Zoomorphologie 94, 133–149 (1980)

Zoomorphologie

Projections of Auditory Ventral-Cord Neurons in the Supraesophageal Ganglion of *Locusta migratoria**

Annette Eichendorf and Klaus Kalmring**

Fachbereich Biologie-Zoologie, Philipps-Universität, Lahnberge, D-3550 Marburg/Lahn, Federal Republic of Germany

Summary. The neuropile regions in the supraesophageal ganglion of *Locusta migratoria* were revealed by Bodian staining of frontal and parasagittal sections.

A combined recording and staining technique (CoS method, Rehbein et al., 1974) was used to identify physiologically five different types of auditory ventral cord neurons and mark the course of their axons and the positions of the terminal arborizations. The boundaries of the projection regions are described; they include the various multimodal neuropile regions in the ventrolateral protocerebrum.

Previously demonstrated instances of convergence with neurons of other sensory systems, and others likely to exist, are considered with respect to their possible significance in neuronal processing within the auditory system.

A. Introduction

As a rule, neurophysiological data obtained by single-cell recording does not in itself offer a useful basis for analysis of information processing within the central nervous system. This goal can be approached more closely by combining such recordings with staining of the penetrated cells (with Procion Yellow or cobalt sulfide; Iles and Mulloney, 1971; Pitman et al., 1972), so that the structure and function of single central neurons can be compared directly. During such experiments it is possible to interrupt certain receptor inputs or individual pathways; thus the function of particular parts of the neurons can often be determined. However, clarification of the way the incoming information is fur-

---

* Supported by the Deutsche Forschungsgemeinschaft, as part of the program Sonderforschungsbereich Bionach, Bochum. The investigations were done at Lehrstuhl für Allgemeine Zoologie, Ruhr-Universität, D-4630 Bochum

** Send reprint requests to K. Kalmring, Fachbereich Biologie – Zoologie der Philipps-Universität, Lahnberge, D-3550 Marburg, Federal Republic of Germany

0340-6725/80/0094/0133/$03.40

ther processed can be accomplished only if the structure and function of the projection regions of central neurons are known. In the case of the auditory elements in the orthopteran supraesophageal ganglion, little is known of either the courses of the fibers or their projection regions.

For tettigoniids no relevant morphological data and only a few physiological observations (Rheinlaender and Kalmring, 1973; Rheinlaender, 1975) are available. In the supraesophageal ganglion of the cricket *Gryllus bimaculatus*, Rheinlaender et al. (1976) demonstrated the course followed by a large-caliber, auditory ventral cord neuron down to its terminal arborizations, but did not describe the individual projection regions.

Data on the auditory pathway in the supraesophageal ganglion of the acridid *Locusta migratoria* (Linnaeus, 1758), again, are primarily physiological; Adam (1969) recorded the responses of auditory neurons in the lateral boundary region of the protocerebrum. The morphology of only one auditory neuron in this region has been described (Rehbein, 1976).

The present work was undertaken to fill this gap. The approach was twofold: (1) silver impregnation (e.g., modified Bodian staining) was used to map the most important neuropile regions in the supraesophageal ganglion of the migratory locust, and (2) the terminal arborizations of auditory ventral cord neurons were revealed by a combined recording and staining technique (the cobalt sulfide method of Rehbein et al., 1974) so that their projection regions could be demarcated. Finally, the structure and function of these projection regions are discussed, with reference to other sensory inputs (Boeckh et al., 1976; Ernst et al., 1977; O'Shea and Williams, 1974).

B. Materials and Methods

Male and female imagines of *Locusta migratoria*, three weeks following the final molt, were used in all experiments.

The following methods were used to mark the courses of auditory-neuron fibers in the supraesophageal ganglion, their terminal arborizations and their projection regions:

(a) the combined staining and recording technique (CoS method) of Rehbein et al. (1974); this procedure permits direct comparison of the morphology and function of single neurons.

b) axonal cobalt-iontophoreses of fiber bundles in split circumesophageal connectives; this technique provides supplementary information about fibers which, as often happens, are only partially stained by method (a).

(c) the silver intensification method of Tyrer and Bell (1974), which makes even a slight cobalt-sulfide precipitate visible.

(d) the silver intensification of whole preparations, by the method of Bacon and Altman (1977).

(e) Bodian staining as modified by Boeckh (1975), for detailed histological study of the neuropile regions in the supraesophageal ganglion. Sections stained by this method provided the basis for description of the auditory projection regions; the terminology of Strausfeld (1978) was adopted.

1. Electrophysiology

a) Preparation

Prior to experiments using the combined recording and staining technique the animals were anesthetized with CO_2 and, after removal of the legs and wings, glued to a metal holder, dorsal side down, with a wax-colophonium mixture (Kalmring, 1975). The supraesophageal ganglion was exposed by dissection from the ventral surface.

b) Recordings with microelectrodes

The activity of single nerve fibers at the point of entry of the circumesophageal connective into the tritocerebrum was recorded with glass microelectrodes. The method was that used by Pitman et al. (1972) for combined recording and staining, modified for extracellular recording by Rehbein et al. (1974). The apparatus and experimental procedure have been described by Kalmring (1975).

The glass microelectrodes were filled with $CoCl_2$ or $Co(NO_3)_2$ solutions. The concentrations of the electrolytes varied between 1 and 3 M; in some cases a 2:1 mixture of 3 M KCl and 3 M $CoCl_2$ was used. Electrodes filled with 3 M $CoCl_2$ allowed particularly good staining and were used when the morphology was of prime interest. The resistance of the microelectrodes was 5–15 MΩ. The reference electrode was a silver wire inserted into the abdomen.

Just prior to recording, the perineurium was removed at the recording site. As a rule, the recordings were extracellular. At the end of the recording session the ganglion was soaked in a 1% solution of $(NH_4)_2S$, until the CoS produced became apparent as a black precipitate. Then the tissue was prefixed in situ, dissected out, carefully cleaned, and fixed in alcoholic Bouin solution. The results of staining via the recording electrode were verified by comparison with those obtained by splitting the connective and subsequently filling small fiber bundles iontophoretically with $CoCl_2$.

This axonal iontophoresis was developed by Iles and Mulloney (1971) for the transport of Procion Yellow, and used by Tyrer and Altman (1973) for cobalt chloride. 8–12 h proved to be a favorable exposure time.

2. Histology

a) Preparation of Whole Mounts

After the tissue had been penetrated with Bouin solution it was dehydrated in an ascending series of alcohols and acetone and made transparent.

