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ORIGINAL PAPER

Robustness of an innate releasing mechanism against degradation of acoustic communication signals in the grasshopper *Chorthippus biguttulus*

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Abstract

Noise is a challenge for animals that use acoustic communication to find a mate. A potent source of noise in animal communication is that arising from other conspecific signals, whose co-occurrence can result in extensive interference—evident as the so called "cocktail-party problem"—that may affect the receiver mechanisms to detect potential mates. We studied grasshopper females to explore how modifications of the song pattern influence song recognition. First, we degraded an attractive model song with random fluctuations of increasing amplitudes out of different frequency bands, and determined "critical degradation levels" at which the females ceased to respond. A masker band with frequencies between 0 and 200 Hz, which covers the frequency range of the natural song envelope, was by 3–5 dB more destructive in hampering signal recognition than frequencies above 200 Hz. As second approach, we applied temporal disturbances such as accentuations or gaps at different positions within the song subunits and observed how response behavior was affected. Accentuations at subunit start increased, whereas those in the midst or at the end of a subunit reduced attractiveness. Gaps at these positions had diverse effects. The results are discussed with respect to neuronal filtering.

Keywords Acoustic communication · Signal degradation · Noise · Masking · Mate choice

Abbreviations

CDL	Critical degradation level
AM	Amplitude modulation
NSR	Noise–to-signal ratio

Introduction

The identification and correct interpretation of a potential mating partner's communication signals are crucial tasks in an animal's life which exert strong selection pressures both on signal production as well as on the sensory systems of the receivers. In general, features of the signals and properties of the receivers are matched in a process of coevolution (von Helversen and von Helversen 1994; Boughman 2002; Wiley 2013). However, as a rule, the mutual selection pressures exerted by signalers and receivers are asymmetric, depending on the partners' respective investment in the offspring (Trivers 1972; Andersson 1994; von Helversen and von Helversen 1994). An important parameter influencing both partners is the quality of signal transmission from signaler to receiver, which depends on modality and intensity of the signals and transmission properties of the habitat that delimit the signal-to-noise ratio of signals arriving at the receiver (Klump 1996; Brumm and Slabbekoorn 2005). When acoustic signals are transmitted from a signaler to a distant receiver they are likely to be modified by different sources of masking sounds and signal degradation (Michelsen and Larsen 1983; Römer 2001, 2013; Brumm 2013). Wiley (2006) emphasizes the necessity to investigate a receiver's preferences under noise, because features of effective signals may differ in the presence of high and low background stimulation (see, e.g., van Staaden and Römer 1997; Couldridge and van Staaden 2004; Reichert and Ronacher 2015). Thus, environmental conditions may contribute to shape female preference functions as well as male signals (Brumm and Slabbekoorn 2005; Reichert and Ronacher 2015). Especially

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in long distance communication conspicuous, high contrast signals are advantageous (Boughman 2002; Gerhardt and Huber 2002; Brumm 2013; Römer 2013).

Here we investigated how a receiver copes with a widespread problem of signal transmission, that is, with degraded and distorted signals. Our study system is the acoustic mate recognition system of the grasshopper *Chorthippus biguttulus*. The recognition of acoustic signals is an important barrier against hybridization between species (Gottsberger and Mayer 2007; Finck and Ronacher 2017), and it is therefore likely that there was a strong selection on receivers to identify the signals of conspecifics.

Environmental noise can be broadband, and this type of noise has received much attention in studies of insects (van Staaden and Römer 1997; Ronacher et al. 2000; Schmidt et al. 2011; Schmidt and Römer 2011; Römer 2013; Lampe et al. 2012; Reichert and Ronacher 2015; Reichert 2015) as well as in frogs (Gerhardt and Huber 2002; Vélez et al. 2013). However, much environmental noise contains amplitude modulations, and this creates special challenges for communication (Ronacher and Hoffman 2003; Vélez and Bee 2011). Many experiments have demonstrated that in grasshoppers, acoustic signal recognition and the identification of conspecific mates depend primarily on the species-specific pattern of amplitude modulations (von Helversen 1972; von Helversen and von Helversen 1997, 1998; Klappert and Reinhold 2003; Schmidt et al. 2008). However, since grasshoppers are often found in dense aggregations (Kriegbaum 1988, 1989), and *Chorthippus biguttulus* males are easily stimulated to stridulate by other singing males (Jacobs 1953), signals from conspecifics, as well as signals from other sympatric species, are likely to interfere with the signal of a specific sender and degrade its species-specific temporal pattern. Thus, females have to detect the relevant signals in a background of similar sounds, a challenge faced by many species that signal in aggregations and that is similar to the human cocktail party problem (Bee and Micheyl 2008; Schmidt and Römer 2011; Vélez and Bee 2011). In addition, reflections and reverberations also may cause modifications of the signal's amplitude modulation pattern (Michelsen and Larsen 1983; Römer 2001; Brumm and Slabbekoorn 2005).

