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RESEARCH ARTICLE

Maintaining acoustic communication at a cocktail party: heterospecific masking noise improves signal detection through frequency separation

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SUMMARY

We examined acoustic masking in a chirping katydid species of the *Mecopoda elongata* complex due to interference with a sympatric *Mecopoda* species where males produce continuous trills at high amplitudes. Frequency spectra of both calling songs range from 1 to 80 kHz; the chirper species has more energy in a narrow frequency band at 2 kHz and above 40 kHz. Behaviourally, chirper males successfully phase-locked their chirps to playbacks of conspecific chirps under masking conditions at signal-to-noise ratios (SNRs) of −8 dB. After the 2 kHz band in the chirp had been equalised to the level in the masking trill, the breakdown of phase-locked synchrony occurred at a SNR of +7 dB. The remarkable receiver performance is partially mirrored in the selective response of a first-order auditory interneuron (TN1) to conspecific chirps under these masking conditions. However, the selective response is only maintained for a stimulus including the 2 kHz component, although this frequency band has no influence on the unmasked TN1 response. Remarkably, the addition of masking noise at 65 dB sound pressure level (SPL) to threshold response levels of TN1 for pure tones of 2 kHz enhanced the sensitivity of the response by 10 dB. Thus, the spectral dissimilarity between masker and signal at a rather low frequency appears to be of crucial importance for the ability of the chirping species to communicate under strong masking by the trilling species. We discuss the possible properties underlying the cellular/synaptic mechanisms of the 'novelty detector'.

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INTRODUCTION

Reproductive isolation of acoustically communicating animals can be maintained by reliable detection and recognition of conspecific calling songs (Shaw, 1999; Gerhardt and Huber, 2002). Receivers discriminate between conspecific signals and those from other sympatric species by evaluation of species-specific signal features. In a similar way, taxonomists make use of these features to identify the species composition of calling communities (Walker, 1964; Otte, 1992; Riede, 1998; Walker et al., 2003; Nityananda and Balakrishnan, 2006). However, recognition is challenging for receivers in a social environment where many coactive signallers result in masking interference and contribute to what has been called a cocktail party situation (Cherry, 1953; Bronkhorst, 2000; Bee and Micheyl, 2008; Ryan and Brenowitz, 1985; Narins and Zelick, 1988; Andersson and McGregor, 1999; Amézquita et al., 2006; Schmidt et al., 2011). Empirical evidence in katydids suggests that even the acoustic competition of one species with a highly redundant signal can result in strong masking and silencing of a sympatric species with discontinuous songs (Greenfield, 1988; Römer et al., 1989).

In order to avoid masking interference, signallers could partition their signalling activity in time, frequency and space [for a review of insects, see Römer (Römer, in press)]. Signalling in 'silent windows' has been found in birds (Brumm, 2006), frogs (Schwartz and Wells, 1983; Paez et al., 1993; Wong et al., 2009) and insects (Latimer, 1981; Gogala and Riede, 1995; Greenfield, 1988). Signal detection is improved by peripheral or central nervous filters that reduce masking interference by frequencies beyond the filter-specific sensitivity range (the 'matched filter hypothesis') (Capranica and Moffat, 1983; Wehner, 1987; Kostarakos et al., 2008; Schmidt and Römer, 2011). Spatial niche partitioning has been documented in a vertical stratification of calling heights of tropical insect communities, with three main layers corresponding to the canopy, understorey and ground layer (Diwakar and Balakrishnan, 2007; Jain and Balakrishnan, 2012; Schmidt et al., 2013). It is also evident that a combination of parameters does improve acoustic niche partitioning (Sueur, 2002; Diwakar and Balakrishnan, 2007).

In contrast to those of crickets, the calling songs of many katydids are broadband signals with a frequency spectrum that extends far into the ultrasonic range; some include only ultrasonic frequencies, in single cases of tropical species up to more than 100 kHz (Heller, 1988; Morris et al., 1994). Furthermore, their ears are not tuned to a particular frequency but exhibit high sensitivity in a broad frequency range including audio and ultrasonic frequencies (Rheinlaender et al., 1972; Rheinlaender and Römer, 1986; Faure and Hoy, 2000a; Stumpner and Molina, 2006). Thus, katydids cannot discriminate conspecific signals from heterospecific ones in the background, or from predatory bat cues simply based on spectral information. Schul and colleagues suggested that the only reliable information for discrimination should be based on temporal properties of conspecific signals (Schul et al., 2000).

The fact that frequency partitioning appears not to be an option for katydids using broadband communication signals has substantial consequences for the detection of behaviourally relevant signals in a noisy background. From a sensory and neuronal perspective,

receivers can improve signal discrimination by (1) reliable classification of temporal properties of bursts of action potentials encoded in sensory neurons that respond to signals and background (Hartbauer et al., 2012; Pfeiffer et al., 2012), and/or (2) selective neuronal responses to behaviourally relevant sound signals (Faure and Hoy, 2000b; ter Hofstede and Fullard, 2008). The latter can be the outcome of auditory stream segregation, which describes the ability of receivers to form perceptually different objects on the basis of mixed auditory streams that are related to different sound sources (Bee and Micheyl, 2008; Nityananda and Bee, 2011). At the single neuronal level, Schul and colleagues (Schul and Sheridan, 2006; Schul et al., 2012) described the highly selective encoding of bat-like calls despite the simultaneous presence of a repetitive conspecific signal in the katydid *Neoconocephalus retusus*. Such a 'novelty detector' would allow this katydid to respond with evasive reactions to echolocation bat calls while listening to conspecifics (Schul and Sheridan, 2006).

Novelty detection may also play a role in the context of species recognition. Here, we report such a case for two katydid species of the genus *Mecopoda* where males of a chirping species attract females with highly periodical chirps, while another sympatric species produces trills at high broadcast levels [103 dB sound pressure level (SPL) at 15 cm] (Krobath, 2013). Importantly, the broadband spectra of the signals of the two species are rather similar. Males of the chirper species synchronise their signals with those of conspecific males to form a chorus (Sismondo, 1990; Hartbauer et al., 2005), and this synchrony is rather robust to realistic intensities of rainforest background noise (Hartbauer et al., 2012). Noise robustness finds its neuronal correlate in the activity of an interneuron (TN1) selectively encoding conspecific chirps even under such background noise conditions (Siegert et al., 2011).

We investigated whether the continuous trills of one *Mecopoda* species affects signal detection of the *Mecopoda* chirper in behavioural entrainment experiments. The neuronal basis of signal detection was studied using the activity of TN1 in response to conspecific chirps under various 'trill noise' background levels. By manipulating the frequency composition of the trills, we can show that novelty detection in this neuron is based on a small difference in the low frequency component of the broadband calling songs.

MATERIALS AND METHODS

Insects

We used two katydid species of the genus *Mecopoda* (Serville 1831, Ensifera, Tettigoniidae, Mecopodini), occurring in sympatry in the Malaysian rainforest. One species produces calling songs consisting of chirps repeated regularly with a chirp interval of 2 s (herein termed 'chirper') and the other species generates long-lasting trills (herein termed 'triller'). Chirps of the chirper are identical to those of 'species S' described by Sismondo (Sismondo, 1990), and songs of the trilling species are identical to those of '*Mecopoda* sp. 2' described by Korsunovskaya (Korsunovskaya, 2008) (Fig. 1A). Individuals were taken from two separate laboratory breeds that were originally established with individuals collected in the rainforest (Ulu Gombak, Selangor, Kuala Lumpur, Malaysia). Insects were reared in crowded colonies at a temperature of 27°C, 70% relative humidity, on a 12 h:12 h light:dark schedule. They were fed *ad libitum* with fish food, oat flakes and fresh lettuce.