By this procedure one obtains a transparent ganglion within which can be seen a deep black neuron, often stained even in the finest branches. The preparations were mounted with Styrol in a hollowed-out microscope slide and viewed under a microscope equipped with a drawing attachment (Leitz Laborlux); drawings were made in anterior-posterior and lateral projection.

b) Silver Intensification

An advantage of the recording technique used is that CoS often appears even in the smaller branches of the neuron, and that fairly small neurons can be stained. But it frequently happens that the CoS precipitate is not detectable, because the concentrations of CoS are too low to be visible through the dense nervous tissue of the ganglion. The deposits can be so slight that it is impossible to see either the terminal structures – which often contain very little CoS because the fibers are so thin – or the somewhat larger branches. Two methods can be used to reveal such structures.

(1) Tyrer and Bell (1974) developed a method of staining serial sections in which silver deposits both intensify the CoS precipitate and bring out the background structures in the surrounding nervous tissue. The basis of this 'Timm's sulfide method' is the reduction of silver nitrate to elementary silver in anacid solution of gum arabic and hydroquinone as a developer. The reaction is catalyzed by heavy metals; in this case cobalt serves as the seed for silver deposition.

Frontal serial sections 10 or 20 µm thick were prepared. The silver-impregnation procedure used here differs from that of Tyrer and Bell in that our $AgNO_3$ concentration was less (0.5%) and the temperature lower. Under these conditions the staining process is prolonged and the time when the correct intensification is reached can be determined more accurately. The resulting sections show black neurons which contrast with a tobacco-brown background.

(2) A block intensification method was developed by Bacon and Altmann (1977). This is a modification of Timm's sulfide method for silver impregnation of whole preparations, in which the viscosity of the developer substance is reduced and the preparation is transferred to an incubation solution.

c) Bodian Staining

Where a number of different structures in the supraesophageal ganglion were of interest, a modification of Boeckh's (1975) Bodian method was used. The supraesophageal ganglion was fixed in hot saturated Bouin solution for 6–12 h, immediately after removal from the animal. After fixation it was washed in 70% alcohol to which a drop of a 0.1% ammonia solution had been added, to eliminate the yellow color left by the fixative mixture. Then the preparations were dehydrated in an ascending series of alcohols and transferred to paraplast via methylbenzoate or chloroform. When throroughly penetrated they were embedded in paraplast. Strips of 10 µm sections were cut with the serial-section microtome and impregnated.

This method of staining is superior to others because of the excellent definition of nuclei, fibers, and neuropile regions, especially in phase contrast micrographs. This method was preferred for description of the regions of neuropile in which the auditory neurons terminate because Timm's technique does not reveal the structures as distinctly.

C. Results

I. Structural Organization of the Supraesophageal Ganglion

As is usually the case among insects, the supraesophageal ganglion (SupEG) of *Locusta migratoria* is divided into proto-, deuto-, and tritocerebrum. The ganglion comprises a number of neuropile regions and fiber structures, as well as a cortical layer containing cell bodies.

The following important neuropile regions are found within the protocerebrum: mushroom bodies, central complex, a very large, multimodal (primarily visual) neuropile, and the optic ganglia. The mushroom bodies are regarded as the highest-level association centers for all sensory inputs. An uninterrupted, very dense mass of neuropile, the mushroom body with its characteristic subdivisions of stalk and calyx is readily distinguishable from the remainder of the protocerebrum. Its complicated structure, with intrinsic and extrinsic fibers, has been described in detail by Schürmann (1973a, b). The central complex comprises the central body, ellipsoid body, protocerebral bridge, ventral body, and antennoglomerular tract. This complex is thought to play an important role in organizing motor excitatory patterns.

The entire lateral protocerebrum is taken up by multimodal neuropile. This system consists of several sections, each surrounded in a characteristic way by large fiber tracts that link the different sections. This neuropile is the main projection region of the auditory ventral-cord neurons in the SupEG. In addition, visual neurons from the medulla externa and neurons from the antennal lobe project into this neuropile.

The deutocerebrum consists essentially of the antennal lobe and the antennomechanosensory region. The antennal lobe bulges out of the ganglion on the

Fig. 1. Frontal section through the supraesophageal ganglion (Bodian stain); the plane of section is indicated by a line in Figure 2. *MB*, mushroom body; *CB*, central body; *OF*, optic focus; *PL*, protocerebral lobe; *LH*, lateral horn; *AM*, antenno-mechanosensory region. These abbreviations are used in all other illustrations of this kind. For further description see text

frontal aspect of the deutocerebrum; it is the input station for receptor fibers of the antennal nerve (Gewecke, 1967; Ernst et al., 1977). The non-olfactory receptor fibers from the antenna are thought to terminate in the antenno-mechanosensory region, as also do a few side branches of auditory ventral-cord neurons.

The structure of the tritocerebrum resembles that of the ventral cord. The stomatogastric system arises here (Hanström, 1968).

Figure 1 shows a frontal section through the SupEG, in the plane in which the auditory fibers run (the plane of section is indicated in the lateral view in Fig. 2). In this region of the SupEG the following structures are clearly visible: 1, parts of the mushroom body (MB) with stalk and calyx; 2, the caudal part of the central body (CB); 3, the multimodal neuropile of the lateral protocerebrum, consisting of the optic focus (OF), protocerebral lobe (PL), and lateral horn (LH). In this plane the multimodal neuropile reaches its greatest extent; it is the main projection region of the auditory ventral-cord neurons in the SupEG.

Fig. 2. Parasagittal section through the left half of the SupEG, in the region of the mushroom body and the antennal lobe (*AL*); Bodian stain. *VB*, ventral body

