

## RESEARCH ARTICLE

# Decision making and preferences for acoustic signals in choice situations by female crickets

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## ABSTRACT

Multiple attributes usually have to be assessed when choosing a mate. Efficient choice of the best mate is complicated if the available cues are not positively correlated, as is often the case during acoustic communication. Because of varying distances of signalers, a female may be confronted with signals of diverse quality at different intensities. Here, we examined how available cues are weighted for a decision by female crickets. Two songs with different temporal patterns and/or sound intensities were presented in a choice paradigm and compared with female responses from a no-choice test. When both patterns were presented at equal intensity, preference functions became wider in choice situations compared with a no-choice paradigm. When the stimuli in two-choice tests were presented at different intensities, this effect was counteracted as preference functions became narrower compared with choice tests using stimuli of equal intensity. The weighting of intensity differences depended on pattern quality and was therefore non-linear. A simple computational model based on pattern and intensity cues reliably predicted female decisions. A comparison of processing schemes suggested that the computations for pattern recognition and directionality are performed in a network with parallel topology. However, the computational flow of information corresponded to serial processing.

**KEY WORDS:** Decision making, Acoustic communication, Female choice, Phonotaxis

## INTRODUCTION

Mate choice can be viewed as a computational chain of information-processing steps at the end of which a decision is made (Bateson and Healy, 2005). Numerous studies have evaluated choice behaviour by measuring preference functions on a one-dimensional scale (Kirkpatrick et al., 2006). Yet the signals sent by a potential mate are often composed of multiple characteristics that have to be assessed by the females (Gerhardt et al., 2007; Márquez et al., 2008). The problem of efficient decision making is especially relevant in situations in which these different attributes are not positively correlated, so that no single option is the best of all alternatives (Gigerenzer et al., 1999).

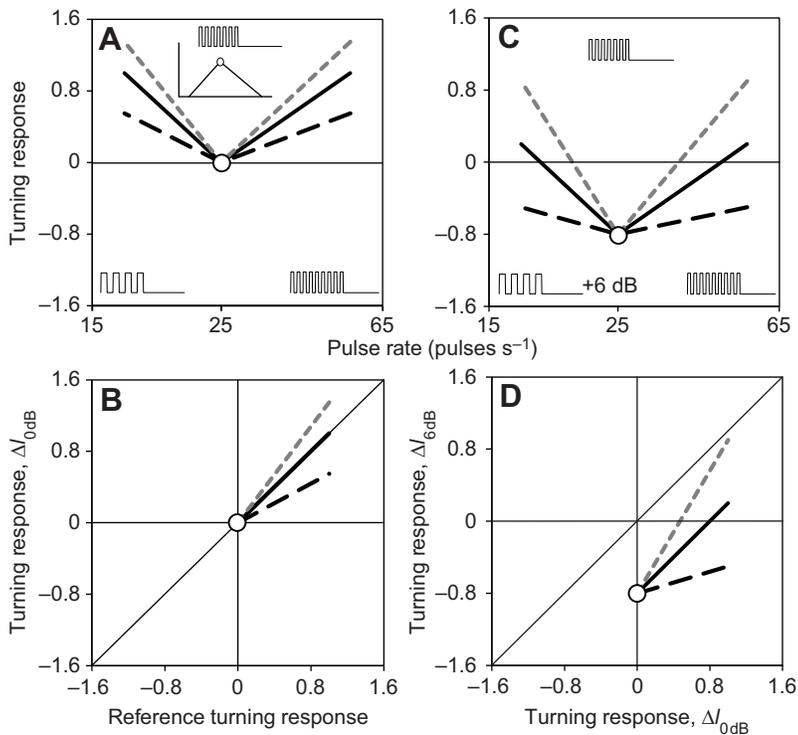
Female choice in crickets for acoustic signals produced by males is a case in point. Between species, and even within a species, male songs differ in multiple attributes such as carrier frequency and sound intensity or in temporal parameters given by the pulse and/or the chirp pattern. Since male crickets form calling aggregations in

the field (Simmons, 1988) females are usually confronted with several males singing at the same time from different distances and directions, a situation not unlike the human cocktail-party problem, which describes the challenge of perceiving and localizing a sound source in a noisy social environment (Cherry, 1953; Bee, 2008; Bee and Micheyl, 2008). Therefore, the quality of a male song does not necessarily exhibit a positive correlation with its loudness, as, for instance, a conspecific male with an attractive song pattern at a larger distance will be perceived less loudly than a heterospecific male with an unattractive song at close range because of sound attenuation by spherical spreading. Although previous studies have tested female crickets in choice paradigms (Popov and Shuvalov, 1977; Doherty, 1985; Pollack, 1986), it is still debated how females compute and integrate perceived information to form a decision for the song of a particular mate. Behavioural experiments with female crickets in choice situations are potentially ambiguous for several reasons. Unlike many animals, including humans, crickets do not appear to perform an auditory scene analysis, in which the perception and recognition of different acoustic objects is linked to their location. Rather, crickets are known to form acoustic hemispheres in their auditory pathways (Pollack, 1988) and are therefore expected to suffer from masking effects if confronted with several sound sources from one side. Also, it is still debated whether female crickets become more selective in choice situations, in which a direct comparison of acoustic signals is possible, compared with no-choice paradigms and conflicting evidence exists (cf. Popov and Shuvalov, 1977; Doherty, 1985; Pollack, 1986; Wagner, 1998). Finally, it is still unresolved whether female crickets employ serial or parallel processing of pattern and directional information during auditory processing as both scenarios have been proposed (Wendler, 1989; Stabel et al., 1989; Poulet and Hedwig, 2005). In a parallel-processing scheme, the attractiveness of a signal will depend solely on pattern quality as attractiveness will only gate the information about intensity differences for a directional decision. In a serial-processing scheme, both pattern quality and intensity will contribute to the attractiveness of an acoustic signal and drive the directional decision.

To separate these different scenarios and to understand the computational outcome of decision making in crickets, we tested females on a trackball system (see Materials and Methods for details) in choice situations in which two uncorrelated parameters were varied – pulse rate and sound intensity. Female crickets are known to exhibit stabilizing preferences for pulse rate, but prefer the louder of two signals over a wide intensity range (Hennig, 2009). First, the attractiveness of different pulse rates was determined in a no-choice paradigm. Then, these pulse rates were tested in a choice paradigm against a constant pulse rate of high or intermediate attractiveness, in order to assess possible changes in the tuning of the preference function for pulse rate. There are three scenarios for how the selectivity of preference functions for pulse pattern will be affected in a choice situation compared with a no-choice situation

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**Fig. 1. The shapes of preference functions in a choice paradigm.** (A) Preference functions for a constant attractive stimulus (positive responses) versus a stimulus with varied pulse rates (negative responses). Inset shows preference function for pulse rate in a no-choice paradigm. Solid black line shows expected turning responses in a choice paradigm at equal intensities, if the preference function remains unchanged from a no-choice test. Dashed lines indicate wider (black) or narrower (grey) preference functions in a choice situation when absolute values are compared. (B) Turning responses from A plotted against the inverted preference function from a no-choice test (equal to black solid line in A). An unchanged preference function (black solid line in A) shows a slope of the regression equal to 1, a wider preference function as in A will result in slope of the regression smaller than 1, narrowing will lead to slopes larger than 1. (C) Preference functions and corresponding regressions in a choice paradigm as in A, with stimuli at different intensities (negative values indicate turning responses towards the louder side). (D) Regressions as in B for stimuli with unequal intensities. Slopes smaller and larger than 1 indicate wider or narrower preference functions, respectively, in C. See text for a detailed description.  $\Delta$ , difference in intensity.

