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ORIGINAL PAPER

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Noise filtering in the auditory system of *Locusta migratoria* L.

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Abstract Many acoustically communicating grasshoppers live in crowded populations where sound of many individuals may cause permanent noise. Tympanic receptors and first-order auditory interneurons of *Locusta migratoria* code such noise tonically, whereas many higher order interneurons react only weakly. In response to simultaneously presented sound they exhibit a better signal-to-noise ratio than their presynaptic elements. Two possible filter mechanisms are suggested for noise reduction in higher-order interneurons: (i) high-pass filtering of receptor spike frequencies and (ii) filtering due to synchronization of receptor spikes. Different receptor spike frequencies were elicited by series of short noise pulses with variable repetition rates. Receptor activities differing in their degree of synchronization were elicited by sound stimuli with variable rising times. In contrast to the first order interneurons some higher order interneurons responded best to receptor spike frequencies above 150–200 Hz, thus showing the postulated filtering. Only one higher order interneuron (AN4) distinguished between synchronous and asynchronous receptor activities. It is suggested that high-pass filtering of receptor spike frequencies is responsible for the noise filtering observed in these interneurons. The synchronization selectivity of AN4 is proposed to be responsible for temporal pattern detection of conspecific sounds.

Key words Noise filter · Auditory system · Locust · Spike frequency · Spike synchronisation

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Introduction

The acoustic communication of acridid grasshoppers is based on sending, receiving and recognizing sound signals, the temporal structure of which is very diverse among different species (Jacobs 1953). Differences in temporal structure of the species-specific songs are known to form an effective isolation mechanism for sympatric living species (Helversen 1972, 1984, Helversen and Helversen 1987). The songs are broad-band signals which contain maximal amplitudes in a low-frequency range (6–10 kHz), and in most species a broadly tuned ultrasonic maximum [25–30 kHz; Meyer (1994)]. In some species like *Chorthippus biguttulus* a difference in frequency content between male and female songs plays an important role in the recognition of sex (D. von Helversen and O. von Helversen, unpubl. obs.). Although the low-frequency maxima may differ among species (Meyer 1994) there is still no evidence that the song frequency is equally important for species recognition as the temporal structure.

An acridid grasshopper which moves about in dense grassland in a dense population of stridulating conspecifics faces severe problems in analyzing the messages sent out by a conspecific animal: (i) the sound pressure of a calling song produced by a small grasshopper like *Ch. biguttulus* is low (only 65–70 dB SPL at a distance of 10 cm) compared to the sound produced by crickets and bushcrickets, thus leading to a small active space of the signal. (ii) The animal is sitting in a very complex sound field in which these soft sound signals are strongly absorbed, reflected and diffracted by the ground and the vegetation (Michelsen 1978). These properties of the habitat lead to distortion of the signal and to a strong attenuation of amplitudes thus reducing the hearing distance at least by a factor of 2 compared to the distance expected from geometric spreading of sound (Rheinlaender and Römer 1986; F. Lang, unpubl. obs.). They also cause a minor distortion

of phase information (A. Michelsen, pers. comm.) which for the grasshoppers is important for localization of sound (Michelsen 1994; Michelsen and Rohrseitz 1995). (iii) Another problem results from the noise caused by other animals living in the same habitat and communicating in the same frequency range. The animal must somehow be able to overcome the masking effect and to select the signals of a single conspecific from the background noise (Römer 1994; Pollack 1988). (iv) Finally, acridid grasshoppers have to face the problem of "internal noise" caused by vibrations of their tympanic membranes which are placed in the side wall of the first abdominal segment, as a result of hindleg movements, respiration etc.. All these activities of the animal lead to a non-acoustic activation of the tympanic receptors (Hedwig 1989, Lang and Elsner 1994, Hedwig and Meyer 1994).

Altogether these factors reduce the precision with which the acoustic information is perceived. Information processing in the CNS thus operates at a lower signal-to-noise ratio than under ideal conditions. Using the Omega-neuron of bushcrickets as a "biological microphone" it was shown that the conspecific sound patterns are masked by a high level of background noise (Römer et al. 1989). Similarly, recordings from the tympanic nerve of the gomphocerine grasshopper *Ch. biguttulus* in the field also showed a severe disturbance of the responses to conspecific song patterns caused by a high level of background noise (A. Werner, pers.comm.). However, despite these difficulties these grasshoppers are able to recognize and localize a conspecific song in their habitat up to distances at which in the tympanic nerve recording there is no response to the song observable (Gilbert and Elsner 1995, Werner and Elsner 1995). Thus, in the CNS there must be available a signal which copies the original temporal structure of the song. This raises the question of whether a noise filter on a higher level of the auditory system improves the signal-to-noise ratio for acoustic communication.

The intention of this paper is to show that the auditory system of a grasshopper is able to carry out a form of noise filtering, thus reducing the noise received by the receptors. As a model system the migratory locust *Locusta migratoria* L. was chosen, because the thoracic part of the auditory system to a large extent corresponds to that of gomphocerine grasshoppers (Römer and Marquart 1984, Stumpner and Ronacher 1991). In order to comprehend the information processing within the auditory system, the activities of the tympanic nerve, single tympanic receptor fibres and different auditory interneurons were recorded in response to sound signals under various background noise conditions. For a more detailed understanding of the filter properties within the auditory system neuronal responses to different receptor spike rates and to different states of receptor synchronization were analyzed.

Materials and methods

Animals

Locusts (*Locusta migratoria* L.) at 1–2 weeks after their final moult were taken from the crowded culture of the Zoological Institute. The culture is frequently supplemented with animals from other cultures.

