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Structure and Function of Acoustic Neurons in the Thoracic Ventral Nerve Cord of *Locusta migratoria* (Acrididae)*

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Summary. 1. Individual acoustic neurons were investigated by a combined recording and staining technique (CoS). Recordings were done with $CoCl_2$ filled glass-microelectrodes; structural identification of the fibres was achieved by precipitating the Co^{2+} with $(NH_4)_2S$.

2. The fibres of acoustic receptor neurons in the metathoracic ganglion have terminal branches only in the acoustic neuropiles. Fibres of high- and low frequency receptors were found electrophysiologically, which also differ in structure.

3. The thoracic low frequency neurons are interneurons of complex structure; they are limited to the thoracic ventral nerve cord.

4. The response patterns of acoustic neurons ascending to the supraoesophageal ganglion (B, K, C, I, and D neurons) are essentially generated in the frontal acoustic neuropiles of the metathoracic ganglion. Most of these neurons are connected with non-acoustic neuronal systems by their axon branches.

A. Introduction

A better understanding of neuronal processes is achieved if one can visualize the structure of those neurons from which electrophysiological recordings were made. Origin, course, and connections of nerve cells to certain neuronal centres can be ascertained by positively knowing the underlying structures. Also individual neurons can be identified with more certainty.

Physiological investigations of the afferent auditory pathway of tettigoniids and gryllids (Suga, 1963; Zhantiev, 1971; and Zhantiev and Chukanov, 1972) have shown that there are not only T-shaped neurons but also ascending and descending acoustic neurons in the ventral nerve cord. The first synaptic connection in the auditory pathway of both families occurs in the prothoracic ganglion (Rehbein, 1973).

Primary and secondary acoustic neurons are connected in this synaptic region. Most of the information processed in the first synaptic region is conducted not only to the supraoesophageal ganglion but also into certain centres of the caudal thoracic nerve cord (Rheinlaender and Kalmring, 1973).

In the acridids the tympanic organs are situated on the pleurits of the first abdominal segment whereas they lie on the tibiae of first legs in tettigoniids. Most of the synaptic transmission between primary and secondary acoustic neurons takes place in the metathoracic ganglion. Acoustic neurons which connect

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the receptor cells of the tympanic organ with higher centres of the supraoesophageal ganglion are ascending neurons in locusts (Popov, 1969; Kalmring, Rheinlaender and Rehbein, 1972; Rehbein, 1973). By physiological investigations alone it is hardly possible to determine whether these neurons in locusts also conduct their information to thoracic centres already at this neuronal stage.

A combined recording and staining technique enables us to record extracellularly from acoustic neurons, and to determine simultaneously the structure of these neurons. This method is a variation of the intracellular injection technique of Pitman, Tweedle and Cohen (1972). Thus we are able to test the presumptions made above and to clarify further structural details of acoustic neurons.

B. Material and Methods

150 adult *Locusta migratoria* of either sex were used at about 4 weeks after the last moult.

The combined recording and staining technique applied by us consists of an electrophysiological and an immediately succeeding histological part. The electrophysiological methods concerning preparation, apparatus, experimental procedure, and registrations are described in detail by Kalmring, Rheinlaender and Römer (1972). There is only one difference in the recording technique: the glass microelectrodes for the recordings were filled with 3 M $CoCl_2$ instead of 3 M KCl. The electrode resistance was normally 2–8 MΩ. Recordings were made from various regions of the thoracic ventral nerve cord.

In some cases the responses of neurons were registered on tape and conducted to a computer (PDP-12[1]) to show the time course of response patterns for a duration of 409.6 ms. This time was divided into 128 classes of 3.2 ms each. Every spike corresponds to a standard value, which was added one to another in each class during 28 response recordings. The sum of these standard values within each class was plotted as Peri-Stimulus-Time Histogram[2].

Succeeding the electrophysiological experiments the three thoracic ganglia were bathed in 1% $(NH_4)_2S$, then dehydrated in alcohol and cleared in styrol (vinyl benzene). Camera lucida drawings and photographs were made from the stained neurons in dorso-ventral and lateral projections.

The recording and staining technique introduced here differs from the intracellular $CoCl_2$-injection technique of Pitman, Tweedle and Cohen in the following points:

1) The recording electrode was not DC-coupled; the cobalt ions were not iontophoretically injected.

2) Recordings were made extracellularly with AC-coupled electrodes.

3) Staining of the nerve cell happened simultaneously during the AC-recordings.

The stained nerve cell is most likely identical with the one of which recordings were obtained because of the following reasons:

1) There is a consistent correspondence between the structure of the stained neurons and those neurons which show the same reaction types electrophysiologically.

2) If recordings were made from only one acoustic neuron then only one neuron is stained. Successive recordings from several neurons will stain a corresponding number of nerve cells. The simultaneous recording of e.g. two acoustic neurons results in the staining of two neurons.

3) Staining of one or several neurons takes place only under the following conditions: a) the recording electrode must be placed very close to the nerve cell (spike amplitude of several mV); b) the recording time must be several minutes.

An important advantage of the method described above is the possibility to analyse structure and function of neurons with relatively small axon diameters (1–5 μm ⌀).

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1 On loan from DFG to Prof. Schwartzkopff.

2 The computer program was kindly supplied by Dr. H. Leppelsack.

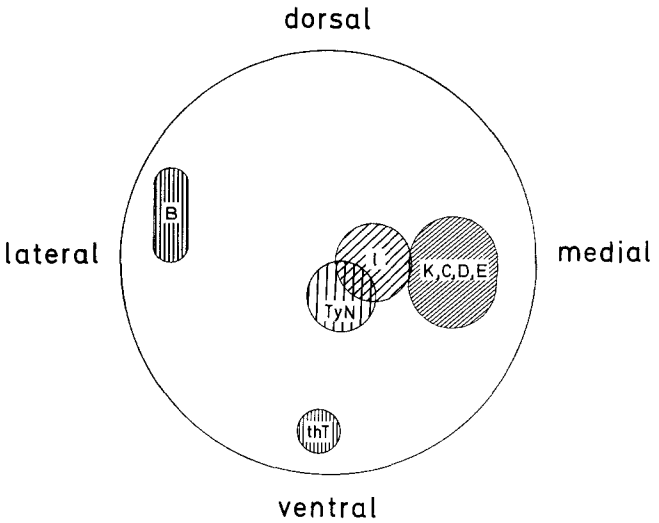

Fig. 1. Schematic presentation of some acoustic fibres in the cross section of a meso-metathoracic connective. *B*, *K*, *C*, *D*, *E*, and *I* higher order acoustic neurons ascending to the supraoesophageal ganglion; *thT* thoracic low frequency neuron; *TyN* tympanic nerve fibres

The mechanism of cobalt migration along the nerve cell is still unknown. Under good recording conditions staining can be traced over a distance of 6 mm.

