J Comp Physiol A (2016) 202:823–837
DOI 10.1007/s00359-016-1124-x

ORIGINAL PAPER

How females of chirping and trilling field crickets integrate the 'what' and 'where' of male acoustic signals during decision making

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Received: 14 July 2016 / Revised: 3 September 2016 / Accepted: 6 September 2016 / Published online: 16 September 2016

Abstract In crickets acoustic communication serves mate selection. Female crickets have to perceive and integrate male cues relevant for mate choice while confronted with several different signals in an acoustically diverse background. Overall female decisions are based on the attractiveness of the temporal pattern (informative about the 'what') and on signal intensity (informative about the 'where') of male calling songs. Here, we investigated how the relevant cues for mate choice are integrated during the decision process by females of five different species of chirping and trilling field crickets. Using a behavioral design, female preferences in no-choice and choice situations for male calling songs differing in pulse rate, modulation depth, intensities, chirp/trill arrangements and temporal shifts were examined. Sensory processing underlying decisions in female field crickets is rather similar as combined evidence suggested that incoming song patterns were analyzed separately by bilaterally paired networks for pattern attractiveness and pattern intensity. A downstream gain control mechanism leads to a weighting of the intensity cue by pattern attractiveness. While remarkable differences between species were observed with respect to specific processing steps, closely related species exhibited more similar preferences than did more distantly related species.

Keywords Decision making · Auditory processing · Gain-control mechanism · Female choice · *Gryllus*

Introduction

Mate choice is a major decision-making task that a sexually reproducing animal has to solve (Miller and Todd 1998). This includes the perception and evaluation of sexual cues that provide information about a potential partner, a judgement of overall sexual attractiveness and in many cases the task of localization (Miller and Todd 1998). Thus mate choice is the result of an information processing chain under the constraints of restricted time, predation risk, diminishing resources and potentially noisy backgrounds (Leonard and Hedrick 2009). In crickets males produce conspicuous mating signals which attract sexually receptive females (Regen 1913). Females use these signals to recognize and locate the correct signal while being confronted with several males singing at the same time in a complex acoustic background. Song signals arrive at the position of the female from different directions and distances which results in both differences in perceived signal intensity and variation in signal attractiveness of male songs. Overall, decision making in female crickets is based on pattern attractiveness (informative about the 'what') and on signal intensity (indicative of the 'where', Popov and Shuvalov 1977; Doherty 1985; Hirtenlehner and Römer 2014; Gabel et al. 2015). For the cricket *Gryllus bimaculatus* the integration of both cues is provided by a gain-control mechanism which leads to a non-linear weighting of signal

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Electronic supplementary material The online version of this article (doi:10.1007/s00359-016-1124-x) contains supplementary material, which is available to authorized users.

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intensity by pattern attractiveness (Doherty 1985; Pollack 1988; Poulet and Hedwig 2005; Gabel et al. 2015).

Because most prior research was performed with only a few species of field crickets, decision rules among species were rarely compared. Hence it is less clear whether the algorithm of computation and the integration of cues follows the same rules in different species. Divergence in signal recognition and processing during evolution of communication systems often requires changes in sender and receiver (Alexander 1962). The integration of cues during mate choice may be based on the same computational algorithm with specific adaptations or may potentially differ greatly between species. Here we aimed to examine the contribution of pattern attractiveness and signal intensity during the decision process in five species of *Gryllus* field crickets differing in their degree of relatedness (Fig. S1, *G. firmus*, an unnamed species [DB Weissman and DA Gray manuscript name *Gryllus* sp 15, hereafter *"staccato"*], *G. personatus*, *G. rubens* and *G. texensis*). We focused on the cues relevant for decision making on a short time scale such as pulse rate, pulse modulation depth and the relative timing of chirps and trills. A comparison of the decision rules for this variety of species is particularly interesting as they differ in several attributes such as phylogenetic relatedness (Fig. S1), geographic distribution, sympatric and allopatric occurrence, song patterns of males, and female song preferences (Table S1). *G. firmus*, *G. "staccato"* and *G. personatus* males all produce short chirps whereas *G. rubens* and *G. texensis* males produce long trills (Table S1). Pulse rates range from 18 to 96 pulses per second between species (Alexander 1957; Doherty and Storz 1992; Blankers et al. 2015; Gray et al. 2016b; Hennig et al. 2016). Females of *G. rubens* and *G. texensis* prefer species-typical long trills with high pulse rates (Blankers et al. 2015). *G. "staccato"* and *G. personatus* females prefer intermittent chirp patterns (Hennig et al. 2016). *G. firmus* females prefer rather low pulse rates compared to the other species and respond to chirps as well as long trills although males produce only the former (Gray et al. 2016a).

The aim of the present study was to give insight into the integration of different cues for the decision process of the five *Gryllus* species and to examine common features and/or differences in signal processing between them. Therefore, each species was examined in both choice and no-choice tests for their responses to song patterns with different pulse rates, modulation depths, intensities, chirp/trill arrangements and temporal shifts of synchronously presented signals. Additionally, for each species we compared the relative contribution of signal intensity and temporal cues to decision making by constructing the corresponding equivalence functions (Ronacher 1979, 1983). Furthermore, we sought to determine if female responses to synchronously presented signals with varying levels of overlap support a signal processing model based on separate left–right signal processing or combined processing of summed or superimposed signals. Results are discussed in the context of neurobiological mechanisms as well as phylogeny and ecology of the acoustic communities.

Materials and methods

Animals and trackball system

All females were obtained from a laboratory stock. Laboratory populations were initiated with field caught animals: *G. firmus*, Gainesville, Lake City and Live Oak, Florida; *G. "staccato"*, Agua Fria National Monument, Yavapai Co., Arizona; *G. personatus*, Winslow, Navajo Co. Arizona; *G. rubens* and *G. texensis* were collected from allopatric localities: *G. rubens*, Gainesville, Lake City and Live Oak, Florida; *G. texensis*, Austin, Lancaster and Round Rock, Texas. The crickets were raised in 19-L containers with gravel, shelter and food ad libitum. Females were separated from males before reaching adulthood and acoustically isolated during the experimental phase which started from 1 week after the final molt.

Female preferences were tested using a trackball system (Dahmen 1980) described in detail in Gabel et al. (2015). In brief, female crickets, tethered to a metal pin, were placed in a naturally walking position at the top of a hollow Styrofoam ball (diameter 10 cm, weight 1.2–1.8 gm) which was placed in a wooden anechoic box (50 × 50 × 50 cm) and supported by an airstream to rotate with minimal friction. Female movements (longitudinal/X-rotation and lateral/Y-rotation) were monitored by either one optical sensor (Agilent ADNS-2051) at the bottom of the trackball or by two sensors (ADS-500, Avago Technologies) with a focusing lens positioned laterally at an angle of 90°. Two loudspeakers (Piezo Horn Tweeter, PH8, Conrad Electronics) were placed at an angle of 45° left and right to the animals' length axis and with a distance of 25 cm frontal to the cricket. Females were able to face the loudspeakers but a complete rotation around the horizontal axis was not possible. Each speaker was calibrated with a condenser microphone (Brüel & Kjær type 4133 relative to 2×10^{-5} Pa fast reading) and a measuring amplifier (Brüel & Kjær type 2231, Nærum, Denmark) on top of the ball where the females were placed during experiments. Experiments were performed at 24.1 ± 1.5 °C.

