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MULTISEGMENTAL INTEGRATION AND DIVERGENCE OF AFFERENT INFORMATION FROM SINGLE TACTILE HAIRS IN A CRICKET

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SUMMARY

The long tactile hairs of crickets contribute to intersegmental receptive fields of interneurones that integrate input from different types of tactile mechano-sensory hairs. Afferent input from the identified long hairs studied converges on a group of multisegmental interneurones of the abdominal and thoracic ganglia. Conversely, the input from each tactile hair receptor diverges to several multisegmental interneurones and also to motoneurones of their own and neighbouring segments. The interneurones have spike initiating zones in each ganglion they reach. Spikes initiated by hair afferents can travel caudally and rostrally in an interneurone. These interneurones spreading tactile information from single sensory cells to several ganglia are not suited for fine discrimination of sources of touch which could elicit specific somatotopically oriented motor behaviour of the cricket. More specific pathways from long tactile hairs to motoneurones exist in abdominal and thoracic segments.

INTRODUCTION

In insects and other arthropods movements of appendages or the whole body can be elicited when mechanosensitive hairs on their body are bent upon contact with the environment. The areas of mechanosensory stimulation apparently are identified by the animal, for often reflexes or more complex motor responses follow. Grooming, kicking or antennal probing responses may be directed at the site of contact in order to reach or avoid the source of touch to tactile hairs and sometimes also retraction of limbs, change of body position or escape may occur as more general avoidance reactions. The movements do not appear to follow fixed patterns; rather, they are organized as touch-oriented motor acts with concurrent motor activation extending to several segments of limbs and of the body. The decisions to perform these movements and the subsequent motor coordination must be organized in the CNS according to the intensity and

Key words: Touch-sensitive, interneurones.

localization of stimuli to the tactile mechanoreceptors. Recent studies have shown that in locusts tactile afferents converging from small hairs influence the discharge rate of local interneurones (Siegler & Burrows, 1984; Burrows & Siegler, 1984) which seem to be primary integrating neurones to these tactile afferents.

As a first step towards understanding how intersegmental central neurones are influenced by the primary afferents from tactile mechanoreceptors, the intersegmental pathways of divergent and convergent information from identified single receptor cells must be traced.

For the present paper the cricket *Gryllus bimaculàtus* was used as a model system, for its body and limbs are covered with numerous hairs and bristles, many of which have already been studied in other crickets as to their localization (Honegger, 1977; Hustert, 1978; Eibl, 1978; Fudalewicz-Niemczyk, Olesky & Rosciscewska, 1980; Klein, 1981), their receptor responses (Neumann, 1975; Gaffal & Theiß, 1978; Hustert, 1980, 1981) and their primary projections in the ventral nerve cord (Honegger, 1977; Hustert, 1978; Eibl & Huber, 1979). The long tactile hairs protruding over neighbouring bristles have been the primary objects of this study, because they can be identified in every animal by their characteristic localization and because their afferents excite several intersegmental interneurones of the ventral nerve cord (Hustert, 1981).

MATERIALS AND METHODS

Adult male and female crickets of the species *Gryllus bimaculatus* from a laboratory culture were used. On their cuticle, smaller hairs and bristles showed considerable variation in thickness, length and relative distribution on the cuticle. The results obtained with long tactile hairs of different animals did not show significant physiological differences in their afferent and higher order neurone responses.

The projections of the single hair's afferents in the CNS were determined by a cobalt backfilling method through the base of single hair sensilla as described earlier (Hustert, 1978) and the distribution of fine peripheral nerves was visualized by centripetal cobalt filling of the whole nerves (Hustert, 1974, 1978). Cobalt precipitated in the neurones was usually silver intensified using the method of Bacon & Altmann (1977) and also with a slightly modified technique (Hustert, 1978). Projections of sensory afferents stained from sensilla situated at greater distance from the CNS, for example those on the tibia, often required heavy intensification and subsequent destaining of the ganglionic surface (Pitman, 1979).

Afferent signals from sensory receptors were recorded *via* suction electrodes with their polyethylene tips placed in a position on a peripheral nerve where the spike amplitude of a single sensory hair axon was larger than those of the other units recorded from the same nerve. The afferent unit of the hair was identified by its phase-locked responses upon selective mechanical stimulation of the hair to be studied.

The stimulation device was a tongue-shaped piezoelectric bender (Valvo PXE 5) with a minuten needle mounted at its end for moving the sensory hair. A function generator and power amplifier imposed various waveforms on the bender.

Spiking discharges of two interneurones (mechanosensory hair interneurones MHI1 and MHI4)) were recorded routinely from the ventral surface of connectives with extracellular focal suction electrodes of 20–60 μm tip diameter (for a preliminary account of MHI1 responses see Hustert, 1981).

Single unit and intracellular recordings from axons in the connectives (and from neuropile processes of the MHI1) in several types of interneurones were obtained with glass microelectrodes of 20–40 MΩ tip resistance. The electrodes were filled with 2 mol l^{-1} potassium acetate or the fluorescent dye Lucifer Yellow (5 % in 1 mol l^{-1} $LiCl_2$, Stewart, 1978). The morphology of stained neurones was studied in whole mounts after fixation in buffered paraformaldehyde, dehydration in ethanol and clearing in methyl salicylate. Interneurones were considered as identified when they showed the same morphological features and physiological characteristics in at least three different animals (MHI1–4).

The recordings from the CNS were made in preparations turned ventral side up. These preparations were reduced to the ventral half of the thorax and the abdominal sternites. Head, tergites, gut and the genital segments posterior to the sixth abdominal segment were removed. The CNS of the remaining segments was left intact and the sclerites and legs were immobilized with minuten needles. Removal of some parts of the ventral cuticle exposed the CNS for recording ventrally. Platforms of different shapes were used to support the ganglia and connectives when recording with microelectrodes.