Sound recordings

Calling songs of both species were recorded from isolated males singing in a sound-proof incubator maintaining a constant temperature of 27°C. Sound recordings were performed at a distance of 15 cm relative to the signalling individual using a calibrated 1/2 in free-field condenser microphone (type 40AC, G.R.A.S. Sound & Vibration A/S, Holte, Denmark) with a flat frequency response between 10 Hz and 40 kHz. The microphone output was amplified using a preamplifier (type 26AM, G.R.A.S. Sound & Vibration A/S) and a power module (type 12AK, G.R.A.S. Sound & Vibration A/S). For analysis of the frequency spectra at higher ultrasonic frequencies we performed recordings with a 1/4 in free-field condenser microphone (type 40BE with type 26AC preamplifier, G.R.A.S. Sound & Vibration A/S) with a frequency response of ±3 dB between 10 Hz and 100 kHz. A/D conversion was performed *via* an external audio interface (Edirol FA-101, Roland Inc., Tokyo, Japan) operating at a sampling rate of 192 kHz. Sound recordings were analysed with the audio software Cool Edit Pro 2.0 (Syntrillium Software, Phoenix, AZ, USA).

Playback signals and sound calibration

Acoustic signals used in playback experiments are representative examples of songs of both species (Fig. 1). The chirp used in entrainment experiments (Fig. 1A, left) consisted of 15 syllables (chirp duration 285 ms, syllable period 20 ms) with a gradually increasing amplitude; the same chirp was also used as a stimulus in neurophysiological experiments (see below). The trill consisted of the stereotypical pattern of a soft syllable followed by two syllables of higher amplitude. This unit was repeated with a period duration of 30 ms.

Playback of sound signals in entrainment and neurophysiological experiments was controlled in Cool Edit Pro 2.0 driving an Edirol A/D audio interface operating at a sampling rate of 96 kHz. Sound signals were attenuated (PA-5, Tucker Davis Inc., Alachua, FL, USA) and amplified using an amplifier with a flat frequency response up to 100 kHz (NAD 214, NAD Electronics, Pickering, ON, Canada). A pair of leaf tweeters (EAS-10TH400A, Technics, Kadoma, Japan) with a rather flat frequency response between 200 Hz and 40 kHz was used in playback experiments. Because of the loudspeaker frequency response and the reduced sampling rate of the Edirol A/D audio interface, the signal playback resulted in a strong attenuation of frequencies higher than 40 kHz. We thus simulated the frequency spectrum of a signal as being perceived at medium sender–receiver distances of about 2 m, where ultrasonic frequencies are strongly attenuated (our own measurements at sites where the two species have been collected in the rainforest) (Keuper et al., 1986; Römer and Lewald, 1992). The conspecific chirp signal was calibrated to a SPL of 65 dB at the position of the insect preparation and the position of males in entrainment experiments. Sound recordings obtained from 15 males showed that this chirp amplitude refers to an average sender–receiver distance of 1.8 m. From the field we know that this distance allows singing males to uphold synchrony in the presence of a background trill. Sound calibration was performed during continuous loop mode presentation of three subsequent syllables with the highest amplitude using a 1/2 in microphone (type 2540, Larson Davis, Depew, NY, USA) connected to a sound level meter (CEL 414, Casella, Bedford, UK) operating in fast reading mode (time constant 125 ms). In masking experiments, periodical chirps were simultaneously broadcast with a representative trill motif with a total duration of 12 s. This trill sequence was broadcast in loop mode with a calibrated amplitude that refers to the root mean square (RMS) amplitude of two representative repeatable units (fast reading mode).

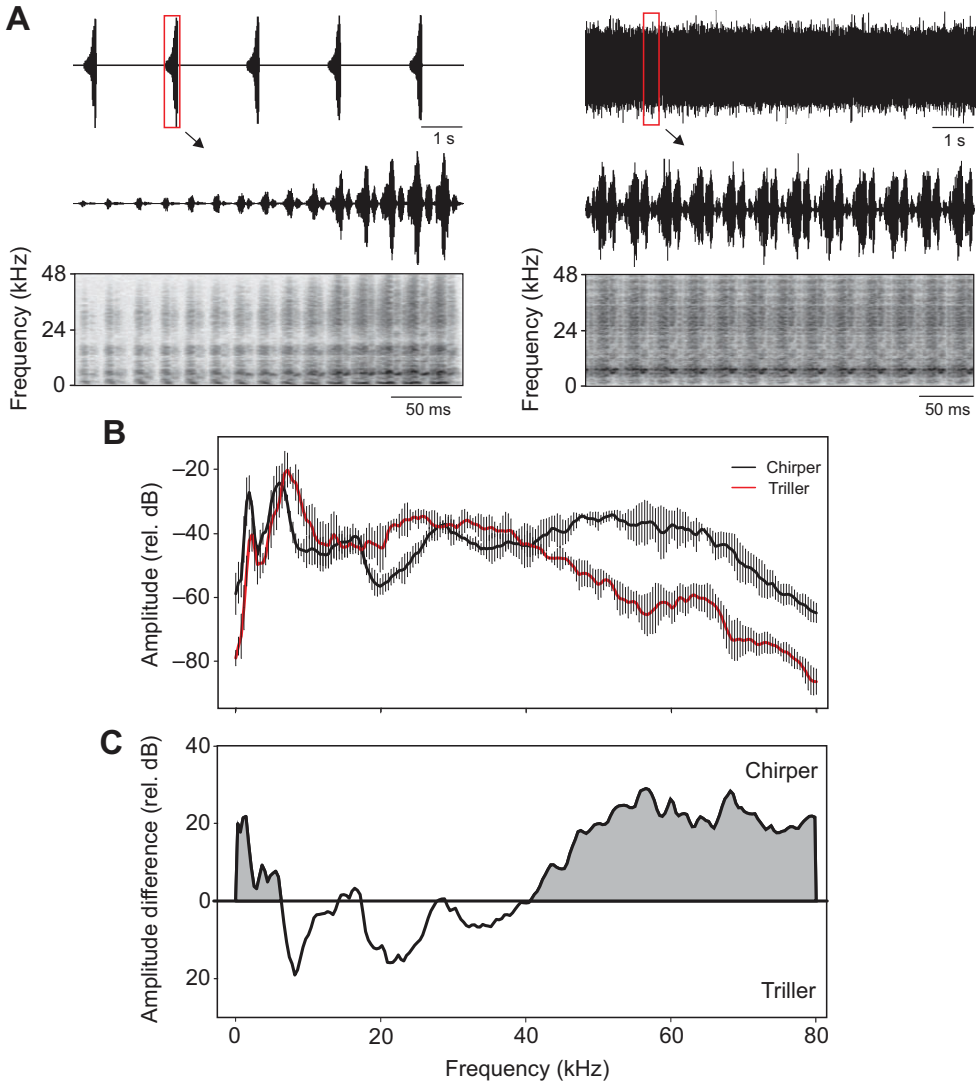

Fig. 1. Characteristics of acoustic signals used in behavioural playback and neurophysiological experiments. (A) Oscillograms and spectrograms of a chirp (left) and a trill (right) of the two *Mecopoda* species. (B) Power spectra of calling songs obtained from five *Mecopoda* chirper (black) and triller (red) males. Error bars indicate standard deviation. (C) Difference spectrum of the calling songs of both species.