In order to determine the course of the entire tympanic nerve within the thoracic ventral nerve cord the method of axonal Co^{2+} iontophoresis was additionally used. In this procedure the peripheral end of the tympanic nerve was put into a solution of 50 mM $CoCl_2$ and a DC-current of 1 μA was applied. The migrated cobalt ions were precipitated as CoS.

C. Results

The axons of the acoustic neurons of higher order leave the metathoracic ganglion in bundles. The connectives between the meta- and mesothoracic ganglia include 4 regions where the acoustic fibres run closely together: a medial, central, ventral, and lateral bundle. Their relative position to one another remains constant throughout the thoracic nerve cord (Fig. 1).

I. Acoustic Receptor Neurons

a) Course of Tympanic Nerve Fibres in the Ventral Nerve Cord

The acoustic receptor neurons (tympanic or primary acoustic neurons) enter the metathoracic ganglion dorso-laterally between the neuromers of the third thoracic and the first abdominal segments. They run ventro-medially until reaching a bundle of connective fibres at the ventral side of the ganglion. At this point a part of the primary neurons send collaterals into a "caudal acoustic neuropile" (Figs. 2, 3). All the tympanic nerve fibres branch extensively into a clearly separated "frontal acoustic neuropile" of the metathoracic ganglion. Because of its relatively large area it can be assumed that this neuropile is the

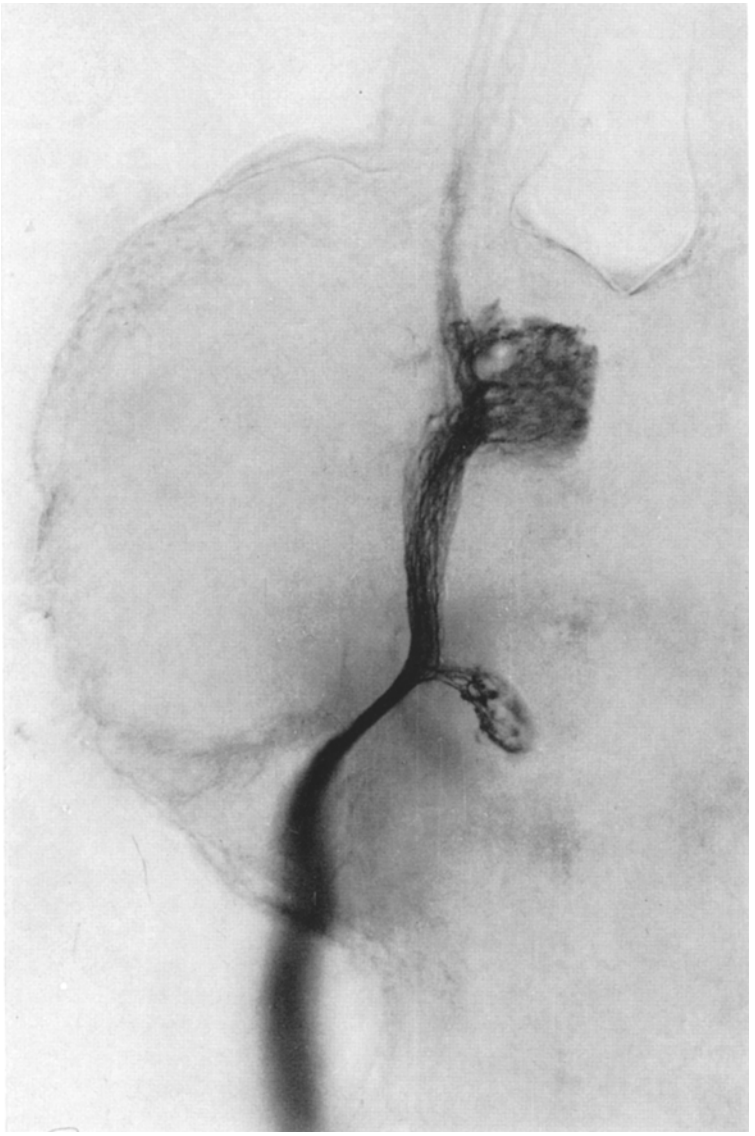

Fig. 2. Course and ramifications of the tympanic nerve fibres of one side in the metathoracic ganglion of *Locusta migratoria*. CoS-staining; whole mount preparation

most important region, where first and second order acoustic neurons are synaptically connected.

Collaterals of most of the receptor neurons reach the mesothoracic ganglion over the ipsilateral meso-metathoracic connective. There they form another neuropile, the "frontal acoustic neuropile" of the mesothoracic ganglion. A caudal acoustic neuropile does not exist in this ganglion, as suggested before (Rehbein, 1973).

