Biol. Cybern. 79, 467–476 (1998)

Biological Cybernetics

Acoustic pattern recognition in a grasshopper: processing in the time or frequency domain?

Dagmar von Helversen, Otto von Helversen

Zoologisches Institut der Universität Erlangen, Staudtstrasse 5, D-91058 Erlangen, Germany

Received: 4 October 1997 / Accepted in revised form: 26 August 1998

Abstract. Males of the grasshopper *Chorthippus biguttulus* produce songs which consist of the stereotyped and rhythmic iteration of a sound unit (termed syllable) separated by distinct syllable pauses. Virgin females respond to this signal, and to similar artificial signals, with song phrases of their own. In behavioural experiments the response probability of virgin females can be measured with artificial acoustic stimuli. The stimuli consisted of an amplitude modulated noise the envelope of which was altered. We investigated several hypotheses on the mechanisms of conspecific song recognition with special emphasis on the question whether recognition occurs in the frequency domain or in the time domain. (1) Females of *Ch. biguttulus* required only the first five Fourier components of the envelope function (corresponding to 50 Hz for a fundamental frequency of 10 Hz) to detect the syllable/pause structure. In addition, they detected small gaps within syllables if the signal contained at least ca. 15 Fourier components (corresponding to a frequency of 150 Hz). Further experiments showed that the correct phase information of the Fourier components is necessary for recognition, indicating that pattern recognition is not achieved merely on the basis of band pass filtering. (2) A cross correlation between the signal and an assumed internal template yields only inconsistent predictions of the response probabilities. (3) The recognizer system probably works in the time domain, possibly by direct comparison of adjacent syllable and pause durations. It is not yet clear whether the duration of a syllable is evaluated with respect to the preceding or succeeding pause. We emphasize that the neural recognizer of the grasshopper does not only examine a signal for its similarity to an internal template, but that it also takes into account features that indicate an incorrect signal. This may be a general feature of neuronal pattern recognition systems which have been shaped by natural selection.

1 Introduction

Pattern recognition is a basic prerequisite of communication. Acoustic communication systems have evolved in many different animal taxa, in vertebrates, for example frogs, birds and mammals, as well as in insects, for example crickets, grasshoppers and cicadas. Since insect nervous systems consist of very few neurons as compared to vertebrates, it was expected that their recognizing systems may be simpler to understand. To date, however, no biological pattern recognizing system has been understood in detail, in any animal, on the level of neurons and their connections, despite some promising approaches (e.g. Schildberger 1984).

In the following we report on behavioural experiments with the grasshopper *Chorthippus biguttulus*. Females of this species recognize the song pattern of their males with astonishing accuracy. We use this example to draw attention to some peculiarites of pattern recognition in biological systems in comparison with artificial pattern recognition systems.

1.1 The acoustic communication system of Ch. biguttulus

Males of many grasshopper species produce sound by rubbing a file of cuticular teeth on the inner side of their hind femora against a specialized protruding vein on each forewing. The spectral properties of the song are therefore determined by the resonance spectrum of the wings; this is similar in many grasshopper species (Meyer and Elsner 1996). The decisive, species-specific information of the signal – apart from a few exceptions – is not contained in the carrier spectrum, but in the *amplitude modulation* of the carrier. The amplitude modulation is produced by the species-specific movement pattern of the hindlegs during the song (Elsner 1974; von Helversen and Elsner 1977).

The song of a *Ch. biguttulus* male consists of the stereotyped repetition of a sound unit, termed syllable

---

Correspondence to: O. von Helversen

Dedicated to Bernhard Hassenstein on the occasion of his 75th birthday

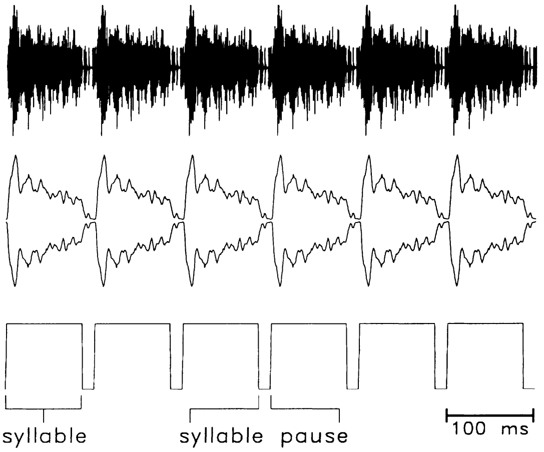

Fig. 1a–c. Part of the song pattern of a *Chorthippus biguttulus* male and the envelopes of artificial models used in the experiments. **a** Oscillogram of six syllables of a phrase; **b** envelope of this part of the song; **c** rectangularly modulated amplitude function which, when multiplied with a carrier of broad band noise, is an effective song model for the female

(Fig. 1); every syllable is produced by three (sometimes two or four) down-and-up movements of the hindlegs, followed by a short syllable pause. The durations of syllables (s) and syllable pauses (p) depend on temperature (at 30 °C, $s = 70$–90 ms and $p = 12$–20 ms; von Helversen 1972). The syllables and syllable pauses constitute a phrase (2–3 s in length) and several phrases (mostly 3–4) form a song.

On warm, sunny days, *Ch. biguttulus* males roam through the meadows which they inhabit and produce their calling song from time to time, normally at intervals of one half to several minutes. When a virgin female which is ready to mate hears the song of a conspecific male, she will respond with a song phrase of her own (Jacobs 1953; von Helversen and von Helversen 1994, 1997). A male, upon hearing a female answer, immediately responds and a duet ensues, in the course of which the male approaches the female and eventually copulates with her.

We used the response singing behaviour of the female to gain insight into pattern recognition mechanisms. The fact that playback of artificial song patterns (for instance, amplitude modulated noise) is effective in eliciting female response songs indicates that the values of certain stimulus parameters in these patterns match those of natural male songs. The artifical songs can be played back automatically with the aid of a computer, and the response song of the female can be picked up by a microphone connected to the computer so that the entire experiment can be performed using a fully automatic set-up (von Helversen and von Helversen 1983). With this experimental approach, using an input-output comparison, the functional organization of the recognizing system of the female can be investigated.

In neuroethology, recognizing systems are often called "neuronal filters". In this sense, a filter is not only a transfer function which changes an input to an output function. Instead, the output (if there is one) is considered to activate a subsequent neuronal circuit. In general, a "recognizer" is a neuronal system which, for every possible combination of pattern parameters, generates a weighting function, the value of which activates subsequent neurons, and, thereby, on crossing a threshold will lead to a response.