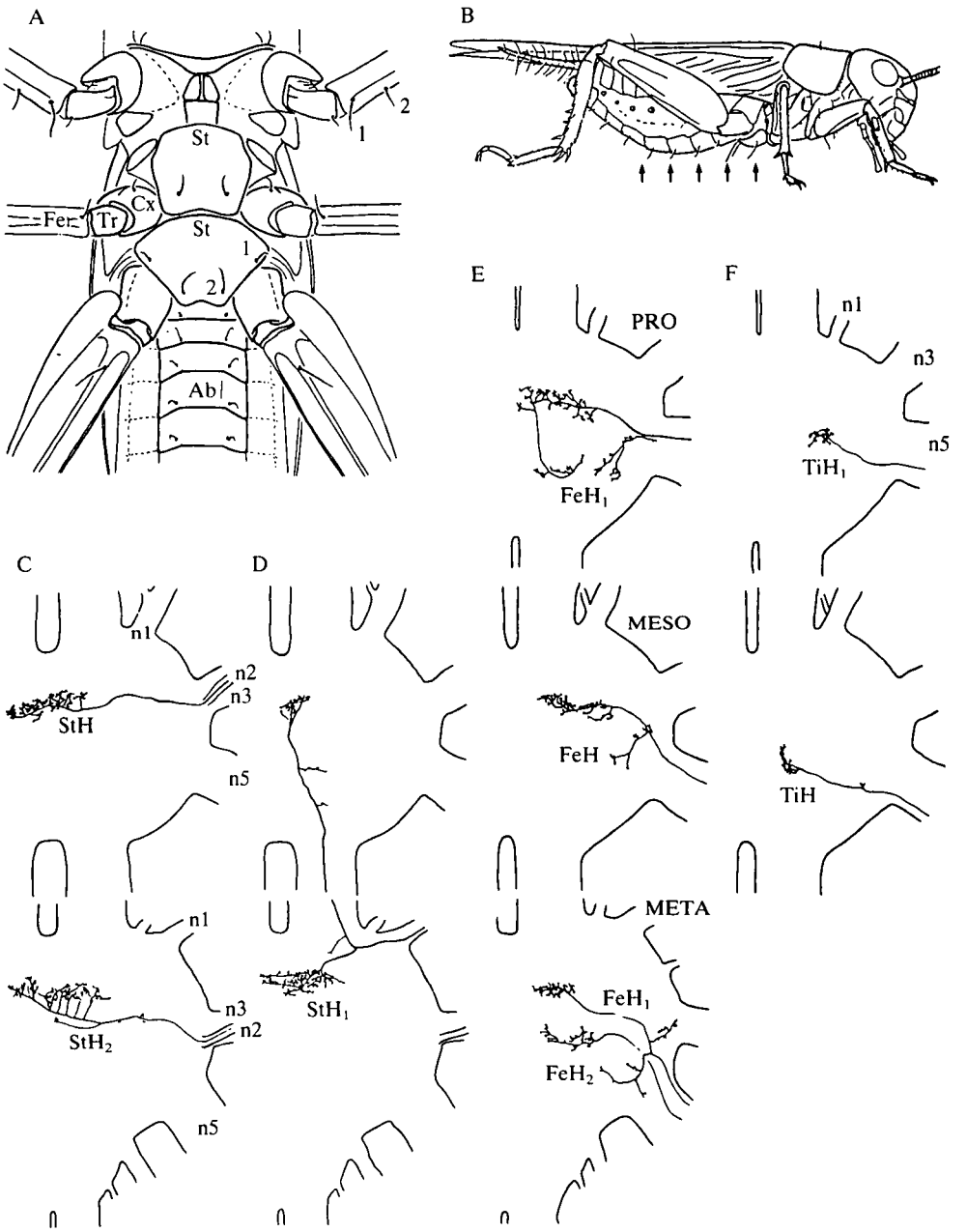
Nerves were named as in the locust thorax (Campbell, 1961) where homology to crickets is obvious, and the sense organs were named as in locusts by Hustert (1978) and Pflüger, Bräunig & Hustert (1981). $ProFeH_1$ for example means: first (proximal) long tactile hair on the femur of the prothoracic leg. The mechanosensory hair interneurones (MHI) with thoracic somata were named MHI1–3, and MHI4 is the interneurone arising from the first free abdominal ganglion (Ag3).

RESULTS

Localization and properties of long tactile hairs

The location of mechanosensitive hairs

The bodies of crickets are covered with numerous mechanosensitive hairs, each supplied with one sensory cell at its base. Their cuticular structures range from tiny to long (20–2000 μm) and from wide to slender (5–80 μm) at their base. All tactile hairs insert in a relatively rigid base of the cuticular skeleton. At the edges of legs and thoracic segments, stout bristles (hairs with a wide base) and large spines (larger than bristles with mechanosensitive neurones at their base) prevail. The distribution pattern of smaller hairs shows no regularity that could allow reliable identification of single hairs in different animals.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MESO
FeH
TiH
META
StH1
StH2
FeH1
FeH2

Fig. 1

In contrast, the long tactile hairs (500–2000 μm) are found at constant locations on sternites and leg segments of adult crickets and of larval instars. The positions of those pointing ventrally on the body of the adult *Gryllus bimaculatus* are shown in Fig. 1A,B. In addition to these, tibial, dorsal femoral and pronotal hairs exist (but are not visible in Fig. 1). Occasionally pairs of longer hairs of the same type develop on the coxae and trochantera and sometimes also (in addition to the regular abdominal hairs) laterally on the sternites, close to the pleural folds.

Central projections of the primary axons

The pattern and extent of central projections from the long tactile hairs are known for the abdominal sternite hairs of *Acheta domesticus* (Hustert, 1978). Their locations and central projection are very similar in *Gryllus bimaculatus*. Therefore, only projections of tactile hair afferents of the thorax and legs will be described (Fig. 1C–F).

All projections from long tactile hairs take a ventral and medial course upon entering the segmental ganglion and reach the most ventral level of the neuropile (ventral association centre, VAC, including the very ventral association centre, vVAC). The projections of sternite hairs cross the midline (Fig. 1C,D) and have no early arborizations in the lateral neuropile. Only the second hair of the metathoracic sternite ($MetaStH_2$) sends an intersegmental collateral into the mesothoracic sensory neuropile. Femoral hairs are the most proximal long hairs seen regularly in all legs of each animal (although the coxa and trochanter of some animals may carry relatively long hairs also). Their primary projections extend less far than those of sternal hairs but almost reach the ganglionic midline and arborize extensively there (Fig. 1E). In the prothoracic projection of FeH_1 projection an additional collateral runs to the posterior part of the median ventralmost neuropile. In all projections of the proximal femoral long hairs, one collateral turns posteriorly (and one is also directed anteriorly in the metathoracic FeH_1) after the axon has entered the ganglion. Only in the projection of the more distal and dorsal $MetaFeH_2$ is the main arborization in a posterior part of the ventralmost neuropile. Projections from the tibial long hairs (TiH) which are the

Fig. 1. Peripheral location and central projection of long tactile hairs in the cricket body. (A) Schematic ventral view of the thoracic and anterior abdominal segments with the first leg segments coxa (Cx), trochanter (Tr) and Femur (Fe). Of the mechanosensory hairs only the long tactile hairs are shown (their thickness is exaggerated). When more than one long hair is located on a sternite or leg segment (St, Ab) they are identity numerals (1, 2). (B) Lateral view of the cricket *Gryllus bimaculatus* showing the position of long tactile hairs, specifically those which point ventralwards (arrows). (C)–(F) Projections of the primary sensory cells of long tactile hairs in the pro-, meso- and metathoracic ganglia (PRO, MESO, META). *Camera lucida* drawings from the dorsal side. Lateral nerves are indicated by numbers (n1–5). (C) Projection of the mesothoracic sternite hairs MesoStH and the second metathoracic sternite hair ($MetaStH_2$). (D) Shows the intersegmental projection of the first metathoracic sternite ($MetaStH_1$). (E) Homologuous hair projections of the proximal femoral hairs ($ProFeH_1$, MesoFeH, $MetaFeH_{1,2}$). (F) Homologous projections from the prothoracic first long tibial hair (TiH_1) and the single mesothoracic long tibial hair. The metathoracic tibia carries no long tibial hair.

most distal long hairs of cricket legs reach the lateral part of the vVAC only (Fig. 1F).