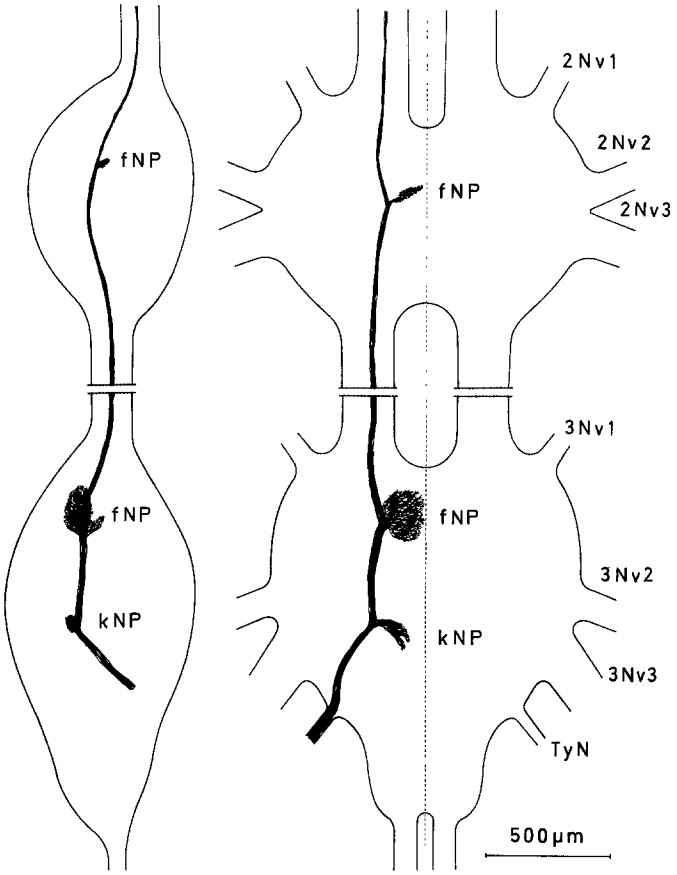

Fig. 3. Schematic presentation of the course of the tympanic nerve fibres in the meta- and mesothoracic ganglion. *fNP, kNP* frontal, caudal acoustic neuropile; *2Nv1, 2Nv2, 2Nv3* wing, muscle, leg nerve of the mesothoracic ganglion; *3Nv1, 3Nv2, 3Nv3* wing, muscle, leg nerve of the metathoracic ganglion; *TyN* tympanal nerve. These abbreviations are the same for all further figures. Left side lateral view, right side dorsal view

Part of the acoustic receptor neurons send collaterals further to the prothoracic ganglion (Fig. 3). All the tympanic nerve fibres run ipsilaterally, having no crossing branches.

b) Structure of Individual Receptor Neurons

The structure and function of single receptor neurons were investigated with the combined recording and staining technique only in the region of the metathoracic ganglion. Two different shapes (shape 1 and 2) were found (Fig. 4). Both branch extensively into the frontal acoustic neuropile of the metathoracic ganglion and send a collateral to the mesothoracic ganglion. Shape 1 has additional branches in the caudal acoustic neuropile.

Some stainings indicate other shapes (Fig. 4: 3, 4, and 5) but it is not clear if these are perhaps incomplete stainings of shapes 1 and 2.

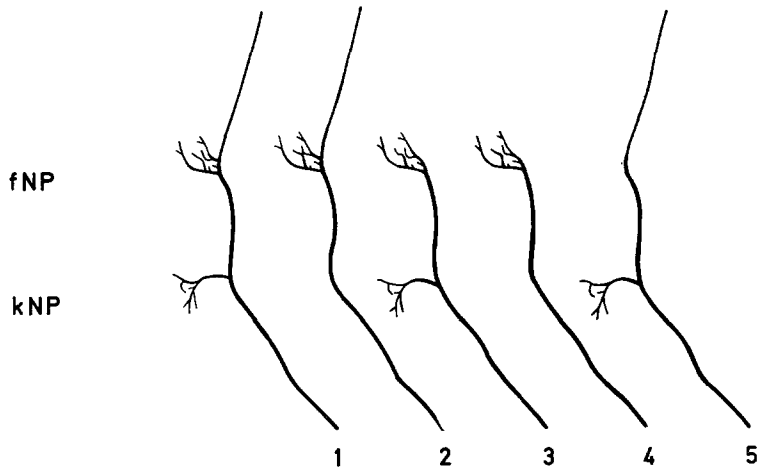

Fig. 4. Schematic presentation of single receptor neurons with their terminal branches in the metathoracic ganglion

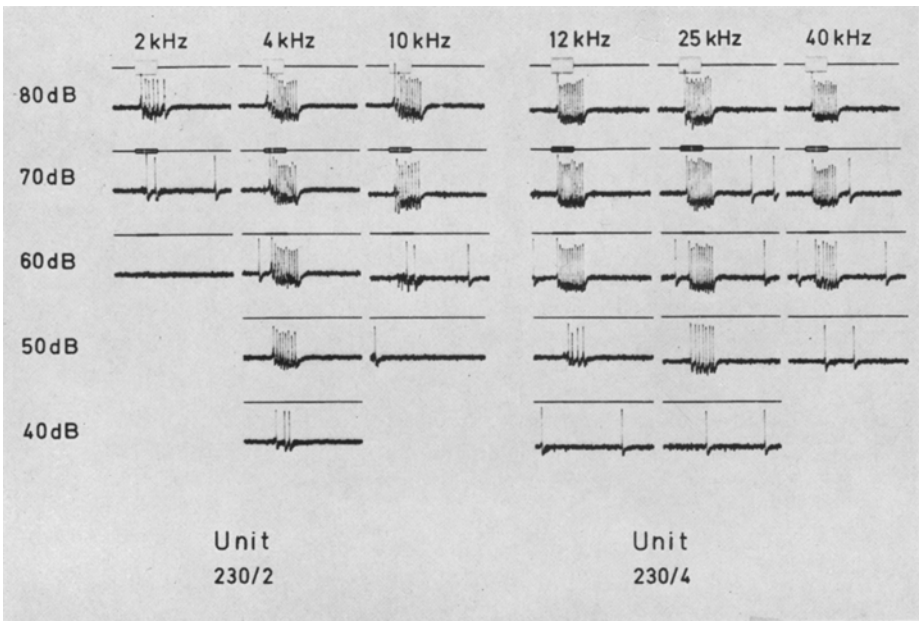

Fig. 5. Response patterns of two acoustic receptor neurons in the metathoracic ganglion of one experimental animal (ipsilateral recordings). Unit 230/2 shows maximal sensitivity to 4 kHz (kcps) stimulation; unit 230/4 to 25 kHz stimulation (low and high frequency neurons, respectively). Stimulations with different intensities (dB SPL); duration 20 ms; repetition rate 2 ps

A final classification of the various shapes into "morphological types" is only possible if further investigations also reveal the structure of the receptor neurons in the meso- and prothoracic ganglia.

Electrophysiological investigations show that shapes 1 and 2 correspond with two groups of neurons; each group consists of receptor neurons with similar reactions: shape 1 is represented by "low frequency neurons" (maximal sensitivity of the response patterns in the frequency range from 3–5 kHz); shape 2 is represented by "high frequency neurons" with maximal sensitivity in the frequency range from 12–25 kHz (Fig. 5).

The characterization into "low" and "high" frequency neurons was chosen with respect to the frequency range where acoustic communication of locustids takes place.