Signal generation and presentation

Sound signals were generated digitally with LabView Software (National Instruments, TX, USA). A given signal envelope with 1 ms rise and fall times was multiplied

Table 1 Song stimuli and parameters used

Species	Freq. (kHz)	Pulse rate (p/s)	Pulse duty cycle	Chirp or trill rate#/s	Chirp or trill duty cycle	Modulation depth (%)
G. firmus	4.5	18.5 (8–33)	0.5	2	0.38	0, 12.5, 25, 37.5, 50, 62.5, 75, 87, 5, 100
G. "*staccato*"	5.5	83.3 (33–333)	0.66	3	0.34	0, 25, 50, 75, 100
G. personatus	5.0	55.6 (29–167)	0.5	3	0.35	0, 25, 40, 50, 75, 100
G. rubens	5.0	50.0 (29–83)	0.5	1	0.89	0, 25, 50, 75, 100
G. texensis	5.0	62.5 (42–100)	0.5	1	0.89	0, 25, 50, 60, 75, 100

For each species, the parameters of the attractive reference stimulus are given. Test series varied pulse rates across the range given in parentheses and also varied sound amplitude and sound energy (see text). Sound energy was varied by changing the modulation depth of the pulse pauses. In all tests, carrier frequency, pulse duty cycle, and chirp or trill rate were held constant

with a sine wave (see Table 1 for used frequencies). Sound signals were broadcast via one or both loudspeaker after D/A-Conversion (update rate 100 kHz, PCI 6221, National Instruments, TX, USA), adjustment to a given intensity by a digital controlled attenuator (PA5, Tucker Davis Technologies, FL, USA) and amplification (Raveland, Conrad Electronics, SE, Germany). The generated pulses were grouped into chirps or trills mimicking the calling song of *G. firmus*, *G. "staccato"*, *G. personatus, G. rubens* or *G. texensis* (see Table 1 for details). Reference functions for varying pulse rates (Table 1) were measured initially in no-choice paradigms at sound amplitudes of 74, 80, and 86 dB SPL. Different modulation depths of the pulse pauses of the attractive reference pattern were measured at sound amplitudes of 77, 80, and 83 dB SPL in no-choice tests. Choice tests were conducted to test for the influence of signal intensity given by sound amplitude (dB SPL) or signal energy (stimulus integration over time) and timing differences on female decisions by presenting an attractive reference pattern (Table 1, chosen from Fig. 1a–e) versus an alternative pattern with a difference either in sound amplitude (dB SPL), in signal energy (as given by the modulation depth of the pulse pauses, see Fig. 1g and S2 for pattern examples) or in time delay between the two presented patterns (for more details see "Results").

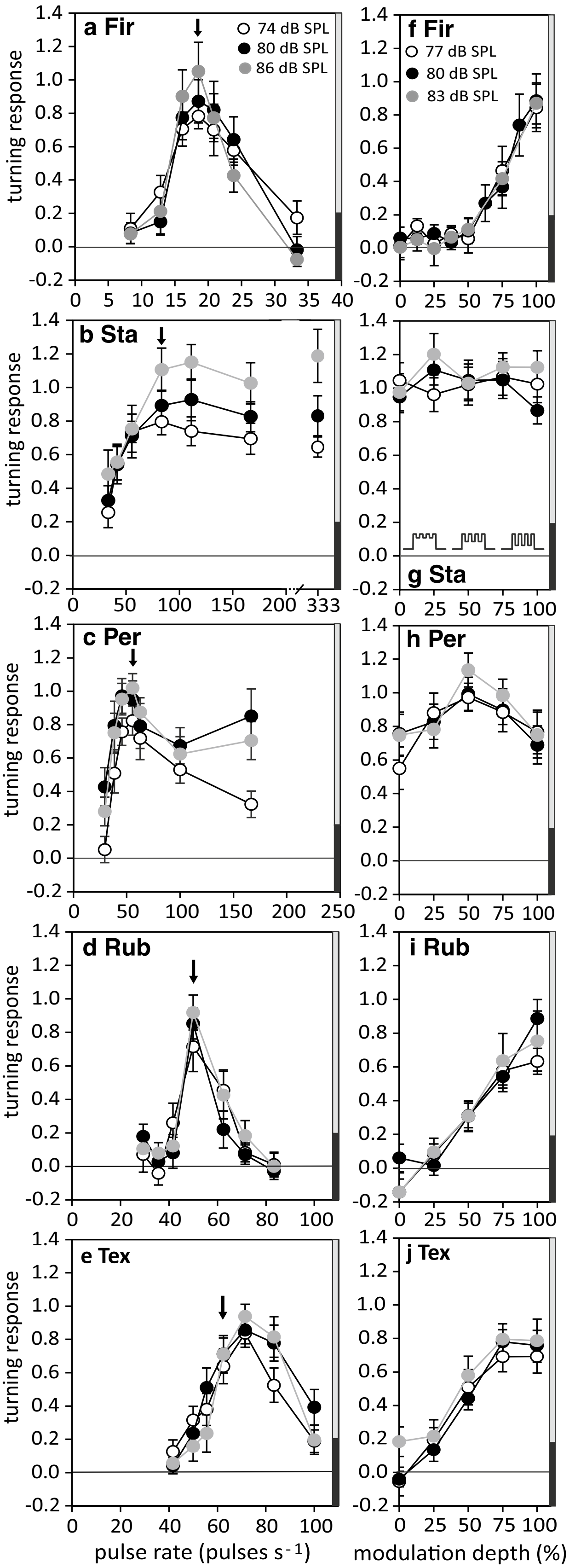
Each test series contained two positive and two negative controls as well as 7–10 test stimuli, and lasted for 24–30 min. In each test series one positive control was given at the beginning and one at the end to control for strength and change of motivation by females. Likewise one negative control was given at the beginning as a silent interval to monitor baseline activity and one negative control was given at the end as a continuous tone to test for female selectivity. In-between the stimulus sequence was randomized. All stimuli and the positive and negative controls were presented for 45 or 60 s from each speaker consecutively and between the presentations a break of 10 s was given to avoid possible carry over effects from the previous signal (see Weber et al. 1981, Poulet and Hedwig 2005 who reported time constants of 5–7 s for the decay of phonotaxis after signal presentation).

Data evaluation

To evaluate female decisions, the lateral deviation of a female during signal presentation from both speakers was averaged and normalized to the mean of the two positive controls and is termed "turning response". Therefore, responses usually reached values between 0 and 1 except when females responded stronger to the test stimuli than to the positive controls. In this case responses above 1 were obtained. In no-choice tests a response to the presented pattern is indicated by a positive value and values around zero indicate no response due to random orientation. During choice tests values ranged between +1 and −1, where positive values indicate a preference for the reference pattern and negative values refer to a preference for the alternative pattern. Turning responses around zero then indicated equal attractiveness of the patterns and thus no preferred orientation.

Data from 12 to 19 females per stimulus set are given as mean values with standard errors in the figures. Females exhibiting a value below 0.4 during the positive controls were excluded from the analysis as were females which showed strong responses during the negative controls. All responses were compared to the silent control with a paired *t* test. Statistical significance ($p < 0.05$) is indicated in the figures by a grey bar on the right hand side of the diagrams: a preference for the reference pattern corresponds to the region marked by a light grey bar; a preference for the alternative pattern by a dark grey bar; responses not significantly different ($p > 0.05$) from the silent control are marked by a black bar. In the diagrams abbreviations for species were as follows: Fir for *G. firmus*, Sta for *G. "staccato"*, Per for *G. personatus*, Rub for *G. rubens* and Tex for *G. texensis*.

Fig. 1 Female response functions in no-choice situations. **a**–**e** Turning responses of females for different pulse rates in no-choice experiments at 74 (*unfilled circles*), 80 (*filled black circles*) and 86 dB SPL (*filled grey circles*). **a** *G. firmus*, *n* = 12 for all sound amplitudes, **b** *G. "staccato"*, *n* = 13 for 74 and 80 dB SPL, *n* = 12 for 86 dB SPL, **c** *G. personatus*, *n* = 12 for 74 and 80 dB SPL, *n* = 16 for 86 dB SPL, **d** *G. rubens* females, *n* = 12 for 74 and 86 dB SPL, *n* = 13 for 80 dB SPL, **e** *G. texensis*, *n* = 14 for 74 dB SPL, *n* = 12 for 80 and 86 dB SPL. *Arrows* mark pulse rate which was used as reference pattern in the subsequent choice tests. **f**–**j** Turning responses of females for an attractive pulse pattern chosen from **a**–**e** (marked by *arrows*) with increasing modulation depths of the pulse pauses at 77 (*unfilled circles*), 80 (*filled black circles*) and 83 dB SPL (*filled grey circles*). **f** *G. firmus*, *n* = 12 for all sound amplitudes **g** *G. "staccato", n* = 12 for 77 and 83 dB SPL, *n* = 15 for 80 dB SPL, **h** *G. personatus, n* = 12 for 77 dB SPL, *n* = 13 for 80 and 83 dB SPL, **i** *G. rubens*, *n* = 16 for 77 dB SPL, *n* = 13 for 80 dB SPL, *n* = 12 for 83 dB SPL, **j** *G. texensis*, *n* = 15 for 77 dB SPL, *n* = 17 for 80 dB SPL, *n* = 13 for 83 dB SPL. Illustrations in **g** show test patterns with different modulation depths of the pulse pauses



