

Walking in Fourier's space: algorithms for the computation of periodicities in song patterns by the cricket *Gryllus bimaculatus*

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Abstract Is discrimination of the envelope of an acoustic signal based on spectral or temporal computations? To investigate this question for the cricket *Gryllus bimaculatus*, pattern envelopes were constructed by the addition of several sine waves and modified by systematic phase changes. The phonotactic response of female crickets towards such sinusoidal but also rectangular pulse patterns was quantified on a locomotion compensator. Envelope patterns that exhibited a modulation frequency of 25 Hz as the dominant frequency were attractive and although changes of phase modified the temporal pattern, the values of attractiveness remained unaffected. Removal of the 25-Hz component reduced the phonotactic scores. Patterns in which other frequency components exhibited a larger amplitude than the 25-Hz component were less attractive. However, the combination of an unattractive pulse period with the attractive modulation frequency of 25 Hz in a pattern revealed that such stimuli were unattractive despite the presence of the 25-Hz component. A comparison of the attractiveness of all patterns revealed that female crickets evaluated the duration of pulse period over a wide range of duty cycles. The combined evidence showed that pattern envelopes were processed in the time- and not in the spectral domain.

Keywords Acoustic communication · Auditory processing · Fourier analysis · Pattern recognition · Signal envelope

Introduction

How do female crickets discriminate the songs of their own species from others? A brief inspection of their acoustic signals deems this a simple task: a sinusoidal carrier is amplitude modulated such that a periodical series of sound pulses with silent pauses results. Since the auditory organ of crickets cannot perform a frequency analysis of the carrier with high resolution, it is the amplitude modulation or envelope of the signal that transmits the relevant information for song discrimination (Huber et al. 1989). Variation in the temporal pattern of pulses is the decisive means by which crickets can encode their species identity. However, there are two constraints that limit the coding space for different signal envelopes for crickets: first, the resonant mechanism of sound production curtails the possibility to include temporal detail and second, temporal resolution for amplitude modulations in the auditory pathway will limit the decoding of temporal detail in patterns (Gerhardt and Huber 2002; Huber et al. 1989). Indeed, most species use simple series of continuous pulses (trills) or groups of pulses (chirps) separated by some longer pause (Fig. 1a). Only few species exhibit more complex rhythms in their songs as for instance in the genus *Teleogryllus* (Otte 1992).

From a technical point of view, the simplest algorithm for the analysis of such a periodical pattern is the computation of the autocorrelation function that would instantly reveal the most common interval (Hartmann 1998). From a researcher's point of view, however, it has turned out to be remarkably difficult to determine the algorithm by which crickets analyse their songs. The first extensive investigation proposed a 30-Hz filter for the cricket *Gryllus bimaculatus* (Thorson et al. 1982) and thus suggested that the algorithm operates in the frequency domain, equivalent to a

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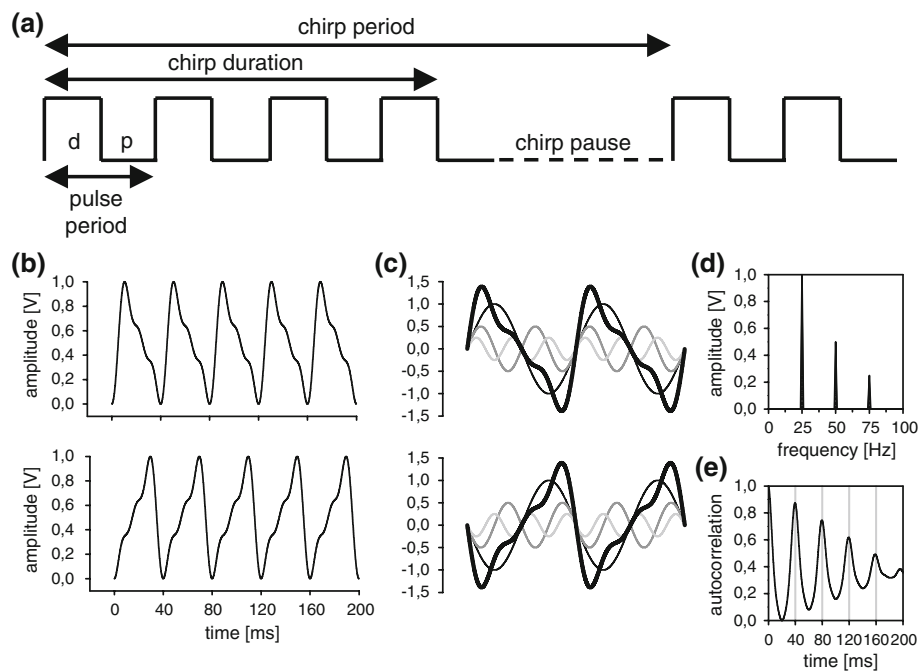


Fig. 1 Temporal and spectral cues of periodical signals. **a** Envelope of a song pattern composed of groups of pulses is typical for the cricket, *G. bimaculatus*, with terms describing the temporal cues available for evaluation (*d* pulse; *p* pause duration; duty cycle (not shown) is calculated as $d/(d + p)$; pulse period). **b** Envelopes of sinusoidal pulse patterns build from the addition of sine waves as shown in (c). **c** The triangular pulse shapes in (b) result from the

addition of three frequencies that are multiples of each other and are added at halving the amplitude for each higher harmonic. Due to the change of phases from 0° (upper panel) by 180° (lower panel), patterns are inverted and correspond to time reversed versions of one another. **d** Amplitude spectrum and **e** autocorrelation function for the two patterns in (b) are identical, because both computations are phase insensitive

spectral analysis of the envelope. The observation of high-, low- and bandpass-properties of neurons in the brain of crickets supported this view (Schildberger 1984). However, evidence for an analysis in the time domain by measuring pulse periods or pulse durations by computation of the cross-correlation function with an internal template also exists (Hennig 2003). Moreover, for bushcrickets that use similar patterns of pulses as crickets but filled with a broadband carrier, a temporal analysis is also observed (Schul 1998).

The present report focuses on the algorithm of computation (Marr 1982) and not on its physiological implementation (see for example Schildberger 1984; Nabatiyan et al. 2003; Webb et al. 2007). Computational algorithms for a time series can be divided into two groups, spectral computations that decompose the signal into the amplitude and phase spectra of its frequency components and temporal computations that measure durations of signal elements in time (Hartmann 1998). The main difference between algorithms that operate in the spectral and the temporal domain arises from their phase dependence. If an algorithm operates in the frequency domain, only the amplitude spectrum of its frequency components is evaluated. Then, only the presence of a single fundamental frequency—or a set of frequencies—should suffice for

song discrimination and all temporal information as introduced by phase differences should be irrelevant (as explained in Fig. 1b). Such an algorithm corresponds to the prediction of the 30-Hz filter that suggests a simple band-pass filter composed of elements with high- and low-pass filter properties (Thorson et al. 1982; Schildberger 1984). *Sensu strictu* all signals with identical spectral content should then elicit the same response irrespective of their temporal pattern (see Fig. 3 for such a set of patterns). In contrast, if the algorithm operates in the time domain, temporal measures such as pulse duration, pause duration or pulse period should be important (Schul 1998; Bush and Schul 2006, Hennig 2003). In these cases, the phase spectrum of a Fourier analysis does matter, because the temporal pattern is unequivocally described only, if both the amplitude and phase spectra are known (Hartmann 1998; Michelsen et al. 1985; von Helversen and von Helversen 1998; Schmidt et al. 2007). The computation of a correlation function may be viewed as a method to derive periodicities in a signal; while an autocorrelation compares the signal with itself and is independent of phase (Fig. 1b), a cross-correlation compares the signal with a template and thus operates in the temporal domain.

The goal of the present study was to devise a set of experiments by which an identification of the algorithm

of pattern analysis in crickets is possible. The cricket *G. bimaculatus* was chosen since with this species the original experiments suggesting a spectral analysis were performed. First, the transfer function of the auditory filter in the cricket *G. bimaculatus* for sinusoidal stimuli was determined. Second, stimuli with different phase spectra but identical amplitude spectra were tested and the amplitude of the fundamental frequency was varied in order to determine its role for positive phonotaxis. Finally, the responses of crickets to spectral and temporal properties of a variety of patterns were compared.

Materials and methods

Animals

Gryllus bimaculatus were obtained as nymphs from a commercial supplier and raised to adulthood in isolation from males. Virgin females were tested from the ninth day after their final moult.

Phonotaxis experiments

Behavioural tests were performed on a locomotion compensator (Kramer treadmill; for details see Weber et al. 1981) in an anechoic chamber at $25 \pm 2^\circ\text{C}$. Experiments were conducted in the dark except for the infrared light used to monitor the movements of the cricket. Crickets were placed on top of a sphere, free to walk but kept in place by compensatory sphere rotations, while song models were presented from loudspeakers in their horizontal plane. The rotations of the sphere were monitored by displacement transducers. After sampling their output signal by an AD-board (PCI-6221, National Instruments, TX, USA), the walking velocity and virtual track of the insect were calculated.

Stimulus generation and presentation

Song models were generated digitally by multiplication of a given signal envelope with a sine wave (4.5 kHz) using LabView Software (National Instruments, TX, USA). Envelopes of sinusoidal stimuli were constructed by addition of sine waves and the resulting waveform was normalized to the maximum such that the signal envelope varied between zero and 1 V (Fig. 1b, c). When introducing phase changes, the envelope for some stimuli was shifted in time in order to ensure zero levels at the beginning (see Schmidt et al. 2007 for a similar approach). Changing the phase of all frequencies by 180° always results in an inversion of signal (Fig. 1b, c) and in some cases this is equivalent to a reversion of a signal in time

(Fig. 1b; see Figs. 3, 4, and 5 for several examples of such inversions and reversions; von Helversen and von Helversen 1998; Hartmann 1998). Note that pairs of patterns with a reciprocal duty cycle (e.g., 0.1 and 0.9 or 0.3 and 0.7 as in Fig. 6) also represent inverted, but not reversed versions from one another and thus possess the same amplitude spectrum but different phase spectra (see also Hennig et al. 2004).