Frequency manipulation of playback signals

Manipulation of the spectral composition of chirps allowed us to study the effect of certain frequency bands on signal detection in behavioural entrainment experiments, and on the response of TN1 in neurophysiological experiments. The most prominent frequency bands in chirps have been identified in a narrow range around 2 kHz, and at frequencies higher than 45 kHz (see difference spectrum in Fig. 1C). However, because of the frequency restriction of the playback system (see above), these ultrasonic frequencies in the chirp did not exist in the playbacks. A smaller frequency band at 6 kHz with more energy in the chirp resulted from the fact that in both signals the most prominent component is at 6–7 kHz, with a shift towards 7 kHz in the trill. Thus, the main difference in the frequency spectra between the chirp signal and the masker was the higher energy at 2 kHz for the chirp, whereas the masker had more energy starting at frequencies higher than 9 kHz. For the experimental approach, the respective frequency band in the chirp at 2 or 6 kHz was attenuated to the same level as in the spectrum of the trill, using the fast Fourier transform (FFT) filter function provided by Cool Edit Pro 2.0. The quality of the spectrum of the playback signals was evaluated by Fourier analysis of microphone recordings performed at the distance of receivers (see supplementary material Fig. S1).

Entrainment experiments

Individual males (N=10) of the chirping species were entrained as followers to a periodic chirp broadcast with a constant period between 1.8 and 2 s, and an amplitude of 65 dB SPL at the position of the singing male (35 cm male–speaker distance). Variation of the broadcast chirp period between 1.8 and 2.0 s for each male was necessary in order to achieve their entrainment as followers. After males had successfully established phase-locked synchrony, the playback of the trill was started with an amplitude that was gradually changed from 55 to 73 dB SPL. Trill amplitude was maintained constant for 3 min and varied in steps of 3 dB. The proportion of phase-locked chirps was evaluated off-line within the last minute of each amplitude interval. A deviation of the phase-locked chirp period of more than 64 ms from the stimulus period was regarded as asynchrony. The experiment was repeated using a chirp with an attenuated 2 kHz band.

Neurophysiology

TN1 is a first-order auditory interneuron with an axon on the soma-contralateral side ascending from the prothoracic ganglion to the brain (Suga and Katsuki, 1961; McKay, 1969). Action potential (AP) activity can be recorded unequivocally from the cervical connective using hook electrodes (Rheinlaender, 1984; Schul,

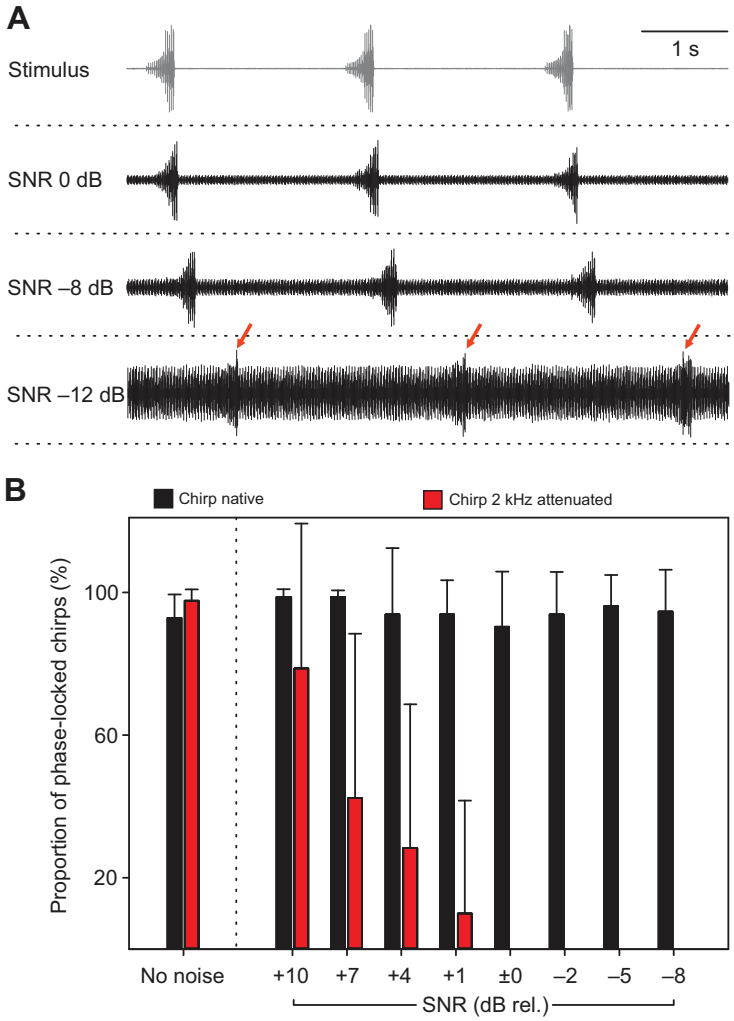

Fig. 2. Synchronous entrainment of chirper males under masking conditions with the trilling species. (A) Examples of phase-locking to the entrainment stimulus at different signal-to-noise ratios (SNRs). Note that the microphone recording the chirps of the singing male was acoustically isolated from the trill signal and thus the illustration does not reflect the real masker amplitude. There is a loss of phase-locking at a SNR of −12 dB. Arrows indicate the final part of masked chirps. (B) Results of entrainment experiments with the native frequency spectrum (black bars) and a chirp spectrum with a 2 kHz component equalised to the amplitude in the masker (red bars). *N*=10 males.

1997; Faure and Hoy, 2000b; ter Hofstede et al., 2010). Intracellular recordings and staining confirmed that we recorded from a neuron in *M. elongata* that has the typical TN1 morphology as described for several bushcricket species. Details concerning dissection and extracellular recording of TN1 activity have been described elsewhere (Rheinlaender and Römer, 1980; Faure and Hoy, 2000a). In brief, the ipsilateral cervical connective was surgically exposed and mounted using a tungsten hook electrode. The preparation was placed ventral side up in an anechoic chamber equipped with two loudspeakers positioned at a distance of 30 cm from the preparation. Electrode signals were amplified using an extracellular amplifier equipped with a headstage (EXT-02F/1, NPI, Tamm, Germany). A/D conversion (PowerLab/4SP, AD Instruments, Spechbach, Germany) of the electrode signal was accomplished at a sampling rate of 40 kHz. All stimuli were broadcast from the ipsilateral side and, if not stated otherwise, calibrated to 65 dB SPL at the position of the preparation. For comparison, we also extracellularly recorded the activity of the omega neuron (ON1), a local prothoracic first-order auditory interneuron with tonic response characteristics, in a few *Mecopoda* chirper individuals. For details concerning these recordings see Römer et al. (Römer et al., 2002).