The acoustic pattern recognition system of *Ch. biguttulus* is relatively well studied (e.g. von Helversen 1972; von Helversen and von Helversen 1983, 1987, 1997). An effective minimal song model is rectangularly modulated white noise, wherein the syllable duration s and the syllable pause duration p have values similar to the male song ($s = 80$ ms and $p = 12$–15 ms; von Helversen 1972, Fig. 1). Interestingly, the recognition system accepts syllables and pauses in a fairly large range provided that the patterns have a ratio of syllable: pause durations of around 6. This seems to be an adaptation to the temperature dependence of the song (von Helversen and von Helversen 1981, 1994).

1.2 Aim of the study

In the following we test several hypotheses on the neuronal mechanisms, which could allow the recognition of the species-specific song pattern in *Ch. biguttulus*.

1. The stereotyped repetition of the syllable-pause pattern suggests that the recognition system works in the *frequency domain* (of the amplitude modulation) and not in the time domain. In the cricket species *Gryllus campestris* and *G. bimaculatus*, an essential part of the filter system can be described as a simple *band-pass* (Thorson et al. 1982; Huber and Thorson 1985; Schildberger 1984; Schildberger et al. 1989). Can this hypothesis be applied to song pattern recognition in *Ch. biguttulus*?
2. In some cases, for example in birds, the song pattern received by the nervous system appears to be compared to an internal "template". We ask whether a *cross-correlation* with an internal template could be the basis of recognition in *Ch. biguttulus*.
3. Alternatively, the process of filtering could work in the *time domain*, so that durations of syllables and pauses are compared. If this is the case, is the *order* of correct pauses and correct syllables important?

Further, we also discuss the basic question of whether the recognition process is mainly an analysis of the *similarity to an internal template*, accepting patterns on the basis of the degree of matching to such a template (as do most artificial recognition systems, and as assumed by most models of biological recognition systems, e.g. Ronacher 1998), or whether an *exclusion principle* is also applied, such that patterns that contain wrong components are rejected. These questions will be covered in three consecutive sections.

2 Materials and methods

Virgin females of *Ch. biguttulus* were used in all experiments. These were caught as subadults in the field and raised to adults in the laboratory. Five days after moulting, most females started to respond to the species-specific male song.

The experiments were run in an automatic computer-controlled set-up (von Helversen and von Helversen 1983). The female was placed in a small gauze cage within a thermostatic chamber (temperature constant at 30 °C) lined with sound-dampening material. The different song models were generated on a computer by modulating broad band noise (2–40 kHz) with an envelope function, and were presented to the female via a piezo-electric speaker (at 70–76 dB SPL). The number, sequence and timing of stimuli could be manipulated. In most cases the stimuli, consisting of three phrases (each 3 s in length), were replayed at intervals of 30 s or 60 s, such that effective and ineffective models followed randomly. The computer also monitored the female's response by way of a microphone, and recorded the number of responses to the different test stimuli. The effectiveness of a stimulus was measured as the proportion (in percent) of presentations of that stimulus that evoked a response. For further details of the experimental procedure, see von Helversen and von Helversen (1983).

3 Is the recognition system based on frequency analysis and subsequent band-pass filtering of the envelope function?

The cricket species *Gryllus campestris* and *G. bimaculatus* use band-pass filters to recognize the envelope function of the species-specific song pattern (the carrier frequency is a 5 kHz sinewave). Thorson et al. (1982) showed that the 30 Hz component which is given by the syllable period plays the most important role in song recognition in these crickets, and that indeed only the rate, not the duty cycle (s/p ratio), is evaluated. Doherty (1985) demonstrated that the animals also evaluate the chirp rate (3 Hz), and finally Wendler (1990) showed, in an elegant experiment, that the recognition system of these two species works like a double-band-pass filter for 30 Hz and for 3 Hz, and that (at least when the motivation of the female was high enough) either of the two band-passes sufficed for a well-oriented phonotactic approach. This would correspond to the idea of one double-band pass or of two separate band-pass filters, the outputs of which are connected by a logical OR. Hennig and Weber (1997) suggested, for the recognition system of another cricket species, *Teleogryllus commodus*, a filter system which could be best explained as consisting of two band-pass filters (a chirp and a trill filter) which are connected by a logical AND, since, for the phonotactic reaction of the animal, activation of both filters was necessary.

In the following we test the hypothesis whether band-pass filters or possibly parallel band-pass filters, the outputs of which are connected by logical functions, could explain the recognition process in *Ch. biguttulus* females. In particular we investigated the following questions. What is the range of frequencies within which the envelope function is evaluated by the recognition system of the grasshopper? How many Fourier components of the envelope are evaluated? Is the phase spectrum important or are signals discriminated only on the basis of the amplitude spectrum?

Before designing an appropriate experiment, the following considerations should be kept in mind:

1. Band-pass filtering is meaningful only with respect to the envelope function, i.e. the amplitude modulation, and not with respect to the carrier frequencies. The carrier spectrum also plays a role, for example in the recognition of sex, but it can be varied within a broad range without reducing the effectiveness of a sound stimulus (von Helversen and von Helversen 1997).
2. In the Fourier analysis of an envelope and the subsequent multiplication of parts of a Fourier spectrum with a carrier for the construction of new sound models, it must be guaranteed that all envelopes have only positive signs. Therefore we could not start from envelopes with a rectangular modulation down to zero. Since for the grasshopper a signal-to-noise ratio of 8–10 dB is sufficient for recognition (von Helversen 1979) and, in the natural song, pauses are not completely silent (von Helversen and von Helversen 1997), we started with a stimulus with a modulation between 0.2 and 0.8 instead of 0 and 1.
3. The recognition system of *Ch. biguttulus* is adapted to the temperature dependence of the song (von Helversen and von Helversen 1981). As the male song rate changes by a factor of 4 within the suitable temperature range, the fundamental frequency of the envelope function (>20 Hz at 40 °C and as low as <6 Hz at 20 °C) is not very important. The decisive factor is the syllable-pause ratio, that is the amplitudes and phases of the Fourier components and not their fundamental frequency. Therefore we kept the fundamental frequency constant at 10 Hz in all experiments; all frequency components in Figs. 2 and 3 are multiples of 10 Hz.

3.1 What is the effective frequency range of the amplitude modulation?

In a first series of experiments we decomposed the envelope of the effective pattern "rectangular modulation with a syllable duration $s = 86$ ms and syllable pause $p = 14$ ms" into its Fourier components and tested how many components are necessary for the animals to recognize the signal. The results (Fig. 2, upper part) revealed that for four out of six females only the first five components were necessary to reach the maximum response level. Since the fundamental frequency was 10 Hz, this corresponds to a highest Fourier component of 50 Hz. The two less motivated females also showed a rise of response probability at higher Fourier components.