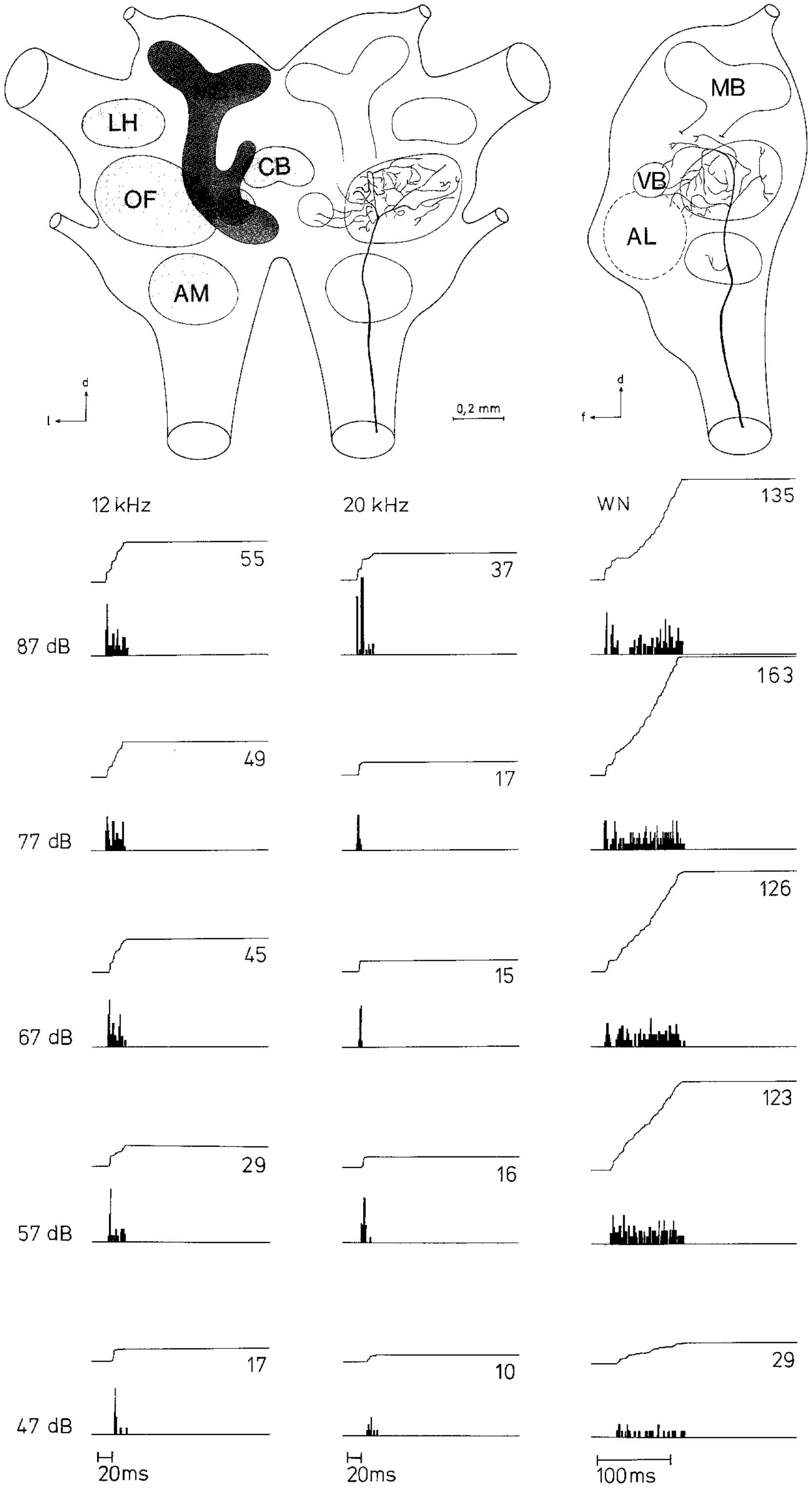
In the deutocerebrum the section passes through the boundary region between antennal lobe (AL) and antenno-mechanosensory region (AM).

Figure 2 shows the fronto-caudal extent of the same structures. This parasagittal section passes through the stalk of the mushroom body and through the antennal lobe and the antenno-mechanosensory region.

II. The Auditory Ventral-Cord Neurons in the Supraesophageal Ganglion

For five different types of auditory ventral-cord neurons, the courses of the fibers, including the terminal arborizations, could be followed and the projection regions demarcated.

Fig. 3. *Upper part:* course of the axon and projection of the terminal arborization of a G_1 neuron in the SupEG. *d*, dorsal; *f*, frontal; *l*, lateral (this notation applies to all other illustrations of this kind). *Lower part:* responses of a G_1 neuron to ipsilateral sound stimuli (12 kHz, 20 kHz, and white noise). Stimulus duration, 20 ms or 100 ms, repetition rate 2/s, intensity as indicated. Each graph represents the responses to 15 successive identical stimuli in the form of a post-stimulus-time histogram (*PST* histogram) generated by a computer (Didac 800, from the firm Intertechnique). Bin width 1 ms; response monitored for 240 ms (12 kHz and 20 kHz) or 280 ms *(WN)* following stimulus onset. Above each PST histogram is the associated curve of the cumulative frequency distribution; the numbers at the ends of the curves indicate the total number of impulses in the 15 responses


LH
MB
CB
OF
AM
d
l
0,2 mm
MB
VB
AL
d
f
12 kHz
20 kHz
WN
55
37
135
87 dB
163
49
17
77 dB
126
45
15
67 dB
123
29
16
57 dB
17
10
29
47 dB
20ms
20ms
100ms

The following are features common to all the neurons:

(i) One neuron of each type ascends in each half of the SupEG.

(ii) The axons of the auditory neurons pass through the posterior part of the ganglion.

(iii) The main branching region is the ventrolateral protocerebrum.

(iv) In no case could a direct connection to the superordinate centers mushroom body and/or central body be observed.

(v) The diameter of the axon can vary by a factor between two and three at different points along its length.

1. The G_1 Neurons

There are about 15 auditory neurons that ascend to the SupEG on each side of the ventral cord. The largest of these is the G_1 neuron. Its dendrites lie in the mesothoracic ganglion, where the axon divides into a descending branch, which runs to the metathoracic ganglion, and a branch ascending to the supraesophageal ganglion. The latter passes through the ventral cord together with the B neurons (Rehbein, 1976)

In the upper part of Figure 3 the position of a G_1 neuron and its branching in the SupEG is shown. The axon runs through the lateral third of the tritocerebrum and the caudal part of the deutocerebrum. In the deutocerebrum it sends a short collateral into the antenno-mechanosensory region (AM). On entry into the protocerebrum the axon divides into three branches. This pattern of branching is always present, although inter-individual variations are frequent. Figure 4 shows this first branching of the axon, in the neuropile of the optic focus (OF), for six different animals. The fibers of the G_1 neurons are of relatively large but highly variable caliber. Fibers 10 µm in diameter often expand – especially at branch points – to as much as 15 µm. At some constrictions the diameter can be as little as 6.5 µm.

The main projection region of the G_1 neuron is in the multimodal neuropile of the lateral protocerebrum (Fig. 3). The extensive terminal arborizations of the axons are limited almost entirely to the optic foci (OF). Only a few branches pass mediad behind the ventral body (VB), and two others run laterad next to the mushroom bodies (MB).

The responses of the G_1 neurons are distinguished by marked habituation when the stimulus is a series of sound signals. The responses of neurons in the habituated state to stimulation with various frequencies and with white noise are shown in the lower part of Figure 3. 12-kHz stimuli 20 ms in duration, repeated at 2/s, elicit only about two or three spikes, and the response to each such stimulus at a frequency of 20 kHz is a single spike. Only at high intensities (87 dB) does each 20-kHz stimulus elicit two spikes. White noise pulses 100 ms in duration produce weakly tonic responses, which at high intensities (87 dB) are often suppressed for 10–20 ms following the first one or two spikes in the response.

