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Review Article

Processing of acoustic signals in grasshoppers – A neuroethological approach towards female choice

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ABSTRACT

Acoustic communication is a major factor for mate attraction in many grasshopper species and thus plays a vital role in a grasshopper's life. First of all, the recognition of the species-specific sound patterns is crucial for preventing hybridization with other species, which would result in a drastic fitness loss. In addition, there is evidence that females are choosy with respect to conspecific males and prefer or reject the songs of some individuals, thereby exerting a sexual selection on males. Remarkably, the preferences of females are preserved even under masking noise. To discriminate between the basically similar signals of conspecifics is obviously a challenge for small nervous systems. We therefore ask how the acoustic signals are processed and represented in the grasshopper's nervous system, to allow for a fine discrimination and assessment of individual songs. The discrimination of similar signals may be impeded not only by signal masking due to external noise sources, but also by intrinsic noise due to the inherent variability of spike trains. Using a spike train metric we could estimate how well, in principle, the songs of different individuals can be discriminated on the basis of neuronal responses, and found a remarkable potential for discrimination performance at the first stage, but not on higher stages of the auditory pathway. Next, we ask which benefits a grasshopper female may earn from being choosy. New results, which revealed correlations between specific song features and the size and immunocompetence of the males, suggest that females may derive from acoustic signals clues about condition and health of the sending male. However, we observed substantial differences between the preference functions of individual females and it may be particularly rewarding to relate the variations in female preferences to individual differences in the responses of identified neurons.

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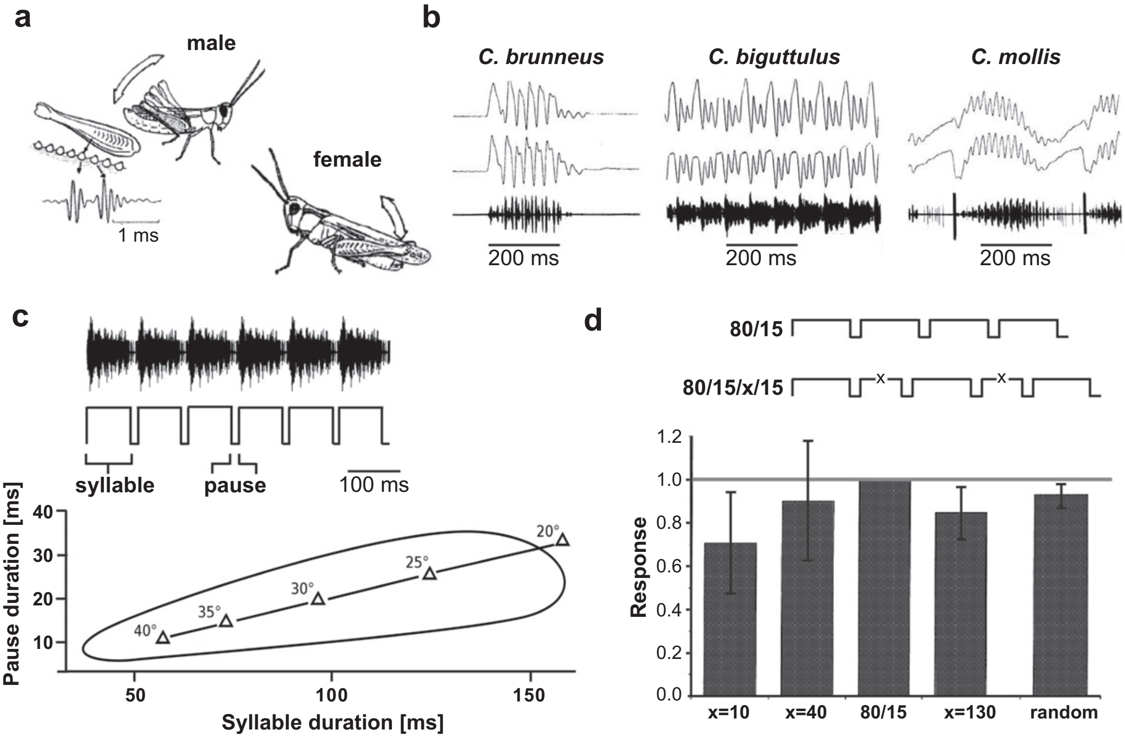

Fig. 1. (a) Singing male and female grasshopper (drawing: O. von Helversen). (b) Song of *Chorthippus brunneus* and details of *C. biguttulus* and *C. mollis* songs (from von Helversen and von Helversen, 1994); lower trace sound, upper traces movement pattern of the two hind legs. C. brunneus songs are short, ca 200–250 ms, while the songs of the other two species have durations of 2–5 s, and 15–30 s, respectively. (c) Enlarged detail of a *C. biguttulus* song and envelope of the song models used in behavioural tests; below: combinations of syllable-pause patterns accepted by females. Triangles show the syllable and pause durations observed in male songs produced at different temperatures between 20° and 40 °C. (Modified after von Helversen (1979; von Helversen and von Helversen, 1994)) (d) Responses of *C. biguttulus* females to song models with changed rhythm (see envelopes). Insertion of sound pulses of varying duration *x* had small effect on the females' response probability (the data were normalized to the responses to the standard model of 80 ms syllables combined with 15 ms pauses). (a) from von Helversen and von Helversen, 1997; (b–d) combined and modified after von Helversen (1979), von Helversen and von Helversen (1994, 1998), by courtesy of Springer Science and Business Media and Elsevier.

1. Introduction

In this review we want to introduce and discuss grasshoppers as a model system for the processing of acoustic signals in the context of mate attraction and sexual selection. This system is particularly interesting since the recognition of the species-specific communication signals is of vital relevance in the life of grasshoppers: acoustic signals provide the major cues for species identification and are crucial to prevent hybridization between species. If the acoustic communication is experimentally prevented, hybridization may occur (von Helversen and von Helversen, 1975a,b). Thus, a high fitness premium is laid on the processing and correct recognition of acoustic signals. The neuronal processing is, however, not confined to species identification. Grasshopper females exert a sexual selection on males, by preferring or rejecting songs of individual conspecific males. This *female choice* entails the detection and discrimination of small variations of the species-specific song pattern. Obviously, this is a more demanding task with respect to signal processing than to accept conspecific songs and to avoid songs of different species – whose patterns usually differ considerably (see Fig. 1b).