TN1 thresholds for pure tone signals were determined in steps of 1 kHz within a frequency range of 1 to 20 kHz. Threshold was determined as the lowest SPL of the stimulus eliciting a response in at least 50% of stimuli. The pure tone signals were presented at intervals of 2 s; they consisted of three pulses with a pulse duration of 10 ms and an inter-pulse interval of 1 ms. In experiments with simultaneous playback of a pure tone signal and trill, the pure tone signal had the same temporal parameters as described above.

Data evaluation and statistics

Raster plots and peri-stimulus time histograms (PSTHs) of TN1 responses were calculated in Spike 2 (v5.2.1, Cambridge Electronic Design, Cambridge, UK). The average neuronal response to a chirp signal was calculated for each individual over 30 stimulus presentations (chirper *N*=20, triller *N*=10). We also calculated the percentage of chirps eliciting a TN1 response under various masking conditions. Mean percentage values were averaged across individuals.

Spectrograms of sound signals were computed in Audacity 2.0 (http://audacity.sourceforge.net) using a FFT with a window size of 512 points and a Hanning window function. Mean spectrograms were prepared by averaging the spectrograms of five *Mecopoda* chirper or triller males after equalising RMS amplitude of signals. All figures and statistics were generated in SigmaPlot 12.3 (Systat Software Inc., Chicago, IL, USA). In order to account for multiple testing of single individuals, all significance values were Bonferroni corrected.

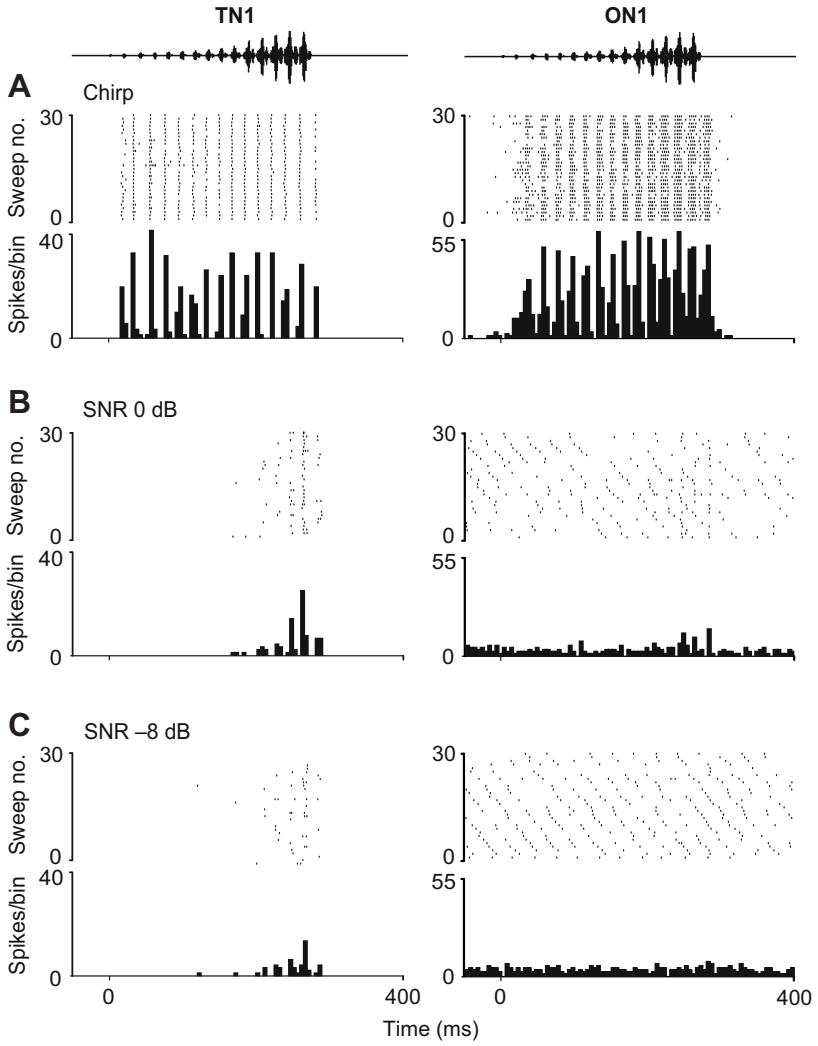

Fig. 3. Representative examples of responses to chirps presented at various SNRs of two interneurons (TN1 and ON1). Raster plots and peri-stimulus time histograms (PSTHs) of responses without the masker (A), and under masking conditions at a SNR of 0 dB (B) or −8 dB (C). Note the complete loss of a stimulus-related response in the ON1 response at a SNR of −8 dB.

RESULTS

Signal characteristics

The signals of the chirper and triller species differed strongly in their temporal characteristics, but less so in their frequency components, including frequencies from less than 2 kHz up to 80 kHz (Fig. 1B). Oscillograms of both signals used in the playback experiments are shown in Fig. 1A at different time scales. The direct comparison revealed more energy around 2, 6 and beyond 44 kHz in the chirper signal, whereas prominent energy differences favouring the trill occurred at frequencies between 9 and 44 kHz (Fig. 1B,C).

Signal synchronisation under masking noise of the trilling species

The ability of *Mecopoda* chirper males to synchronise with acoustic signals of other males in a chorus can be used to study the perception of conspecific signals under the masking conditions of the heterospecific trill. All males phase-locked their chirps to the regularly repeated playback chirp under a SNR of +10 dB (Fig. 2B, black bars). Surprisingly, all males were able to maintain phase-locked synchrony even at a SNR of −8 dB, when the masker was 8 dB higher than the playback chirp amplitude (94.6±11.7%, mean ± s.d. of phase-locked chirps). A further reduction of the SNR to −12 dB resulted in a breakdown of synchronous entrainment (see example in Fig. 2A). Even when the masker had no effect on the amount of phase-locking, it nevertheless resulted in a shift of a male's chirp relative to the stimulus (compare phase-locked chirps at SNRs of 0 and −8 dB in Fig. 2A). Obviously, this is caused by the masking of the soft initial syllables in the stimulus by the continuous trill background.

The high amount of phase-locking at unfavourable SNRs up to −8 dB is surprising given the continuous background of the trill, and the fact that the conspecific stimulus and background are rather similar in their spectral composition. In the comparison between the spectra of both chirps and trills there is a low frequency component at 2 kHz with consistent larger amplitude in the chirp. In order to investigate its contribution to signal perception under trill noise conditions, entrainment experiments were repeated with a chirp in which the 2 kHz band was attenuated, so that signal and masker were not different in this frequency band (Fig. 2B). Even at a high SNR of +10 dB, the proportion of phase-locked chirps was only 80% and further decreased to 10% at a SNR of +1 dB. Phase-locked entrainment completely disappeared at a SNR of 0 dB or lower (Fig. 2B, red bars). Moreover, 8 out of the 10 studied males ceased signalling after breakdown of synchrony, a behaviour that was never observed during entrainment to the full spectrum chirps.