For comparison, afferents from the intersegmental axon of the PronH and from long and short bristles (FelB and FesB) lying adjacent to the MesoFeH on the femur were stained (Fig. 2). The projection of FelB reaches the posterior extension of the VAC where the long tibial hair afferents arborize and from here a collateral extends in the anterior VAC to the area lateral to the StH and FeH projections. The short bristle afferents (FesB) reach the anterior VAC area *via* a direct course. The shaded area in Fig. 2 outlines the ventral neuropile area of the mesothoracic ganglion in which tactile hair projections can terminate.

Response characteristics of the long tactile hairs

Long tactile hairs emerge from a narrow cuticular base as described for the tibia (Neumann, 1975). Their tapering shafts either extend perpendicular to the surface of the cuticle or are curved posterior-medially in sternite hairs and distally in hairs of the legs. The extremely fine tips of the long hairs on the sternites bend

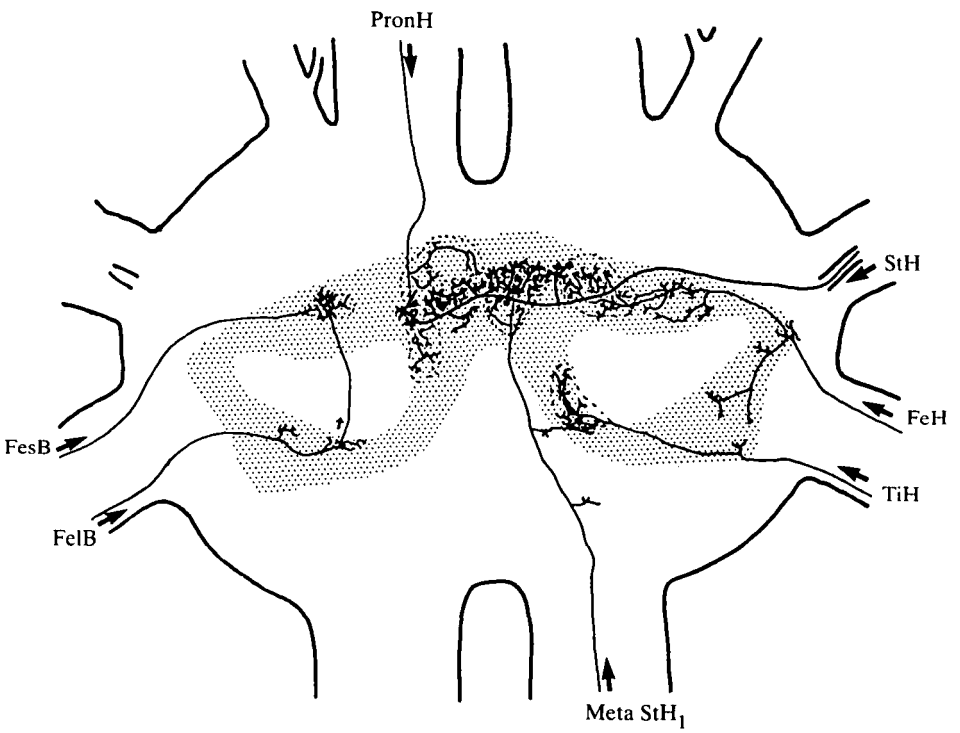

Fig. 2. Distribution and convergence of mechanosensory hair projections in the ventral association centre (VAC) with its extending lateral and posterior areas of hair projections (shaded area) in a composite drawing of the mesothoracic ganglion. Mesothoracic hair axons enter *via* the lateral nerves (n1–5) sternite (StH), femoral (FeH) and tibial (TiH) long hairs are compared with femoral long (FelB) and short (FesB) bristle projections. The intersegmental projections of the pronotal long hair (PronH) and the first metathoracic long sternite (MetaStH$_1$) enter *via* the connectives.

under light touch and cause mainly lateral movements of the shaft in the hair base in response to mechanical stimulation from any direction. Slow air currents (below $9\,m\,s^{-1}$) are not able to bend long hairs of the body and legs, in contrast to the wind-sensitive filiform hairs of the cricket cerci. Touch upon a long hair from any direction elicits a phasic high frequency response from its sensory cell, which adapts only little upon repetitive stimulation and then maintains a steady level (Fig. 3). When continuous sinusoidal stimuli are applied to a hair, the spiking responses may follow the cycles of stimuli at frequencies up to 140 Hz in a 1:1 ratio (Hustert, 1980). The responses of most long hairs to displacement show no pronounced directional characteristic in polar plots of discharge rates. Occasionally, when identical stimuli are applied from different angles, an increased intensity of response is elicited by a stimulus oriented in the plane in which the curved shaft to the hair lies. 'Trapezoidal' stimulation (bending a hair from its resting position into a constant angle of deflection) causes phasic responses. The adaptation times increase with larger angles of deflection and may end in low frequency tonic discharges during extreme deflection of the hair shaft (Fig. 3).

A peculiar feature of the abdominal long hairs is that, when the sternites become wet, the hairs come to lie in a posterior shallow groove of the sternal cuticle extending from the hair base (probably shaped by the newly developing hair before ecdysis). In this position the sensory cell of the hair discharges continuously. When dried and erect again, these hairs respond physically as before.

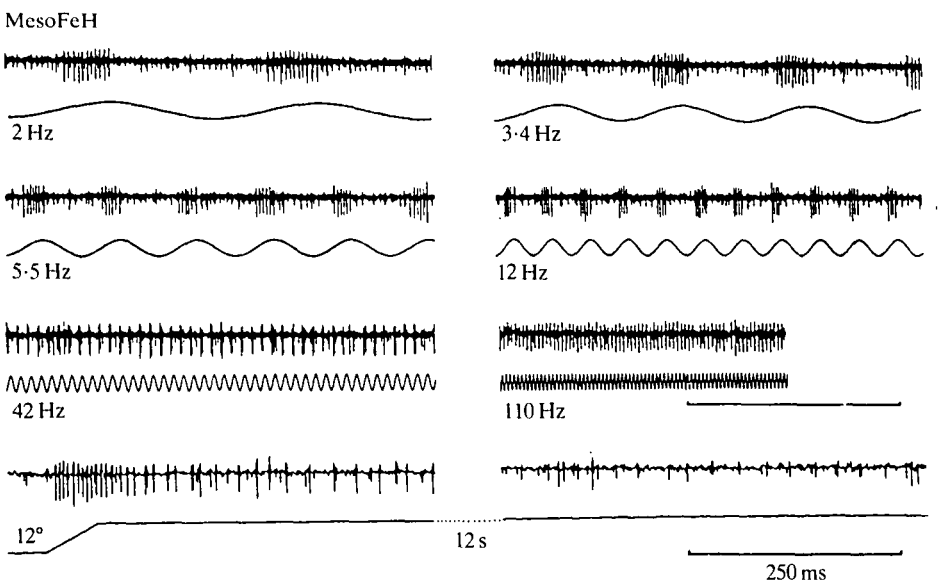

Fig. 3. Primary afferent responses of the mesothoracic femoral long hairs (MesoFeH) are recorded from the leg nerve close to the mesothoracic ganglion (upper traces, smaller spikes from other axons). Sinusoidal stimuli of 5° angular deflection from resting position are applied to the hair (lower traces) at different frequencies. The last line shows the adapting response of the sensory cell to a 12° deflection with a step-like stimulus from the resting position of the hair.