Results

Female responses in no-choice situations

First female responses to different pulse rates and modulation depths were measured in no-choice situations to obtain reference functions for choice experiments. For pulse rate variations the test patterns were presented at 74, 80, and 86 dB SPL (Fig. 1a–e). The results for pulse rate variation revealed that *G. firmus*, *G. rubens* and *G. texensis* females exhibited closed response functions centered upon their respective species typical pulse rates; *G. "staccato"* females exhibited a threshold-type preference function with high responsiveness to pulse rates equal to or higher than the species typical pulse rate; *G. personatus* females showed a response pattern that peaked at species typical pulse rates, but they also responded well to higher pulse rates (Fig. 1a–e). Considering the entire range of pulse rate variation, *G. firmus* females responded to very low pulse rates compared to the other species (Fig. 1a; Gray et al. 2016a) and *G. rubens* and *G. texensis* to intermediate pulse rates (Fig. 1d, e; Blankers et al. 2015). *G. personatus* and *G. "staccato"* failed to respond to low pulse rates, but revealed intermediate to high turning responses to high pulse rates (Fig. 1b, c). *G. "staccato"* responded to the widest range of pulse rates, up to 333 pps (Fig. 1b). Female responses to different pulse rates were intensity invariant as females showed similar response levels at all sound amplitudes (Fig. 1a–e) except for *G. "staccato"* and *G. personatus* at pulse rates of 100 pps or higher (Fig. 1b, c).

Next female responses to an attractive pulse pattern with different modulation depths of the pulse pauses were determined in a no-choice situation at sound amplitudes of 77, 80, and 83 dB SPL (Fig. 1f–j) since an increase of 3 dB in sound energy corresponds to an increase of 6 dB in sound amplitude in Fig. 1a–e. The results revealed remarkable differences between species (Fig. 1f–j). *G. firmus* females showed no responses to pulse patterns with modulation depths lower than 50 % and increasing responses to pulse patterns with modulation depths higher than 50 % (Fig. 1f). *G. "staccato"* and *G. personatus* females showed strong responses towards a wide range of modulation depths, even to chirp patterns that exhibited no pulse structure at a modulation depth of 0 % (Fig. 1g, h, see illustrations in Fig. 1g for test patterns with different modulation depths). Reponses of *G. rubens* and *G. texensis* females increased with increasing modulation depth (Fig. 1i, j). All species showed very similar response levels at all sound amplitudes indicating intensity invariance as before (Fig. 1f–j).

Female responses to the different pulse rates were also tested at different modulation depths in a no-choice situation to assess how responses to different pulse rates were affected by modulation depth (Fig. S2). Responses of female *G. firmus* for different pulse rates at a modulation depth of 75 % were strongly reduced (Fig. S2a) as well as responses of female *G. rubens* for different pulse rates at 40 % modulation (Fig. S2d). Female *G. texensis* showed weaker responses for pulse rate patterns at 60 and 75 % modulation except for the most attractive pulse rate of 71 pps (Fig. S2e). *G. "staccato"* and *G. personatus* females exhibited similar preferences for different pulse rates at different modulation depths (Fig. S2b, c) consistent with their already observed tolerance for this parameter (Fig. 2g, h). However, both species still revealed reduced response scores at lower pulse rates (Fig. S2b, c).

Overall the results revealed that the response functions for pulse rate and modulation depth differ between species but were more similar between closely related species (*G. "staccato"*/*G. personatus* and *G. rubens*/*G. texensis*) than between more distantly related species.

Female choice behavior

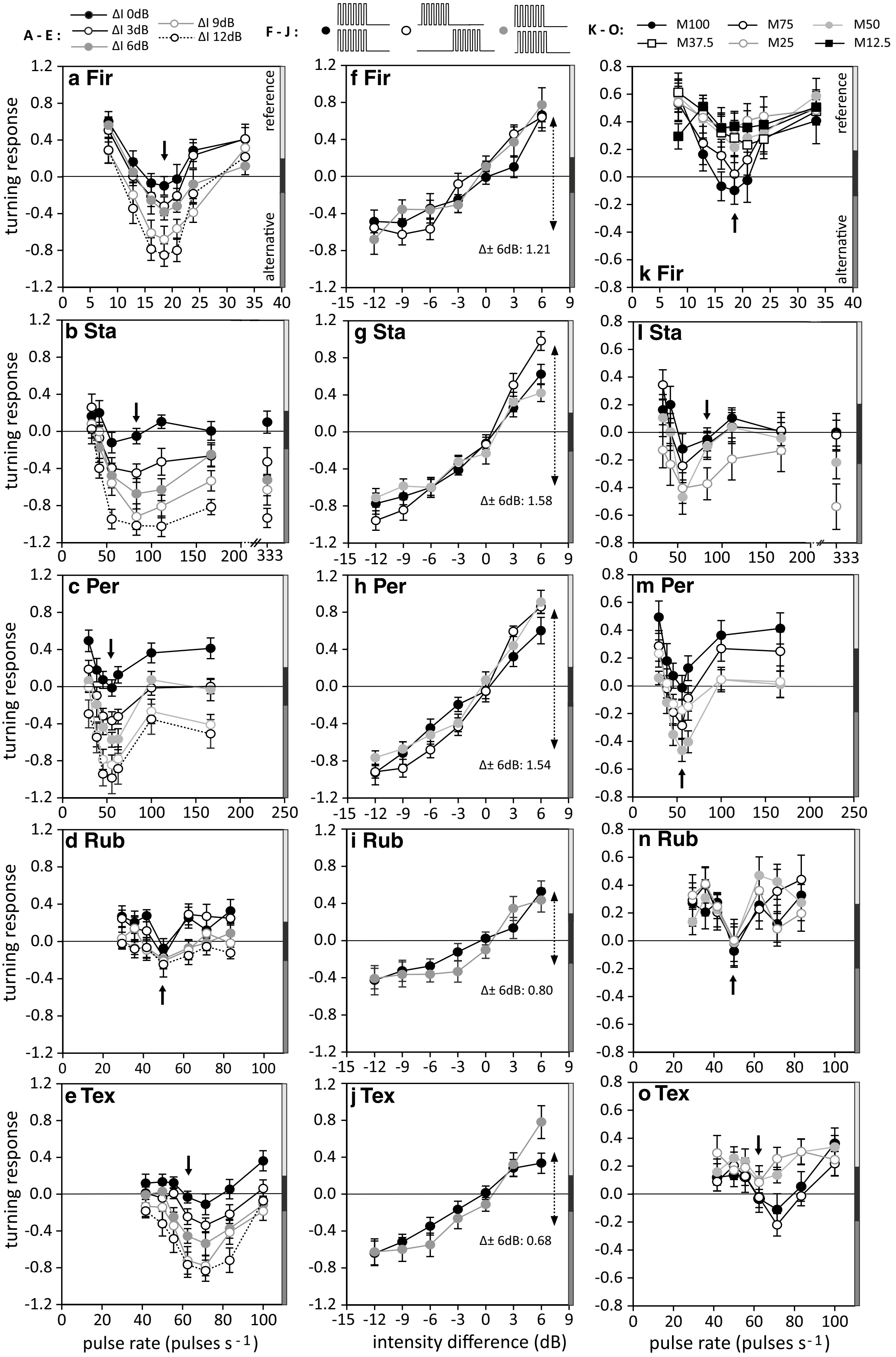
The impact of sound amplitude

To determine how female crickets evaluated pattern attractiveness and sound amplitude in a choice situation we conducted test series presenting an attractive reference pattern from one speaker and an alternative pattern with variable pulse rates (from Fig. 1a–e), respectively, from the other speaker (pulse rates are given in Table 1). The tests were first conducted at equal sound amplitude of 80 dB SPL and in the next step the patterns were presented with differences in sound amplitude of 3, 6, 9, and 12 dB (Fig. 2a–e). To keep the overall sound intensity constant the difference was symmetrically changed around a mean sound amplitude of 80 dB SPL. Thus, at a difference in sound amplitude of 3 dB the attractive reference pattern was presented at 78.5 dB SPL and the alternative pattern at 81.5 dB SPL (see Figure legend for details).