Preparation

The experiments were performed in an non-echoic Faraday-cage at room temperature (20–22°C). The animals were fixed ventral side up. Meso- and metathoracic ganglia were dissected free and lifted on a metal spoon which also served as an indifferent electrode. From the upper side a metal ring was gently pressed on top of the ganglia to reduce movements of the neural tissue. In order to prevent strong respiratory movements all peripheral nerves of meso- and metathoracic ganglia and the abdominal connectives were cut except the metathoracic nerves 6 (tympanic nerves). The ganglia were continuously covered with Ringer solution.

Recording and staining

The intracellular activity of single receptor fibres and auditory interneurons was recorded with thick-walled glass microelectrodes (resistance 100–150 MΩ) in or near the frontal auditory neuropile of the metathoracic ganglion. The tip of the electrode was filled with lucifer yellow (Sigma), the shaft with 5% LiCl. At the beginning of some experiments the sheath of the ganglion was treated with pronase for 2 min. After recording the dye was injected by hyperpolarising current (1 nA for 3–5 min). The ganglia were then excised, fixed and dehydrated for fluorescence microscopy, photographed and drawn as a whole-mount.

In some experiments, simultaneously to the intracellular recordings the summed tympanic nerve activity was recorded extracellularly with a hook electrode.

Acoustic stimulation

The animals were stimulated via two loudspeakers (Dynaudio D21/2) placed at a distance of 30 cm at each side of the animal. The sound stimuli were created by a custom-made programmable stimulator controlled by a computer (Lang et al. 1993).

In the experiments concerning noise filtering, model songs imitating the temporal structure of the species-specific sounds of *Locusta migratoria* were presented from one side. They consisted of five double syllables of white noise each with a rising time of 4 ms, a plateau of 2 ms and a falling time of 15.5 ms (Fig. 1A). These model songs, presented at intensities from 45–75 dB SPL, were either presented alone or superimposed with permanent white noise from both sides with a level of 40, 50 or 60 dB SPL. The noise which was played back by the same speakers as the model songs, was switched on 5 s before the songs. Under these conditions the activity of 10 tympanic receptors and 44 auditory interneurons and 6 tympanic nerve preparations was recorded.

In further experiments neuronal responses to pulsed stimuli with different pulse rates and to stimuli with different rising times were analyzed. Pulsed stimuli were used to create synchronized receptor activities the spike frequency of which could be varied. Stimuli with different rising times were applied to create receptor activities with different degrees of synchronization (Krahe and Ronacher 1993):

(i) The pulsed stimuli consisted of a series of 50 short pulses (white noise of 90 dB SPL) each with a duration of ca. 100 µs. The

repetition rate of these pulses was varied from 100 to 1000 Hz (Fig. 1B). Under these experimental conditions, the responses of 7 tympanic receptors, 21 auditory interneurons and 3 tympanic nerve preparations were recorded.

(ii) Finally, pure tone stimuli were presented with either a rising time of 1 ms and a falling time of 10 ms, or a rising time of 10 ms and a falling time of 1 ms. These two types to stimuli containing the same sound energy, elicited receptor activities with strong resp. low synchronization (Fig. 1C). Data from 7 tympanic receptors, 36 auditory interneurons and 3 tympanic nerve preparations, recorded under these conditions, were analyzed.

Data processing

All recordings were stored on magnetic tape (RACAL 4D). The data were digitized with an A/D-converter (Data Translation DT2825-DI A/D-board and TurboLab by Stemmer Software) with a sample rate of 10 kHz and stored on MO-discs. The data were analyzed by means of Neurolab (Hedwig and Knepper 1992). In case of intracellular recordings, spike frequency, spike count and latency of the first spike following a sound stimulus, were analyzed. In case of extracellular nerve recordings the integral of the rectified signal was used as a measure for nerve activity.

Single data sets were checked for normal distribution. After verifying this, standard deviations were calculated. *t*-Tests were used to estimate significances.

Results

Noise filtering

The intention of this section is to demonstrate that under noisy conditions in some higher order auditory interneurons the signal-to-noise ratio is higher than in the presynaptic elements of the auditory system. Therefore, the reactions of tympanic receptors, of tympanic nerve recordings, of first-order and higher-order auditory interneurons to song models with and without background noise are shown (Fig. 1A, 2).