Neurophysiological correlates of signal detection under masking conditions

In *Mecopoda* chirper, the TN1 neuron ipsilateral to the stimulus reliably encoded conspecific chirps in its response when broadcast

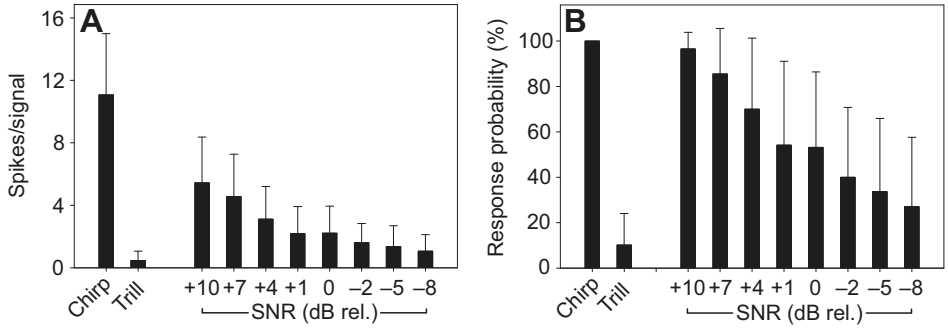

Fig. 4. The response of TN1 in preparations of *Mecopoda* chirpers to chirps and trills (left bars), or to chirps under masking when trills were broadcast at various SNRs (right bars). Response magnitude was analysed as average spikes per chirp (A) or TN1 response probability to chirp presentations (B).

at 65 dB SPL (Fig. 3A). Specifically, the temporal pattern of syllables was encoded with a high precision of 1 AP per syllable. The simultaneous broadcast of the trill at equal amplitude strongly reduced the response to the soft syllable at the beginning of the chirp, but still elicited a robust response to the final, high amplitude syllables (Fig. 3B). Even at a SNR of −8 dB, the TN1 response was not completely masked, and about 30% of stimuli elicited at least 1 AP per stimulus. As a comparison, we studied the coding of the omega neuron (ON1) under the same unmasked and masked conditions of the trilling species. Without the masker, ON1 of the *Mecopoda* chirper showed a strong, tonic response to each of the 13 syllables (Fig. 3A). However, starting at SNRs of 0 dB the response to chirps was completely masked (Fig. 3B,C, right).

Fig. 4 summarises quantitative data of TN1 responses in conditions without the trill masker, and at various SNRs relative to the masker. Conspecific chirps in the absence of the trill background elicited an average TN1 response of 11 APs, whereas the trill elicited almost no response at all (N=20 males; Fig. 4A). The trill playback reduced the TN1 response to 6 APs at a SNR of +10 dB (Fig. 4A) or to an average of 1 AP per chirp at a SNR of −8 dB (black bars; P<0.001; ANOVA on ranks). Increasing levels of the trill background also reduced the percentage of chirps eliciting a TN1 response at all (Fig. 4B). Only about 50% of chirps elicited a TN1 response at a SNR of 0 dB, which was further reduced to 30% at a SNR of −8 dB. Playback of the same stimuli to *Mecopoda* triller individuals resulted in weaker TN1 responses for all stimuli and SNRs (data not shown).

Manipulation of the frequency composition of the chirp

The relevance of the particular frequency composition of the chirp for a selective TN1 encoding in the *Mecopoda* chirper was investigated by manipulating the spectral composition of the conspecific chirp. A chirp with native temporal pattern of the syllable but trill-like frequency content elicited a significantly weaker TN1 response compared with native chirps (P<0.001, N=10, Mann–Whitney rank sum test; Fig. 5). Interestingly, the softer syllables of such a manipulated chirp evoked a higher TN1 activity than the high amplitude syllables at the end (Fig. 3A). If either one or a combination of the spectral energy peaks at 2 and 6 kHz had been attenuated, the response in TN1 was not different to the response to native chirps (Fig. 5B).

Under masking conditions at a SNR of 0 dB (65 dB SPL), the chirp with the trill-like spectrum elicited almost no response at all compared with the response to the native chirp (2.21 APs per chirp; P<0.01, N=10, Mann–Whitney rank sum test; Fig. 5B). This experiment demonstrates that the selective TN1 response is sensitive to differences in species-specific frequency components in the masker and chirp.

However, when either the 2 kHz component in the chirp, or both the 2 and 6 kHz component in the chirp had been attenuated to the level as in the trill, the response of TN1 was almost completely abolished (0.61 and 0.34 APs per chirp; P≤0.005, Mann–Whitney rank sum test; Fig. 5B). By contrast, attenuation of the 6 kHz frequency component alone had no effect on the average TN1 response under masking conditions, when compared with the native chirp.

TN1 threshold measurements

Under masking conditions, an improved TN1 response to signals with a prominent 2 kHz frequency band may be the result of specific tuning characteristics of TN1 in *Mecopoda* chirpers. Therefore, we determined TN1 thresholds in the frequency range between 1 and 20 kHz in both *Mecopoda* species (Fig. 6). Over all frequencies tested, TN1 in the *Mecopoda* triller was significantly less sensitive across all tested frequencies, with the largest difference of 16 dB between 10 and 20 kHz (Fig. 6). In both species the highest thresholds were found between 3 and 5 kHz (chirper 77 dB SPL, triller >80 dB SPL). The average TN1 threshold at 2 kHz was 5 dB lower in the *Mecopoda* chirper.

The masker trills improve the detection of chirps

Although the above results indicate a somewhat lower TN1 threshold at 2 kHz in the *Mecopoda* chirper, this frequency band remains subthreshold at a playback level of 65 dB SPL for chirps. We therefore investigated the hypothesis of whether simultaneous presentation of the trill might even improve the detection of a signal with a carrier frequency of 2 kHz. First, in a neurophysiological experiment the threshold of TN1 for a 2 kHz stimulus was determined in the unmasked condition, where in about 70% of stimuli the neuron elicited a suprathreshold response (68.1±10.2%, mean ± s.d.; Fig. 7, left black bar). As a control, the same experiment was performed with a stimulus of 6 kHz, which yielded an identical response probability (Fig. 7, red bar). Notably, reducing the SPL for both stimuli by only 1 dB resulted in a reliable drop in the response probability well below 50%, and thus below the threshold criterion.

When the continuous trill masker was broadcast at 65 dB SPL and the 2 kHz stimulus at the previously determined threshold amplitude of the TN1 (i.e. 0 dB relative to the unmasked threshold; Fig. 7), the response probability still remained at 60%. Even a further reduction of the SPL of the 2 kHz stimulus to 10 dB below the unmasked level did not reduce the response probability. At a level of −2 dB the response was even significantly increased under the masking condition (P=0.04, paired t-test, N=10). In individual preparations, we reduced the stimulus level down to −14 dB relative to the unmasked condition and still recorded response probabilities of 59.5±32.6% (mean ± s.d.; data not shown). However, the same series tested with the 6 kHz stimulus revealed complete masking at any level from +2 to −10 dB (Fig. 7, red bars). The same was true for an ultrasonic stimulus of 45 kHz (data not shown).

