J Comp Physiol A (1998) 183: 729–735

ORIGINAL PAPER

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Song recognition in the grasshopper *Chorthippus biguttulus* is not impaired by shortening song signals: implications for neuronal encoding

Accepted: 1 September 1998

Abstract The communication signals in many grasshopper species are composed of multiple repetitions of highly stereotyped subunits, and thus provide redundancy. In a behavioural paradigm, we tested the ability of males of the grasshopper *Chorthippus biguttulus* to recognize shortened versions of the communication signals of conspecific females. Males reliably responded to a three-subunits signal (250 ms), i.e. to a signal of less than a quarter of the natural duration. This performance is remarkable in view of the substantial adaptation and the variability present in the spiking responses of auditory interneurones. These behavioural results will impose constraints for investigating possible encoding mechanisms used by the grasshoppers' auditory system.

Key words Grasshoppers · Acoustic communication · Neuronal encoding · Adaptation · Neuronal reliability

Introduction

Many gomphocerine grasshoppers use acoustic signals in order to find a sexual partner. It is the temporal pattern of the sound signals which is decisive for the recognition of conspecifics, so preventing hybridization with other species (von Helversen and von Helversen 1975, 1994). Several species produce long songs (up to 30 s or even more) that are periodic, in that they are composed of many repetitions of much shorter stereotyped subunits (Elsner 1974; Elsner and Popov 1978; see also Fig. 1a).

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In this paper, we focus on possible consequences of signal duration for *song recognition* by the receiver's auditory system. Two properties of auditory neurones are of special interest in this context. First, many interneurones show considerable variability in their responses to identical stimuli (Stumpner 1989; Stumpner and Ronacher 1991; Stumpner et al. 1991). The monotonous repetition of subunits in grasshopper songs might thus be important to compensate for the rather low reliability of neuronal responses. Second, most auditory interneurones show a pronounced adaptation of their spiking responses, which is particularly prominent during the first 100–200 ms after stimulus onset. Therefore, a minimum song duration might be necessary to overcome such transient adaptation effects in auditory neurones.

We performed behavioural tests in which we measured the ability of *Chorthippus biguttulus* males to recognize the species-specific and sex-specific patterns of artificially shortened female songs. These behavioural data may become important for an understanding of the encoding and processing of temporal patterns by an insect's nervous system.

Materials and methods

Animals

Behavioural experiments were performed on 47 males of the grasshopper *Ch. biguttulus* L. (Gomphocerinae, Acrididae, Orthoptera), that were caught in the field in Northern Bavaria.

In this species both sexes stridulate and respond to the signals of conspecifics (for review see von Helversen and von Helversen 1994, 1997). Males and females produce basically similar songs, which are composed of subunits of 80–100 ms duration. Male calling songs have durations of 1.5–4.5 s (von Helversen 1972; Elsner 1974). The response songs produced by females in mating condition are somewhat shorter, around 1–1.5 s (von Helversen and von Helversen 1975). Males use the female's response as a cue for phonotaxis. As males perform phonotaxis only towards singing females and not towards other singing males (von Helversen 1993), their auditory system must discriminate the sex-specific characteristics of female stridulation signals from those of conspecific males. *Ch. biguttulus* males exploit three cues for the recognition of female

signals: (1) slow rise of sound pulse amplitude, (2) presence of short sound pulses that are separated by small gaps (cf. Fig. 1a), and (3) spectral content (for details see von Helversen 1993; von Helversen and von Helversen 1997).