There are three basic questions we have to consider in the context of female choice: (i) How are acoustic signals represented in the receiver's CNS, and how well can different signals be discriminated on the basis of variable spike trains? (ii) What features of a male's song make it attractive, and on which features do females rely for the discrimination between individual males? (iii) Do the songs contain information about the sender's quality and what aspects of quality can be inferred from specific song features?

1.1. Basic features of the communication system

Many grasshopper species rely primarily on acoustic signals to attract and to identify sexual partners. Gomphocerine grasshoppers usually produce their signals ("songs") by rhythmically moving a file on the hind legs against the forewings (Fig. 1a and b). Both the song production, i.e. the patterns of leg movements, as well as the song recognition are innate behaviours and differ between species (von Helversen and von Helversen, 1975a,b; Saldamando et al., 2005; Vedenina et al., 2007). To avoid hybridization with foreign species is probably the most important function of acoustic signalling (von Helversen, 1986; Stumpner and von Helversen, 1994; von Helversen and von Helversen, 1994; Safi et al., 2006). By experimentally preventing the song production of heterospecific males it was possible to induce related species to interbreed and to produce fertile hybrids (Perdeck, 1957; von Helversen and von Helversen, 1975a,b; Gottsberger and Mayer, 2007). Acoustic communication thus constitutes *the* major pregamic hybridization barrier, and has direct consequences for the animals' reproductive success (Kriegbaum and von Helversen, 1992; Tregenza et al., 2000). In addition, however, it may be important to extract from these signals clues about the quality of a potential mate (e.g. Anderson, 1994; Anderson and Simmons, 2006). This aspect is particularly relevant for females, whose large investment in eggs limits their reproductive output – males in these species contribute only "cheap" sperm and do not provide any resources for the offspring. Indeed, there is evidence that, for example, *Chorthippus biguttulus* females exhibit preferences for the songs of individual conspecific males, and thereby exert a *sexual selection* on males (Kriegbaum, 1989; Kriegbaum and von Helversen, 1992; Klappert

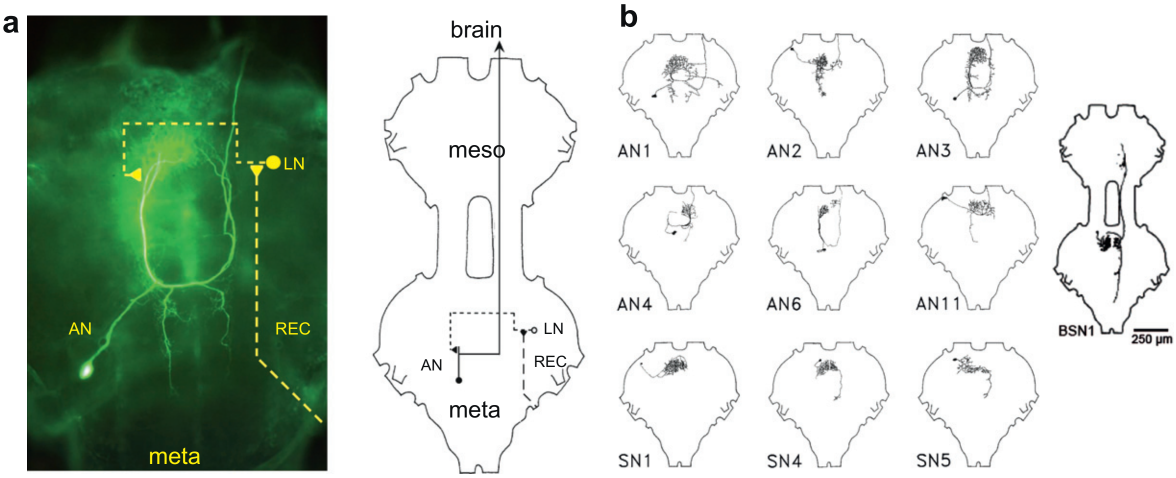

Fig. 2. (a) Scheme of the grasshoppers' auditory pathway. Meta, meso: metathoracic ganglion complex and mesothoracic ganglion; REC receptor axon, LN local neuron, AN Lucifer yellow staining of the ascending neuron AN3 (from Ronacher et al., 2008, with permission of the American Psychological Association. (b) morphologies of some local and ascending auditory neurons (courtesy of A. Stumpner). SN local segmental neurons, BSN1 bisegmental neuron, AN neurons with axon ascending to the brain (terminology after Römer and Marquart, 1984, and Stumpner and Ronacher, 1991).

and Reinhold, 2003, 2005; Einhäupl et al., 2011). Female preferences can be easily and automatically recorded in this species since females respond to the calling songs of males with a song of their own (von Helversen, 1972; von Helversen and von Helversen, 1997, see Fig. 1a).

1.2. The cues for song recognition reside in the temporal pattern of amplitude modulations

What cues do grasshoppers use to extract information about species identity or mate quality from acoustic signals? The ears of grasshoppers exhibit only a poorly developed frequency resolution (Römer, 1976; Stumpner and von Helversen, 2001; Hennig et al., 2004). Furthermore, the carrier frequency spectra of songs overlap considerably between species (Meyer and Elsner, 1996). A spectral analysis of the signal's frequency content is therefore not likely to contribute substantially to species identification. Indeed, the most obvious differences between the songs of different species reside in the species-specific patterns of amplitude modulations (see Fig. 1b, and Elsner, 1974; Elsner and Popov, 1978; von Helversen, 1986; Stumpner and von Helversen, 1994). Pioneering experiments performed on *Chorthippus biguttulus* by Dagmar von Helversen and many follow up studies showed that it is indeed the pattern of amplitude modulations, i.e. the sound envelope, which provides the major cues for species identification and mate choice (von Helversen, 1972, 1979; von Helversen and von Helversen, 1994, 1997; Stumpner and von Helversen, 1992). *C. biguttulus* females seem to evaluate a ratio between syllable duration and pause duration (see Fig. 1c, and von Helversen, 1972, 1979). By relating two temporal parameters that depend both on temperature, this species circumvents the recognition problems caused by the temperature induced time-warp of the songs, whereas other species can be led astray by temperature changes (Bauer and von Helversen, 1987). The club-shaped acceptance area of females of *C. biguttulus* in Fig. 1c thus encompasses the song features of males singing at different temperatures (von Helversen, 1979; Creutzig et al., 2009, 2010). Unexpectedly, the regularity of the song subunits is not essential, song models in which sound pulses of varying duration were inserted retained high attractiveness in spite of changed rhythm (Fig. 1d, von Helversen and von Helversen, 1998; Klappert and Reinhold, 2003). This latter result renders potential processing mechanisms, like a cross correlation with a stored internal template, unlikely (von Helversen and von Helversen, 1998).