At equal sound amplitude of reference and alternative pattern all species showed no preference for one of the presented patterns if they exhibited the same pulse rate (Fig. 2a–e; Table 1). At lower and higher pulse rates of the alternative pattern and equal sound amplitudes the attractive reference pattern was preferred (black circles in Fig. 2a–e). With increasing difference in sound amplitude female preferences were shifted towards the louder alternative patterns (Fig. 2a–e). The preference functions of *G. rubens* females differed from the other species as they exhibited a smaller shift and never preferred a louder, but less attractive alternative pattern (Fig. 2d, Fig. S3 d). The strength of the shift at different pulse rates was quantified by plotting the turning response for each pulse rate against the respective difference in sound amplitude (Fig. S3). The observed shift in turning response at different sound amplitudes was generally stronger for attractive pulse patterns than for less attractive patterns. For example the shift of preferences towards the louder alternative patterns of *G. firmus* females was twice as strong for the most attractive pulse rate of 18 pps than for the less attractive pulse rate of 33 pps (Fig. 2a, Fig. S3a). Of all species, *G. "staccato"* and *G. personatus* exhibited the strongest shift towards the louder alternative pattern (see values below −1 in Fig. 2b, c, Fig. S3b, c).

In a further step the impact of differences in sound amplitude on the turning response for a constant attractive pulse rate at different temporal chirp/trill arrangements was examined. For that, a reference pattern was presented against an equal alternative pattern and the sound amplitude of the reference pattern increased from 68 to 86 dB SPL whereas the sound amplitude of the alternative pattern was kept constant at 80 dB SPL. Different chirp pattern arrangements were tested for *G. firmus*, *G. "staccato"* and *G. personatus* to examine whether female responses differed for chirps presented in a simultaneous, alternating or interleaved fashion (see inset in Fig. 2). For *G. rubens* and *G. texensis* only the simultaneous and interleaved presentation was possible as trills were presented in an alternating fashion. Positive turning responses in Fig. 2f–j indicated a preference for the reference pattern and negative values indicate a preference for the alternative pattern. On the abscissae dB-values refer to the differences in sound amplitude between sound patterns from both sides, with positive values indicating a louder reference pattern.

All arrangements of the chirp and trill patterns resulted in similar, intensity dependent responses of all species (Fig. 2f–j). At a difference of 0 dB females showed no preference for one of the presented patterns. With increasing difference in sound amplitude the preference for the


A - E :
ΔI 0dB
ΔI 3dB
ΔI 6dB
ΔI 9dB
ΔI 12dB
F - J :
K - O:
M100
M75
M50
M37.5
M25
M12.5
a Fir
b Sta
c Per
d Rub
e Tex
f Fir
g Sta
h Per
i Rub
j Tex
k Fir
l Sta
m Per
n Rub
o Tex
reference
alternative
turning response
Δ± 6dB: 1.21
Δ± 6dB: 1.58
Δ± 6dB: 1.54
Δ± 6dB: 0.80
Δ± 6dB: 0.68
pulse rate (pulses s-1)
intensity difference (dB)
pulse rate (pulses s-1)

◂**Fig. 2** Female preferences in a choice situation depending on pattern attractiveness and sound amplitude or sound energy. **a**–**e** Female preferences in choice situations presenting an attractive reference pattern from one speaker and the variable pulse rates as in Fig. 1a–e of an alternative pattern from the other speaker. Signals were broadcast at equal sound amplitude of 80 dB SPL and then with 3 dB difference (*black line unfilled circles*, reference at 78.5 dB SPL, alternative at 81.5 dB SPL), 6 dB difference (*grey line filled circles*, reference at 77 dB SPL, alternative at 83 dB SPL), 9 dB difference (*grey line unfilled circles*, reference at 75.5 dB SPL, alternative 84.5 dB SPL) and 12 dB difference (*black dotted line unfilled circles*, reference at 74 dB SPL, alternative at 86 dB SPL). **a** *G. firmus*, $n = 12$ for 0, 3 and 6 dB difference, $n = 13$ for 9 and 12 dB difference, **b** *G. "staccato"*, $n = 12$ for a difference of 0, 3, 6, 9 dB, $n = 16$ for 12 dB difference, **c** *G. personatus* females, $n = 13$ for 0 and 12 dB difference, $n = 14$ for 3 dB difference, $n = 12$ for 6 and 9 dB difference, **d** *G. rubens*, $n = 12$ for all differences in sound amplitude, **e** *G. texensis*, $n = 12$ for 0, 3 and 9 dB difference, $n = 14$ for 6 dB difference, $n = 13$ for 12 dB difference. **f**–**j** Female responses to equally attractive chirp patterns presented simultaneously (*black line filled circles*), alternatingly (*black line unfilled circles*) or interleaved (*grey line filled circles*, see inset at top) at varying intensity differences. **f** *G. firmus*, $n = 12$ for all presentations, **g** *G. "staccato"*, $n = 12$ for all presentations, **h** *G. personatus*, $n = 12$ for simultaneous presentation, $n = 16$ for alternating and interleaved presentation, **i** *G. rubens*, $n = 12$ for both presentations, **j** *G. texensis*, $n = 12$ for both presentations. *Arrows* mark the dynamic range of female responses from an intensity difference of −6 to +6 dB. **k**–**o** Female preferences in choice situations presenting an attractive reference pattern with 100 % modulation of the pulse pauses from one speaker and an alternative pattern with variable pulse rates as in Fig. 1a–e. The modulation depths of the alternative pattern was varied as in Fig. 1f–j. Preference function M100 (both patterns with 100 % modulation) corresponds to the preference function with 0 dB difference in Fig. 2a–e. **k** *G. firmus*, alternative patterns with 75 ($n = 12$), 50 ($n = 15$), 37.5 ($n = 12$), 25 ($n = 12$), 12.5 % ($n = 12$) modulation depth. **l** *G. "staccato"*, alternative patterns with 75 ($n = 16$), 50 ($n = 13$), 25 % ($n = 12$) modulation depth. **m** *G. personatus*, alternative patterns with 75 ($n = 12$), 50 ($n = 19$), 25 % ($n = 16$) modulation depth. **n** *G. rubens*, alternative patterns with 75 ($n = 12$), 50 ($n = 13$), 25 % ($n = 14$) modulation depth. **o** *G. texensis*, alternative patterns with 75 ($n = 12$), 50 ($n = 13$), 25 % ($n = 14$) modulation depth. *Arrows* mark points of equal pulse rate of reference and alternative pattern

louder pattern increased (Fig. 2f–j). The dynamic range of female responses between +6 and −6 dB was marked by an arrow. This range was largest for *G. "staccato"* and *G. personatus*, intermediate for *G. firmus* and smallest for *G. rubens* and *G. texensis* (Fig. 2f–j).The observed increase in the range of turning responses was in agreement with the results of Fig. 2a–e as the shift of female preferences towards the louder patterns was strongest for *G. "staccato"* and *G. personatus*.

The impact of signal energy

To determine how females integrate signal energy (as given by sound intensity and modulation depth) and pattern attractiveness in choice situations a set of test series was conducted which presented an attractive reference pattern with 100 % modulation depth against an alternative pattern with variable pulse rates and increasing modulation depth of the pulse pauses (Fig. 2k–o). Both patterns were always presented at 80 dB SPL. The choice situation with a modulation depth of 100 % of the pulse pauses of both patterns (black filled circles, M100 in Fig. 2k–o) corresponded to the choice situation at equal sound amplitude of 80 dB SPL (black filled circles, ΔI 0 dB in Fig. 2a–e).

The preference functions of *G. firmus* females showed that at modulation depths lower than 75 % females always preferred the attractive reference pattern (Fig. 2k) consistent with the responses for *G. firmus* for variation of modulation depth in the no-choice paradigm (Fig. 1f). Female preferences of *G. "staccato"* and *G. personatus* females were shifted towards the alternative patterns with lower modulation depths and thus higher signal energy (Fig. 2l, m). *G. rubens* females exhibited similar preferences across all choice situations irrespective of the modulation depth of the alternative patterns and never turned towards the alternative pattern with lower modulation depth but higher sound energy (Fig. 2n). Preferences of *G. texensis* females revealed a small shift towards the alternative patterns, if these had a modulation depth of 75 % (Fig. 2o). At lower modulation depths of the alternative patterns females preferred the attractive reference pattern with 100 % modulation depth (Fig. 2o).