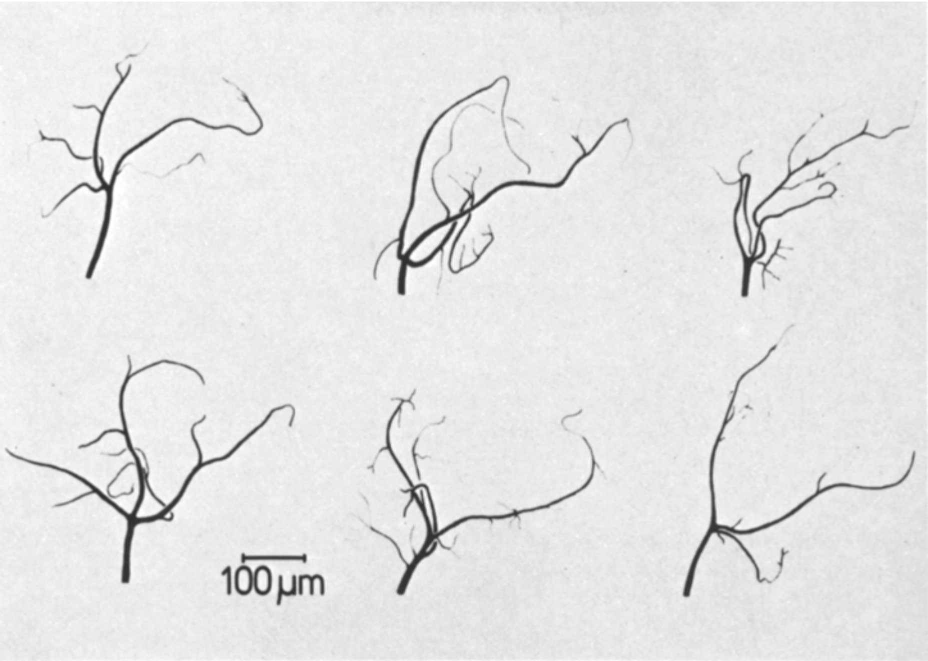


Fig. 4. Individual differences among the first large axonal arborizations of six different G_1 neurons in the protocerebrum

2. *The B_1 Neurons*

The B neurons are among the largest ascending auditory ventral cord neurons. Their axons are thick, with extensive terminal arborizations in the protocerebrum.

The dendrites of the B_1 neuron are in the metathoracic ganglion, on the side contralateral to the axon. The axon ascends to the SupEG together with that of the G_1 neuron, in the lateral part of the ventral cord (Rehbein, 1976).

The upper part of Figure 5 shows the course of the B_1 neuron in the SupEG. Entering the tritocerebrum from a lateral position, it moves to the caudal side and then shifts medially as it passes through trito- and deutocerebrum. At the medial edge of the antenno-mechanosensory region (AM) there is a small collateral. Up to this point the axon has remained in the caudal part of the ganglion. After entering the protocerebrum the axon bends laterally and sends out further collaterals as it passes through the dorsal region of the optic foci (OF) and into the lateral horn (LH), at the dorsolateral limit of which it terminates. Most of the terminal branches are in the lateral horn; they extend nearly to the bridge to the optic ganglia.

The responses of the B_1 neuron also show habituation. Stimuli 20 ms in

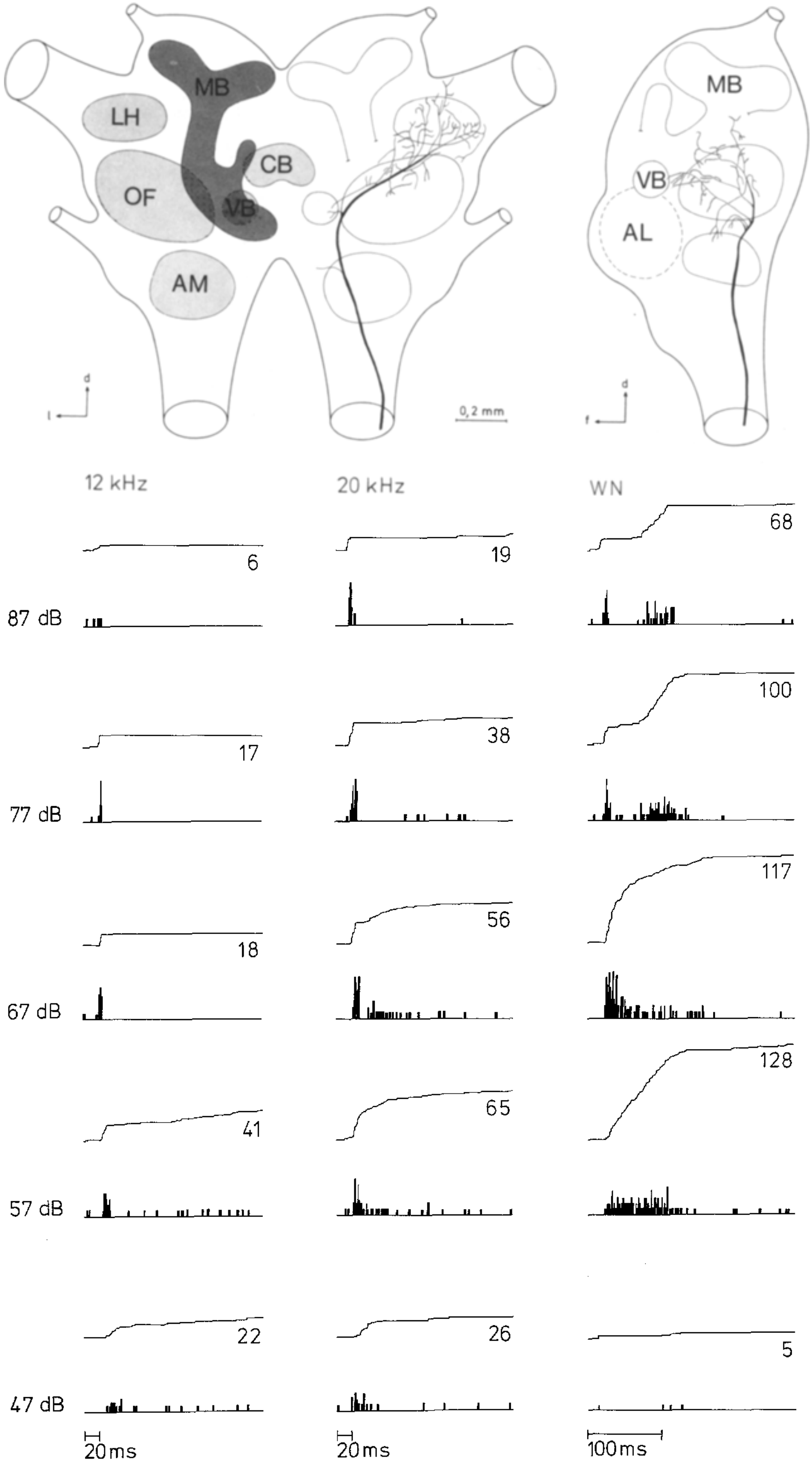


Fig. 5. *Upper part:* course of the axon of a B_1 neuron and projection of its terminal arborizations in the SupEG. *Lower part:* responses of a B_1 neuron to ipsilateral sound stimuli; parameters and manner of presentation as in Figure 3

