

Neurophysiological Aspects of Song Pattern Recognition and Sound Localization in Grasshoppers¹

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SYNOPSIS. In their intraspecific communication females of the grasshopper *Chorthippus biguttulus* are able to detect minute gaps in songs. Males of this species can lateralize sound with less than 1 dB difference between the two ears. Behavioral experiments suggested that separate pathways exist for song recognition and sound localization. As for the neurophysiological basis, auditory receptors respond tonically and necessarily carry all information explaining behavioral performances in their spiking responses. However, for pattern recognition as well as for coding of directional information, it seems necessary for the animal to evaluate a whole set of parallel receptor fibres to achieve the precision observed in behavior. The information of receptors converges onto thoracic neurons which drive neurons ascending to the brain. Some of these ascending neurons exhibit dramatic response differences either for various temporal patterns or for sound from different directions and therefore may represent pathways specialized for song recognition or for sound localization.

INTRODUCTION

Among some groups of acridid grasshoppers highly specialized acoustic communication has evolved. In many Gomphocerine species in Europe, males produce songs and females can respond by a song of their own. Like all other acoustically active species they have to solve two basic problems, namely *recognition* and *localization* of the relevant signal. In *Chorthippus biguttulus*, both sexes are able to distinguish conspecific from heterospecific signals and both can discriminate between male and female songs (for reviews see von Helversen and von Helversen, 1983, 1987, 1994). Although the phonotactic approach usually is the male's task, both sexes essentially are able to perform positive phonotaxis. It has to be emphasized that production as well as recognition of the songs are "innate" behaviors

(there is no overlap between generations and thus no possibility of learning from parents).

Under normal conditions, the male initiates communication by spontaneously singing. Only females which are inclined to mate, may respond to the male's song. By means of this response song the male can localize the female. Repeated song alternations between the sexes enable the male to approach the female.

Song pattern recognition

The songs of *Chorthippus biguttulus* males are broad band signals with a highly stereotyped temporal structure (Fig. 1). Females of *Ch. biguttulus* are very choosy in accepting a potential mate. Their highly selective singing response is most convenient for investigating the underlying recognition mechanisms. By playing back various song models to a female and counting the female's responses it is possible to find out the critical "sign stimuli" for the recognition of the species-specific song pattern. In these experiments the females turned out to be very selective for certain temporal parameters of a song. A model song is attractive to a female if it consists of a series of syllables (white noise) separated by pauses (Fig.

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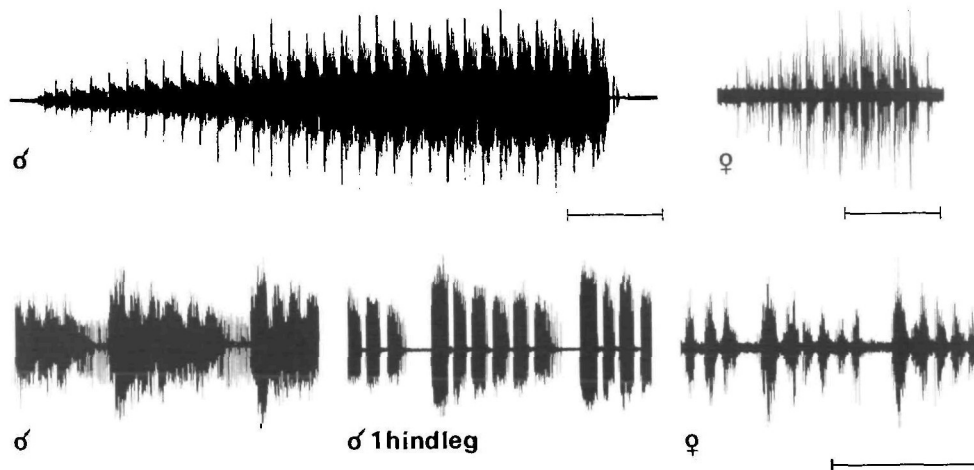


FIG. 1. Songs of *Chorthippus biguttulus*. The upper traces show a single verse of a male (left) and a female (right). Bars: 500 ms. The lower traces show expanded portions (single syllables) of songs of a male singing with both hindlegs (left), a male singing with only one hindleg (after autotomy of the second; middle) and a female (right). Note the gaps occurring within a syllable after one hindleg is lost (left and middle) and note the differences in onsets between male and female sound pulses (middle and right). Bar: 100 ms. Data: courtesy of D. and O. von Helversen.