To quantify the relative contribution of pattern attractiveness and intensity to decision making in the different species an equivalence function was constructed. If females exhibited a turning response of 0 in a choice situation as in Fig. 2a–e, k–o, the difference in pattern attractiveness was compensated by the difference in sound intensity. Then the louder, less attractive alternative pattern was rated as equivalent to the softer, attractive reference pattern. For construction of the equivalence functions the zero crossings of the preference functions in Fig. 2a–e, k–o were used (Fig. 3a). For signal attractiveness, first the pulse rates of the alternative patterns at which the turning response was 0 in a choice situation were extrapolated from the diagrams (Fig. 2a–e, k–o) as illustrated in Fig. 3a. Then the no-choice turning responses for these pulse rates were extrapolated for an intensity of 80 dB from Fig. 1a–e as a measure for signal attractiveness (see Fig. 3a for an example for *G. firmus*). For differences in stimulus energy the corresponding no-choice reference function M75, M50 or M25 was used (shown in Fig. S2). For intensity differences, the given differences in sound amplitude and sound energy from Fig. 2a–e, k–o were converted to a common measure for sound intensity in dB using the formula: $dB = 10\log\left(\frac{I1}{I2}\right)$. In a last step these turning responses in a no-choice situation indicative of pattern attractiveness were plotted against the corresponding intensity differences (Fig. 3b–f). The resulting equivalence functions revealed a logarithmic

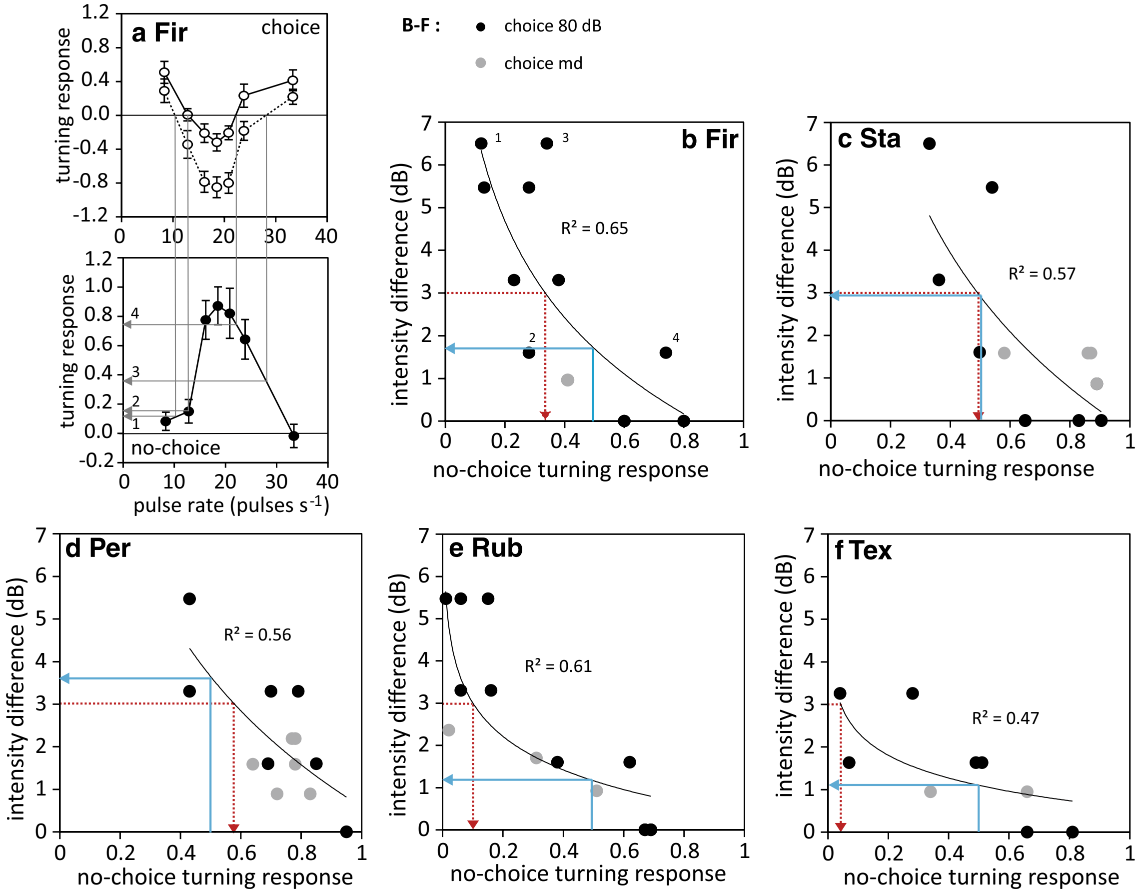


Fig. 3 Equivalence functions for pattern attractiveness and sound intensity. **a** Illustration for the extrapolation of equivalence points from Fig. 2a–e, k–o. In the upper diagram preference functions of a choice situation with 3 and 12 dB difference for *G. firmus* from Fig. 2a are shown. The lower diagram shows the response function at 80 dB SPL in a no-choice situation for *G. firmus* of Fig. 1a. The pulse rates of the alternative patterns at which females exhibited no preference were extrapolated from preference functions in a choice situation (*upper diagram*). For these pulse rates the no-choice turning responses were extrapolated from the response function in a no-choice situation (*lower diagram*, indicated by *dashed arrows*). These turning responses were *plotted* against the corresponding intensity difference. Corresponding points in **a** and **b** are numbered with 1, 2, 3, and 4. **b**–**f** Equivalence functions. Equivalence points were taken from zero crossings of the preference functions in Fig. 2a–e with increasing difference in sound amplitude (*black filled circles*) or from the preference functions with difference in sound energy (*grey filled circles*, **a**–**e**, see text for details). The values for pattern attractiveness as given by variation of pulse rate and/or modulation depth were interpolated from data in Fig. 1 and Fig. S2. **a** logarithmic regression was used to show the trend of the equivalence function. The *red dashed arrow* marks the attractiveness of the alternative pattern which is compensated at a difference of 3 dB. The *blue arrow* marks the difference in dB which compensates an attractiveness of the alternative pattern of 0.5

trend for all species indicating again the non-linear shift of female preferences in the choice experiments. The higher the difference in pattern attractiveness between alternative and reference pattern (thus the lower the attractiveness of the alternative pattern) the higher the intensity of the alternative pattern had to be in order to be rated as equivalent to the reference pattern.

To compare the impact of signal intensity for the different species the turning response (or pattern attractiveness of the alternative pattern) which was compensated by an intensity difference of 3 dB were marked with a red dashed arrow in the diagrams (Fig. 3b–f). The intensity difference which compensated a pattern attractiveness of 0.5 were shown with a blue arrow. A difference of 3 dB was sufficient to compensate patterns of low attractiveness (turning response <0.4) in *G. firmus, G. rubens* and *G. texensis* (Fig. 3b, e, f). In *G. "staccato"* and *G. personatus* 3 dB compensated a higher attractiveness of a pattern (turning response >0.5, Fig. 3c, d). In *G. firmus, G. rubens* and *G. texensis* a pattern attractiveness of 0.5 of the alternative pattern was compensated by less than 2 dB, whereas in *G. "staccato"* and *G. personatus* 3–4 dB were necessary (Fig. 3b–f). These measures again revealed that the lower the attractiveness of the alternative pattern the higher the intensity of the alternative pattern had to be in order to be rated as equivalent. The equivalence functions of *G.*

"staccato" and *G. personatus* were shifted along the *x*-axis as female responses in no-choice situations at 80 dB SPL did not decrease to zero and the response values towards the alternative patterns in a no-choice situation were higher than in the other species (Fig. 1a–e).

To verify if a difference in sound amplitude lead to an additional shift of female preferences towards alternative patterns with a lower modulation depth and thus higher signal energy, a reference pattern with 100 % modulation was played back from one loudspeaker and an alternative pattern with a lower modulation depth from the other loudspeaker first at equal sound amplitude of 80 dB SPL and second with an intensity difference of +6 dB (Fig. S4). For all species the results revealed a distinct shift towards the alternative patterns with a lower modulation depth presented at a higher sound amplitude (Fig. S4).