Our present study aimed at specifically degrading a signal's amplitude modulation pattern, its envelope. We modified the signal envelope in a twofold approach, focusing either on the frequency domain or on the temporal domain. First, we degraded an attractive model song with random fluctuations of increasing amplitudes out of different frequency bands, and determined "critical degradation levels" at which the females ceased to respond. Comparing different masker frequency bands revealed that a masker covering the frequencies between 0 and 200 Hz, which overlaps with the male song spectrum, was by 3–5 dB more destructive for signal recognition than maskers with modulation frequencies above 200 Hz.

In a second, complementary experiment—now focusing on the time domain—we applied temporal disturbances such as accentuations or gaps at different positions within the song subunits and observed how signal attractiveness was affected. *Chorthippus biguttulus* females are known to pay attention to specific characteristics within the song subunits, e.g., onset accentuations, offsets, gaps (von Helversen and von Helversen 1997). Among these features, gaps and accentuations appear to be particularly important for sex recognition and mate quality evaluation (von Helversen and von Helversen 1997; Stange and Ronacher 2012). By comparing the effects of confined envelope modifications, we show that dependent on their specific position within a song subunit, accents or gaps in a song subunit strongly reduce signal attractiveness.

Methods

Animals

Behavioral experiments were performed on virgin females of *Chorthippus biguttulus* (Orthoptera, Acrididae) that were caught as nymphs in the field near Göttingen or were raised in the lab from eggs (collected from the same population). After the final moult females were kept separated from males in large cages in a 14/10 h light–dark cycle and were fed ad libitum with a mixture of grasses (see Schmidt et al. 2008 for details). Animals were marked individually with a three-point color code and were tested at the age of 10–20 days after adult moult.

Acoustic stimuli

Since earlier investigations demonstrated that the crucial features for song recognition lie in its pattern of amplitude modulations (AM), we specifically aimed at manipulating the song envelope. To better control the song features, we did not use a natural song of a *C. biguttulus* male as the experimental stimulus but rather used synthetic song models. Synthetic male songs have been previously shown to be highly attractive to females (von Helversen and von Helversen 1997; Balakrishnan et al. 2001). The basic song model consisted of 33 rectangular 80 ms noise 'syllables' (rise and fall time = 1 ms) separated by 15 ms silent pauses. The total song duration was ca 3 s which is in the range of natural songs and well accepted by females (von Helversen 1972; Krämer and Ronacher unpublished results). In a second song model, the noise syllables started with an onset accentuation (6 dB higher than the syllable plateau for 10 ms). The major Fourier components of these envelopes are concentrated below 100 Hz (see Fig. 1a). We degraded the envelopes using two different approaches.

Stochastic degradation

We used six bands of broad band noise (0–100; 100–200; 0–200; 200–400; 400–600; and 600–800 Hz) with which the signal envelope was stochastically degraded in 3 dB steps, relative to the variance of the original envelope (see Fig. 1b, c for two examples). The noise-to-signal ratio is given in decibels as NSR = 10 log (noise variance)/(original song variance). Thus, the degradation level of 0 dB corresponds to a NSR of one (for details of the procedure see Neuhofer et al. 2011). For each degradation level, a new stochastic degradation was chosen but the envelope noise was identical for different trials at a given degradation level ("frozen noise"). All resulting envelopes were filled with a broad band carrier (noise 5–40 kHz) and played back at a plateau intensity of 70 dB SPL, which is well accepted by *C. biguttulus* females (von Helversen and von Helversen 1997; Krämer 2017).