1, lower left), both having definite durations (*cf.*, von Helversen, 1972, von Helversen and von Helversen, 1987). An especially fascinating capacity is the detection of minute gaps of 1 to 2 ms duration in model songs (von Helversen, 1972, 1979; see shaded area in Fig. 4C). Figure 2A demonstrates the gap detection of these small grasshoppers being equal to or even exceeding that of most vertebrates. In *Ch. biguttulus*, these gaps destroy the behavioral effectiveness of a model completely. Gaps in the ms-range may occur in songs of males with *e.g.*, one hindleg missing (Fig. 1, lower middle) and obviously reduce the fitness of those males (Kriegbaum, 1989).

Sound localization

In *Chorthippus biguttulus* it is usually the male's task to localize a rather stationary female. For the majority of possible stimulus directions males only can determine whether the sound source is located on their right or on their left side (von Helversen and Rheinlaender, 1988). The phonotactic approach of a male is based on a repetition of such left/right decisions. Due to their smallness (interaural distance approx. 2mm or less) the grasshoppers are severely hand-

icapped in localizing a sound source: intensity differences and time differences between the two ears are very low in small animals. Notwithstanding these physical limitations males of *Ch. biguttulus* are unrivalled in exploiting minute intensity differences of less than 1 dB for sound lateralization (von Helversen and Rheinlaender, 1988). For a comparison with intensity discrimination capacities of vertebrates see Fig. 2B. Considering this precision of lateralization, one might expect that the stridulation signals of females should contain many steep sound onsets. However, sound pulses produced by females have a ramplike rise (Fig. 1 lower right)—a feature that is important for the male's Innate Releasing Mechanism (von Helversen, 1993). As we will show, this shape of the female's stridulation signals actually also facilitates directional hearing.

Parallel pathways for pattern recognition and sound localization

The ears of grasshoppers are situated in the first abdominal segment. They contain at least four types of auditory receptors. Central projections form a distinct neuropile in the metathoracic ganglion (TG3, Römer, 1985). Smaller neuropiles in the first

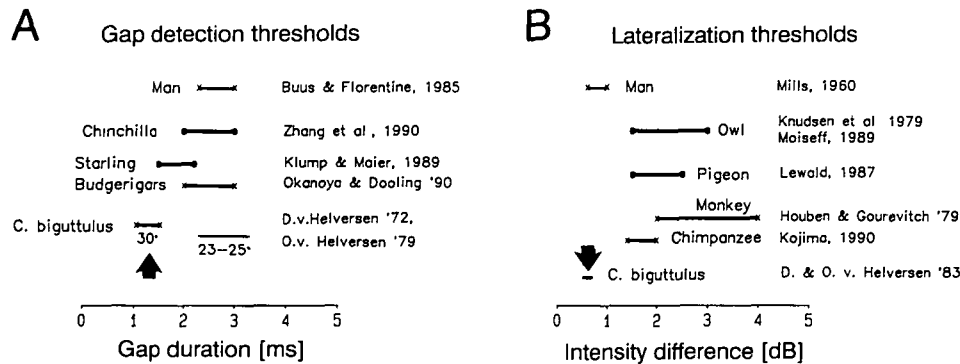


FIG. 2. Comprehension of published data on (A) detection of gaps in sound and (B) of detection of intensity differences between the two ears. Authors are indicated next to the respective values. For gap detection by *Chorthippus biguttulus* two temperatures are given, room temperature and 30°C. Note that *Ch. biguttulus* is well in the range of highest precision found among vertebrates.

abdominal ganglion (fused to the TG3), in the other thoracic ganglia and in the subesophageal ganglion exist as well. Receptors probably do not project into the brain (*e.g.*, Halex *et al.*, 1988), where the final decision of song recognition is made. Lesion experiments have unequivocally demonstrated that for the recognition process receptor projections anterior to the metathoracic ganglion are not necessary (Ronacher *et al.*, 1986). Therefore, auditory neurons ascending from the metathoracic ganglion to the brain must take an important part in the process of pattern recognition and sound localization.