II. Acoustic Neurons of Higher Order

Most of the acoustic neurons of higher order studied here have already been described and classified into certain reaction types (Kalmring, 1971; Kalmring, Rheinlaender and Rehbein, 1972; Kalmring, Rheinlaender and Römer, 1972). In the electrophysiological experiments reported here, the neurons were identified in the same way. Additionally, their structure was revealed by CoS-staining. Comparison between structure and reaction of the acoustic neurons shows that normally each reaction type corresponds to only one morphological type. Only if neurons are comparable in structure, i.e. in (a) the course of their axons, (b) their branching patterns, and (c) in the position of their somata are they classified as a distinct morphological type.

If neurons differ from other ones in their response patterns (reaction type) as well as in their morphology (morphological type) we call them a neuronal type. These neuronal types are normally represented by only one neuron on each side of the nerve cord.

1. Thoracic Acoustic Neurons

There are acoustic interneurons which are limited to the thoracic nerve cord. They never have been found in the suboesophageal ganglion. Because of their physiological properties we call them "thoracic low frequency neurons". They have the following characteristics: their reaction range on frequency stimulation lies between 2 and 20 kHz with a maximal sensitivity from 3–5 kHz. The V-shaped threshold curve rises sharply below 4 kHz and more gradually from 4–20 kHz; the maximal difference in intensity is 20–30 dB. The neurons react with tonic response patterns and show an intensity discrimination only near the threshold. At higher intensities they measure the stimulus duration (Fig. 6). The response patterns of these neurons are essentially generated by influences of the ipsilateral tympanic organ. This was proved by destruction of the contralateral tympanic organ which had no effect on the response patterns.

Although the physiological findings suggest several similarly reacting thoracic low frequency neurons on each side of the nerve cord, this is not finally proved. The thoracic low frequency neurons connect several centres of the meta-, meso-, and prothoracic ganglia with each other. The structure of such a neuron has the

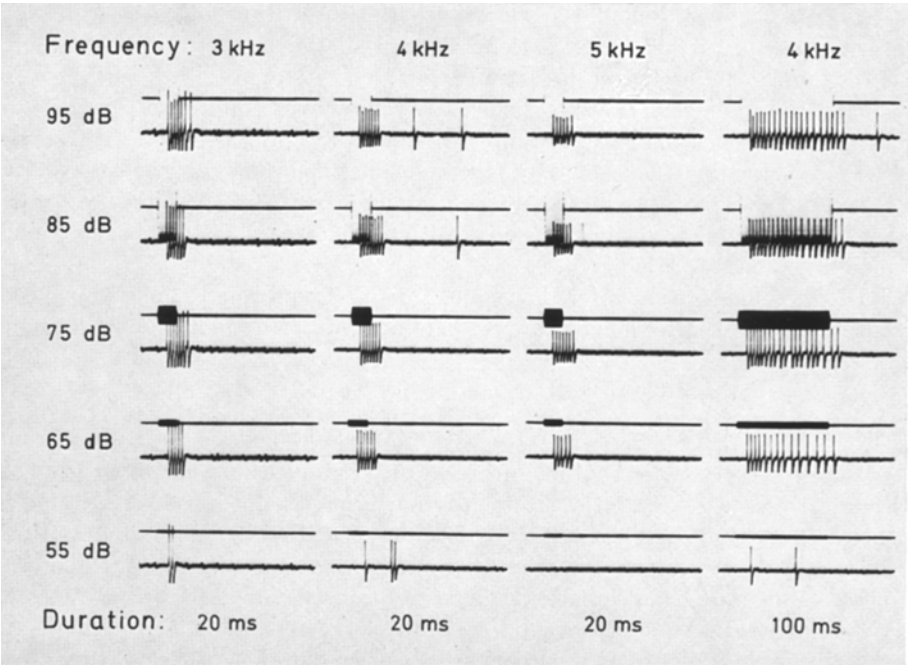

Fig. 6. Response patterns of a thoracic low frequency neuron of the metathoracic ganglion (ipsilateral recordings; intact auditory system). Repetition rate 2 ps

following characteristics: its soma is situated in the caudal region of the metathoracic ganglion near the entrance of the tympanic nerve (Fig. 7). The relatively thick axon runs parallel to the midline of the metathoracic ganglion and leaves it in the ventral bundle of the connective (Fig. 1). An exceptionally strong side branch of the axon (6–10 μm ⌀) runs fronto-ventrally in the region of the frontal acoustic neuropile to the opposite side (Figs. 7 and 8). From this collateral several branches go to the acoustic neuropiles of both sides. The contralateral neuropile usually receives a greater number of branches.

A small branch to the contralateral caudal neuropile starts at the place where the axon runs perpendicular dorsad in the direction of the soma (Fig. 7). At the same site root-like branches, which are not connected with the acoustic neuropiles, radiate laterally.

Within the mesothoracic ganglion the axon of the thoracic low frequency neuron runs also parallel to the midline of the ganglion. Besides a few smaller branches which end ipsilaterally near the midline, a stronger axon branch runs in the frontal ganglion region to the contralateral side. Only one of its branches ends in the region of the contralateral acoustic neuropile. The axon leads via the pro-mesothoracic connective to the prothoracic ganglion. The structure of the thoracic low frequency neurons in the prothoracic ganglion have not yet been investigated.

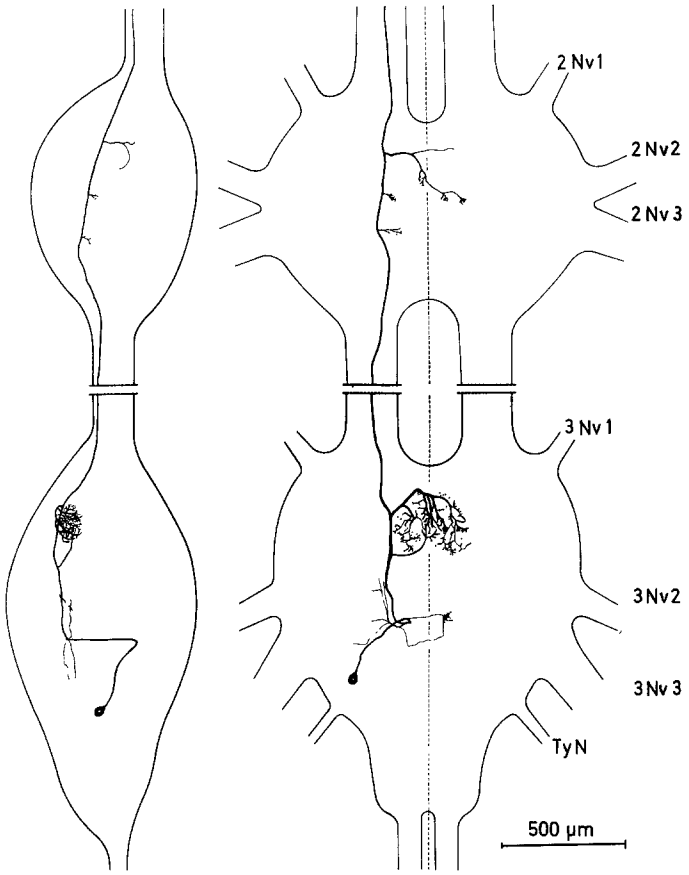

Fig. 7. Camera lucida drawing of the structure of a thoracic low frequency neuron in the region of meso- and metathoracic ganglia. Left side lateral view, right side dorsal view

