

STRAND RECEPTORS ASSOCIATED WITH THE FEMORAL CHORDOTONAL ORGANS OF LOCUST LEGS

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SUMMARY

The so-called flexor strand of the femoral chordotonal organ of the locust jumping leg was found to be innervated by a single sensory neurone with its cell body in the metathoracic ganglion. The strand is therefore a new mechanoreceptor of the strand receptor class. It is sensitive to extension of the femoro-tibial joint. The innervation is rather unusual in the hind leg as well as in the fore and middle legs.

INTRODUCTION

The morphology and physiology of the mechanoreceptors of insect legs have been well studied, particularly in the femora and tibiae of locusts. Thus we know that in all three locust leg pairs the femoro-tibial joint has one chordotonal organ (Slifer, 1935; Usherwood, Runion & Campbell, 1968; Burns, 1974), five multipolar sensory neurones arranged in three groups (Coillot & Boistel, 1968; Williamson & Burns, 1978) and, in the pro- and mesothoracic legs, one multipolar muscle tension receptor (Theophilidis & Burns, 1979).

In subsequent physiological investigation it has been assumed that additional sense organs are not present (Burrows & Horridge, 1974; Bässler, 1979; Field & Burrows, 1982). As will be shown here, one sense organ at least has so far been overlooked.

The present study was initiated by the discovery of a particular nerve during an investigation of coxal mechanoreceptors of the hind leg (Bräunig, 1982*a*). This nerve was not listed in the more detailed descriptions of locust leg innervation (Campbell, 1961; Coillot & Boistel, 1968; Heitler & Burrows, 1977); it had a rather small diameter and appeared to carry a single sensory axon towards the femoro-tibial joint. A previous study (Bräunig, 1982*a*) showed this axon to belong to a neurone of the strand receptor type, that is a sensory neurone, the cell body of which is located in the central nervous system (Bräunig & Hustert, 1980), but failed to reveal its peripheral structures. The present study describes the morphology of the peripheral end organs innervated by these neurones for all three leg pairs and investigates some physiological properties of metathoracic organ.

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MATERIALS AND METHODS

Experiments were performed on adult locusts, *Locusta migratoria migratorioides* (R. & F.), obtained from a crowded laboratory culture.

Parts of the peripheral nervous system were stained with cobalt chloride (Pitman, Tweedle & Cohen, 1972) using essentially the method of Hustert (1978). Best results were obtained using isolated legs, cobalt chloride concentrations of 1.5–3% and filling times of 3–5 h at room temperature. To prevent desiccation of the extremely fine nerves under study (diameter frequently less than 5 μm) it was essential to perform all experimental steps with the preparation completely covered with locust saline (Clements & May, 1974).

Conventional extracellular recordings from sensory nerves were obtained with fine hook electrodes made out of sharpened stainless steel insect pins. Signals were preamplified, displayed on an oscilloscope screen and stored on tape for processing or transfer at 1/16 original speed to a pen recorder.

Sense organs were stimulated either by rotating the femoro-tibial joint by means of a feedback controlled d.c.-motor, or directly. In the latter case the strand of a sense organ was exposed and gripped with a pair of fine forceps forged from small insect pins mounted on a piezo-electric stimulator. Stimulating devices were carefully positioned with micromanipulators and were driven by function generators.

The terminology will be that of Snodgrass (1929) for muscles and sclerites, that of Bräunig (1982a) for metathoracic nerves and all sense organs, that of Theophilidis & Burns (1979) for pro- and mesothoracic nerves and that of Hoyle & Burrows (1973) for metathoracic motor neurones.