(Fig. 1A,B). In a no-choice situation, crickets will exhibit the strongest turning response (lateral deviation towards a test pattern during the experiment, see Materials and methods) to the most attractive pulse rate and weaker responses to less-attractive pulse rates reflected in the tuning of a preference function (Fig. 1A, inset). By contrast, in a choice paradigm a turning response of zero is expected, if the pulse rates presented from both sides possess equal attractiveness and intensities (open circle in Fig. 1A; Wendler, 1989). Variation of the pulse rate from one side will confront the female cricket with less-attractive pulse rates from one speaker (lower part of Fig. 1A) and with an attractive pulse rate from the other speaker, held constant for all choice tests (top part in Fig. 1A). Female crickets are then expected to turn towards the more-attractive pulse rate, yielding positive turning responses in Fig. 1A. In terms of absolute turning responses, these preference functions can be wide (dark dashed line in Fig. 1A) or narrow (light stippled line in Fig. 1A). In order to compare the preference functions of the choice paradigm with the one from the no-choice situation, the response to the most attractive pulse rate in the no-choice test has to be set to zero (open circle in Fig. 1A) and all other values from the preference function have to be calculated as the absolute difference from the maximal response. Such a calculation will effectively turn the preference function from the no-choice paradigm upside down (black solid line in Fig. 1A). This inversion allows a direct comparison with the absolute turning response from the choice paradigm as in Fig. 1B. Here, the turning responses from the choice paradigm (ordinate of Fig. 1B) are plotted versus the (inverted) responses from the no-choice situation (abscissa of Fig. 1B). If the absolute width and strength of the preference function for pulse rates is unchanged between the no-choice and choice situation, all points will then fall on the diagonal (black line in Fig. 1B). A wider or narrower preference function as indicated in Fig. 1A will result in a changed slope (illustrated by the dashed lines with different grey shading in Fig. 1B, corresponding to the preference functions shown in Fig. 1A).

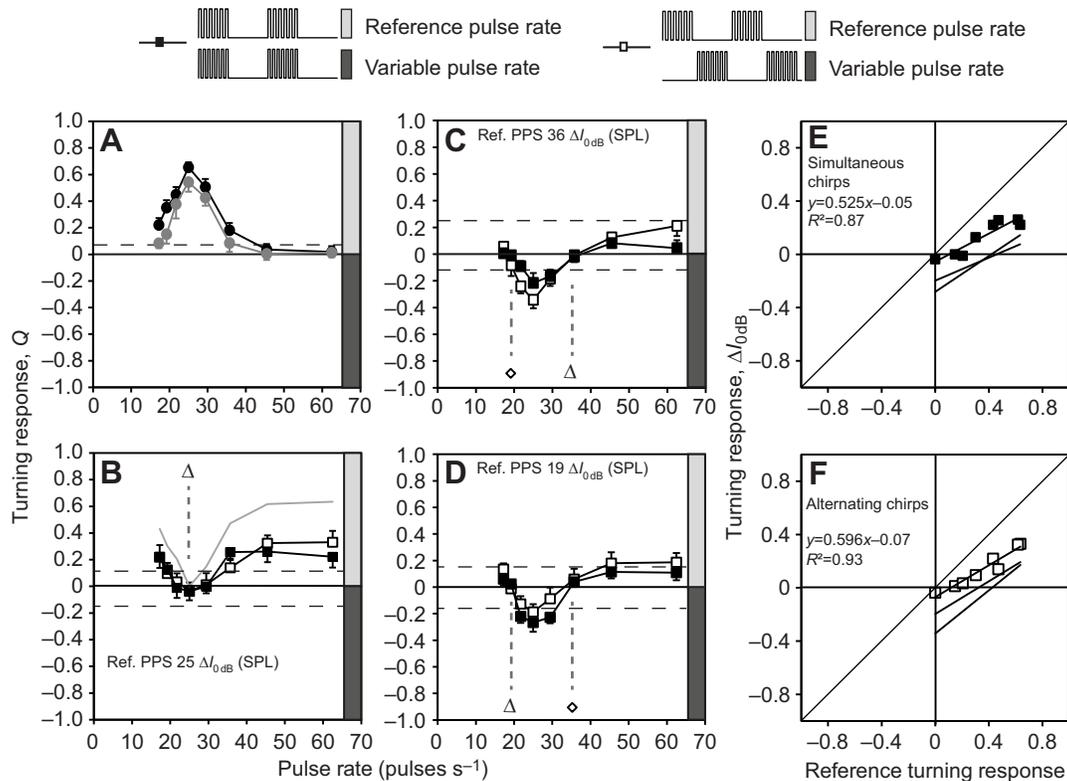
The rationale outlined in Fig. 1A,B also applies if pulse rates of different attractiveness are presented 6 dB louder (lower part in Fig. 1C) than the attractive reference pattern (upper part in Fig. 1C) in order to evaluate how intensity differences affect the directional decisions. Then a shift of the preference function to the side with the louder signal is expected (Fig. 1C). If these responses are plotted against the responses from a choice test without intensity difference (e.g. the black line in Fig. 1A), a slope of one refers to a parallel and constant shift to the louder signals, whereas other slopes suggest a non-linear influence of an intensity difference, indicative of a changed tuning of the preference function (Fig. 1D).

Several sets of experiments as outlined in Fig. 1 were performed with different reference pulse rates and intensities (74 dB and 80 dB). Signals during the choice tests were presented in simultaneous or alternating chirp patterns to control for masking effects. Thereby, we aimed to separate the contributions of pattern attractiveness and signal intensity for phonotactic orientation and thus decision making in female crickets. The integration of both cues can be modelled by weighting signal intensities with the respective quality cue of a given sound signal. We argue that such an operation corresponds to a serial computation of the cues for pattern and direction, executed within a parallel network topology.

## RESULTS

### Weighting of cues in choice situation

The first test series was designed to obtain a reference function of female preferences for different pulse rates (17–63 pulses s<sup>-1</sup>) in a no-choice paradigm. The preference function exhibited maximal turning responses at a pulse rate of 25 pulses s<sup>-1</sup>, if sound patterns were presented at 80 dB SPL or 74 dB sound pressure level (SPL) (Fig. 2A). The preference functions measured for pulse rate at different intensities were very similar, indicating a minor influence of sound intensity in a no-choice situation. On average there was a small reduction in the turning strength at 74 dB (mean  $\pm$  s.d.: 0.09  $\pm$  0.06) compared with tests at 80 dB SPL. Pulse rates higher than



