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Research Paper

The heterospecific calling song can improve conspecific signal detection in a bushcricket species

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ABSTRACT

In forest clearings of the Malaysian rainforest, chirping and trilling *Mecopoda* species often live in sympatry. We investigated whether a phenomenon known as stochastic resonance (SR) improved the ability of individuals to detect a low-frequent signal component typical of chirps when members of the heterospecific trilling species were simultaneously active. This phenomenon may explain the fact that the chirping species upholds entrainment to the conspecific song in the presence of the trill. Therefore, we evaluated the response probability of an ascending auditory neuron (TN-1) in individuals of the chirping *Mecopoda* species to triple-pulsed 2, 8 and 20 kHz signals that were broadcast 1 dB below the hearing threshold while increasing the intensity of either white noise or a typical triller song.

Our results demonstrate the existence of SR over a rather broad range of signal-to-noise ratios (SNRs) of input signals when periodic 2 kHz and 20 kHz signals were presented at the same time as white noise. Using the chirp-specific 2 kHz signal as a stimulus, the maximum TN-1 response probability frequently exceeded the 50% threshold if the trill was broadcast simultaneously. Playback of an 8 kHz signal, a common frequency band component of the trill, yielded a similar result. Nevertheless, using the trill as a masker, the signal-related TN-1 spiking probability was rather variable. The variability on an individual level resulted from correlations between the phase relationship of the signal and syllables of the trill. For the first time, these results demonstrate the existence of SR in acoustically-communicating insects and suggest that the calling song of heterospecifics may facilitate the detection of a subthreshold signal component in certain situations. The results of the simulation of sound propagation in a computer model suggest a wide range of sender-receiver distances in which the triller can help to improve the detection of subthreshold signals in the chirping species.

1. Introduction

In the nocturnal tropical rainforest, many insect and anuran species communicate via airborne sound simultaneously. In this situation, which is somewhat like that of a cocktail party, the background noise level is usually high (Lang et al., 2005; Riede, 1997; Ellinger and Hödl, 2003; Hartbauer et al., 2010; Römer, 2013), and receivers must face challenges while listening and responding to the signals of conspecifics due to potential masking interference (Bee and Micheyl, 2008). Signalers usually evaluate the temporal signal pattern to discriminate conspecific from heterospecific signals, but this task is difficult to perform when a multitude of heterospecific signals degrade the amplitude modulations of calling songs that contain information about species identity. Some animals have found a solution to this problem in that the frequency of their calling songs matches the sensitivity of the receiver (Schmidt and Römer, 2011; Schmidt et al., 2012). However, this type of frequency tuning in receivers is less effective in communication systems whereby the signaler generates songs with more broadband frequencies. This is exactly the case in many bushcricket species in which the males attract phonotactically-responding females from a distance.

In the genus *Mecopoda*, several sibling species are morphologically similar, but these can easily be distinguished by differences in their species-specific calling song patterns (Nityananda and Balakrishnan, 2006; Siegert et al., 2011; Schneider and Römer, 2016). Two *Mecopoda* species live sympatrically in forest clearings

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Abbreviations

SR	Stochastic resonance
TN-1	T-shaped interneuron
SPL	Sound pressure level
SNR	Signal-to-noise ratio
ISI	Interspike intervals

of the Malayan tropical rainforest: a trilling species and a chirping species, the males of which advertise themselves by producing periodic signals with frequency compositions that strongly overlap those of the songs of the trilling species (Fig. 1). Since both species are active at the same time (i.e., after sunset), and the calling songs of the trilling species are of high intensity, it was expected that the trilling species' song would mask the calling song of the chirping species. On the contrary, Siegert et al. (2013) demonstrated that a rather low frequency component at 2 kHz allowed males to establish synchronous entrainment even when the trill of the sympatric *Mecopoda* species was broadcast 8 dB louder than the conspecific calling song. This frequency component is weak in the calling song of the trilling species but rather high in the chirping one. Surprisingly, Siegert et al. (2013) found an improvement in the detection of periodic 2 kHz signals in the response of an auditory neuron (TN-1) when the heterospecific masking trill was broadcast simultaneously. This unexpected result may be attributed to a phenomenon known as stochastic resonance (SR), which explains noise-enhanced signal detection due to the resonance of random and uncorrelated noise with the signal (Benzi et al., 1981; Benedix et al., 1994; Wiesenfeld and Moss, 1995).