1.3. Organization principles of the grasshopper's auditory pathway

The basic processing stages have been elucidated by lesion experiments (Ronacher et al., 1986) and by selective heating of different ganglia (Bauer and von Helversen, 1987). These experiments revealed that a first important stage of auditory processing is located within the metathoracic ganglion complex. In this ganglion a reciprocal inhibition occurs which improves the processing of sound direction (Ronacher et al., 1986; von Helversen, 1984; von Helversen and von Helversen, 1995). However, the final decision whether or not the sender belongs to the same species or about the quality of song signals takes place within the "brain", the supraoesophageal ganglion (Ronacher et al., 1986; Bauer and von Helversen, 1987).

The ears of grasshoppers are located on both sides of the first abdominal segment. About 60–80 auditory receptors, assembled in Müller's organ, are attached to the inside of each tympanum. The majority of receptors are tuned to the range between 4 and 7 kHz, only around 10–15 cells are tuned to high frequencies, above 15 kHz (Michelsen, 1971; Römer, 1976; Jacobs et al., 1999). The receptor axons enter the metathoracic ganglion complex where they arborize to form an auditory neuropil with local interneurons (Fig. 2). Several local neurons have been identified on the basis of their characteristic morphologies (Römer and Marquart, 1984; Stumpner and Ronacher, 1991; Stumpner et al., 1991). The basic organization seems to be a 3-layer feed-forward network: receptors connect to about 15 local neurons, but normally not directly to ascending neurons, and local neurons in turn pass information to ascending neurons that send their axons to the brain (Stumpner, 1988; Stumpner and Ronacher, 1991; Prier and Boyan, 2000; Vogel and Ronacher, 2007; Clemens et al., in press). Ascending neurons – so far approximately 20 unique types have been identified – thus provide the output of the metathoracic processing module, and the only information, which is available to the brain for the final decision of whether or not to accept a calling song. The manifold of types of ascending neuron in grasshoppers (Fig. 2b) stands in sharp contrast to the auditory system of crickets and many bushcrickets, for which in general only two to three neurons have been described that ascend to the brain (Wohlers and Huber, 1982; Römer et al., 1988; Schildberger, 1994; Stumpner and von Helversen, 2001; Hennig et al., 2004; Stumpner and Molina, 2006; Triblehorn and Schul, 2009). A possible consequence of this difference between the auditory systems of Caelifera and Ensifera is an expansion of the space of stimulus patterns which is potentially available for

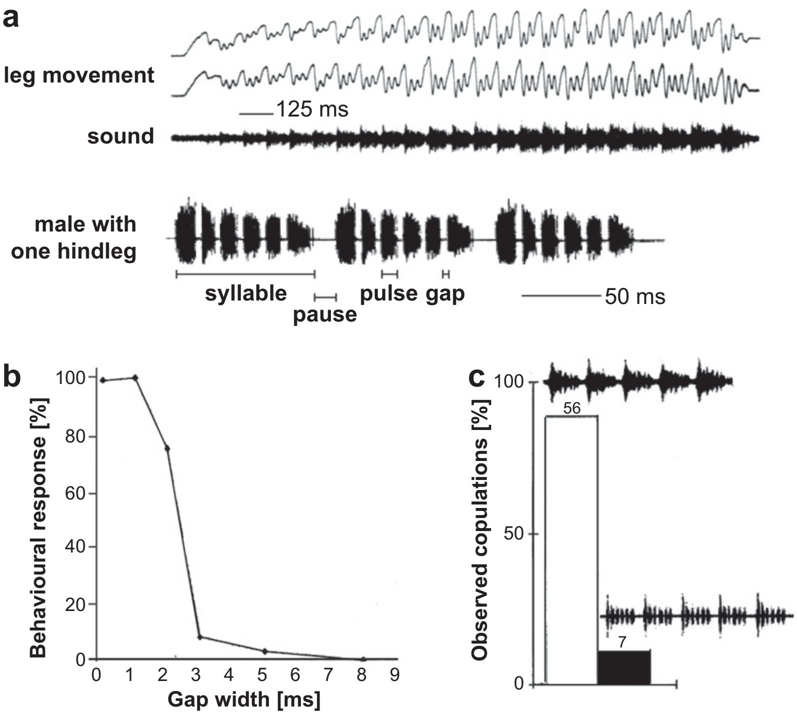

Fig. 3. (a) song of an intact *C. biguttulus* male and detail of the song of a male singing with only one hind leg; note the gaps within the syllables (combined from Ronacher et al., 2004 and Krahe et al., 2002 with permission from Springer Science and Business Media. (b) Response of a *C. biguttulus* female to song models with gaps, modified after von Helversen, 1972 with permission of Springer Science and Business Media (c) mating success of intact (open column) and impaired males (filled column); from Kriegbaum, 1989, with permission of Springer Science and Business Media.

grasshopper. The capacity of a more sophisticated analysis of sound patterns may have enabled the evolution of highly complex songs in acridid grasshoppers, while crickets and bushcrickets mostly produce rather simple song patterns (von Helversen, 1986; Stumpner and von Helversen, 1992; Gerhardt and Huber, 2002; Vedenina et al., 2007; for bushcricket songs see Heller, 1988; Schul, 1998; Bush et al., 2009). A similar observation has been reported for a different sensory modality, the electrosensory system, in which a more elaborate brain structure allows for the detection of more complex signals (Carlson et al., 2011).