duration at a repetition rate of 2/s, of various frequencies (12 kHz and 20 kHz), elicit on-responses at high and sometimes at intermediate intensities. In the near-threshold region the responses comprise several spikes per stimulus. The responses to white-noise pulses 100 ms in duration are like those of the G_1 neurons, particularly in the high-intensity range.

3. The C_1 Neurons

The C_1 neurons, like some of the other C neurons, have fibers about 5–6 μm in diameter. Thus their axons are thinner than those of the G_1 and B_1 neurons, but thicker than those of F and K neurons.

The axon enters the mediocaudal part of the tritocerebrum (Fig. 6, top), and keeps this position until it is in the protocerebrum. The first branches are sent out in the dorsal part of the antenno-mechanosensory region (Am). The main projection regions of these neurons, again, are the optic foci (OF) in the lateral protocerebrum.

The C neurons are characterized by tonic responses to sound stimuli varying in duration. These responses habituate slightly or not at all. The direct response to 12 kHz or 20 kHz stimuli 20 ms in duration, repeated at 2/s, is a series of impulses lasting as long as the stimulus or, in some cases, even longer. The same kind of response is elicited by white noise pulses 100 ms in duration (Fig. 6, lower part). The responses to sounds at the frequencies tested here are greatest at intermediate and moderately high intensities (67 and 77 dB). A distinguishing feature of the C neurons is their spontaneous discharge. Following the direct response to stimulation described above, the spontaneous discharge is suppressed for a period depending on the intensity and duration of the stimulus. With certain stimuli in the threshold region it may appear, as an afterdischarge, as early as 10 ms after the end of the response. At intermediate intensities, however, the spontaneous impulses are suppressed for up to 100 ms after the response has ended (cf. Fig. 6, 12 kHz and 20 kHz).

4. The F_2 Neurons

The F neurons are relatively small-caliber auditory ventral cord neurons. They run together with most of the C neurons, in a bundle in the middle of the ventral cord. The course of their axons through the trito- and deutocerebrum closely resembles that of the C_1 neuron (Fig. 7, top). The terminal arborizations of the F_2 neuron, apart from one branch, lie entirely in the neuropile of the optic focus (OF).

The responses of the F neurons are characterized by marked directionality and by the absence of both spontaneous activity and afterdischarge. As a rule the responses last considerably longer than the stimulus (Fig. 7, lower part). The responses to relatively high-intensity stimuli are marked by long latencies (cf. 20 kHz, 87 dB). The F_2 neurons respond only to frequencies above 10 kHz.