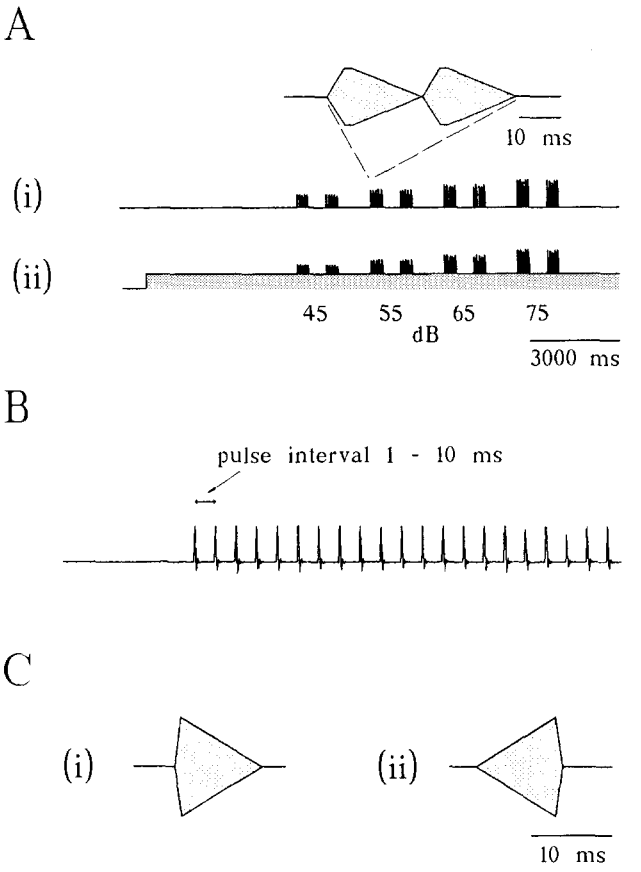


Fig. 1 A–C Sound stimulation patterns: **A** models of species-specific sound pattern of *Locusta migratoria* consisting of white noise of different intensities (45–75 dB SPL). Each double series of five stimuli was (i) either presented alone or (ii) superimposed with permanent noise of 40, 50 and 60 dB SPL; **B** stimulation with series of 50 short pulses (white noise, 90 dB SPL) with a duration of ca. 100 µs the intervals of which were varied from 1 to 10 ms (repetition rate between 100 and 1000 Hz); **C** pure tone stimuli (4 kHz and 16 kHz) which were either applied (i) with a rising time of 1 ms and a falling time of 10 ms or (ii) with a rising time of 10 ms and a falling time of 1 ms

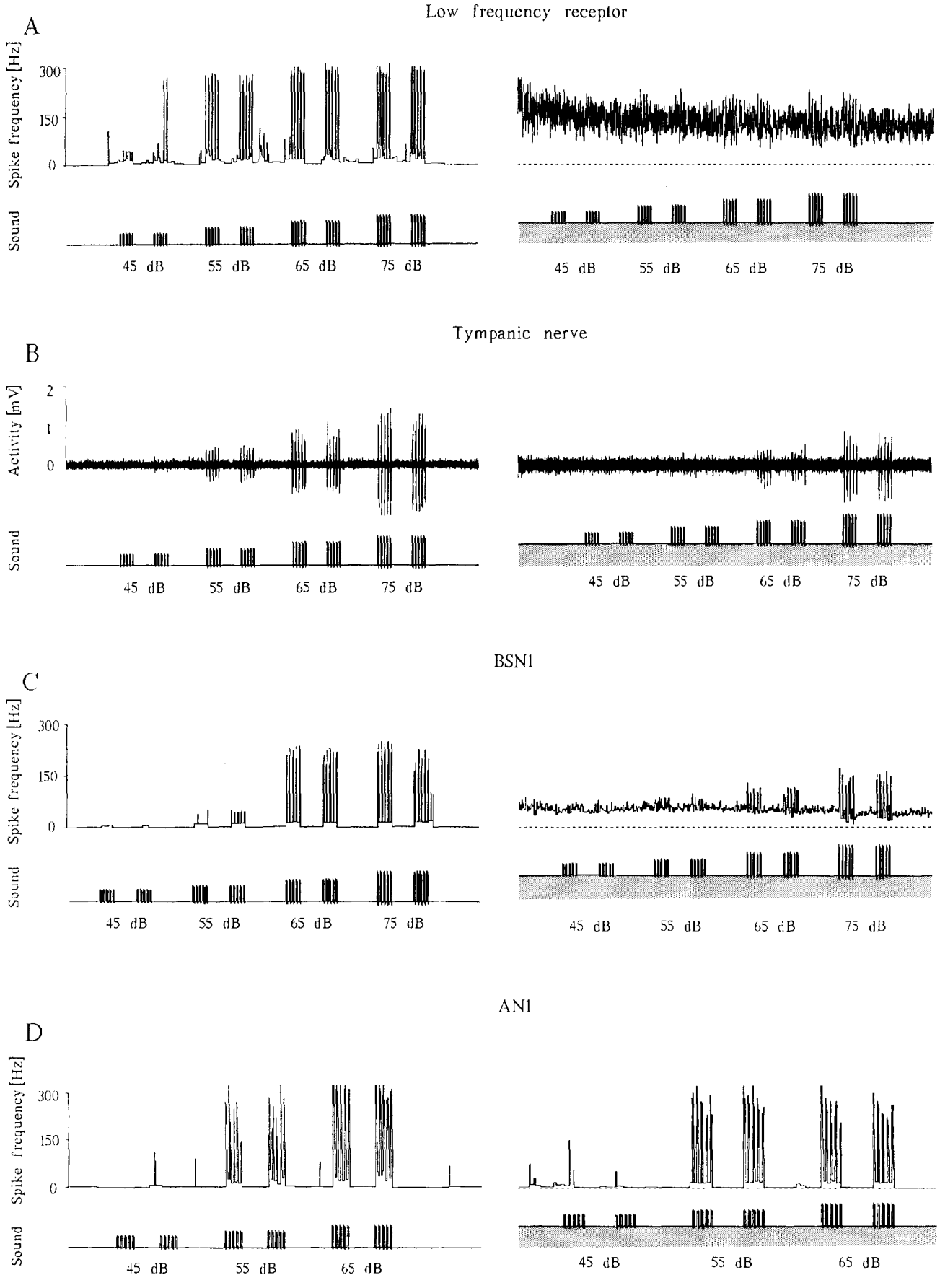
Tympanic receptors

The intracellularly recorded receptor fibres (Fig. 2A, left side) responded to each syllable of the song models with a burst of action potentials (APs) with an initial spike frequency of more than 300 Hz. Only at threshold intensities (45 dB SPL in Fig. 2A) was the spike frequency lower. The background noise elicited spike frequencies from less than 100 Hz at threshold level up to 200 Hz at 60 dB SPL. The right side of Fig. 2A shows the responses of the same receptor fibre to the song models superimposed with 50 dB SPL background noise. In this case the responses to the song models are hardly detectable because the noise elicits spikes with a frequency of ca. 120 Hz. This type of reaction was found in all tympanic receptor types.