The envelope for song models with rectangular pulses and pauses was generated with rise and fall times of 1 ms. Pulsed stimuli were either continuous or contained groups of pulses, mimicking a chirp of *G. bimaculatus* (c.f. Figs. 1, 2). Chirps had a duration of 200 ms followed by a pause of 133 ms, corresponding to a chirp rate of 3 Hz, unless otherwise specified. Acoustic stimuli were stored on disk and broadcast after DA-conversion (16-bit resolution, 100 kHz sampling rate; PCI-6221 National Instruments, Texas) via one of two loudspeakers (Piezo Horn tweeter PH8) separated by an angle of 90° . Signal amplitude was calibrated with a condenser microphone (Bruel & Kjaer Type 4133) and a measuring amplifier (Bruel & Kjaer Type 2231). Sound measurements were obtained 0.5 cm above the sphere, with the microphone directed towards the loudspeaker. Sound intensities were 80 ± 2 dB SPL (re. 2×10^{-5} μPa , fast reading).

Temporal measures of patterns were obtained with a threshold at 15% of the maximum that returned the values for pulse and pause duration. From these values, period duration and duty cycle (pulse duration divided by period duration; Schildberger 1984, Verburt et al. 2007) were computed. For patterns with rectangular pulses these values were rather robust for variation of the threshold due to the fast rise time of 1 ms; patterns with sinusoidal pulses for which equivocal or ambiguous values due to small variations in threshold resulted were excluded from presentation in Fig. 7, but included in Fig. 8. For the computation of amplitude spectra only the chirp part of a signal without the following chirp pause was used. By this constraint the 3-Hz component due to the chirp structure and not relevant for the present investigation was removed from the spectra. Note that the spectral content does not principally change by that procedure, but that side bands of spectral peaks are reduced. Before computation of a spectrum, the mean value of the envelope pattern was subtracted, in order to remove the f_0 -component in the spectrum that has an effect on amplitude values. This procedure is justified, since the effect of adaptation of sensory neurons on the coding of patterns has the same effect (Benda and Hennig 2007). The amplitude values of frequencies used are given in the text and the respective figure captions. Phase values were chosen such that distinct differences in temporal patterns arose. Note that phase values are relative, because of the phase rules of spectral analysis (Hartmann 1998).

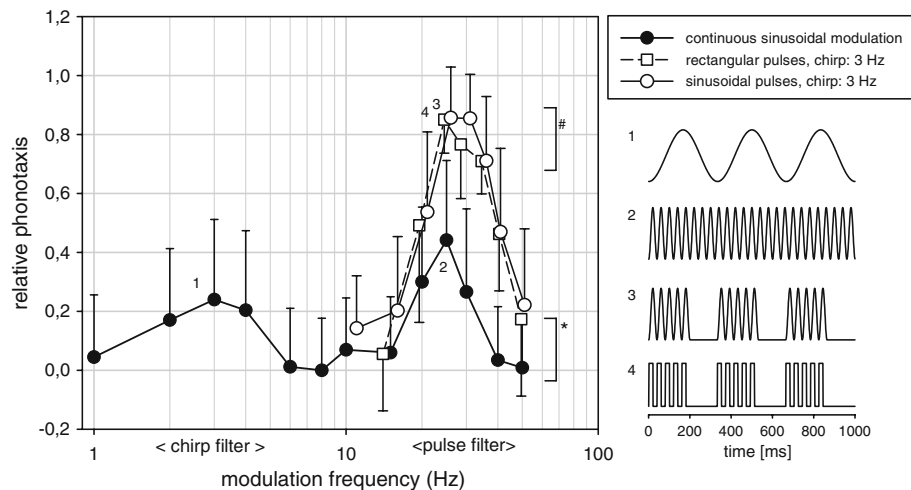


Fig. 2 Transfer function of phonotactic response for females of *G. bimaculatus* in response to envelope patterns with different modulation frequencies. Presented stimuli consisted of continuous modulations (black circles, see envelope patterns 1 and 2) or groups, i.e. chirps of sinusoidal (white circles, pattern 3) or rectangular (white squares, pattern 4) pulses. The modulation frequency for the latter stimuli was calculated as the inverse of the pulse period and corresponded to the fundamental frequency of the amplitude

spectrum. Envelopes of all stimuli were filled with a carrier of 4.5 kHz. Chirp and pulse filters refer to responses at 3 and 25 Hz, respectively. Responses marked with a '#' were not significantly different from the positive control stimulus, responses marked with a '*' were not significantly different from the negative controls. Responses without a mark were significantly different from the positive as well as the negative control stimuli (see "Materials and methods")

Stimulus protocol and data evaluation

Acoustic stimuli were presented for 100 s from each loudspeaker consecutively. A control stimulus, similar to the calling song of males (5 pulses at pulse/pause durations of 20/20 ms, pulse period of 40 ms, chirp period 333 ms; see Fig. 2, pattern 4), was presented at the beginning and also the end of each session in order to control for a change of motivation (positive control). Female crickets were tested with 4–7 test stimuli in each session (25–40 min). Further controls included the presentation both of continuous unmodulated tones at 4.5 kHz as well as silent intervals for 100 s, in order to obtain measures for baseline activity of individual females (negative control). Before the presentation of a stimulus from a respective loudspeaker a silent break of 10 s was maintained, in order to minimize possible hysteresis effects from the previous pattern (see Weber et al. 1981 and Poulet and Hedwig 2005 who reported a time constant of 5–7 s for the decay of phonotactic orientation after presentation of an attractive signal).

For each walking track, the walking distance, vector length (L) and angle towards the loudspeaker (γ ; after correction for the respective loudspeaker position) were calculated and referenced to the measures of the walking track obtained for the initial control stimulus according to the following formula (see Schul 1998 for a detailed description):

$$\text{relative phonotaxis}_{[\text{test}]} = \left(\frac{\text{distance}_{[\text{test}]}}{\text{distance}_{[\text{control}]}} \right) * L_{[\text{test}]} * \cos |\gamma_{[\text{test}]} - \gamma_{[\text{control}]}|$$

The value of relative phonotaxis for the first presentation of the positive control was therefore the value of the vector length and crickets then typically achieved scores of 0.8. Consequently, this measure of relative phonotaxis indicated positive or negative phonotaxis at values of 0.8 or -0.8 , respectively. Values around zero indicate no preferred orientation and were usually the result of circular walking tracks. The measure of 'relative phonotaxis' served as valid indicator for the attractiveness of a stimulus and exhibited two major advantages over singular readings of phonotactic orientation. First, individual variations with respect to walking distance and biases in the directional orientation of individual females towards a loudspeaker are compensated for. Second, readings larger than 1.0 indicate that a test stimulus is more attractive than the control (i.e., a supernormal stimulus, Lorenz 1943, Tinbergen 1951).

Since phonotactic scores of female crickets to the first presentation of the positive control were typically at 0.8, experiments were aborted, if the response was below 0.6. Test sessions in which the response to the final control was more than 20% below that of the first control or in which the responses to continuous tones or silent intervals serving as negative controls was higher than 0.2 were excluded from the data set. Unless specified otherwise mean values and standard deviation are indicated.

Statistical analysis was performed with raw data that is the value of relative phonotaxis obtained for one female for a particular test or control stimulus. For a test series, a minimum of 15 and a maximum of 42 different females

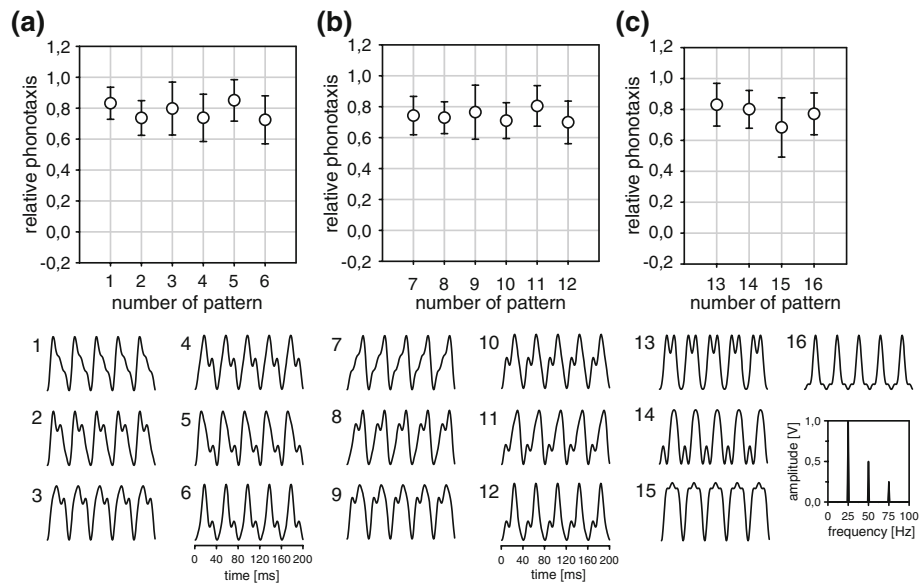


Fig. 3 Phonotactic response towards envelope patterns that were composed by addition of three sine waves (25, 50, and 75 Hz at amplitudes of 1.0, 0.5 and 0.25, respectively; see Fig. 3c, inset). Due to the variation of phase, different envelope patterns (the chirp part of 200 ms is shown below the respective panels) emerged in the time domain, although the amplitude spectrum is identical for all stimuli in (a) to (c). Stimuli with triangular appearance were grouped according to the rise time (a steep onset, b shallow onset). In c symmetrical stimuli are shown. a–c Females responded to all patterns equally well.