Position-specific envelope degradation

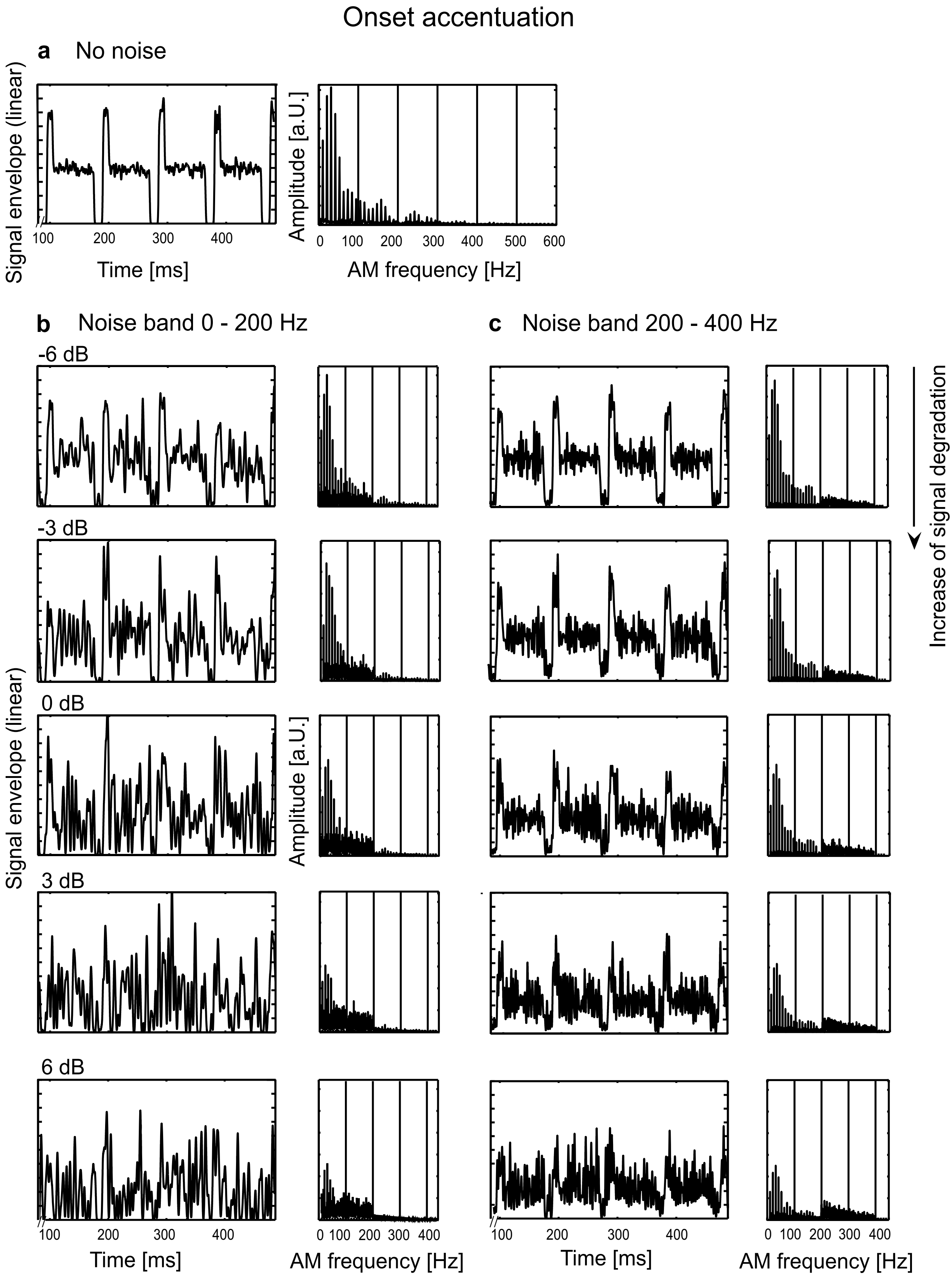
The results of the stochastic degradation experiments suggested that the strong additional amplitude modulations imposed onto the syllables of a song were particularly destructive (see "Results"). This was an incentive to introduce, as a second approach, position-specific perturbations onto the syllable envelopes, by introducing accentuations or gaps at different positions within the syllable. As an attractive basic model, we chose rectangular syllables (72 ms, rise and fall time = 1 ms) separated by 12 ms pauses. The perturbations consisted of either an intensity rise (accentuation) of 6, 12 or 18 dB, or a 6, 12 or 18 dB lower intensity ("gap"), or a combination of accentuations and gaps. The accentuations were either a single 24 ms accent or two 6 ms accents separated by a 6 ms plateau; similarly, the gaps were either a single intensity drop of 24 ms ("long gap"), or two 6 ms gaps separated by a 6 ms plateau (Fig. 2). For the combined perturbations a 6 ms accent was followed by a 6 ms gap or vice versa; this combination was repeated once. These modifications were applied either in the first, the second or the last third of each syllable ("start", "middle", "end"), see Fig. 2. The 12-dB data for the combined perturbations were already presented in a different context in Fig. 1 in Meckenhäuser et al. (2014), all other data are unpublished.

These stimuli are interesting in view of their Fourier component composition. First, the perturbations were primarily in the frequency range below 100 Hz. Second, there is a major difference in the spectra between, on the one hand, the onset and end stimuli (which have identical or almost identical spectra), and on the other hand, the perturbation in the middle of the syllable (see supplemental Figures). A translation of these disturbances in the frequency of Fourier components would lead to the prediction that the animals should respond similarly to onset and end stimuli because of their similar spectra, and differently to middle stimuli (but see "Results", and von Helversen 1998).

Behavioral tests

The protocol of behavioral tests is described in detail elsewhere (Schmidt et al. 2008; Reichert and Ronacher 2015), so here only a short summary is given. Females were placed in a small sound transparent cage situated at 30 cm from the loudspeaker (Adam Audio AX5, Adam Audio GmbH, Berlin, Germany, or Dynaudio D21, Skanderborg, Denmark) within a sound proof chamber. The temperature during experiments was kept constant at 30 ± 2 °C. Female response songs were recorded via a small microphone (GH-183. Conrad electronics, Germany) placed near the female. Before a test cycle started, a control stimulus (80/15 ms syllable pause duration) was presented to check for responsiveness. If a female did not respond to this control stimulus, the program paused for 120 s before the next presentation of the control (see Schmidt et al. 2008). Only if the female responded to that control, a playback cycle was started in which all stimuli were presented once; between stimulus presentations pauses of 8 s were inserted. Before the next playback cycle started, again the control stimulus had to be answered. To minimize carryover effects between stimuli, the stimulus order was newly randomized for each playback cycle. A complete session consisted of 18 playback cycles. To control for selectivity, a "negative" control stimulus without any species-specific temporal structure was included (a 3-s continuous noise). Females that responded to the negative control more than two times (out of 18 presentations) were excluded as less selective. The response probability for each stimulus was calculated as the percentage of stimuli to which the female responded relative to the total number of stimulus presentations (18 responses corresponds to 100%).