**Fig. 2. Preference functions of phonotactic responses for female crickets in no-choice and choice paradigms.** (A) Preference function for pulse rate in a no-choice test presented at 80 dB (black line,  $N=22$ ) or 74 dB (dark grey line,  $N=15$ ). (B) Turning responses in choice experiments where an attractive reference pattern with a pulse rate of 25 pulses  $s^{-1}$  was played back from one speaker and a pattern with varied pulse rates from the opposite speaker at equal intensities (80 dB SPL). Positive values indicate turning strength towards the attractive reference pattern. Turning responses for simultaneous (filled squares,  $N=12$ ) and alternating chirp patterns (open squares,  $N=16$ , see insets at top). Grey line shows the inverted reference function from A, the triangle marks the pulse rate of the reference stimulus, 25 pulses  $s^{-1}$ . (C,D) Same test situation as in B but with different reference patterns (C: 36 pulses  $s^{-1}$ , D: 19 pulses  $s^{-1}$ ). Filled (C:  $N=12$ , D:  $N=13$ ) and open squares (C:  $N=23$ , D:  $N=15$ ) as in B, see insets at top. Symbols in C,D mark turning responses for patterns that had the same pulse rate (triangles) or same attractiveness (diamonds). Data points between the dashed lines in A–D are not significantly different from the mean of the negative controls. All data points above the upper dashed line or below the lower dashed line are significantly different from the negative controls. (E,F) Linear regressions between turning responses of the choice tests in B–D and turning responses of the inverted reference function (grey line in B) for (E) simultaneous playback and (F) alternating playback. Data points are shown only for tests with the most attractive reference pattern of 25 pulses  $s^{-1}$ . Insets at top refer to stimulus presentation for simultaneous and alternating chirp patterns, grey bars indicate the direction of turning responses as plotted in A–D.  $\Delta I$ , difference in intensity.

40 pulses  $s^{-1}$  did not elicit a significant turning response at either intensity (Fig. 2A). To determine if the pattern quality or attractiveness – here defined solely by the pulse rate – was a simple predictor for the decision of a female in a choice situation, two test sessions were carried out, presenting an attractive reference pattern with a pulse rate of 25 pulses  $s^{-1}$  from one speaker and variable pulse rates of the reference function (Fig. 2A) from the opposite speaker. Both stimuli were broadcast at an equal intensity of 80 dB SPL and chirps were presented in either a simultaneous or alternating fashion (see stimulus presentation at top of Fig. 2). The results of the simultaneous as well as of the alternating playback revealed that females showed no significant preference for one of the two presented patterns, if the alternative pattern was in the range of 22 to 29 pulses  $s^{-1}$ . At lower and higher pulse rates of the alternative pattern, females significantly preferred the attractive reference pattern with a pulse rate of 25 pulses  $s^{-1}$  as indicated by the positive turning responses (Fig. 2B). However, the strength of turning towards the standard pattern was not as strong as during the no-choice tests (grey line in Fig. 2B, see also black symbols in Fig. 2A).

Next, we tested the linearity of female responses by replacing the reference pattern of 25 pulses  $s^{-1}$  with stimuli of either 19 or 36 pulses  $s^{-1}$ . These stimuli were chosen because they had an intermediate, but similar attractiveness (c.f. Fig. 2A, triangles and

diamonds in Fig. 2C,D mark turning responses for a choice between patterns that had the same attractiveness i.e. 19 and 36 pulses  $s^{-1}$ , the triangle indicates the pulse rate of the reference pattern). Females maintained their preference for pulse rates of 25 pulses  $s^{-1}$  during the simultaneous as well as the alternating playback situation, as indicated by the negative turning responses (Fig. 2C,D). During presentation of equal pulse rates from both speakers, females exhibited no significant turning response (see triangles in Fig. 2C,D). Also, at less-attractive pulse rates, females showed no significant turning response except for the alternating playback with a reference pattern of 19 pulses  $s^{-1}$  (Fig. 2D). Here, females preferred the standard pattern with 19 pulses  $s^{-1}$  over the alternative pattern with 46 pulses  $s^{-1}$  and 63 pulses  $s^{-1}$ , as indicated by the positive turning responses.

To determine whether the behavioural tuning for pulse rate is the same in no-choice and choice situations, the responses of the choice experiments in Fig. 2B–D were compared with the responses of the inverted reference function from no-choice tests (calculated from Fig. 2A, grey line in Fig. 2B) as in Fig. 1B. The slopes of the regression functions obtained from all three choice experiments (Fig. 2B–D) are plotted in Fig. 2E,F. All slopes were smaller than 1 (between 0.43 and 0.67 for simultaneous presentation of chirps, and between 0.60 and 0.81 for alternating chirps and not significantly

different for simultaneous,  $P=0.29–0.37$  or alternating stimuli,  $P=0.054–0.85$  indicative of a wider preference for pulse rates in a choice situation (compare black dashed line in Fig. 1A,B). In Fig. 2E,F data points are shown only for tests with the most-attractive reference pulse rate of 25 pulses  $s^{-1}$  from Fig. 2B, as only then did the regression intercept the ordinate at zero. For other reference pulse rates as in Fig. 2C,D, the regression functions revealed similar slopes but were shifted to lower values, because of the lower attractiveness of the reference pattern (Fig. 2E,F).

In a second series of choice tests, the influence of an intensity difference between the two presented stimuli on the turning strength was assessed. All test pulse rates as in Fig. 2 were used, but the reference patterns were broadcast at 74 dB SPL and the patterns with varying pulse rates were presented at 80 dB SPL, again in both a simultaneous and alternating fashion. The results of all tests revealed a distinct shift of the preference function towards the louder patterns (Fig. 3A–C). This shift towards patterns with higher intensity was strongest for attractive pulse rates between 20 and 30 pulses  $s^{-1}$  and smaller for less-attractive pulse rates. The pulse rates with intermediate attractiveness of 19 pulses  $s^{-1}$  and 35 pulses  $s^{-1}$  again scored equal response levels (compare turning responses for patterns marked with diamonds and triangles in Figs 2C,D and 3B,C). To quantify and to examine the trend and magnitude of the observed shift as illustrated in Fig. 1C,D, the turning response at an intensity difference of 6 dB was plotted against the turning response at equal intensities for both test paradigms (Fig. 3D,E, data from Fig. 2B–D). As before, data points are plotted only for tests with an attractive pulse rate of 25 pulses  $s^{-1}$  as a reference pattern (data from Fig. 3A) but the regressions for all test series are shown. Notably, all regressions exhibited an increased slope higher than 1 (between 1.626 and 2.006 for simultaneous presentation of chirps, and between 1.674 and 1.864 for alternating chirps and were not significantly different for simultaneous,  $P=0.084–0.93$  or alternating stimuli,  $P=0.25–0.62$ ). The observed slopes were similar to the grey dashed line in the scheme presented in Fig. 1D, indicative of narrower preference functions. Therefore, the data suggested a stronger impact of intensity differences at attractive pulse rates and thus a non-linear influence of the intensity difference on the turning strength.

### Predicting female preferences with a simple model

Since both pulse rate and intensity affected female turning responses, we used a simple model to predict female decisions. For that, we assumed that there are two bilateral recognizers in the cricket's brain that evaluate acoustic signal from each side separately, as proposed earlier (Pollack, 1986; Doherty, 1991). The predicted strength of the turning response was calculated as the difference in turning responses measured for each of the two test patterns when presented alone. At equal intensities from both sides, as in Fig. 2B–D, this is:  $P=Q_{\text{Pattern1}}-Q_{\text{Pattern2}}$  where  $P$  is the predicted turning response,  $Q_{\text{Pattern1}}$  is the observed turning response to the reference pattern and  $Q_{\text{Pattern2}}$  is the observed turning response to the respective pulse rate presented from the opposite speaker from which different pulse rates were presented. The computed difference in turning response was used as a prediction and could attain values between  $-1$  and  $1$ , as in the test sessions. A positive value indicated a preference for the reference pattern and a negative value indicated a preference for the alternative pattern. A value of zero indicated equal strength of activation from both sides.