After dissection of the meso-metathoracic connectives the characteristic response patterns of the thoracic low frequency neurons remain unchanged. This means that their response patterns are generated in the metathoracic ganglion. Therefore the axon branches in the mesothoracic ganglion do not receive any (or at least no pattern changing) tympanic acoustic information. Via these branches acoustic information could be delivered and/or received from other neuronal sensory systems.

The branches in the frontal and also in the caudal neuropiles of the contralateral side of the metathoracic ganglion are mainly delivering structures (presynaptic). This can be proved by electrophysiological means: the same characteristic response patterns of the neuron can be recorded from these contralateral branches. The thoracic low frequency neurons are synaptically connected to receptor neurons on the ipsilateral side. So far the available results do not indicate in which of the two ipsilateral neuropiles these connections are located.

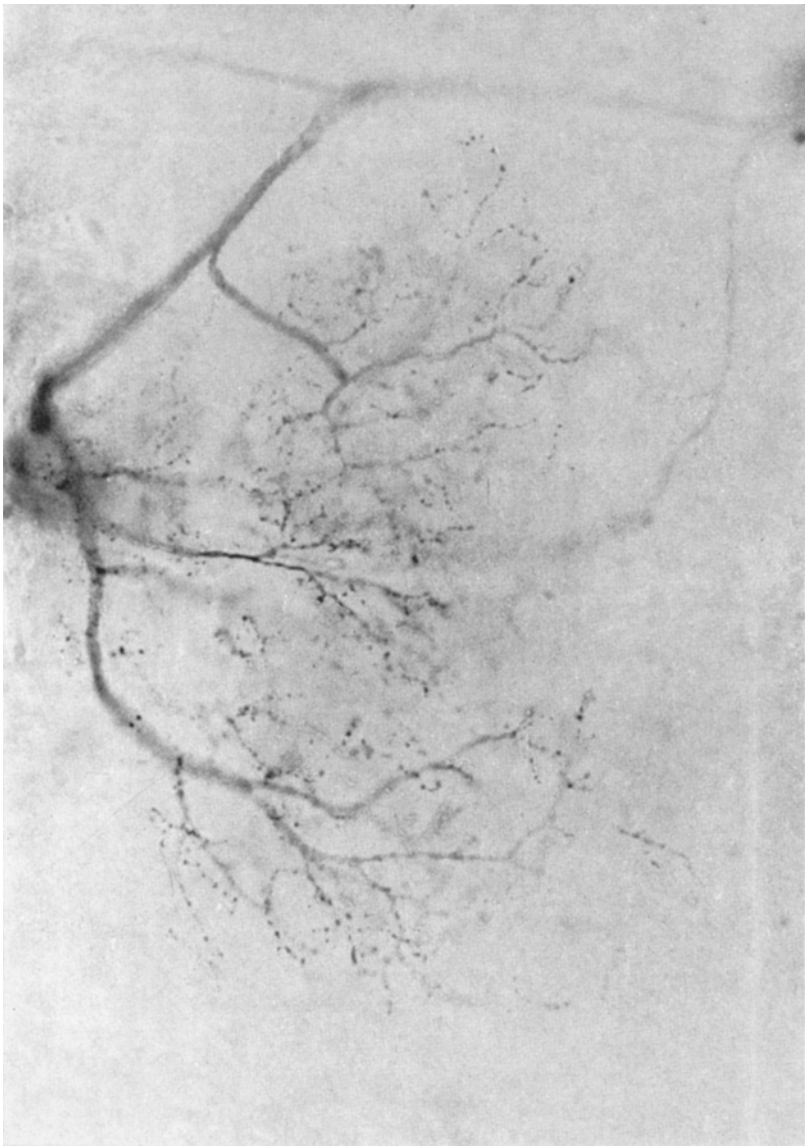

Fig. 8. Ramifications of a thoracic low frequency neuron in the region of the frontal acoustic neuropile of the metathoracic ganglion

2. Acoustic Neurons Ascending to the Supraoesophageal Ganglion

These neurons directly connect the acoustic centres of the ventral nerve cord with those of the supraoesophageal ganglion.

a) Neurons of Type B. The physiological properties of B-type neurons have already been described by Popov (1969), Kalmring (1971), Kalmring, Rhein-

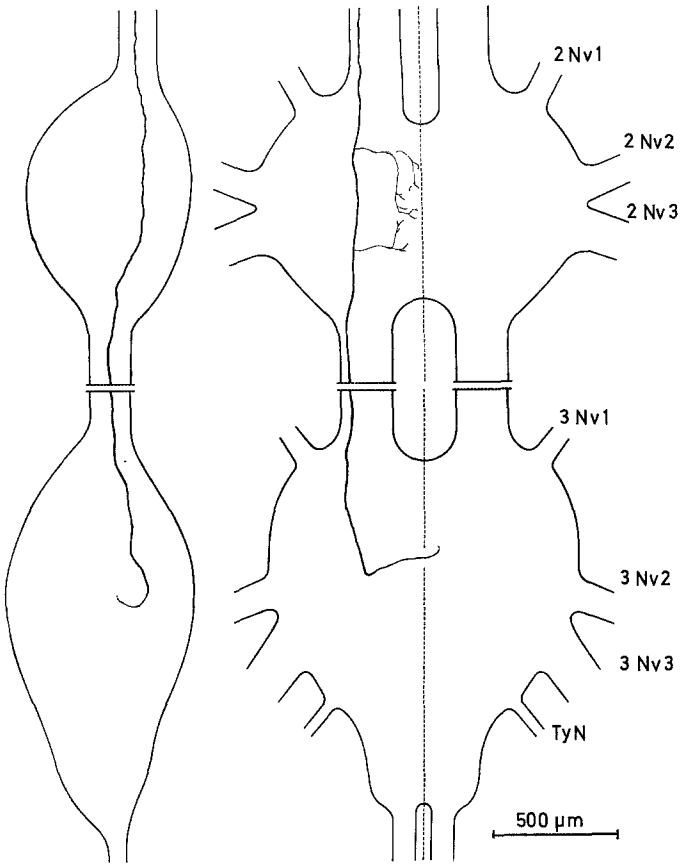

Fig. 9. Camera lucida drawing of the structure of a B-type neuron in the region of the meso- and metathoracic ganglia. Left side lateral view, right side dorsal view