In addition, we conducted the same experiment with the natural song; in a natural syllable the sound pressure function was rectified, the moving average of the amplitude of this rectified signal calculated and this function Fourier analysed. We obtained the same result as in the first experiment (Fig. 2, lower). With more than ca. five Fourier components the response probability did not increase further.

Previous experiments have shown, however, that *Ch. biguttulus* females do not ignore modulation frequencies higher than 50 Hz: females are able to detect

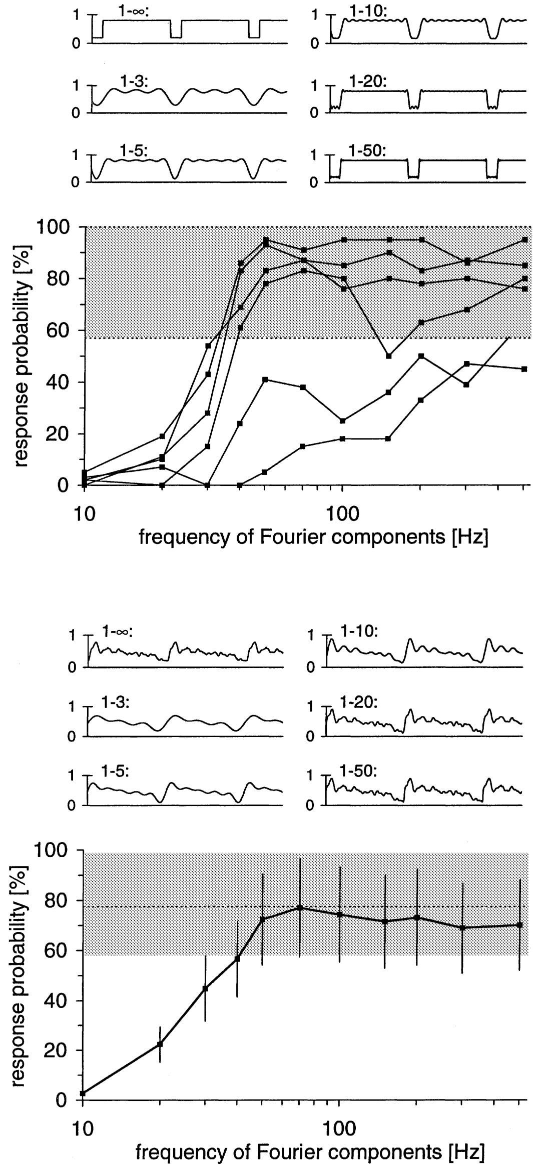

Fig. 2. Minimum number of Fourier components of the envelope function of the song necessary for recognition. *Above*: the envelope function of an effective pattern (rectangularly modulated broad band noise with syllable and pause durations of $s = 86$ ms and $p = 14$ ms) was Fourier analysed and restored stepwise from the Fourier component 1 (only fundamental frequency), the Fourier components 1 and 2, 1 to 3, and so on until 1 to 50 (see *insets*). These functions were multiplied with broad band noise and used as sound models. The response probability of six individual females was measured in an automatic, computer-controlled setup (n = 21–60 tests/data point). The response probability (in % of presented stimuli) is plotted against the frequency of the highest Fourier component present in the envelope (logarithmic scale). As the fundamental frequency was 10 Hz, the frequency of the kth Fourier component is k*10 Hz. The *hatched band* marks the range of response probability to the reference pattern (containing all Fourier components). *Below*: the same procedure was applied to the amplitude modulation of the natural song (see text). Means and SE for 5 females; 76 tests per point. The *hatched band* represents the SE of the mean response probability to the reference pattern (containing all Fourier components)

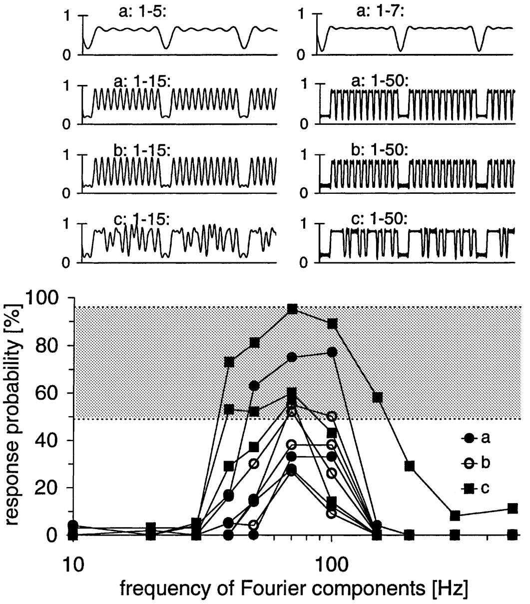

Fig. 3. Minimum number of Fourier components necessary for the detection of small gaps within the syllable. Three different models (a, b, c) which are not effective because of the gaps in their syllables (*inset, right side*) were Fourier analysed and stepwise restored from the Fourier components according to the process described in Fig. 2. Response probability is plotted against the frequency of the highest Fourier component (log. scale); as the fundamental frequency was 10 Hz, the frequency of the kth Fourier component is k*10 Hz. The symbols a, b, c correspond to the three different reference models.The test stimuli between 15 and 100 Hz contain sufficient information on the syllable structure, but obviously not enough information on the gaps; therefore they were responded to by the grasshopper females (N = 3, 4, 3 females for stimulus series a, b, c respectively, n = 22–65 tests/data point). The *upper line* of the *inset* gives the envelope functions for the Fourier components 1–5 and 1–10 which are similar for all three stimulus types; *below*: components 1–15 and 1–50 are given for the stimulus types a, b and c as examples

very short gaps (1.5–2 ms duration at higher intensities) within syllables and they do not respond to songs with "gappy" syllables (von Helversen 1972, 1979). Thus, higher frequency components can completely destroy the effectiveness of a pattern. We therefore repeated the experiment with patterns that were expected to be ineffective because of the gaps within the syllables.

Indeed we found, independent of whether the gaps were 2 ms or 3 ms long (Fig. 3 inset a, b) and whether they were regularly spaced or not (Fig. 3 inset c), that high frequency components are detected (Fig. 3): the artificial stimuli which had too few Fourier components (≤4) were not responded to, as it was the case in the first experiment. Stimuli with 5–10 Fourier components evoked good responses, because the frequency range of the Fourier components was not large enough to depict the gaps. Stimuli with frequency components of more than 150 Hz were again not answered. This indicates that the grasshoppers can detect modulation frequencies up to at least 150 Hz.