In a first step, we used the experimental data from the no-choice tests and predicted the turning responses for the choice tests at equal

intensity (Fig. 2). Although high correlation values were obtained, the slopes of the regressions were clearly larger than 1 (Fig. 4A,B). The steep slopes were a result of the higher turning responses found for no-choice tests which predicted stronger turning responses than actually observed in a choice test (Fig. 2). Effectively, the steep slopes were therefore a result of the changed width of the preference functions from no-choice to choice tests (Figs 1A,B and 2E,F).

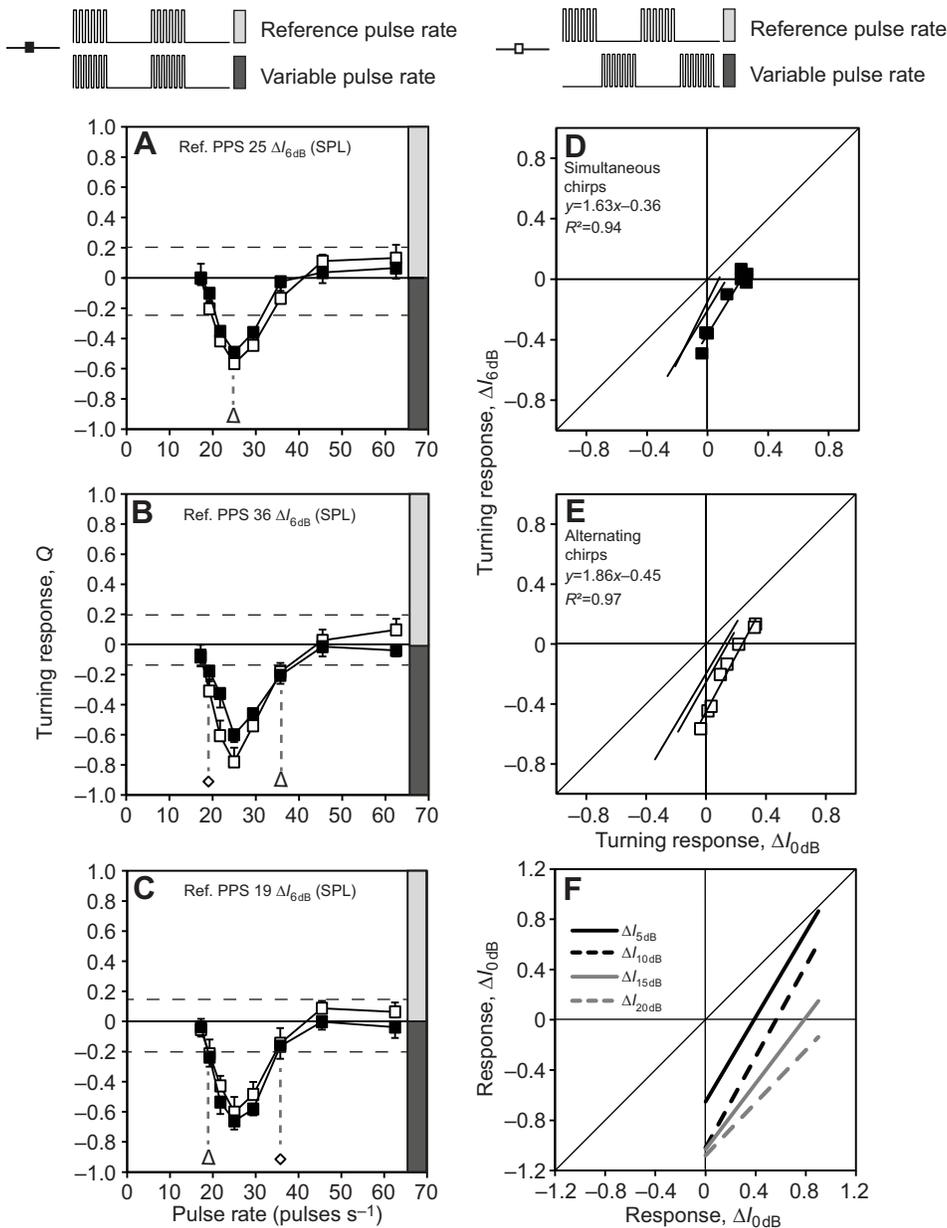
In a second step, we therefore used the turning responses observed in a choice paradigm with an attractive pulse rate of 25 pulses  $s^{-1}$  as a reference pattern (from Fig. 2B) to predict the turning responses at different reference patterns (from Fig. 2C,D). Predictions were calculated as above and the regressions now exhibited slopes closer to 1 (Fig. 4C,D) indicative of a better prediction of female turning responses by a model with two bilateral recognizers.

For the prediction of turning responses towards stimuli with different pulse rates and intensities, the signal from each side was assigned two values that were added together. One value reflected the attractiveness of a pattern and was determined from the choice tests at equal intensity (Fig. 2B). The other accounted for the influence of intensity on the turning response. Therefore, predicted values were calculated as follows:  $P=Q_{\text{Pattern1}}-Q_{\text{Pattern2}}-\Delta I_{6\text{dB}}$ . Tests at different intensities in the no-choice paradigm had revealed that there is only a small change in the strength of the turning responses from 80 dB to 74 dB SPL (Fig. 2A). Since the effect of intensity on the choice behaviour of female crickets was evidently much stronger (Fig. 3A,B,C), we obtained values for intensity from data in Fig. 3 in two steps. First, a constant value for the intensity difference of  $\Delta I_{6\text{dB}}$  was determined from the  $y$ -intercept of the regression lines plotted in Fig. 3D,E. However, this procedure ignored the non-linear influence of intensity differences that were evident from Fig. 3D,E and therefore did not produce good predictions of female choice behaviour (not shown). In order to account for the non-linear influence of intensity, we calculated a single regression over all data points, as in Fig. 3D,E and thereby obtained an estimate with a mean slope of 1.37 for simultaneous stimulus presentation and 1.46 for alternating stimulus presentation and a negative  $y$ -intercept (0.24 for simultaneous presentation and 0.28 for alternating presentation). For every choice pair, we calculated the distance of the regression function to the angle bisector which reflects the contribution of  $\Delta I_{6\text{dB}}$  to the turning response. Although the predictive power of the model for the experimental data from choice situations with an intensity difference (Fig. 3A–C) was generally good (Fig. 4E,F), the slopes of both regression functions were slightly lower than 1. Combining the predictions of the model for the complete data set from choice situations (Figs 2B–D and 3A–C), shown separately in Fig. 4C–F resulted in a slope of the regression close to 1, indicative of a good overall prediction (Fig. 4G,H).

The high predictive power of the model demonstrated that female decisions can be explained by a comparison of auditory inputs from both sides. However, our calculations also revealed that the strength of turning responses of female crickets in choice tests cannot be predicted quantitatively from female preferences in a no-choice situation.