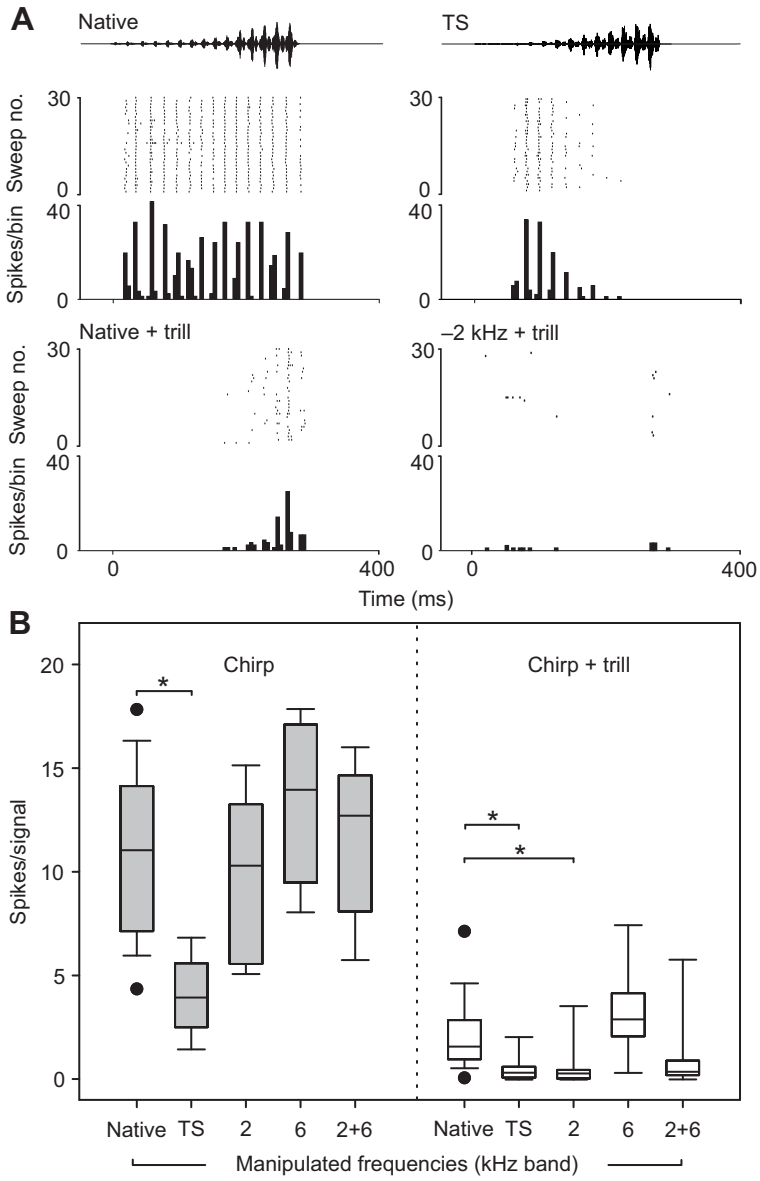

Fig. 5. TN1 response to frequency-manipulated chirps in *Mecopoda* chirpers. (A) Representative examples of TN1 responses shown as raster plots and PSTHs to a chirp with the native frequency spectrum (Native) and the frequency spectrum of the trilling species but with the same waveform as the native chirp (TS). The masked condition using the chirp with the native frequency spectrum is shown beneath the native spectrum (Native + trill). The TN1 response to a 2 kHz frequency-manipulated chirp presented under masked conditions is also shown (–2 kHz + trill). (B) Average TN1 response to chirps with the native spectrum or to chirps with a manipulated frequency spectrum (2 and 6 refer to the frequency bands attenuated to the same level as in the triller spectrum. Chirps were broadcast either without noise (left; 65 dB SPL) or under masking conditions of the trill at a SNR of 0 dB (right; 65 dB SPL). Note that attenuation of the 2 or 6 kHz component has no effect for the response without masking, but that the 2 kHz component is essential for the response under masking conditions. *Significant difference (P<0.005; Mann–Whitney rank sum test; N=10). Boxes contain 25–75% of the data points, horizontal lines represent median values, black circles represent outliers and whiskers indicate the 90th and 10th percentiles.

As these results strongly indicate a significant improvement of signal detection under masking conditions if the signal contains higher energy in the 2 kHz band compared with the masker, we also examined the degree of temporal overlap between signal and masker necessary for such improvement. We introduced silent gaps of 40 ms duration into the continuous trill at intervals of 2 s, so that the 2 kHz stimulus interacted to a different degree of temporal overlap with the masker. In these experiments, the SPL of the stimulus was maintained at −6 dB relative the threshold determined under unmasked conditions, and the masker SPL was 65 dB SPL. Successively shifting the stimulus towards the silent gap in the masker reduced the probability of responses in TN1 (P<0.02, paired t-test) from 95% with complete overlap (Fig. 8, no. 1) to 32% when the stimulus coincided with the silent gap (Fig. 8, no. 5). A further shift of the stimulus towards overlap with the masker after the gap resulted in a recovery of response probability.

It should be noted, however, that in 30% of the preparations TN1 did not respond to the 2 kHz stimulus under masking conditions and, therefore, these were excluded from the statistics.

DISCUSSION

Males of the *Mecopoda* chirper species face a complicated ‘cocktail party-like’ problem when they try to communicate with either conspecific females or males in the nocturnal tropical rainforest. The general rainforest background noise in the audio and ultrasonic frequency bands may cause a strong masking effect for the perception of their chirps. Indeed, in controlled playback experiments the proportion of phase-locked chirps was reduced to 50% when presented at a SNR of −1 dB (Hartbauer et al., 2012). In addition to this background, *Mecopoda* chirpers live in sympatry, and communicate at the same time, with another species of the *Mecopoda elongata* complex, which produces highly redundant, long lasting signals at SPLs of more than 100 dB at a distance of 15 cm (Krobath, 2013). Moreover, the frequency composition of the calls of the triller and chirper species are broadly similar, so that the chances of receivers in the chirper species being able to detect the signal under the continuous noise of the triller species in the same frequency range appear to be rather low. Previous studies on other katydids have indeed demonstrated the strong detrimental effect of acoustic competition of only one species with a highly

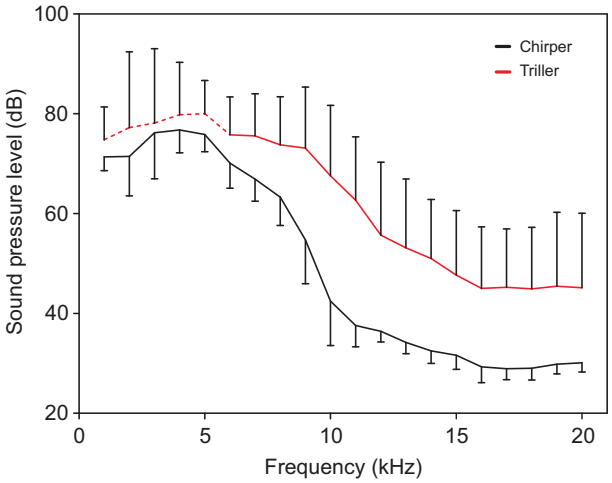

Fig. 6. TN1 threshold curves. Average threshold curve of TN1 neurons of *Mecopoda* chirpers (black; *N*=10) and triller (red; *N*=9). Error bars indicate standard deviation of the mean TN1 response. Note that some TN1 neurons in triller preparations had thresholds above 100 dB SPL at frequencies below 6 kHz. These data were excluded from statistical analysis and the reduced data set is shown as a dashed line.