RESULTS

Connections between nerves 3B and 5B in the hind leg

There are two anastomoses between nerves 3B and 5B. One is found where the axons of the SET_i- and CI-neurones join the anterior branch of the crural nerve (5B₁) (Hoyle, 1955). A second anastomosis is formed by nerves 3B_{5c} and 5B_{1c} proximally in the femur (Bräunig, 1982a). Nerve 3B_{5c} is one of the numerous fine coxal branches of nerve 3B, nerve 5B_{1c} is the second femoral branch of nerve 5B₁. Branch 5B_{1c}, immediately after leaving the main nerve 5B₁, fuses with nerve 3B_{5c} and runs across the ventral surface of the most proximal anterior bundle of the extensor tibiae muscle, called the 'fan' by Hoyle (1978), towards the lateral (outer) femoral cuticle (Bräunig, 1982a). From here it travels distally between the cuticle and an underlying longitudinal trachea along the ventro-lateral ridge for about one-half the length of the femur (Fig. 1). Apart from the single axon of nerve 3B_{5c}, nerve 5B_{1c} contains axons from sensory hairs standing on that ridge and between adjacent muscle fasciculi (in the distal half of the femur this task is taken over by another branch of nerve 5B₁).

To confirm these anatomical findings (Bräunig, 1982a) hook electrodes were placed on nerve 5B_{1c} in the proximal half of the femur and on nerve 3B₅ in the coxa. The

recordings confirm a common unit in both nerves and show that it is sensory, since the spike is propagated towards the central nervous system (Fig. 3A).

Since the central projections of nerve 5B₁c have revealed a single strand receptor neurone cell body in the metathoracic ganglion (Bräunig, 1982a) and the recording from that nerve showed a sensory unit sensitive to extension of the tibia, it was concluded that there must be a strand receptor associated with the joint between femur and tibia.

Search for the femoro-tibial strand receptor in the hind leg

Attempts were made to reveal the peripheral structure of the femoro-tibial strand receptor by staining nerve 5B₁c distalwards with cobalt chloride starting from the proximal femoral region. These attempts failed so the axon was followed by physiological methods. A recording electrode was placed on nerve 5B₁c proximally in the femur, the cuticle of the ventro-lateral femoral ridge carefully removed distally and fine nerve branches thus exposed were probed with a second electrode for the activity of the unit in question. In this fashion the axon could be traced as far as the femoral chordotonal organ.

Once a distal nerve branch was known to contain the axon it was stained with cobalt. These stainings showed a single axon travelling from the ventro-lateral ridge of the

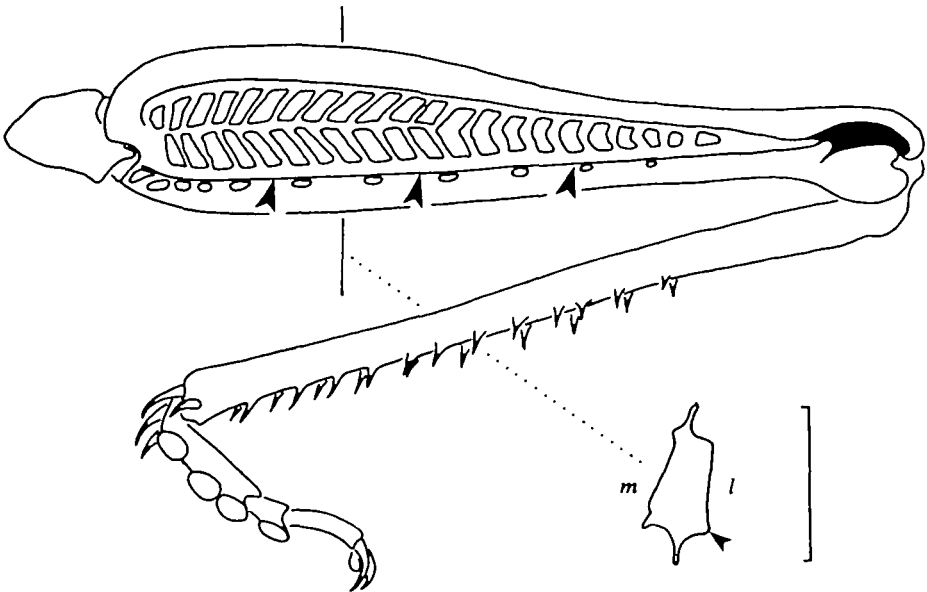


Fig. 1. Lateral view (dorsal to the top) and cross-section profile of the left locust hind leg. Arrowheads point out the ventro-lateral ridge of the femur underneath which the axon of the femoro-tibial strand receptor travels towards its peripheral target. *m*, medial (inner); *l*, lateral (outer) face of femur; scale bar, 5 mm.