Experimental setup and test procedure

As an indicator for song recognition, we observed the conspicuous turning reaction of males to female songs, which is the first step of the phonotactic approach (von Helversen and Rheinlaender 1988; von Helversen 1993). All experiments with individual males were run in an anechoic room. The noise level in the experimental room was 20 dB in the range 3–20 kHz, and 25 dB in the range 1–40 kHz. The temperature during the tests was kept between 29 and 32 °C. For these experiments, the loudspeaker (AKG Type DKL 29/51) was positioned laterally to the animal (between 80 and 100°, left or right, distance 20 cm). This was done in order to provide good lateralization cues. D/A conversion of the digitally stored song models was performed by a 12-bit DT 2821-board (Data Translation) at 100 kHz. The board was controlled by the signal analysis software TURBOLAB V.4.2. (Stemmer), which was also used for the construction of the stimuli (see below). Sound intensity was adjusted by an attenuator (Heineke) and a power amplifier (Diora stereo amplifier WS 504). For calibration of sound intensity we used a sound-level meter (Brüel and Kjäer type 2235) and a 1/2" condensor microphone (Brüel and Kjäer type 4133). Most experiments were performed at an intensity of 45 dB SPL (re $2 \cdot 10^{-5}$ $N \cdot m^{-2}$; fast reading); this intensity has been established to be very effective in this type of experiment (von Helversen 1993).

In the main experiment (Fig. 2a), we used female models composed of 8 or 12 identical subunits as a reference stimulus, and shortened versions of 5–2 subunits for the critical tests (not all stimuli could be tested with all individuals). Testing began with a standard female stimulus (12 or 8 subunits), after which shortened song models were presented in varying order, frequently switching between stimuli. We took care to avoid conceivable influences of stimulus presentation sequence. Tests with the reference stimulus were occasionally interspersed in order to control for a high response level of the experimental animals (for additional controls see Results). Each stimulus type was presented to an individual between 10 and 50 times (mean 25 times), and the percentage of turning responses was calculated from each individual's responses. Usually, males were tested on 2–5 consecutive days. In the figures the median and quartiles derived from the percentage values of different individuals are shown together with the mean values. As tests for statistical significance of differences in response levels we used the Kruskal-Wallis *H*-test or, in case of paired observations, the Wilcoxon signed rank test (Sokal and Rohlf 1981).

Construction of stimuli for behavioural tests

For the main experiment, we constructed song models based on a natural song of a *Ch. biguttulus* female, recorded at 30 °C. The song was digitized and one subunit, i.e. a syllable plus adjacent pause (see Fig. 1a), was cut out. This basic unit was then repeated 2, 3, 4, 5, 8 or 12 times (the 3-subunits model is shown in Fig. 1a). The respective durations of these models were 165 ms (2 subunits), 250 ms (3), 335 ms (4), 420 ms (5), 675 ms (8), and 1015 ms (12).

As additional stimuli we used models derived from male songs (kindly provided by Dagmar and Otto von Helversen), and also female song models, in which the syllable-pause structure of the subunits was modified while the female-like pulse structure with slowly rising intensity was preserved (see insets in Fig. 3). For these experiments, a normal three-subunits female model served as reference stimulus. In stimulus No. 4 (see Fig. 3a) the pauses between syllables were excised. For stimulus No. 5 the pauses were excised *and* the pronounced first pulse of each syllable was replaced by a pulse of normal intensity, so that this model consisted of 18 female-type pulses without any conspicuous subunit structure. Another type of model consisted of two prolonged syllables of nine pulses separated by a single pause of 12 or 18 ms (stimuli Nos. 2 and 1 in Fig. 3a; two different pause durations were used since *Ch. biguttulus* females are known to prefer longer pauses if the syllable duration is increased; von Helversen and von Helversen 1994).

The male song models were based on two types of male song: (1) the song of an intact male stridulating with both hindlegs, and (2) the song of the same individual stridulating with only one hindleg. The "gappy" songs of males that stridulate with only one hindleg combine features of a female song (six distinct sound pulses per syllable) and that of a male (steep pulse onsets; see Fig. 1a). Gap durations in our "one-hindleg male" song model were between 2.9 and 3.8 ms. The models of the male songs were slightly longer than the corresponding female models (see Fig. 1a). Since we were