Behavioral studies have also suggested that for song recognition a summation of the inputs of both ears takes place, while for sound localization, the two inputs inhibit each other (von Helversen and von Helversen, 1987). Therefore, parallel pathways for song recognition and localization must exist. We will show that this separation into parallel pathways takes place on the level of the just mentioned auditory interneurons ascending from the thorax to the brain.

METHODS

We recorded from auditory receptor fibres and auditory interneurons originating in the metathoracic ganglion (TG3) of *Ch. biguttulus* and *Locusta migratoria*. The methods of intracellular recording and morphological identification of neurons were conventional and are described in detail elsewhere

(Stumpner and Ronacher, 1991; Krahe and Ronacher, 1993).

For assessing the directionality cues present in the spike activity of auditory receptors of *L. migratoria* we used sawtooth-shaped sound pulses (white noise) of 10 ms duration. In order to compare stimuli of equal energy and frequency content, a ramp stimulus and its temporal inverse were used (compare insets in Fig. 5; for details see Krahe and Ronacher, 1993). Auditory receptors of locusts were taken as a model system for the receptors of *Ch. biguttulus* due to their greater convenience for electrophysiological recordings. Earlier studies failed to reveal obvious differences in the receptor responses of these two species apart from slight shifts in characteristic frequencies and thresholds (Ronacher and Römer, 1985, Stumpner and Ronacher unpublished).

In a standard test program for interneurons, each cell was sequentially stimulated from the soma-ipsilateral (*ipsi*) and from the soma-contralateral side (*contra*) with 100 ms noise syllables of increasing intensity. As a measure of a neuron's directionality, we compared the number of spikes evoked by ipsilateral and contralateral stimulation, at a given intensity (in the behaviorally relevant intensity range of 50–80 dB SPL). Since most ascending neurons produce more spikes when stimulated from soma-contralaterally (*i.e.*, from the side with the ascending axon; Stumpner and Ronacher, 1991),

the number of spikes is expressed as percentage of the spike number with contralateral stimulation (Fig. 6A). A 100% value in Figure 6A means that ipsilateral and contralateral stimulation evoked the same response magnitude, and therefore the neuron had no directionality. A 0% value would indicate a complete inhibition with somapsilateral stimulation and thus maximal directionality. The (mean) distance of a neuron's response function from the 100 percent level therefore can be taken as an indicator of the neuron's directionality.

A similar procedure was applied in order to assess a neuron's capacity for gap detection. The neuron's spike response to uninterrupted syllables was taken as a reference value, and compared to the spike number evoked by a syllable containing gaps (*cf.*, Stumpner *et al.*, 1991). It has to be mentioned that the minimal gap duration that influenced the female's response in behavioral tests strongly depended on temperature and on sound intensity. At 52 dB the change in the female's response occurred with only 4ms gap duration, while at intensities of 64 or 76 dB gaps of 1 to 1.5 ms were already detected by the females (at 30°C, von Helversen, 1979). Thus, for evaluating a neuron's gap detection capacity we decided to take into account only the intensity range between 60 and 80 dB SPL.

RESULTS

Detection of short gaps in model songs by the female

As mentioned above, the recognizing-system of female *Chorthippus biguttulus* beside others is sharply tuned to detect minute gaps in songs. It must be the auditory receptors which transmit information about these gaps to the CNS, despite their inter-spike intervals often being larger than the detected gaps. Spike numbers of receptor responses to models with different gaps (Fig. 3A) do not differ in a range, where behavior shows perfect discrimination (compare Fig. 4C). Therefore, only the temporal distribution of spikes during a response can serve as a cue in which information on gaps is encoded. The most obvious ways of the nervous system to evaluate this temporal distribution

are either evaluating interspike intervals or summing up activity of a set of parallel fibres.