For the stochastic degradation test, a playback cycle contained 34 stimuli. The tests with onset accentuated syllables were performed on 40 females, 7 of which were excluded as unselective; the tests with rectangular syllables on 18 females, 4 of which were excluded. The tests with position-specific envelope degradations had to be performed on different cohorts due to the large number of stimuli. Short accentuations and short gaps were tested on 26 individuals; 24 ms accentuations and 24 ms gaps were tested on 20 females; the combination of accentuations and gaps was tested on 33 females.


Onset accentuation
a No noise
Signal envelope (linear)
Time [ms]
100
200
300
400
Amplitude [a.U.]
AM frequency [Hz]
0
100
200
300
400
500
600
b Noise band 0 - 200 Hz
c Noise band 200 - 400 Hz
-6 dB
-3 dB
0 dB
3 dB
6 dB
Increase of signal degradation
Signal envelope (linear)
Amplitude [a.U.]
100
200
300
400
Time [ms]
0 100 200 300 400
AM frequency [Hz]
100
200
300
400
Time [ms]
0 100 200 300 400
AM frequency [Hz]

◂**Fig. 1** Stochastic degradation of signal envelopes. **a** Stimulus envelope of four song subunits with 6 dB onset accentuation (left), and the corresponding Fourier spectrum (right). Songs consisted of 33 subunits with a total duration of ca 3 s. **b** Stimulus envelopes degraded with uniform amplitude noise in a frequency band from 0 to 200 Hz (see spectra next to the envelopes). Noise levels increase from top to bottom; 0 dB corresponds to a noise-to-signal ratio of 1. **c** Degradation with the noise band 200–400 Hz. Plot as in **b**

Data evaluation and statistics

Following Neuhofer et al. (2011), we determined for each noise band a critical degradation level (CDL) as that degradation at which the behavioral response dropped below 50%. This is exemplified with the data of one female in Fig. 3. Since there was a substantial interindividual variation of CDLs, the effects of different noise bands were statistically evaluated in pairwise comparisons (repeated measures ANOVA with Tukey–Kramer multiple comparisons post hoc test). The second experiments with position-specific envelope degradations were analyzed with the non-parametric Friedman test, combined with Dunn's multiple comparisons test.

Results

Effects of envelope degradation by different frequency bands

The effect of degradation is shown in Fig. 4a for the song model with onset accentuation. The degradation with the 0–200 Hz masker resulted in a median CDL of − 2.6 dB while the medians for higher frequency bands were shifted by 3.5–5 dB to larger, positive values. The stronger degrading effect of the low frequency masker (0–200 Hz) is further supported by the tests with two narrower masker bands (0–100; 100–200 Hz), as their CDLs were − 3.4 and − 4.0 dB, respectively. All CDLs for the maskers above 200 Hz are highly significantly different from the CDLs for 0–200 Hz as well as from the 0–100 and 100–200 Hz CDL values ($p < 0.001$; repeated measures ANOVA with Tukey–Kramer multiple comparisons post hoc test, $N = 33$). The CDLs for frequency bands 200–400, 400–600 and 600–800 Hz did not differ significantly from one another; the same was true for the comparison of 0–100 and 100–200 Hz. The 0–200 Hz CDL did not differ from that of 0–100 Hz, while it differed weakly significantly from that of 100–200 Hz ($p < 0.05$). The results obtained with the stimuli without onset accentuation ('block syllables') underpin these results, although significance levels were weaker, likely due to the smaller sample size (Fig. 4b). Masker frequencies above 200 Hz resulted in higher CDLs than the 0–200 and the 0–100 and 100–200 Hz maskers. The 0–100 and 100–200 Hz bands yielded CDLs of − 4.8 and − 3 dB, respectively. Both values were highly significantly lower than the CDL for 200–400 Hz (0 dB, $p < 0.001$), and weakly significantly lower than the CDLs for 400–600 and 600–800 Hz ($p < 0.05$); all other comparisons revealed non-significant differences ($p > 0.05$; repeated measures ANOVA with Tukey–Kramer multiple comparisons post hoc test, $N = 14$). For the song model with a 6 dB onset accentuation, there was a trend that the animals tolerated an approximately 2 dB higher degradation level as compared with block syllables without such an accentuation (compare Fig. 4a, b). However, this positive effect seemed to be restricted to masker frequencies above 200 Hz; for the low frequency maskers the onset accentuation provided no consistent advantage against degradation.