The impact of timing differences

In the final set of experiments the impact of timing differences during a nearly simultaneous presentation of two patterns from both loudspeakers was investigated (Fig. 4). A reference pattern was played from one side and the same pattern was also broadcast from the other side, but with an increasing time delay such that the relative timing of pulses within a chirp or trill changed as illustrated in Fig. 4a.

The results revealed a delay dependent change in response values for all species (Fig. 4b–f). At delays of zero equivalent to a simultaneous stimulus presentation, females showed no preference for one of the two presented patterns (Fig. 4b–f). At small time delays of the alternative pattern female responses towards the leading reference pattern increased. At intermediate time delays female responses decreased again and at a time delay corresponding to an interleaved stimulus situation females again showed no preferred orientation (open squares in Fig. 4d–f). With a further increase of time delays of the alternative pattern female preferences were shifted towards the alternative pattern. The magnitude of turning responses differed between species: the three chirping species showed lower turning responses compared to the two trilling species (Fig. 4b–f).

To compare the time window in which females of the different species showed maximal turning responses, values for the time delay at the maximal turning response were plotted as absolute time delays on the abscissa and as relative time delays with respect to the pulse period on the ordinate (Fig. 4g). A relative delay of 50 % corresponded to an interleaved stimulus situation. For the absolute time delay the time a pulse of the alternative pattern was lagging or leading (see Fig. 4a) with respect to the pulse of the reference pattern was used. The plot revealed that all species exhibited maximal turning responses at a relative delay between 21 and 44 % (Fig. 4g). With respect to absolute time delays most species were rather similar and ranged between 4 and 8 ms, except for *G. firmus* which exhibited maximal turning responses at much longer absolute time delays compared to the other species (Fig. 4g).

Discussion

Contribution and consequences of signal processing

The present results revealed similar trends in auditory processing of acoustic cues for decision making between species of field crickets although characteristic differences also emerged. All five species evaluated pulse rate and modulation depth for the attractiveness of song patterns (Fig. 1). In choice experiments sound intensity differences influenced female responses (Fig. 2) as did the temporal shift of two competing signals (Fig. 4). These data sets specifically indicated that the general scheme of information processing was similar if not identical between species with respect to (1) bilateral pattern recognizers (2) separate evaluation of pattern attractiveness and sound intensity and (3) a gain control mechanism linking pattern recognition to localization.

First, the type of chirp arrangement (simultaneous, alternating, interleaved) could have an effect on female preferences if incoming patterns from both sides were superimposed externally or internally or summed up as it is the case in grasshoppers (von Helversen and von Helversen 1995). The present results indicate that the type of chirp arrangement had no effect on turning responses (2f–j). In an interleaved stimulus arrangement superposition from both sides would lead to patterns with continuous tones for trilling species or to tone-chirps for chirping species. Both were unattractive at least for *G. firmus*, *G. rubens* and *G. texensis* supporting a separate representation of patterns from both sides (Fig. 1f, j, i, Blankers et al. 2015; Gray et al. 2016a). In an alternating chirp situation, superposition would create near continuous trills which are unattractive for *G. "staccato"* and *G. personatus* (Hennig et al. 2016). Thus, there was no evidence for an external or internal superposition or summation of patterns in any of the arrangement types which should have led to a reduction of pattern attractiveness. Incoming patterns from different sides were likely analyzed by separate left and right neuronal networks which process pattern attractiveness independently (Doherty 1985; Pollack 1986; Gabel et al. 2015). In ecologically relevant settings with multiple simultaneously calling males, independent processing of pattern attractiveness may facilitate song comparison, either interspecific or intraspecific, rather than rendering multiple incoming calls to noise (Pollack 1988).

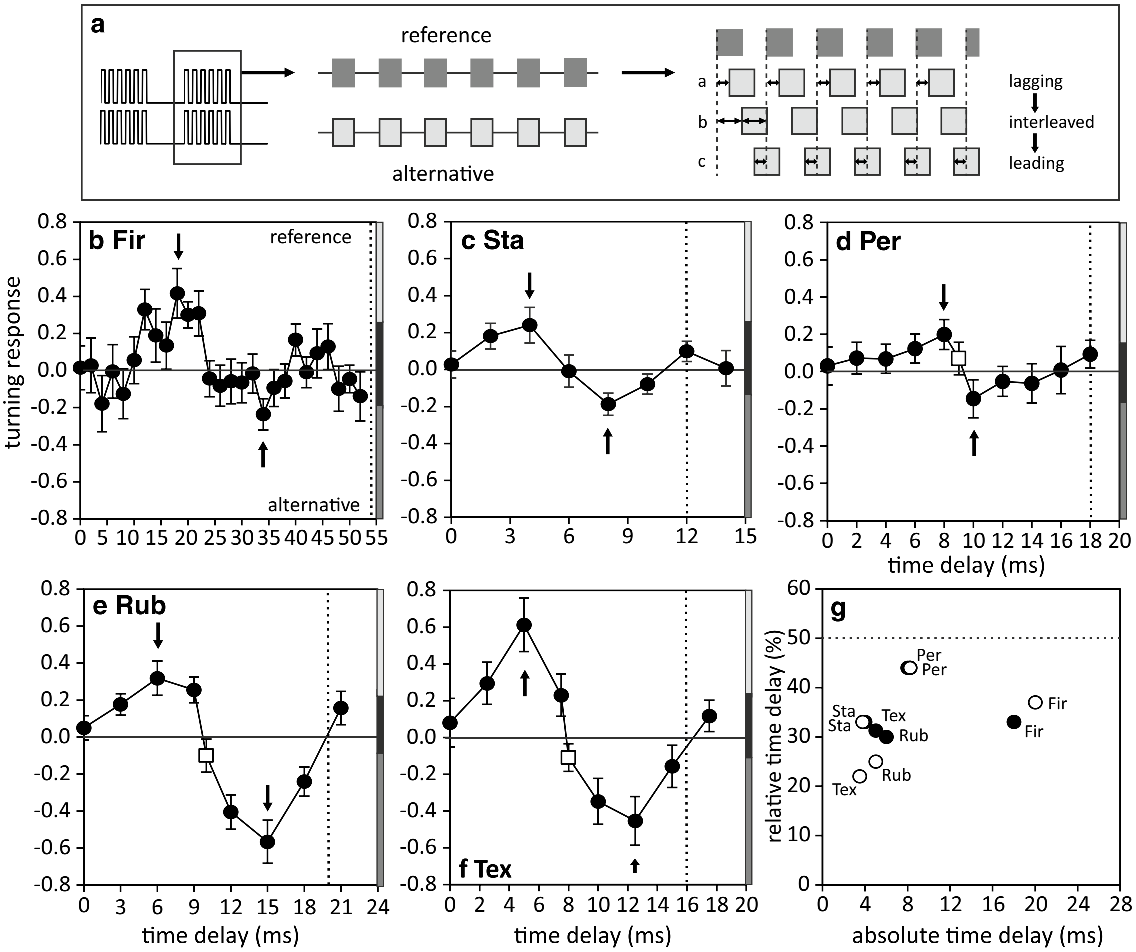


Fig. 4 Female responses to chirp patterns presented at different time delays. **a** Scheme of chirp pattern arrangement. Illustration to the *left* shows patterns at a delay of zero which represented simultaneous presentation. Illustration to the *right* shows different time delays of the lower alternative pulse pattern (*light grey squares*) relative to the *upper reference* pulse pattern (*dark grey squares*). *Dotted lines* mark the starting point of the first pulse pattern. **a** Second pulse pattern delayed at a half pulse duration meaning the second pulse pattern was lagging, **b** Second pulse pattern interleaved relative to the first, **c** Second pulse pattern a three-quarter pulse period delayed meaning that (except for the very first pulse of the first pattern) the second pulse pattern was leading relative to the first pulse pattern. **b**–**f** Female preferences for chirp patterns with timing differences. A reference stimulus and an alternative stimulus of equal attractiveness were presented with varying timing differences while the alternative stimulus was delayed. *Black dotted line* in **b**–**f** marks the duration of one pulse period. *Arrows* mark the maximal turning response towards the *reference* and *alternative* pattern. *Open squares* in **d**–**f** mark interleaved pattern presentation (data points taken from the interleaved pattern presentation in Fig. 2h–j). **b** *G. firmus, n* = 12–13, **c** *G. "staccato", n* = 15, **d** *G. personatus, n* = 15, **e** *G. rubens, n* = 12, **f** *G. texensis, n* = 12. **g** *Plot* of the absolute time delay for the maximal turning response towards the reference pattern (*black circles*) and the maximal turning response towards the alternative pattern (*open circles*) against the relative time delay (=absolute time delay normalized to the pulse period). *Dotted line* marks a relative time delay of 50 % which correspond to an interleaved stimulus situation

Second, the view that pattern recognition is evaluated separately from an intensity dependent localization (Schöneich et al. 2015) was confirmed here as pattern recognition with respect to pulse rate and modulation depth was intensity invariant for all five species with the exception of high pulse rates for *G. "staccato"* and *G. personatus* (Fig. 1). Third, in a choice situation all five species weighted the intensity differences between patterns with pattern attractiveness (Figs. 2a–e, k–o, 3, Fig. S3,) which is in support of a gain control mechanism linking both results of sensory processing as demonstrated before (Doherty 1985; Pollack 1988; Poulet and Hedwig 2005; Gabel et al. 2015).