The dependence of the receptors' interspike intervals on intensity, however, is much larger than the dependence on gaps (Ronacher and Römer, 1985). Therefore, spike intervals do not seem to be the best neuronal trait for gap detection. As for the summed responses of many receptor fibres, one can pick these up experimentally by means of a hook electrode around the tympanic nerve. From a hook electrode recording it becomes immediately obvious, that with gaps above a certain duration a marking of each pulse onset following a gap takes place (inset in Fig. 3B). This pulse onset marking must come about by synchronization of spikes on parallel fibres, which therefore seems to be the relevant mechanism for a set of auditory receptors to transfer information on gaps (Ronacher and Römer, 1985).

Is this information also represented in the responses of auditory interneurons? Actually, it is represented to various degrees in different neuron types. However, only one neuron type, AN4 (Fig. 4A), shows a spiking response, which very closely represents the behavioral responses (Fig. 4C). Song models with gaps of more than 3 to 4 ms (at 23 °C) nearly completely suppress spiking activity of AN4. Probably by some undescribed local interneuron (Stumpner, unpublished) each peak of synchronization in the tympanic nerve is converted to an inhibitory potential in AN4, and these IPSPs sum up to a complete inhibition of AN4's responses in a model with pulses and gaps (Fig. 4B).

Sound localization

Grasshopper males are small and therefore handicapped in gaining directional cues from any sound. A male most probably cannot use the physical interaural time differences which amount to 5–6 microseconds at most. Instead, it must rely on interaural intensity differences that result from the diffraction of sound waves around the body and from pressure gradient properties of its ears (see Michelsen, 1979, 1983, 1992 for reviews). Behavioral and neurophysiological experiments in *Chorthippus biguttulus* indicated an intensity difference between left

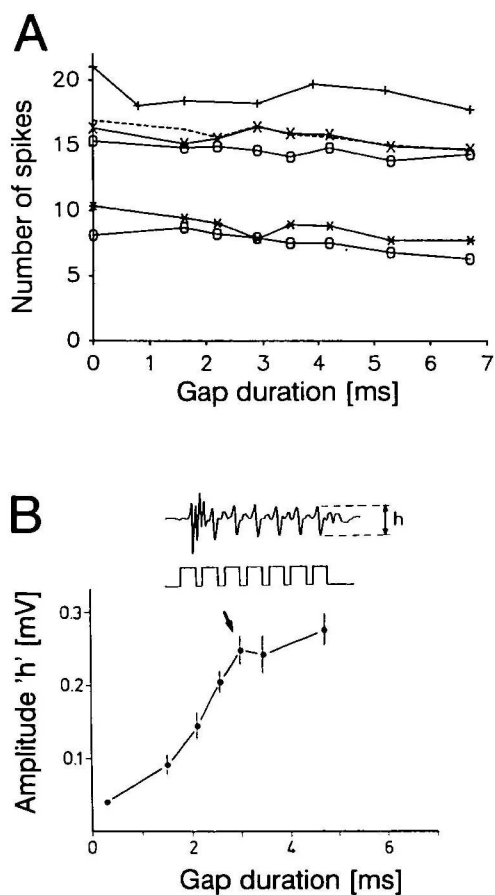


FIG. 3. (A) Responses of 6 different auditory receptors in 4 different individuals of *Ch. biguttulus*, 15–20 dB above threshold. Stimuli were white noise syllables with gaps of different durations inserted (pulse duration 7.5 ms). (B) Hook electrode recording of the tympanic nerve in a *Ch. biguttulus* female: response magnitude (amplitude 'h') of the averaged summed activity to models with different gap durations. The highest value of any peak after the first burst was measured. The inset indicates the averaged response with 3 ms gaps. Each response was averaged from 20 stimulus presentations, temperature 33°C. Modified after Ronacher and Römer, 1985, and Ronacher unpublished results.

and right ear in the range of 6–9 dB for white noise stimuli (von Helversen, 1984; Wolf, 1986). Such an intensity difference has a twofold effect upon the tympanic receptor discharges: receptors on the louder side, in their dynamic range, will respond with a higher spike rate than the contralateral receptors; in addition, the first spikes will be evoked earlier, due to the intensity