The results depicted in Fig. 3 do not demonstrate the presence of a band-pass filter, although they appear to at first glance, since a band-pass filter would ignore the addition of higher Fourier components. Rather they suggest that the grasshopper, in a two-tailed process, tests the stimulus for its similarity with a template and, on the other hand, also examines parameters (in this case

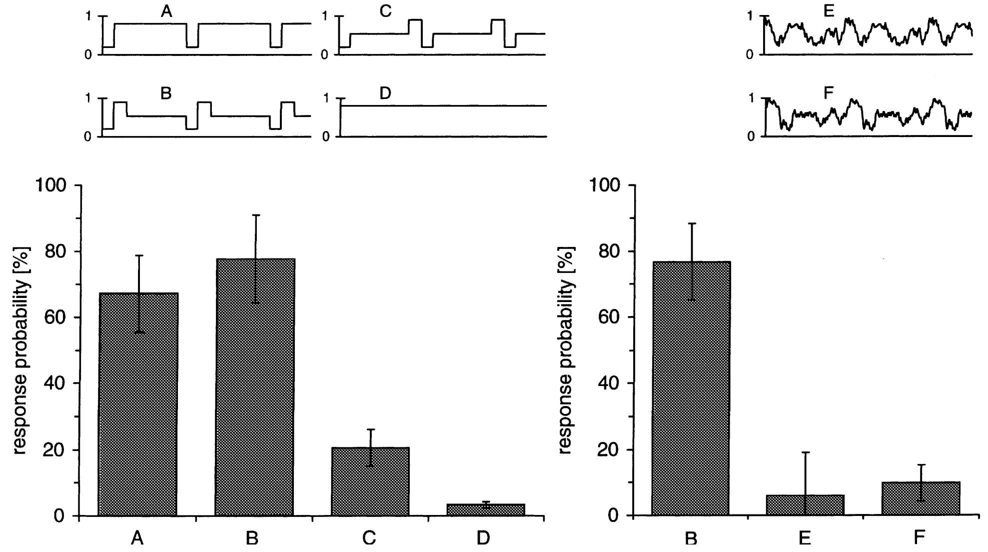

Fig. 4. Phase information of the envelope Fourier spectrum is necessary for song recognition. *Left side*: four different artificial song models were offered to the females. *A*: rectangular modulation with the effective syllable-pause combination ($s = 86$ ms, $p = 14$ ms); *B*: the same model, but with the first 10 ms of each syllable enhanced in amplitude; *C*: the same model as *B*, but played backwards; *D*: a phrase of continuous noise as a control. *Right side*: for all 50 Fourier components of the effective stimulus pattern *B* (*inset left side*), the amplitude values were kept constant; the phase values were retained (*B*), or taken from a random generator (*E* and *F*). The resulting envelope functions (see *insets*) were used to modulate broad band noise. $N = 4$ females, $n = 14$–63 tests per point

high frequency components) which might prove that the signal is *incorrect*. The frequency ranges of the two processes, analysis of the basic pattern and gap detection, are different.

3.2 Is the amplitude spectrum sufficient for recognition ?

Typical biological band-pass filters only rely on the amplitude or power spectra of the signal, while neglecting the phase information. Therefore we tested whether the correct phase relations of the Fourier components are of importance for the song recognizing system of this grasshopper:

1. When a signal is played backwards, all phases are mirrored, whereas the amplitude information is held constant [1]. Do the grasshoppers respond independent of whether the signal is played forwards or backwards?
2. In a second experiment, we used the Fourier transformation of the above-mentioned pattern ($s = 86$, $p = 14$), retained all amplitudes up to component number 50, but replaced all phases by values that had been chosen by a random generator.

Both experiments (Fig. 4) clearly demonstrate that the grasshoppers need not only the correct amplitude but also the correct phase information: stimuli B and C (left side) and stimuli B, E, and F (right side) differ only with respect to their phase spectra, but only B is effective. Therefore the recognizing system cannot be a band-pass filter, or combination of band-pass filters, evaluating only the power spectrum. (The term "filter" is used here in the above-mentioned sense as usual in neuroethology).

4 Is the recognition system based on a cross-correlation with a template function?

The idea of "acoustic templates" underlying recognition received support mainly from observations on birds. Marler (e.g. 1990, 1996) and Konishi (e.g. 1985) found that young birds first develop a template for their population-specific song pattern in an imprinting-like process and that this template is later used by the females to recognize the correct male song and by the males to adjust their own song to the template. It is not known how an incoming acoustic pattern is matched to the template, but, interestingly, in electrophysiological experiments Vicario (1994) found excitation patterns in the motor cortex of song birds that were coupled to the song input. In insects, the same idea has been discussed, particularly in combination with the "genetic coupling" hypothesis (Hoy 1978, Doherty and Hoy 1985).

The simplest way to compare a time pattern to a template is a cross-correlation between the two functions (Weber and Thorson 1989). Cross-correlation, for instance, seems to play an important role in the comparison of call and echo in bats (e.g. Altes 1981; see also Menne and Hackbarth 1986). In artificial pattern recognition systems, cross-correlation is commonly used to test for similarity between a known model element and an input pattern (e.g. sonagram analysis; Williams and Slater 1991).

Therefore we tested the hypothesis whether the song recognition system of *Ch. biguttulus* functions as a cross-

---

[1] This hint we owe to B. Hassenstein

correlator, comparing the input with an internal template. We used two different approaches:

1. A cross-correlation compares two rhythmic processes and the correlation is maximal when both rhythms coincide; therefore disruption of the rhythm of the stimulus signal should diminish the maximum value of the cross-correlation.
2. If the periods of signal and template are equal, then in the case of two functions which have values only of "0" and "1", the cross-correlation procedure will measure similiarity only by counting the time intervals in which both functions are "1", independent of how these values are distributed over the period.

Approach 1: We played artificial song models to the grasshopper, in which the effective syllable-pause combination $s = 80/p = 15$ ms was interrupted by syllables of different durations (see Fig. 5). Such intercalated syllables did not significantly affect the females' responses, even though the rhythm was drastically altered. Even when we randomly inserted syllables of a different duration between consecutive pairs of correct syllables and pauses (Fig. 5, rightmost column), thereby destroying the basic rhythm almost totally, the females were able to recognize these signals without any difficulty and judged them as correct.