2. Choosy females discriminate between songs of conspecific males

2.1. Behavioral evidence for female choice

As mentioned in the Introduction, grasshopper females show clear preferences for the songs of certain conspecific males, thereby exerting a sexual selection on males. A particularly striking example is a rigid rejection exerted by *C. biguttulus* females against the songs of impaired males, i.e. males that have lost one hind leg (von Helversen, 1972, 1979; Ronacher and Stumpner, 1988; von Helversen and von Helversen, 1997). The critical cue, on which rejection depends, are miniature gaps of only 2–4 ms duration that occur in the sound syllables of impaired males (Fig. 3a). Songs of *C. biguttulus* males are composed of 20–40 uniform sound syllables that are separated by pauses. Each syllable is produced by usually 3 up- and down-movements of the hind legs (see Figs. 1b, 3a). Since sound cannot be produced at the upper and lower reversal points of the leg movement, tiny gaps occur in the syllables if only one hind leg is left (lower trace in Fig. 3a). Females of this species do reject songs with “gappy” syllables and cease to respond if the gaps exceed 2–3 ms duration (see Fig. 3b and von Helversen, 1972, 1979). Intact males circumvent this problem by a slight phase shift between the movements of the two legs by which the gaps are masked (Elsner, 1974; Ronacher, 1989). The females’ gap detection response directly influences the mating success of males. In a large-scale field experiment the mating success of intact males has been compared to that of an equal number of males with only one hind leg, which therefore did produce songs with gaps (Kriegbaum, 1989). The latter group had a drastically reduced chance to mate (Fig. 3c).

So far, the majority of studies used artificial song models, in which several parameters could be varied independently (see e.g. von Helversen and von Helversen, 1997, 1998; Balakrishnan et al., 2001; Schmidt et al., 2008; Wittmann et al., 2011). In recent studies *C. biguttulus* females were found to exhibit also distinct preferences among a sample of songs of intact males (Klappert and Reinhold, 2003; Einhäupl et al., 2011; Stange, 2011; Stange and Ronacher, 2012). Due to the large number of different features present in natural songs it is not easy to pinpoint which cues determine the females’ decision (cf. Schmidt et al. 2008). Klappert and Reinhold (2003) found that in addition to the absence of gaps in the syllables the maximum amplitude (loudness) of songs contributed most to their attractiveness. Song attractiveness correlated significantly with the body condition of males, and was a good predictor for a male’s mating success (Klappert and Reinhold, 2003, 2005). Interestingly, the rhythm of syllables and pauses did not significantly influence attractiveness, which is in line with the experiments mentioned above, in which the regularity of artificial model songs was changed without affecting attractiveness (Fig. 1d).

2.2. Female preferences are preserved under masking noise

In a recent study we tried to reduce the number of distinguishing song features by rescaling natural songs to a constant subunit duration and filling the envelopes with the same natural carrier

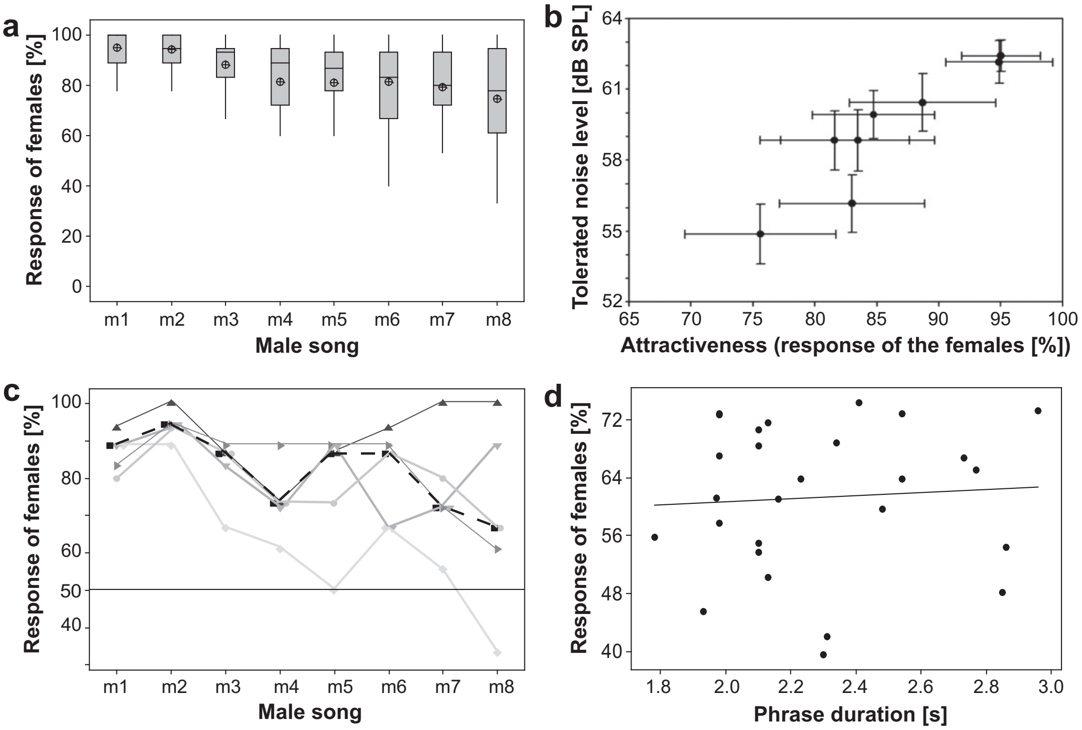

Fig. 4. (a) Responses of *C. biguttulus* females to songs of 8 males (m1–m8, arranged according to their attractiveness (the differences in attractiveness between songs were highly significant, $p < 0.001$, Friedman ANOVA, $N = 23$ females). Boxes indicate median and quartile ranges, whiskers 10 and 90 percentiles, crosses mean values. b) attractive songs are more robust against noise (abscissa: response of females to uncontaminated songs, ordinate: noise level at which the female's responses dropped to 50%, for details see Einhäupl et al., (2011). (a and b) from Einhäupl et al. (2011), with permission of Oxford University Press). (c) individual females differed considerably in their preferences for m3–m8 (Einhäupl et al. unpublished). (d) Total song duration had no significant influence on attractiveness (each point represents the average response of 15 females to the song of a male; $N = 27$ males, $r = 0.0099$, $p = 0.961$; N. Stange, unpublished results).