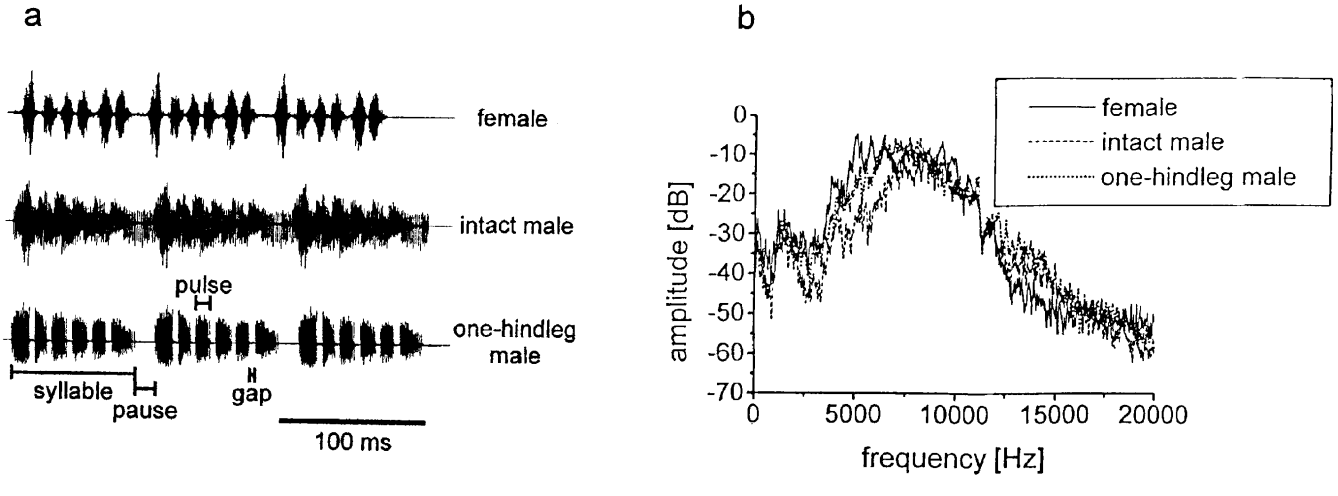

Fig. 1 **a** Song models composed of three identical subunits (i.e. "syllable" plus "pause"), used for behavioural tests. The songs of males and females of *Ch. biguttulus* share the basic structure of syllables and pauses, but differ in several details. Sound pulses of females show a slow rise in intensity, in contrast to the steep onsets of a male's sound pulses (compare top and lowest trace). In the song of females the sound pulses are clearly discernible and separated by small gaps, while in the song of an intact male the gaps between sound pulses are masked by a phase shift between the movements of left and right hindleg (Elsner 1974). However, in songs of a male that has lost one hindleg the sound pulses become discernible (*lowest trace*; same animal as in middle trace). **b** Spectra of the low-pass-filtered songs used for the behavioural tests. The filter (cutoff at 10 kHz) was applied in order to exclude the sex-specific differences in the high-frequency range as a cue for discrimination (cf. Meyer and Elsner 1997; von Helversen and von Helversen 1997)

interested in the grasshoppers' ability to recognize the *pattern* of such shortened songs, and not in a possible discrimination based on differences in the carrier-frequency content (see von Helversen and von Helversen 1997), all songs were low-pass filtered (KEMO VBF8, cut off frequency 10 kHz). The resulting spectra are shown in Fig. 1b.

Results

Three types of behaviour were observed after stimulating males with song models: (1) *turning response*; (2) *singing response without turn* (when stimulated with a male song, males sometimes stridulate but do not show their characteristic turning response); (3) *no response* (animal sitting without response song). These behaviours are also observed in response to natural female songs. Other behaviours as jumps and runs (without prior turning) occurred very rarely in our experimental situation, and were not included in this analysis. The proportion of turning responses related to the sum of all responses is a reliable indicator of whether the male's auditory system recognized a sound signal as conspecific *and* classified it as 'female' or not (von Helversen 1993).

