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Sound source segregation in grey treefrogs: spatial release from masking by the sound of a chorus

MARK A. BEE
Department of Ecology, Evolution, and Behavior, University of Minnesota, Twin Cities

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Animals that communicate acoustically in noisy social environments face the problem of perceptually segregating behaviourally relevant signals from background noise. Studies of humans indicate improvements in speech perception tasks when target speech and a masking noise with the frequency spectrum of speech come from different locations. Thus for humans, spatial release from masking is an important mechanism of sound source segregation that functions in acoustic communication in noisy, real-world environments. Little previous work has investigated the mechanisms of sound source segregation in nonhuman animals that rely on acoustic signalling. I investigated spatial release from masking in the grey treefrog, *Hyla chrysoscelis*. Grey treefrogs form large breeding aggregations in which males produce loud advertisement calls that are necessary and sufficient for species recognition, source localization and selective mate choice by females. I tested the hypothesis that females would experience a release from masking when a synthetic advertisement call (target signal) and an artificial noise with the spectrum of a grey treefrog chorus (masker) were spatially separated. Using a phonotaxis paradigm, I assessed females' responses to the target signal at four signal-to-noise ratios (SNR) and two angular separations. Female responsiveness to the target signal increased as the SNR increased from −12 dB to +6 dB. More important, phonotaxis responses were faster at a 90° angle of signal−masker separation compared to one of just 7.5°. These results support the hypothesis that spatial release from masking is a potentially important mechanism for sound source segregation in animal acoustic communication.

Keywords: acoustic communication; cocktail party problem; communication; grey treefrog; *Hyla chrysoscelis*; receiver psychology; sound source segregation; spatial release from masking; spatial unmasking; vocal communication

Acoustic communication mediates diverse animal behaviours (Hauser 1996; Bradbury & Vehrencamp 1998; Owings & Morton 1998). To understand the magnitude of the computational problems involved in perceiving acoustic signals in the real world, it is important to appreciate that acoustic signals and other environmental noises are composed of sound pressure waves that add together to form a single complex pressure waveform that impinges on a receiver's hearing organs. Hence, receivers face a fundamental problem known as 'sound source segregation', which involves perceptually segregating behaviourally relevant acoustic signals from the numerous sources of masking and interfering noise in the environment (Klump 1996; Fay & Popper 2000; Cooke & Ellis 2001; Carlyon 2004; Brumm & Slabbekoorn 2005; Langemann & Klump 2005).

A familiar and well-studied example of human sound source segregation is the aptly named 'cocktail party problem' (Cherry 1953; Bronkhorst 2000), which refers to the difficulty we have in perceiving speech under noisy social conditions. Studies of sound source segregation in humans have identified a number of mechanisms that contribute to a release from masking by exploiting spectral, temporal and spatial features of the multiple sound sources in the environment. For example, human listeners experience improved speech perception when two competing speech signals differ in frequency (e.g. Brokx & Nooteboom 1982). Humans also experience improved speech perception in noise by exploiting 'dips' in the

Correspondence: M. A. Bee, Department of Ecology, Evolution, and Behavior, University of Minnesota, 100 Ecology, 1987 Upper Buford Circle, St Paul, MN 55108, U.S.A. (email: mbee@umn.edu).

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amplitude envelope of temporally modulated maskers (e.g. Gustafsson & Arlinger 1994; Dubno et al. 2002; Nelson et al. 2003; Fullgrabe et al. 2006). Correlated envelope fluctuations across the spectrum of a temporally modulated masker may also contribute to improved speech perception in the form of 'comodulation masking release' (e.g. Grose & Hall 1992; Festen 1993; Kwon 2002). Finally, numerous studies of a phenomenon known as 'spatial release from masking' or 'spatial unmasking' (Shinn-Cunningham et al. 2005) have reported improvements in speech perception when a speech signal and a so-called 'speech-shaped' masker (noise with the frequency spectrum of natural speech) are perceived as originating from different locations (e.g. Bronkhorst & Plomp 1992; Arbogast et al. 2002; Culling et al. 2004; Hawley et al. 2004).