were tested. In most cases but not all the scores of relative phonotaxis were normally distributed. Therefore, a non-parametric test was chosen (Friedman Test (Nonparametric Repeated Measures ANOVA) with Dunn post-test in GraphPad Software, California) considering multiple tests of individual females in different test series. For all test series the relative phonotactic scores for the positive control (first and last control pattern in a test series) were not significantly different from one another. Equally, there was no significant difference between two negative controls (the silent and continuous tone control). In Figs. 2, 3, 4, 5, and 6, the scores obtained from test patterns were compared to both the positive and the negative control stimuli and thus three classes of attractiveness emerged for all test patterns. In Figs. 2, 4b, 5, and 6, test patterns that were not significantly different from the positive control are marked by a ‘#’ indicating high attractiveness, test patterns not significantly different from the negative control are marked by a ‘*’ indicating low attractiveness due to random orientation and test patterns significantly different from both control types indicating intermediate attractiveness (data points unmarked). In Figs. 3 and 4a, levels of significance are given in the legend. In general, the scores of relative phonotaxis for two given test patterns had to differ by 0.20–0.25 in order to become significantly different. The method used for interpolation of data in Figs. 7a, h was

Differences in the temporal detail of the envelope patterns appeared to be unimportant. Differences in rise time and duty cycle between patterns did not significantly change the phonotactic response. Note that stimuli in panels a and b represented inverted versions from one another, as for instance patterns 1 and 7, and thus correspond to forward (1) and backward (7) played versions. Stimuli in c also show pairs of inverted patterns (13, 14 and 15, 16), but these cases do not correspond to inversions in time. All responses in a to c were not significantly different from the response to the positive control stimuli

based on a triangulation of the data and cubic interpolation (Barber et al. 1996).

Results

The transfer function of female crickets for modulation frequencies was determined by presentation of sinusoidal signals from 1 to 50 Hz with a carrier frequency of 4.5 kHz (Fig. 2, filled circles). Test stimuli were broadcast continuously for 100 s from each loudspeaker and sinusoidal pulses were not grouped into chirps as they occur in the calling song of *G. bimaculatus*. The transfer function revealed a bimodal distribution with increased scores for relative phonotaxis at 3 and 25 Hz, significantly different from a random orientation (Fig. 2). However, high values of relative phonotaxis were only obtained, if the presented modulation pulses were grouped into chirps that were broadcast at a period of 333 ms (equivalent to 3 Hz with a chirp duration of 200 ms, Fig. 2, open symbols, e.g., patterns 3, 4). Best responses for modulation frequencies between 25 and 35 Hz were not significantly different from the positive control stimulus. The shape of the response curve for modulation frequencies higher than 10 Hz was the same for both sinusoidal and rectangular pulses (Fig. 2 open symbols). This set of experiments suggested that

female crickets employ two tuned filters (a chirp filter at 3 Hz and a pulse filter at 25 Hz) both of which have to be activated for strong positive phonotaxis (c.f. Doherty 1985). At 15 and 50 Hz, the values of relative phonotaxis for chirp patterns were of the same magnitude as for a continuous modulation frequency of 3 Hz and may be due to the activation of the chirp filter alone (Fig. 2). Since the algorithm of the pulse filter was in the focus of the present investigation, the chirp structure as in patterns 3 and 4 of Fig. 2 was maintained for further test stimuli. Chirp duration was kept at 200 ms and chirp period was set to 333 ms equivalent to 3 Hz. The amplitude spectra of those stimuli are rather similar to that of a continuous pattern without the chirp structure, but reveal an additional frequency component at 3 Hz and side bands for all frequency components with higher magnitude (see Materials and methods and Hartmann 1998). In order to be able to compare spectra for different patterns directly, the 3-Hz component was removed from the spectra shown in the following figures. Viewed in the frequency domain, a frequency of 25 Hz elicited best responses of the pulse filter, which corresponded to a pulse period of 40 ms in the time domain.

Properties of the pulse filter in the frequency domain

An algorithm for pattern analysis that evaluates the amplitude spectrum of a signal in the frequency domain should be insensitive for variation of the phase in the signal and depend on the relative magnitude of the relevant frequency component; that is 25 Hz for females of *G. bimaculatus* (Fig. 2). Therefore, if the observed peak at 25 Hz was strictly due to a plain bandpass filter that evaluates the pattern envelope in the frequency domain, then the filter's response as measured by the relative phonotaxis of crickets should be independent of phase variations in the pattern provided the 25-Hz component is present.

In a first set of experiments, a basic pattern was chosen that contained three frequency components 25, 50 and 75 Hz at amplitudes of 1.00, 0.50 and 0.25, respectively (inset in Fig. 3c). If all frequencies are added with phase values of zero, then a triangular temporal pattern with a strong onset results (Figs. 1b, c, 3a-1). Variation of phases produced a set of different temporal patterns that all share the same pulse period of 40 ms and differed mainly in pulse and pause duration, duty cycle and rise time, despite the identical spectral content of all patterns (Fig. 3, see patterns below panels). Female crickets accepted all these patterns equally well and responded with high values of relative phonotaxis that were not significantly different from the response to the positive control stimuli (Fig. 3). In Fig. 3, the responses towards these patterns are grouped according to fast (Fig. 3a) and slow rise time (Fig. 3b), in order to demonstrate that this temporal cue had no

influence on the values of relative phonotaxis. In Fig. 3c, stimuli with symmetrical pulse shapes are shown. Thus, variation of phases in this set of patterns did not affect the high levels of relative phonotaxis. Consequently, this data set appeared to provide strong evidence for processing in the frequency domain without the influence of phase information. However, in the time domain all patterns also revealed a pulse period of 40 ms that could account for the high levels of attractiveness if processing is rooted in the time domain. Therefore, several controls were necessary in order to exclude processing in the temporal domain. If processing was based on frequency analysis by a bandpass filter tuned to 25 Hz, best responses of female crickets should depend on (1) the presence and (2) magnitude of the 25-Hz component and should (3) be maintained, if the 25-Hz component was introduced as a harmonic frequency component. Furthermore, variations of phases should not lead to different responses for patterns composed from the same amplitude spectrum.

In a second set of experiments, the fundamental frequency of 25 Hz was removed from the spectrum that produced a triangular pattern (c.f. Fig. 3) in order to test the importance of the 25-Hz component. In the time domain stimuli with faster temporal modulations appeared (Fig. 4a). For these patterns the phase was also varied, in order to control for the possibility that patterns with particular phase combinations were more attractive than others. This variation of phase changed the temporal pattern, but regular peaks with a pulse period of 40 ms were retained (Fig. 4a—1, 2, 3, 4). Female crickets did not respond to any of these patterns with a missing fundamental of 25 Hz very well. However, the scores of relative phonotaxis were significantly different from the negative controls. A basic response level at 0.2 remained for all patterns that was possibly due to the activation of the chirp filter as previously observed (Fig. 2 at 3 Hz). Thus, the frequency component of 25 Hz appeared to be crucial for positive phonotaxis and further supported the view of spectral processing regardless of phase information. Temporal processing appeared unlikely, since female crickets failed to respond well although the temporal period of 40 ms was present in all four test patterns. However, viewed from the temporal domain the failure of crickets to respond to these patterns with a pulse period of 40 ms (Fig. 4a) may have been due to a masking effect of the pulse period partly due to insufficient modulation depth in the presented patterns. Therefore, a control experiment was added to determine the level of masking in the temporal domain that female crickets would accept (Fig. 4b). These tests revealed that crickets respond with high values of relative phonotaxis, if the modulation depth was at least 50% but not below. Unmodulated blocks of sound (0% in Fig. 4b) were still significantly different from the responses

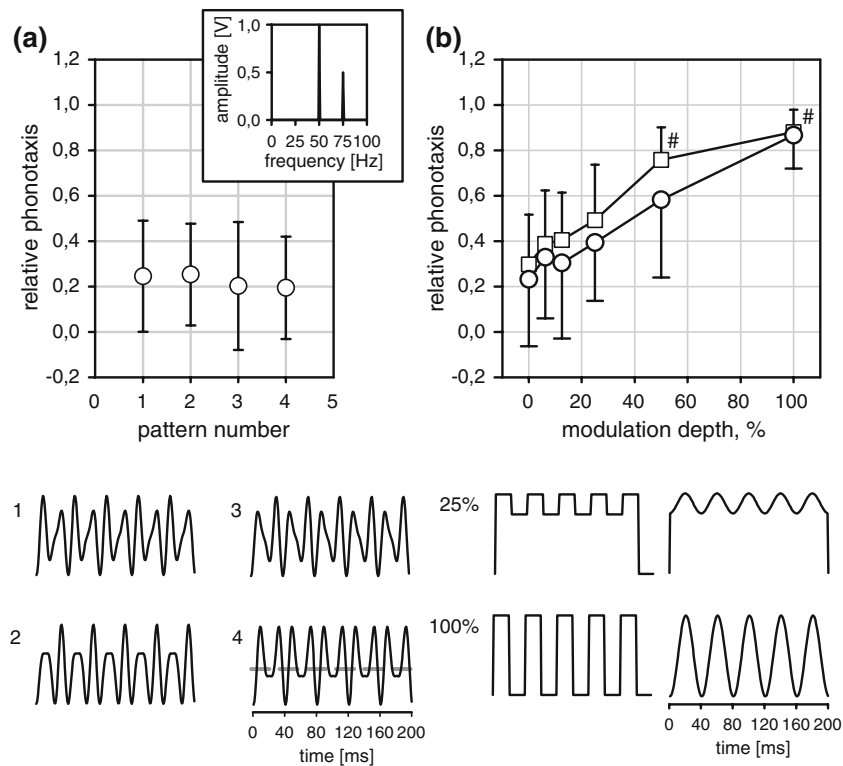


Fig. 4 Phonotactic response towards envelope patterns that were composed by the addition of sine waves as in Fig. 3, but without the fundamental frequency of 25 Hz and towards patterns with different modulation depth. **a** Patterns without the fundamental frequency of 25 Hz (see inset for spectrum) elicited only low relative phonotactic scores. Presented patterns are shown below the panel in the time domain. Patterns 1–3 reveal a pulse period of 40 ms measured from peak to peak. All responses were significantly different from the response to the negative control stimuli. The grey stippled line in pattern 4 indicates a modulation depth of 50%. **b** Relative phonotaxis

to envelope patterns with a pulse period of 40 ms (i.e., 25 Hz) but different modulation depth. Two sets of stimuli were presented (sinusoidal modulation: *open circles*, pulse modulation: *open squares*; see examples below). Only patterns with a modulation depth of 50% or higher elicited a relative phonotactic score as high as the control. Responses marked with a '#' were not significantly different from the positive control stimulus. Responses without a mark were significantly different from the positive as well as the negative control stimuli

to the negative controls and may again reflect the response of the chirp filter. Nevertheless, the patterns tested in Fig. 4a had a level of masking due to a reduced modulation depth of approximately 50% (indicated by a grey stippled line for pattern 4 in Fig. 4a). Although female crickets tolerated a masking of 50% in experiments in which the modulation depth was varied (Fig. 4b), test patterns that revealed a modulated rather than a continuous masking may require higher signal to noise ratios for signal detection (Ronacher and Hoffmann 2003). Therefore, the observed drop in the response can also be explained in the temporal domain due to masking effects of the pulse period of 40 ms.