frequency spectrum (taken from one male). The maximal intensity of the songs was also adjusted to a constant level of 70 dB (Einhäupl et al., 2011). Hence, the main cues left for a female to discriminate between these rescaled songs were overall phrase duration and the fine pattern of amplitude modulations within the subunits. Although none of the individual songs used in this experiment was particularly unattractive – as e.g. stemming from a male singing with only one hind leg – females showed significant preferences (Fig. 4a and c). These observations underline the auditory system's capacity to detect rather subtle differences between songs of conspecific males. To what degree this discrimination capacity may help to assess the quality of potential mates will be discussed later, in Chapter 4. Interestingly, the overall phrase duration had only a weak influence on attractiveness (Einhäupl et al., 2011), and this was confirmed for a larger sample of 27 male songs presented to a different cohort of females (Fig. 4d).

Even though females preferred the song of certain males when tested in the lab, we have to ask how robust such preferences are under more natural conditions, that is, in a noisy environment as the animals will normally experience. We mimicked this condition by presenting the same song stimuli under different levels of broadband noise (Einhäupl et al., 2011). Our null hypothesis was that noise would mask the cues used to discriminate between individual songs and therefore the differences in attractiveness would disappear under increased levels of noise. Most remarkably, this was not the case: in contrast to this prediction, the songs that were most attractive under low-noise conditions turned out to be most robust against masking noise as well; attractive songs tolerated up to 5 dB higher noise levels. There was a strong correlation between female response probabilities (to the unmasked song) and the tolerated noise level (Fig. 4b; $r = 0.922$, $p = 0.0011$, $N = 8$, Spearman rank correlation).

3. Neurophysiological basis for the discrimination of individual songs

The central nervous system has no other information about acoustic stimuli than the spike trains that arrive via the auditory receptors and auditory interneurons. Hence, a necessary prerequisite to discriminate two acoustic signals is that the spike trains that they elicit are sufficiently different to be discriminated by a higher recognition centre in the grasshopper's brain. However, nervous systems face a fundamental problem that constrains stimulus discrimination: the intrinsic variability of spike trains. This variability is caused by the stochastic nature of ion channel function. Various stages of neuronal encoding depend inextricably on the stochastic opening and closing of ion channels, beginning with sensory transduction, synaptic transmission and generation of action potentials (e.g. White et al., 2000). The resulting variability of neuronal signals entails a fundamental problem for any analyzer network: the intrinsic stochasticity leads to a substantial trial-to-trial variability of spike trains, even if the identical object is present in the outer world (Fig. 5a). The brain thus has to decide whether two spike trains that differ by a certain amount may represent two different objects in the external world, or whether the differences may have been caused by the intrinsic noisiness of spike trains (Neuhofer et al., 2011). Given the unreliability of spike trains, the detection of gaps as small as 2–3 ms becomes a particular challenge (Ronacher and Römer, 1985; Ronacher and Stumpner, 1988; Machens et al., 2001). A detrimental influence of intrinsic neuronal noise can, of course, be reduced by averaging across several neurons with similar properties. Indeed, a sampling from a pool of 6–13 auditory receptor neurons has been proposed to explain the high accuracy in directional hearing of *C. biguttulus*

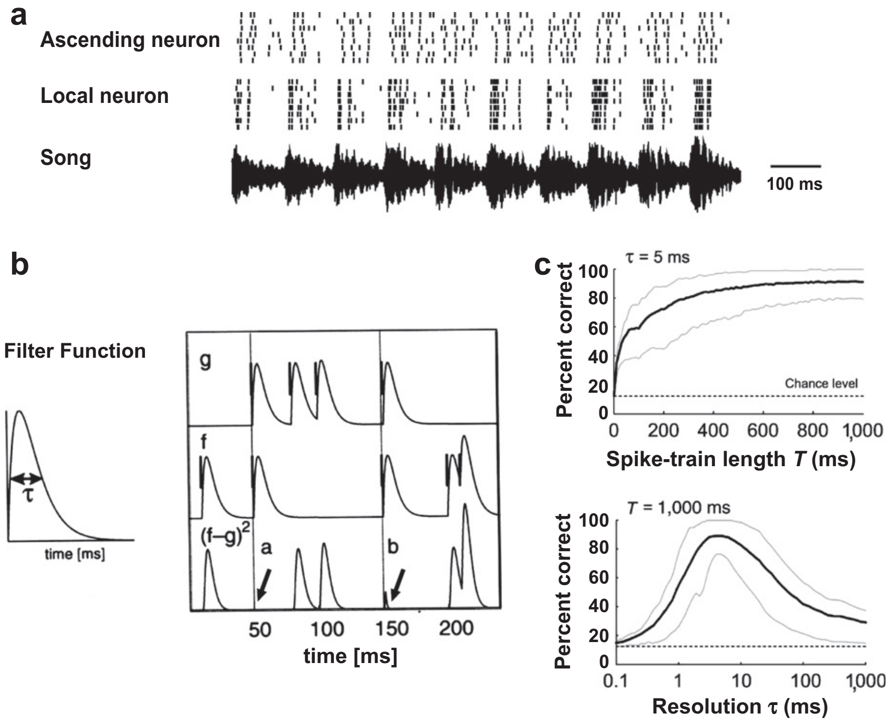

Fig. 5. (a) Responses of a local and an ascending auditory neuron to repeated presentations of a male song. In this 'spike raster plot' the occurrence of spikes is indicated by small vertical bars, the stimulus was presented 8 times. Note the trial-to-trial variability of spike trains. (b) Principle of the spike train metric method introduced by van Rossum, 2001; for explanations see text. (a and b) from Ronacher et al., 2008, with permission of the American Psychological Association). (c) Discrimination performance of auditory receptor neurons, in dependence of the length of spike trains (upper graph) and the temporal resolution (τ). The task was to assign any given spike train to the specific song (out of 8 songs) by which he was elicited (for details of the procedure see Machens et al., 2003 and Wohlgemuth and Ronacher, 2007). (c) from Machens et al., 2003, with permission of Nature Neuroscience.