laender and Römer (1972). The response patterns of the B-type neurons are characterized as follows: the intensity region close to the threshold is answered preferentially with tonic reactions. Higher intensities are answered with on-reactions or not at all. Destruction of one tympanic organ during the experiments prove that the response-pattern-generating influences come from the primary neurons of the ipsilateral side. The destructions also show inhibitory interactions from the respective contralateral side which enhances the contrasts of the direction response within the preferentially answered region. In contrast to most of the other higher order acoustic neurons the answers of the B-type neurons show certain variations within an experimental sequence when stimulated with the same sound parameters, though the characteristic response pattern remains unchanged. The physiological results suggest that there is only one B-type neuron on each side of the ventral nerve cord.

The morphological structure of the B-type neurons have been largely elucidated within the area of the meta- and mesothoracic ganglia. The axon of the B-type

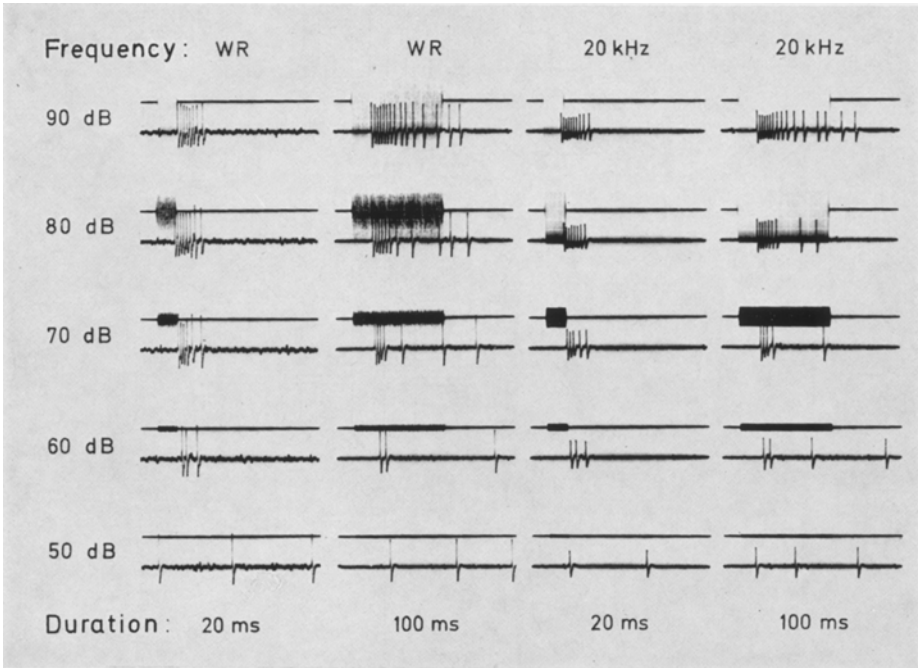

Fig. 10. Response patterns of a K-type neuron from the metathoracic ganglion (ipsilateral recordings; intact auditory system). Repetition rate 2 ps

neuron runs from the frontal region of the metathoracic ganglion to the supra-oesophageal ganglion without intercalated synapses. Its extreme dorso-lateral position within the connectives remains constant (lateral bundle, Fig. 1). In the metathoracic ganglion the axon of the B-type neuron crosses to the contralateral side (Fig. 9). Only on this side a connection to the frontal acoustic neuropile can be shown. In the mesothoracic ganglion axon branches have been found which are very thin in comparison to the large calibre of the axon. These branches run ventro-medially; their terminal branches have a beaded appearance and lie exclusively on the ipsilateral side.

The physiological results indicate that the response patterns of B-type neurons are generated in the metathoracic ganglion. These neurons only have connections to the contralateral frontal acoustic neuropile of the metathoracic ganglion, but their response patterns are generated by receptor neurons of the ipsilateral side. Therefore, the pattern—generating activity can only be conducted by crossing acoustic interneurons. This means that the B-type neuron is an acoustic neuron of third or higher order.

b) Neuron of Type K. The K-type neurons react tonically to stimuli of 20 ms duration. Their responses are characterized by the fact that the number of impulses per stimulus rises linearly when related to logarithm of the sound pressure (intensity measurement). In this respect they differ from the C-type neurons which also react tonically but measure intensities only in the region

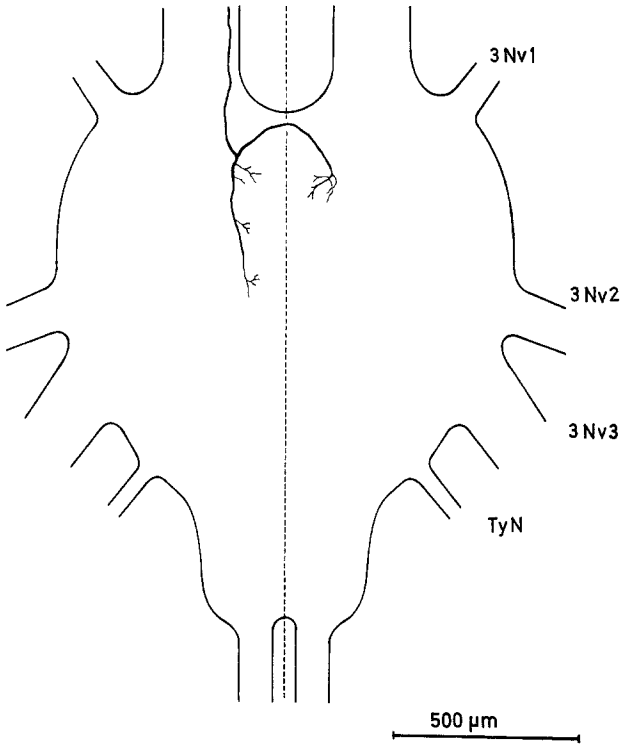

Fig. 11. Camera lucida drawing of the structure of a K-type neuron in the metathoracic ganglion (dorsal view)