In a third set of experiments, other frequency components were added to the frequency component of 25 Hz (Fig. 5). If processing was based on a plain bandpass tuned to 25 Hz, other frequency components in the signal should not affect the filters response (see sketch in Fig. 5d, upper panel). Frequency components of 15 and 50 Hz were chosen for addition, since these elicited only low response

levels if presented alone (Fig. 2, open symbols). In the series of tests shown in Fig. 5 amplitude values for the added modulation frequencies were calculated as dB-values referenced to the amplitude of the 25-Hz component. At 0 dB, the added frequency component was of the same magnitude as the 25-Hz component. With increasing amplitude of the added frequency component, relative phonotaxis was reduced (Fig. 5a, b). Within each group of test patterns with a particular combination of amplitudes, the phase was varied in order to test whether the attractiveness of a set of test patterns with the same amplitude values was dependent on temporal properties. The small variation of relative phonotaxis values within each group of amplitude values suggested that phase and thus temporal information had little influence on the values of relative phonotaxis in these tests (Fig. 5a, b, see patterns below each panel). The response of female crickets deteriorated in a similar manner, if both lower and higher frequency components were added (Fig. 5c). The data for the test patterns at -6 dB in Fig. 5b confirm the results shown in

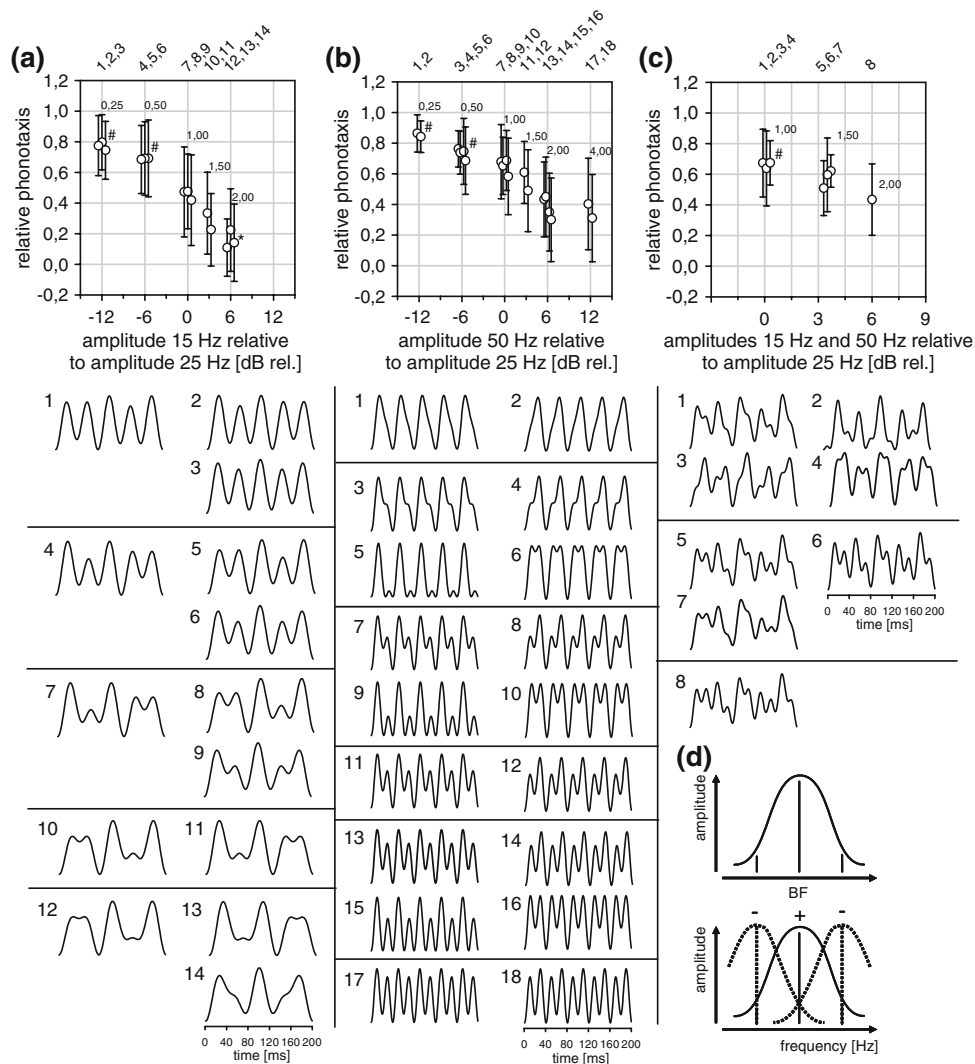


Fig. 5 Phonotactic response to envelope patterns composed by the addition of sinus of different amplitudes. **a** Response to patterns to which a modulation frequency of 15 Hz was added to 25 Hz (set to 1 V) at increasing amplitudes. The amplitude of the 15-Hz component is indicated in dB relative to the amplitude of the 25-Hz component at the abscissa. Negative dB-values indicate a lower amplitude of the 15-Hz component, 0 dB indicates equal amplitude of both components. The respective patterns are shown below in the time domain and are indexed by a number given above the panel. Patterns below panels represent inverted and reversed version from one another (see “Materials and methods” and Fig. 1b, c). Numbers within the panel refer to the amplitude of the added 15-Hz component. Note that the values of relative phonotaxis were slightly shifted at their respective dB-values according to the pattern index above for better visibility. The phonotactic score decreased with increasing amplitude of the 15-Hz component. **b** Response to patterns for which a modulation frequency of 50 Hz was added to 25 Hz (set to 1 V) at increasing

amplitudes. Patterns and dB-values are shown as in **a**. The phonotactic score decreases with increasing amplitude of the 50-Hz component, however, the reduction is not as strong as for the addition of the 15-Hz component as in **(a)**. **c** Response to patterns to which modulation frequencies of 15 and 50 Hz were added to 25 Hz (set to 1 V) at increasing amplitudes. Patterns are shown as in **(a)**; dB-values indicate the summed amplitude of both added frequency components (15, 50 Hz) relative to the amplitude of 25-Hz component. Note that the envelope of such a pattern was normalized to maximum of 1 V after the addition of frequencies. **d** Sketch of a plain bandpass filter tuned to a best frequency (BF, *upper panel*). Sketch of a bandpass filter with suppressing filters at lower and higher frequencies (*lower panel*). Responses marked with a ‘#’ were not significantly different from the positive control stimulus, responses marked with a ‘*’ were not significantly different from the negative controls. Responses without a mark were significantly different from the positive as well as the negative control stimuli

Fig. 3, since the amplitude spectra of these patterns were identical except for the weak 75-Hz component and patterns 3–6 in Fig. 5b also resemble those in Fig. 3. From the viewpoint of a frequency analysis, this reduction argued against a plain 25-Hz filter, since then other frequency

components should not affect the response. However, a frequency analysis cannot be excluded, since adjacent filters that are tuned to the lower and higher frequency components may suppress the response of the bandpass filter tuned to 25 Hz (see sketch in Fig. 5d, lower panel).