The first question was to what extent the song of a *Ch. biguttulus* female can be shortened without impairing the male's recognition of the signal. Fig. 2a presents the percentage of turning responses of males when stimulated with female songs of different durations. Males showed a high level of turning responses with model durations ranging between 1000 ms and 250 ms, corresponding to 12–3 subunits (no significant difference for the 3- to 12-subunit data according to the Kruskal-Wallis test, $P > 0.5$). Although there is a slight drop in the mean percentage of turning responses between the 4-subunits and the 3-subunits stimulus, the high level of turning responses to the 3-subunits signal indicates that males correctly classified this signal as stemming from a female (11 animals showed a response level of over 90%, the lowest observed response to a 3-subunits female song was 56%). There is a steep decline in turning responses visible between 3 and 2 subunits ($P \ll 0.001$, $\chi^2 = 45.4$, $df = 5$, Kruskal-Wallis): in response to a 2-subunits model most individuals turned either rarely or not at all. However, there were 4 (out of 20) individuals producing more than 35% turning responses with the 2-subunits-model, one of them even 78%! Thus, the minimum structure that allows a reliable recognition of a female song pattern appears to be a 3-subunits song model or – for some individuals – perhaps even a 2-subunits model.

For the interpretation of this result it is crucial to know whether the animals still responded in a discriminative way to these shortened stimuli. Therefore, we performed two additional experiments. In the first, we tested males with shortened male songs, and in the second experiment, males were stimulated with shortened female songs in which the syllable-pause pattern had been modified.

Figure 2b shows the results of experiments with shortened male song models. None of the 10 males tested ever performed the characteristic turn in response to the three-subunits version of an intact male song (this stimulus elicited only a response song but not a turn, or no response at all). Nine out of 13 males showed occasional turning responses to the stimulus derived from a male song produced by only one hindleg (shaded bar). However, the highest turning percentage observed with an individual for this stimulus type was 35%. A pairwise

