



A gain control mechanism governs the weighting of acoustic signal intensity and attractiveness during female decisions



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In many acoustical communication systems song signals serve for mate selection. Animals thus need to make a decision about which is the best mating partner in a choice situation by integrating the cues of the available signals. In female crickets, choice behaviour is based on the attractiveness of the temporal pattern of a male's calling song and on its intensity. Signal intensity is affected by both sound amplitude and sound energy as given by the amplitude modulation. Here we targeted the psychometric functions that relate these physical cues to sensory perception in female crickets, *Gryllus bimaculatus*. First, no-choice tests were conducted to examine the response functions for pattern attractiveness and intensity. Second, we systematically varied pattern attractiveness and sound amplitude or sound energy of two competing signals which were presented from opposite sides in a choice situation. To examine the relative contribution of both cues to female choice behaviour an equivalence function for pattern attractiveness and signal intensity was derived which indicated at which levels both cues compensated for each other. The psychometric data and the equivalence function revealed that for patterns of high attractiveness there was a strong impact of even small intensity differences, whereas for patterns with low attractiveness large intensity differences were required to influence female decisions. Thus the integration of pattern attractiveness and intensity is provided by a gain control mechanism that reflects a nonlinear weighting of intensity differences by pattern attractiveness.

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From an evolutionary point of view, decision making should be economical to utilize available resources best and to maximize benefits at a given energy expenditure. The bases of decision making are the sensory capacities and processing schemes, which become particularly relevant if multiple cues have to be integrated for a robust representation as the basis for the best choice (Barlow, 1961; Stevens, 2008). Commonly, psychometric functions are examined as these capture the sensory basis of decision making by relating a physical stimulus to sensory perception (Gleich, Hamann, Kittel, Klump, & Strutz, 2006).

Much attention has been paid to economical decision making with respect to optimal foraging and nutrition (Monteiro, Vasconcelos, & Kacelnik, 2013; Nachev, Thomson, & Winter, 2013; Nachev & Winter, 2012; Shafir, Waite, & Smith, 2002; Shafir & Yehonatan, 2014; Waite, 2001). Communication systems present a similar challenge in a choice situation, yet here a decision about which individual is a suitable mating partner has to be made. In

many animals, song signals serve for mate selection (Catchpole & Slater, 1995; Gerhardt, 2001; Gerhardt & Huber, 2002; Searcy & Andersson, 1986). Commonly several senders transmit multicomponent information at the same time and the receiver has to evaluate this information during decision making which requires neuronal networks tuned to the species-specific song and processing mechanisms that extract and integrate the relevant information (Gerhardt & Huber, 2002). Acoustic communication in crickets is a case in point. Only male crickets produce calling songs and sexually receptive females respond to these songs by phonotaxis (Popov, Shuvalov, & Markovich, 1976; Regen, 1913). Females therefore have to recognize and localize the species-specific song (Pollack, 2000) and are faced with choosing one of several males singing at the same time (Simmons, 1988).

In this study we aimed to determine the psychometric functions for acoustic signals relevant for mate choice in crickets. For their decision crickets evidently integrate two cues: signal attractiveness (given by temporal parameters, e.g. pulse rate) and signal intensity (Doherty, 1985; Gabel, Kuntze, & Hennig, 2015; Hirtenlehner & Romer, 2014; Pollack, 1986; Popov & Shuvalov, 1977). These cues are not necessarily positively correlated, as an attractive singer may be perceived at a lower intensity by the female simply because it is

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further from the receiver. The auditory system of crickets is particularly good for analysing such issues as the neural basis of sensory processing is well investigated at the level of individual neurons, sensory processing schemes, signal recognition and sound localization (Gabel et al., 2015; Grobe, Rothbart, Hanschke, & Hennig, 2012; Hennig, 2009; Hennig & Weber, 1997; Huber & Thorson, 1985; Pollack, 1986, 1988; Schildberger, 1984; Schöneich, Kostarakos, & Hedwig, 2015; Stabel, Wendler, & Scharstein, 1989; Wendler, 1989; Wohlers & Huber, 1978). As only a limited number of auditory neurons are involved in the sensory processing chain forming the basis for choice behaviour, decision making is constrained and simple but optimal solutions may be expected.

We evaluated no-choice and choice behaviour for conditions of different signal attractiveness and intensity as differences in both will determine the turning direction of the female (Gabel et al., 2015; Poulet & Hedwig, 2005; Stabel et al., 1989; Wendler, 1989). To create differences in pattern attractiveness we selected the pulse rate of acoustic signals as this cue is generally seen as the most important for species recognition (Gerhardt & Huber, 2002). For differences in signal intensity, both sound amplitude as given by the peak level and sound energy over time as given by the modulation pattern or modulation depth were changed. The robustness of female preference for the more attractive of two signals was tested over a wide range of differences in sound amplitude (Doherty, 1985; Gabel et al., 2015). The influence of sound energy on female choice behaviour was also examined by varying the modulation depth of the pulse pauses of one of two competing signals. If sound energy is a relevant cue for integration in sensory neurons (Gabel et al., 2015; Gollisch, Schütze, Benda, & Herz, 2002) a distinct shift of female preferences towards the patterns with lower modulation depth and therefore higher sound energy is expected, similar to the choice situation between patterns with different sound amplitudes. However, a change in modulation depth of the pulse pauses will also affect pattern attractiveness (Hennig, 2009). Finally, we aimed to construct an equivalence function which quantifies the relationship between the internal representations of two perceptual parameters (Ronacher, 1979, 1980; Terhardt, 1968). Thus the equivalence function will measure the relative contribution of pattern attractiveness and of sound intensity to decision making in crickets.

