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Intracellular Studies on Auditory Processing in the Metathoracic Ganglion of the Locust

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Summary. 1. Postsynaptic potentials of various auditory interneurons were recorded intracellularly in the metathoracic ganglion of the locust. Although the sound stimulus consisted of bursts of pure tones (20 or 100 ms duration), only a minority of intracellular responses (8 out of 43) exhibited simply configurated depolarizing potentials (Fig. 2a, b). Most responses were composed of excitatory and inhibitory postsynaptic potentials (Fig. 2c–e) with different temporal interactions between EPSP and IPSP. Thus the multifold spike patterns, known in principle from previous extracellular recordings, can be explained.

2. In the neuron of Fig. 3a the threshold curves of EPSP and IPSP differ significantly in the frequency-intensity field. Based on a comparison with previous findings on receptors and one thoracic interneuron (Rehbein et al. 1974), a model for synaptic connectivity is proposed, although detailed morphological data are not available.

3. The degree of EPSP- and IPSP-interaction depends strongly on sound direction. The ipsilaterally generated excitation can be totally eliminated when the contralateral ear is more strongly stimulated (Figs. 4, 5). Two different modes of temporal interaction between EPSP and IPSP can be detected: on the one hand – if both potentials appear – the inhibition follows the excitation. Thus the resulting spiking activity is modified without changing the latency of the corresponding response (Figs. 4, 6). On the other hand the inhibition precedes excitation (Fig. 5), which in addition influences the initial phase (latency) of the response. These data indicate the existence of an underlying synaptic mechanism for previous extracellular findings (see Mörchen 1980).

Abbreviations: *EPSP* excitatory postsynaptic potential; *IPSP* inhibitory postsynaptic potential

Introduction

In the insects' auditory pathways most of the interneurons, though stimulated with pure sound pulses, exhibit rather complex response patterns compared with those of receptors (for review see Elsner and Popov 1978). This phenomenon can be explained by the assumption that these units must be activated by manifold presynaptic inputs originating from different receptors within the tympanic organ. Furthermore, many interneurons receive additional input from the opposite organ and thus are favored candidates for binaural processing.

In the locust, the frontal acoustic neuropile in the metathoracic ganglion represents the first center for synaptic transmission in the auditory pathway (Rehbein 1973). On the one hand, the axon collaterals of tympanic receptor fibres each terminate here on the ipsilateral side. On the other hand, we know from morphologically identified interneurons that they branch into both the right and the left neuropile (Rehbein et al. 1974). This bilateral organization of such central units implies the existence of crossing segments which are assumed to be enlarged in diameter as compared with the other dendritic structures in the ventral nerve cord (Rehbein 1976; Pearson and Goodman 1979; Pearson et al. 1980). Thus this locus is well suited for intracellular recordings.

In this study we present intracellular responses concerning complex auditory processing in the metathoracic ganglion of the locust which so far have been restricted to crickets and cicadas (Wiese 1978; Wohlers and Huber 1978; Huber et al. 1980; Boyan 1980). By the application of the intracellular technique we are thus able to describe some synaptic mechanisms underlying the generation of auditory responses important for pattern recognition and directional coding.

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Materials and Methods

Thirty-six adult male and female locusts (*Locusta migratoria* L.) were used 4 weeks after the last moult. After removing the wings and legs the animal under investigation was waxed ventral side down on a small, thin metal sheet. The study focussed on auditory processing in the metathoracic ganglion. Therefore this ganglion was exposed and the ganglion sheath was carefully dissected from a small area above the acoustic neuropile for further penetration of the microelectrode. To prevent muscular movement of the preparation all but the tympanic nerves were severed.

In the frontal region of the metathoracic ganglion a paired acoustic neuropile can be found (Rehbein 1973) in each part of which the axonal collaterals of auditory receptor fibres terminate each on the ipsilateral side. Information about the detailed synaptic connectivity between those receptor fibres and subsequent auditory interneurons is limited. Extracellular cobalt stainings (Rehbein et al. 1974) revealed that several interneurons exist with bilaterally organized dendritic structures thus connecting both halves of the auditory pathway in the metathoracic ganglion of the locust. So far it is unknown whether both dendritic structures are postsynaptic or whether these interneurons transfer auditory information from one side to the other as is suggested for the omega-cell in crickets (Huber and Wohlers, pers. communication). Certainly the midline crossing segments of such interneurons seem to be enlarged in diameter thus facilitating intracellular penetration. Therefore in our study the micropipette was preferentially inserted along the midline of the metathoracic ganglion where stable intracellular recordings could be achieved for periods varying from 5 min up to about one hour.