### Effect of a tone stimulus on female preferences in choice tests

In the choice tests, females were confronted with different pulse rates from both sides that could conceivably hamper recognition due to masking effects, particularly during simultaneous stimulus presentation. To assess the magnitude of possible interferences,



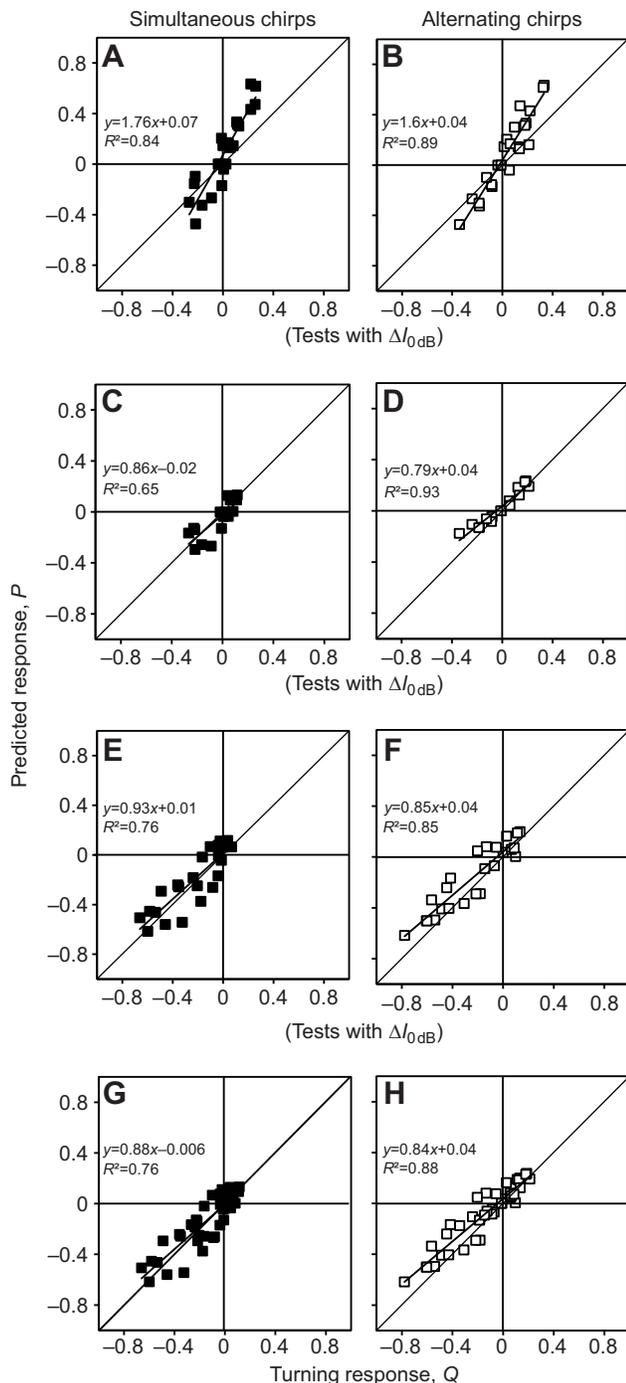
**Fig. 3. Female responses in a two choice paradigm with an intensity difference of 6 dB between reference (74 dB SPL) and alternative pattern (80 dB SPL).**

(A–C) Stimulus patterns and data presentation as in Fig. 2B–D. Filled squares show responses for simultaneous (A:  $N=12$ , B:  $N=13$ , C:  $N=12$ ) and open squares for alternating chirp patterns (A:  $N=16$ , B:  $N=15$ , C:  $N=15$ , see insets at top). Triangles and diamonds in A–C as in Fig. 2B–D. Insets at top refer to stimulus presentation for simultaneous and alternating chirp patterns, grey bars indicate the direction of turning responses as plotted in A–C. (D,E) Linear regressions between responses of choice tests with intensity difference and choice tests without intensity differences (data from Fig. 2B–D) for D simultaneous and E alternating chirp patterns. Data points are only shown for choice tests with an attractive reference pattern of 25 pulses s<sup>-1</sup>. (F) Linear regression between responses in choice test with and without intensity differences, data replotted from Doherty (1985). The reference pattern was attenuated by 5, 10, 15 or 20 dB relative to the alternative pattern. Preference was quantified as the percentage of females who tracked the reference or the alternative pattern. In F 100% is referenced as 1.0. pulses s<sup>-1</sup>.  $\Delta I$ , difference in intensity.

females were tested with four stimulus series in a choice paradigm, in which a stimulus with an attractive pulse rate of 28 pulses s<sup>-1</sup> was presented from one speaker and a tone stimulus from the opposite speaker (see inset to the right of Fig. 5). The chirp rate was kept at 2 chirps s<sup>-1</sup> as before, and stimuli were presented in an alternating as well as a simultaneous fashion. In the test series shown in Fig. 5A, the sound intensity for the tone was increased from 68 to 86 dB SPL in steps of 3 dB, whereas the intensity for the attractive pulse rate remained constant at 80 dB SPL. At low tone intensities, the pulse rate stimulus was clearly preferred, but at higher tone intensities, the turning strength was strongly reduced for both alternating and simultaneous chirp presentation (Fig. 5A). A second, similar pair of test series was also performed in which the intensity of the tone was kept constant at 80 dB SPL and the intensity of the pulse rate stimulus was increased from 68 to 86 dB SPL. The results of these tests mirrored those of Fig. 5A, except that the turning response for the pulse rate stimulus increased with intensity (not shown). From these two pairs of choice tests, the turning responses due to intensity differences relative to 80 dB SPL

were determined (Fig. 5B). The response strength for tone and pulse stimulus is also given, if presented in a no-choice test at 80 dB SPL (left of Fig. 5B). In all choice tests at equal intensity of pattern and tone stimulus, the pattern was preferred (Fig. 5B). For softer tones (pattern 3 dB or 6 dB louder than the tone), the preference for the pattern increased close to the response level observed, when the pulse rate stimulus was presented in a no-choice test (Fig. 5B). For louder tones (intensity of the pattern –3 dB or –6 dB relative to the tone), the preference decreased (Fig. 5B). At a 3 dB louder tone, females still preferred the attractive pattern, but at a 6 dB louder tone, females showed no preference. The turning responses during the simultaneous playback were slightly lower than during the alternating playback (Fig. 5B) indicative of a masking effect of the tone stimulus.

To examine whether the model with bilateral recognizers would also account for the responses with a tone stimulus when the pattern was 6 dB softer than the tone (Fig. 5B), the predicted responses were calculated as above (Fig. 4G,H). Values for pattern attractiveness were derived from the test situation without an



**Fig. 4. Linear regression between predicted and experimentally obtained responses for simultaneous and alternating chirp patterns.**

(A,B) Regression between predicted and experimentally obtained responses during choice tests without intensity difference ( $\Delta I_{0\text{dB}}$ ; Fig. 2). The predicted responses were calculated with the responses during the no-choice paradigm. (C,D) As in A and B, but the predicted responses were calculated with the data from the choice test in Fig. 2B. (E,F) Regression between predicted and experimentally obtained responses during choice tests as in C,D with different intensities ( $\Delta I_{6\text{dB}}$ ). (G,H) Overall linear regression for all choice tests from C,E and D,F. See text for the calculation of predicted responses.

intensity difference in Fig. 5B. To determine  $\Delta I_{6\text{dB}}$ , we used the regression formula of the mean regression of Fig. 3D,E and calculated the distance of the regression function to the angle bisector. For this dataset, the model predicted significantly higher

turning responses than obtained during the choice tests (diamonds in Fig. 5B), which indicated that intensity values contributed by tone pulses were not accurately accounted for.