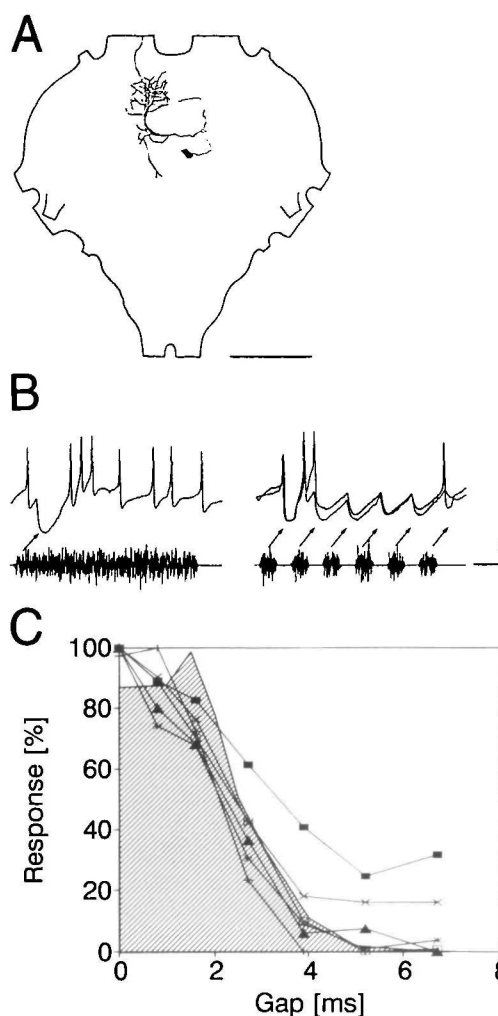


FIG. 4. (A) Morphology of the AN4 neuron in a *Ch. biguttulus* female (bar: 250 μ m). (B) AN4's spiking responses to a syllable with gaps (right) and without gaps (left). Note the summation of inhibitory potentials (arrows) in the right trace (two repetitions shown; bars: 10 ms, 5 mV). The diagram in (C) gives the numbers of spikes produced by four AN4 neurons in response to stimuli with different gap durations at intensities between 66 and 78 dB SPL. A behavioral response function (mean of three females) obtained at the same temperature is indicated by the shaded area. Modified after Ronacher and Stumpner, 1988.

dependence of the receptor's latency (Mörchen *et al.*, 1978). In principle, the CNS of a grasshopper could exploit both types of information. Indeed, behavioral experiments demonstrated that the animals are able to evaluate artificially generated inten-