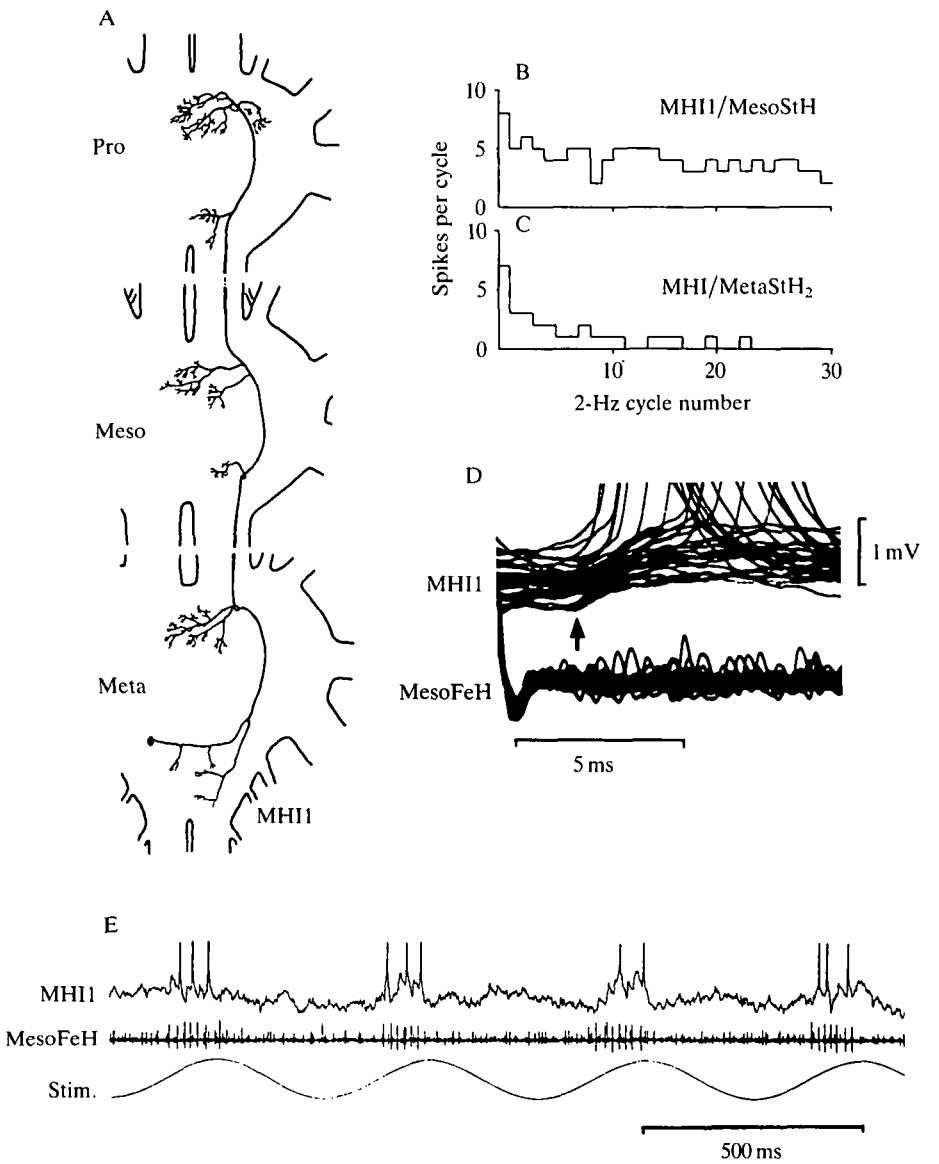

Fig. 4.(A) Morphology of the mechanosensory hair interneurone 1 (MHI1) in all three thoracic ganglia. Composite drawing from two Lucifer Yellow stains with injection of the dye in the pro-mesothoracic and the meso-metathoracic connective. The delicate collaterals in the abdominal neuromeres of the metathoracic ganglion may be stained incompletely. All anterior collaterals branch in the very ventral neuropile area (vVAC). (B) Adapting discharge in the previously unstimulated interneurone MHI1 to 2-Hz repetitive stimulation of the primary afferent input, deflecting the mesothoracic (MesoStH) and in (C) the second metathoracic sternite long hair ($MetaStH_2$). (D) Traces of 28 sweeps triggered by the afferent spikes of the MesoFeH (lower trace) and resulting EPSPs and spikes of the MHI1. Same recording as in E, except for upper traces in a.c.-mode. Arrow, beginning of EPSPs. Spikes are cut off. (E) Response of the MHI1 to selective stimulation of the single femoral hair of the ipsilateral mesothoracic leg (MesoFeH). Upper trace: recording from a mesothoracic neuropile process of the MHI1 which subsequently was identified morphologically (Fig. 4A). Middle trace: the afferent spikes from the axon of FeH (large unit) are recorded from the surface of the main leg nerve (n5). Lower trace (Stim.): waveform of the 2-Hz stimulus applied to the hair with a deflection of 5° amplitude.

Integration of mechanosensory hair afference

The specific thoracic tactile hair interneurone (MHI1)

The most pronounced responses to stimuli that deflect long hairs of the thorax and leg are seen in the multisegmental mechanosensory hair interneurone MHI1 (and its contralateral homologue) which extends from the metathoracic to the prothoracic ganglion (Fig. 4A,B). Its soma lies dorsally and contralateral to the axon, close to the division between metathoracic and abdominal neuromere in the metathoracic ganglion. The axon takes a very ventral course through the connectives (a feature which allows reliable recording with focal suction electrodes from both pro-meso- and meso-metathoracic connectives) and in each ganglion the axon follows the outer ventral lateral tract (a.VLT, Tyrer & Gregory, 1982). Two homologous regions of medial arborizations are seen in each ganglionic neuropile, a smaller medio-ventral one in the posterior part of each neuropile and an extensive anterior one proceeding through parts of the VAC into the 'very ventral association centre' (vVAC, Pflüger *et al.* 1981), where most of the tactile hair afferents terminate (Figs 2, 4A).

The MHI fires action potentials *only* after tactile hairs have been stimulated. The non-adapting response to stimulation of the long MesoFeH (Fig. 4B) was used to measure delay times between afferent spikes and MHI1 response (Fig.4E) in the mesothoracic neuropile. Delays of 2·7–2·8 ms were measured between the axon of the MesoFeH in the leg nerve and the first rising of resulting EPSPs in the ipsilateral neuropile processes of the MHI1 (Fig. 4D). Taking into account an axonal conduction time of 1 ms from the leg nerve (lateral sternal region) to the mesothoracic neuropile, the synaptic delay time of 1·7–1·8 ms indicates monosynaptic connection between tactile afferent and intersegmental interneurone.

