



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

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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  $90^\circ$  angle of signal–masker separation compared to one of just  $7.5^\circ$ . These results support the hypothesis that spatial release from masking is a potentially important mechanism for sound source segregation in animal acoustic communication.

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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

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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

they both remained until the female was tested in a subsequent test. All phonotaxis tests were performed at  $20 \pm 2^\circ\text{C}$ . For females collected from populations that are sympatric with *H. versicolor*, I always tested the female in an initial two-choice discrimination experiment in which I alternated broadcasts of natural *H. chrysoscelis* and *H. versicolor* calls to confirm the female's species identity. Only females that approached the *H. chrysoscelis* call were used as subjects in this study. At the completion of all testing (typically within 1–3 days of collection), I released females with their mates at their original location of capture.

I tested females in a temperature-controlled, walk-in sound chamber (inside dimensions:  $245 \times 215 \times 250$  cm,  $L \times W \times H$ ). The floor of the chamber was covered by black carpet with a Quiet Floor NP (Acoustical Surfaces, Inc., Chaska, MN, U.S.A.) sound control floor underlay. The inside walls and ceiling of the chamber were covered with dark grey melamine acoustic foam wedges (15.24 cm thick) to reduce acoustic reflections. The baseline sound pressure levels (SPL re.  $20 \mu\text{Pa}$ ) inside the chamber ranged from 9 to 20 dB SPL (fast RMS, unweighted) over the 500-Hz to 4-kHz octave bands, which span the frequency range of primary interest here. I used a Brüel & Kjær Type 2250 sound level meter to measure sound levels in the chamber and to calibrate the playback levels of acoustic signals and masking noises. Sound level measurements were made by placing the microphone of the sound level meter at the approximate position of a female's head at the location from which females were released.

I tested females under infrared (IR) illumination using two IR light sources that were mounted near the ceiling on opposite walls of the sound chamber. Behavioural responses were observed using an overhead, IR-sensitive Panasonic WV-BP334 video camera that was mounted from the centre of the chamber ceiling. The video feed from inside the chamber was monitored in real time using an analogue-to-digital encoder (Canopus) installed in a Dell Optiplex GX620 PC computer located outside the chamber. Acoustic signals and masking noises were broadcast through A/D/S L310 speakers using a second Dell Optiplex GX620 computer also located outside the chamber. The acoustic stimuli consisted of digital sound files (44.1 kHz sampling rate, 16-bit resolution) that were broadcast using Adobe Audition 1.5 interfaced with an M-Audio FireWire 410 multichannel soundcard. Output from the soundcard was amplified using a Sonamp1230 multichannel amplifier (Sonance).

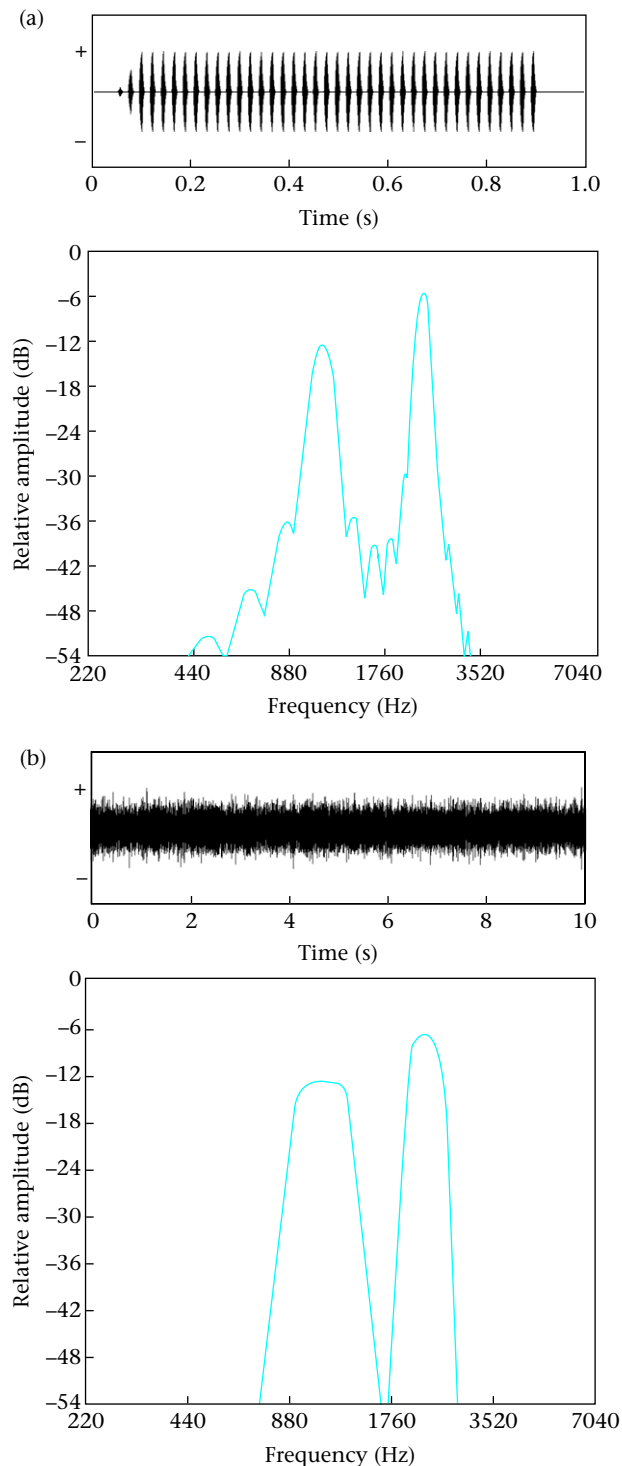
I conducted phonotaxis tests in a circular test arena (2 m diameter) inside the sound chamber. The perimeter of the arena floor was marked off into 24 bins of  $15^\circ$ . The walls of the arena were constructed from hardware cloth (60 cm high) and covered by visually opaque, but acoustically transparent, black cloth. Playback speakers were positioned on the floor of the chamber just outside the wall of the test arena and aimed towards the centre of the arena. This arena design eliminates any visual cues to the speaker location that may remain under IR illumination. Target signals were always placed at the centre of one of the  $15^\circ$  bins around the edge of the arena. At the beginning of a test, the female was removed from the