Approach 2: We constructed signals that had the same maximum value (0.85) of cross-correlation with the template $s = 80/p = 15$ ms, but a different distribution of "0" values. By transferring parts of a syllable pause into gaps within the syllable it is possible without difficulty to find patterns with the same cross-correlation value but with one of them effective and the other ineffective (Fig. 6). Finally, we examined for many different stimuli the relation between stimulus effectiveness (female response probability) and the maximum value of the cross-correlation. There was no correspondence between effectiveness and the maximum value of cross-correlation (Fig. 7).

These results contradict the idea that cross-correlation with an internal template plays a role in the recognition process in the grasshopper. The results of Fig. 5 show in addition that the rhythm of the song does not carry important information. Thus, "similarity" as measured by a cross-correlation is not a sufficient criterion for recognition. Obviously, the recognition system also evaluates additional parameters which show that the signal should be classified as "incorrect" or "wrong".

5 The importance of neighbouring syllables and pauses and their order

As the two hypotheses derived from other taxa (bandpass filtering and cross-correlation with an internal template, both of which make use of the stereotyped rhythmic repetition of the syllables) do not correctly predict the behaviour of the animals, it seems likely that the recognition system works in the time domain rather than in the frequency domain. The neuronal system then may evaluate neighbouring syllable and pause durations. This is suggested by the result (Fig. 5) that stimuli in

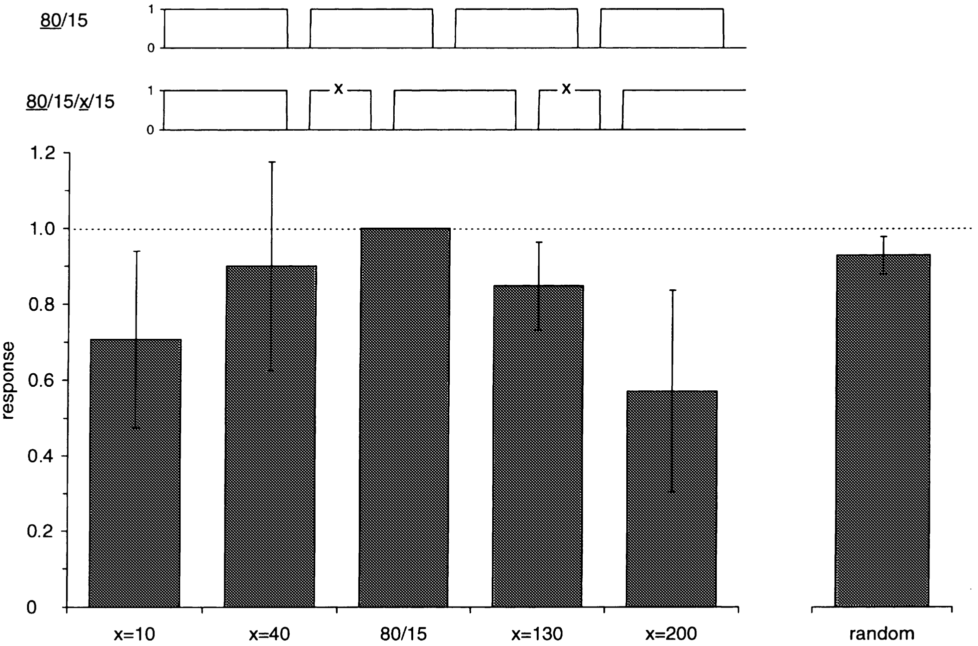

Fig. 5. Effectiveness of song models in which the rhythm was disturbed. Starting from the effective pattern with a syllable duration $s = 80$ ms and a pause duration $p = 15$ ms (short notation 80/15), every second syllable duration was changed, resulting in a pattern (syllable underlined) ...x/15/80/15/x/15/80/15... with $x = 10$, 40, 130 or 200 ms. Female response probability was not much reduced by insertion of the "wrong" syllables, though the rhythm was drastically altered. *Right-most column*: even when every second syllable was replaced by a syllable of different duration (here in the order 10, 130, 40, 200 ms), the model was nearly as effective as the original 80/15 combination. Obviously, for the grasshopper the reiteration of the combinations ... 15/80/15... was sufficient for recognition, although there was no constant rhythm. $N = 40$ females; ordinate normalized to the response probability to 80/15

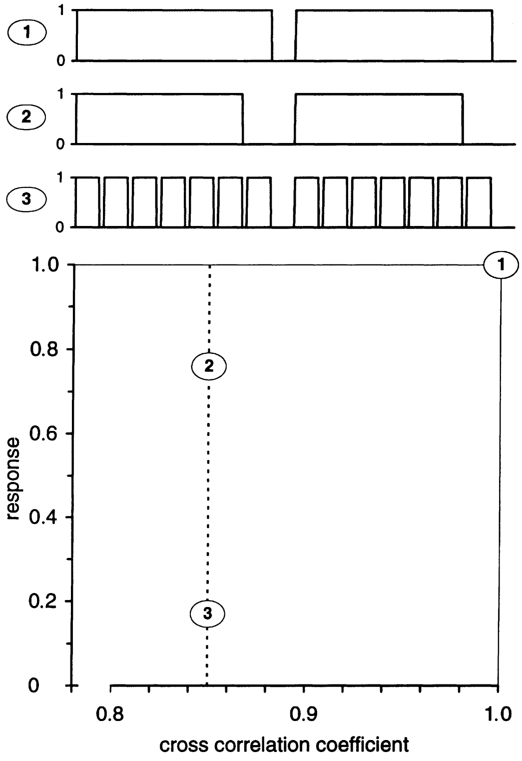

Fig. 6. Comparison of the effectiveness of two patterns (*2* and *3*) with the same maximum value of the cross-correlation with a template. Models (*2*) and (*3*) have the same maximum value of the cross-correlation function relative to model (*1*), the pattern 80/12, because they have the same overall duration of pauses: model (*2*) is the pattern 70/22, with pauses 10 ms longer than normal, (*3*) with 5 gaps of 2 ms within the syllable. Both axes normalized; *circles* (*2*) and (*3*) give the mean response value of 4 females (n = 27–74 tests). Obviously, cross-correlation with an internal template did not determine the effectiveness