The multisegmental receptive field of the MHI1 can be subdivided according to the response characteristics of the interneurone. (i) Fast or rapid responses of the MHI1 are elicited by stimuli to abdominal long hairs (AbdStH), to posterior metasternal hairs ($MetaStH_2$; Fig. 4C), to all leg hairs contralateral to the MHI1 axon, to most small tactile bristles of thoracic sternites and ipsilateral legs, and to tibial long hairs. (ii) Ipsi- and contralateral long sternite hairs ($MetaStH_1$ and MesoStH) and ipsilateral long femoral hairs elicit persistent interneurone responses during repetitive stimulation (Fig. 4B) although the gain (ratio of interneurone to afferent spikes) decreases after the onset of periodic stimulation of one hair.

Coinciding afferent inputs from two hair receptors in different segments of the interneurone's receptive field each elicit independent responses from the interneurone. Thus, when long single hairs of two different segments are stimulated simultaneously they elicit separate responses which simply superimpose in the axon of the MHI1 as recorded from the connective between both segmental ganglia (Fig. 5A). This indicates that interneurone spikes can be initiated independently in the sections of the interneurone which belong to different

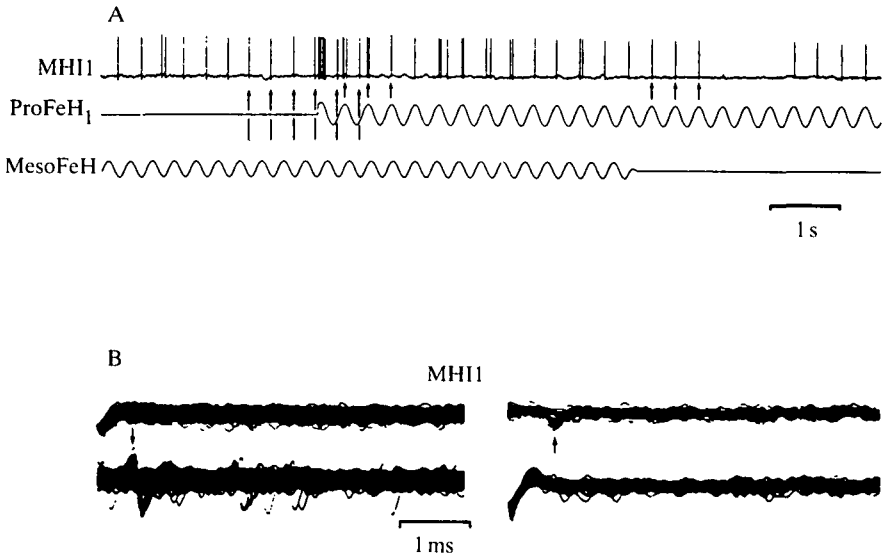

Fig. 5.(A) Convergence of input to the MHI1 from two different segments. The prothoracic FeH was stimulated first (upper trace) while the MHI1 was recorded from the ipsilateral pro-mesothoracic connective (middle trace) then the mesothoracic FeH was stimulated (lower trace) simultaneously, but with a slightly different frequency. The spikes descend from the prothoracic ganglion and ascend from the mesothoracic ganglion. (B) Ascending (left) and descending (right) conduction of spikes recorded from the axon of the MHI1 in the pro-mesoconnective with two extracellular electrodes, one close to the mesothoracic ganglion (upper trace), one close to the prothoracic ganglion (lower trace). Traces on the left are triggered by spikes ascending from the mesothoracic neuropile (elicited by the MesoFeH) and traces on the left are triggered by spikes descending from the prothoracic neuropile (elicited by the ProFeH).

segmental neuropiles. The spikes travel (at a speed of $0{\cdot}9\,m\,s^{-1}$ between pro- and mesothoracic ganglion) both anteriorly and posteriorly from the neuropile of origin (Fig. 5B). The responsiveness of the interneurone to hair afferents is sometimes altered by other neuronal influences, for example during strong ventilatory or other motor activity. There is no evidence for mutual influence between the bilateral pair of left and right MHI1, for stimulation of one long hair of the mesothoracic sternite MesoStH results in spiking responses of both the ipsi- and contralateral MHI1 axons, while stimulation of the long femoral hair on the same side can elicit spiking in the ipsilateral MHI1 axon only.

Mechanosensory influence mediated *via* spike propagation along the interneurone to thoracic motoneurones was not observed. This was tested by stimulating long hairs (usually the $ProFeH_1$ in this study) in one segment in order to excite motoneurones in a different segment *via* the MHI1 (e.g. recording afferent discharges of motor nerves containing mesothoracic leg motoneurones). If the MHI1 had been able to elicit motor responses (other than general arousal) this experiment should have shown motor responses in other thoracic segments, but these were never observed in any preparation (but see local responses to tactile hairs below).

Other thoracic interneurones with responses to tactile stimuli

Afferent information from different tactile hairs of the sternites and legs not only converges onto the bilateral pair of MHI1 but also diverges to additional pairs of identified thoracic interneurones which extend between pro- and metathoracic ganglia (Fig. 6A,B). These exhibit continuous spiking discharges upon which are superimposed responses to afferents from stimulated tactile hairs (Fig. 7A). Their receptive fields and their response characteristics to repetitive stimulation of single sensory afferents are very similar to those of the MHI1 although their morphology is different. The MHI2 usually responds to stimulation of a single long hair (MesoFeH) with a typical time lag of 2–3 ms after the spikes ascending in the MHI1 (Fig. 7B,C). This time lag indicates that in the afferent-to-MHI2 pathway one more neurone than in the afferent-to-MHI1 pathway may intervene.

The axon of one spontaneously active interneurone (MHI2) descends ipsilaterally from a medial postero-dorsal cell body in the prothoracic ganglion to the metathoracic level (Fig. 6A). Most of its collaterals arborize in the ventral plane of the prothoracic and mesothoracic neuropile and ramify most profusely at the medio-ventral level but reach the VAC also. The axon follows the ventral intermediate tract (VIT).

The soma of the second spontaneously active interneurone (MHI3) is situated dorsally in the metathoracic ganglion (Fig. 6B), ipsilateral to the course of its axon which extends both anteriorly and posteriorly in the thoracic CNS. Within the ganglia the axon follows the ventral intermediate tract (VIT). Anteriorly it leaves the prothoracic ganglion and the posterior branch extends to the first free abdominal ganglion (belonging to the third abdominal segment). Its most extensive arborization was stained in the ventral neuropile of the mesothoracic ganglion where it covers the area of most ipsi- and contralateral tactile hair projections.

A tactile interneurone with a predominantly abdominal receptive field (MHI4)

In the connective between metathoracic and first free abdominal ganglion (Ag3) the axon of a ventrolateral interneurone (MHI4) can be recorded routinely with focal suction electrodes (Fig. 8B). This interneurone is not spontaneously active and consistently responds with little adaptation to stimulation of any ipsi- or contralateral long hair of the abdominal sternites (Fig. 8C). It responds to most of the sternal meta- and mesothoracic long hairs also but adapts more rapidly to this input. The MHI4 type neurone extends from its (contralateral) soma in the first free abdominal ganglion (third abdominal segment) anteriorly further than the metathoracic ganglion (Fig. 8A). Its major arborizations branch in the mechanosensory VACs and vVACs in the abdominal and metathoracic neuropile regions. Since it is known that all abdominal long hairs have direct projections extending to the first free abdominal segment, these could connect to the MHI4 directly in this neuropile or in the abdominal neuromeres of the metathoracic ganglion.