incubator and placed in a small (9 cm diameter), acoustically transparent release cage located on the floor and positioned at the centre of the test arena. Females were able to freely move about and reorient inside the release cage, and I did not quantify a female's orientation prior to her release. After a 1-min acclimation period, I started broadcasts of the target signal, which was broadcast continually during the entire duration of a test. In the masked conditions, I started broadcasting the masker 30 s into the 1-min acclimation period, which was 30 s prior to the start of the signal broadcast. After 1 min of signal presentation, I remotely released the female from the release cage using a rope and pulley system that could be operated from outside the chamber. Timing of the test began concurrently with the female's release. The absolute positions of the playback speakers around the perimeter of the circular arena were systematically varied to control for any possibility of a directional response bias in the sound chamber. No such bias was evident in female responses.

## Experimental Design

I used a series of 'no-choice' experiments in which I measured a female's latency to approach a synthetic target signal that was modelled after natural *H. chrysoscelis* calls (Gerhardt 2001). The target signal (Fig. 1a) was composed of 39 pulses that were 11 ms in duration and separated by 11-ms interpulse intervals (45.5 pulses/s; pulse duty cycle = 50%; 847-ms call duration). Each pulse was created by adding two phase-locked sinusoids with frequencies (and relative amplitudes) of 1.1 kHz ( $-6$  dB) and 2.2 kHz (0 dB). The envelope of each pulse was shaped with an inverse exponential rise time and an exponential fall time that were both 48% of the pulse duration. The temporal envelope of the call was shaped with a 50-ms linear rise time. In all tests, the target stimulus repeated with a period of 4.5 s, which corresponds to a natural calling rate in this species. Under conditions of masking, females were presented with the target signal in the presence of a continuous chorus-shaped noise (Fig. 1b). This noise was created using the Adobe Audition software to generate and digitally filter the same broadband noise of 6.5-min duration into two separate narrowband noises (440-Hz bandwidth at the 6-dB down points). The two narrowband noises had centre frequencies (and relative peak amplitudes) of 1.1 kHz ( $-6$  dB) and 2.2 kHz (0 dB). These two noises were digitally added together to create a single masking noise (Fig. 1b) that had a steady-state envelope and a frequency spectrum simulating that of a grey treefrog chorus. Females are not attracted to this chorus noise in the absence of a target signal (Swanson et al. in press).