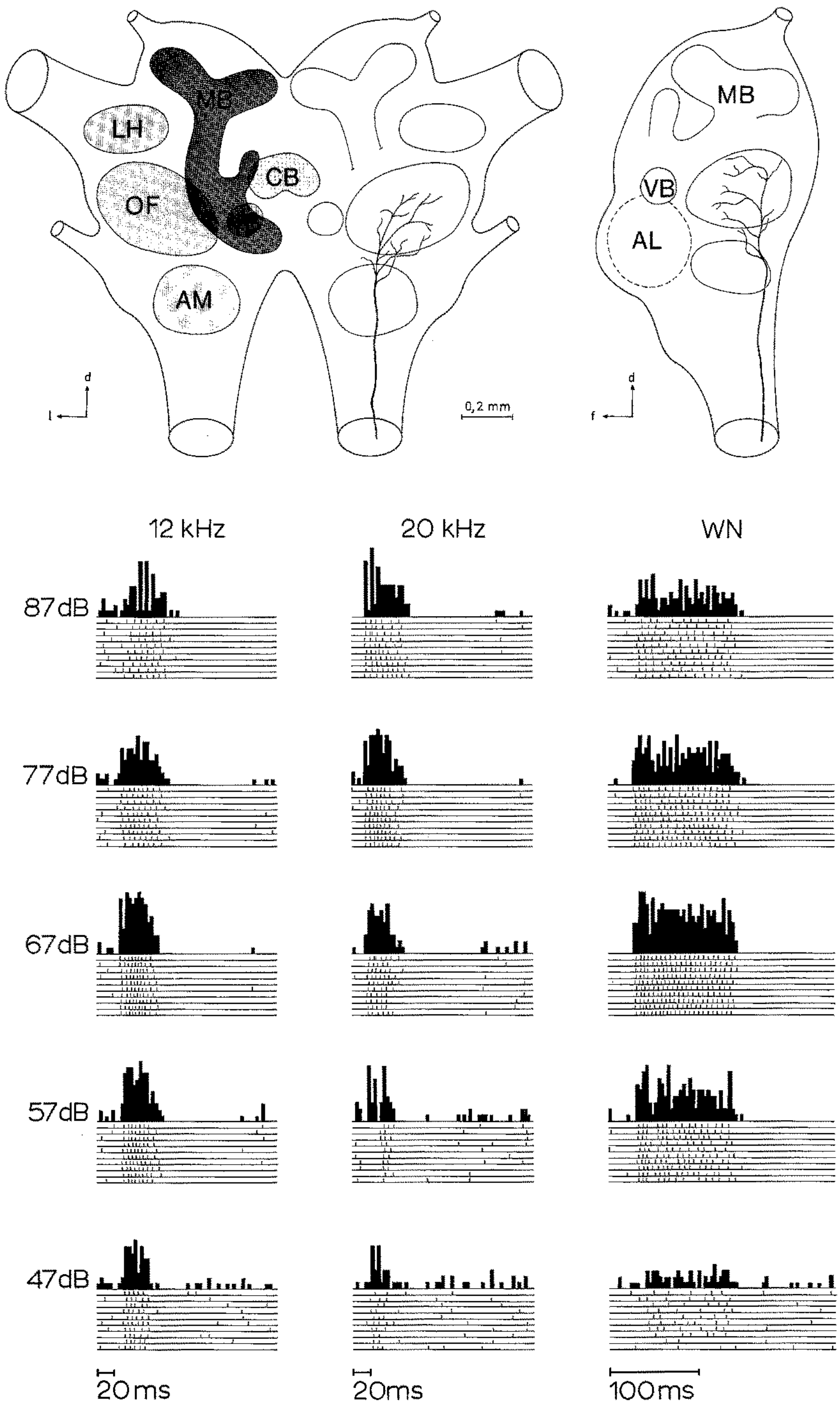


Fig. 6. *Upper part:* course of the axon of a C_1 neuron and projection of its terminal arborizations in the SupEG. *Lower part:* responses of a C_1 neuron to ipsilateral sound stimuli; parameters as in Figure 3. Each PST histogram represents ten successive responses, constructed with a PDP-12 computer. Bin width, 3.2 ms. Below the PST histograms are the ten individual responses, monitored for 200 ms (12 kHz and 20 kHz) or 240 ms *(WN)* following stimulus onset. Each impulse is represented by a vertical line

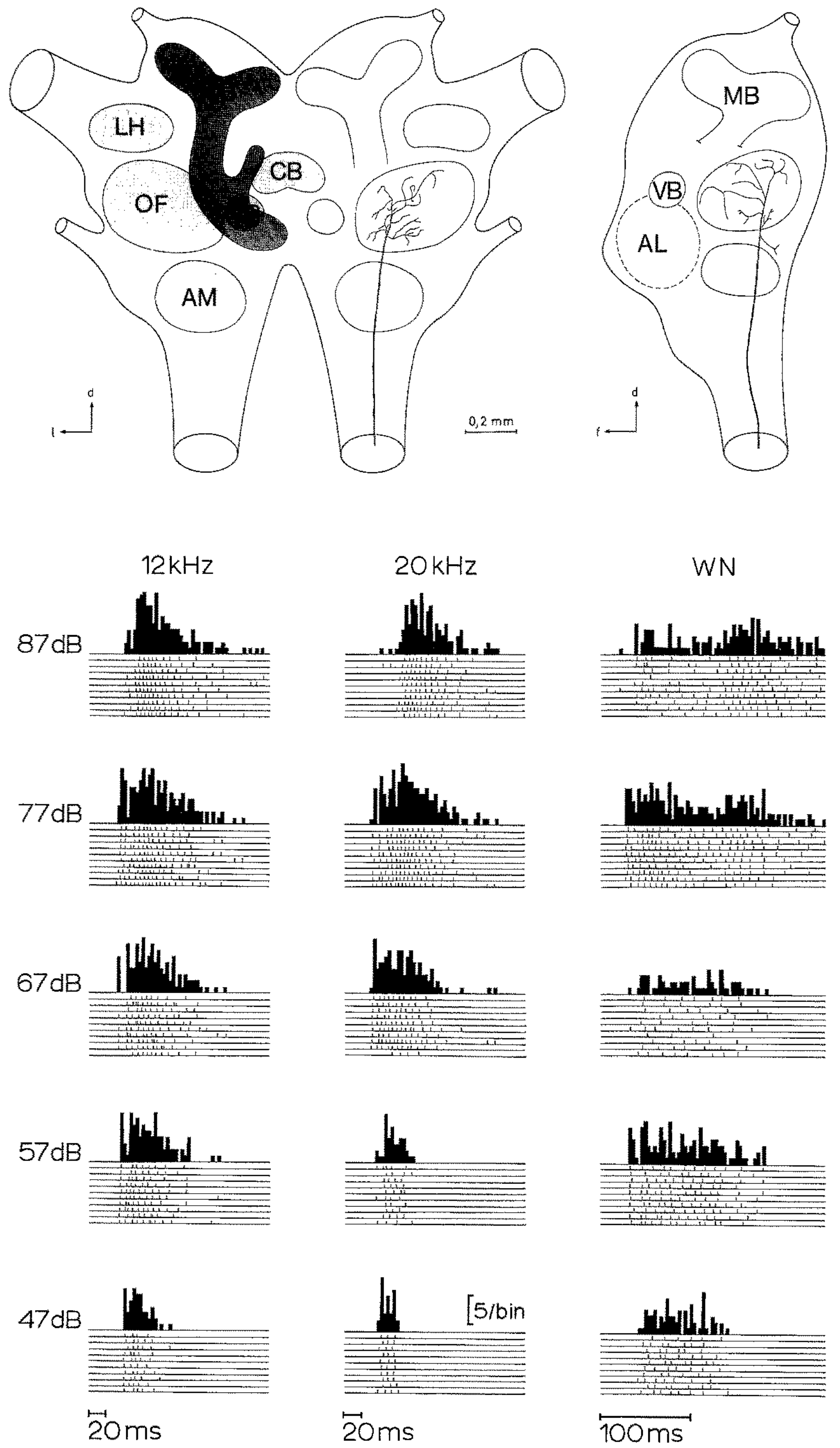


Fig. 7. *Upper part:* course of the axon of an F_2 neuron and projection of its terminal arborizations in the SupEG. *Lower part:* responses of an F_2 neuron to ipsilateral sound stimuli; parameters and manner of presentation as in Figure 6