males (Ronacher and Krahe, 2000). However, this solution is less likely to be realized at higher stages of processing due to the size limitations of insect nervous systems. Alternatively, the manifold repetition of redundant song subunits (Figs. 1 and 3) could also be exploited to reduce the effects of noise by means of temporal integration, that is, by averaging across multiple subunits. However, behavioral experiments on males have shown that two to three subunits suffice to enable the recognition of a female song, and even under masking noise no more than five subunits contribute to signal recognition (Ronacher and Krahe, 1998; Ronacher et al., 2000). Obviously, these animals do not rely much on a long-term temporal integration. Moreover, it is not clear how such a processing scheme could be implemented in a grasshopper's relatively small nervous system. One would postulate a mechanism similar as the 'multiple looks model' proposed by Viemeister and Wakefield (1991) for the processing of acoustic signals by humans (for a detailed discussion of the potential contribution of temporal integration, see Ronacher et al., 2004, 2008).

3.1. Quantifying the similarity of spike trains by a metric

The behavioral tests described in Fig. 4a and c have set the benchmark figures for discrimination performance. If we want to explore how well two basically similar signals – in our example the songs of two male grasshoppers belonging to the same species – can be discriminated by the auditory system, we must take the viewpoint of the brain and measure the similarity or dissimilarity of spike trains. The method of choice is a 'spike train metric', which quantifies the distance between two spike trains by a single number – two basically equivalent methods have been introduced by Viktor and Purpura (1997) and van Rossum (2001). We applied the van Rossum metric, the principle of which is explained in Fig. 5b. First, each spike of the two spike trains *g* and *f* is replaced by a filter function; as a second step the difference of the two resulting functions is squared and then the integral is taken (for details see van Rossum, 2001). The crucial step is the subtraction, since by this operation the contribution of coincident spikes cancels out (see arrows in Fig. 5b). Obviously, two spike trains that share many coincident spikes are similar, and the metric will yield a small distance value, which fits perfectly to our intuition of distances. By varying the width τ of the filter function one can adjust the temporal precision of the metric evaluation. A small τ emphasizes the timing of spikes, whereas with a large $\tau > \sim 500$ ms the timing of spikes is largely ignored and only differences in spike count contribute to the distance between two spike trains. Thus, by varying τ this metric allows one to investigate neuronal coding schemes based on spike rates or on spike timing, respectively.

We used this metric to explore how well the songs of eight *C. biguttulus* males can be discriminated on the basis of spike trains produced by single auditory neurons (Machens et al., 2003). As a prerequisite for a reliable discrimination the spike trains that were elicited by a specific song should cluster together. In other words, the spike trains produced at repeated presentations of song X – which will differ due to trial-to-trial variability – must be more similar to each other than to the spike trains elicited by song Y. To exclude a rather trivial discrimination based on different durations of the song subunits we equalized the subunit durations and the carrier frequency content of eight songs, as well as the maximum amplitude (the same songs were used for the behavioral experiments mentioned above in Fig. 4). As a consequence of this procedure, the songs differed only in the fine temporal structure of their sound envelope, i.e. the amplitude modulations within the syllables. Although several potential cues for discrimination were eliminated – i.e. differences in intensity, in carrier frequency content and subunit duration – the discrimination was almost perfect (>90%) at the level of auditory receptor neurons, provided that the spike trains were evaluated with a high temporal resolution in the range of 5 ms (Fig. 5c). That is, the timing of spikes was essential for this high classification performance. Note that already a single spike train of a single receptor provided the basis to extract such a high amount of information (Machens et al., 2003). The classification success exceeded 80% for a spike train length of 400 ms (upper diagram in Fig. 5c), which corresponds to just a few song subunits. Thus, this excellent discrimination is based on spike trains that comprise only around 50 action potentials (typical spike rates ranged between 100 and 200 Hz; see Machens et al., 2003).

These data evaluations have shown that a remarkable discrimination between similar signals is possible at the most peripheral input stage, based on the responses of a *single* receptor neuron. One may expect a further improvement when we ascend in the auditory pathway, due to the potential of sampling across a population of receptor neurons. But contrary to this expectation the good discrimination of stimuli is lost at higher processing stages (Vogel et al., 2005; Vogel and Ronacher, 2007). The reliability of a single neurons' responses is reduced at the next two processing stages: most local interneurons, and in particular ascending interneurons exhibit a higher trial-to-trial variability and, consequently, a reduced classification success for natural stimuli, as well as for artificial stimuli with sinusoidal or rectangular amplitude modulations (see Fig. 5a for an example, and Wohlgemuth and Ronacher, 2007; Wohlgemuth et al., 2011). The likely explanation for this observation is that a change in coding principles occurs between local and ascending neurons. Whereas a 'summed population code' describes the neuronal responses at the level of receptor neurons and most local neurons, in ascending neurons the information seems to be distributed among a population of neurons with different properties. Thus, already at a rather peripheral stage of the auditory pathway a 'labeled-line code' appears to be realized, for which the exact timing of spikes is less crucial (Clemens et al., in press).

4. Female preferences and information content of natural songs

What makes a male's song attractive? What kind of information about the sending male can a female grasshopper extract from a song that impinges on her ears?