Individual females were tested in a sequence of five phonotaxis tests and were given a brief 'time-out' of 5–15 min between consecutive tests. Three of five tests in a sequence were considered unmasked 'reference conditions'. In these conditions, the females heard the target signal presented alone at a sound pressure level of 76 dB SPL (fast RMS, C-weighted) measured at the female release site (1 m from the source). Each sequence of five tests



**Figure 1.** Oscillograms (top traces) and power spectra (bottom traces) of the digital sound files of (a) the synthetic call used as a target signal and (b) a 10-s segment from the 6.5-min long 'chorus-shaped' noise used in the masking conditions.

began with two consecutive tests of the reference condition (Reference 1 and Reference 2) and ended with a third test of the reference condition (Reference 3). The remaining two tests in a sequence were considered masked conditions in which females heard the target signal in the

presence of the chorus-shaped masker, which was presented at an overall level of 70 dB SPL (1 m from the source). This level falls within the range of background noise levels that can be measured in grey treefrog choruses (M. A. Bee, unpublished data). The two masked conditions were always tested between Reference 2 and Reference 3. In one of these two tests, the masker speaker was located adjacent to the signal speaker, which corresponded to an angular separation of  $7.5^\circ$  around the circular arena; in the other test, the masker and signal speakers were separated by  $90^\circ$  around the arena. I tested the two levels of angular separation in a randomly determined order for each subject. The relative positions of the target and masker speakers were also varied systematically so that the masker speaker was displaced to the left or right of the target speaker in approximately 50% of tests. I scored a 'no response' in the masked conditions if a female did not touch the wall of the arena in the  $15^\circ$  arc centred in front of the target speaker within 5 min. Separate groups of females were tested at one of four SNRs ( $-12$  dB,  $-6$  dB,  $0$  dB and  $+6$  dB) in the two masking conditions ( $N = 20$  per group, total  $N = 80$ ). These SNRs were created by manipulating the overall level of the target signal in the presence of the 70-dB masker, so that at the  $+6$ -dB SNR, the level of the target signal was the same in the masked conditions and the unmasked reference conditions. Hence, the design of the experiment for the masked conditions was a 2 (angular separations,  $7.5^\circ$  and  $90^\circ$ , within-subjects)  $\times$  4 (SNRs,  $-12$  dB,  $-6$  dB,  $0$  dB or  $+6$  dB, between-subjects) factorial design.

## Data Analysis

To ensure a high level of motivation over the duration of a test sequence, I used four response criteria for including a female in the final data set. These four criteria were based on her responses to the target signal in the unmasked reference conditions. First, I required that, during each test of a reference condition, females show characteristic phonotaxis movements (e.g. head scanning and zigzag patterns of walking or hopping towards the speaker). Second, I excluded females that first touched the wall of the arena in any reference condition outside of the  $45^\circ$  arc centred in front of the target speaker. Third, I only included females that eventually touched the wall of the arena inside the  $15^\circ$  arc centred in front of the target speaker within 5 min in all three reference conditions. Finally, I excluded a female if her latency to touch the wall in the  $15^\circ$  arc in front of the target speaker during the final reference condition (Reference 3) was more than twice her latency to respond in the second reference condition (Reference 2). Of the 80 females that were collected and tested in this experiment, 13 were excluded from statistical analyses because they did not meet one or more of these criteria, yielding a final sample size of 67 females ( $-12$  dB:  $N = 17$ ;  $-6$  dB:  $N = 16$ ;  $0$  dB:  $N = 17$ ;  $+6$  dB:  $N = 17$ ). I compared the latencies of these females in the reference conditions using a 3 (reference conditions, within-subjects)  $\times$  4 (SNRs, between-subjects) ANOVA with the Greenhouse–Geisser correction (Greenhouse & Geisser 1959).

To test the spatial unmasking hypothesis, I analysed normalized 'phonotaxis scores' based on a female's latency to respond to the target signal in the two masked conditions relative to her latency to respond in the unmasked reference conditions. Following previous studies (Bush et al. 2002; Schul & Bush 2002; Beckers & Schul 2004), I computed phonotaxis scores for each masking condition as a percentage by dividing the mean latency from Reference 2 and Reference 3 by a female's latency to respond to the target signal in the particular masked condition of interest. I assigned a phonotaxis score of zero if females scored a 'no response' in a masked condition. Thus, phonotaxis scores close to 100% indicate that the target signal in a masked condition was as effective at eliciting phonotaxis as the unmasked target signal in the reference conditions, whereas phonotaxis scores less than 100% indicate that the target signal was less effective at eliciting phonotaxis. I analysed phonotaxis scores using a 2 (angular separations, within-subjects)  $\times$  4 (SNRs, between-subjects) ANOVA with the Greenhouse–Geisser correction. I used a linear contrast across levels of SNR to test the general prediction that phonotaxis scores would increase as a function of increasing SNR. According to the spatial unmasking hypothesis, I further predicted that phonotaxis scores would be higher when the signal and masker were separated by 90° compared to the conditions with only 7.5° of separation between signal and masker. I used planned contrasts to test this prediction by separately comparing phonotaxis scores in the 7.5° and 90° conditions at each level of SNR. I used Statistica 7.0 to compute all ANOVAs and contrasts and used a significance criterion of  $\alpha = 0.05$  in all statistical tests.