femur across the scoloparium of the femoral chordotonal organ into the so-called 'flexor strand' (Field & Burrows, 1982), a structure first described by Usherwood *et al.* (1968) as a 'ligament' connecting the chordotonal organ with the apodeme of the flexor tibiae muscle (Fig. 2A).

On this 'ligament' over a distance of about 500 μm the stained axon exhibits the peripheral branching pattern typical for strand receptor neurones (Bräunig, 1982*a,b*). A few first order branches were followed by numerous ramifications of higher order, becoming finer and finer. The region containing the terminal ramifications is located in the proximal quarter of the 'ligament' and appears slightly thickened.

Thus the so-called 'flexor strand' or 'ligament' of the femoral chordotonal organ is a separate mechanoreceptor of a different morphological class. It inserts on the chordotonal organ proximally and on the apodeme of the flexor tibiae muscle distally (Fig. 2A). In the following sections it will be called the femoro-tibial strand receptor, abbreviated fetiSR.

Afferent responses of the metathoracic femoro-tibial strand receptor

Extension of the tibia causes elongation of the flexor muscle apodeme which in turn causes elongation of the fetiSR receptor strand (compare Field & Burrows, 1982), and thereby stimulation of its receptor neurone (Fig. 3). Direct stimulation of fetiSR by pulling its strand (Fig. 3E) increases its discharge rate just as does extension of the tibia (Fig. 3B–D). All strand receptor neurones known so far are sensitive to elongation of their receptor strands (Bräunig & Hustert, 1980; Hustert, 1983; Bräunig, 1983).

The fetiSR neurone is active over almost the entire range of tibial positions (Fig. 3B). When the receptor has adapted after changing position, spiking is very regular (see small deviations of discharge rate in Fig. 3B,E). Only in the fully flexed position (0° , joint position defined as by Usherwood *et al.* 1968 and Siegler, 1981) is it completely silent in most preparations. It increases its discharge rate in proportion to joint angle almost linearly between 30° and 120° joint position and goes into saturation with further extension of the joint (Fig. 3B). At the fully extended position of the tibia (170°) fetiSR tends to give erratic responses like high frequency bursts interrupted by silent periods. This phenomenon is probably due to overstretching and is also frequently observed with coxal strand receptors (Bräunig, 1983).

The phasico-tonic response to ramp stimuli (Fig. 3C) shows that the receptor not only reacts in proportion to joint position, but also to its first derivation, i.e. velocity. This is also shown by the slight phase advance during sinusoidal stimuli (Fig. 3D), and the halt or decrease of the spike discharge rate at negative velocities during ramp or sinusoidal stimuli (Fig. 3C,D). Thus the fetiSR not only encodes joint position, but also provides the central nervous system with information about the velocity of active or passive movements of the femoro-tibial joint.

The femoro-tibial strand receptor in the fore and middle legs

The location of the receptor in the pro- and mesothoracic legs is homologous to that in the hind leg. The receptor strand lies parallel to the distalmost anterior bundle of