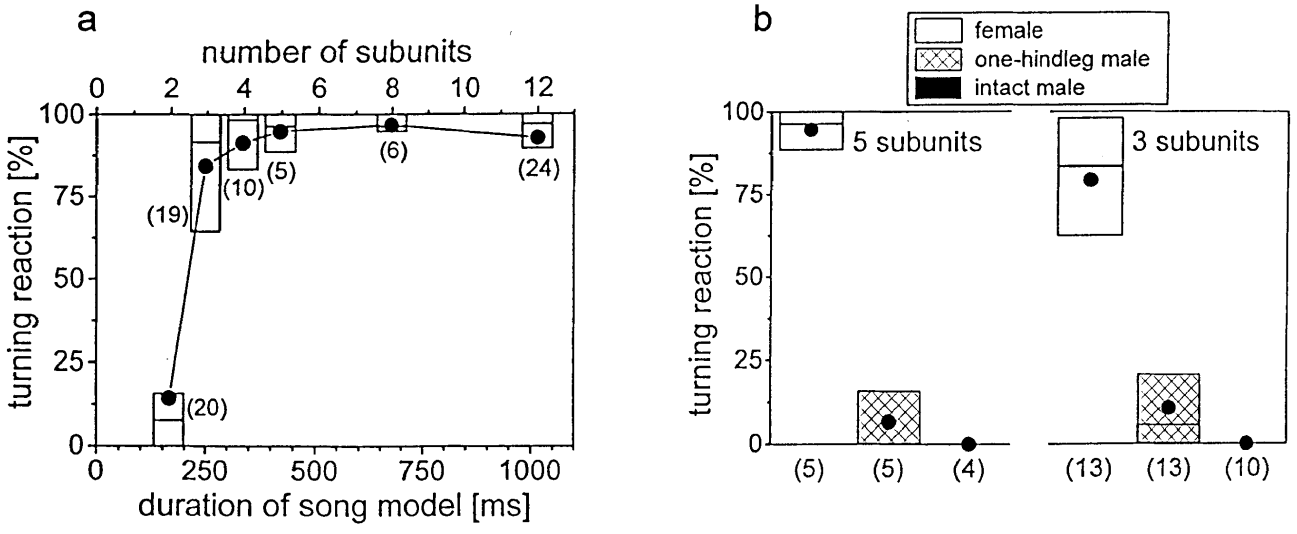

Fig. 2 a Occurrence of phonotactic responses of *Ch. biguttulus* males (*ordinate*) to female songs of different durations (*abscissa*). On the top axis the respective number of subunits is indicated. *Boxes* indicate the median and quartile ranges; in some cases the median and one of the quartiles coincide at 100 or 0%. For comparison mean values are also shown (*filled circles*). Numbers in parentheses give the numbers of individuals tested for each stimulus type. **b** Turning responses of males to shortened songs of a female, a "one-hindleg-male", and an intact male. The *columns on the left* show responses to five-subunits stimuli, on the *right* to three-subunits stimuli. Males never showed turning responses towards an intact-male song but responded well to a female song. *Numbers in parentheses* below the columns give the number of individuals tested for each condition. All song models were low-pass filtered (see Fig. 1b). See text for further explanations

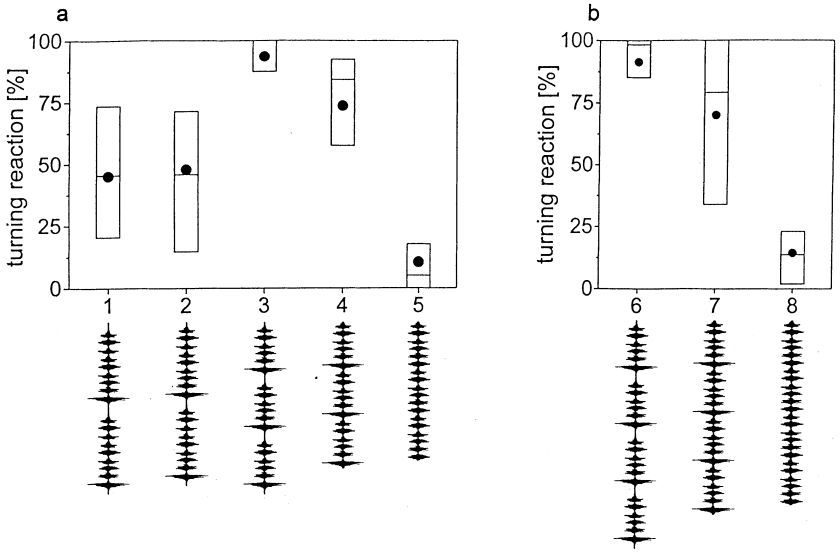

Fig. 3a, b Responses of *Ch. biguttulus* males to female songs with altered subunit structures. **a** Stimuli modified on the basis of a three-subunits female song (stimulus No. 3 = control). **b** Stimuli modified from a four-subunits female song (stimulus No. 6 = control). Stimuli are shown as insets and numbered consecutively in order to facilitate referencing in the text. *Boxes* median and quartiles; *filled circles* mean values

comparison within the 13 individuals tested with both female and one-hindleg-male songs (three-subunits data in Fig. 2b) indicates a highly significant difference ($P < 0.001$, Wilcoxon signed-rank test). All males occasionally turning in response to the "one-hindleg" male song were also tested with intact male song (three or five subunits) but never performed phonotactic turns in response to this stimulus.

In order to exclude the possibility that the missing turning responses could have been due to a specific fatigue of turning, we tested the males after every 'missing' turning response to a male song with a 5- or 3-subunits female song. We scored the 'no' responses only as such if the animal immediately afterwards performed a turn in response to the female song, which was the case in over 90% of stimulus presentations. This control shows unequivocally that the failure of turning responses to shortened male song models was due to a true discrimination from female song, and not to fatigue.

