



## Research paper

# Spatial release from masking in a free-field source identification task by gray treefrogs

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## ABSTRACT

Humans and other animals often communicate acoustically in noisy social groups, in which the background noise generated by other individuals can mask signals of interest. When listening to speech in the presence of speech-like noise, humans experience a release from auditory masking when target and masker are spatially separated. We investigated spatial release from masking (SRM) in a free-field call recognition task in Cope's gray treefrog (*Hyla chrysoscelis*). In this species, reproduction requires that females successfully detect, recognize, and localize a conspecific male in the noisy social environment of a breeding chorus. Using no-choice phonotaxis assays, we measured females' signal recognition thresholds in response to a target signal (an advertisement call) in the presence and absence of chorus-shaped noise. Females experienced about 3 dB of masking release, compared with a co-localized condition, when the masker was displaced 90° in azimuth from the target. The magnitude of masking release was independent of the spectral composition of the target (carriers of 1.3 kHz, 2.6 kHz, or both). Our results indicate that frogs experience a modest degree of spatial unmasking when performing a call recognition task in the free-field, and suggest that variation in signal spectral content has small effects on both source identification and spatial unmasking. We discuss these results in the context of spatial unmasking in vertebrates and call recognition in frogs.

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## 1. Introduction

The “cocktail party problem” refers to the difficulty we have understanding speech when multiple people are speaking simultaneously (Bronkhorst, 2000; Cherry, 1953; McDermott, 2009). Importantly, this problem is not unique to humans and can be viewed in a broad, evolutionary framework as a general problem in hearing and sound communication that we share with numerous other animals (Bee and Micheyl, 2008; Hulse, 2002). Compared to our understanding of how humans perceive speech in noisy settings, however, we know little about how nonhuman animals solve evolutionarily analogous problems (Bee and Micheyl, 2008; Hulse, 2002). Such considerations are important for understanding the mechanisms and evolution of auditory perception and vocal communication, especially in light of the evolutionary

history of hearing, which had multiple, independent origins (Webster et al., 1992). Moreover, some key features of auditory systems have even arisen independently multiple times in some lineages (Christensen-Dalsgaard and Carr, 2008; Hoy, 1992; Manley et al., 2004; Schnupp and Carr, 2009; Webster et al., 1992).

A key feature of natural soundscapes that we exploit in segregating sources is spatial separation between signals of interest and competing signals or sources of noise. Signals are more easily detected or recognized when they are separated in space from other sounds compared with co-localized conditions (Gilkey and Good, 1995; Kidd et al., 1998; Litovsky, 2005; Saberi et al., 1991; Santon, 1987; Shinn-Cunningham et al., 2005). In speech recognition tasks, for example, adults with normal hearing experience a “spatial release from masking” (SRM) of about 6–10 dB when competing speech or speech-like noise is displaced from target speech by 90° in azimuth compared with a co-localized configuration (reviewed in Bronkhorst, 2000). The purpose of the present study was to investigate SRM in a sound source identification task in frogs.

Anuran amphibians (frogs and toads) are ideally suited for studies of hearing and sound communication in noisy social settings (Feng and Schul, 2007; Narins and Zelick, 1988). Male frogs often form dense breeding choruses where they compete to attract

Abbreviations: ANOVA, analysis of variance; RMS, root mean square; SD, standard deviation; SRM, spatial release from masking; SPL, sound pressure level.

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females using advertisement calls (Gerhardt and Huber, 2002). Advertisement calls are loud (e.g., 95–110 dB peak sound pressure level at 1 m; Gerhardt, 1975), sustained ambient noise levels in active breeding choruses can be quite intense (Narins, 1982; Swanson et al., 2007), and some frog choruses can be heard from distances of up to 2 km (Arak, 1983). Within a chorus, reproductive females must be able to detect advertisement calls, localize their source, and identify the source as a male of her own species (Gerhardt and Bee, 2007). The noise in breeding choruses and the concurrent calls of nearby males can reduce signal active space (Bee, 2007; Bee and Swanson, 2007; Bee and Schwartz, 2009; Gerhardt and Klump, 1988; Wollerman, 1999), impair species recognition (Bee, 2008a; Marshall et al., 2006; Schwartz, 1987; Schwartz and Gerhardt, 1995), call type discrimination (Schwartz and Gerhardt, 1989), and source localization (Marshall et al., 2006), as well as limit the expression of female mate choice preferences (Bee, 2008b; Richardson and Lengagne, 2010; Schwartz et al., 2001; Wollerman and Wiley, 2002). In spite of these challenges, female frogs nevertheless find suitable mates in the acoustic scenes of breeding choruses. Two features of the anuran auditory system present interesting challenges to understanding how female frogs segregate sources in chorus environments.