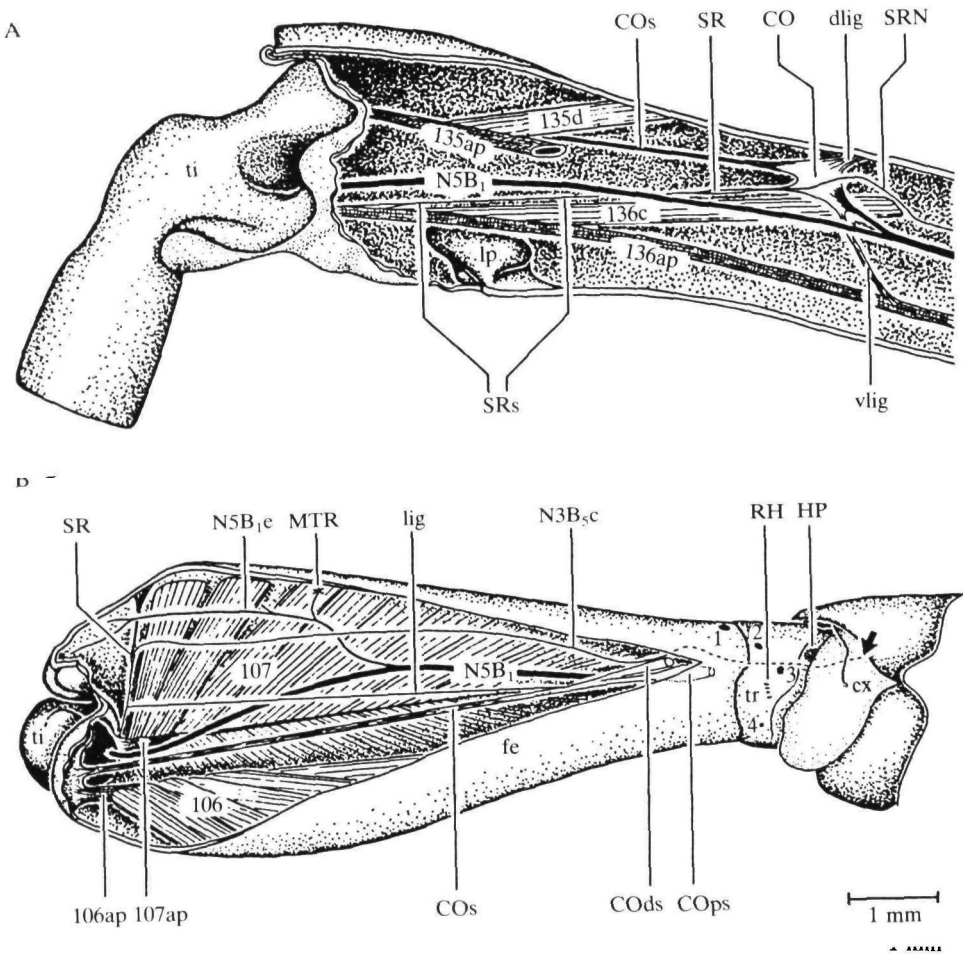


Fig. 2. Position and innervation of the femoro-tibial strand receptors. (A) Inner view of the anterior distal femoral region of the left hind leg (dorsal at the top, distal on the left). Most muscle bundles of flexor and extensor have been removed as well as air sacs, tracheae and some nerves to expose the femoral chordotonal organ (CO) with its dorsal (dlig) and ventral (Vlig) ligaments, its strand (COs) and its innervation by a branch of nerve 5B₁ (N5B₁). Note the strand receptor (SR) with its innervation (SRN) and strand (SRs) connecting the chordotonal organ with the apodeme of the flexor muscle (136ap) parallel to the anterior accessory flexor muscle (136c). ti, tibia; lp, lump (Heitler, 1974); 135d, anterior accessory extensor; 135ap, extensor muscle apodeme. (B) Dorsal view of the left middle leg (anterior at the top, distal on the left). Femur has been opened antero-dorsally by a longitudinal cut between attachments of flexor and extensor muscle bundles. The dorsal cuticle of the femur (fe) with the extensor (106) has been displaced to the rear and air sacs, tracheae and some nerves have been removed to allow an unobstructed view of the flexor muscle (107), proximal (COPs) and distal (CODs) scoloparia and strand (COs) of the femoral chordotonal organ, the femoro-tibial strand receptor (SR) and its innervation (N3B_{5c}). Note the ligament (lig) connecting the strands of chordotonal organ and strand receptor. On femur (fe) and trochanter (tr) hairplate (HP), row of hairs (RH) and fields of campaniform sensilla (1-4) are shown for orientation, arrow on coxa (cx) marks origin of nerve 3B_{5c}. MTR, muscle tension receptor (Theophilidis & Burns, 1979); ti, tibia; 106ap, 107ap, apodemes of extensor or flexor muscle.