All experiments were performed in a custom-made anechoic chamber with the speaker (Audax TW 8 spc.) at a distance of 50 cm rotating horizontally around the animal in 30° steps. Sound stimuli were produced by an amplitude modulated generator (Akustischer Stimulator II, Burchard) and thus pure sound pulses of variable flat-top duration (20 and 100 ms) and rise and fall times of 1 ms could be generated. Stimulus frequency was varied between 3–40 kHz, sound intensity attenuated in 10 or 1 dB steps. The sound pressure level at the preparation was measured by a Brüel and Kjaer $^1/_2''$ condensor microphone and is expressed in dB re 2×10^{-5} N/m^2 (for further acoustic configurations of the recording chamber see Rheinlaender and Römer 1980). Ambient temperature inside the chamber was 20 ± 2 °C.

Glass micropipettes filled with 3 M potassium-chloride or potassium-acetate (30–60 MOhm resistance) were used as different electrodes and connected to a 10× gain DC amplifier (LM 1, List electronics) which permitted the passing of current through the electrode and the measurement of electrode resistance via a bridge circuit. Potentials were monitored on an oscilloscope (502, Tektronix) and stored on a DC-tape recorder (Racal store 4D). For further analysis playbacks of the recordings were photographed from the oscilloscope display by a camera (Recordine, Tönnies).

The micropipettes were aligned at a right angle to the ganglion surface under optical control and then advanced in steps of one or a few µm into the tissue. Three criteria were used to determine whether a recording was intracellular:

1. Membrane potential had to be between 40–70 mV. Usually the potential drop was measured at the end of the experiment when the electrode was being withdrawn from the cell.

2. Spontaneous activity, monitored extracellularly before penetration, should not change significantly or in the case of an increase, had to return to the normal level within 30 s after penetration.

3. Either spontaneous activity or amplitudes of excitatory or inhibitory postsynaptic potentials should change significantly when a small current (ca. 1–2 nA) was passed through the electrode. In the example of Fig. 1 the neuron generates a depolarizing potential when the sound pulse is given at resting potential (0 nA, no current injection, Fig. 1, middle traces). When simultaneous to sound presentation the membrane is additionally depolarized by the injection of current of +2 nA lasting for 1 s (Fig. 1, upper traces), the same sound stimulus configuration then elicits a synaptic potential of smaller amplitude and spontaneous activity is increased. In contrast, the depolarizing potential is increased by an injection of current of −2 nA and spontaneous activity is nearly eliminated (Fig. 1, lower traces).

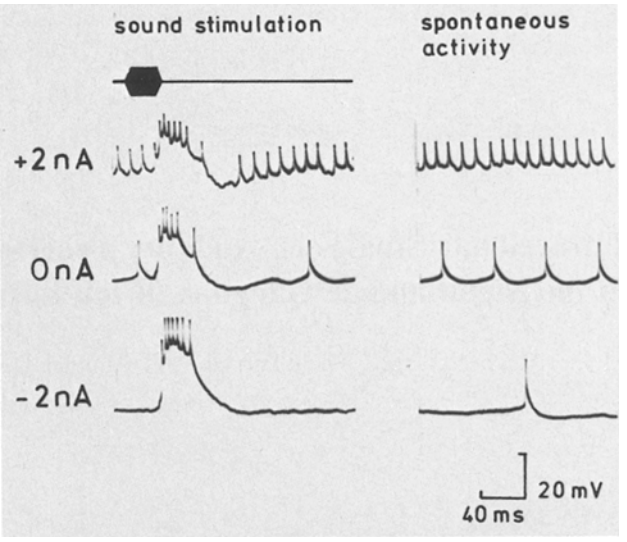

Fig. 1. Modulation of EPSP-amplitude and spontaneous activity by current injection (+2 nA depolarizing; −2 nA hyperpolarizing current; 0 nA: without current injection) and additional sound stimulation. Stimulus frequency 8 kHz, duration 20 ms; rise and fall time 1 ms; repetition rate 1/s