The pauses between syllables are presumed to be of particular importance for song recognition in *C. biguttulus* (von Helversen and von Helversen 1994, p 257). Here we examined whether the pauses in the song models were affected at the median critical degradation levels. However, for the 0–200 Hz masker band, the pauses between syllables are not severely masked at − 3 dB, the median CDL for the accentuated syllables, and the same is true for the 200–400 Hz signals at 0 and + 3 dB (see Fig. 1) and for the block stimuli without onset accentuation (data not shown). Thus, we concluded that the crucial features that led to a rejection of the degraded signals did not depend on a complete masking of the pauses but rather must be assigned to the strong additional amplitude modulations imposed onto the syllables. This observation was an incentive to introduce a second type of subunit degradation in which only the syllable plateaus were systematically modified at different positions.

Position-specific envelope degradation with accentuations and/or gaps

The two different types of accentuation used, a single 24 ms accent or two 6 ms accents, influenced the response behavior in a similar way (Fig. 5a, b). Placed at the start of the syllable, the accents resulted in highly attractive song models (median responses > 90%, only the for 18 dB accentuation the median response level was reduced to 60 and 70%, respectively). More importantly, the same accents placed in the middle or at the end of a syllable led to drastically reduced response levels (Fig. 5a, b).

An ongoing lowering of amplitude (24 ms "gaps") affected the song's attractiveness differently (Fig. 5c). Introducing a 6 dB drop had the opposite effect on stimulus attractiveness as a 6 dB accent. Syllables with a lowered amplitude at the start were rejected (median response 30%) while the same reduction at middle or end position still yielded attractive stimuli (Fig. 5c). In contrast, the accent at the start strongly increased the response level (median

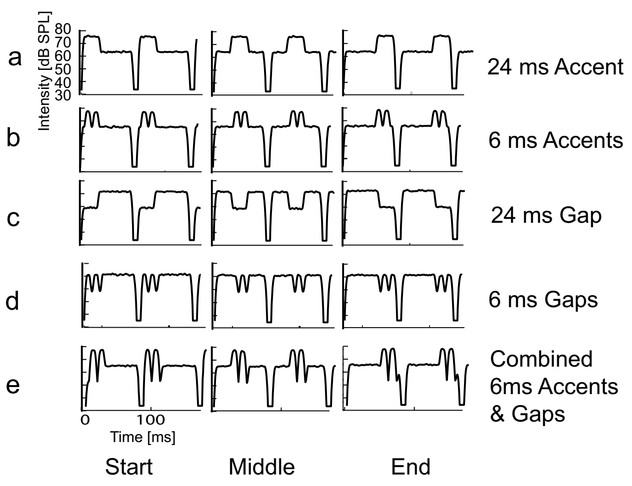


Fig. 2 Position-specific degradation of song subunits. Envelopes of song subunits with amplitude modifications either at the start, the middle or the end of a subunit. Two subunits with 12 dB amplitude steps are depicted; 6 and 18 dB amplitude steps were also used

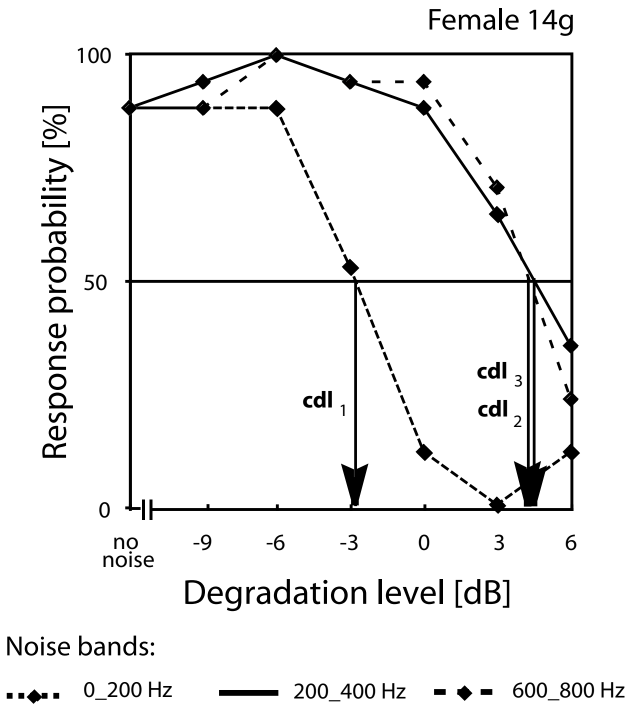


Fig. 3 Quantification of the critical degradation levels (CDL). Shown are the responses of an individual female (#14g) to songs that were degraded with three noise bands (0–200, 200–400, 600–800 Hz). The CDL was determined as the intersection of the respective linear interpolation of the adjacent data points with the 50% response level. Note that for the 0–200 Hz band the response drops steeply between −6 and 0 dB, whereas for the two other band the drop occurs between 0 and +6 dB