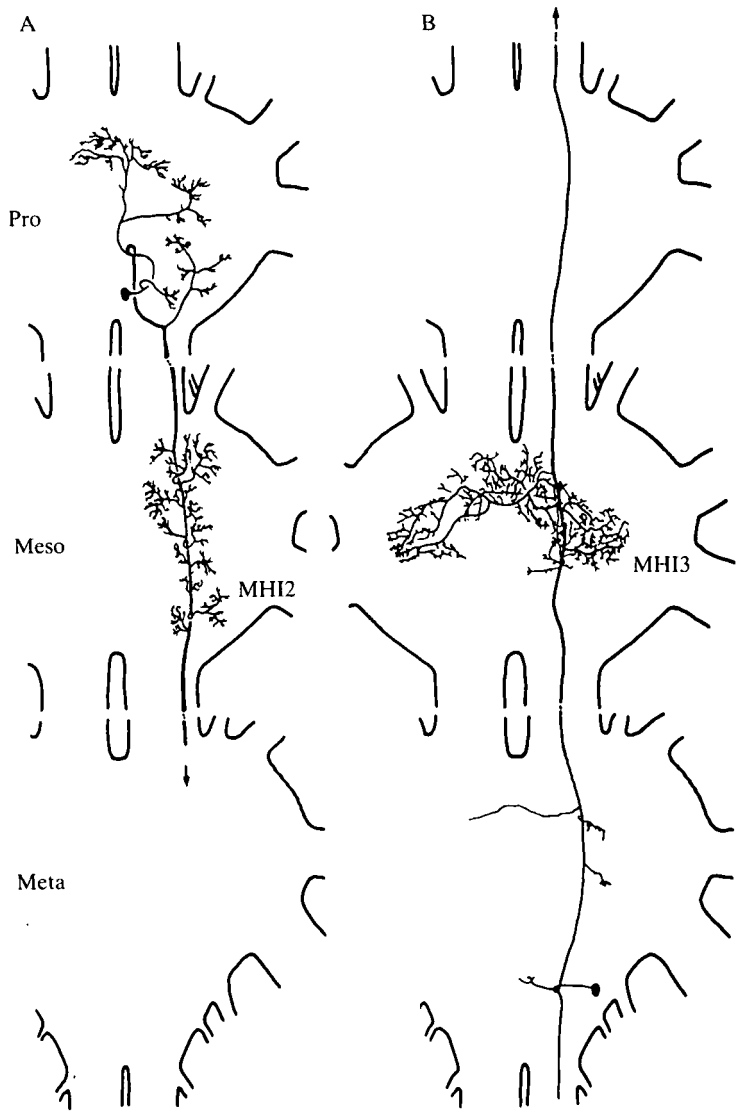

Fig. 6.(A) Morphology of an interneurone (MHI2, stained with Lucifer Yellow) with a receptive field of tactile hairs similar to that of MHI1. Staining *via* the axon in the pro-mesothoracic connective was not sufficiently intensive to visualize its metathoracic branching pattern. This interneurone fires spontaneously and the tactile hair afferents superimpose their input. (B) Morphology of a mechanosensory hair interneurone (MHI3) responding to long tactile hair afferents. Although the detailed branching morphology is only known in the mesothoracic ganglion its axon was seen to enter the connective between the metathoracic and first free abdominal ganglia, and also the connective between prothoracic and suboesophageal ganglia.

Motor responses to stimulation of the long tactile hairs

The motor responses elicited by touch of single long hairs in a preparation are usually local motor reflexes involving just the muscles of appendages on which the stimulated hair is situated. Stimulation of the MesoFeH causes flexion move-

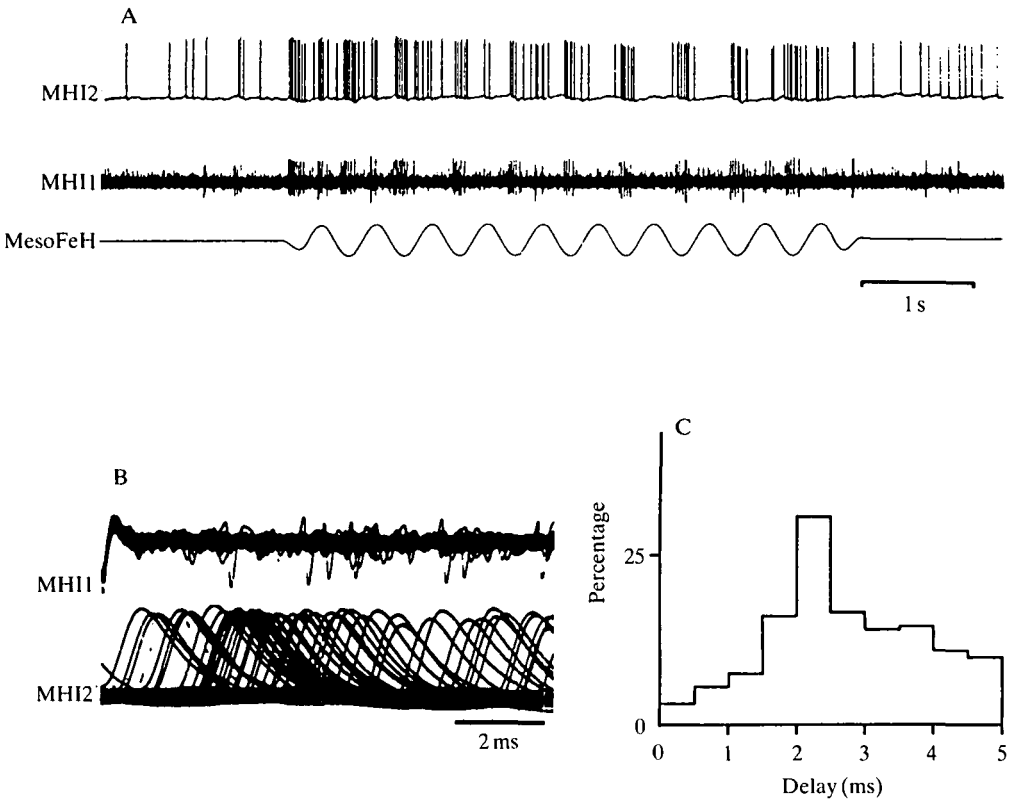

Fig. 7.(A) Divergence of tactile hair input from a single sensory cell (FeH) on a mesothoracic leg (lower trace) to two interneurones (MHI1 and MHI2) recorded in close vicinity to the ipsilateral pro-mesothoracic connective. MHI1 was recorded extracellularly (large amplitude units in middle trace) and MHI2 intracellularly (upper trace). (B) Time lag between ascending spikes of the MHI1 (upper trace, triggering the oscilloscope sweep) and the MHI2 (lower trace) when stimulating and recording as in A. (C) Histogram of the distribution of time lags between MHI1 and MHI2 spikes; data from 100 consecutive sweeps as in B; abscissa: delay in ms; ordinate: percentage of MHI2 spikes following a spike in MHI1.

ments of the tarsus by means of the tarsal depressor muscle in the same leg (Fig. 9), but tibial spurs of this leg may elicit the same reaction. Afferent discharge from the ProFeH$_1$ increases motoneurone discharges in the prothoracic nerve 5c, which mainly contains axons to the ipsilateral trochanter levator muscles. Stimulation of an abdominal hair can excite motoneurones to sternite levator muscles (expiratory muscles) in the same and also in adjacent segments (Hustert, 1980). Most of these responses rapidly adapt upon repetitive stimulation.