close to the threshold—though very exactly (Kalmring, 1971). The K-type neurons usually answer to stimuli of 100 ms duration with on-bursts followed by some after-discharge. Only high intensity stimuli cause phasic-tonic reactions (Fig. 10). The structure of these neurons shows that they receive their pattern-generating influences in the metathoracic ganglion. The K-type neurons have terminal branches in the frontal acoustic neuropiles of both sides. The connection to the contralateral neuropile is a characteristically bow-shaped axon branch (Fig. 11). The axon of this type of neuron runs parallel to the midline of the ganglion and has some branches toward the midline. These neurons are connected to the supraoesophageal ganglion via the medial bundle (Fig. 1).

c) Neuron of Type I. The physiological porperties of the I-type neurons have also been described by Kalmring, Rheinlaender and Römer (1972). The maximal responses of these neurons to stimuli of 20 ms duration never show more than 2–4 spikes per stimulus. Their threshold lies between 50 and 70 dB SPL. The destruction of the contralateral tympanic organ during the experiments shows that the response patterns of these neurons are mainly generated by receptor neurons of the ipsilateral side.

The physiological as well as the morphological results indicate that there is only one I-type neuron on each side of the ventral nerve cord.

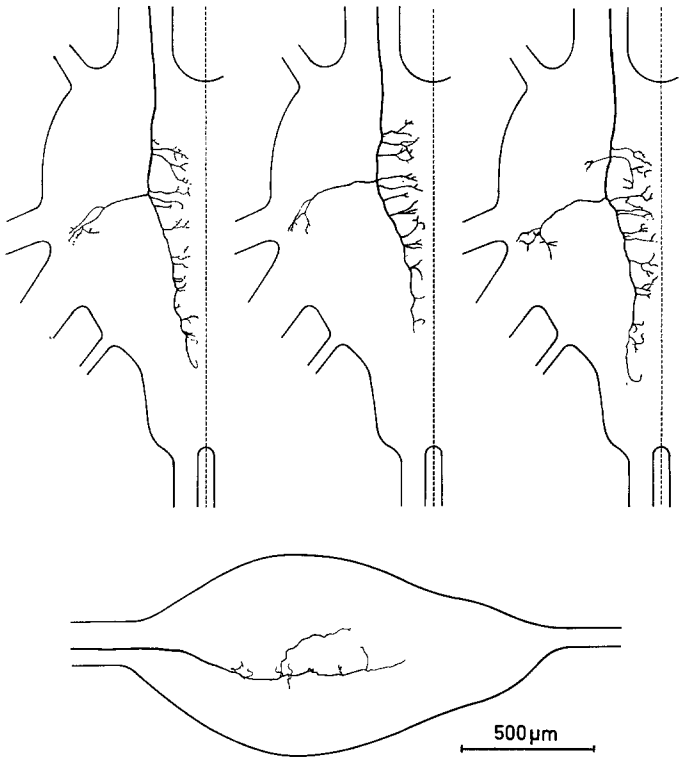

Fig. 12. Camera lucida drawing of the structure of I-type neurons in the metathoracic ganglia of 3 different animals. Above dorsal view, below lateral view

So far the morphological structures of the I-type neurons have been demonstrated only for the metathoracic ganglion. The nerve cell is easily identified by its characteristic ramifying pattern (Fig. 12). The axon runs through the ganglion, parallel to the midline and terminates near the caudal end of the ganglion, gradually becoming thinner. There are series of medial branches along the entire axon, their finest ramifications nearly reach the midline of the ganglion without ever crossing to the contralateral side. A strong axon branch bifurcates to the lateral periphery of the ganglion and branches near the entrance of the muscle and leg nerves (3Nv2 and 3Nv3). All the fine ramifications of the axon branches have a beaded appearance.

The axon of the I-type neuron ascends to the mesothoracic ganglion within the central bundle of the meso-metathoracic connectives (Fig. 1).

d) Neurons of Type C. The reactions of the C-type neurons have been extensively described earlier (Kalmring, 1971; Kalmring, Rheinlaender and Rehbein, 1972). Their answer to sound stimuli of various durations is a sustained discharge pattern. Recent investigations show that this type of reaction is represented by several individual neurons on each side of the ventral nerve cord.

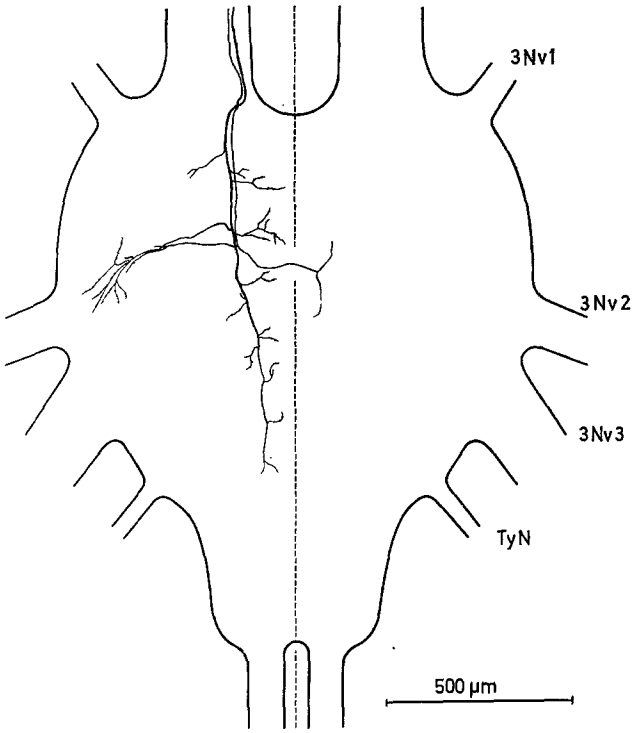

Fig. 13. Camera lucida drawing of the structures of a C-type and a D-type neuron (dorsal view)

The essential structure of one of these C-type neurons was established in the metathoracic ganglion. A neuron with a typical phasic response (D-type) was simultaneously recorded and stained together with this C-type neuron (Kalmring, Rheinlaender and Rehbein, 1972) (Fig. 13). Each of these two neurons sends one axon branch to the lateral periphery of the ganglion, near the entrance of the leg and muscle nerves. Acoustic information is probably also conducted via these axon branches to non-acoustic neuronal centres, as described above for the I-type neuron.