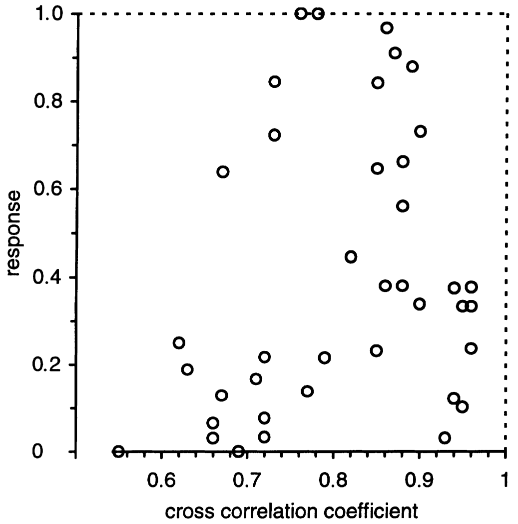

Fig. 7. Relation between effectiveness of a sound pattern and the maximal value of its cross-correlation to an effective template. In analogy to Fig. 6, the effectiveness of many different stimulus patterns was compared to their maximal value of cross-correlation to the template s = 80, p = 15. No dependence could be found. (Both coordinates are normalized, the ordinate to the response probability released by the template, the abscissa to the autocorrelation value of the template)

which a correct syllable was framed by correct pauses evoked good responses. The reciprocal question "will a stimulus be effective when a correct pause duration is framed by two correct syllables?" cannot be answered in a simple experiment, as introducing pauses which are too long drastically reduces the response [Fig. 8; interestingly, this is in contrast to introducing syllables which are too long (Fig. 5: x = 130, 200 ms) – we had chosen syllables and pauses which are about four times longer than the optimal values, giving s = 300 ms and p = 60 ms].

If we assume that the recognition system measures and relates the duration of neighbouring syllables and pauses, the next question is whether the order in time is also important. That the order of units in a biological signal may be of importance with respect to recognition has been shown for another grasshopper species (Stumpner and von Helversen 1992) in behavioural experiments, and for birds (Lewicki 1996) in both behavioural and electrophysiological experiments.

We designed two experiments to investigate the significance of the order "correct syllable/correct pause" or "correct pause/correct syllable". In the first (Fig. 9) we inserted a "wrong" syllable-pause combination before or after the correct syllable and pause. The "wrong" combination was $s = 30/p = 5$ ms. This results in two possible patterns (syllables underlined) ...5/80/15/30/5... and ...15/80/5/30/15..., so that the values which belong together are combined in a different order. The result of this experiment revealed no difference in the effectiveness of the two patterns (Fig. 9E, F; A–D serve as controls).

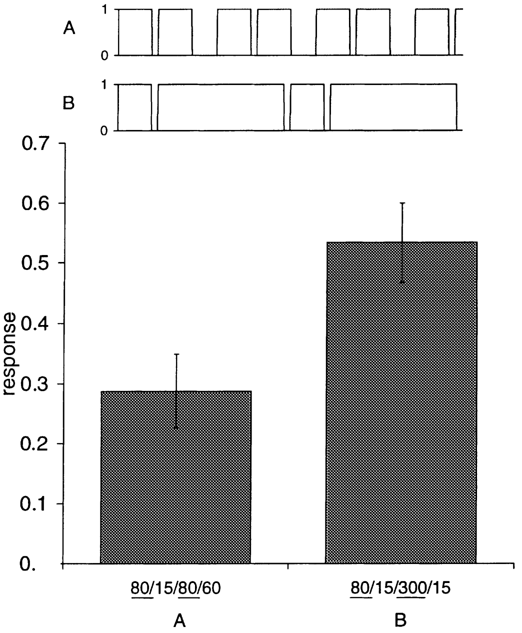

Fig. 8. Effectiveness of sound models in which a correct pause was framed by two correct syllables (*A*) or a correct syllable was framed by two correct pauses (*B*), achieved by insertion of pauses (*A*: p = 60 ms) or syllables (*B*: s = 300 ms; compare insets) that were four times their normal length. Very long pauses reduced effectiveness more than did long syllables. Mean and SE for 11 and 6 females for *A* and *B* respectively

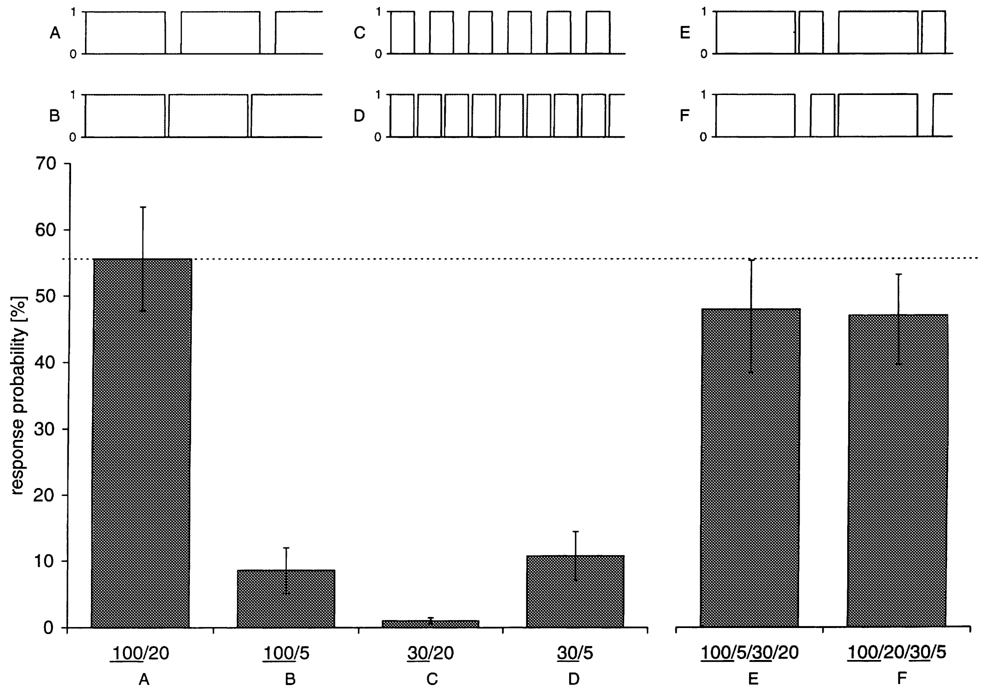

Fig. 9. Importance of the order of syllable and pause. We started with the effective syllable/pause combination $s = 100$ ms, $p = 20$ ms (*A*). None of the control combinations $s = 100/p = 5$ (*B*), $s = 30/p = 20$ (*C*), and $s = 30/p = 5$ ms (*D*) was effective. The two critical combinations, (*E*) with correct pause after the correct syllable and (*F*) with correct pause leading the correct syllable, were equally effective. Means and SE for 5 females

In the second experiment we inserted a syllable block consisting of 2 ms long pulses with 2 ms long pauses, which were repeated 20 times, to produce an 80 ms long "interrupted syllable". This interrupted syllable was inserted before or after the correct syllable/pause combination, producing stimuli with the order "correct pause before or after correct syllable" (Fig. 10). In this experiment, the combination "correct pause *before* correct syllable" was clearly preferred.