The general picture of sensory processing underlying decisions in female crickets, therefore, emerges as rather similar between species (Fig. 5): incoming song patterns are analyzed separately by bilaterally paired networks for pattern attractiveness (P_L, P_R) and differences in pattern intensity ($I_{L\text{-}R}$, $I_{R\text{-}L}$; Pollack 1986, 1988; Stabel et al. 1989; Wendler 1989; Poulet and Hedwig 2005; Gabel et al. 2015). A downstream gain-control mechanism (circles with

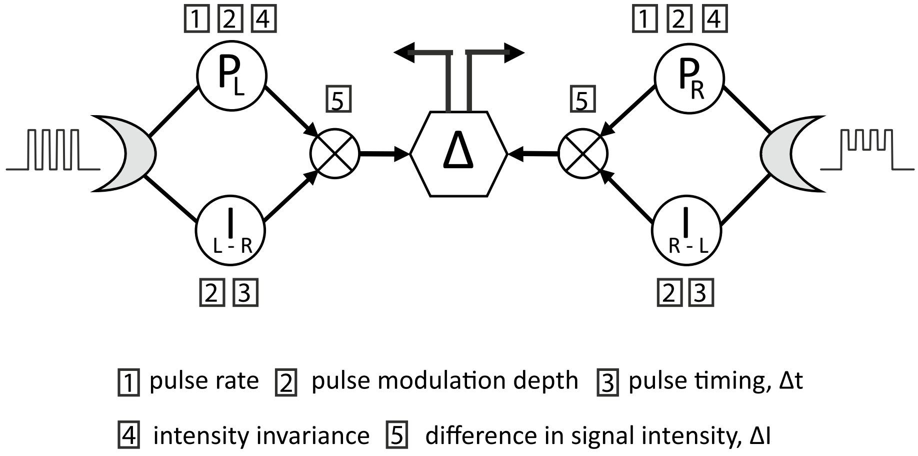


Fig. 5 Scheme of auditory processing with points in the processing chain marked at which differences between species were observed. Computation of pattern attractiveness and directional information. The auditory input from both sides is analyzed for the temporal pattern (P_L, P_R) and the difference in intensity ($I_{L\text{-}R}$, $I_{R\text{-}L}$). Both cues are integrated by a gain control mechanism (*circles with crosses*) which results in a non-linear weighting of the intensity cue by pattern attractiveness. A comparison between both sides leads to a directional decision (*unfilled triangle*). See text for details

crosses) leads to a weighting of the intensity cue by pattern attractiveness (Figs. 2, 3, 5, Poulet and Hedwig 2005; Gabel et al. 2015; Gabel et al. 2016). Finally, a comparison between both sides leads to a directional decision (unfilled triangle, Fig. 5). Therefore, pattern recognition and direction are evaluated in a parallel network but the gain-control mechanism fuses the outcomes of both computations which corresponds to a serial flow of information (Poulet and Hedwig 2005; Gabel et al. 2015).

Despite the shared general scheme specific differences between species were observed at all three processing points (P_L, P_R–pattern recognition, $I_{L\text{-}R}$, $I_{R\text{-}L}$–pattern intensity, gain-control mechanism), as indicated in Fig. 5. The following parts of the discussion aims to assess at which processing modules specific cues such as pulse rate, modulation depth and pulse timing will have an impact on turning decisions in choice situation and at which points intensity invariance and differences in signal intensity emerged (Fig. 5).

Divergence in the functionality of the pattern recognition module

In crickets the activation of two filters, the temporal filter for the pulse pattern which operates on a short time scale and the filter for the chirp pattern which operates on a long time scale, is important for pattern recognition and evaluation (Doherty 1985; Grobe et al. 2012; Blankers et al. 2015; Hennig et al. 2016). Here, only the properties of the filter for the pulse pattern were examined and generally confirmed previous measurements for pulse rate selectivity (Fig. 1a–e, Fir: Gray et al. 2016a, Rub, Tex: Blankers et al. 2015; Sta, Per: Hennig et al. 2016), with the exception that *G. personatus* revealed an acceptance of higher pulse rates, albeit reduced from the species-typical peak response, not seen in Hennig et al. (2016) data. At present this deviation in female responses at higher pulse rates remains unexplained, but we note that the crickets used in each study were derived from field collections in separate years and partly raised under different conditions. For all species, except for *G. "staccato"*, the response to pulse rates was strongest at the conspecific pulse rate, an observation typical for crickets, katydids and frogs (Gerhardt and Huber 2002). Differences in tuning are likely due to the computational outcome of a pattern recognition module (Fig. 5, P_L, P_R) consisting of a small circuitry of neurons sensitive to changes in pulse rate (Schöneich et al. 2015).

Variation of modulation depth had a twofold effect in choice experiments. While resulting differences in sound energy between patterns will influence the turning response (Fig. 2k–o), the attractiveness of song signals is also affected (Fig. 1f–j). Three types of selectivity for modulation depth were observed (Fig. 1f–j): *G. firmus* with the lowest pulse rate was the most sensitive species for changes in modulation depth, while species with intermediate to high pulse rates were either most tolerant (*G. "staccato"* and *G. personatus*) or accepted modulation depths larger than 50 % but not below (*G. rubens* and *G. texensis*). While the findings for the latter two species are in accordance with reports for *G. bimaculatus* (Hennig 2009) the observed tolerances for modulation depth are rather counter-intuitive with respect to signal detection in noise. At low modulation frequencies neuronal phase coupling across the auditory systems of vertebrates and insects is known to be more robust to changes in modulation depth than at higher modulation frequencies (Prinz and Ronacher 2002; Joris et al. 2004; Wohlgemuth et al. 2011). However, species with low pulse rates were very sensitive to modulation depth, whereas species with high pulse rates appeared to be insensitive for changes in modulation depth (Fig. 1f–j). Most likely these responses reflect species-specific differences in the pattern recognition module since at least for *G. "staccato"* an increase in pulse duty cycle as given by an increase in pulse duration is known to increase pattern attractiveness (Hennig et al. 2016) and renders a tone-like chirp without pulse rate modulation as attractive as a pulsed chirp (Fig. 1g, see also Schul et al. 1998; Deily and Schul 2004, 2009 for similar observations in *Tettigonia viridissima* and the genus *Neoconocephalus*). Physiologically, these differences remain unexplained at present (Schöneich et al. 2015), while computational models suggest differences in the template for pulse rate recognition (Clemens and Hennig 2013; Hennig et al. 2014).