A cautionary word about interpreting phonotaxis scores and response probabilities is in order. Because of the difficulties with conditioning frogs to respond to acoustic signals in traditional psychoacoustics experiments, phonotaxis assays represent an important tool for investigating auditory perception in frogs (Gerhardt 1995; Gerhardt & Huber 2002). One major advantage of phonotaxis is that it exploits the animals' natural behavioural repertoire to assess the biologically important perceptual tasks faced by females in nature, namely those of detecting, recognizing and localizing a calling male. Phonotaxis towards a speaker indicates that the female has detected the signal and recognizes it as that of an appropriate mate; arrival at the speaker indicates successful sound localization. Differences in response latencies and response probabilities in no-choice experiments, however, cannot readily distinguish between effects related to signal detection, sound pattern recognition and source localization. Distinguishing among effects on these three different elements of call perception was not the purpose of the present study. Rather, the purpose was to test the hypothesis that spatial unmasking improves call perception, which could include effects related to improvements in signal detection, recognition and localization. Therefore, the underlying assumption of this study was that females would show faster phonotaxis under stimulus conditions that promote spatial release from masking in the perception of male calls. The data reported below support the validity of this assumption.

## RESULTS

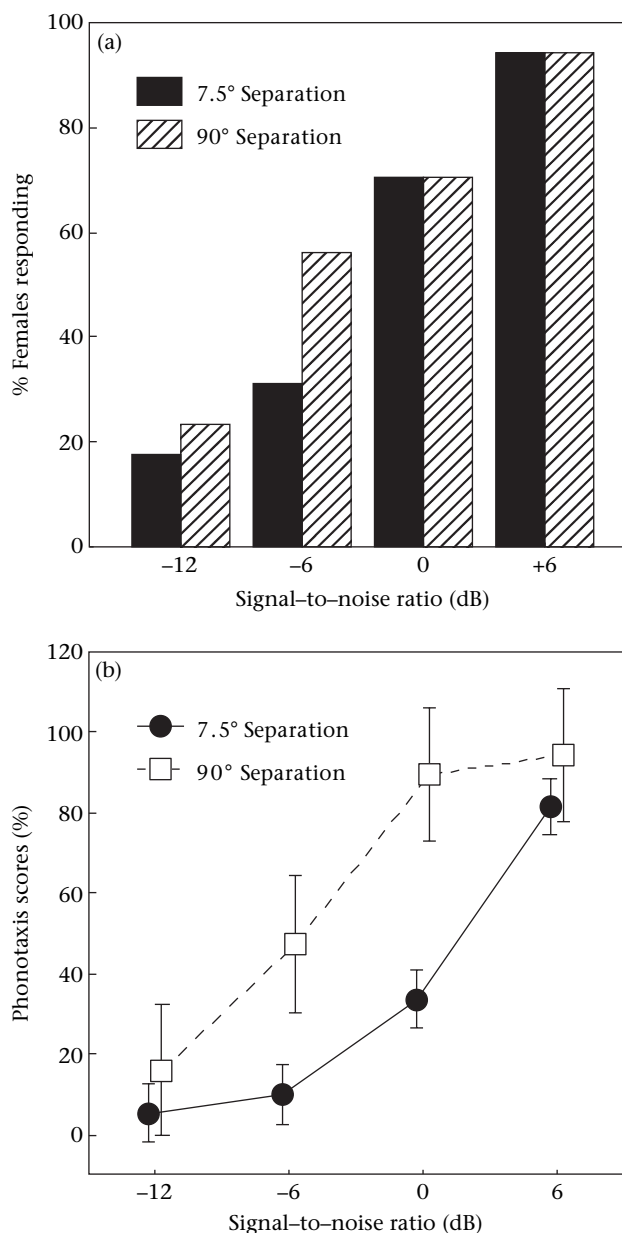
### Responses in the Unmasked Reference Conditions

The inclusion criteria were effective at including only females that showed similar high levels of responsiveness over the entire duration of a test sequence. In all three unmasked reference conditions, females typically showed positive phonotaxis directly towards the target speaker and required just over a minute to touch the arena wall in the 15° arc directly in front of the speaker. The mean  $\pm$  SE latency to touch the wall of the arena in front of the speaker varied between 65.5  $\pm$  4.1 s in Reference 2 and 71.4  $\pm$  5.4 s in Reference 1 ( $N = 67$ ). There were no significant differences in response latency across the three reference conditions, nor were there differences in latency between groups of females tested at the four SNRs (reference condition:  $F_{2,63} = 0.81$ ,  $P = 0.4194$ ; SNR:  $F_{3,63} = 1.87$ ,  $P = 0.1435$ ; interaction:  $F_{6,63} = 0.86$ ,  $P = 0.5079$ ). Together, these results confirm that response motivation did not decline over the course of repeated testing within a test sequence.