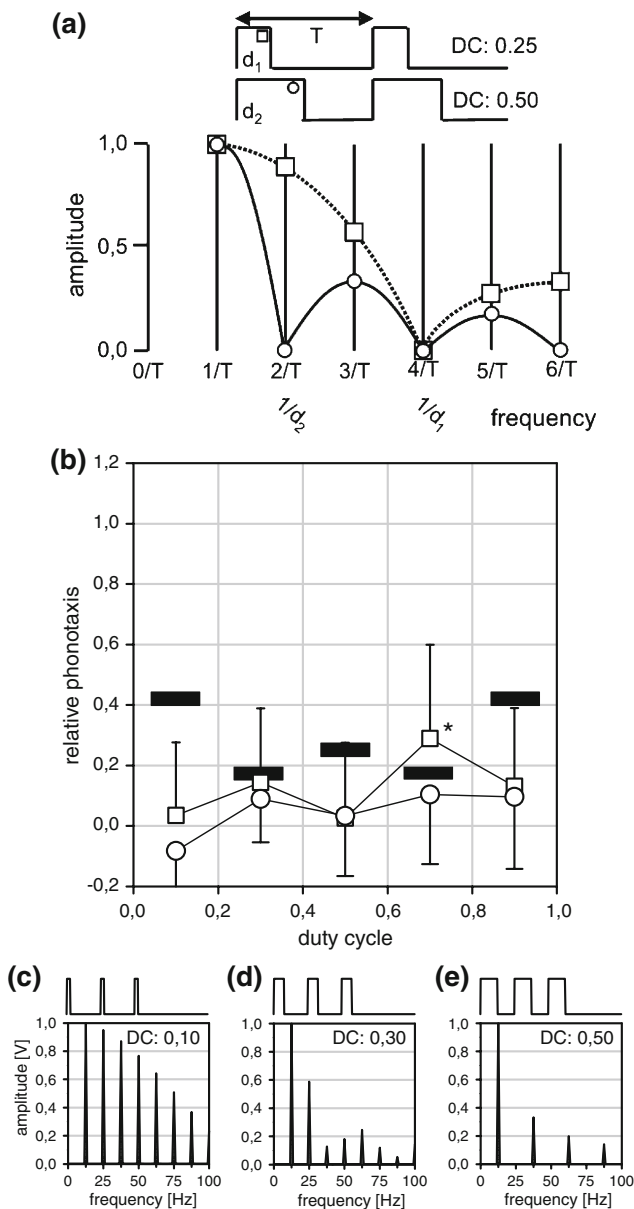


Fig. 6 Phonotactic response to envelope patterns of groups of pulses with a pulse period of 80 ms and different duty cycles. **a** Amplitude spectra for patterns with different duty cycles. This panel illustrates how at a given pulse period T , the amplitude of harmonics in the spectrum (x/T) depends on the duration of the pulse d_i and thus the duty cycle. At a duty cycle of 0.5, the first harmonic ($2/T$) disappears completely (i.e. 25 Hz for a fundamental frequency of 12.5 Hz). See text for further explanation. **b** Response to pulse patterns with a pulse period of 80 ms and different duty cycles. Two sets of stimuli with different numbers of pulses were presented (*open circles* 3 pulses; *open squares* 4 pulses) in order to control for a possible influence of pulse number and chirp duration. The response marked with a ‘*’ was significantly different from the negative controls, all other responses were not significantly different from the negative controls. *Black bars* indicate expected responses, see text. **c–e** Envelope and amplitude spectra of test patterns with different duty cycles. Note that the amplitude spectra of patterns with a duty cycle of 0.7 and 0.9 are identical to those in **(d)** and **(c)**, respectively (see text)

Also, variations in phase did not affect the responses to these patterns as previously observed (Figs. 3, 4a). However, if viewed in the temporal domain, the reduction in the scores of relative phonotaxis can also be explained by a shift of the pulse period from 40 to 66 ms (i.e., the period of 15 Hz) in Fig. 5a (patterns 7–14) and by an increased masking of and thus difficulty to detect the pulse period of 40 ms as was also the case in Fig. 4a (Fig. 5, b patterns 13–18; c, patterns 5–8).

The conclusion from these first three sets of experiments was that the attractiveness of patterns can be explained by both a frequency based and time based filter process. Certainly, all patterns with a dominant frequency of 25 Hz were attractive but these also revealed a clear period of 40 ms. Conversely, unattractive patterns revealed a low or masked 25-Hz component, but in the time domain this was also the case for the period of 40 ms: stimuli in which the magnitude of the 25-Hz component was reduced also increased the masking of the period of 40 ms (Figs. 4, 5). The lacking influence of phase information on the attractiveness of patterns in Figs. 3, 4, and 5 appeared to support processing in the frequency domain. However, viewed from the time domain, the temporal variations as introduced by phase may have been too small to be detected due to a limited temporal resolution of auditory processing in crickets.

A fourth set of experiments was devised, in which patterns with a period of 80 ms were presented that nevertheless contained the frequency component of 25 Hz. In the time domain, these patterns should be unattractive due to the long pulse period twice as long as the pulse period of 40 ms (see responses to a modulation frequency of 12.5 Hz in Fig. 2, open symbols, that correspond to the fundamental frequency of a pulse period of 80 ms). However, in the frequency domain these patterns should reveal some level of attractiveness, since the amplitude spectrum contains the 25-Hz component as a higher harmonic (Hartmann 1998; Gerhardt and Huber 2002). Variation of the duty cycle in a pattern with a pulse period of 80 ms produces spectra that contain 12.5 Hz as the fundamental frequency and 25 Hz as the first harmonic frequency. The amplitude of the 25-Hz component depends on the duty cycle as sketched in Fig. 6a. Patterns with rectangular pulses reveal a fundamental frequency that corresponds to the pulse period ($1/T$ in Fig. 6a) and harmonic frequencies at n/T . By variation of the duty cycle at a constant period the pulse duration d_i is varied (Fig. 6a, upper panels). In the amplitude spectrum of such a pattern both the line spectrum due to the period T and the spectrum of the pulse duration d_i are convolved. Patterns with short pulse durations at small duty cycles will reveal numerous harmonic frequencies in their amplitude spectrum (Fig. 6a, open squares). However, at a duty cycle

of 0.5 every second harmonic of the fundamental frequency will assume an amplitude value of zero and thus disappear from the amplitude spectrum (Fig. 6a, open circles; Hartmann 1998). Therefore, at a fundamental frequency of 12.5 Hz the first harmonic frequency of 25 Hz will disappear from the spectrum at a duty cycle of 0.5, but will be present with varying amplitude at all other duty cycles. Note that the amplitude spectra of patterns with reciprocal pairs of low and high duty cycles are identical (i.e., 0.1 and 0.9 or 0.3 and 0.7, see Materials and methods). Therefore in Fig. 6c–e, only the spectra for duty cycles up to 0.5 are shown for the tested patterns. The phase spectra of such pairs of patterns are nevertheless different, because a pattern with a low duty cycle represents an inverted version of a pattern with a high duty cycle (see Materials and methods, Hartmann 1998, Hennig et al. 2004).

This experiment was designed as a crucial test whether female crickets analyse patterns in the temporal or the spectral domain. In the former case, none of these test patterns should be attractive due to the long pulse period of 80 ms. In case of spectral processing only patterns with low and high duty cycles should be attractive, while a duty cycle of 0.5 should be unattractive due to the lack of the 25-Hz component (see spectra in Fig. 6c–e). The spectral masking of the 25-Hz component in these patterns was similar to the masking by the addition of other frequency components tested previously (Fig. 5). In order to control for possible effects of the number of pulses in these experiments, two sets of patterns with 3 and 4 pulses respectively were tested (Fig. 6b). The values of relative phonotaxis were low for all patterns and not significantly different from the negative controls except for one pattern (marked with an asterisk, Fig. 6b). If processing is rooted in the frequency domain, the expected response levels can be estimated with some caution from the previous data set in which other frequency components were added to the 25-Hz component (Fig. 5) and are indicated as black bars in Fig. 6b. The spectra of patterns with duty cycles 0.1 and 0.9 (Fig. 6c) roughly correspond to pattern 8 in Fig. 5c and the spectra of duty cycles 0.3 and 0.7 correspond to patterns 12–14 in Fig. 5a. In the spectral domain these patterns are most similar to the signals in Fig. 6, but there are differences in the number of frequencies in the respective spectra (Figs. 5, 6). Furthermore, the effect on response levels by adding lower or higher frequencies than 25 Hz may also differ (c.f. Fig. 5a, b). Both differences somewhat limit the reliability of the expected response levels in Fig. 6b. Nevertheless, especially at low and high duty cycles the expected response levels were not reached (Fig. 6b). The test series in Fig. 4a in which the fundamental frequency of 25 Hz was removed did not closely resemble the spectrum of a pattern with a duty cycle of 0.5 as in Fig. 6e, since those patterns were composed from 50

and 75 Hz (Fig. 4a) that are not present in the spectrum of Fig. 6e. Yet, tests without the 25-Hz component had revealed scores of relative phonotaxis at 0.2 (Fig. 4a) and were higher than those obtained for the tests in Fig. 6b. Similarly, a test pattern with the 15-Hz component alone (Fig. 2, open symbols) that is similar to the spectrum of the 12.5 Hz tested in Fig. 6b, e at a duty cycle of 0.5, scored values of relative phonotaxis were at 0.2 and different from the negative controls. Furthermore, previous experiments had shown that a basic response level was always observed at a relative phonotaxis of 0.2 most likely due to the sole activation of the chirp filter (Figs. 2, 3, 4, 5). Such a response level is not observed for almost all patterns in Fig. 6b and may indicate a suppression of the phonotactic response to patterns with a pulse period of 80 ms. In conclusion, the results presented in Fig. 6 suggested that the pulse period of 80 ms does not activate the pulse filter, although a frequency component of 25 Hz is clearly present in all patterns with a duty cycle other than 0.5. Consequently, pattern evaluation of the pulse filter does not operate in the frequency domain but in the temporal domain.