Processing of pattern intensity and time delays

The intensity of a song signal is given by its sound amplitude and sound energy (modulation depth) both of which are evaluated by female crickets to arrive at a directional decision (Figs. 2, 5). Differences between species became evident by the dynamic range, *G. "staccato"* and *G. personatus* exhibited the strongest dependence of turning responses on intensity, while *G. rubens* and *G. texensis* revealed a lower dependence (Fig. 2f–j). A further component contributing to the strength of a directional response is given by contralateral inhibition from neuronal processing for contrast enhancement between the input from both ears (Römer et al. 2002; Hartbauer and Römer 2016). The effects of time delays on female choice behavior can be most parsimoniously explained as a consequence of contralateral inhibition, since females of all species preferred the leading stimulus at a given time delay (Fig. 4) at which the effects of contralateral inhibition were likely the strongest (Römer et al. 2002, Selverston et al. 1985; Horseman and Huber 1994; Hildebrandt et al. 2015). Therefore, it is likely that a leading stimulus is perceived louder as its contralateral counterpart is inhibited. For all species except for *G. firmus* the observed time delays at which a leading pattern is preferred correspond to the 4–8 ms time delay which the omega neurons are known to need for inhibition of their counterparts (Selverston et al. 1985; Horseman and Huber 1994). For *G. firmus* females showed a maximal response at longer absolute time delays than the other species. Even longer time delays than a single pulse period are also known to drive female turning responses in other cricket species towards the leading sound pattern (Wyttenbach and Hoy 1993; Hedwig and Poulet 2004, 2005).

The present data set of choice tests with time delays also revealed a surprising difference in the magnitude of turning responses between species (Fig. 4), as *G. "staccato"* and *G. personatus* showed the weakest turning responses to time delays and thus enhanced intensity differences, whereas *G. rubens* and *G. texensis* exhibited the strongest turning response, somewhat contradictory to the strength of turning towards intensity differences observed before (Fig. 2f–j). Most likely this difference was due to a summation of contralateral inhibition over a longer time, thus yielding a stronger effect, in trilling species (Rub, Tex) than in chirping species (Fir, Sta, Per, see Römer and Krusch (2000) for time constants of up to 5 s in a katydid).

The functionality of the gain-control mechanism and differences between species

The experiments with differences in sound amplitude (Fig. 2a–e) and signal energy (Fig. 2k–o) as well as the equivalence functions (Fig. 3b–f) exemplified the presence of a gain-control mechanism which weighs the intensity cue by pattern attractiveness in all species (Doherty 1985; Pollack 1986; Poulet and Hedwig 2005; Gabel et al. 2015). Except for *G. rubens* there was a strong impact of intensity differences at a high gain for attractive pulse rates in all species whereas the impact of intensity differences was small for patterns of low attractiveness. Thus, it required high intensity differences to shift a decision towards a pattern with low attractiveness (Fig. 3b–f). In contrast in *G. rubens* the shift was smallest for the most attractive pulse rate and females never significantly preferred a louder less attractive pattern over the softer attractive reference pattern (Fig. 2d, n). Evidently pattern intensity is given less weight by the gain-control mechanism in *G. rubens*.

Sound amplitude and signal energy seem to have a similar influence on female choice behavior (Fig. 3b–f) indicating that signal energy is integrated by sensory neurons (Gollisch et al. 2002; Gabel et al. 2015) in all studied cricket species. Nevertheless, pattern attractiveness is evaluated separately in the crickets brain (Schöneich et al. 2015) and is intensity invariant (Fig. 1a–e) which is most likely caused by the intensity invariance of the auditory system above intensities of 60 dB SPL generated by spike frequency adaptation (Benda and Hennig 2008). Only *G. "staccato"* and *G. personatus* showed an intensity dependence at high pulse rates in a no-choice situation (Fig. 1b, c) which may also be caused by the gain-control mechanism as in these two species in choice situations sound intensity also had a stronger impact on female preferences than in the other species.

The role of phylogeny and ecology

The present results revealed remarkable differences in choice behavior between the species examined. The most consistent similarities between species were observed for close relatives as they exhibited preferences more similar than between less closely related species (Figs. 1, 2, 3, 4, Fig. S1). Further potential common denominators between species such as chirped or trilled songs or preference thereof, geographical, sympatric or allopatric distributions (Tab. S1) did not show a consistent linkage with the similarities and differences of choice behavior examined. In terms of phylogenetic distance we observed three groups: the two species pairs (*G. rubens*/*G.texensis* and *G."staccato"*/*G.personatus*) and the more distantly related species *G. firmus* (Fig. S1).

G. rubens and *G. texensis* are cryptic sister species with extensive areas of sympatry and allopatry (Gray et al. 2008). Pulse rate is the key feature to distinguish between species (Gray and Cade 2000) and song recognition is also primarily dependent on pulse rate with a shift in the peak preference between both species (Fig. 1a, Blankers et al. 2015). Our results revealed only one additional difference in choice behavior between these two species. *G. rubens* females never significantly preferred a louder less attractive pattern over the reference pattern which exhibited the most attractive conspecific pulse rate at lower sound amplitude or with lower signal energy (Fig. 2d, 3d) which differs from choice behavior of female *G. texensis* (Fig. 2e, o). Thus, pulse rate was weighed much stronger in *G. rubens*, which is potentially a specific adaptation to the occurrence in sympatry with *G. texensis*. Female *G. rubens* will not track calling songs with a wrong pulse rate, e.g. calling songs of *G. texensis* males, even if males are singing louder or at closer distances. In contrast, female *G. texensis* might be attracted to male *G. rubens* pulse rate if the song were nearby or especially loud, however, even in those circumstances close-range courtship interactions would inhibit hybridization (Gray 2005) which appears to be minimal (Izzo and Gray 2004, Blankers et al. 2016).

G. "staccato" and *G. personatus* are allopatric very closely related species (along with *G. lineaticeps*) and showed similar preferences which differ from the other studied species in pulse rate preference, preference for modulation depth and weighting of signal intensity (Fig. 1, 2, 3). As these species are allopatric with respect to each other, differences could be due to genetic drift or to selection caused by sympatry with other congeners. Especially in *G. "staccato"* the differences in auditory processing led to less selective preferences as females accepted a wide range of pulse rates, and modulation depths and signal intensity had a strong influence (Figs. 1b, g, 2, 3). They are the least discriminative of these five species which is particularly interesting as they live in the most acoustically diverse community (D.A. Gray personal observation, Hennig et al. 2016) which is in contrast to the suggestion of an increasing filter selectivity and thus sharper tuning of preference functions with a higher complexity of acoustic communities (Schmidt et al. 2011). Thus, one could expect a detrimental effect of the low selectivity on mate finding in the field as females prefer signals with temporal parameters which are not produced by conspecific males (i.e. pulse rates above 100 p/s) and signal intensity has a strong influence on female decisions (Fig. 1b, g, Gray et al. 2016b; Hennig et al. 2016). Potentially other mechanisms or parameters of male songs operating on different time scales and not taken into account here contribute to a more selective choice in females.

G. firmus is not closely related with another species studied here but occurs together with *G. rubens* and somewhat with *G. texensis*. Females will discriminate against the songs of these trilling species because of their preference for very low pulse rates (Fig. 1a, Gray et al. 2016a). *G. firmus* females discriminated against pulse patterns with modulation depths below 50 % (Fig. 1f) and preferred the reference pattern with 100 % modulation over alternative patterns with lower modulation depths (Fig. 2k). Thus, the pulse structure is highly important for pattern recognition. Moreover, females even preferred the reference pattern with the most attractive conspecific pulse rate attenuated by 12 dB over an alternative pattern with lower and higher pulse rates (Fig. 2a). Doherty and Storz (1992) also found that females preferred a song with the conspecific pulse rate over an alternative song with lower pulse rates when it was attenuated by 6 or 12 dB. Potentially this strong weighting of signal intensity by pattern attractiveness is a specific adaptation to the occurrence in sympatry with the sister species *Gryllus pennsylvanicus* (Harrison and Arnold 1982; Doherty and Storz 1992). Male songs of these two sister species are similar, consist of rhythmic chirps each of which is composed of three to five pulses (Doherty and Storz 1992). But *G. pennsylvanicus* males sing at faster rates than *G. firmus* males (Alexander 1957; Weissman et al. 1980; Doherty and Storz 1992) and thus *G. firmus* females will discriminate against their songs even if males are singing louder or at closer distances.

Acknowledgments We thank Bernhard Ronacher for critical and constructive discussions about the data analyses and the manuscript. We appreciate Elisa Becker, Pascal Kolja Haß, Anne Görlitz, Daria Ivanova and Ailyn Yilmaz for the help with some of the experiments. All applicable international, national and/or institutional guidelines for the care and use of animals were followed. This work was supported by the German Research Foundation [he2812/4-1].

Compliance with ethical standards

Conflict of interest The authors declare no competing or financial interest.

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