The results of Fig. 2 demonstrate that males can recognize a female signal and discriminate it from a male song pattern even if it is shortened to three subunits. It is conceivable, however, that the males classified these song models only on the basis of the slowly rising amplitude modulations of sound pulses typical for female songs. If the animals' recognition of a female song pattern was mainly based upon the presence of ramp-like versus steep pulse onsets, there were still 18 sound pulses that could have been evaluated by the animals. The question now is whether the presence of female-like sound pulses is sufficient for recognition of short song models by the males, or whether the males also need the species-specific syllable-pause structure, as they do in signals of normal duration (von Helversen and von Helversen 1997). In a second experiment we therefore tested males with female song models in which the subunit structure had been modified (see Materials and methods and insets in Fig. 3). Compared to the typical female stimulus (stimulus No. 3 in Fig. 3a), these manipulations reduced the attractiveness of song models (the Kruskal-Wallis H-test yields $P < 0.001$ for a comparison of all stimuli, and $P < 0.01$ for stimuli Nos. 1–4). In the mean, the stimuli with longer syllables and only a single pause (Fig. 3a, stimuli Nos. 1 and 2) evoked fewer turning responses than the control, the interindividual variability, however, was enormous. The same is true for the stimulus without pauses (No. 4). Remarkably, several individuals responded quite well to this stimulus type in which the syllable-pauses were missing but the pronounced first pulses were still present. A similarly large interindividual variability was also observed in a repetition of this experiment with stimuli based on four subunits (stimulus No. 7 in Fig. 3b). All individuals, however, showed a drastic reduction of turning responses with the model without any subunit structure (compare responses to stimuli Nos. 3 and 5 in Fig. 3a, and stimuli Nos. 6 and 8 in Fig. 3b). Obviously, the presence of 18 or even 24 female-like sound pulses alone is not sufficient to elicit the turning response of *Ch. biguttulus* males. These results corroborate that the syllable-pause structure was still important for the recognition of shortened female songs.

Discussion

Cues for pattern recognition with short models

The results in Fig. 2 show that *Ch. biguttulus* males reliably recognize the sex-specific stridulation signals of conspecific females even if shortened to three subunits. This recognition must have been based on envelope cues (e.g. ramp-like versus steep pulse onsets, see Fig. 1a), since in our song models the carrier-frequency differences between male and female songs in the high-frequency range had been removed as a potential cue by low-pass filtering (cf. Materials and methods). [The small spectral differences around 5–7 kHz between the three song

models used in our experiments (Fig. 1b) are within the interindividual variability of one sex (cf. Meyer and Elsner 1997), and therefore are unlikely to constitute a reliable cue for sex discrimination]. Figure 3 demonstrates that recognition did not depend solely upon the sex-specific shape of female sound pulses, but that the species-specific subunit structure was also important, in the three-subunits model as well as in long song models (cf. von Helversen and von Helversen 1997). Furthermore, these tests revealed that the pronounced first pulses of the subunits can – though perhaps not for all individuals – be sufficient to mark the subunit structure even in case that the syllable pauses are missing. This result may help to assess the contribution to the encoding of temporal patterns of different ascending neurones, in particular of phasically responding elements (cf. Stumpner et al. 1991).

Information processing in the auditory system of grasshoppers

Earlier experiments (Ronacher et al. 1986; Bauer and von Helversen 1987) provided evidence that the decisive steps of song recognition occur within the brain while the metathoracic ganglion complex, in which the auditory receptors synapse onto interneurones, harbours an important first station of auditory preprocessing. The relevant information about the temporal structure of song patterns must be transmitted to the brain via auditory interneurones ascending from the thoracic ganglia (cf. Ronacher et al. 1986). To date no single ascending neuron has been found that would be able to encode the complete information about the song pattern (cf. Ronacher and Stumpner 1988; Ronacher 1990; Stumpner et al. 1991; Stumpner and Ronacher 1994). Rather the information necessary for pattern recognition seems to be distributed amongst an ensemble of several ascending neurones (Krahe 1997).