the flexor tibiae muscle (Fig. 2B) which probably corresponds to the anterior accessory flexor of the metathoracic leg (muscle 136c in Fig. 2A). The innervation of the receptor, however, as well as its association with the femoral chordotonal organ, differs from that in the hind leg.

In the pro- and mesothoracic legs the fetiSR nerve leaves other branches of nerve 3B in the coxa (arrow in Fig. 2B) and, clinging to the cuticle, travels anterodorsally through the trochanter towards the distal scoloparium of the femoral chordotonal organ. From here it passes freely through the femoral lumen towards the receptor strand located distally in the femur. In contrast to the situation in the hind leg there is usually no anastomosis with a side branch of nerve 5B: in the pro- and mesothoracic leg the fetiSR nerve (3B_{5c}) pursues its way through almost the entire length of the femur without joining other nerves and apparently not adhering to other structures such as tracheae or muscles (Fig. 2B).

In some preparations, nerve 3B_{5c} fused with nerve 5B_{1e}, a nerve supplying the muscle tension receptor and sensory hairs on the anterior distal wall of the femur (Theophilidis & Burns, 1979) with distal branches very close to the fetiSR receptor strand. This alternative route for the strand receptor axon is shown schematically in Fig. 4.

While there is a direct connection between the femoral chordotonal organ and fetiSR in the hind leg, in the fore and middle leg this connection is indirect: a very thin and fragile ligament (lig in Figs 2B, 4) connects the strands of both mechanoreceptors.

DISCUSSION

Implications from strand receptor innervation

A strand receptor is an insect mechanoreceptor consisting of a connective tissue strand that is innervated by one or more sensory neurones. The cell bodies of these neurones are not found in the periphery like those of the great majority of arthropod sensory cells, but are located in the central nervous system (Bräunig & Hustert, 1980). Furthermore the strand receptor neurones exhibit a typical morphology, and thereby can easily and unequivocally be distinguished from motor and other sensory neurones in the central projections of major peripheral nerves (Bräunig, 1982*a,b*). No neurones morphologically resembling strand receptor cells, in cobalt backfills, have been found in any peripheral nerves other than nerve 3B (Burrows, 1975; Bräunig, 1983).

Fig. 3. Afferent responses of the hind leg femoro-tibial strand receptor. (A) Simultaneous recording from nerve 5B_{1c} (upper trace) proximally in the femur and from nerve 3B₅ (lower trace) in the coxa (recording sites are shown as black triangles in Fig. 4). Ten sweeps of the oscilloscope were triggered from the fetiSR spike in nerve 5B_{1c}, which arrives in nerve 3B₅ with constant latency. (B) Static discharge rate of the fetiSR unit (impulses s⁻¹) at various angles of the femoro-tibial joint (0°, fully flexed; 150°, almost fully extended), vertical bars represent maximum deviation of discharge rate observed after 1 min of adaptation following a change of joint position. Sample time, 2 min. (C) Instantaneous frequency plots of fetiSR response to 30° ramp stimuli with 30° s⁻¹ (upper record) and 60° s⁻¹ (lower record). Arrows indicate drop to or return from zero activity. Between single steps 1 min intervals of continuous record have been omitted. (Definition of joint angular position as in B.) (D) Response of fetiSR to sinusoidal extension (Ext.) in four different sectors of joint angular position as defined in B (montage synchronous with stimulus trace). (E) Response of fetiSR towards direct 0.5-mm elongation of its strand (upward deflection of stimulus trace) at a tibial position of approx. 90°.