Compared to the vast literature related to the human cocktail party problem, relatively few studies have investigated the mechanisms of sound source segregation in the context of animal acoustic communication (Feng & Ratnam 2000; Hulse 2002; Bee & Micheyl, in press). Yet, for animals that acoustically communicate in large social aggregations, such as many insects, frogs and birds, the problem of perceiving acoustic signals is equivalent to the human cocktail party problem because the signals of other conspecifics represent a particularly potent source of masking noise (Klump 1996; Aubin & Jouventin 1998; Brumm & Slabbekoorn 2005; Langemann & Klump 2005; Bee & Micheyl, in press). In addition, for receivers that extract information in extended communication networks (McGregor 2005), for example, by eavesdropping on acoustic interactions between other individuals (Otter et al. 1999; Peake et al. 2001, 2005), sound source segregation is imperative for accurately assigning signals to the correct signallers. Further insights into the perceptual mechanisms that facilitate acoustic communication in a noisy world could be made by investigating sound source segregation in the acoustic communication systems of nonhuman animals.

Anuran amphibians (frogs and toads) represent a taxonomic group for which sound source segregation is likely to be especially important for acoustically mediated behaviours. During periods of active breeding, frogs often form large, multispecies aggregations in which males produce loud, species-specific advertisement calls. In many species, these calls are both necessary and sufficient for species recognition and source localization, and they are important in female mate choice and male–male competition (reviewed in Gerhardt & Huber 2002; Gerhardt & Bee 2006; Wells & Schwartz 2006). Previous studies suggest that the high levels of background noise generated in a chorus can potentially mask the perception of acoustic signals (Gerhardt & Klump 1988; Wollerman 1999; Schwartz et al. 2001; Wollerman & Wiley 2002). Results from previous behavioural (Schwartz & Gerhardt 1989) and neurophysiological (Ratnam & Feng 1998; Lin & Feng 2001, 2003) studies suggest that spatial release from masking might contribute to sound source segregation in frogs.

The aim of the present study was to test the hypothesis that spatial separation between an advertisement call (the target signal) and a 'chorus-shaped' noise (the masker) leads to an improvement in call perception in grey treefrogs, *Hyla chrysoscelis*. In this study, the masking noise had a spectrum simulating that of a natural chorus. A chorus-shaped masker parallels the use of speech-shaped maskers in previous human studies of masked speech perception. I used a 'no-choice' paradigm (Gerhardt 1995; Ryan & Rand 2001) in which I broadcast a synthetic mating call of known attractiveness to gravid females. I compared responses in unmasked reference conditions (target signal alone) to conditions in which the target signal was broadcast in the presence of the chorus-shaped masker at one of four signal-to-noise ratios (SNRs: −12 dB, −6 dB, 0 dB and +6 dB) and one of two levels of angular separation between the signal and masker (7.5° and 90°). One general prediction was that female responsiveness would increase as a function of increasing SNR, as shown in other frogs (Ehret & Gerhardt 1980; Wollerman 1999; Wollerman & Wiley 2002). According to the spatial unmasking hypothesis, I predicted that females would also show increased phonotaxis towards the target signal when the signal and chorus-shaped masker were separated by 90°.

METHODS

Subjects and Study Sites

Hyla chrysoscelis (Cope's grey treefrog) is the diploid member of a cryptic diploid–tetraploid species complex; *Hyla versicolor* (the eastern grey treefrog) is the tetraploid (Gerhardt 1994; Ptacek et al. 1994; Holloway et al. 2006). The two species have spectrally similar advertisement calls that differ primarily in their temporal properties (Gerhardt 2001). Both grey treefrogs are common in Minnesota, where this study was conducted, and occur in broad areas of sympatry throughout the state. Isolated populations of pure *H. chrysoscelis* can be found south and west of Minneapolis and Saint Paul. Nightly collections of gravid females were made between 5 May and 29 June 2006 from ponds and marshes at three field sites located within 80 km of the Saint Paul campus of the University of Minnesota. These field sites included areas of both current allopatry (Carver Park Reserve, Carver County, MN, 44°55′06″N, 93°23′42″W) and sympatry with *H. versicolor* (Lake Maria State Park, Wright and Sherburne counties, MN, 45°01′17″N, 93°30′21″W; Tamarack Nature Center, Ramsey County, MN, 45°06′02″N, 93°02′09″W). I collected females in amplexus between 2100 and 0200 hours, stored the pairs in small plastic containers, and returned them to the laboratory where they and their mates were maintained at 2°C to delay egg deposition prior to testing.

General Testing Procedures

On the day of testing, the pair was transferred to a 20°C incubator and held there at least 1 h until their body temperatures had reached 20 ± 1°C. For testing, the female was separated from her mate, tested in a phonotaxis test, and then returned to her mate in the incubator where