In contrast, more widespread motor responses in several segments can be aroused occasionally by touching a single long hair. In preparations these are seen as struggling movements of all legs and as abdominal contractions mediated by motoneurones of the thoracic and abdominal ganglia. The responses adapt rapidly when the same mechanoreceptor is stimulated repetitively.

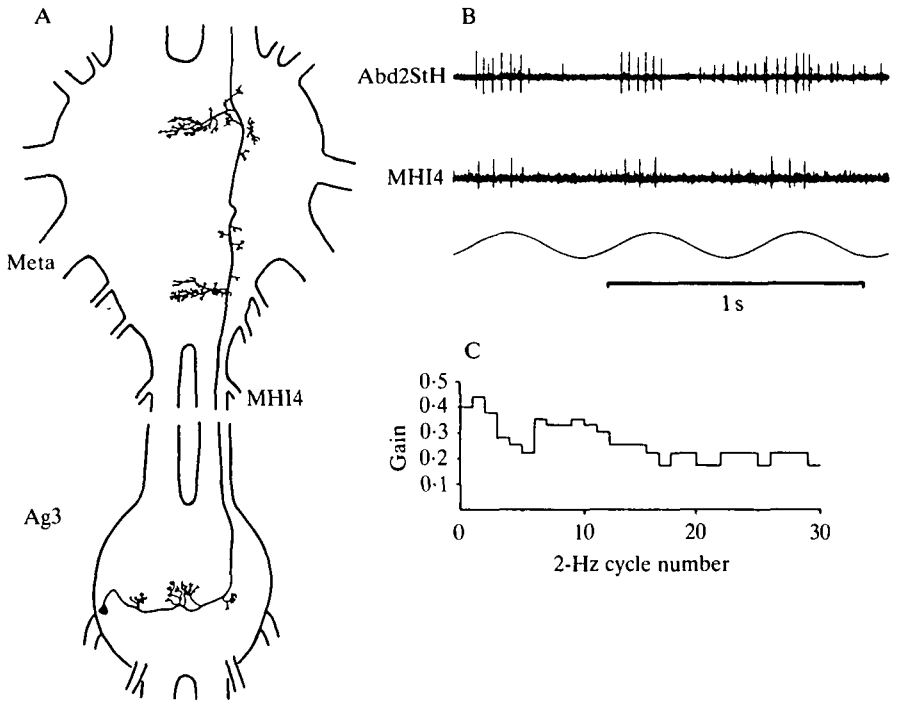

Fig. 8.(A) Ventral view of the abdominal interneurone (MHI4) ascending from its dorsal soma in the Ag3 (first free abdominal ganglion) contralaterally to the metathoracic and mesothoracic ganglion. All large collaterals turn ventrally in the neuropile. Staining with Lucifer Yellow. (B) Response of the interneurone MHI4 to stimaulation of a single abdominal long hair (Abd2StH). (C) Gain of the interneurone MHI4 when stimulated *via* the AbdStH. The ordinate indicates gain as ratio of interneurone-to-afferent spike numbers.

In intact animals, bending of single tactile hairs often elicits antennal probing, directed towards the source of touch, but also grooming of the stimulated area and avoidance reactions by means of the legs occur, ranging from leg withdrawal to escape or vigorous defensive kicking (W. Gnatzy, personal communication). In some crickets these behavioural responses cannot be provoked at all; in others, any touch causes escape behaviour.

DISCUSSION

The function of the long tactile hairs

The long tactile hairs on the body of insects serve as little mechanical antennae similar to whiskers and to other protruding stiff hairs in mammals. They function as an early warning system in that they bend under external contact before the approaching object touches the smaller mechano- and chemosensitive hairs or even the cuticular surface of the animal.

In all cricket species, the long ventral sternite and leg hairs are seen in homologous positions. They monitor first contacts of the ventral parts of the body

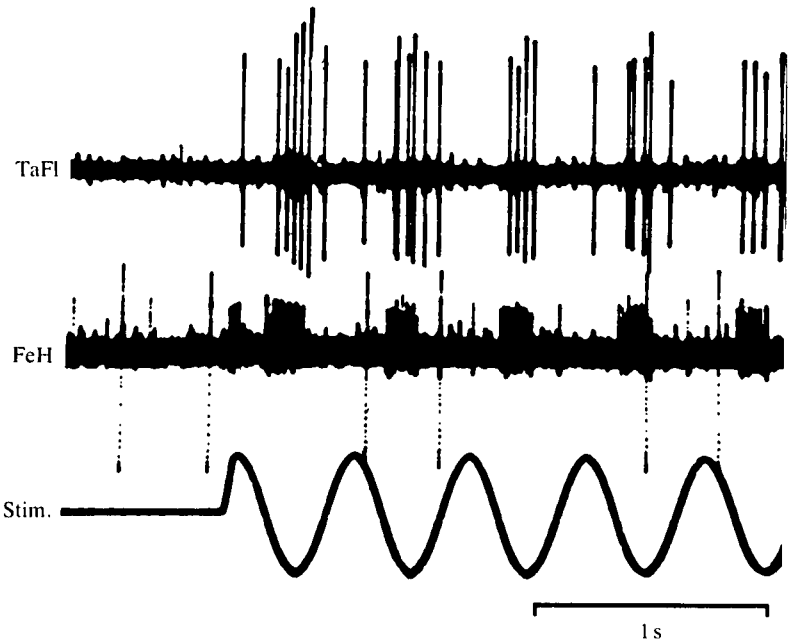

Fig. 9. Response of motoneurones to the tarsal flexor muscle (TaFl) upon stimulation (Stim.) of the long mesothoracic sternite hair (MesoFeH).

with the substrate or with protruding obstacles (Hustert, 1978, 1981; for cockroaches: Spencer, 1974). The lateral tibial hairs signal lateral contact (Schwabe, 1906; Pumphrey, 1940; Neumann, 1975) and the dorsal pronotal and the dorsal metafemoral hairs respond primarily to dorsal contact. The responses of a single long tactile hair alone must be able to drive postafferent neurones if their function is early warning of approaching contact. Conflicting information from other, unstimulated tactile mechanoreceptors is avoided because all tactile hairs respond phasically and without a tonic resting discharge in their afferent axons. Continuous discharge is only seen in axons from the abdominal long hairs when they are wet and lying flat on the sternite cuticle. The persistent discharge in this situation may provoke cleaning responses.

The function of the long tactile hairs should also be considered in context with the other tactile hairs and bristles of the body surface in crickets. Their arrangement in general could serve several tactile functions: (i) to increase the capability of perceiving contact in places of the body surface which are densely covered with hairs (object, social and predator contact); (ii) to give an exact topological representation of contact; (iii) to identify the approach of an object by the sequence of longer-to-shorter hair stimulation until finally contact with the cuticle can be recorded by vibration-or deformation-sensitive sensilla (campaniform sensilla, chordotonal organs); (iv) to monitor body-to-mouth orientation during grooming of the body (localization and regulation of the degree of contact)

and (v) to elict grooming when tonic discharge of hairs indicates constant deflection by obstacles or dirt.