As stated above, the microelectrode was generally placed along the midline of the ganglion to provide stable intracellular recordings. This complicates the definition of an ipsilateral stimulus situation with reference to the speaker location and the geometrical configurations of the recorded unit. As we did not use any intracellular staining techniques, the morphological features of the units studied remained unknown and we therefore defined ipsilateral stimulation simply according to that speaker position on the right or left side of the preparation where the threshold for excitatory responses was lowest. From previous physiologically and morphologically identified auditory interneurons in the locust we know that this definition coincides with the course of the ascending axon from the metathoracic ganglion through one of the two connectives up to the brain (Rehbein et al. 1974; Rehbein 1976).

Results

In the following section we present some exemplary intracellular recordings in order to reveal the complex mechanisms of auditory processing in the metathoracic ganglion of the locust. Though morphological evidence as the result of stainings is lacking, we are confident that each documented response pattern is characteristic for a specific type of neuron. First of all, they differ significantly concerning the interaction of excitation and inhibition. Furthermore each pattern described below was recorded at least 3 to 5 times in different specimens, often two of them regis-

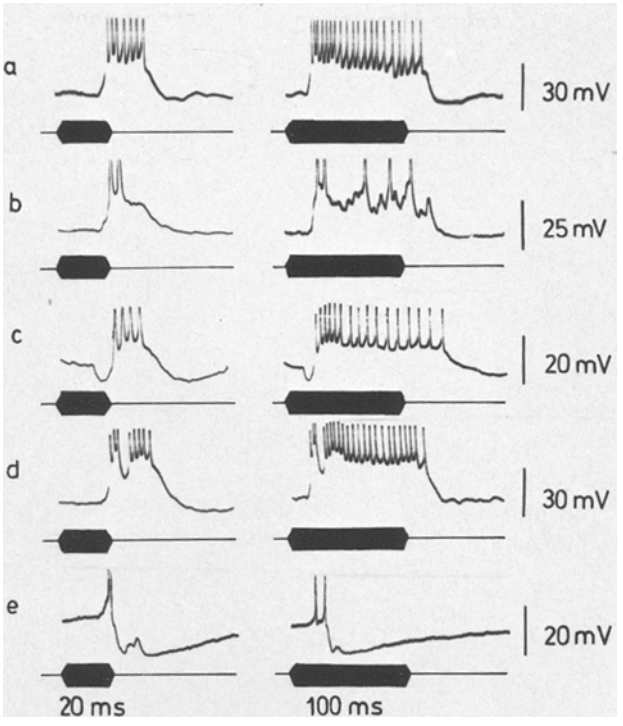

Fig. 2. Intracellular responses of 5 different interneurons (**a**–**e**) recorded in the metathoracic ganglion of the locust, stimulated with sound pulses of 20 and 100 ms duration, rise and fall time 1 ms; repetition rate 1/s. Stimulus frequency in **a**: 25 kHz, in **b**, **c**, **d**: 12 kHz, in **e**: 5 kHz (representing the best frequency of each neuron). Sound intensity: 20 dB above threshold, respectively. In most displays of this and the following figures spikes are truncated. Note in **c**–**e** that inhibition occurs at different instants relative to excitation

tered successively within one preparation. In order to facilitate the comparison between the responses of different units we will demonstrate only those recordings generated at the cell's best frequency and stimulated 20 dB above threshold (for one exceptional case see Fig. 3a).

It should be noted that in all units the intracellular electrode recorded both subthreshold synaptic activity and superimposed spikes.

1. Description of Different Response Patterns

Though all auditory receptor fibres exhibit tonic response patterns (Michelsen 1971; Römer 1976; Mörchen et al. 1978), we recorded only relatively few auditory interneurons reflecting this simple kind of neuronal discharge pattern (Fig. 2a and b). The unit in Fig. 2a copies the duration of the sound pulse with regard to the excitatory postsynaptic potential (EPSP) and spiking activity very precisely. With regard to the postsynaptic potential this is also true for the unit in Fig. 2b. However, the spiking pattern represents the tonic postsynaptic input rather imprecisely. This is also true for higher sound intensities tested (not shown here), and so far we do not know to which specific membrane properties this neuronal behavior must be ascribed.