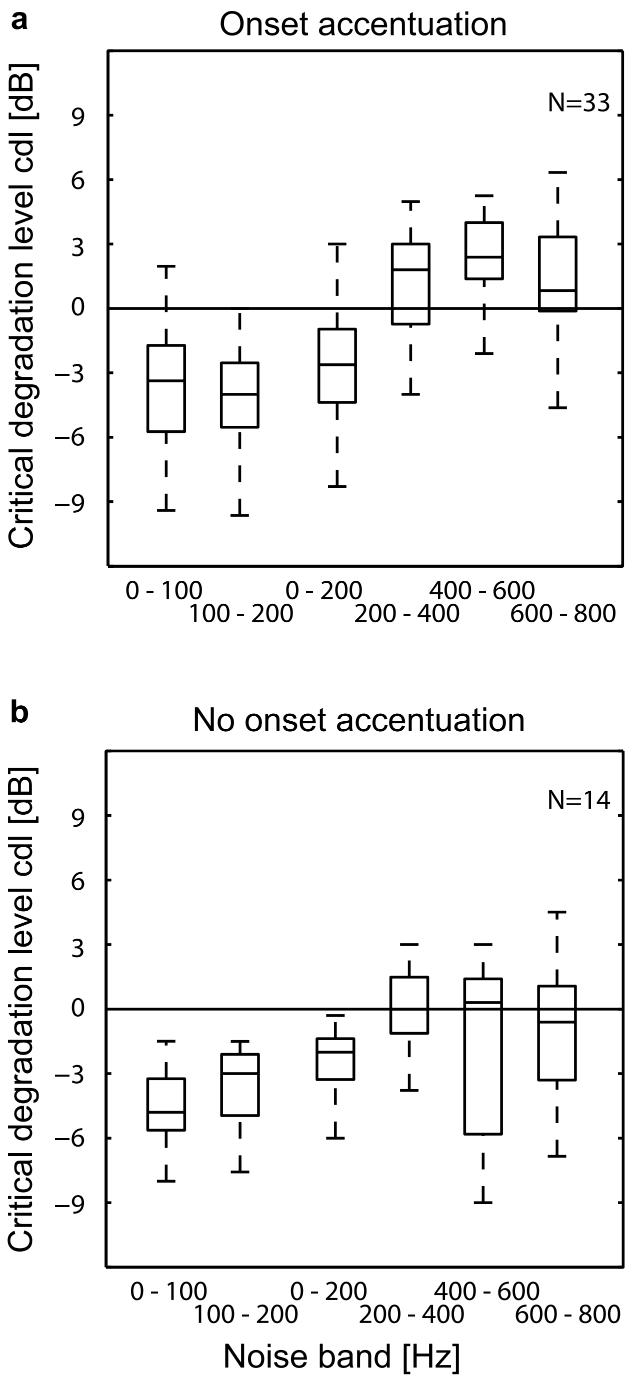


Fig. 4 Effects of degradation by different frequency bands. Critical degradation levels for stimuli as in Fig. 1 are shown as box plots (median and interquartile ranges; whiskers denote 10 and 90 percentiles) for the different frequency bands. **a** Stimuli with onset accentuation, $N = 33$ females tested; **b** stimuli without onset accentuation 14 females tested

100%), but resulted in reduced responses (45 and 30%) if placed in the second or third position (Fig. 5a). At amplitudes of 12 and 18 dB, this negative effect of an accent at the middle or end of a syllable was even more pronounced. 12