Tympanic nerve

When the tympanic nerve activity was recorded under the same conditions (Fig. 2B), during background noise the responses to the song models were much more obvious than in the single receptors (cf. Fig. 2A). The responses to the song models were though weaker during background noise (right side of Fig. 2B) than without background noise (left side of figure). The detection threshold was increased by about 10 dB. The reaction to the permanent noise itself was low at all intensities.

When interpreting summed nerve potentials one has to take into account that only well-synchronized single activities elicit a strong extracellular summed potential, whereas asynchronous activities can happen to delete each other's extracellular potential (Adam 1977). Thus, the low summed nerve activity during permanent noise


Low frequency receptor
A
Spike frequency [Hz]
300
150
0
Sound
45 dB
55 dB
65 dB
75 dB
Tympanic nerve
B
Activity [mV]
2
1
0
BSN1
C
AN1
D

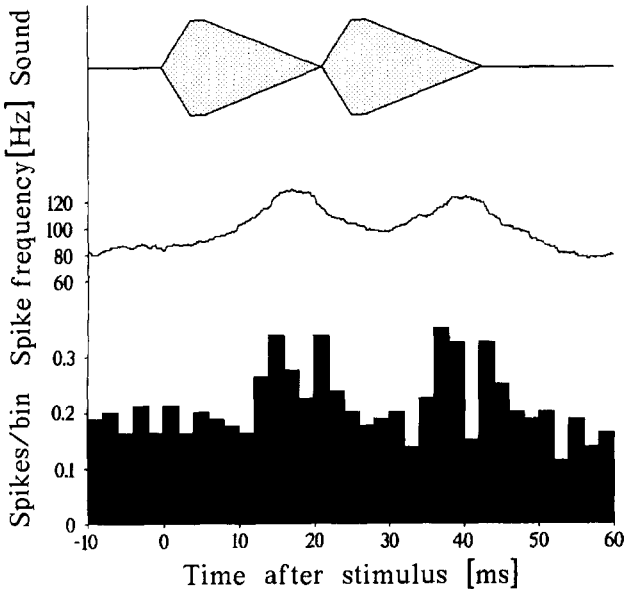


Fig. 3 Averaged responses of a tympanic receptor fibre. The responses of a low frequency receptor (type 3) to model songs of 65 dB SPL during background noise of 60 dB SPL were averaged over 60 song syllables (bin width 2ms)

can be interpreted as asynchronous activity of many active receptor fibres. The clear responses of the summed nerve activity to the song models suggest that the single receptor activities are synchronized by each syllable.

In order to confirm this prediction, the activity of a single receptor was averaged over 60 syllables during background noise, imitating the response of a whole receptor population consisting of 60 cells (Fig. 3). Spike frequency as well as spike count increased 15–20 ms after the beginning of each syllable, indicating both a higher spike rate and a gain in synchronization.

First-order auditory interneurons

There is strong evidence that the local and biganglionic neurons are mainly activated monosynaptically by the tympanic receptors. The activation of these interneurons occurs mainly from the side ipsilateral to the soma (Marquart 1985).

Above threshold these neurons responded to the song models with bursts of APs (Fig. 2C, left side). As with tympanic receptors the spike frequency of these bursts was reduced during permanent noise. At the same time these neurons reacted to permanent noise with tonic activity – as shown for BSN1 in Fig. 2C (right side). [Especially for BSN1, being a double or triple neuron (Römer and Marquart 1984; Stumpner 1989) there can be distinguished "tonic" and "phasic-tonic" types (Stumpner 1988; Stumpner and Ronacher 1991). In the "phasic-tonic" types the elicited spike frequency during permanent noise was lower than in the "tonic" type shown in the figure.]

Compared with the tympanic receptors the local interneurons reacted to permanent noise with a lower spike frequency and they showed slightly clearer responses to simultaneously applied song models. The signal-to-noise ratio of these interneurons was thus better than that of the receptors but still relatively low.

Ascending auditory interneurons

The ascending auditory interneurons which were analyzed (AN1, AN2, AN3, AN4, AN8), show more complex responses to sound stimulation than the supposed first-order interneurons. From the arborisation pattern of their dendrites and from their long response latencies it can be concluded that they are mainly or exclusively activated polysynaptically via interconnected excitatory and inhibitory first-order interneurons (Römer and Marquart 1984, Marquart 1985, for AN1: Pearson et al. 1985). Most of these neurons are direction sensitive because of inhibition from the side ipsilateral to the soma.

Above threshold these neurons (AN1 shown as an example) responded with one or more spikes to the syllables of the song models (Fig. 2D, left side). During simultaneous background noise the response activity to the song models remained almost unchanged. The background noise itself elicited only very little activity (Fig. 2D, right side). In these interneurons, the signal-to-noise ratio for responses to the song models during background noise was noticably enhanced compared to that of the receptors and first-order interneurons.

Comparison of receptor and interneuron activities

The responses of the receptors to the song models differ in two aspects from their reactions to permanent noise: song models elicit (i) higher spike frequency and (ii) stronger synchronization among parallel fibres than permanent noise (Figs. 2A, B, 3). These two response properties of receptors are thus available for a noise filtering mechanism in higher-order interneurons. One mechanism would thus be to respond exclusively to receptor activities above a minimal spike *frequency*. The other mechanism would be a preferential response to well-*synchronized* receptor activities. These two possible mechanisms are to be investigated in the following.