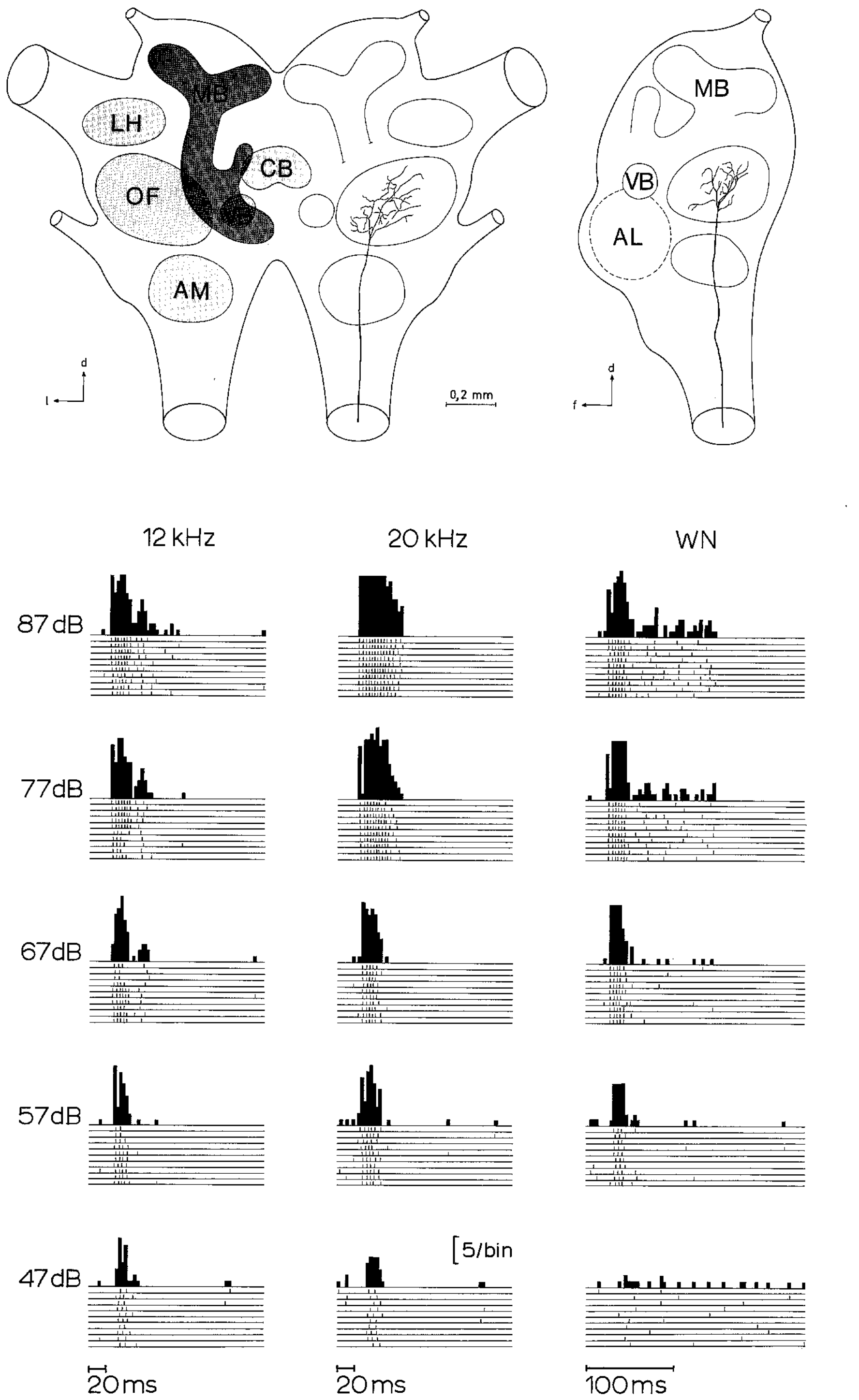


Fig. 8. *Upper part:* course of the axon of a K_2 neuron and projection of its terminal arborizations in the SupEG. *Lower part:* responses of a K_2 neuron to ipsilateral sound stimuli; parameters and manner of presentation as in Figure 6

5. *The K_2 Neurons*

These, like the F neurons, are of small caliber. The K_2 neurons enter the tritocerebrum in a bundle together with the F_2 and C_1 neurons, and pass to the protocerebrum without branching (Fig. 8, top). The terminal arborizations lie in the middle region of the optic foci (OF).

The K_2 neurons give tonic responses to stimuli lasting up to 15–20 ms. Longer stimuli elicit responses like those to 20-ms stimuli, except that at high intensities there may be a scattered afterdischarge (cf. white noise, 100-ms duration, 77 dB and 87 dB in the lower part of Fig. 8). These neurons have only slight spontaneous activity and exhibit little afterdischarge. Habituation is normally negligible or entirely absent.

D. Discussion

The main projection region of the five auditory ventral-cord neurons studied here is the large multimodal neuropile of the ventrolateral protocerebrum. The area of greatest overlap among the terminal arborizations of the different neurons is in the optic foci (OF); the K_2, F_2, and G_1 neurons terminate here, as do many of the branches of the C_1 neurons. By contrast, the B_1 neurons project predominantly to the lateral horn (LH) and to parts of the protocerebral lobe (PL) near the optic ganglia. Only the dorsal parts of the optic foci are reached by branches of the B_1 neurons. Small collaterals, ending chiefly in the antenno-mechanosensory region (AM) of the deutocerebrum, are sent out by the G_1 and B_1 neurons and to an even greater extent by the C_1 neurons.

The five auditory ventral cord neurons described here have different response characteristics. The G_1 and B_1 neurons are strongly habituating; they give phasic responses to brief repeated sound signals and respond to the syllables of the conspecific song with one or two spikes (syllable-counting function; Kalmring, 1975 II). The C_1 and F_2 neurons usually give tonic responses with little or no habituation, so that the duration of the response corresponds to that of the stimulus. The K_2 neurons respond similarly to stimuli no longer than 20–30 ms. A special feature of the F_2 neurons is the marked direction-dependent component in their responses. Taken together, the responses of the five neurons transmit the most important parameters of the locust song. The remaining auditory ventral-cord neurons, not investigated here, give responses that resemble in one respect or another those of the five cells described (Kalmring et al., 1978). Their axons enter the tritocerebrum together, in bundles. Thus one may infer that they follow similar courses through the supraesophageal ganglion and project to comparable regions.

All the ascending auditory ventral cord neurons studied so far are multimodal neurons (Čokl et al., 1977). That is, they transmit information not only from the tympanal organs, but also from other sense organs. The interactions demonstrated so far are effects of the vibration receptors in the subgenual organs and of the campaniform sensilla in all six legs upon the responses to sound stimuli.

The projection regions of these 'auditory-vibratory' neurons in the SupEG consist of multimodal neuropile into which both visual neurons from the third optic ganglion (O'Shea and Williams, 1974) and sensory neurons from the antennal lobe (AL) and the antenno-mechanosensory region (AM) (Ernst et al., 1977) project. It is of interest to consider how this situation may affect the further processing of auditory information. Is information about sound signals in the animals' environment processed in isolation or only in relation to signals from other sensory systems?

Evidence favoring the first alternative is provided by experiments on auditory behavior. Orthopterans display a clear ability to distinguish and localize sound signals, when these are the only stimuli presented (Huber, 1977; Popov and Shuvalov, 1977; Elsner and Popov, 1978).

Thus the auditory system does not require any additional information from other sensory systems to perform basic recognition processes. However, the information channels in this system are used by other systems at a fairly low level. The morphological results presented here – that the projection regions of the auditory-vibratory ventral-cord neurons are also the site of inter-neuronal transmission and processing of the information from visual and antennal neurons – suggest that processing in these regions is complex and normally multimodal. Horridge et al., as early as 1965, described neurons in the optic ganglia and the lateral protocerebrum with responses affected by both visual and auditory stimuli. Findings of O'Shea and Williams (1974) also support the second of the above alternatives; the visual movement-detector neurons they studied have auditory inputs.