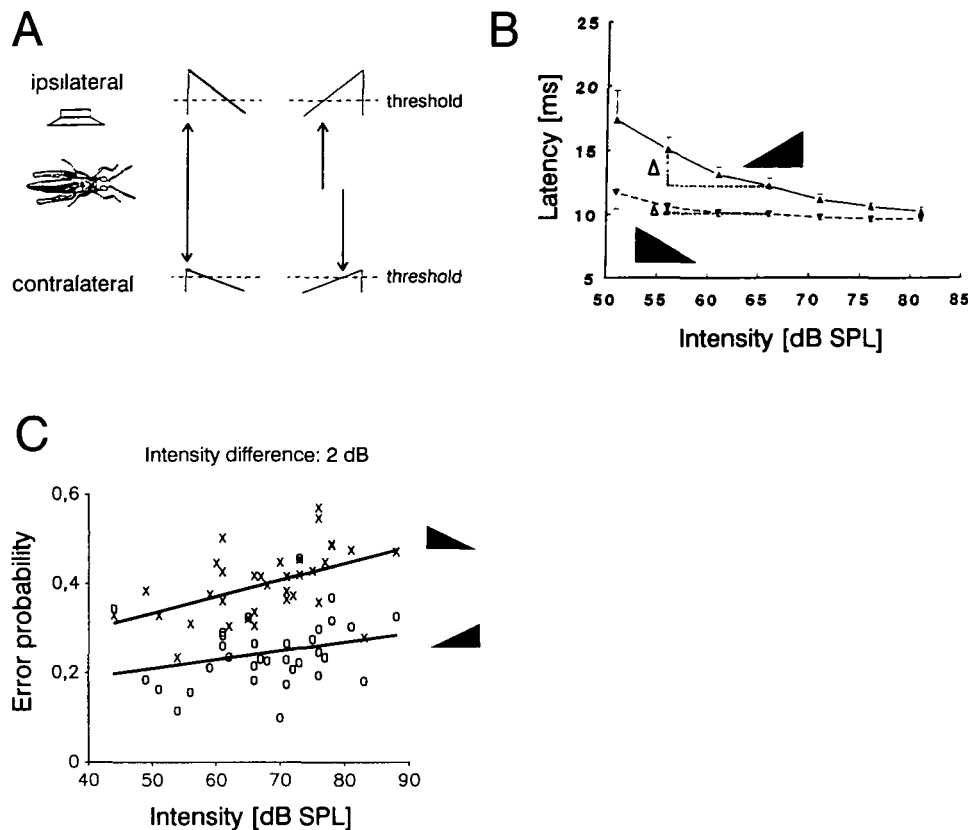


FIG. 5. Effect of pulse rise time on latency in auditory receptors of *Locusta migratoria*. (A) Scheme demonstrating, why slowly rising ramps in theory evoke larger latency differences between two given intensities than steep onsets. (B) shows that a steeper response function (see inserted 10 dB differences) can actually be observed in receptor cell responses. Note, however, the larger standard deviations with slowly rising ramps (50 stimulus repetitions per data point). In (C) the calculated error probabilities for an interaural intensity difference of 2 dB are shown for both response types; data from 8 receptor cells. See methods and text for details. Modified after Krahe and Ronacher, 1993 and unpublished results.

sity differences as well as time differences for phonotactic orientation (von Helversen and Rheinlaender, 1988).

As mentioned above, the songs of female *Chorthippus biguttulus* consist of sound pulses with long rise times (ca. 10 ms; Fig. 1 lower right), while the sound pulses in male songs show steep onsets (Fig. 1 lower middle; von Helversen, 1993). At first glance a steep intensity rise seems to be better suited to allow an exact comparison of the arrival times of spikes within the CNS. However, it has been suggested by Adam (1977) that slowly rising stimuli could improve directionality cues by virtue of producing an additional gain in latency difference between the receptors of both ears. Given a sound

pulse with a slowly rising ramp, it will take a shorter time to exceed the firing threshold of a receptor on the sound facing side than on the contralateral side (see Fig. 5A). Fig. 5B shows the latency vs. intensity curves of a single receptor fibre, for the two stimulus types indicated by insets. The curve for the slowly rising ramp is shifted towards higher latency values as compared with the mirror image stimulus type. Most importantly, however, the upper curve has also a steeper slope (see 10 dB differences indicated in Fig. 5B). This corresponds to the above mentioned gain in latency difference at a certain intensity difference. However, the response functions for ramp-like onsets do not only have a steeper slope, but data points also

show a distinctly higher variance compared to the other stimulus type (Fig. 5B). This increase in variance could counteract the mean gain in latency. In order to quantitatively assess the interaction of these two factors, a Monte Carlo simulation was performed. In this simulation the probabilities of errors of left/right-decisions were calculated a grasshopper would make by basing its decisions on the comparison of a pair of left and right receptors. The results of this calculation, for two data sets fitted to an intensity difference of 2 dB, are shown in Fig. 5C. As can be seen from that figure, the error probabilities are definitely lower for a stimulus with slowly rising ramp. This type of signal, therefore, obviously improves the directionality cues present in the receptors' responses. (It has to be mentioned that a similar evaluation based on spike count data revealed no significant differences between the two stimulus types. This means, however, that the use of ramplike communication signals would improve the latency cues while not affecting the other available cue for directional hearing, namely spike count.)

Nonetheless, it is also evident that in both cases the error probabilities of Figure 5C are high, as compared to an almost errorless behavioral response at an intensity difference of 2 dB. Obviously, the information that can be obtained from the comparison of a pair of receptors is not sufficient to explain the behavioral accuracy of the animals. Model calculations show that sampling from a larger population of parallel receptors (about 30) could decrease the error probability drastically. It remains to be investigated, however, whether the animals also might improve these directional cues by sampling over a longer period of time—at least the stridulation signals of females of this species last for about one second (Krahe and Ronacher, 1993).