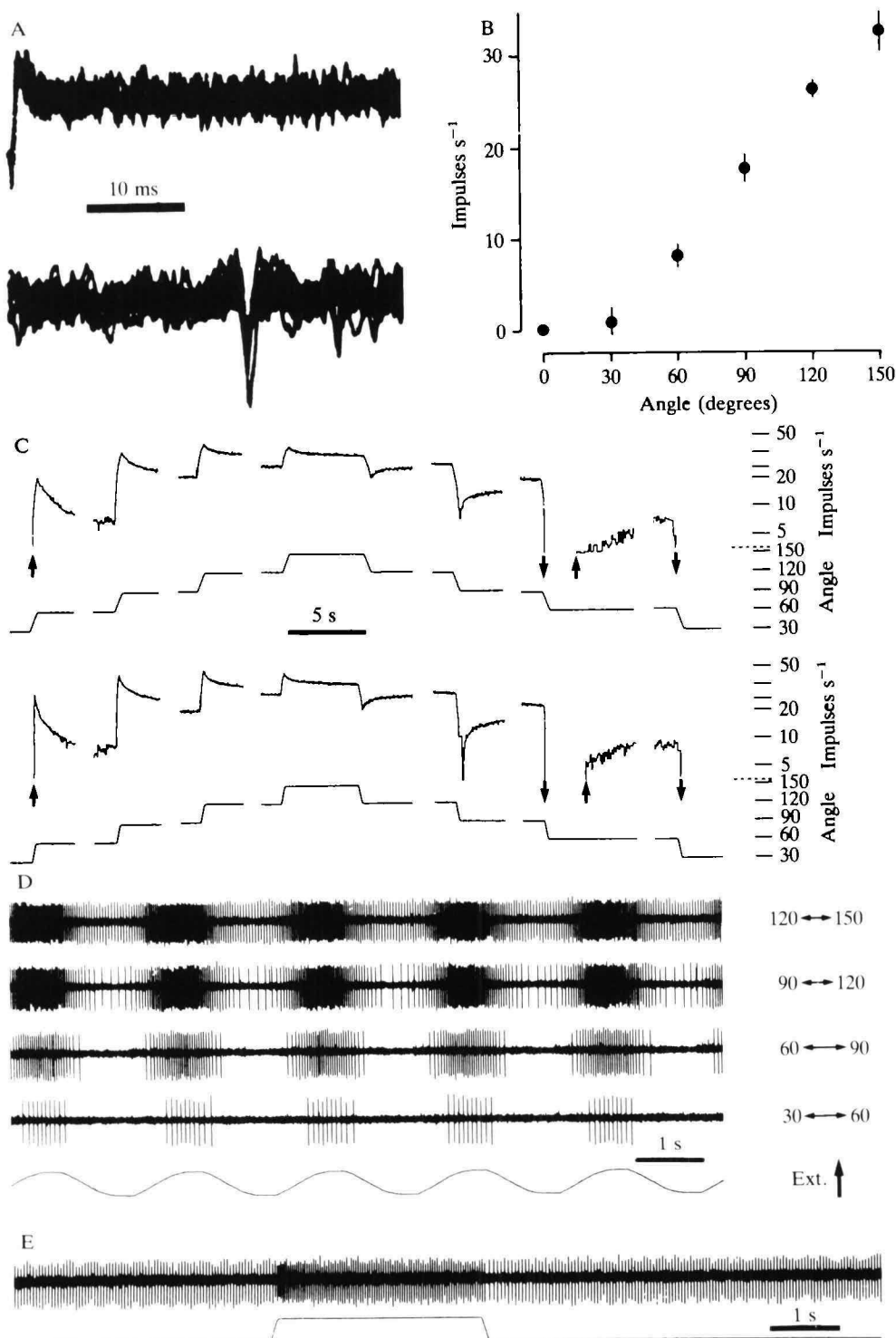


Fig. 3

So far, four strand receptor organs have been described for each locust leg: one in the subcoxal joint (Bräunig & Hustert, 1980; Bräunig, Hustert & Pflüger, 1981; Hustert, 1983), two in the coxo-trochanteral joint (Bräunig, 1982*a,b*) and the fetiSR in the present study. All of them are innervated by branches of nerve 3B.