In contrast to these findings most of the units show response patterns which are composed of excitatory and inhibitory postsynaptic potentials. In the following three examples (Fig. 2c–e) we demonstrate that in particular the temporal relationship between EPSP and IPSP activity results in very different spiking activities of the corresponding cells. In Fig. 2c, for example, the inhibitory response precedes the excitatory one. Thus the latency of the first spike within the response is sharply 'controlled' by this initial inhibitory potential, lasting for approximately 5–10 ms. It can be noted that the durations of both excitatory and inhibitory processes are quite different. Whereas the IPSP is more or less independent of the stimulus duration, the EPSP follows rather precisely the time course of the sound signal.

The spike pattern of the neuron shown in Fig. 2d consists of two pulse trains evoked by a tonic EPSP which is interrupted by a short inhibition. The IPSP is – similar to the case in Fig. 2c – independent of stimulus duration. However, in contrast to the preceding example, the inhibition is delayed by about 5–10 ms relative to the onset of the depolarization. The resulting effect of this temporal relationship leads to a spike pattern comprising of two parts although the stimulus is a pure sound pulse.

Figure 2e demonstrates the feature of a phasic spike response. Again it seems to be generated by the interaction of EPSP and IPSP, the IPSP following the EPSP with a delay of a few milliseconds. In contrast to Fig. 2c and d the inhibition lasts longer and thus all but the very first part of the excitatory response is suppressed.

The response patterns of auditory interneurons generated in the metathoracic ganglion of the locust seem to be characterized by a common feature: The postsynaptic membrane is activated by a depolarization lasting as long (or even longer) than the stimulus. In more than 50% of the units recorded from this depolarization is superimposed by inhibitory processes (Fig. 2c–e) occurring with different time delays and durations relative to excitation.

In some neurons where the intracellular penetration lasted for a longer period of time, we were able to study the postsynaptic responses within the whole frequency-intensity field. We found that the amplitudes of both depolarizing and hyperpolarizing potentials can depend heavily on stimulus frequency. This finding is shown in detail in Fig. 3a for a unit similar to the one in Fig. 2c. To differentiate the effect of