Interestingly, so far no interneuron was found that strongly discriminates between the two stimulus types presented here, although the more phasic responses of certain neurons are clearly affected (Rammes and Ronacher, unpublished). Similar results have been reported for anurans (Hall, 1994).

We conclude that it is not by chance that

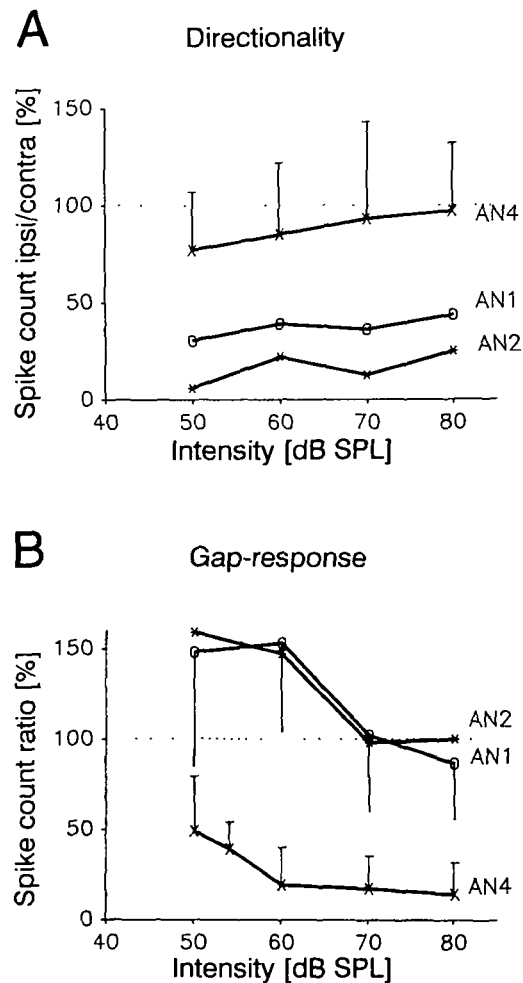


FIG. 6. Intensity response functions of three ascending auditory interneurons of *Ch. biguttulus*. (A) Differences between spike numbers for ipsilateral and contralateral stimuli (100% compares to "no difference"). (B) Differences between spike numbers for a stimulus with and without gaps (100% means "no difference", while 0 means "no response to stimulus with gaps"). Some standard deviations inserted only. Number of cells per function in A and B: AN1: 12, AN2: 6, AN4: 8. Modified after Ronacher and Stumpner, 1993 and Stumpner, unpublished results.

female grasshoppers utter this type of communication signals. It might well be an adaptation to support the males in performing their phonotactic approach towards the female. It could be worthwhile to investigate whether similar arguments apply also to the communication signals of other species, e.g. frogs that in their songs show also