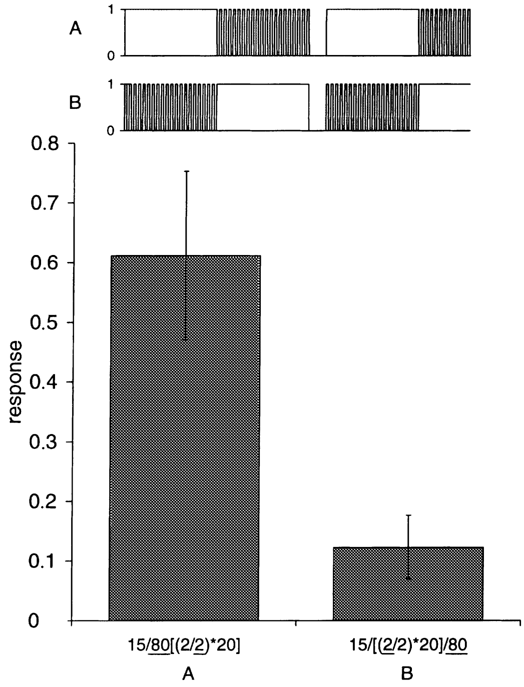

Fig. 10. Importance of the order of syllable and pause. An "interrupted syllable" constructed by 20 repetitions of a pulse of 2 ms duration and a gap of 2 ms duration was inserted to separate the syllable $s = 80$ ms from the pause $p = 15$ ms. This is possible in two ways, producing the combinations "correct pause/correct syllable" (*A*) and "correct syllable/correct pause" (*B*). The first order was much more effective than the second one. $N = 4$ females, $n = 31$–177 tests per column

The results presented in Figs. 5, 8, 9 and 10 suggest that the recognizing system of the grasshopper *Ch. biguttulus* evaluates neighbouring syllables and pauses in the time domain and relates their values. It remains unclear whether and under what conditions the order of syllables and pauses does play a role.

6 Discussion

The songs of many Orthopteran species, including crickets, bushcrickets and grasshoppers, consist of rhythmic repetitions of highly stereotyped sound units. This suggested that the neuronal pattern recognizing systems might work in the frequency domain. Our experiments with the grasshopper species *Ch. biguttulus* reveal that pattern recognition in this species does not occur on the basis of two simple mechanisms proposed: band-pass filtering and cross-correlation with an internal template.

The idea of band-pass filtering, including more complex versions such as parallel band-pass filters, the outputs of which are connected by logical operations, can be refuted for the grasshopper, because the phase information cannot be neglected. In this respect, the neural mechanism enabling pattern recognition seems to be more complex in grasshoppers than in crickets, as several studies suggest that recognition in crickets may well be mediated by a band-pass filter or a combination of two band-pass filters (Schildberger 1984; Wendler 1990 for *Gryllus*; Hennig and Weber 1997 for *Tel-*

eogryllus commodus). Interestingly, in crickets, Weber and Thorson (1988, 1989) also demonstrated that higher frequency Fourier components do not inhibit the song recognition provided the 3 Hz and 30 Hz components are present in the signal. When they presented a signal with a syllable rate of 60 Hz, the females showed excellent phonotaxis as soon as every second pulse was decreased by ca. 3 dB, thereby generating a 30 Hz component. These experiments support the idea that the song recognizing mechanisms in crickets are simple band-pass filters that ignore the phase information.

Cross-correlations between time functions which compare the incoming auditory excitation pattern to an internal template are also not sufficient to explain the response selectivity in the grasshopper *Ch. biguttulus*. The same conclusion was drawn by Pollack and Hoy (1979) from their "shuffled song" experiments with the cricket *Teleogryllus oceanicus*.

Therefore, the neuronal recognition network of the grasshopper probably works in the time domain. The simplest idea is that the neuronal excitation caused by syllable onsets and by syllable offsets is tested for coincidence after a certain delay. Models of this type have been suggested (e.g. Reiss 1962, 1964), but, to date, there is no electrophysiological evidence supporting this idea from recordings from brain neurons.

Why then are the units so rhythmically and stereotypically repeated in the songs of so many species? The most probable answer seems to be that repetition is the simplest way of improving the signal-to-noise ratio.

6.1 Two ways to recognize a signal: 'evaluation of similarity' and 'rejection of incorrect features'

A signal can be detected by two ways: (1) an analysis of similarity to a template can measure the degree of matching of the signal to this template and classify the signal as "accepted" or "correct", when the difference is smaller than a certain threshold, or (2) an exclusion principle can be used, and the signal will be classified as "incorrect" as long as certain features are detectable, and as "correct" only when none of these features is present or detectable. These two principles, of course, are not mutually exclusive.

Typically, in the environment of an acoustically communicating animal a limited number of "signal competitors" exist. Thus biological recognition systems are expected not only to evolve mechanisms that detect correct signals but also *exclude incorrect signals*. The task of detecting incorrect signals and excluding them may sometimes be easier to solve than an extensive evaluation of a large number of parameters. Having evolved as opportunistic and unpredictable responses to the forces of selection, biological pattern recognition systems are therefore often difficult to understand in terms of the principles of design engineering. A combination of the two major principles of pattern recognition (analysis of similarity versus rejection of incorrect components) may well be a general feature of neuronal mechanisms of pattern recognition which have been shaped by natural selection.

Our experiments revealed at least two features of acoustic signals which strongly reduce the effectiveness of song models in *Ch. biguttulus*:

1. The insertion of small gaps into syllables totally destroys the effectiveness of a signal. This implies that relatively high frequency components of the signal envelope can be measured (see Fig. 3).
2. In contrast to long syllables (up to ca. 300 ms or more) which reduce effectiveness only slightly (see Fig. 8), the insertion of long pauses (> 60 ms) drastically reduces the response.

Neuronal networks always combine excitatory and inhibitory processes. In the nervous system of *Ch. biguttulus* all known data indicate that auditory information is in a first stage distributed over a number of parallel channels, each with its own filter properties. Only in the brain do the different channels with their excitatory and inhibitory inputs converge upon an as-yet unidentified "neuronal pattern recognizer" (see, for example, Stumpner et al. 1991).

It is surprising that, until now, artificial speech recognition systems and similar technical signal detection systems do not, to our knowledge, use the dual principles of acceptance and rejection, but rely only on measures of similiarity.