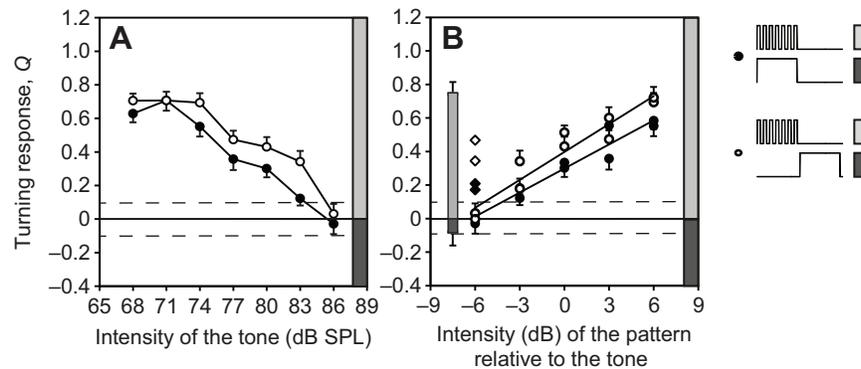
## DISCUSSION

### Signal representation and cues for decision making

Sensory computations for decision making require some form of internal representation of signals. In situations with multiple sound sources, insects face the potential problem of masking interference by conspecific and heterospecific signals originating from different distances (Pollack, 2000). Therefore, the quality of a given signal is not necessarily positively correlated with intensity. In addition, further sound sources such as abiotic (Brumm and Slabbekoom, 2005; Reichert and Ronacher, 2015) or even anthropogenic noise (Lampe et al., 2012, 2014; Schmidt et al., 2014) may impede signal representation and recognition. Crickets, bushcrickets and grasshoppers are known to employ several processing tools to reduce the detrimental effects of masking and noise (Einhäupl et al., 2011; Schmidt and Römer, 2011; Neuhofer and Ronacher, 2012; Hildebrandt et al., 2015), most prominently by forward masking, selective attention, formation of acoustic hemispheres and stream segregation (Pollack, 1986; Schul and Sheridan, 2006; Triplehorn and Schul, 2009; Schmidt and Römer, 2011). Our experiments support the observations from former studies (Pollack, 1986; Doherty, 1985), which demonstrated that female crickets are able to choose between two patterns and express a clear phonotactic preference irrespective of simultaneous or alternating stimulus situation or intensity differences (Figs 2, 3 and 4). Our data in Fig. 2 are consistent with previous observations by Wendler (1989) and Stabel et al. (1989) as females turn towards the side with the more attractive pattern at equal intensities. Moreover, our results of the experiments with the tone burst from one side also confirm their observations, although their experimental design was different, as the attractive pattern was presented from above. Nevertheless, as in our experiments, females turned away from the tone signal (Fig. 5).

The choice behaviour of female crickets was accurately predicted by a computational model that simply compared the auditory inputs from both sides (Fig. 4). These observations suggest that decision making by female crickets is based on separate, bilaterally organized recognizers, as suggested previously (Pollack, 1986; Doherty, 1991). This view is also supported by the bilateral organization of neuronal elements for song recognition in the cricket's brain (Kostarakos and Hedwig, 2012, 2015). A direct comparison of two or more sound signals could conceivably result in a higher selectivity than in a no-choice situation, which would be evident in a narrower tuning of a preference function (Fig. 1A,B; Popov and Shuvalov, 1977; Doherty, 1985; Pollack, 1986). However, at equal intensities of both stimuli female crickets exhibited wider preference functions in a choice paradigm (Fig. 2, cf. Fig. 1A,B). The model calculations suggest that the observed reduction in selectivity is a direct outcome of the comparative evaluation of acoustic signals from both sides, wherefore the observed turning responses are not as strong as predicted from the no-choice paradigm (Fig. 4A,B).

In our study, pulse rate was varied as a cue for pattern quality independent of signal intensity. Female responses revealed that both cues were integrated for signal evaluation and turning response (Figs 3 and 4). Also, female responses were reliably predicted by a model representing the bilaterally organized recognizers in the cricket's brain (Fig. 4). Although one might have expected a constant shift of the turning response at a constant directional cue, as given by an intensity difference of 6 dB between signals from two sides, this was not observed (Figs 2 and 3). Indeed, this



**Fig. 5. Turning responses in choice experiments with an attractive pattern and a tone stimulus, presented simultaneously or in an alternating fashion.** Attractive pattern was 28 pulses  $s^{-1}$ . Tone stimulus was presented simultaneously (filled circles,  $N=17-18$ ) or in an alternating fashion (unfilled circles,  $N=18-19$ ). The intensity of either the pattern or the tone stimulus was held constant at 80 dB SPL while the intensity of the alternative pattern was varied from 68 to 86 dB SPL in 3 dB steps (overall four test series). (A) Example of preference functions where the intensity of the pulse pattern was held constant at 80 dB SPL; the intensity of the tone stimulus was increased from 68 to 86 dB SPL. (B) Female responses at identical intensity differences between pulse pattern and tone stimulus, data extracted from four test series relative to 80 dB SPL. Female responses from no-choice paradigms are given by shaded bars for the pulse pattern (grey,  $N=16$ ) and tone stimulus (dark,  $N=12$ ). Model predictions for a test situation with an intensity difference of 6 dB are shown by diamonds. Insets on the right illustrate presentations of simultaneous and alternating stimuli.

phenomenon is already evident in the data of Doherty (1985) over a range of intensity differences up to 20 dB, if tracking responses of females on a Kramer treadmill are replotted (Fig. 3F). Therefore, the observed widening of the preference function for pulse rate from a no-choice to a choice paradigm (Fig. 2A,B) was counteracted, if intensity differences were available as a further cue (Figs 2 and 3). These observations imply that the influence of intensity differences on the turning response was not linear, but depended on the quality of the sound pattern (Figs 1B,D and Fig. 3D,E): for patterns with high attractiveness, the intensity difference was weighted more strongly than for patterns with low attractiveness.