SR refers to a paradox phenomenon that improves the sensitivity of a system to external stimuli at rather weak levels of noise (e.g., Collins et al., 1995, 1996; Gluckman et al., 1996; Gammaitoni et al., 1998; Russell et al., 1999; Henry, 1999; Tougaard, 2000; Ward et al., 2002; Lyttle, 2008). Noise is usually considered to be something detrimental that should be minimized whenever possible; however, noise is enhancing the detection of weak periodic signals in certain cases. Therefore, McDonnell and Abbott (2009) described SR as a “noise benefit in a signal-processing system”, or “noise-enhanced signal processing”. Low levels of stochastic noise usually improve the detection of subthreshold signals, while higher noise levels adversely affect signal detection because signals are masked by noise (e.g., Collins et al., 1996; Gammaitoni et al., 1998; Henry, 1999).

To date, SR has been found in many different receiver systems, either of biological or technical origin. SR has generally been found in a nonlinear input-output system (for an exception, see Fuliński and Góra, 2000) when signals are broadcast at subthreshold levels (but see Collins et al., 1995) and moderate levels of noise are added. The detection of subthreshold, periodic signals is improved, which reduces the probability of missing signals by increasing the hit rate at the same time according to signal detection theory (Tougaard, 2002). SR can be investigated by studying the receiver's ability to detect signals during steadily-increasing noise levels.

Several studies have shown that SR can improve signal detection in various organisms. For example, SR seems to improve the sensitivity of mechanoreceptor hair cells in the crayfish (Douglass et al., 1993). SR was also found in a study by Russell et al. (1999), who investigated the feeding behavior of paddlefish. Their results demonstrated that the success of capture rate was increased in the presence of low electrical background noise levels. Moreover, Levin and Miller (1996) conducted SR experiments to examine the cercal system of crickets. They believe that adding noise to a weak periodic air flow is improving the detection of predatory wasps. SR was additionally found to play a role in the mating system of the stink bug *Nezara viridula*, in which it improved the detection of weak vibratory signals in a noisy environment (Spezia et al., 2008). As another positive effect, SR was found to improve the nervous processing of auditory information in the brains of frogs. In this case, the response of midbrain auditory neurons to a weak periodic input signal was enhanced in the presence of broadband noise (Ratnam and Feng, 1998; Bibikov, 2002).

Currently, it is unclear whether SR plays a vital role in acoustically-communicating organisms that live in habitats that have rather high levels of background noise such as the nocturnal tropical rainforest. One reason for this lack of knowledge is that many SR studies use white noise as a masker because the characteristics of this artificial noise strongly deviates from natural signals that are characterized by a species-specific spectral content as well as temporal structure. Furthermore, the noise intensity must be moderate to favor SR, which is not necessarily the case when heterospecific signalers are in close proximity to one another or when their signals are of high intensity. In order to study whether SR improves the acoustic communication in *Mecopoda*, we studied the

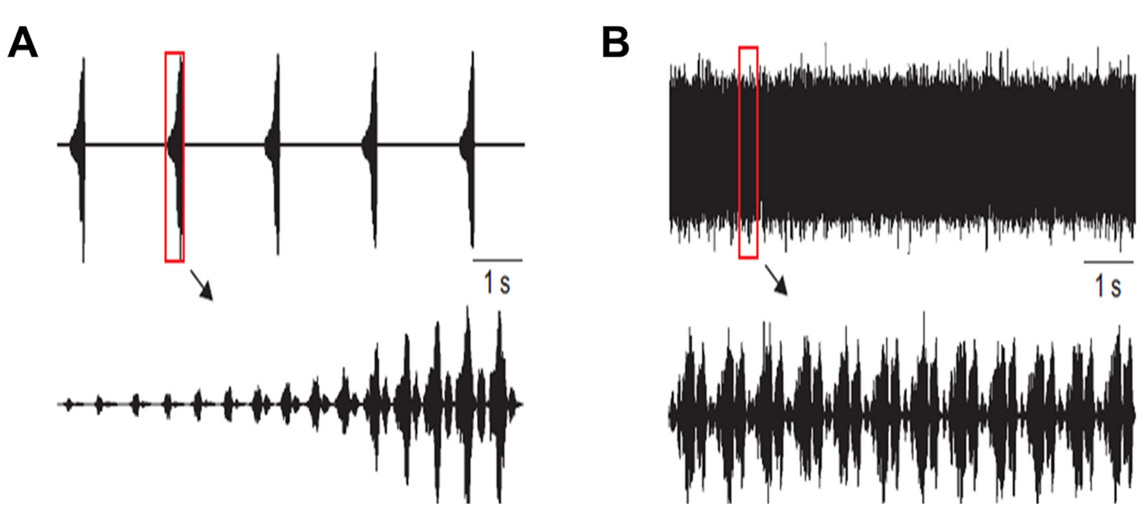

Fig. 1. Oscillograms of the calling song of the two *Mecopoda* species (reprinted with permission from Siegert et al., 2013). (A) Calling song of the chirping species and the temporal pattern of a single chirp (below). (B) Calling song of the trilling species and the train of syllables magnified below. A two-second part of this trill was used for playback in this study.