Relevant cues for the pulse filter in the temporal domain

The combined evidence from the experiments in the previous section indicated that female crickets of *G. bimaculatus* evaluated the pattern envelope with an algorithm that measures temporal cues. The data set also showed that several temporal details in a pattern did not strongly influence the attractiveness of a stimulus, since variations of phases at a particular amplitude distribution of spectral components did not result in significant differences of attractiveness between such patterns (Figs. 3, 4a, 5). Therefore, female crickets were likely to assess only the gross temporal structure of a pattern that is completely described by the pulse, pause and pulse period duration and the respective duty cycle. In order to examine which of these four variables provided decisive cues for the attractiveness of a pattern, female crickets were tested with another four test series in which each of these parameters was varied systematically. For tests of pulse and pause duration one variable, i.e., pulse or pause duration was kept constant at 20 ms, while the respective other value was varied (Fig. 7b, c open squares). For the test of pulse period, a duty cycle of 0.5 was chosen (Fig. 7d, open squares; see also Schildberger 1984). The duty cycle was tested at a period duration of 40 ms and at two intensities (70 dB and 80 dB) in order to control for a possible effect of sound energy on the level of attractiveness (Fig. 7e, open squares and diamonds). For each of these variables a tuning curve resulted that for pulse and pause duration

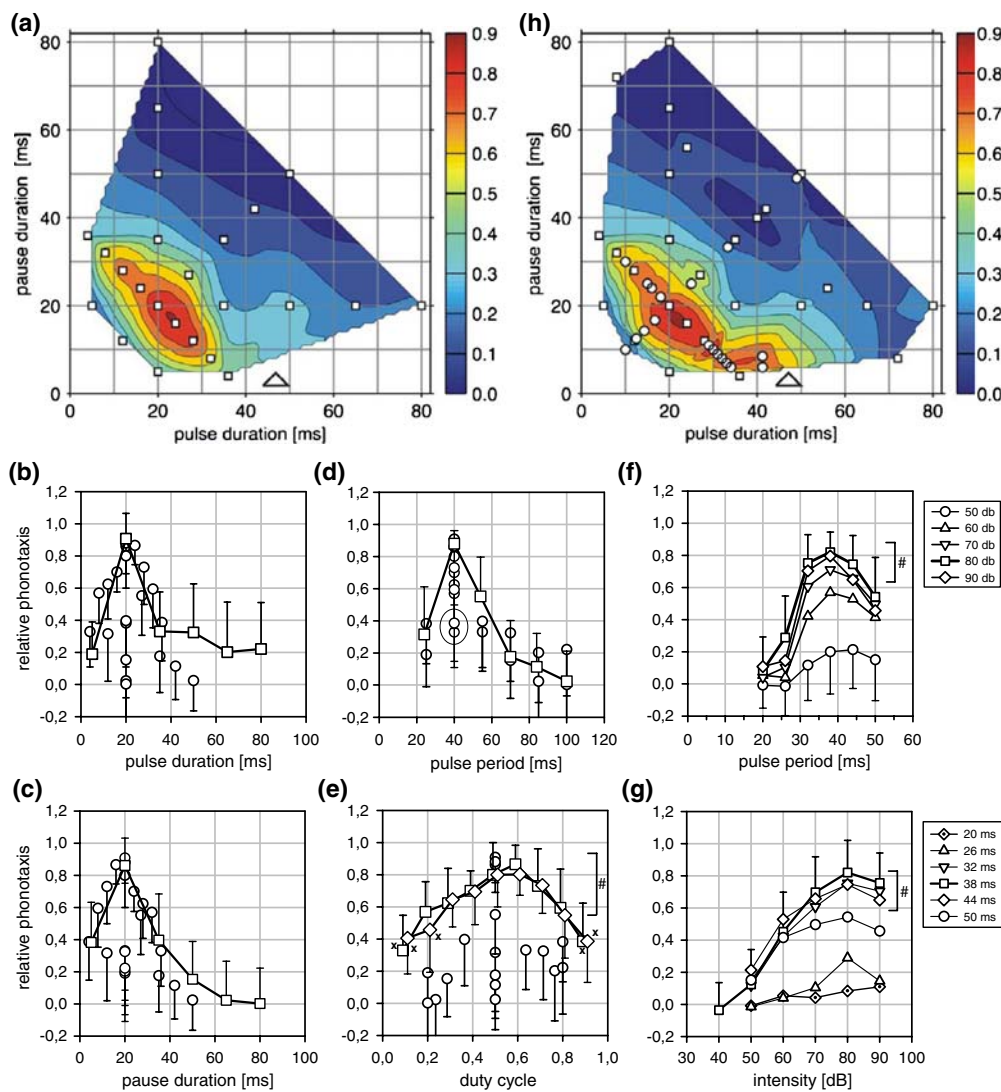


Fig. 7 Phonotactic response to envelope patterns built from rectangular pulses and presented in chirps (duration of 200 ms, 3 Hz) with different pulse, pause and period durations, different duty cycles and sound intensities. **a** Phonotactic responses plotted in an array that refers to the presented pattern (abscissa indicates the pulse and ordinate the pause duration of the test pattern). Measured data points are indicated by *white squares*; response ranges were calculated by cubic interpolation (Barber et al. 1996). The data points along the diagonal to the upper right represent patterns with different periods, but a constant duty cycle of 0.5, data on the diagonal from 40 ms pulse duration to 40 ms pause duration represent patterns with a period of 40 ms, but different duty cycles. The response field showed an extension on the diagonal with a period of 40 ms, largely independent of the duty cycle. **b–e** Phonotactic responses from a plotted according to the **(b)** pulse, **(c)** pause, **(d)** period duration and **(e)** duty cycle of the presented pattern. In **b–e**, data points measured along the respective axis and diagonals in **(a)** as referred to by the abscissae in **(b–e)** are indicated by *open squares*, all other data points from **(a)** are indicated by *open circles*. **b** Pulse duration: *open squares* show the response to patterns with a constant pause duration of 20 ms, **c** Pause duration: *open squares* show the response to patterns with a constant pulse duration of 20 ms, **d** Period duration: *open squares* show the response to patterns with a constant duty cycle of 0.5, **e** Duty cycle: *open squares* and *diamonds* show the response to

patterns with a constant period duration (40 ms; *diamonds* 70 dB, *squares* 80 dB). **f** Control experiment for the influence of sound intensity and sound energy due to different duty cycles and other temporal measures of the patterns presented in **(a)**. Patterns with a constant duty cycle of 0.5, but a variation of the pulse period [along the diagonal to the upper right in **(a)**] were presented at intensities from 50–90 dB SPL in steps of 10 dB. The shape of the response curve for pulse period remains the same for intensities above 70 dB. **g** Data from **f** plotted as an intensity response function. **h** Phonotactic responses plotted in an array as in **(a)**. Responses of all stimulus patterns with sinusoidal (*open circles*) and rectangular pulses (*open squares*) grouped in chirps (3 Hz) as shown in Figs. 2, 3, 4, 5, 6. For sinusoidal patterns, temporal measures were determined by a threshold of 15% from the maximum. The response field revealed a similar shape as in **(a)** and high phonotactic responses along the diagonal with a constant pulse period of 40 ms. See text for the response to patterns with a period of 40 ms and high duty cycles that differ from the responses to similar patterns in **(a)**. The *bold triangles* in **a** and **h** indicate weakly increased response ranges to patterns with a higher duty cycle. Responses marked with a '#' were not significantly different from the positive control stimulus. Responses marked with a 'x' in **(e)** were significantly different from both positive and negative controls

peaked at 20 ms and at 40 ms for pulse period (Fig. 7b–d open squares; open circles refer to other patterns in Fig. 7a). For the duty cycle, a wide range of values between 0.2 and 0.8 was accepted equally well at both intensities (Fig. 7e).

With these test patterns it was possible to construct an array (Fig. 7a) in which each pattern is characterized by its respective pulse (abscissa) and pause duration (ordinate). For each pattern the mean values of relative phonotaxis were used to compute response ranges (Barber et al. 1996). By their phonotaxis female crickets showed that they accept patterns that fulfil two criteria: a pulse period duration of 40 ms and a duty cycle between 0.2 and 0.8 (Fig. 7a). In Fig. 7b–e, the values of relative phonotaxis from other test series on which the response areas in Fig. 7a were based are also included as open circles. Figure 7d shows that pulse period is the major cue for the attractiveness of a pattern since at a pulse period of 40 ms only duty cycle values below 0.2 and above 0.8 revealed lower values of relative phonotaxis (marked by a circle in Fig. 7d, c.f. Fig. 7e). In the other panels (Fig. 7b, c), there were numerous patterns with a pulse or pause duration of 20 ms that were not attractive (open circles). Similarly, patterns with a duty cycle between 0.2 and 0.8 were only attractive, if the pulse period was also at 40 ms (Fig. 7e).

Since the reduction in the response to low duty cycles may have been the result of low energy levels in the acoustic signal, a further set of experiments was devised in order to control for the role of intensity on attractiveness and phonotactic scores (Fig. 7f, g). Female crickets were tested with a series of patterns that varied in the duration of pulse period at a duty cycle of 0.5 similar to Fig. 7d. In order to capture possible changes in the shape of the response curve for pulse period due to differences in intensity, a finer resolution for pulse period was used. This series was tested at different intensities from 50 to 90 dB in steps of 10 dB. Female crickets revealed the same preference curve for pulse period at intensities from 70 to 90 dB and exhibited the highest values of relative phonotaxis at pulse period between 32 and 44 ms that were not significantly different from the positive control (Fig. 7f). In Fig. 7g this data is plotted as a function of intensity, in order to estimate at which intensity a significant reduction of the scores of relative phonotaxis occurred. At 60 dB, the phonotactic scores were between 0.4 and 0.5 and thus similarly lower compared to the control at 80 dB as the phonotactic scores to a low duty cycle at 0.1 in Fig. 7e. The reduction in intensity for a duty cycle of 0.1 from 0.5 corresponds only to -14 dB (intensity) or -7 dB (energy) and is therefore lower than the reduction of -20 dB from the control at an intensity of 60 dB in Fig. 7g. Therefore, sound intensity alone is unlikely to completely account for the reduced response to low duty cycles (Fig. 7a, e).

Furthermore, if the reduction at low duty cycles was due to intensity, the drop in the response should be stronger for the test series with lower intensity, which is however not the case (Fig. 7e). At a high duty cycle of 0.9, the pause duration of 4 ms (Fig. 7e) may be too short with respect to the resolution of the auditory pathway and likely explain the observed reduction in attractiveness.