The basic information conveyed by the songs certainly has to be about species identity. For *C. biguttulus* the syllable-to-pause pattern has been found to be a crucial cue for species identification (von Helversen, 1972, 1979, see also Fig. 1). Additional features of the amplitude modulation patterns, however, influence the attractiveness of songs (see above and Klappert and Reinhold, 2003, 2005). Most remarkably, females of *C. biguttulus* also preferred songs of conspecific males that had a higher dissimilarity to songs of other sympatric grasshopper species (Safi et al., 2006). This indicates that exclusion of a potential hybridization risk may be a factor that also shaped the preference functions of females (von Helversen and von Helversen, 1994).

To identify potential attractiveness cues let us have a closer look at the natural songs. An obvious feature of the song of *C. biguttulus* is the onset accentuation of its "syllables" (see Figs. 1c and 5a). Onset accentuation seems a means to preserve the syllable pause structure in the presence of masking noise and thus may facilitate signal recognition under natural conditions in the habitat where a substantial amount of background noise is normally present (e.g.

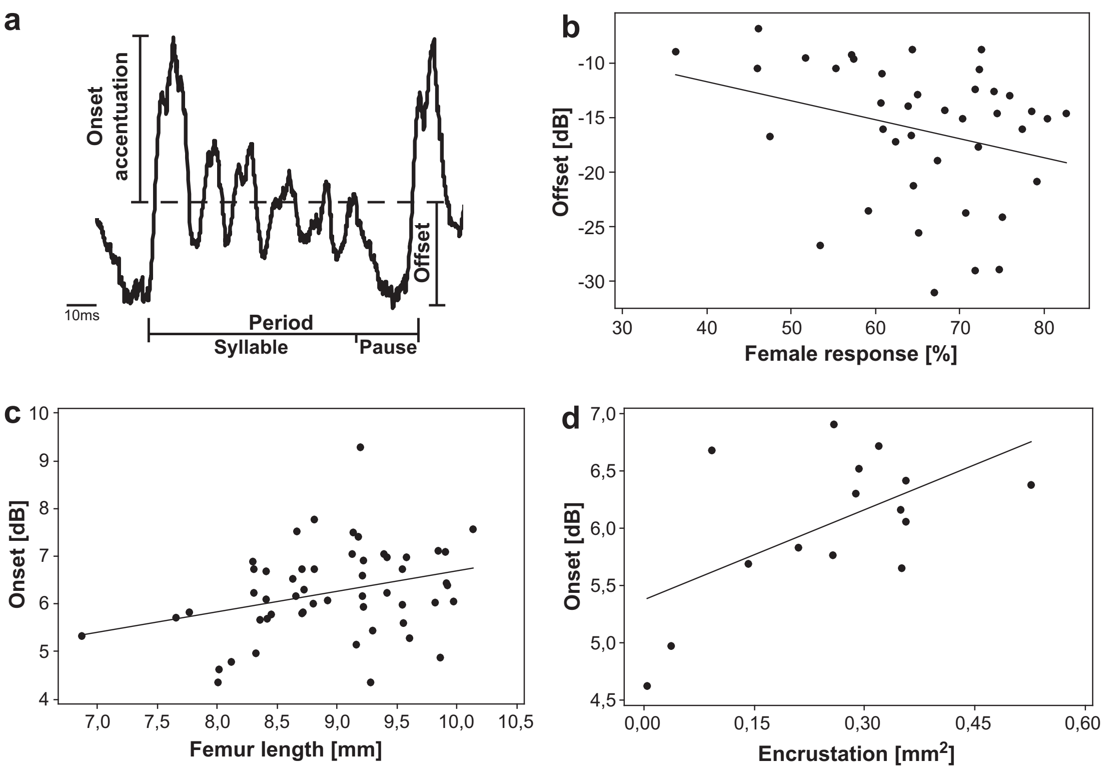

Fig. 6. (a) definitions of song features exemplified on the envelope of a song subunit (syllable plus pause) of *C. biguttulus*. (b) Song with deeper offsets elicit stronger responses of females (Spearman $r = -0.312$; $P = 0.05$; $N = 15$ females tested with 40 male songs (Stange, 2011). (c) Correlations between syllable onset accentuation and length of the hind femur, or (d) an indicator of immunological competence (encrustation of a nylon thread introduced into the thorax of males for 1 week, for details of the method see Stange and Ronacher, 2012). (c) $N = 54$ males caught in the field near Göttingen, $r = 0.307$, $p = 0.024$ ($p = 0.096$ after Bonferroni-Holm correction). (d) $r = 0.572$, $p = 0.026$ ($p = 0.156$ after Bonferroni-Holm correction), $N = 15$ males, Stange, 2011).

Michelsen and Larsen, 1983; Römer, 1998, 2001; Gilbert and Elsner, 2000; Lang, 2000; Brumm and Slabbekoorn, 2005). Thus, it was not surprising that in behavioral experiments with model songs this onset feature has been found to enhance attractiveness (von Helversen, 1979; Balakrishnan et al., 2001; von Helversen et al., 2004).

Interestingly, males do not normally produce completely silent pauses between the sound syllables (see example in Fig. 1c). Rather they produce a series of very short clicks in the "pause", which are due to a soft movement of one of the hind legs (which produces the so called pattern II) while the other leg (pattern I) stops completely (Elsner, 1974; Balakrishnan et al., 2001). Thus, a natural song exhibits not only a distinct onset accentuation but also a variable offset, depending on the number of clicks within a "pause". As a rule, earlier experiments used song models with completely silent pauses, but it has been shown that an offset of 9 dB difference was sufficient to elicit response saturation in females (von Helversen, 1979).