Evidently, the precision with which temporal patterns can be encoded by an ensemble of neurons will depend on the variability of neuronal responses (see e.g. König et al. 1996; Rieke et al. 1997). In principle, the nervous system could reduce the detrimental effects of neuronal variability in two ways: either by averaging the responses of different neurones with similar response characteristics (cf. Ronacher and Römer 1985), or by temporal averaging, in case of the grasshopper songs over several stereotyped subunits. As far as is known, the first possibility is unlikely to be realized in the grasshopper: probably there are not so many ascending interneurones that the CNS could compensate for the variability of spike count and spike timing by averaging over the responses of several elements with similar response characteristics (Römer and Marquart 1984; Stumpner 1989; Stumpner and Ronacher 1991; Stumpner et al. 1991; Krahe 1997). Considering the second possibility, our behavioural data (Fig. 2) define a clear upper limit of 250 ms for a possible temporal integration. Remarkably, auditory interneurones show different degrees of adaptation during the first 200 ms after stimulus onset. To illustrate the extent and time course of adaptational changes, Fig. 4 shows spike count and latency data for three ascending auditory neurons of *Ch. biguttulus*. In two of them, AN4 and AN12, which are

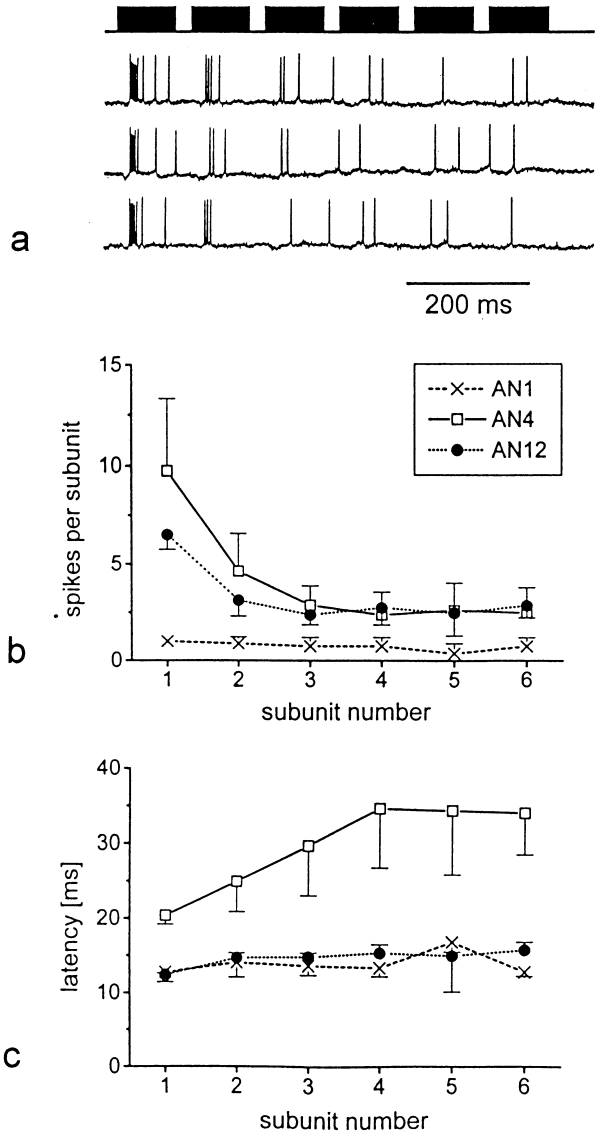

Fig. 4a–c Adaptation and variability of responses of ascending auditory interneurones of *Ch. biguttulus*. **a** Response of an AN4 neuron to three presentations of a song model; note the variability of responses. **b** Spike count data for three neurones. Adaptation affects the spiking response mainly during the first two subunits. **c** The latency (relative to the subunit onset) of the respective first spikes evoked by each subunit shifts towards larger values (same cells as in **b**). Intracellular recordings from auditory interneurones of *Ch. biguttulus* were obtained with conventional methods at room temperature (the experimental procedure is described in detail in Stumpner and Ronacher 1991). Neurones were identified morphologically by lucifer yellow (Sigma) injection. Artificial sound stimuli consisted of six noise syllables (100 ms) and 25-ms pauses. *Bars* indicate standard deviations. Eight stimulus presentations per point (at 72 dB SPL). Data kindly provided by Dr. Andreas Stumpner (Göttingen)