METHODS

Animals

Gryllus bimaculatus females were taken as last instars from stock or were obtained from a commercial supplier (Das Futterhaus, Berlin, Germany) and were raised to adulthood in isolation from males. The experimental phase started 1 week after their final moult. During this phase each female was kept separately in a box with water-storing gel and food ad libitum and an egg box as shelter at natural day and night rhythm. After the experimental phase females were kept together in 19-litre containers under the same conditions. The experiments comply with the 'Principles of animal care', publication No. 86 23, revised 1985 of the National Institutes of Health, and also with the current laws of Germany.

Song Models and Phonotaxis Experiments

Behavioural experiments were performed on a trackball system (Dahmen, 1980), similar to the set-up used by Hedwig and Poulet (2004) at 23.7 ± 0.8 °C. A hollow Styrofoam ball (diameter 10 cm, weight 1.2–1.8 gm), placed in a dark anechoic wooden box and fitting into a half sphere, was lifted by a constant air stream to rotate with minimal friction. Females, tethered to a metal pin, were

placed in a natural walking position on top of the ball. The longitudinal (X-rotation) and lateral (Y-rotation) movements of the females were monitored by two sensors (ADS-500, Avago Technologies, San Jose, CA, U.S.A.) with focusing lens positioned laterally at an angle of 90 degrees or a single optical sensor (Agilent ADNS-2051, Agilent, Santa Clara, U.S.A.) at the bottom of the half sphere. Sensor signals were sampled at 10 kHz per channel (ADNS-2051) via an A/D board (PCI-6221, National Instruments, Austin, TX, U.S.A.) or transmitted via a handshaking protocol using digital lines (ADNS-5050). Two loudspeakers (Piezo Horn Tweeter, PH8, Conrad Electronics, SE, Hirschau, Germany) at a distance of 25 cm frontal to the cricket were each placed at an angle of 45° to the female's length axis and at an angle of 90° to each other. The females could not rotate completely around their horizontal axis but were able to orient towards the loudspeakers until they just faced them.

For song models a given signal envelope with 1 ms rise and fall times was multiplied with a sine wave (4.5 kHz) using LabView Software (National Instruments, TX, U.S.A.). During a test the signals were broadcast via one of two (no-choice) or both loudspeakers (choice tests). The digital sound signals were converted to analogue signals with a D/A-board (update rate 100 kHz, PCI 6221, National Instruments), adjusted to a chosen peak amplitude by a digital controlled attenuator (PA5, Tucker Davis Technologies, Alachua, FL, U.S.A.) and amplified (Raveland, Conrad Electronics). Both speakers were calibrated with a measuring amplifier (Brüel & Kjær type 2231, Nærum, Denmark) and a condenser microphone (Brüel & Kjær type 4133) relative to 2×10^{-5} Pa, fast reading, at the walking position of the female using a continuous tone of 1 s with a carrier frequency of 4.5 kHz.

The stimuli contained groups of pulses mimicking a chirp of male *G. bimaculatus*. The chirp rate was kept constant at 3 chirps/s and the pulse duty cycle of all pulsed stimuli was kept constant at 0.5. In choice tests chirps were presented in an alternating fashion. Each test series contained seven test stimuli, two positive and two negative controls and lasted for 24 min. The acoustic stimuli were presented for 45 or 60 s from each loudspeaker consecutively. The stimuli sequence during a test session was randomized except the positive and negative controls. One positive control (similar to the male's calling song, 25 pulses/s, 3 chirps/s) was given at the beginning and one at the end of a test series in order to control for a change in motivation of the female. Similarly, one negative control was given at the beginning and one at the end of a test series. The first negative control included the presentation of a silent interval in order to monitor baseline activity and the second negative control included the presentation of a continuous unmodulated tone at 4.5 kHz to control for female selectivity. Between the presentation of each control or test pattern a break of 10 s was maintained to minimize possible carryover effects from the previous signal.

Data Evaluation

To evaluate female preferences, we used the overall steering direction or lateral deviation (Y-rotation) of a female measured over the complete time window of stimulus presentation. This lateral deviation or turning response of a female during signal presentation towards the loudspeakers was normalized to the positive controls such that response values between 0 and 1 were obtained. In no-choice tests, positive values indicated a preference for the presented pattern whereas values around zero indicated no preference due to random orientation. In the choice tests, positive values indicated a preference for the reference pattern and negative values indicated a preference for the alternative pattern from the opposite speaker. In choice situations, values around zero indicate no preferred orientation to either loudspeaker due to equal

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