The nerve branch innervating fetiSR is unusual in pursuing its own way through the leg. Although the fetiSR axon may use side branches of the main leg nerve (5B) for part of its way into the distal femoral region (nerve 5B_{1c} in the hind leg and sometimes

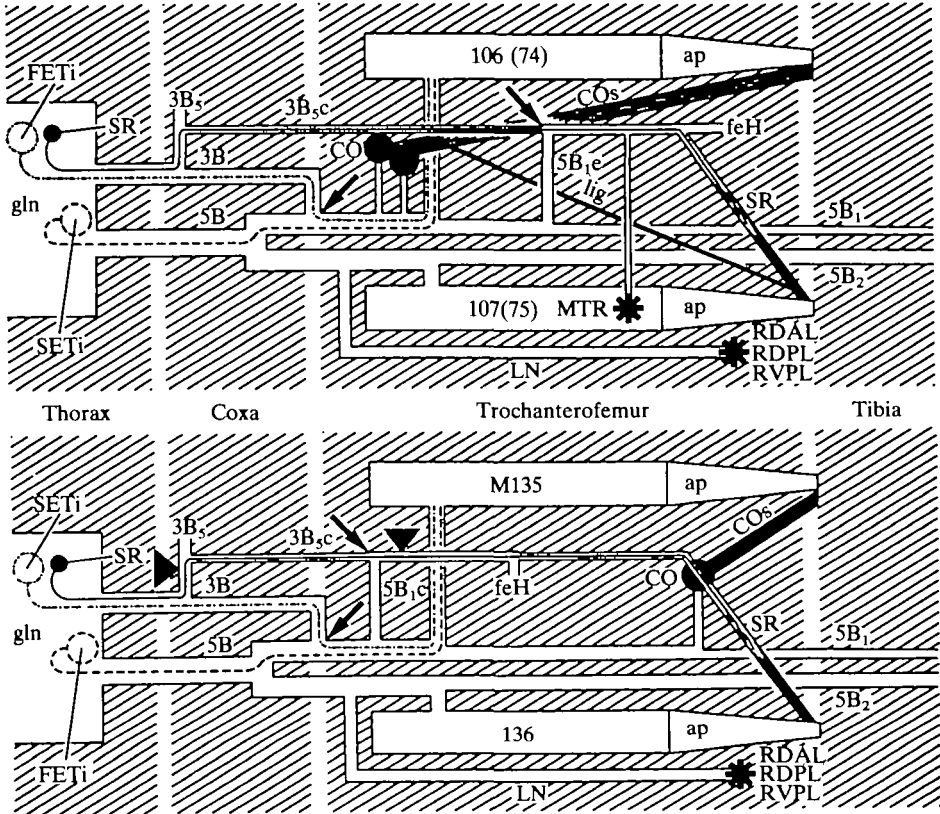


Fig. 4. Sensory supply of the femoro-tibial joints of the fore and middle legs (top section) and the hind leg (bottom section). The schematic representation combines results of earlier publications with those of the present study and shows the thoracic ganglia (gln), nerves 3B and 5B with their branches to sense organs and muscles of the joint. Additionally illustrated are the cell bodies of two extensor motor neurones (SETi, FETi; Hoyle, 1955; Hoyle & Burrows, 1973; Wilson & Hoyle, 1978) and that of the fetiSR neurone (SR) as well as the course of their axons through the two anastomoses between nerves 3B and 5B marked by arrows. (Black triangles mark recording sites of Fig. 3A.) The scheme puts stress on the homologies between all legs, therefore only few differences are outlined: the chordotonal organ (CO) has only one scoloparium and is located distally in the hind leg. There is no ligament (lig) connecting the chordotonal organ (CO) and the strand receptor (SR) and no muscle tension receptor (MTR) has yet been found in the hind leg (compare upper and lower scheme). ap, apodeme; CO, femoral chordotonal organ; COs, strand of CO; feH, femoral sensory hairs; LN, lateral nerve (Heitler & Burrows, 1977); RDAL, RDPL, RVPL, multipolar sensilla (Coillot & Boistel, 1968); 74, 106, 135, extensor muscles of the pro-, meso- or metathoracic leg; 75, 107, 136, flexor tibiae muscles of pro-, meso- or metathoracic leg.

nerve 5B_{1e} in the other legs), in the pro- and mesothorax it is normally able to find its peripheral target without making use of the leg nerve.

Nerve 3B, a major peripheral nerve in adult locusts and larvae, is established early during embryogenesis by a pioneer neurone growing out from the central nervous system into the leg bud (Bentley & Keshishian, 1982*a,b*; Ho & Goodman, 1982). It is believed that this pioneer neurone becomes the SETi motor neurone of the extensor tibiae muscle in the adult (C. S. Goodman, personal communication).