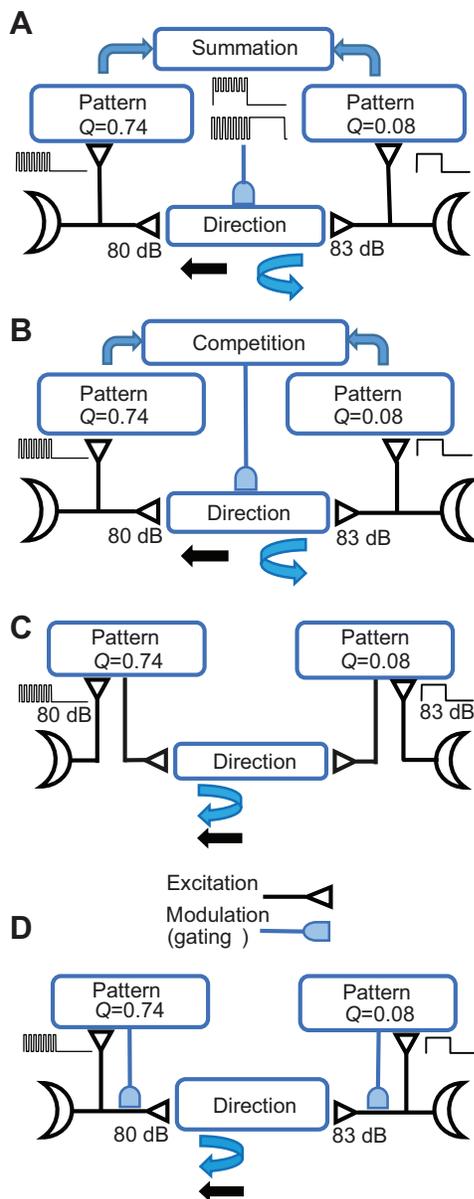
The observed integration of quality and intensity cues during sensory processing therefore required a weighting function that attenuates intensity difference and thus turning responses for unattractive sound signals (Fig. 3; Doherty, 1985). If, in our simple model, both cues were considered appropriately a good prediction of female preferences and turning responses was obtained (Fig. 4). However, for our experiments with a tone stimulus we obtained much higher predicted responses than were observed experimentally (Fig. 5). Although the peak intensity of the tone was correctly described by sound intensity in dB SPL, this is not the case for the sound energy. The sound energy of the tone stimulus can be obtained by integration of sound intensity over the whole duration of the tone (Gollisch et al., 2002). Therefore, the stimulus energy of the tone stimulus was almost twice as high as the stimulus energy of a pattern built from pulses and pauses, if presented at equal peak intensity. If stimulus energy rather than peak intensity is the relevant cue for integration by sensory neurons (Gollisch et al., 2002), the impact of intensity differences will be underestimated by our present model for tone stimuli with high sound energy. Nevertheless, the computational model demonstrated that the decision of a female can be explained by a simple weighting process for pattern quality and intensity. However differences in pattern quality are weighted more during the decision process than differences in pattern intensity.

In the field, female crickets will profit from such a computational scheme, as responses to conspecific males with high-quality patterns will be stronger than responses to heterospecific singers producing songs at different pulse rates. Arena and outdoor studies also revealed that differences in SPL are relevant for female

decisions; however, larger differences in intensity were necessary for a significant choice than in experiments on a trackball system (Hirtenlehner and Römer, 2014). This may be due to the propagation of signals parallel to the ground as Kostarakos and Römer (2010) reported a discontinuous intensity gradient of an acoustic signal over distances between 1 to 16 m. Given these unpredictable intensity gradients, it may be advantageous for a female to weigh pattern quality higher than intensity differences for decision making. It has also been shown that decisions are based more on song quality than intensity for other species that use acoustic communication for mate attraction. Gerhardt et al. (1996) found that female *Hyla versicolor* and *Hyla chrysoscelis* preferred a call with high pulse number over a call with low pulse number and high call rates over low call rates even though the sound intensity of the preferred stimuli was 6 dB less than that of the alternative.

#### Serial or parallel processing of recognition and localization

Positive phonotaxis requires both the recognition and localization of conspecific signals. For insects, scenarios of parallel and serial processing of pattern recognition and localization have both been discussed in the past. In grasshoppers, the cues for recognition and localization are evidently processed independently and in parallel (von Helversen, 1984; von Helversen and von Helversen, 1995). For evaluation of the song pattern, the inputs from both ears are summed internally to form a composite pattern, which is independent of direction. Intensity differences between both sides determine the turning direction (Fig. 6A, von Helversen and von Helversen, 1995). In the present tests with crickets, an internal summation would result in less-attractive patterns and thus reduced turning responses, especially if a tone stimulus is presented from one side (Fig. 6A). Furthermore, present evidence in crickets suggests a separate representation of acoustic signals from two sides (Fig. 4, Pollack, 1986), a view that is supported by a bilateral organization of neurons selective for pulse rate (Kostarakos and Hedwig, 2012). Parallel processing always predicts turns towards the louder side, if an attractive signal is presented (Fig. 6A); however, this was not observed here (Figs 2, 3 and 5) nor by Doherty (1985). In our experiments, the sound intensity of the tone stimulus with a difference of +3 dB to the pulsed pattern was even twice as loud (+6 dB), if stimulus energy was considered.



**Fig. 6. Schemes of auditory processing of pattern recognition and direction from auditory input.** Parallel processing with internal (A) summation and (B) competition of patterns. (C) Serial processing. (D) Parallel wiring network, but serial computation by modulation. Numbers in A–D refer to turning responses ( $Q$ ) for pulsed patterns or tone stimuli (see pattern insets) as presented in Fig. 5, intensities are given as dB. Central patterns in A refer to pattern representation after summation. Curved arrows show responses predicted by network topology, black arrows refer to observed responses by female crickets. Wiring symbols given as inset above D refer to excitatory or modulatory connections. See text for details.

In an alternative scenario of parallel processing, two bilaterally separate recognizers could compete to determine signal attractiveness (Fig. 6B), but the directional decision would still predict a turn towards the louder side, contrary to observations in crickets (Fig. 5; Doherty, 1985; Wendler, 1989). Both scenarios of parallel processing can be excluded for crickets, as they are incompatible with the observed turns towards the softer but more-attractive signal (Fig. 5). Indeed, both implementations of parallel processing are inferior for decision making in a choice situation, because pattern recognition is independent of the

localization process. In this situation, it is impossible for a female cricket to choose a male with a high-quality pattern to achieve maximal reproductive success. The observed implementation of parallel processing and internal summation in grasshoppers appears to be optimized for high signal to noise ratios of pattern representation in no-choice situations, possibly enhanced by their limited active space of signalling (Lang, 2000). No-choice situations may then be common for the detection of a single singing male or female, or even for an individual predator, such as a bat. The observed processing scheme may therefore rather reflect an old evolutionary property of an auditory pathway as evidenced by its conserved neuronal elements (Neuhofer et al., 2008).

In the schemes of serial processing proposed for crickets and bushcrickets, the inputs of both ears remain separated and the patterns are recognized by two bilaterally paired neuronal networks (Doherty, 1985; Pollack, 1986, 1988; Stabel et al., 1989; Wendler, 1989; Schul et al., 1998; Römer and Krusch, 2000). Intensity differences, but also quality differences, between both sides will then determine the turning direction (Stabel et al., 1989). For our model prediction, both pattern quality and intensity values were used. In the simplest form, both cues could be evaluated by two bilateral recognizers as shown in Fig. 6C, to obtain the correct turning responses. However, this model would assume equal weights – or a fixed ratio – between signal quality and intensity, which was not observed (Fig. 3D,E).

Instead, the strength of the intensity cue was modulated by signal attractiveness and therefore the turning response was not linearly dependent on intensity differences (Fig. 3). In principle, such a modulation could be implemented within the recognition network in the cricket's brain; however, present evidence for an acoustic steering reflex clearly makes a peripheral realization more likely (Fig. 6D; Hedwig and Poulet, 2004; see also Doherty, 1991). In this latter scenario, the topology of the processing network is parallel as in Fig. 6A,B, but the processing scheme corresponds to a serial operation because the directional decision is modulated by the pattern recognition network. Thus localization is not independent of pattern recognition. Earlier experiments confronting females with choice situations are consistent with our results and the scheme of serial processing because females showed either no preference for one of two equal patterns presented at the same sound intensity, or turned towards the louder of two patterns (Doherty, 1985; Weber and Thorson, 1988; Wendler, 1989; Stabel et al., 1989).