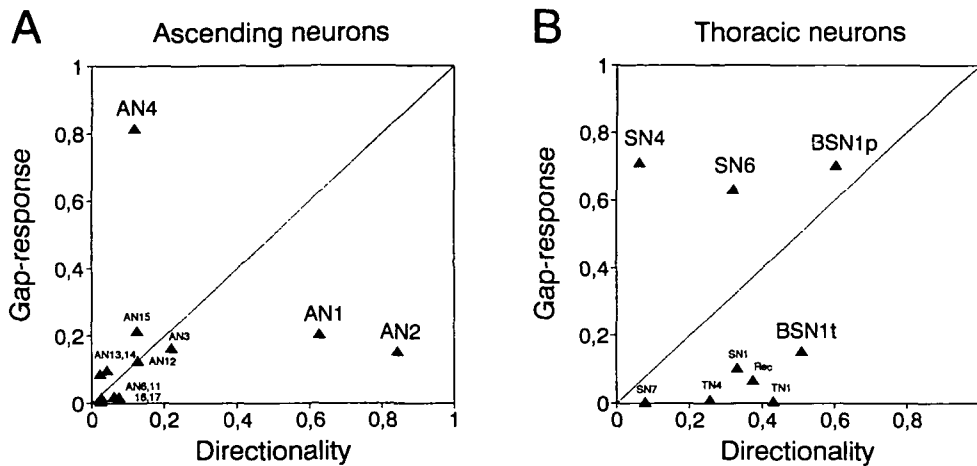


FIG. 7. Correlation between coding of sound direction and gap detection in (A) 12 ascending interneurons (=AN) and (B) 9 thoracic neurons (local=SN, bisegmental=BSN, T-shaped=TN; receptors=Rec) of *Ch. biguttulus* females. The higher the score, the stronger the representation of the respective information in the neuron's response. Normalization was done in such a way that only scores between 0 and 1 are possible. Names of neurons, which had at least one score above 0.5 were printed larger than the others. N cells evaluated: 3–20. For neuron names see Stumpner and Ronacher, 1991. (A): Modified after Stumpner *et al.*, 1993.

a variety of amplitude modulations with long rise times.

Parallel processing of sound pattern and sound direction

As mentioned in the Introduction, there is clear evidence from several behavioral studies for the existence of independent pathways for processing of song pattern and sound direction. On what level in the CNS does this separation take place? We investigated the responses of thoracic neurons (most probably with direct input from receptors) and of ascending neurons (most probably second order interneurons, see Römer *et al.*, 1988, Stumpner and Ronacher, 1991). For all interneurons we compared gap-detection as an example for pattern recognition (see above), and coding of directional information, as seen in response differences for sound from left and right side (ipsi- and contralateral).

In Figure 6A the data of 3 ascending auditory neurons of *Ch. biguttulus* are presented. AN1 and AN2, at most intensities, show higher responses to soma-contralateral stimuli than to soma-ipsilateral stimuli. These neurons, however, do not show reliable detection of gaps in a song model (Fig. 6B). The reverse is true for the AN4 inter-

neuron. This interneuron reliably detects syllables without gaps in a song model and is inhibited by syllables containing gaps. This response difference is nearly independent of intensity (Fig. 6B). However, directional responses of this neuron are relatively weak (Fig. 6A).

Fig. 7A shows a plot of "gap response" vs. "directionality" for ascending neurons. The scores are calculated from data as shown in Fig. 6 (see Methods). The majority of 12 neurons tested neither express high and intensity-independent directionality nor do they consistently discriminate between stimuli with and without gaps. AN4 shows a high score for gap response combined with low directionality. AN2 and AN1 show the reverse characteristic.

This separation of information onto independent channels for directional hearing and pattern recognition is less clearly expressed on the level of thoracic neurons (Fig. 7B). At least one of these cell types, BSN1p (the more phasically responding member of the BSN1-twin neurons; Stumpner, 1989) has a high score in both parameters. Interestingly, this neuron type also might be important for a further aspect of pattern recognition, namely marking of syllable onsets (Stumpner *et al.*, 1991).

These results suggest that among thoracic (1st order) interneurons song pattern and sound direction can be represented by the same neuron type. Ascending (2nd order) neurons, however, may constitute the parallel pathways postulated from behavioral results.

Conclusions

The extraordinary capacities of grasshoppers shown in Figure 2A and B obviously are adaptive for increasing the mating success and for preventing hybridization (see von Helversen and von Helversen, 1994; Kriegbaum, 1989; Kriegbaum and von Helversen, 1992). As for their neuronal basis, spike synchronization on parallel receptor fibres and improvement of directional cues by using ramp-like communication signals may constitute mechanisms relevant not only for grasshoppers (see articles by Hall, 1994; Schwartz, 1994). The high degree of information processing in unique members of 2nd order interneurons, however, may be characteristic for insects with nervous systems of relatively restricted numbers of nerve cells (see also Atkins, 1994). The selective advantage for a specific neuron to reliably respond to a certain stimulus parameter, therefore, may be higher in insects than in vertebrates having populations of neurons with similar response characteristics. The separation of different aspects of sound processing on lower levels and convergence on higher levels, on the other hand, may again be more widespread among different taxa (*e.g.*, Suga, 1989, Konishi, 1993, see also Walkowiak and Luksch, 1994), although it is disputed for crickets (Stabel *et al.*, 1989, Doherty, 1991). Switching from sensory to motor pathways for acoustic communication seems to involve higher centers in the brain—in grasshoppers and crickets as well as in vertebrates (see Walkowiak and Luksch, 1994; Huber, 1962).

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