Fig. 2A–D Responses to background noise. Response patterns of a tympanic receptor (type 3) (**A**), an extracellularly recorded summed potential of the tympanic nerve (**B**), responses of a biganglionic (**C**) and of an ascending auditory interneuron (**D**) being stimulated with model songs alone (*left side*) and with simultaneous background noise of 50 dB SPL (*right side*)

Filtering of spike frequencies

In order to test the reactions of auditory neurons to different spike frequencies of the tympanic receptors, series of pulsed stimuli were presented with variable repetition rate (Fig. 1B).

Tympanic receptors

When stimulated with a repetition rate up to 250 Hz the receptors reacted with ca. 1 spike/pulse (Fig. 4A). The latency of these spikes was strongly coupled to the single pulses, the receptors thus probably spiked synchronously (see arrows in Fig. 4A). At higher pulse rates the receptors were no longer able to respond to each pulse because the pulse rate exceeded their maximal spike rate. The receptors reacted to these stimuli with an initial spike frequency of 300–350 Hz which then decreased to ca. 250 Hz.

Tympanic nerve

The shape of the summed nerve potential reflected the state of synchronization among the tympanic receptors (Fig. 4B): up to 250 Hz the nerve recording showed peaks which were latency coupled to the pulses (see arrows in Fig. 4B). At higher pulse rates there was an initial period of synchronous receptor activity the duration of which increased from 10 ms at 250 Hz to 25 ms at 1000 Hz, followed by asynchronous activity. This lead to high average activities at low pulse rates with highly synchronous receptor activities, and to low average activities at high pulse rates which elicited asynchronous receptor activities.

First-order auditory interneurons

All recorded interneurons of this type responded less accurately to pulsed stimuli than the tympanic receptor fibres. Every response started with an initial burst of high spike frequency (up to 250 Hz), followed by tonic activity of 100–150 Hz (BSN1 in Fig. 4C). The spikes were not latency coupled to the single pulses, the spike pattern thus mainly reflected the duration of the stimulus and not the pulse pattern. SN1 and TN1 reacted in a similar way responding with lower spike frequencies.

Ascending auditory interneurons

The ascending inteneurons which were tested under these conditions reacted differently from the previously described cells. The response patterns of AN1 and AN4 are shown as examples (Fig. 4D, E).

AN1 responded weakly to stimuli with pulse rates up to 200 Hz. Pulse rates from 200 to 300 Hz elicited maximal tonic activity. At higher pulse rates the spike frequency in this neuron slightly increased, the spike count decreased with decreasing stimulus duration. This type of activity was also found in other ascending interneurons.

AN4 showed a more complex response pattern: pulse rates up to 150 Hz did not elicit any response. This was caused by a strong inhibition which followed each pulse. At pulse rates of about 200 Hz the excitatory responses reached a maximum. They consisted of a phasic onset followed by tonic activity. At still higher pulse rates a strong phasic response was elicited only.

Filter mechanisms

Although there was synchronous receptor activity at low pulse frequencies the ascending auditory interneurons either responded weakly or not at all. In case of AN1 one might speculate that the reason was an interval between the receptor spikes too long to be integrated to a suprathreshold response (see arrows in Fig. 4D). In the case of AN4 such a mechanism may also have been effective, but additionally a strong pulse-coupled inhibition occurred suppressing any suprathreshold response. These response properties lead to high-pass filtering of receptor spike frequencies.