Acknowledgements. We acknowledge gratefully the help of Alfred Schmiedl and Johannes Hofmann in designing the hard- and software of the computer-aided experiments. We thank U. Habbe for developing the preliminary stimulus programs concerned with Fourier analysis and the generation of sinewave envelope functions, and H. U. Kleindienst for providing us with the final computer programs in this field. Our thanks are also due to Maria Bauer for running numerous experiments and preparing most of the figures and to Rohini Balakrishnan who improved the English translation immensely. We thank B. Ronacher and D. Varju for making valuable suggestions to improve an earlier version of the manuscript. This article is dedicated to Bernhard Hassenstein, whose clarity of thought and rational approach to all problems was an inspiration to us.

References

Altes RA (1981) Echo phase perception in bat sonar? J Acoust Soc Am 69:505–508

Doherty JA (1985) Trade-off phenomena in calling song recognition and phonotaxis in the cricket *Gryllus bimaculatus* (Orthoptera, Gryllidae). J Comp Physiol 156:787–801

Doherty JA, Hoy RR (1985) The auditory behavior of crickets: some views of genetic coupling, song recognition, and predator detection. Q Rev Biol 60:457–472

Elsner N (1974) Neuroethology of sound production in gomphocerine grashoppers. I. Song patterns and stridulatory movements. J Comp Physiol 88:67–102

Helversen D von (1972) Gesang des Männchens und Lautschema des Weibchens bei der Feldheuschrecke *Chorthippus biguttulus* (Orthoptera, Acrididae). J Comp Physiol 81:381–422

Helversen D von, Helversen O von (1981) Korrespondenz zwischen Gesang und auslösendem Schema bei Feldheuschrecken. Nova Acta Leopoldina 245:449–462

Helversen D von, Helversen O von (1983) Species recognition and acoustic localization in acridid grasshoppers: a behavioural approach. In: Huber F, Markl H (eds) Neuroethology and behavioural physiology. Springer, Berlin Heidelberg New York, pp 95–107

Helversen D von, Helversen O von (1997) Recognition of sex in the acoustic communication of the grasshopper *Chorthippus biguttulus* (Orthoptera, Acrididae). J Comp Physiol A 180:373–386

Helversen O von (1979) Angeborenes Erkennen akustischer Schlüsselreize. Verh Dtsch Zool Ges 1979:42–59

Helversen O von, Elsner N (1977) The stridulatory movements of acridid grasshoppers recorded with an opto-electronic device. J Comp Physiol 122:53–64

Helversen O von, Helversen D von (1987) Innate receiver mechanisms in the acoustic communication of orthoperan insects. In: Guthrie DM (ed) Aims and methods in neuroethology. Manchester University Press, Manchester, pp 104–150

Helversen O von, Helversen D von (1994) Forces driving coevolution of song and song recognition in grasshoppers. Prog Zool 39:253–284

Hennig RM, Weber T (1997) Filtering of temporal parameters of the calling song by cricket females of two closely related species: a behavioural analysis. J Comp Physiol A 180:621–630

Hoy RR (1978) Acoustic communication in crickets: a model system for the study of feature detection. Fed Proc 37:2316–2323

Huber F, Thorson J (1985) Cricket auditory communication. Sci Am 253:60–68

Jacobs W (1953) Verhaltensbiologische Studien an Feldheuschrecken. Z Tierpsychol Beih 1:1–228

Konishi M (1985) Birdsong: from behaviour to neuron. Ann Rev Neurosci 8:125–170

Lewicki MS (1996) Intracellular characterization of song-specific neurons in the zebra finch auditory forebrain. J Neurosci 16:5854–5863

Marler P (1990) Song learning: the interface between behaviour and neuroethology. Phil Trans R Soc Lond 329:109–114

Marler P (1996) Sensory templates in species specific behavior. In: Fentress J (ed) Simpler networks and behavior. Sinauer, Sunderland, Mass, pp 314–329

Menne D, Hackbarth H (1986) Accuracy of distance measurement in the bat Eptesicus fuscus: Theoretical aspects and computer simulations. J Acoust Soc Am 79:386–397

Meyer J, Elsner N (1996) How well are frequency sensititivities of grasshopper ears tuned to species-specific song spectra? J Exp Biol 199:1631–1642

Pollack GS, Hoy RR (1979) Temporal pattern as a cue for species-specific calling song recognition in crickets. Science 204:429–432

Reiss RF (1962) A theory and simulation of rhythmic behavior due to reciprocal inhibition in small nerve nets. In: Proc AFIPS Spring Joint Computer Conf, vol 21. National Press, Palo Alto, pp 171–194

Reiss RF (1964) A theory of resonant networks. In: Reiss RF (ed) Neural theory and modeling. Stanford University, Stanford, Calif., pp 105–137

Ronacher B (1998) How do bees learn and recognize visual patterns? Biol Cybern 79:477–485

Schildberger K (1984) Temporal selectivity of identified auditory neurons in the crickets brain. J Comp Physiol A 155:171–185

Schildberger K, Huber F, Wohlers WD (1989) Central auditory pathway: neuronal correlates of phonotactic behavior. In: Huber F, Moore TE, Loher W (eds) Cricket behavior and neurobiology. Cornell University Press, Ithaca, N. Y., pp 423–458

Stumpner A, Ronacher B, Helversen O von (1991) Auditory interneurones in the metathoracic ganglion of the grasshopper *Chorthippus biguttulus*. II. Processing of temporal patterns of the song of the male. J Exp Biol 158:411–430

Stumpner A, Helversen O von (1992) Recognition of a two-element song in the grasshopper *Chorthippus dorsatus* Zett. (Orthoptera: Gomphocerinae). J Comp Physiol A 171:405–412

Thorson J, Weber T, Huber F (1982) Auditory behaviour of the cricket. II. Simplicity of calling-song recognition in *Gryllus*, and anomalous phonotaxis at abnormal carrier frequencies. J Comp Physiol 146:361–378

Vicario DS (1994) Motor mechanisms relevant to auditory-vocal interactions in songbirds. Brain Behav Evol 44:265–278

Weber T, Thorson J (1988) Auditory behaviour of the cricket. IV. Interaction of direction tracking with perceived temporal pattern in split-song paradigms. J Comp Physiol A 163:13–22

Weber T, Thorson J (1989) Phonotactic behavior of walking crickets. In: Huber F, Moore TE, Loher W (eds) Cricket behavior and neurobiology. Cornell University Press, Ithaca, N. Y., pp 310–339

Wendler G (1990) Pattern recognition and localization in cricket phonotaxis. In: Gribakin FG, Wiese K, Popov AV (eds) Sensory systems and communication in arthropods. Birkhäuser, Basel, pp 387–394

Williams JM, Slater PJB (1991) Computer analysis of bird sounds: a guide to current methods. Bioacoustics 3