supposed to participate in pattern encoding (Stumpner et al. 1991), the spike count per syllable drops by more than 50% from the first to the second subunit (Fig. 4b). Apart from spike count, adaptation also influences the timing of spikes, different neurones being affected to a different degree (Fig. 4c). If the pattern processing by the song recognizing filters depends on a temporal integration over several subunits, one is inclined to assume that the profound changes in spike responses occurring during the first 200 ms after stimulus onset must affect this processing. [Note that the grasshopper males did not exclusively rely upon the shape of sound pulses, but also assessed the syllable-pause structure of short model songs (Fig. 3)!] It appears more likely that the song recognizing neuronal filters operate with short integration times. Further tests must now follow to clarify whether recognition may even be possible on the basis of a single correct subunit (see Hennig and Weber 1997, for an example of very short integration times of neuronal filters in gryllids).

Why do females produce songs longer than necessary for recognition by the male?

Natural songs of *Ch. biguttulus* females last around 1 s (1.18 ± 0.23 s, range 0.8–1.5 s; von Helversen and von Helversen 1975), which is approximately four to six times the minimum length required for reliable recognition by the male in the experiment in Fig. 2. Of course, in our laboratory experiments, the males had especially favourable conditions for song recognition, since the tests were performed with rather undistorted patterns at low noise levels (see Materials and methods). In the field the animals will face signals that are degraded between sender and receiver and masked by noise, due, for example, to other singing individuals of the same or other species. By the multiple repetition of subunits females may seek to improve signal transmission in a noisy biotope (Michelsen and Larsen 1983; Römer 1992; Römer and Lewald 1992). Thus, the natural durations of female songs probably reflect a compromise mainly between the necessity to reliably transmit the signal to the receiving male and the risks of sound production (for a discussion of these and other influences see von Helversen and von Helversen 1994; Kriegbaum 1989; Kriegbaum and von Helversen 1992; Stumpner and von Helversen 1992). The pronounced first pulses in each syllable – which can be sufficient to mark the subunit structure (cf. Fig. 3) - may be a 'cheap' means to improve the signal-to-noise ratio in a noisy biotope.

In the vibratory communication of the spider *Cupiennius salei* the lower limit for the number of syllables necessary to elicit a respone was also 3 syllables, while natural courtship signals were much longer (12–50 syllables, Schüch and Barth 1990). It would be interesting to relate these results to the noise and signal degradation in the spider's biotope.

Are long songs necessary to improve directional cues?

In order to find a responding female, a male must not only recognize the female signal but also extract from it directionality cues that allow a phonotactic approach towards the sender (von Helversen and Rheinlaender 1988; von Helversen 1993; von Helversen and von Helversen 1997; Krahe and Ronacher 1993; Ronacher and Krahe 1997a; see also Michelsen 1994; Michelsen and Rohrseitz 1995, 1997). Therefore, one might postulate that the natural duration of female songs is essential for this localization task. By temporal integration males could enhance the otherwise poor directionality cues. This possible function of long song durations, however, is ruled out by behavioural experiments, in which we assessed the lateralization accuracy for female song models with different durations. Lateralization accuracy was the same for a 250-ms song and for a 1000-ms song (3 and 12 subunits, respectively; Ronacher and Krahe 1997b, and unpublished observations).

The grasshoppers' central nervous system must detect conspecific signals from the rather unreliable responses of auditory neurones, and it is able to do so on the basis of a single presentation of a three-subunits stimulus in 'real time'. Hence, the results in Figs. 2 and 3 impose constraints for models of acoustic information processing. Further behavioural, neurophysiological and modelling studies are now in progress in order to specify the contributions of individual neurones to the total pattern information that is transmitted to the grasshopper's brain via ascending interneurones.

Acknowledgements We are very grateful to Andreas Stumpner for his generous permission to use some of his neurophysiological data (Fig. 4). We thank Astrid Franz, Sandra Wohlgemuth, and Corinna Hofmann for help with the behavioural tests, as well as Dagmar von Helversen, Matthias Hennig, and Andreas Herz for valuable comments on the manuscript. The experiments comply with the current German "law of animal care".

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