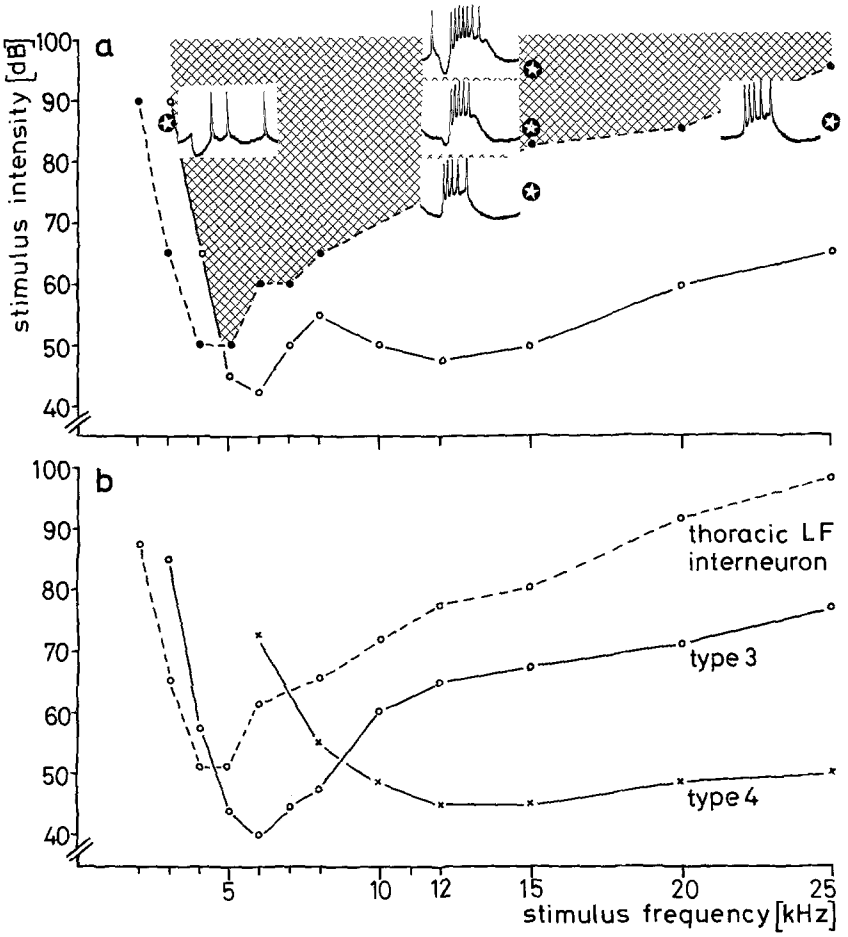

Fig. 3. a Threshold curves of EPSP (*solid line*) and IPSP (*dashed line*) of the unit in Fig. 2c, averaged on the basis of 5 consecutive identical stimuli (sound duration 20 ms; rise and fall time 1 ms; repetition rate 1/s; sound intensity varied in 5 dB steps starting with threshold value). The hatched area represents the compound action of EPSP and IPSP of this neuron. The asterisks indicate the frequency-intensity values at which the inserted displays were established. **b** Threshold curves of type 3 and 4 receptor fibres (after Römer 1976; *solid lines*) and the thoracic low frequency interneuron (after Römer 1975; *dashed line*). Note the high congruence between the threshold curves of type 3 and 4 receptors with the EPSP response in Fig. 3a and between the tuning of the thoracic low frequency neuron with the IPSP response. For further explanations see text

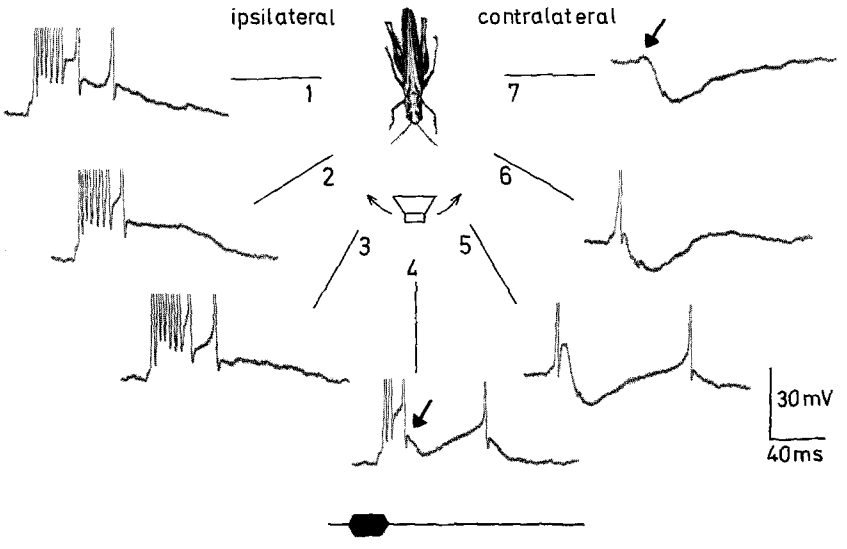

Fig. 4. Intracellular responses of a directionally sensitive interneuron at different sound directions, changed in 30° steps in the frontal field of the preparation (sound frequency 20 kHz; sound intensity 20 dB above ipsilateral threshold, duration 20 ms, rise and fall time 1 ms, repetition rate 1/s). In this and the following figures the stimulus starts at the onset of the scope displays, as indicated for speaker position 4. Arrow at speaker position 4 indicates the first appearance of the inhibitory potential when turning the sound source from ipsilateral to contralateral