Another possibility is that the fetiSR neurone pioneers nerve 3B. This alternative interpretation is supported by the following: in backfills from embryonic limb buds Whittington & Seifert (1981) observed two cell bodies stained *via* nerve 3B, located anteriorly and ventrally in the thoracic ganglion. In the same region of the ganglion in the adult locust, the strand receptor neurones form a cluster of small cell bodies (including that of fetiSR) very close to the large cell body of the SETi motor neurone (Burrows, 1975; Bräunig, 1982*b*). Cobalt backfills of nerve 3B in newly hatched first instar hoppers, however, show SETi and strand receptor cell bodies of equal size (P. Bräunig, unpublished observations). That means that the motor neurone outgrows the sensory ones during postembryonic development, and that it is difficult to distinguish between fetiSR and SETi in embryos: there, both neurones have cell bodies of equal size and location, and their axons leave the ganglion *via* the same nerve towards the primordium of the extensor tibiae muscle (Bentley & Keshishian, 1982*a,b*). For all these reasons, it is possible that the neurone pioneering nerve 3B during embryogenesis of the leg nervous system is in fact fetiSR, not SETi.

Function of the femoro-tibial strand receptor

The functional role of the fetiSR is hard to assess at present. The multipolar neurones at the femoro-tibial joint (Coillot & Boistel, 1968, 1969; Williamson & Burns, 1978), the muscle tension receptor (Theophilidis & Burns, 1979) and many of the scolopidial cells of the femoral chordotonal organ (Usherwood *et al.* 1968; Burns, 1974) respond to extension of the tibia. Perhaps some parameter of tibial extension that they cannot encode is provided by the fetiSR.

Association of fetiSR and the femoral chordotonal organ

The direct insertion of the fetiSR strand on the femoral chordotonal organ in the hind leg as well as the connection of both receptors by a connective tissue ligament in the other two legs means that manipulation of one sense organ may influence the other and *vice versa*. It will be necessary to find out to what extent the techniques applied for dislocating the chordotonal organ apodeme (Bässler, 1979) impair the function of the strand receptor. The behavioural effects observed after these operations could at least partly be due to changed afferent responses of the fetiSR.

For the same reason we need comparative information for other insect species, where similar experiments have been performed (Graham & Bässler, 1981). The overall homology of mechanoreceptor numbers and location in the legs of insects (Bräunig, 1982*a*) make it very likely that the fetiSR is present in all insect legs, and

that study should be made of its location, innervation and possible connection with other sense organs.

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