If pulse period and duty cycle were the decisive temporal cues that determined the attractiveness of a pattern, these cues should allow to predict the responses to sinusoidal pulse patterns tested above (Figs. 2, 3, 4, 5). For that comparison of the pulse and pause duration was determined for all patterns with sinusoidal pulses by a threshold criterion of 15% of the maximum (see “Materials and methods”). Continuous sinusoidal pulse patterns as in Fig. 2 (filled circles) were omitted from this analysis. The scores of relative phonotaxis for sinusoidal patterns and the rectangular patterns with a pulse period of 80 ms were then added to the data points from Fig. 7a (open squares: rectangular patterns; open squares: sinusoidal patterns). The plot of response areas in Fig. 7h was calculated as for Fig. 7a and maintained the same extension along a pulse period of 40 ms. However, at high duty cycles several patterns exhibited high values of relative phonotaxis (Fig. 7h) that were not observed in Fig. 7a. A closer inspection revealed that these values originated from patterns in Fig. 3 (patterns 1–12) and Fig. 5b (patterns 1–6) for which the applied threshold of 15% resulted in relatively high duty cycles. Similarly, the threshold criterion of 15% assigned rather high duty cycle values to patterns from Fig. 5a (patterns 1–6) that also had high values of relative phonotaxis. Despite the large modulation depth of those patterns, the envelope modulation did not return to amplitudes of zero for all sinusoidal pulses and thus duty cycles were rather high. Nevertheless, besides these particular patterns with high duty cycles and high scores of relative phonotaxis, there was a small increase of phonotactic scores for patterns with higher duty cycles in both response areas of Fig. 7a, h (marked by a triangle). This trend was also evident in Fig. 7e. In conclusion, the attractiveness of patterns with sinusoidal pulses can be understood by an evaluation of the pulse period and the duty cycle and thus as the result of an algorithm that operates in the temporal domain.

Comparing autocorrelation and frequency analysis

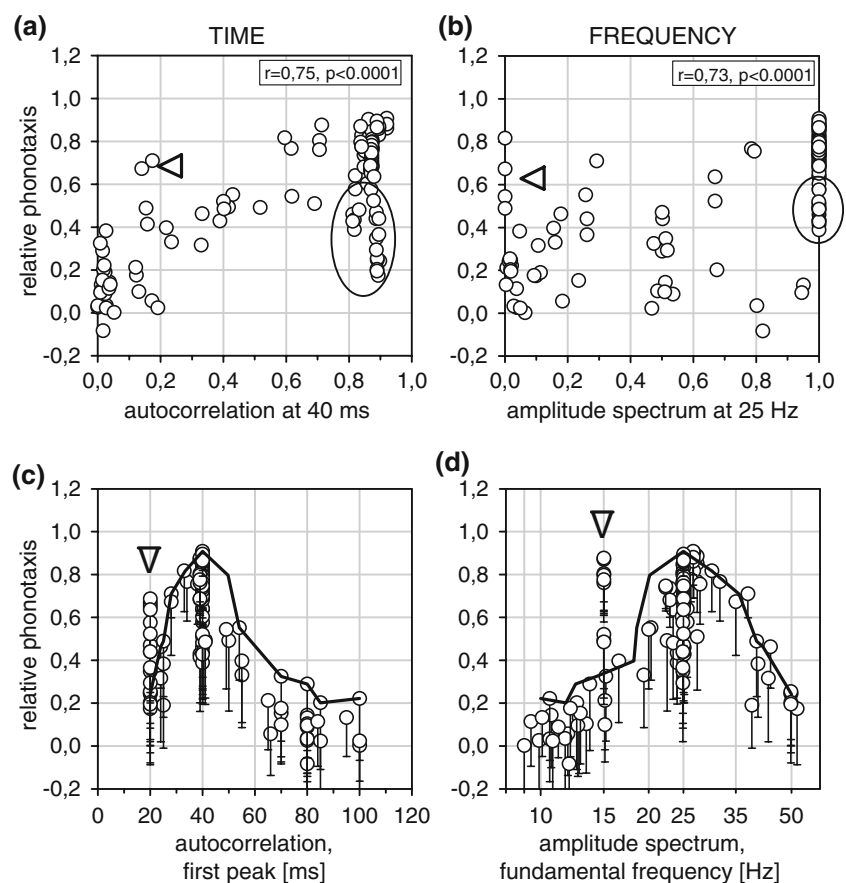
A further algorithm for pattern evaluation other than frequency analysis and temporal processing is provided by the computation of the autocorrelation function. An autocorrelation is closely related to the amplitude spectrum derived by a Fourier-transformation and measures the interval of periodical events in a pattern independent of the

phase spectrum (Fig. 1e; Hartmann 1998). In order to examine whether the values of relative phonotaxis can be explained on the basis of an autocorrelation in the auditory pathway of *G. bimaculatus*, an autocorrelation and, for comparison, the amplitude spectrum was computed for all rectangular and sinusoidal pulse patterns from the previous test series. In Fig. 8a, b, the values of relative phonotaxis were plotted versus the values of an autocorrelation (Fig. 8a) and the amplitude spectrum (Fig. 8b) at a time interval of 40 ms or a frequency of 25 Hz, respectively. The plot for the autocorrelation values revealed a significant correlation (Fig. 8a). However, some patterns with low autocorrelation values revealed high values of attractiveness (triangle in Fig. 8a) and vice versa (encircled values in Fig. 8a). The latter were due to patterns with high modulation frequencies as in Figs. 4a and 5b (patterns 13–18). For a frequency analysis there were also numerous patterns for which the value of the amplitude spectrum at 25 Hz did not predict the value of attractiveness (triangle and encircled values in Fig. 8b), although a significant overall correlation was observed (Fig. 8b).

An implicit assumption of the data plots in Fig. 8a, b was that attractiveness is determined by the pulse period of 40 ms or a modulation frequency of 25 Hz. Conversely, female crickets may evaluate the shortest peak in an

autocorrelation or the lowest frequency, that is the fundamental, in an amplitude spectrum. In a test for the consistency of the data with these processing schemes the plots in Fig. 8c, d show the respective values for an autocorrelation and an amplitude spectrum. For many patterns the values of relative phonotaxis are indeed correctly predicted with the shortest peak at 40 ms (Fig. 8c) and the lowest frequency at 25 Hz (Fig. 8d). The bold line indicates the best responses obtained in previous test series for variation of pulse period (Fig. 8c) and modulation frequency (Fig. 8d). If an autocorrelation or an amplitude spectrum predict the values of relative phonotaxis correctly, all responses should lie at or below the bold lines in Fig. 8c, d. Data points above the bold line would indicate high phonotactic scores for patterns with unattractive temporal (Fig. 8c) or spectral cues (Fig. 8d). Although most data points were not higher than the tuning curves indicated by the bold line, there were also several exceptions observed (bold triangles Fig. 8c, d). The autocorrelation of several patterns revealed a shortest peak at 20 ms but also relatively high values of attractiveness (relative phonotaxis from 0.4 to 0.6, indicated by a triangle in Fig. 8c). These patterns revealed relatively fast amplitude modulations (e.g., Fig. 4, patterns 7–12) that accounted for such a peak in the autocorrelation function at a short interval. The

Fig. 8 Phonotactic responses plotted against autocorrelation and spectral (amplitude) values of patterns with sinusoidal and rectangular pulses (see Figs. 2, 3, 4, 5, 6 for envelope patterns). Only stimuli in which pulses were presented in chirps (chirp period: 333 ms) were included. **a** Phonotactic response versus the autocorrelation value at 40 ms. **b** Phonotactic response versus the amplitude value of the spectrum at 25 Hz. **c** Phonotactic response versus time of the shortest peak of the autocorrelation function. **d** Phonotactic response versus fundamental frequency of the amplitude spectrum of a pattern. **Bold black lines** in **c**, **d** indicate the best responses observed in other test series for variation of pulse period (**c**) or modulation frequency (**d**). **Triangles** and **encircled** data points indicate patterns that contradict the expected response if an autocorrelation or spectral analysis is performed, see text for further explanation



lowest peak in the frequency spectrum was also occupied by some patterns with low modulation frequencies but high values of attractiveness (indicated by a triangle in Fig. 8d). These values resulted from patterns in Fig. 5a (values at -6 and 0 dB) and 5c (values at 3 dB), in which the amplitude of the 15-Hz component was similar to the amplitude of the 25-Hz component and thus accounted for a low frequency peak in the amplitude spectrum. In conclusion, neither a spectral analysis nor an autocorrelation reliably predicted the phonotactic response of crickets, *G. bimaculatus*, to patterns with rectangular or sinusoidal pulses. The evaluation of pulse period as a temporal cue apparently provides a robust measure that is largely independent of noise, modulation depth and sensory thresholds which is not the case for other temporal cues (pulse and pause duration, duty cycle) nor autocorrelation or spectral computations.

Discussion

Spectral versus temporal processing

How do female crickets discriminate the song pattern of their own species from others, by processing of phase-independent spectral or phase-dependent temporal cues? Indeed, there was a remarkable number of patterns and test series that provided evidence for an algorithm operating in the frequency domain for the analysis of the pulse pattern. All stimuli that exhibited a frequency component of 25 Hz as the dominant frequency were attractive (Fig. 2 patterns marked by open symbols, Figs. 3 and 5 all patterns at zero and less dB). Moreover, for these stimuli changes of phase modified the pattern envelope, but the values of attractiveness remained unaffected. Removal of the 25-Hz component significantly reduced the phonotactic scores (Fig. 4a). Patterns in which other frequency components exhibited a larger amplitude than the 25-Hz component were also less attractive (Fig. 5 patterns with dB-values greater than zero). This latter result demonstrated, however, that a plain bandpass filter tuned to 25 Hz (Thorson et al. 1982; Schildberger 1984) alone cannot account for this reduction and that further filters at lower and higher frequencies with a suppressing influence are needed in order to maintain the hypothesis of phase-independent processing in the frequency domain (Fig. 7d). On the other hand, all results in Figs. 3, 4, 5 can also be explained by an algorithm operating in the time domain. Patterns with a distinct pulse period of 40 ms were attractive (Fig. 2 patterns marked by open symbols, Figs. 3, 5 all patterns at zero and less dB). The attractiveness of patterns was reduced, if the period of 40 ms was masked by low modulation depth (Fig. 4b) or distorted by interspersed pulses

that likely aggravated pulse period detection (Fig. 5). The combination of an unattractive pulse period with the attractive frequency of 25 Hz in a set of patterns provided evidence that the signal is processed in the time domain (Fig. 6), since all patterns were unattractive despite the presence of the 25-Hz component. Finally, neither an autocorrelation nor a frequency analysis of an amplitude spectrum that are both phase-independent ways of signal processing can correctly predict all observed responses (Fig. 8). Since the original proposal of the ‘30 Hz filter’ implied phase independence due to spectral analysis based on low-, high- and bandpass filters (Thorson et al. 1982; Schildberger 1984), present evidence shows that crickets operate in the time domain for which not only the amplitude but also the phase spectrum of a pattern is required.