The primary projections

The primary projections of most long tactile hairs of the thorax are restricted locally to their segmental ganglion, with the exception of the MetaStH_1 and the PronH which extend into an adjacent ganglion. All abdominal hair projections reach several ganglia in *Gryllus bimaculatus* as in *Acheta domesticus* (Hustert, 1978); by this arrangement many primary projections from different segments converge in the sensory neuropiles of the segmental ganglia. Therefore in the 3rd abdominal ganglion all abdominal long hair projections can terminate in the vicinity of dendrites belonging to the MHI4 (Fig. 8). Within the ganglionic neuropiles three major projection areas are seen: (i) the anterior part of the ventral asociation centre, which extends bilaterally across the midline of the ganglion; (ii) the posterior VAC which is divided into left and right hemiganglion regions by neuronal cell bodies in the ventral midline and (iii) the lateral branching domains in the latero-ventral neuropile areas. All these regions are also occupied by terminal branches from afferent axons of other tactile hairs and bristles (Fig. 2) and to some extent by collaterals of the MHI1–3 (Figs 4E, 6). The closer a tactile hair is situated to the midline of the cricket in the periphery, the more its primary afferent projections extend towards the middle and contralateral side in the anterior ventral VAC. A similar principle is apparent in the arrangement of some types of mechanoreceptor projection in the thoracic CNS of locusts (Hustert, Pflüger & Braünig, 1981). Some projections branch just in one of the three areas and others in all three. A better defined somatotopic principle of distribution such as that observed, for example, for the clavate hair projections into the cricket terminal ganglia and into the mesothoracic ganglion after transplantation of a cercus to the socket of a mesothoracic leg (Murphey, Bacon, Sakaguchi & Johnson, 1983), could not be found in the pattern of the primary afferents from the long tactile hairs and neighbouring bristles.

Interneurone responses to converging afferents

The large size of the receptive fields formed by the many tactile bristles and the information from long tactile hairs converging upon the thoracic and the abdominal MHIs indicates that these interneurones serve as general pathways for tactile afference and not to represent a detailed somatotopic map of the body surface in crickets. In their largely overlapping receptive fields, only the position of a sensillum as being situated on a sternite or ipsilateral leg is represented in the responses of the thoracic MHIs. A parameter still represented in the MHI is the non-adapting response to bending long tactile hairs in the 'core' of the receptive field which contrasts with the fast adapting responses to all bristle afferents and to those of 'peripheral' long hairs on the contralateral leg and on the distant segments. The persisting MHI responses to afferents of long tactile hairs may serve to recognize repetitive stimuli (from predators, searching antennae of other

crickets) and possibly also extreme deflection of the hairs, as occurs when the animal is crouching or when the hairs are wet and stick to the body surface.

In principle, every tactile hair or bristle of the whole receptive field of an MHI is able to elicit MHI spikes when stimulated singly. With continued stimulation, the interneurone responses to most mechanoreceptors (except the long hairs of the core) adapt rapidly and fall below spiking threshold. The adaptation must be a feature of the individual afferent-to-MHI pathway, since responses to other tactile hairs in the same interneurone remain unaffected. The non- or slightly-adapting responses from long hairs of the 'core' in the receptive field of the MHI1 could be based on monosynaptic connections, in view of the brief delays of 1·7–1·8 ms commonly observed between an afferent spike and the next EPSP in the interneurone (Fig. 4D).

The delays between spikes of the MHI1 and the MHI2 at the same site of a pro-mesothoracic connective indicate that at least one neurone must intervene in the pathway from the tactile hair afferent to the MHI2 (Fig. 7B,C).

None of the MHI were seen to receive afferent excitation other than from tactile hairs. Responses to wind as seen for prosternal hairs and the postafferent intersegmental neurone A4I1 on locusts (Pflüger & Tautz, 1982) were not found in thoracic or abdominal (non-cercal) hairs in crickets. This does not prove that other sensory modalities cannot excite the MHI in the intact and freely behaving animal. The responsiveness of the MHI is often affected by the variable state of excitation in the CNS of the preparation. Naturally, these changes are more pronounced in the spontaneously active MHI2 and MHI3. These latter neurones should be likely candidates for excitation by other, non-tactile, kinds of sensory input.

Divergence from single afferents

Afferent information from a single tactile hair can diverge to the different bilateral pairs of interneurones (type MHI1–3) with the centre of their receptive field in the thoracic segments and the ipsilateral leg, to interneurones with predominantly abdominal receptive fields (MHI4), and to various motoneurones in the abdomen and thorax (motoneurones of the tergo-sternal expiratory muscles, of the trochanteral levator muscles and of the tarsal flexor muscles). Apart from these known functional connections, many other units of the CNS may receive afferent information from a single hair. In locusts, stimulation of many bristle hairs on the hindleg excites local spiking interneurones directly (Siegler & Burrows, 1983, 1984; Burrows & Siegler, 1984), but direct connections to non-spiking local interneurones of the premotor type were not found. In addition the possibility of afferent-to-afferent connectivity of primary hair projections, as demonstrated for locust prosternal hair projections, cannot be excluded (Watson & Pflüger, 1984). Inhibition of a postsynaptic neurone by a tactile hair has been found only in the abdominal CNS (Hustert, 1980).

The excitatory pathways involving only specific, postsynaptic neurones must not be confused with the divergent activation of many motoneurones as seen in

general arousal such as during those struggling movements which occasionally are triggered by touch of a single hair.

At present no definite functional explanation can be given for the divergence of tactile afferent information to several different intersegmental interneurones: The information in the thoracic interneurones represents sternal and ipsilateral touch to legs, and that of the abdominal pair represents similar information about abdominal touch. Neither directly postsynaptic cells of the interneurones were found nor is there behaviour which is elicited specifically *via* the MHIs. Only the spikes of the MHI3 may reach the brain directly and initiate reactions controlled by the brain, such as caudally-directed probing movements of antennae (which are often seen in response to touch of single hairs).

The motoneurone reactions to tactile hair stimulation obviously have more local functions than the intersegmental interneurones. Sternal levator muscles, for example, stop the approach of the abdomen to the ground when the abdominal sternites of a cricket are lowered during expiration and the long tactile hairs touch the ground (Hustert, 1980). In locusts, responses to single tactile hairs of the tarsus can elicit activity in extensor tibiae muscles (Runion & Usherwood, 1968), tibial hair stimulation can evoke tarsal levator responses (Burrows & Siegler, 1982) or, in intact animals, tibial hairs can evoke even motor sequences such as lifting of the whole leg (Pflüger, 1979). In crickets, the response of the trochanteral levator muscles to stimulation of the MesoFeH (Fig. 9) could be interpreted as a localized avoidance reaction, lifting of the whole leg and the response of tarsal depressors may be part of a generalized withdrawal response in which the leg pressing against the ground contributes to raising the body over the substrate.

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