First, frog ears function as pressure-difference receivers (Christensen-Dalsgaard, 2005, 2011; Feng and Shofner, 1981). This fact has important implications for spatial hearing in frogs. In the natural setting of a chorus, frogs may commonly encounter situations in which signals of interest and competing signals or sources of noise originate from different locations. Binaural cues for source localization are negligibly small at the external surfaces of the tympanic membranes given the small size of frog heads in relation to the wavelengths of sound frequencies they typically use for communication (e.g., 0.5–7 kHz) (Christensen-Dalsgaard, 2005, 2011; Gerhardt and Bee, 2007; Rheinlaender et al., 1979). The directionality of the anuran auditory periphery arises from the interaction of sound reaching both the external and internal surfaces of each tympanic membrane. Internal pathways include transmission from the contralateral tympanic membrane or from the body wall and lungs through the mouth cavity via wide Eustachian tubes (Christensen-Dalsgaard, 2005; Gerhardt and Bee, 2007). Though we have a generally good understanding of directional hearing in frogs based on behavioral and physiological studies presenting single sound sources from multiple directions (reviews in Christensen-Dalsgaard, 2005, 2011; Gerhardt and Bee, 2007; Gerhardt and Huber, 2002), we still lack detailed knowledge about how frog ears function in the presence of multiple, simultaneous sound sources (Feng and Schul, 2007). The primary objective of the present study was to provide a quantitative assessment of the extent to which their pressure-difference ears enable frogs to exploit spatial separation between signals and noise in a free-field call recognition task.

Second, amphibians are unique among vertebrates in having inner ears with two sensory papillae that encode different ranges of airborne sound frequencies. In frogs, the amphibian papilla is tonotopically organized and encodes relatively lower sound frequencies (e.g., <1.5 kHz) compared with the basilar papilla, which is broadly tuned to higher frequencies and lacks tonotopic organization (Simmons et al., 2007; Zakon and Wilczynski, 1988). In many frog species, advertisement calls have “bimodal” frequency spectra that contain separate low-frequency and high-frequency components primarily encoded by the separate papillae in the inner ear (Gerhardt and Schwartz, 2001). A secondary goal of this study was to investigate the extent to which processing of sound frequencies primarily encoded by different sensory papillae in the inner ear might contribute to a frog listener’s ability to recognize calls and exploit spatial separation between signals and noise.

Recent psychophysical studies of phonotaxis behavior (approaches toward sound) with females of Cope’s gray treefrog (*Hyla chrysoscelis*) suggest anurans exploit some of the same spectral (Nityananda and Bee, 2011), temporal (Vélez and Bee, 2011), and spatial (Bee, 2007, 2008a, 2010) cues as humans for perceptually organizing complex acoustic scenes. Here, we used phonotaxis experiments to test the hypothesis that spatial separation between signals and noise results in lower signal recognition thresholds (Bee and Schwartz, 2009) in a free-field source identification task. The masker was a “chorus-shaped noise” with the long-term spectrum of natural gray treefrog choruses (Fig. 1), and it was presented either co-localized with the target signal or separated by 90° in azimuth. The target signal simulated a male gray treefrog’s advertisement call, which consists of a short pulse train (Fig. 1). In natural calls, each pulse contains prominent spectral energy at a fundamental frequency (and relative amplitude) of about 1.2–1.3 kHz (–6 to –10 dB) and a dominant second harmonic of about 2.4–2.6 kHz (Fig. 1). These two spectral components are primarily encoded by the amphibian and basilar papillae, respectively (Gerhardt, 2005). In the present study, we manipulated the spectral content of the target signal so that it had either the natural, “bimodal” spectrum (1.3 + 2.6 kHz) or a “unimodal” spectrum containing either just the lower (1.3 kHz) or higher (2.6 kHz) spectral peak alone (Fig. 2). Female gray treefrogs readily respond to calls with both bimodal and unimodal spectra presented at suprathreshold levels (Bee, 2010; Gerhardt, 2005; Gerhardt et al., 2007; Nityananda and Bee, 2011). This manipulation of the target signal’s spectral composition allowed us to assess signal recognition thresholds and the magnitude of spatial unmasking when signals contained frequencies encoded primarily by the amphibian papilla, the basilar papilla, or both.

## 2. Materials and methods

### 2.1. Subjects

Our experiments were conducted between May 15 and July 1, 2010, with female gray treefrogs (*H. chrysoscelis*) of the western mitochondrial DNA lineage (Ptacek et al., 1994). Frogs were collected as breeding pairs in amplexus between 2130 and 0200 h from local ponds and wetlands located in the Carver Park Reserve (Carver Co., Minnesota, U.S.A.), the Crow-Hassan Park Reserve (Hennepin Co., Minnesota, U.S.A.), and the Lake Maria State Park (Wright Co., Minnesota, U.S.A.). Upon return to the laboratory, frogs were maintained at approximately 2 °C to delay egg deposition until tested. On the day of testing, subjects were placed in an incubator set to 20° C until their body temperatures reached 20 ± 1 °C (within 30–45 min), at which time testing commenced. After testing, we reunited subjects with their chosen mates and returned them to their location of capture (usually within 48 h of collection). A total of 164 females were used as subjects in this study, which was carried out in strict accordance with recommendations in the *Guide for the Care and Use of Laboratory Animals of the National Institutes of Health*. Our experimental procedures were approved by the University of Minnesota Institutional Animal Care and Use Committee (#0809A46721).

### 2.2. Acoustic stimuli

#### 2.2.1. Target signals

We conducted no-choice phonotaxis trials (Gerhardt, 1995) in which subjects were presented with an attractive target signal in the presence or absence of masking noise. We used three different target signals (Fig. 2), each consisting of a string of 32 pulses with identical gross-temporal properties that were based on average

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