaniform sensilla (Siegler and Burrows 1983), from mechanoreceptors that monitor the passive movements of the tibial spurs (Burrows and Pflüger 1986), and from a chordotonal organ that acts as a proprioceptor at the femoro-tibial joint (Burrows 1987). Here we have shown that a second proprioceptor, a strand receptor at the femoro-tibial joint, also synapses upon these spiking local interneurones. The one feature that all mechanoreceptors on a leg have in common is therefore that their signals are processed by spiking local interneurones. The afferents from these

mechanoreceptors differ, however, in the connections made with other neurones. Afferents from hairs or campaniform sensilla may also synapse on intersegmental interneurones (Elson 1987; Hustert 1985), but in the adult at least, hair afferents do not synapse directly upon leg motor neurones. By contrast, afferents from chordotonal organs synapse in parallel upon spiking local interneurones, upon specific motor neurones (Burrows 1987) and upon some intersegmental interneurones (Laurent 1986). We do not yet know of other connections made by fe-tiSR, but have found no connections with leg motor neurones. This negative result thus leaves open the possibility that a connection is made to a specific motor neurone, perhaps one of the nine excitatory motor neurones innervating the flexor tibiae muscle, a pathway that could form part of a negative resistance reflex.

Does this pattern of connections give any clue as to how mechanoreceptors might regulate the movements of a hind leg? First, the spiking local interneurones provide a mechanism for mapping the array of exteroreceptors on a leg in a way appropriate for local postural reflexes (Burrows and Siegler 1985; Siegler and Burrows 1986). Thus touching hairs on a particular region of a leg excites a specific array of spiking local interneurones and sets up excitation in the appropriate motor neurones to move the leg away from the source of stimulation. Second, the spiking local interneurones provide an inhibitory path for resistance reflexes initiated by proprioceptors. Thus an imposed extension of the tibia excites particular afferents which in turn directly excite flexor tibiae motor neurones that act to resist the imposed movement. The local spiking interneurones excited by the same afferents could provide the mechanism for inhibition of the antagonist motor neurones in such reflexes, or for the radiation of effects to interneurones and motor neurones controlling other joints of the same leg.

The role of the strand receptor

Interpretation of the role of the strand receptor is complicated by the multiplicity of receptors that monitor extension of the tibia about the femur. The chordotonal organ, the multipolar joint receptors and the strand receptor all provide, at least in part, similar information although there is range fractionation with the multipolar joint receptors spiking at more extended joint angles. At many intermediate angles, however, all will normally be activated together and there is no clear picture of a particular reflex action of the strand receptor. For example, preventing the chordotonal organ from signalling extension either by clamping its receptor apodeme or by cutting its nerve appears to abolish the resistance reflexes of this joint. What our results show here is that the afferent from the strand receptor and afferents from receptors in the chordotonal organ that are sensitive to extension converge at the level of the spiking local interneurones. Our impression is that the strand receptor synapses onto very few of the spiking local interneurones in the midline group, perhaps just one or two. However, this does not imply that its central connections are as restricted as this. The strand receptor may synapse on other interneurones that would ensure its information is not lost at such an early stage of processing that is otherwise implied by its summation with chordotonal afferents on the local interneurones described here. Moreover, we do not know the detailed spike patterns of afferents in the chordotonal organ when the tibia is extended, or the relative weighting given to the fe-tiSR and chordotonal inputs by these local interneurones.

Is anything known of the connections of these spiking local interneurones? One interneurone with properties similar to those described here makes an inhibitory connection with a local nonspiking interneurone (Burrows, in preparation) that in turn makes an excitatory connection with the slow extensor tibiae motor neurone. The effect of exciting the strand receptor would therefore be to prevent excitation of the extensor motor neurone and so curtail an extension movement. In addition, the sensitivity of the strand receptor and hence the weighting of its input to the local interneurones might be altered by the activity of particular slow flexor tibiae motor neurones innervating the accessory flexor muscle. This muscle lies at the distal end of the tibia in parallel to the receptor strand, an arrangement similar to that of a receptor in the coxa (Bräunig and Hustert 1983).

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