In contrast to the schemes of parallel processing (Fig. 6A,B), serial processing of recognition and localization is advantageous for female crickets as they can make a decision for the side where a more attractive song is present. Female crickets achieve this even though they form acoustic hemispheres in their auditory pathway and do not appear to perform a resolved auditory scene analysis like many other animals (MacDougall-Shackleton et al., 1998; Moss and Surlykke, 2001; Hulse, 2002) and also humans (Bregman, 1990, 1993). In conclusion, serial processing enables females to increase their mating success because their response to conspecific singers with higher-quality songs is stronger.

## MATERIALS AND METHODS

### Animals

Experiments were performed with virgin *Gryllus bimaculatus* (DeGeer 1773), which were taken as last instars from stock or were obtained from a commercial supplier (Das Futterhaus, Berlin, Germany). Females were

raised to adulthood in isolation from males and were tested from 1 week after their final molt.

### Phonotaxis experiments

Behavioural tests were performed on a trackball system (in principle as described by Hedwig and Poulet, 2004) placed in a wooden box (50×50×50 cm) lined with sound-absorbing foam to reduce interference with external sounds and echoes. Experiments were conducted in the dark at 24.6±2.6°C. The females were tethered with wax to a metal pin on their pronotum and were placed in a natural walking position on top of a hollow Styrofoam ball (diameter 10 cm, weight 1.2–1.8 g). The trackball fitted into a half sphere which contained holes for a constant air supply. Thus the trackball was lifted and free to rotate with minimal friction. The longitudinal (*X*-rotation) and lateral (*Y*-rotation) movements of the trackball were monitored by either a single optical sensor (Agilent ADNS-2051) at the bottom of the half-sphere or by two sensors (ADNS-5050, Avago Technologies) with a focussing lens positioned laterally at an angle of 90 deg. The sensor signal was either sampled at 10 kHz per channel (ADNS-2051) via an A/D-board (PCI-6221, National Instruments, TX, USA) or transmitted via a handshaking protocol using digital lines (ADNS-5050). Software was programmed in LabView 7.1 or 9 (National Instruments, TX, USA). Sound stimuli were presented via two loudspeakers (Piezo Horn Tweeter, PH8, Conrad Electronics, SE, Germany), which were positioned at a distance of 25 cm frontal to the cricket and each at an angle of 45 deg to the animal's length axis. The females had a certain degree of freedom to orient their body axis towards the loudspeaker just up to facing the loudspeaker, but a complete rotation around the horizontal axis was not possible.

### Song models and test procedures

Song models were generated digitally with LabView Software (National Instruments, TX, USA). A given signal envelope was multiplied with a sine wave (4.5 kHz). Sound pulses had rise and fall times of 1 ms. The digital signals were converted to analogue signals via a D/A-board (update rate 100 kHz, PCI 6221, National Instruments, TX, USA) and transferred to a digitally controlled attenuator (PA5, Tucker Davis Technologies, FL, USA), amplified (Raveland, Conrad Electronics, SE, Germany) and broadcast via one of two or both loudspeakers. The speakers were calibrated with a condenser microphone (Brüel & Kjaer type 4133, Naerum, Denmark) and a measuring amplifier (Brüel & Kjaer type 2231) relative to  $2 \times 10^{-5}$  Pa, fast reading, at the walking position of the female. For calibration, a continuous tone with 4.5 kHz, played back for 1 s, was used. Test signals during experiments were presented at 80 dB SPL, unless otherwise specified.

The stimuli were presented in groups of pulses mimicking a chirp of the song of *G. bimaculatus* or as a tone with the same duration as a chirp. The pulse duty cycle of all pulsed signals was kept constant at 0.5, and the chirp rate was a constant 2 chirps  $s^{-1}$ . First a no-choice reference function for varying pulse rates at 62.5, 45.5, 35.7, 29.4, 25.0, 21.7, 19.2 and 17.2 pulses  $s^{-1}$ , was measured. In the choice tests these pulse rates were presented against a reference pattern with either 25.0, 35.7 or 19.2 pulses  $s^{-1}$  as a simultaneous or alternating chirp pattern first at equal sound intensity and second with the reference patterns broadcast 6 dB softer. All test signals were presented for 60 s. At the beginning and the end of a test session, the female cricket was exposed to an attractive song signal to obtain a reference value for test signals and to control for possible changes in motivation during the session (positive control). Each session also contained a presentation of a continuous unmodulated tone at 4.5 kHz and a silent interval of 60 s to monitor baseline activity to control for motivation and selectivity of female responses (negative control). All test sessions contained the positive and negative controls and 7–8 test stimuli. The presentation of the test signals was randomized and between each presentation from a loudspeaker, a silent interval of 10 s was maintained to minimize possible carry-over effects from the previous signal. Each test signal was presented from both speakers and the mean of both presentations was used to calculate the turning strength. A complete test session lasted 24–28 min.

### Data evaluation

For evaluation of female preference, the turning response was calculated according to the following formula:

$$Q = \frac{Y}{Y_{\max}} \quad (1)$$

where  $Q$  is the normalized turning response,  $Y$  is the measured lateral deviation for a test stimulus and  $Y_{\max}$  is the maximum lateral deviation to the positive controls and test stimuli. For signal presentations from both loudspeakers, a positive value indicated a turning response towards the reference pattern marked by the light grey bar in the diagrams and a negative value indicated a preference for the alternative pattern presented from the opposite loudspeaker marked by a dark grey bar in the diagrams (Figs 2, 3 and 5). A turning response of 0 meant that the females preferred neither pattern over the other. The nearer the turning response was at 1.0 or  $-1.0$  the more attractive was the respective pattern for the females. In our experiments, the turning responses did not reach values of 1.0 or  $-1.0$  as the chirp rate of all used stimuli was 2 chirps  $s^{-1}$ , which was not in the range of maximal attractiveness (Grobe et al., 2012). We used this longer chirp period because it allowed us to present test patterns with different pulse rates without overlap in the alternating stimulus paradigm. Females were excluded from the analysis if the response to the positive controls was below 0.5 or if they exhibited high turning responses during the negative controls. Data from 12 to 27 females per test session are given as mean values with standard error in the figures. In addition, the turning responses to the test stimuli were compared with the mean response to the initial and final negative control (*t*-test). In the diagrams, all data points above the upper black dashed line and below the lower black dashed line are significantly different from the mean of the negative controls, indicating a preference for one of the presented patterns. All data points between the two dashed lines were not significantly different from the mean of the negative controls, indicating low attractiveness of the pattern due to random orientation in single stimuli experiments or equal attractiveness of the patterns in a choice situation. For comparison of the slope of the regression function calculated for choice tests with an attractive reference pattern of 25 pulses  $s^{-1}$  in Figs 2E,F and 3D,E and the regression functions from choice tests with a less attractive reference pattern, a *t*-test for the difference of two slopes was used according to the following formula:

$$t = \frac{b_1 - b_2}{\sqrt{S_{b_1}^2 + S_{b_2}^2}}, df = n_1 + n_2 - 4, \quad (2)$$

where  $b_1$  and  $b_2$  are the slopes of regression lines 1 and 2,  $S_{b_1}$  and  $S_{b_2}$  are the standard errors and  $n_1$  and  $n_2$  are the sample sizes for lines 1 and 2.

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### Competing interests

The authors declare no competing or financial interests.

### Author contributions

The experiments were designed by E.G. and R.M.H. E.G. and J.K. performed the experiments and did the analysis. E.G. and R.M.H. wrote the paper.

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