auditory stimulation upon the EPSP and IPSP alone, the threshold for each component is plotted separately. The solid line in Fig. 3a gives the threshold of the EPSP response with highest sensitivities around 5 and between 10 and 15 kHz. The comparison of this double peaked curve with the frequency tuning of single receptors (Fig. 3b) strongly suggests that both low and high frequency receptors of type 3 and 4 are linked to this interneuron via excitatory synapses. In contrast to this broad band excitatory input the threshold curve of the IPSP response (dashed line in Fig. 3a) has only one peak of maximum sensitivity around 4–5 kHz which precisely reflects the tuning of the thoracic low frequency neuron described elsewhere (Rehbein et al. 1974; see dashed line in Fig. 3b). It should be noted that this low frequency interneuron seems to be directly driven by the tympanic receptors of type 1, as both threshold curves are very similar (see Römer 1975). Thus we assume that this thoracic low frequency unit may function simply as a 'relay' unit converting afferent excitation into inhibitory input in the unit described in Fig. 3a (for some further morphological hints see Discussion). Although the above described presynaptic connectivity of the unit in Fig. 3a seems to be represented by a rather simple network, the resulting response pattern is nevertheless quite complex. Three different response areas can be characterized: The hatched area indicates the influence of both excitatory and inhibitory postsynaptic potentials, whereas on the right hand side of the hatched area an excitatory potential is elicited exclusively and on the left hand side even a pure inhibitory potential appears. Thus the interaction of both synaptic components can be modified by sound intensity as well as by stimulus frequency (see examples in Fig. 3a; for the effect of sound intensity read the displays at 15 kHz from bottom to top, for the effect of stimulus frequency read at a sound intensity of 85 dB SPL from right to left).

2. *Coding of Sound Direction*

Suga and Katsuki (1961) showed that directional coding of insect auditory interneurons is strongly affected by contralateral inhibition. The following section presents three intracellular examples for such bilateral processing and the results reveal that different modes of excitatory versus inhibitory interactions have been evolved. In Fig. 4 with ipsilateral stimulation a strong and – compared with the stimulus duration – long lasting depolarization and resulting spiking activity is generated. When turning the sound source from this position to the animal's longitudinal axis, the amount of EPSP amplitude is reduced by a delayed inhibitory potential (see arrow at speaker position 4) and thus the spike count per stimulus is decreased significantly. A further turn of the speaker to the contralateral side leads to a further increase of the IPSP amplitude. In addition, the delay of the inhibitory potential decreases relative to the onset of the stimulus (note that from speaker position 4 to 7 the latency of inhibition is reduced by about 10 ms). Both effects finally result in a total suppression of the spiking activity of this interneuron with contralateral stimulation. At this stimulus angle it is highly probable that the inhibitory potential prevents the postsynaptic membrane from reaching spiking threshold, which results in a very pronounced right versus left discrimination of this interneuron.

In Fig. 5, with ipsilateral sound stimulation the interneuron generates a burst of spikes per sound pulse. A change of the position of the sound source in the horizontal plane leads to a decrement of the spike response as is the case for the neuron in Fig. 4.

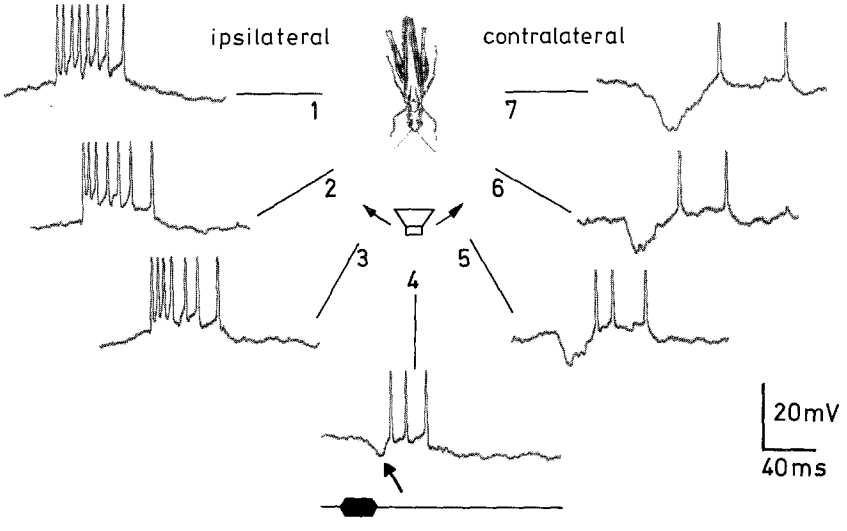

Fig. 5. Intracellular responses of a directionally sensitive interneuron at different sound directions, changed in 30° steps in the frontal field of the preparation (sound frequency 20 kHz, sound intensity 20 dB above ipsilateral threshold, duration 20 ms, rise and fall time 1 ms; repetition rate 1/s). Arrow at speaker position 4 indicates the first appearance of inhibition when turning the sound source from ipsilateral to contralateral