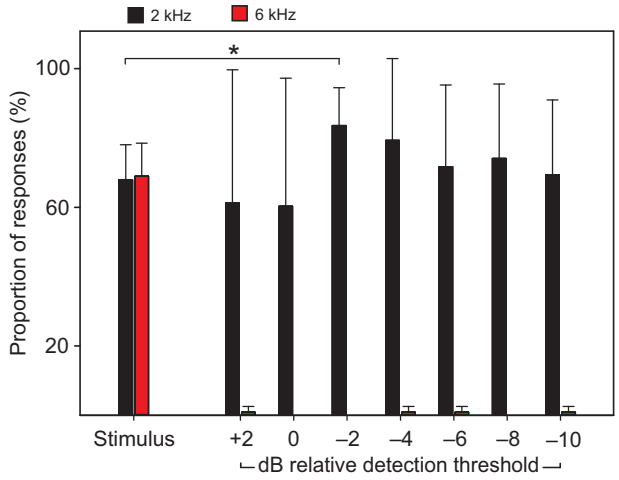

Fig. 7. Average proportion of TN1 responses at the threshold of hearing to pure tone sound pulses of 2 and 6 kHz under masking of the trill. The SPL of the trill was 65 dB; the SPL of 2 and 6 kHz sound pulses was broadcast with decreasing amplitude relative to their unmasked detection threshold. Controls without masking noise are shown on the left. Note that masking noise improves the detection of the 2 kHz sound pulse even at an attenuation of 10 dB. *N*=10 for 2 kHz pulses; *N*=4 for 6 kHz pulses. *Significant difference with *P*=0.04; paired *t*-test.

redundant signal, which can result in complete silencing of a sympatric species with discontinuous songs (Greenfield, 1988; Römer et al., 1989).

Although the same situation exists for the *Mecopoda* chirper and triller species, phase-locked synchrony of *Mecopoda* chirper males was extremely robust against high broadcast levels of calling songs of *Mecopoda* triller males. The ability to establish chorus synchrony was maintained close to 100% even at SNRs of −8 dB (Fig. 2). We concentrated our search for the mechanism of such a performance on the small difference in the spectral composition between signal and noise, given by the amount of additional energy in the signal in the narrow frequency band at 2 kHz. The second component at 6 kHz is only minute and results from the fact that both chirper and triller males have a strong frequency component close to 6–7 kHz, with a slight shift towards higher frequencies in the triller species. At higher frequencies between 9 and about 40 kHz there is more energy in the triller spectrum (Fig. 1), and frequencies higher than 40 kHz, which are in favour of the chirper signal, are rather unlikely to play a role at medium to larger sender–receiver distances because of the strong excess attenuation in the vegetated habitat (Keuper et al., 1986; Römer and Lewald, 1992). Surprisingly, without the 2 kHz component in the chirp signal, its perception under the masked condition is rather limited, and the proportion of chirps phase-locked to the stimulus is reduced to 50% at a SNR as high as +7 dB. Thus, the noise tolerance in the *Mecopoda* chirper appears to differ strongly between rainforest noise, composed of various heterospecific signals differing in amplitude modulation and spectral content, and the trill, in which trains of syllable pairs with rather constant frequency content are regularly repeated. Entrainment experiments revealed that only the former exerts a strong impact on the perception of conspecific signals (Hartbauer et al., 2012). Frequency differences between conspecific calls and a chorus background also enable frogs to segregate concurrent vocalisations, such as those encountered in mixed-species breeding choruses (Nityananda and Bee, 2011).

We focused our search for a neuronal correlate of the high noise tolerance on the TN1 neuron, for several reasons. In a previous study we demonstrated a reliable response in this neuron to conspecific chirps under masking conditions of rainforest noise at a SNR of 0 dB, but almost no response to the noise itself (Siegert et al., 2011). Under the same conditions a selective response to conspecific signals was reduced in the activity of the ON1 (Hartbauer et al., 2012), which is corroborated in our present finding that calling songs of the *Mecopoda* triller strongly masked ON1 responses to conspecific chirps (Fig. 3). This would suggest that ON1 plays a minor role for the detection of conspecific signals under masking conditions. Finally, the homologous TN1 neuron was described in the katydid *Neoconocephalus retusus* (Schul et al., 2012), where it forms the basic mechanism of a neuronal 'novelty detector' that probably enables the detection of predator-related signals (e.g. echolocation calls of bats) while receivers are listening to their conspecific, highly repetitive calling songs. We propose here that a similar mechanism is functional in the TN1 of *Mecopoda* chirpers as well, providing a neuronal novelty detector for conspecific signals rather than predator cues. Neurophysiological experiments revealed that an initial TN1 response to the trill almost completely vanished a few seconds after trill onset. A similar adaptation in spike frequency was absent during playback of conspecific chirps. Therefore, a mechanism known as stimulus-specific adaptation (SSA) (Ulanovsky et al., 2003) seems to be responsible for the selective TN1 response under masking noise conditions. SSA is defined as reduced neuronal activity in response to a highly repetitive stimulus, whereas a reliable neuronal response is maintained to another, often irregular, stimulus. In consequence, receivers are able to perceive and respond to sudden changes in the auditory scene, as reported previously (Schul et al., 2012). Importantly, the 'novelty' character of the conspecific chirp under masking with the trill appears to be entirely based on the small frequency difference between signal and noise at 2 kHz, in both the behavioural entrainment and neurophysiological experiments, as the response of TN1 completely disappeared after frequency manipulation of chirps at 2 kHz. When the spectrum of the chirp was manipulated into a trill spectrum without affecting its temporal structure, the response of TN1 was

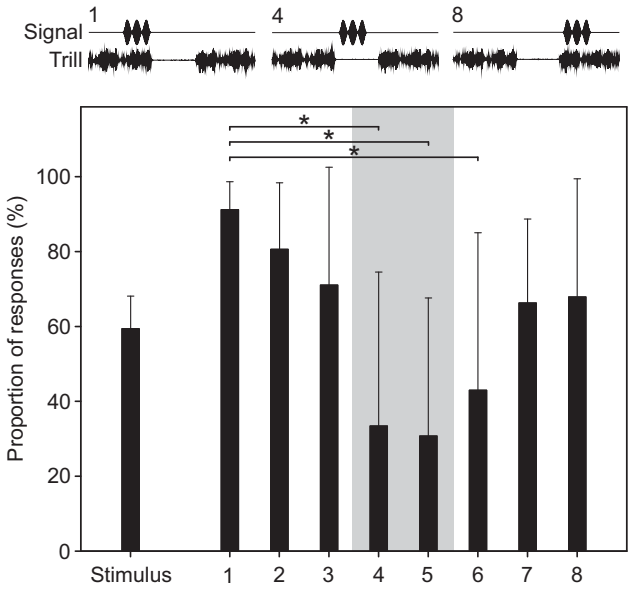

Fig. 8. Test for temporal coincidence of signal and masker for the enhanced threshold response in TN1. Average proportion of TN1 responses to 2 kHz sound pulses with a different temporal relationship to silent gaps inserted in the masker. Note that in no. 1 in the indicated example, signal and masker overlapped entirely before the silent gap, but no overlap occurred in nos 4 and 5; total overlap again occurred after the gap in no. 8. Data from six *Mecopoda* chirpers. Significant difference with $P<0.02$; paired *t*-test.

reduced and clearly different even in the non-masking condition. This indicates that the excess components in the frequency range higher than 9 kHz and/or a missing 2 kHz component induce a stronger SSA due to the fast, repetitive syllables in the chirp, so that responses to the last, high amplitude syllables are prohibited (Fig. 5A).