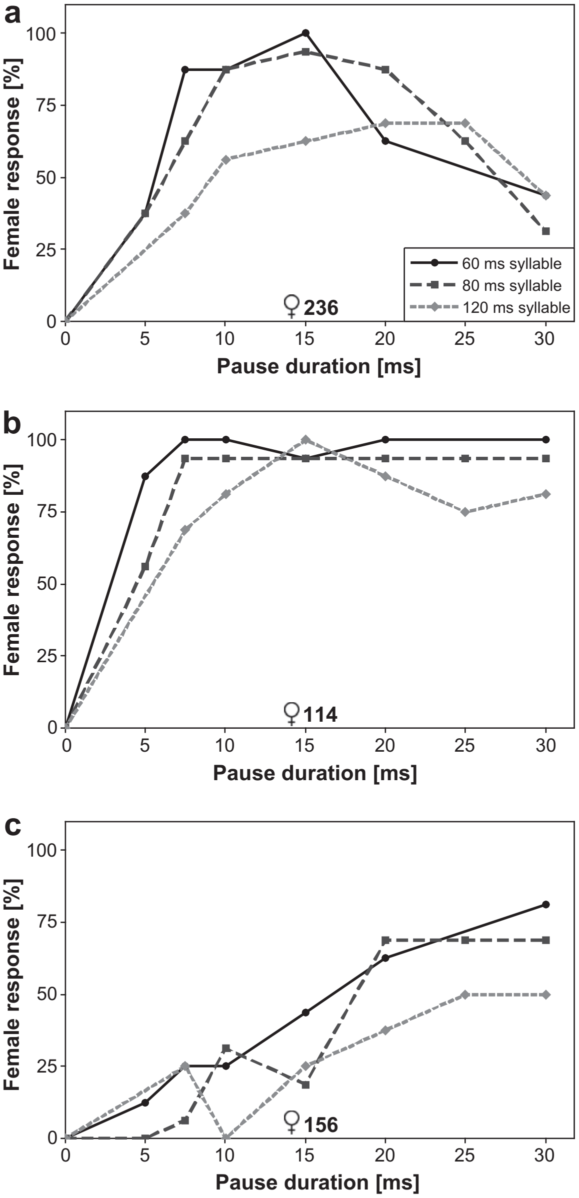

Fig. 7. Individual differences in the shape of female preference functions. Responses of three females to rectangularly modulated (cf. Fig. 1c) song models with 60, 80 or 120 ms syllables and varying pause durations. (a) Female 236 shows the 'typical' response pattern, a bell shaped response combined with a preference for longer pauses at longer syllable durations. (b) Female 114 responded very well to all tested pause durations >7.5 ms, whereas female 156 (c) showed no response saturation even at the largest pause tested (A. Vogt and B. Ronacher unpublished results).

4.1. Potential quality cues in male songs

Since distinct female preferences for natural songs of specific males exist (Fig. 4a), we can ask whether these preferences are oriented towards specific clues about the sender's quality, which may be expressed in some song features (cf. Anderson, 1994). In other words, can females extract information about the quality of the sender from a song they hear?

In a study on a large sample of *C. biguttulus* males, we searched for correlations between song features and morphological characteristics to explore whether specific song features reflect condition or genetic quality of the male, and may therefore appear attractive to females (Stange and Ronacher, 2012). Onset accentuation (for definitions see Fig. 6a) was positively correlated to the length of the hind femur of males (Fig. 6c). Similar positive correlations were observed in a second sample of animals raised in the lab (see Stange and Ronacher, 2012) and in males from three other populations (Stange and Ronacher, unpublished observations). A particularly interesting result was the correlation between onset accentuation and a measure for immunocompetence, the encrustation of nylon threads inserted into the thorax of males (Fig. 6d, $r = 0.572$, $p = 0.026$, $N = 15$ males). Although after Bonferroni correction the significance level of 0.05 was missed, we consider this correlation as reliable since a similar correlation was also observed in a second, independent experiment on lab raised animals (Stange and Ronacher, 2012). The offset depth was also correlated to the immunocompetence indicator – deeper offsets indicating higher immunocompetence (Stange and Ronacher, 2012). Indeed, females preferred songs with larger offsets (Fig. 6b, Spearman $r = -0.312$; $p = 0.05$). Although this correlation was only marginally significant, similar and significant correlations were observed in females from other populations (Stange, 2011). However, the size of the offset was not significantly correlated to the investigated size parameters. The correlations exemplified in Fig. 6c and d suggest that, in principle, a grasshopper female could extract information about the size and the health of a potential mate from the songs he produces.

4.2. Differences between female preference functions

Onset and offset cues have been systematically varied in model songs and found to both influence female response propensity (Balakrishnan et al., 2001; von Helversen et al., 2004). Interestingly, individual females appear to differ in their respective weighting of these two cues. Some females responded to a stimulus without pauses, in which the syllables were marked only with a 12 dB onset, while others responded well to stimuli with an offset of −12 dB, irrespective of the value of onset accentuation. Still other females required the presence of both features to accept a model song (Balakrishnan et al., 2001). To explain the onset and offset responses as well as the differences between individuals these authors proposed a tentative neuronal model composed of an onset detector and a detector for too long pauses.

Also with respect to the optimal pause duration distinct types of female preference functions seem to exist in a population (Fig. 7). We presented song models with varying syllable and pause durations (see Fig. 1c) to virgin *C. biguttulus* females in a computer controlled set up that automatically recorded the responses of females (see Schmidt et al., 2008, for details of the method). Twelve of 24 females exhibited a bell shaped preference, and a shift to longer preferred pause durations with increasing syllable duration (Fig. 7a). This has been described as the response typical for this species (von Helversen, 1972, 1979; von Helversen and von Helversen, 1997). However, for six females all pauses longer than 10 ms were highly attractive (Fig. 7b), whereas for another 3 females attractiveness steadily increased with longer pauses without saturating in the tested range (Fig. 7c). The preference functions of three other animals were intermediate between those of Fig. 7a and b.

In the tests with natural songs as well the preferences of females were not uniform and not all females were choosing the same "super-males" (see Fig. 4c for individual preference functions of six females). In these tests even the on average least attractive song got a 100% response by 4 females (Einhäupl et al., 2011). These differences in female preferences obviously do relieve the strength of sexual selection upon males and also will contribute to maintain genetic variation related to song production within a population.

5. Conclusion and outlook

The large inter-individual differences observed between females also open a promising road for future investigations. It will be particularly interesting to relate the variations in female preferences to individual differences in the responses of identified neurons. One big advantage of these insects is that a large number of their auditory neurons can be morphologically identified (see Fig. 2) and thus the response properties of identified neurons can be compared between individuals, and even between species (Neuhofer et al., 2008). Experiments are now under way to take advantage of this type of variation.

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