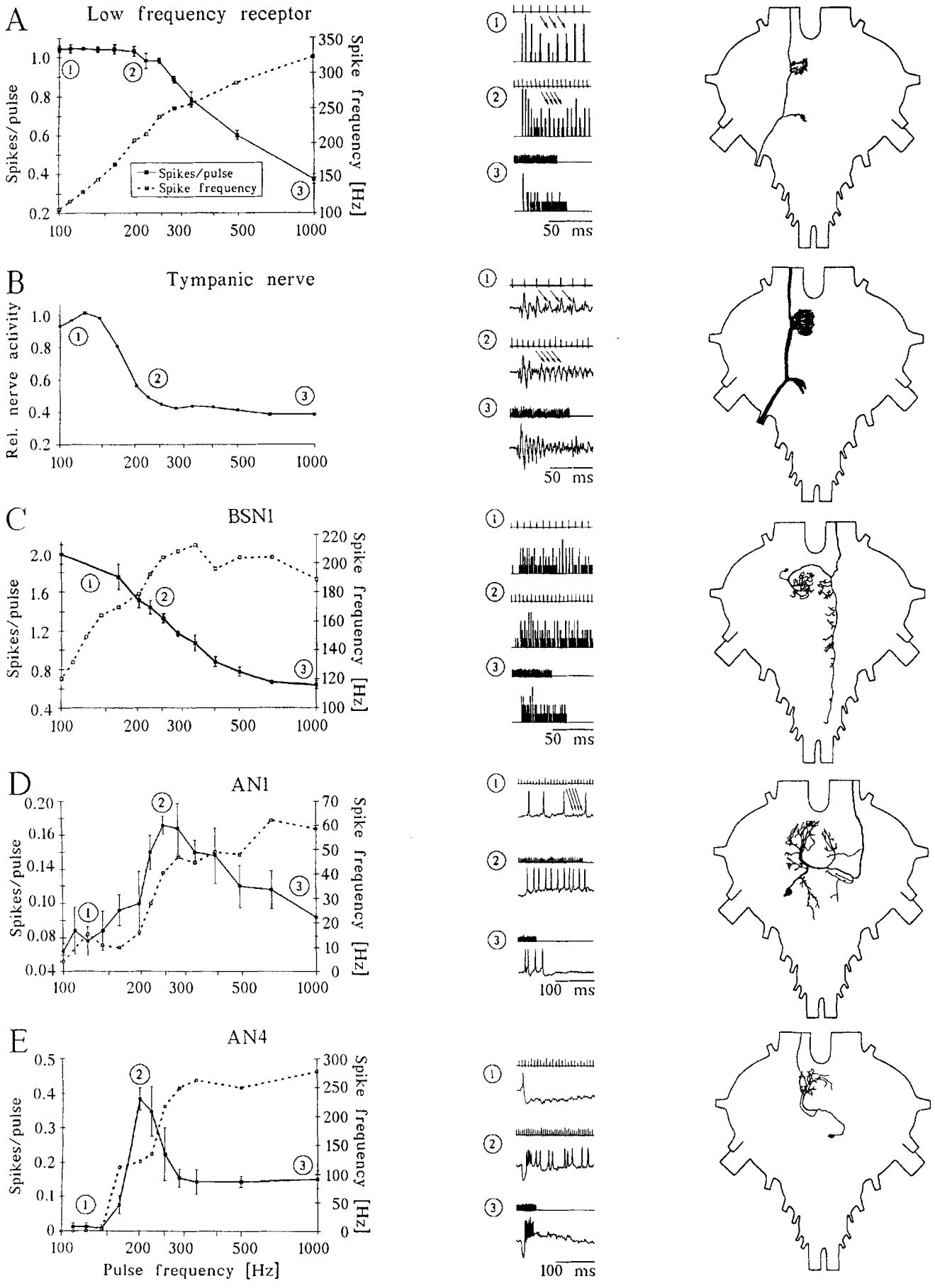
Filtering of receptor synchronization

In order to test the effect of synchronization of receptors on noise filtering stimuli with either a fast or slow rising time (1 ms or 10 ms, Fig. 1C) were applied. All neurons were stimulated at 4 and 16 kHz at intensities from 50 to 90 dB SPL. The results shown in Fig. 5 are taken from stimulations at an intensity within the linear range of the indivual intensity curve.

Tympanic receptors

None of the tested receptors revealed a difference in spike count between stimuli with short and long rising times (Fig. 5A). The spike intervals did not show any significant difference either. Only the latencies for slowly rising stimuli were 6–8 ms longer (highly significant,

Fig. 4A–E Responses to pulsed stimuli. Response activities and metathoracic morphology of a low frequency receptor (type 2) (**A**), of the tympanic nerve (**B**) and of different auditory interneurons (**C–E**) to pulsed stimuli with varying repetition rate. The responses to five stimuli were averaged. The *solid lines* mark spikes/pulse resp. nerve activity (**B**), the *dotted lines* mark spike frequency. The *insets* illustrate the spike patterns resp. nerve activity (**B**) at the indicated pulse frequencies


A
Low frequency receptor
Spikes/pulse
Spike frequency [Hz]
Spikes/pulse
Spike frequency
50 ms
B
Tympanic nerve
Rel. nerve activity
50 ms
C
BSN1
Spikes/pulse
Spike frequency [Hz]
50 ms
D
AN1
Spikes/pulse
Spike frequency [Hz]
100 ms
E
AN4
Spikes/pulse
Spike frequency [Hz]
Pulse frequency [Hz]
100 ms