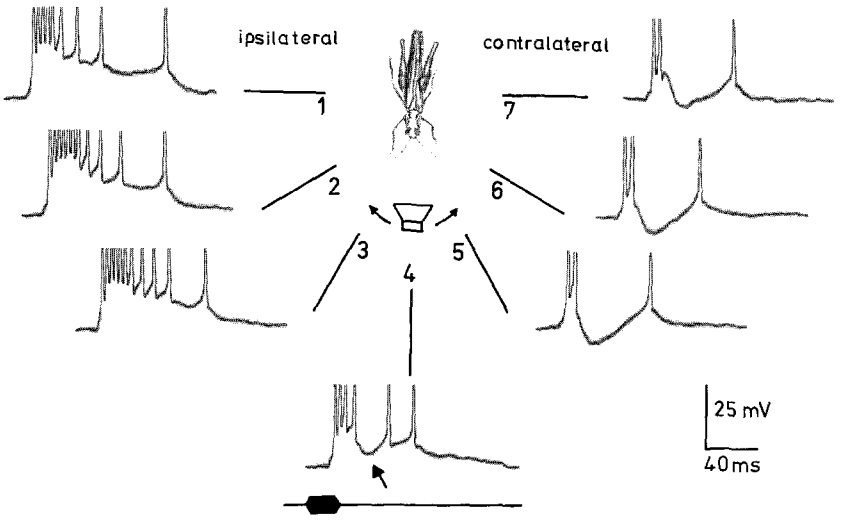

Fig. 6. Intracellular responses of a directionally sensitive interneuron at different sound directions, changed in 30° steps in the frontal field of the preparation (sound frequency 16 kHz, sound intensity 20 dB above ipsilateral threshold; duration 20 ms; rise and fall time 1 ms; repetition rate 1/s). Note that in comparison to Figs. 4 and 5 with contralateral stimulation the spiking activity is still present, although reduced

But the important characteristic of this interneuron is the fact that at frontal, and thus for both ears symmetrical stimulation the IPSP precedes the EPSP. Therefore, in contrast to the example in Fig. 4, already the initial phase of the excitatory response is influenced (see arrow at speaker position 4 and compare with the same speaker position in Fig. 4).

Therefore at frontal stimulation both spike count *and* response latency are modified. As soon as the sound source is moved to the contralateral side (Fig. 5, positions 5–7) these effects become more pronounced: The spike count per stimulus further decreases and there is a dramatic increase of the response latency from about 20 ms at ipsilateral stimulation to about 50 ms at contralateral stimulation. Due to the temporal advantage of inhibition versus excitation at certain speaker positions this interneuron encodes sound direction by means of spike count and response latency, a phenomenon well known from extracellular findings (Mörchen 1980).

Whereas in Figs. 4 and 5 two very pronounced examples of contralateral inhibition are documented, in Fig. 6 responses of an interneuron are shown in which the contralateral sound stimulation does not lead to a total reduction of the spiking activity. With all angular stimulations the EPSP is favored in amplitude and time relative to the IPSP. Therefore, turning the sound source from the ipsilateral to the contralateral side leads to a decrease of the spiking activity with a remaining excitatory response with contralateral sound stimulation.

Discussion

In this study auditory processing by some interneurons in the locust was investigated intracellularly. Thus recent comparable findings on crickets and cicadas are extended (Wiese 1978; Wohlers and Huber 1978; Boyan 1980; Huber et al. 1980).

On the basis of previous extracellular studies on the auditory central nervous processing of the locust it is known that auditory interneurons exhibit rather different and in some cases complex response patterns (Adam 1969; Kalmring 1971; Kalmring et al. 1972a; Kalmring 1975; Mörchen 1980). This kind of variety was found again in the intracellular recordings, but now – due to the intracellular approach – the underlying synaptic mechanisms can be viewed directly.