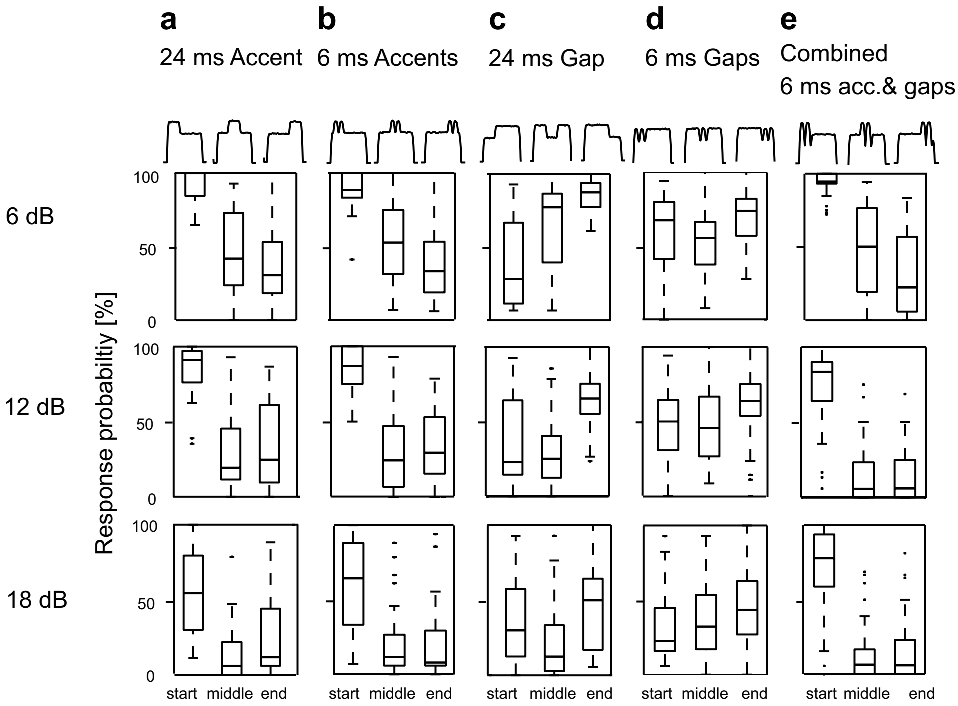


Fig. 5 Effects of position-specific perturbations. **a** Responses of females to a single 24-ms accent of 6 dB (top), 12 dB (midst) or 18 dB (bottom) for stimuli as in Fig. 2 are shown as box plots. For all accent heights, the responses to middle and end accents did not differ significantly, whereas they both differed from the onset position ($p < 0.01$ for middle position at 6 dB, for all other combinations: $p < 0.001$). **b** Responses to two 6-ms accents. Significances as in **a** except for middle position at 6 dB: $p < 0.05$. **c** Responses to a single 24-ms gap. At 6 dB middle and end position: n.s., both differ with $p < 0.001$ from onset position; at 12 dB onset and middle position: n.s., both differ from end position at $p < 0.01$; at 18 dB no significant differences between all positions. **d** Responses to two 6-ms gaps. At all intensities, no significant differences between all positions. **e** Responses to a combination of accents and gaps. The responses to middle and end accents did not differ significantly, whereas they differed both from the onset position (significance levels as in **a**)

and 18 dB troughs were quite unattractive at the first or second position. At the end position, the 12 dB trough resulted in an attractive stimulus while an 18 dB trough also led to a reduced response level. However, even for the 18 dB stimuli there was a non-significant trend towards higher response level at the end position (Fig. 5c). The responses to stimuli exhibiting two 6 ms gaps were largely independent of their position within the syllable, and revealed only a decreasing attractiveness with stronger intensity differences relative to the syllable plateau (Fig. 5d).

Depending on their position within a subunit accentuations and gaps had different effects on female responses (Fig. 5a–d). Which of the two effects would dominate female responses when combined? How would the insertion of both gaps and accentuations influence song attractiveness? As is clearly evident in Fig. 5e, the accent's influence was dominant: the combined manipulation resulted in a very similar response behavior as observed with the pure accent stimuli (compare Fig. 5a, b,e). For all intensities, the combined manipulation in the second or last third of the syllable decreased the responses drastically compared to the accentuation at stimulus onset.

Discussion

Effects of envelope degradation by different frequency bands

Stochastic envelope degradations of song models with frequency bands above 200 Hz were tolerated by *C. biguttulus* females up to a 3–5 dB higher intensity compared to the 0–200 Hz masker. Thus, frequencies below 200 Hz—that overlap with or are close to the song envelope's Fourier components—are roughly twice as destructive maskers compared to the higher frequency bands. Remarkably, the 0–100 and 100–200 Hz maskers had very similar effects, although the latter hardly overlapped with the song's envelope spectrum (see Fig. 1). However, in the temporal domain, these frequencies create gaps in the signal's syllables, which are known to reduce song attractiveness (Fig. 5c, d; von Helversen 1972; Ronacher and Stumpner 1988; von Helversen and von Helversen 1997), and thereby lead to lower critical degradation levels.

Evidently, a masker which covered the song's envelope spectrum had a stronger disturbing effect on females than a masker with a different spectrum (Fig. 4). However, this result is in contrast to a study in which males of *C. biguttulus* were tested with a female's song modified by different maskers (Neuhofer and Ronacher 2012). In Neuhofer's study, the average critical degradation levels did not differ for five maskers that had markedly different overlaps with the main frequencies of the song envelope. These different effects of masking likely reflect the differences between sexes in their innate releasing mechanisms. *C. biguttulus* males require the presence of gaps—and of slowly rising ramps—within a female song subunit, and obviously do not care much about irregularities within syllables. In contrast, females do not respond to subunits with interruptions longer than 2–3 ms (von Helversen and von Helversen 1997).

Effects of onset accentuations

Natural songs of *C. biguttulus* males exhibit an onset accentuation of the "syllables" due to a particularly strong down stroke of the hind legs after a pause (von Helversen and von Helversen 1997; Balakrishnan et al. 2001). The onset accentuations in male songs are mostly between 5 and 8 dB (range 4–11 dB) (von Helversen et al. 2004; Stange and Ronacher 2012). An obvious function of this song feature may be an increased resistance against masking, and may represent an evolutionary adaptation to noisy environments (Wiley 2006; Einhäupl et al. 2011). Indeed, for the song model with a 6 dB onset accentuation there was a trend that animals tolerated an approximately 2 dB higher degradation level as compared with syllables without such an accentuation (Fig. 4). However, this positive effect was restricted to masker frequencies above 200 Hz, whereas for the low frequency maskers the onset accentuation provided no consistent advantage against degradation (Fig. 4).