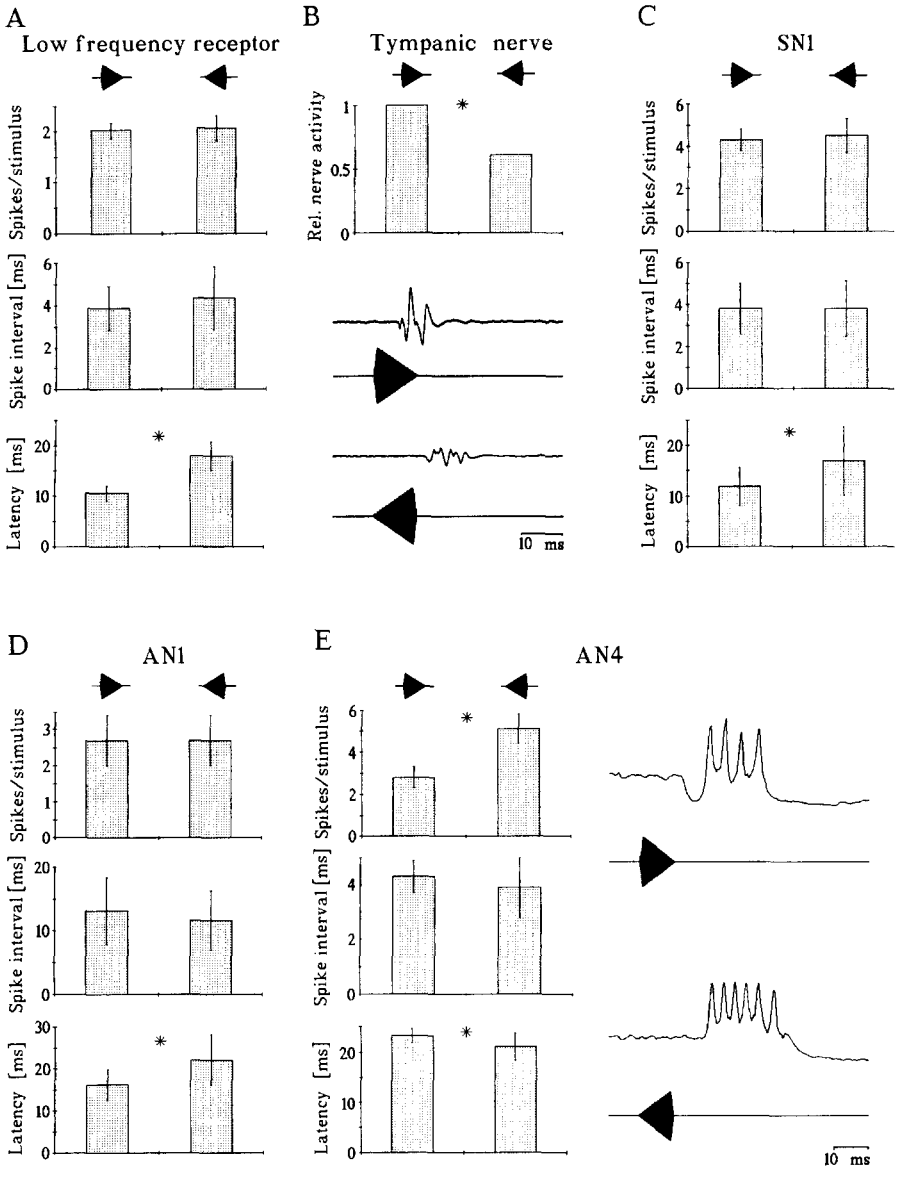


Fig. 5A–E Responses to stimuli with different rising times. Responses of a low frequency receptor (**A**), of the tympanic nerve (**B**) and of different auditory interneurons (**C–E**) to stimuli with a rising time of 1 or 10 ms. The carrier frequencies of the stimuli were 4 kHz (**A**, **B**, **C**, **E**) and 16 kHz (**D**), respectively. The responses to 50 stimuli were averaged. The values marked with *showed significant differences between the fast and slowly rising stimuli

$P < = 0.001$). These data confirm the findings of Krahe and Ronacher (1993) who used white noise stimuli instead of pure tones for sound stimulation.

Tympanic nerve

Although the number of receptor spikes was not affected by the rising time of the stimuli, the summed nerve activity showed strong differences: the amplitude of the response activity was significantly lower for slowly rising stimuli (Fig. 5B, $P < = 0.01$). This indicates that the synchronization of the receptors is lower in response to slowly rising stimuli than to fast rising stimuli.

Auditory interneurons

With the exception of AN4, the tested auditory interneurons (SN1, BSN1, AN1, AN2, AN3 and AN8) showed neither a difference in spike count nor in spike interval when stimulated with fast and slowly rising stimuli. Their latencies were significantly larger for slowly rising stimuli (as examples see SN1 and AN1 in Fig. 5C and D, each $P < = 0.01$). By contrast, AN4 responded clearly stronger, i.e. with higher spike count, to slowly rising stimuli (Fig. 5E, $P < = 0.001$). The spike intervals were slightly lower for slowly rising stimuli. The weak response to fast rising stimuli was caused by an initial IPSP with a duration of 6–7 ms which did not occur at slowly rising stimuli. The

response to fast-rising stimuli occurred about 5 ms before that to slowly rising stimuli. But because of the occurrence of the prominent IPSP, AN4 was the only interneuron which spiked with a significantly longer latency (2 ms) to fast rising stimuli than to slowly rising ones ($P < = 0.01$), whereas all other neurons responded with significantly shorter latencies (5–10 ms).

Discussion

Major aspects of the receptor information are already processed at lower levels of the auditory system of acridid grasshoppers. In addition to interneurons with direction selectivity we find interneurons which are selective for the carrier frequency of a signal (Marquart 1985) and for certain temporal structures (Ronacher and Stumpner 1988, Stumpner et al. 1991). The results presented here suggest a further property of ascending auditory interneurons: the ability to perform noise filtering. This noise filtering improves the signal-to-noise ratio in ascending interneurons under noisy conditions which may exist in their natural habitat or are caused by own body movements, thus improving the detection of biologically relevant signals. The ascending interneurons are able to do so although all presynaptic receptors and interneurons show a distinctly lower signal-to-noise ratio under these conditions.

Spike frequency filtering

The experiments suggest that the mechanism which results in noise filtering in the ascending auditory interneurons uses high-pass filtering of spike frequencies of tympanic receptors. This high-pass filter may be realized in several ways:

(i) In AN4 we observe inhibition which is triggered by each pulse as long as the pulse rate is below 150 Hz. This might also occur in other interneurons but has so far not been observed. In pharmacological experiments with picrotoxin Römer and Seikowski (1985) showed a strong influence of inhibition on the response properties of this neuron. Further experiments of this kind will reveal the actual importance of inhibition for this filter mechanism.

(ii) In the ascending interneurons not showing this pulse-coupled inhibition, a possible mechanism is that the EPSPs of these neurons decay faster than the EPSPs of interneurons which do not show noise filtering. This could prevent the summation of EPSPs which occur with a frequency below 200 Hz, thus keeping the interneuronal activity subthreshold. Exemplary computation of the decay times of EPSPs [$\tau_{1/2}$, Wohlers and Huber (1982)] in some local and ascending interneurons resulted in very short decay times in some AN1 and AN2 from 2 to 3.5 ms, whereas in BSN1 and SN1 the decay times mainly ranged from 4–8 ms. These preliminary results could confirm this idea. Generally the time constancies of potential changes greatly depend on the geometry of the dendritic tree (Sprouston et al. 1994). The measurements thus depend on the position of the recording electrode. Such a filter mechanism was suggested by Boyan and Fullard (1988) who found an auditory interneuron in a noctuid moth which only coded high presynaptic spike frequencies and at the same time had very short EPSPs.