The frequency spectra of calling songs of five *Mecopoda* species from India also show a more or less strong frequency band around 2 kHz (Nityananda and Balakrishnan, 2006), which suggests that low frequency signal components are widespread in the genus *Mecopoda* and potentially improve signal detection in a noisy habitat. The enhancing role of the heterospecific trill for signal detection of the chirp was also demonstrated in our additional experiment, where we manipulated the amount of temporal overlap between masker and a pulsed 2 kHz signal. When the signal coincided with a short time gap in the series of double syllables of the masker, the response probability was significantly reduced (Fig. 8). Thus, it appears that long time constants at the neuronal level are not involved in this enhancing effect.

A frequency difference between the masker (in this particular case the conspecific signal) and the echolocation call of bats was also a prerequisite in the selective TN1 response to the bat call (Schul et al., 2012). Such differences in frequency composition also contributed to the discrimination of calling songs in a behavioural study with the sympatrically occurring *Tettigonia cantans* and *T. viridissima* (Schul, 1998). As a possible sensory mechanism, more receptor cells were found to be tuned to the species-specific low frequency component of 8 kHz, which is enhanced in *T. cantans*, rather than 10–12 kHz, where calling songs of both species exhibit a second peak. In contrast, tuning of receptor cells is more evenly distributed in the array of receptor cells of *T. viridissima* (Schul, 1999).

An unexpected finding in our study was the improvement of the detection of a signal at 2 kHz by the heterospecific masking trill (Fig. 7). When the SPL of the signal was adjusted to the threshold, a reduction by only 1 dB caused a reduction in response probability below the predefined threshold level of 50% without the masker, but under masking conditions the SPL of the signal could be reduced by 10 dB without causing a drop in responses. Response probability was even increased at some levels compared with the unmasked condition. This result deviates from earlier reports demonstrating that even high amplitude, low frequency sound (<10 kHz) elicited weak TN1 responses in *Ancistrura nigrovittata* (Stumpner and Molina, 2006) and *Tettigonia viridissima*, where such low frequency components do not occur in the spectrum (Schul, 1997). Furthermore, low frequency components of *Neoconocephalus ensiger* calling songs even inhibited the TN1 response to ultrasound signal components (Faure and Hoy, 2000b). A positive effect of noise on signal detection in *Mecopoda* chirpers thus appears comparable with the phenomenon of stochastic resonance, which improves the detection of subthreshold fluctuating signals by adding a weak random noise (Wiesenfeld and Moss, 1995). Meanwhile, this mechanism was found in different sensory systems of various species including insects (Levin and Miller, 1996; Spezia et al., 2008), frogs (Bibikov, 2002), mammals (Frisina et al., 1996; Lewis and Henry, 1995; Henry, 1999) and humans (Zhang-Cai et al., 2004; Zeng et al., 2000). However, for two reasons we are not sure whether the phenomenon of enhanced detection of the signal due to background of the trill is identical to stochastic resonance. First, in our experiments the masker was presented at 65 dB SPL, and thus at least 30 dB above the threshold of TN1, which is below 30 dB SPL between 15 and 20 kHz (Fig. 6). Usually, stochastic resonance is found in non-linear systems that are close to their excitation threshold (Lewis and Henry, 1995; Henry, 1999; Tougaard, 2000). However, although the masker was broadcast in our experiments more than 30 dB above the excitation threshold of TN1, the low frequency component in the masker remained subthreshold, as evident in the tuning of the cell. Second, the range of facilitation (about 10 dB; Fig. 7) of the TN1 response appears to be larger than in reported cases of stochastic resonance (e.g. Wiesenfeld and Moss, 1995; Levin and Miller, 1996). Thus, in order to compare these two phenomena, future experiments are necessary in which the experimental paradigms typical for classical reports of stochastic resonance will be used in the *Mecopoda* system.

Schul and colleagues have shown that 'novelty detection' in TN1 of *Neoconocephalus retusus* depends on distinctly different carrier frequencies of transient signals and an on-going pulse train (Schul et al., 2012). They suggested that dendritic processes, rather than receptor cell habituation, contribute to this receiver performance. For *Mecopoda* chirpers we propose a modified dendritic process to be responsible for an improved detection of a chirp with a 2 kHz component in the presence of a highly repetitive train of heterospecific syllables. The detection of the low frequency component in the chirp may be facilitated by a non-linear recruitment of receptors with best frequencies in the low frequency range and strongly overlapping tuning curves.

In katydids, receptors sensitive to airborne sound are tonotopically arranged in the crista acustica (Stumpner, 1996; Strauß et al., 2012), and receptors tuned to low frequencies are located at the proximate end of the array next to the intermediate organ, which is sensitive to both substrate-borne vibrations as well as low frequency airborne sound (Kalmring et al., 1993) [for similar results in cave crickets see Cokl et al. (Cokl et al., 1995)]. Stölting and Stumpner described a 'physiological break' in the frequency tuning of cells in the

intermediate organ of *Pholidoptera griseoaptera*, whereby receptor cells of the proximal part were most sensitive to frequencies below 10 kHz (Stölting and Stumpner, 1998). Even the subgenual organ as the classical vibration-sensitive organ in insects is sensitive to low frequency airborne sound (Shaw, 1994). Such tuning characteristics of the crista acustica and the intermediate organ may constitute adaptations to low frequency components in intraspecific communication signals, which may also exist in *Mecopoda* chirper where it may facilitate signal detection under noisy conditions. In *Mecopoda* chirper the crista acustica consists of 48±2 receptors (Strauß et al., 2012) and thus 15 receptor cells more compared with the ear of *G. gratiosa*. Therefore, 2 kHz components in the chirp may lead to a recruitment of a higher number of low frequency tuned receptors and/or to the additional activation of those of the intermediate and subgenual organ. A coincidence of this 2 kHz component with the trill may result in the non-linear summation of excitatory postsynaptic potentials in the dendrite of TN1 neurons. Obviously, intracellular studies with the TN1 neuron are badly needed for future experiments to validate such postulated subthreshold phenomena.

A further unsolved problem is the finding that males were able to maintain phase-locked synchrony at a SNR of as low as −8 dB in entrainment experiments, but in this situation only about one-third of chirps evoked a TN1 response at all. Thus, in preliminary experiments we investigated the ability of *Mecopoda* chirper males to phase-lock their chirps to playbacks of chirp sequences broadcast at 65 dB SPL in which 67% of randomly selected chirps were removed, thus leaving only 33% of chirps in the playback sequence. With this approach we simulated an unknown ‘decision maker’ looking at the response probability of TN1 for synchronous entrainment by assuming that TN1 is the only neuron providing the information. Males were unable to uphold phase-locked entrainment with this rudimentary stimulus, which may indicate that we need to reject the hypothesis that TN1 neurons are the only basis of noise-robust entrainment. Clearly, further studies are needed to identify the proximate mechanisms at the first synaptic level between receptors and identified interneurons that are involved in selective chirp encoding under noisy conditions.

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AUTHOR CONTRIBUTIONS

M.E.S. conducted the experiments and performed analysis. All authors contributed equally to drafting, writing and revising the article.

COMPETING INTERESTS

No competing interests declared.

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