Synaptic Processing and Possible Connectivity

The recorded postsynaptic potentials reveal a high degree of synaptic processing: Only a minority of interneurons (8 out of 43) reflect the simple tonic response pattern of auditory receptors (Fig. 2a, b). In most of the responses the EPSP's are modified by additional inhibitory potentials generated at different instants relative to excitation. Thus the generation of complex spike patterns must be explained on the basis of the temporal interaction of EPSP and IPSP response (Fig. 2).

As the interneurons studied were not stained by dye injection, there are no direct morphological indications for their synaptic connectivity to auditory receptor fibres and our present knowledge is rather vague for a discussion of this question.

First of all it should be noted that there is a remarkable temporal delay between both neuronal levels. Whereas the latency of receptor fibres is between 7 to 10 ms (recorded just anterior to their branching into the frontal acoustic neuropile), that of auditory interneurons – though studied at comparable sound intensities – varies significantly, ranging from about

18 ms up to 30 ms. This time gap in the order of about 10 ms complicates a general statement concerning synaptic linking of auditory receptors and the interneurons described here. Though auditory processing in the locust metathoracic ganglion has been studied intensively (Kalmring et al. 1972a, b; Rehbein et al. 1974; Kalmring 1975; Rehbein 1976; Mörchen 1980), so far only one interneuron, the thoracic low frequency neuron, with intermediate latencies of about 12 ms was found (Rehbein et al. 1974; Römer 1975). It projects into the frontal acoustic neuropile where the postsynaptic potentials in this study were recorded. Furthermore our physiological findings in Fig. 3a indicate that this thoracic low frequency interneuron can be regarded as a favorite candidate converting sensory excitation into central nervous inhibition. The threshold curve of this segmental unit coincides with both, those of auditory type 1 receptors (see Römer 1975) and the inhibitory area of the studied interneuron shown in Fig. 3a. Consequently for this interneuron the following model of its presynaptic input is suggested: the excitatory input is mediated directly via type 3 and 4 receptors (compare Fig. 3a and b), whereas inhibition is bypassed via one intercalated unit, the thoracic low frequency interneuron (for similar relationships within the cercal system see Levine and Murphey 1980).

There is evidence that the low frequency interneuron inhibits other central units as well (see e.g. the inhibitory frequency area of the B-Neuron; Kalmring 1975). Therefore we assume that compared with the number of ascending interneurons only a few segmental units – at present unknown in structure and detailed morphology – may function as inhibitory channels.

Postsynaptic Correlates for Directional Coding

From most of the experiments in Figs. 2 and 3 it is not possible to say whether the complex postsynaptic responses were generated by monaural or binaural processes. Therefore in about 30% of the recordings the sound source was moved around the animal and thus the central nervous interaction between both auditory inputs could be varied. The intracellular findings in Figs. 4 to 6 reveal that the postsynaptic potentials are composed of excitation and inhibition and, more interestingly, that the degree of their interaction depends heavily on sound direction. In this respect these data confirm our understanding of directional coding in insects based on former extracellular studies (Kalmring et al. 1972b; Kalmring 1975; Mörchen 1980): The excitatory input from one auditory side can be totally cancelled when the contralateral ear is more strongly stimulated. Beside this basic feature of directional coding the examples in Figs. 4 and 5 reveal further two different modes of temporal configuration between depolarization and hyperpolarization. In Fig. 4 in all but the very contralateral position the IPSP 'follows' the EPSP and thus spike count, but not the latency of the response is influenced. This is in contrast to the receptor level where sound direction is encoded by means of both neuronal parameters (see Mörchen et al. 1978).

In the interneuron of Fig. 5 the temporal configuration between EPSP and IPSP is reversed compared to that one of Fig. 4: If present, the IPSP clearly precedes the EPSP. This temporal advantage of IPSP must result in a cancelling of the onset of EPSP when contralateral inhibition increases in amplitude. As a consequence, spike count *and* response latency on the central nervous level depend on sound direction. From these data we must conclude that the different local pathways for EPSP and IPSP produce the characteristic onset latencies of both potentials. These absolute delays may vary from interneuron to interneuron thus leading to different modes of central nervous directional coding.

At present it is not clear whether the lateral inhibition is mediated via the mirror image cell of the studied interneuron (e.g. by postsynaptic branches to the opposite side) or via pre-set units of the kind of the thoracic low frequency interneuron mentioned above.

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