D. Discussion

The investigations of acoustic neurons in the ventral nerve cord of grasshoppers have so far been exclusively done electrophysiologically (Suga, 1963; Popov, 1967, 1969; Rowell and McKay, 1969; Kalmring, Rheinlaender and Römer, 1972). The direct comparison of the physiological and morphological data (received with help of the combined recording and staining technique) enables us to interpret the function of individual neurons in the acoustic system far better than previously. It is indeed possible to get results about the transport of information as well as about the principles of neuronal connections only analysing the electrophysiological results. But only with the help of the morphological correlate of

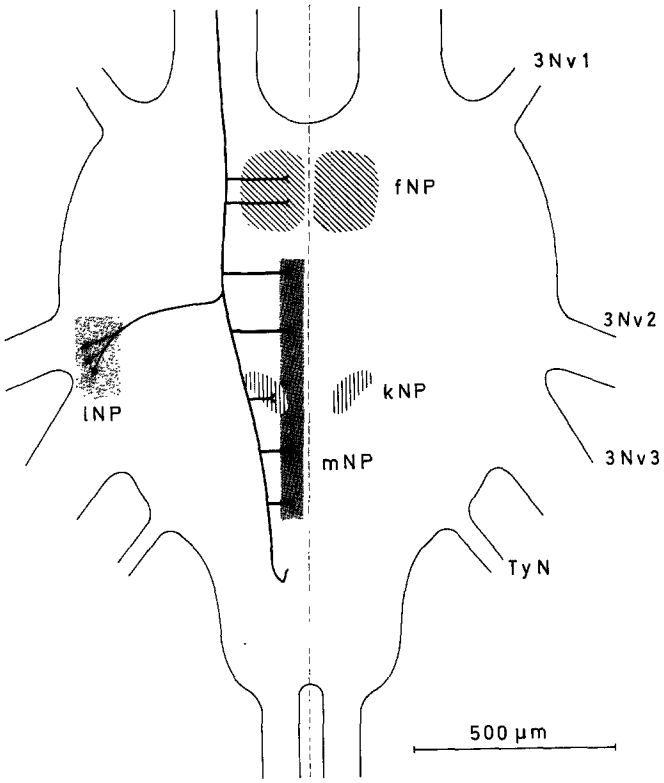

Fig. 14. Schematic presentation of a typical acoustic neuron (ascending to the supraoesophageal ganglion) with its ramifications in the metathoracic ganglion. *lNP* lateral neuropile; *mNP* medial neuropile

the nerve cell the mode and the site of synaptic transmission can be determined. The analysis of structure additionally reveals that in the acoustic neurons of higher order there are complex branches which do not only make connections with the acoustic synaptic regions.

So far neurons could only be separated and classified into certain reaction types by means of their physiological properties. But even with a large number of different combinations (up to 200) of stimulus parameters this does not lead in every case to a unequivocal identification. This identification is definite if morphological details of the neuron (of which recordings were made from) are available. It is often useful to determine additionally the pyhsiological range of variation with the help of statistical procedures such as PST-histograms, etc.

The terminal branches of the tympanic receptor neurons form the acoustic neuropiles of the thorax where they are synaptically connected with neurons of higher order. We cannot exclude that connections to non-acoustic neuronal centres are also established in these neuropiles. But findings in tettigoniids (Rehbein, 1973; Rheinlaender and Kalmring, 1973) favour another kind of neuronal

junctions: in the animals of this family all the axons of the acoustic primary neurons terminate in an acoustic neuropile of the prothoracic ganglion. Nearly the entire acoustic information, after being processed in this acoustic neuropile, is not only transmitted to the supraoesophageal ganglion, but also conducted to the caudal thoracic region. We therefore suggest a connection to non-acoustic centres in the meso- and metathoracic ganglia via acoustic neurons of the nerve cord.

Although the auditory pathways of tettigoniids and acridids differ in structure, the degree of processing in the first synapses is principally the same. Therefore it seems very probable that also in *Locusta migratoria* connections to non-acoustic systems (especially motor systems) are not established via acoustic primary neurons but via the acoustic nerve cord neurons of second or higher order. The following structural findings support this suggestion: acoustic neurons ascending to the supraoesophageal ganglion in the nerve cord of the migratory locust do not only make contact (via axon branches) with the acoustic neuropiles described above, but also with two further neuropile regions in the metathoracic ganglion (Fig. 14). One of these regions ("lateral neuropile") lies at the lateral periphery of the ganglion near the entrance of the leg and muscle nerves the other region ("medial neuropile") lies very near to the midline of the ganglion. A corresponding medial neuropile was also found in the mesothoracic ganglion. In the medial neuropile we found terminal branches of the I-, K-, and C-type neurons. A strong axon branch of the I-, C-, and D-type neurons bifurcates to the lateral side of the metathoracic ganglion. The terminal endings of these axon branches determine the extension of the lateral neuropile.

At the moment it cannot be decided, whether the terminal branches in these non-acoustic neuropiles are pre- or postsynaptic structures, or perhaps both. Since the lateral neuropile is situated in a part of the metathoracic ganglion which is occupied by the dendrites of motoneurons of leg and muscle nerves, it is more likely that the ramifications of the acoustic neurons are presynaptic endings which may be the site for transmission of acoustic information to motoneurons.

In the medial neuropile, however, connections to other sensory systems could be thought to exist. If this is the case pre- and postsynaptic structures of these acoustic neurons lie closely together in this neuropile.

The acoustic systems in the thoracic nerve cord of tettigoniids and acridids are remarkably similar in two respects: connections of acoustic neurons to non-acoustic systems exist; furthermore there are nerve cord neurons of principally similar structures, i.e., also in *Locusta migratoria* we find T-shaped neurons. For example the C-, and K-type neurons receive their acoustic (tympanic) information in the frontal neuropile of the metathoracic ganglion. Since the axons of these neurons run to the supraoesophageal ganglion as well as to the caudal and lateral region of the metathoracic ganglion, acoustic information is conducted simultaneously in frontal and caudal as well as in lateral directions.

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