The filtering of spike frequencies brings about that receptor activities with spike frequencies below 150–200 Hz do not release spikes in the respective ascending interneurons. One advantage of this filter is to suppress slowly modulated noise which effects receptor spike frequencies below 150–200 Hz. Thus, no valuable information about sound stimuli with high modulation frequency, such as conspecific signals, is lost. Besides, various studies showed that the tympanic organ of acridid grasshoppers is not only activated by sound but also by various own movements (Hedwig 1988, Hedwig and Meyer 1994). This causes slowly modulated asynchronous receptor activities at medium spike rates (Lang and Elsner 1994). Like the responses to background noise this non-acoustic activation of receptors could be separated from responses to sound signals with high modulation frequency and could subsequently be suppressed by the mentioned filter (Lang and Elsner 1989).

This filter can, of course, not function without losses, because those ascending interneurons using this filter only respond to receptor activities with high spike frequency. Tympanic receptors respond to fast rising sound stimuli in a phasic-tonic manner (Römer 1976). Computations of intensity curves showed that already a few dB above threshold a receptor-burst begins with an initial spike rate above 150–200 Hz although the average spike rate still remains low. This means the start of the receptor response would pass the proposed filter and elicit a "phasic" response in the ascending interneuron. Thus, the threshold of the interneuron should only be slightly higher than that of the most sensitive presynaptic elements.

Synchronization filter

The results obtained by stimulation with fast and slowly rising stimuli cannot be looked at independently of those obtained with pulsed stimuli. Pulsed stimuli with a pulse frequency below 250 Hz elicited strongly synchronized receptor activities over the entire duration of the stimulus. Those stimuli with a pulse frequency above 250 Hz elicit receptor activities which were strongly synchronized up to 25 ms after the onset of the response only (Fig. 4B). Fast rising stimuli without a pulsed pattern also elicited strongly synchronized receptor activities resembling the high frequent pulses (Fig. 5).

It was shown in this paper that there is at least one auditory interneuron, AN4, which is able to distinguish between synchronous and asynchronous tympanic receptor activities. AN4 responded to fast rising pulses with a strong initial IPSP and a subsequent tonic excitation. A similar response was obtained by stimuli with high pulse frequencies. In contrast, slowly rising sound pulses did not initiate inhibition but only tonic excitation.

A number of studies on the acoustic communication and on the auditory system in acridid grasshoppers indicate that for the evaluation of several parameters of sound signals it is adaptive for the animal to measure receptor synchronization (Ronacher and Römer 1985, Krahe and Ronacher 1993). Behavioural studies on *Ch. biguttulus* (Helversen 1972) demonstrated that females ignore male songs which are interrupted by gaps of more than 2 ms duration. These gaps cannot be detected by a single receptor, but they are coded by the synchronization of the tympanic receptors through the onset following each gap (Ronacher and Römer 1985). Further behavioural studies (Helversen 1993) showed that *Ch. biguttulus* males prefere female songs with slowly rising syllables instead of abruptly rising ones. Slowly rising signals are discussed to facilitate the sound localization (Adam 1977; D. von Helversen and O. von Helversen, (unpubl. obs.).

Ronacher and Stumpner (1988) in *Ch. biguttulus* found that AN4 is able to detect the mentioned gaps in the conspecific male song pattern. Gaps of more than 2 ms duration which elicit strongly synchronized receptor activity inhibit this interneuron completely over a wide range of intensities. In contrast, the neuron responds tonically to uninterrupted songs or gaps of less than 2 ms duration. Thus, in these experiments AN4 also clearly showed synchronization selectivity.

Mechanisms for noise filtering

Comparing the results found for spike frequency filtering and for synchronization filtering makes evident that the spike frequency filtering may represent an adaptive mechanism to cause noise filtering. Most of the considered interneurons performing noise filtering are not synchronization selective. The synchronization filter, although not independent of spike frequency filtering was only found in AN4. Although theoretically being conceivable as a noise filter, it can not explain the noise filter properties in all ascending interneurons. The synchronization selectivity of AN4 might instead be useful for the recognition of the temporal structure of conspecific signals.

Effects in form of a long-lasting inhibition caused by a loud signal suppressing the reaction to less intense noise such as reported by Römer (1994) could not be observed in any of the locust auditory interneurons. This type of forward masking, allowing for a selective attention to the louder signal which could also help in noise reduction has been found for the Omega neuron in crickets and bushcrickets (Pollack 1988; Römer 1994; Sobel and Tank 1994).

Conclusions

The noise filter described in this paper cannot ensure the detection of conspecific sound signals under all circumstances, but it improves the signal-to-noise ratio. It should at least make it possible to detect a new signal, though not its exact temporal structure. Additionally under noisy circumstances it will prevent the animal from reactions to noise which does not carry any relevant information. This holds true for recognition of sound signals in a noisy environment. Also, for the interference with self-induced non-acoustic activation of the tympanic receptors the same holds true: highly active animals, massively disturbing their auditory system, are somehow able to notice a sound (Robert 1989, Hedwig and Meyer 1994); in order to recognize, they might interrupt their activity, if possible, in order to listen to the sound (Meyer and Elsner 1995).

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