As yet it has not been possible to demonstrate direct connections between the auditory-vibratory neurons and the mushroom bodies or other superordinate centers in the SupEG. However, antennal neurons from the deutocerebrum, some of which are multimodal, were shown by Ernst et al. (1977) to project into both the lateral protocerebrum and the calyx of the mushroom body.

Because both the ascending auditory-vibratory neurons and the descending visual-auditory cells (movement detectors) transmit information to various parts of the ventral cord by way of a variety of collaterals, it is to be expected that the sensory information is processed via spatial and temporal influences in several centers of the central nervous system. These centers are not restricted to the supraesophageal ganglion; they are probably linked by ascending and descending pathways (Kalmring et al., 1979, in press). But the ways in which these inferred processes operate remain unclear.

References

Adam, L.J.: Neurophysiologie des Hörens und Bioakustik einer Feldheuschrecke *(Locusta migratoria)*. Z. vergl. Physiol. **63**, 227–289 (1969)

Bacon, J., Altman, J.: A silver-intensification method for cobalt-filled neurons in wholemount preparations. Brain Res. **138**, 359–363 (1977)

Boeckh, J., Ernst, K.D., Sass, H., Waldow, W.: Zur nervösen Organisation antennaler Sinneseingänge bei Insekten unter besonderer Berücksichtigung der Riechbahn. Verh. Dtsch. Zool. Ges. pp. 123–139, Stuttgart: Fischer 1976

Cokl, A., Kalmring, K., Wittig, H.: The responses of auditory ventral cord neurons of *Locusta migratoria* to vibration stimuli. J. Comp. Physiol. **120**, 161–172 (1977)

Elsner, N., Popov, A.V.: Neuroethology of acoustic communication. Adv. Insect Physiol. **13**, 229–355 (1978)

Ernst, K.D., Boeckh, J., Boeckh, V.: A neuroanatomical study on the organisation of the central antennal pathways in insects. Cell Tis. Res. **176**, 285–308 (1977)

Gewecke, M.: Der Bewegungsapparat der Antennen von *Calliphora erythrocephala*. Z. Morph. Ökol. Tiere **59**, 95–133 (1967)

Hanström, B.: Vergleichende Anatomie des Nervensystems der wirbellosen Tiere. Berlin: Springer 1928 (Nachdruck 1968)

Horridge, G., Scholes, J., Shaw, S., Tunstall, J.: Extracellular recordings from single neurones in the optic lobe and brain of the Locust. In: The physiology of the insect central nervous system (Treherne, J., Beament, J., eds.), pp. 165–202. London 1965

Huber, F.: Lautäußerungen und Lauterkennen bei Insekten (Grillen). Abh. Rhein.-Westf. Akad. Wiss. N **265**, 1–66 (1977)

Iles, J.F., Mulloney, B.: Procion yellow staining of cockroach motor neurones without the use of microelektrodes. Brain Res. **30**, 397–400 (1971)

Kalmring, K.: The afferent auditory pathway in the ventral cord of *Locusta migratoria* (Acrididae). I. Synaptic connectivity and information processing among the auditory neurons of the ventral cord. J. Comp. Physiol. **104**, 103–141 (1975)

Kalmring, K.: The afferent auditory pathway in the ventral cord of *Locusta migratoria* (Acrididae). II. Responses of the auditory ventral cord neurons to natural sounds. J. Comp. Physiol. **104**, 143–159 (1975)

Kalmring, K., Kühne, R., Moysich, F.: The coding of sound signals in the ventral cord auditory system of the migratory locust, *Locusta migratoria*. J. Comp. Physiol. **128**, 213–226 (1978)

Kalmring, K., Rehbein, H.G., Kühne, R.: An auditory giant neuron in the ventral cord of *Decticus verruciovorus* (Tettigoniidae). J. Comp. Physiol. (1979) in press

O'Shea, M., Williams, J.L.D.: The anatomy and output connection of a locust visual interneurone: the Lobular Giant Movement Detector (LGMD) neurone. J. Comp. Physiol. **91**, 257–266 (1974)

Pittman, R.M., Tweedle, C.D., Cohen, M.J.: Branching of central neurons: Intracellular cobalt injection for light and electron microscopy. Science **176**, 412–414 (1972)

Popov, A.V., Shuvalov, V.F.: Phonotactic behavior of crickets. J. Comp. Physiol. **119**, 111–126 (1977)

Rehbein, H.G.: Auditory neurons in the ventral cord of the locust: Morphological and functional properties. J. Comp. Physiol. **110**, 233–250 (1976)

Rehbein, H.G., Kalmring, K., Römer, H.: Structure and function of acoustic neurons in the thoracic ventral nerve cord of *Locusta migratoria* (Acrididae). J. Comp. Physiol. **95**, 263–280 (1974)

Rheinlaender, J.: Transmission of acustic information at three neuronal levels in the auditory system of *Deticus verrucivorus* (Tettigoniidae, Orthoptera). J. Comp. Physiol. **97**, 1–53 (1975)

Rheinlaender, J., Kalmring, K.: Die afferente Hörbahn im Bereich des Zentralnervensystems von *Decticus verrucivorus* (Tettigonoiidae). J. Comp. Physiol. **85**, 361–410 (1973)

Rheinlaender, J., Kalmring, K., Popov, A.V., Rehbein, H.G.: Brain projections and information processing of biologically significant sounds by two large ventral-cord neurons of *Gryllus bimaculatus* De Geer (Orthoptera, Gryllidae). J. Comp. Physiol. **110**, 251–269 (1976)

Schürmann, F.W.: Über die Struktur der Pilzkörper des Insektengehirns. III. Die Anatomie der Nervenfasern in den corpara pedunculata bei *Acheta domesticus* L. (Orthoptera): Eine Golgi-Studie. Z. Zellforschung. **145**, 247–285 (1973)

Schürmann, F.W.: Bemerkungen zur Funktion der Corpara pedunculata im Gehirn der Insekten aus morphologischer Sicht. Exp. Brain Res. **19**, 406–432 (1974)

Strausfeld, N.J.: Atlas of an insect brain. Berlin – Heidelberg – New York: Springer 1976

Tyrer, N.M., Altman, J.S.: Motor and sensory flight neurons in a locust demonstrated using cobalt chloride. J. Comp. Neurol. **157**, 117–138 (1974)

Tyrer, N.M., Bell, E.M.: The intensification of cobalt-filled neuron profiles using a modification of Timm's sulphide silver method. Brain Res. **73**, 151–155 (1974)

Received April 25, 1979