From the perspective of processing in the time domain it was rather notable that the temporal detail in numerous patterns did not significantly affect phonotactic scores. Neither the pulse shape (Fig. 2 open symbols, Fig. 5c) nor onset characteristics or rise time (Fig. 3) nor jittered pulses (Fig. 5c) that usually provide crucial cues for discrimination and recognition (Shannon et al. 1995; Grothe et al. 2001; Schmidt et al. 2007) exerted a detrimental influence on phonotactic scores. Within the auditory pathway of cricket the instantaneous firing rates for stimuli with fast rise time are likely higher than for patterns with slow rise times due to different strengths of synchronization amongst afferents (Imaizumi and Pollack 2001; Krahe et al. 2002). If so, the present data set in Fig. 3 does not support the model for pulse rate recognition in crickets based on instantaneous spike frequency presented by Nabatiyan et al. (2003). The observed insensitivity for details of the amplitude modulation (Fig. 3) provided evidence that only the gross structure of a pattern is relevant for processing in the cricket *G. bimaculatus* (Fig. 7). The details of modulation in those patterns may have been below the temporal resolution of processing and thus not available for a computational algorithm. However, it is also possible that crickets do not evaluate fine detail of patterns, although they can resolve these, because signals are easily distorted in real habitats by reverberating structures (Römer and Lewald 1992; Sabourin et al. 2008). The test series in which the duty cycle of an attractive pulse period was varied (Fig. 7e, patterns with high duty cycles and thus short pauses) indicated that the limit of temporal resolution was 4 ms (c.f. Sabourin et al. (2008) for electrophysiological measurements) and was therefore higher than in most other auditory pathways (see Table 1 in Prinz and Ronacher 2002). In this light the strict distinction between spectral and temporal processing for some patterns is also put into perspective. Low temporal resolution will transform most stimuli in Figs. 2, 3, 4, 5 into smoothed sinusoidal patterns and on the basis of such patterns alone a

decision about spectral or temporal processing is hindered, unless spectral and temporal cues diverge as in Fig. 6. However, crickets with a similar temporal resolution but longer pulse periods in their signals (for instance 66 ms for *T. oceanicus*, Pollack and Hoy 1979; Hennig and Weber 1997, Hennig 2003) should be able to discriminate between patterns that contain temporal detail as introduced by the variation of phases (Fig. 3).

The transfer function suggested two combined filters that operate on different temporal scales and both of which needed to be activated for a strong response (Fig. 2, Doherty 1985; Wendler 1990; Deily and Schul 2009). Since the cues for the slow component, the chirp part, was kept constant in most tests, a possible influence on the pulse filter is rather unlikely for the present study (Doherty 1985). Nevertheless, the large standard deviations at the respective peaks of 3 and 25 Hz compared to the valleys in the bimodal distribution reflected large inter-individual differences (Fig. 2). Some individuals would also respond even if only one filter was activated which corroborated previous reports about responses of *G. bimaculatus* to a chirp pattern without modulation by pulses (similar to pattern 1 in Fig. 2, Doherty 1985; Weber and Thorson 1989; Poulet and Hedwig 2005). Since for stimulus construction a chirp period of 333 ms was used, in most test series a residual mean response level at 0.2 remained (Figs. 4, 5), most likely due to the activation of the chirp filter.

The cues for temporal processing—pulse period and duty cycle

Viewed in the temporal domain the cricket *G. bimaculatus* prefers periodical patterns of a pulse period of 40 ms over a range of duty cycles (Fig. 7a, e). The peak of the response to the best pulse period ranged from 30 to 40 ms (Fig. 2). The filter's shape was rather symmetrical, both from a frequency and a temporal view (Figs. 2, 7b, respectively) and corresponded to earlier investigations (Tschuch 1977; Thorson et al. 1982; Poulet and Hedwig 2005; Verburt et al. 2007). The tuning of the filter remained unchanged at intensities higher than 70 dB most likely due to adaptation of receptors and interneurons (Benda and Hennig 2007, see however Pollack and El-Feghaly 1993). The extension of best responses along the axis of pulse periods from 30 to 40 ms suggests that the cricket *G. bimaculatus* solely evaluates the pulse period and not other temporal cues of the gross structure of the pattern as is the case for the cricket *T. commodus* (Hennig 2003). Such a response range for pulse period over a wide range of duty cycles is not uncommon and observed in rather different groups of animals (crickets: Hennig 2003; bushcrickets: Schul 1998; frogs: Schul and Bush 2002). Other than pulse or pause

duration, pulse period is probably one of the most reliable cues in a noisy environment and robust to changes in modulation depth, distortion and noise.

Limitations for the reduced preference of low and high duty cycles are probably due to different constraints (Fig. 7e, see Tschuch 1977 and Verburt et al. 2007 for similar shapes of the duty cycle curve). At low duty cycles, the reduction can partly be understood by the reduction of the energy level as observed for the intensity response curve (Fig. 7g). However, since the response to the variation of the duty cycle was measured at two different intensities and these response curves did not differ at low duty cycles, intensity alone cannot explain the reduced response. Most likely the pulse duration is too short to reliably activate the pulse period detector. At high duty cycles, the response is probably limited by temporal resolution that most likely also accounts for the failure to discriminate temporal detail in other test series (Fig. 3, Sabourin et al. 2008). It is therefore likely that the computational algorithm is solely based on a pulse period detector that is limited by physiological constraints at low (pulse duration) and high duty cycles (temporal resolution).

Crickets, and bushcrickets alike, appear to employ temporal processing for the analysis and discrimination of acoustic signals. Although the computation of an autocorrelation function is an attractive option for the processing of periodical signals and is as compact as the spectra obtained by a Fourier analysis (Friedel et al. 2007), neither of these processing options appears to be employed for analysis by crickets (Fig. 8, see also Weber and Thorson 1989). While temporal processing of acoustic patterns is common across crickets and bushcrickets, the cues and details within this domain differ remarkably. While some species focus on pulse period (*G. bimaculatus*, *Teleogryllus oceanicus*, *Tettigonia cantans*), other species process pulse duration (*T. commodus*), pause duration (*T. viridissima*, see also Schüch and Barth 1990 for a spider) or duty cycle (*T. caudata*; Schul 1998; Hennig 2003). Especially the latter cues are susceptible to noise that poses a particular problem for crickets, since the signal envelope is not buffered by a carrier with a wide frequency spectrum (Römer and Lewald 1992). While the analysis of cues such as pulse period and pulse duration can be unified by cross-correlation that employs short (pulse duration) or long (pulse period) time windows for integration (Hennig 2003), a preference for duty cycle or pause duration is not easily accommodated in such a processing scheme.

From computational algorithm to neural mechanisms

The song discrimination of its own species from that of others in the auditory pathway of female crickets can be viewed as a hierarchical set of processing modules. Each of

these modules has a specific processing task: receptors form a matched filter for the specific frequency channel within which the signal is expected and—due to their rectifying and smoothing nature of response—provide a copy of the signal's envelope by their spike rate for further processing by interneurons (Imaizumi and Pollack 1999; Nabatiyan et al. 2003; Kostarakos et al. 2008); first-order ascending interneurons form a representation of the acoustic signal that is intensity independent as seen by the intensity invariant spike rate due to spike frequency adaptation (Benda and Hennig 2007). Finally, at the level of the brain circuitry a representation of salient features is expected that is invariant to various features and forms the physiological basis for the decision process (Schildberger 1984; Konishi 1990).

When searching for a physiological implementation, it is important to realize that the envelope of the stimuli as seen by the experimental observer is indeed 'perceived' rather differently by neurons. Receptors have a threefold role in stimulus modification: first, they rectify the signal to reflect an envelope by their spike rate; second, their temporal resolution averages across temporal details of the pattern; and third, their adaptation high pass filters the signal (removing stimulus components on longer time scales) and distorts the signal envelope due to the time constant of adaptation. Thus, these properties of receptor responses alone may contribute to the duty cycle preference function measured in behavioural tests which then would not reflect the result of neuronal processing at higher levels. Based on present knowledge, the analysis is most likely performed by few cells connected to a small network (Schildberger 1984). The temporal distribution of excitation and inhibition within the network as well as cellular properties such as membrane time constants, oscillatory and rebound properties represent the most likely candidates for filter properties (Hennig 2003; Webb et al. 2007). For the bushcricket *Tettigonia cantans* a rebound mechanism, possibly even reduced to a single cell can account for the observed period selectivity with a resonant effect that produces distinct preference peaks at higher multiples of the pulse period (Bush and Schul 2006; Webb et al. 2007). For the cricket *G. bimaculatus*, however, no such increased responses at higher multiples were observed (Fig. 7a), although there was a bias towards higher duty cycles (Fig. 7a, e, h).

Generally, time provides crucial cues for auditory processing, both for directional hearing (Konishi 1990; Krahe and Ronacher 1993) as for pattern processing (Langner 1992; Shannon et al. 1995; Schul 1998; Grothe et al. 2001; Joris et al. 2004; Schmidt et al. 2007) across species. Pitch perception and the phenomenon of the missing fundamental remains one of the few examples in which phase insensitivity may play a role at higher processing levels (de Cheveigne 2006; Plack et al. 2006).

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