Besides robustness against noise, the accentuations at syllable onset may also have an additional function since the accentuation height of individual songs was found to correlate with morphological parameters and with an indicator of immunocompetence of the males (Stange and Ronacher 2012). Thus, females could potentially infer information about a male's size and condition from this song feature. Indeed, most females do prefer song models with onset accentuations to rectangular syllables (Balakrishnan et al. 2001, own observations).

Position-specific envelope degradation

First, it should be noted that the results with onset, middle and end accentuations corroborate a conclusion of earlier investigations that grasshoppers process and classify their acoustic signals in the temporal domain and not in the frequency domain (von Helversen and von Helversen 1998; Schmidt et al. 2008). This is supported by the significantly different response percentages to stimuli with identical Fourier amplitude spectra, whereas stimuli with different spectra were treated alike (i.e., rejected). For example, the stimuli with onset accent and end accent in Fig. 5a exhibit the identical Fourier amplitude spectrum (see supplementary figure) but elicited very different responses of the females. In contrast, the mid and end accent stimuli were treated alike in spite of different amplitude spectra.

Let us now compare the effects of accents and gaps in the temporal domain and focus on a single long (24 ms) manipulation. Introducing a 6 dB accent had the opposite effect on stimulus attractiveness as a 6 dB gap (Fig. 5a, c). The stimuli with two 6 ms accents yielded almost identical results as those with a single 24 ms accent (Fig. 5a, b), whereas the responses to two 6 ms gaps differed from those to a single long gap, and revealed only a decreasing attractiveness with stronger intensity differences relative to the syllable plateau, irrespective of their position within the syllable. In combination, these results suggest a particularly strong destructive influence of an intensity rise at inappropriate positions, i.e., an intensity rise that occurs later in the syllable. An accent of 6 dB or more later in the syllable greatly disturbed the recognition mechanism, whereas long gaps at the syllable end had little effect. The strong negative effect of a long gap (12 and 18 dB) in the second position may also be attributable to the intensity rise following the gap. The same reasoning could also explain the strong negative effect of the long gap at the syllable onset (effective at all intensities). The combination of accents and gaps induced behavioral responses that were highly similar to those to accents without gaps. Apparently, the main effect of added gaps was to augment the effects of the intensity rise.

Relating behavioral to neurophysiological data and modeling

The results of the stochastic envelope degradation approach (Fig. 4) demonstrated that degradation frequencies in the range of the song's envelope spectrum are particularly destructive, and conversely, that noise above 200 Hz is efficiently filtered out by properties of auditory neurons. Such filtering is unlikely to occur at the stage of receptors or local neurons since these neurons encode temporal song features in the temporal structure of their spiking responses and because the firing patterns of these neurons generally are capable of reproducing AM rates higher than 200 Hz. Several neurons among them afferents, primary like thoracic neurons (TN1, SN1, partly also BSN1 and even some ascending neurons) showed an all-pass response in their spike rates, with only small changes in spike rates up to modulation frequencies of 500 or 1000 Hz (Franz 2004; Weschke and Ronacher 2008). Spike rates of other neurons, in particular, ascending neurons show low pass, band pass or band stop properties (Weschke and Ronacher 2008; Wohlgemuth et al. 2011). Focusing on how the modulation frequencies influence spike timing, all neurons tested so far exhibit a low pass or band pass characteristic, however their corner frequencies, up to which they may represent amplitude modulations, depend on the processing level (Prinz and Ronacher 2002; Weschke and Ronacher 2008; Wohlgemuth et al. 2011; see also; Neuhofer et al. 2008). Corner frequencies of afferents and local neurons are mostly between 100 and 200 Hz, whereas the majority of ascending neurons exhibits corner frequencies below 100 Hz (median 50 Hz; Ronacher 2014), which would be in line with the filtering of higher frequencies evident in Fig. 4. Yet, a change of coding principles seems to occur between local and ascending auditory neurons: at the level of ascending neurons stimulus features are represented in a labeled line population code that relies predominantly on a spike-count representation (Clemens et al. 2011, 2012).

Summarizing the results of both experimental approaches presented in this study, we hypothesize that the major disturbances for song recognition arise from intensity rises placed at specific positions within the syllable. Several ascending neurons are known that respond to an intensity rise either with additional spikes (AN12, AN3) or with an inhibition (AN4) (Stumpner and Ronacher 1991; Franz and Ronacher 2002; Krahe et al. 2002; Wohlgemuth et al. 2011; see also; Clemens et al. 2011, 2012). However, a corollary of this hypothesis is that the information about an intensity rise at a wrong position within the syllable can only be extracted by comparing the timing of spikes on different ascending neuron types—while the spike timing precision is already reduced at this processing level. This discrepancy strongly suggests the presence of a population code that still relies on the respective timing of action potentials in different ascending neurons (Clemens et al. 2011). A LN model introduced by Clemens postulates a set of parallel feature detectors followed by a temporal integration step by which the exact timing of events is disregarded (Clemens and Ronacher 2013). The behavioral results presented here suggest that this supposed temporal integration step must occur on a later processing stage than at the level of ascending neurons.

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