### Responses in the Masked Conditions

In the masked conditions, responsiveness increased as an increasing function of the SNR. For example, the number of females that touched the wall of the arena in the 15° arc in front of the speaker in under 5 min increased from about 20% at a SNR of  $-12$  dB to about 95% at a SNR of  $+6$  dB (Fig. 2a). The correlations between the number of responsive females and SNR were significant at both levels of angular separation (Spearman rank correlation:  $r_s = 1.0$ ,  $N = 4$ ,  $P_s < 0.05$ ). As illustrated in Fig. 2a, the number of females that responded in the 7.5° condition was lower than that for the corresponding 90° condition at SNRs of  $-12$  dB and  $-6$  dB. While this pattern of results is consistent with the spatial unmasking hypothesis, these differences were not significant in an analysis that treated the number of responsive females in the 7.5° conditions as the 'expected' frequency for responses under masked conditions and the number responding in the corresponding 90° condition as the 'observed' frequencies (over all four SNRs:  $\chi^2_3 = 3.5$ ,  $P = 0.32$ ).

An analysis of phonotaxis scores revealed both a general increase in responsiveness with increasing SNR and a release from masking when the signal and masker were separated by 90° compared to the 7.5° conditions (Fig. 2b). There were significant differences in phonotaxis scores as a function of both the angle of signal–masker separation ( $F_{1,63} = 11.8$ ,  $P < 0.0001$ ) and the SNR ( $F_{3,63} = 13.1$ ,  $P < 0.0001$ ). The two-way interaction between angle and SNR was not significant ( $F_{3,63} = 1.6$ ,  $P = 0.1946$ ). As illustrated in Fig. 2b, phonotaxis scores increased with increasing SNR, and a linear contrast comparing phonotaxis scores as a function of SNR was significant ( $F_{1,63} = 38.9$ ,  $P = 0.0016$ ). As predicted by the spatial unmasking hypothesis, phonotaxis scores were generally higher in the 90° conditions than in the 7.5° conditions across all levels of SNR (Fig. 2b), and these differences were significant at



**Figure 2.** Percentage of females responding and phonotaxis scores in the masked conditions. (a) Histogram showing the percentage of females that touched the wall of the arena in the 15° arc centred directly in front of the target speaker within 5 min. (b) Mean  $\pm$  SE phonotaxis scores as functions of signal-to-noise ratio and angular separation between the target signal and chorus-shaped masker. See text for calculations of phonotaxis scores.

SNRs of  $-6$  dB ( $F_{1,63} = 4.6$ ,  $P = 0.0351$ ) and  $0$  dB ( $F_{1,63} = 10.9$ ,  $P = 0.0016$ ), but not at SNRs of  $-12$  dB ( $F_{1,63} = 0.4$ ,  $P = 0.5310$ ) and  $+6$  dB ( $F_{1,63} = 0.6$ ,  $P = 0.4507$ ).

## DISCUSSION

Acoustic communication in noisy social environments is well documented in the animal behaviour literature. Some of the well-known examples include frog and insect choruses (Gerhardt & Huber 2002; Greenfield 2005),

dawn choruses of songbirds (Amrhein et al. 2004; Goriissen & Eens 2004; Liu 2004), and large crèches of juvenile bats (Balcombe 1990; Balcombe & McCracken 1992) and penguins (Aubin & Jouventin 1998, 2002). Few previous studies, however, have investigated the mechanisms of sound source segregation in animals even though such environments represent the direct animal equivalents of the human cocktail party problem (but see e.g. Schwartz & Gerhardt 1989, 1995; Hulse et al. 1997; Aubin & Jouventin 1998). The objective of this study was to investigate spatial release from masking as a potential mechanism that contributes to sound source segregation in frogs.

## Spatial Unmasking in Grey Treefrogs

The results of this study support the hypothesis that female grey treefrogs experience an improvement in call perception when a target signal and chorus-shaped masking noise are separated in space. When the SNR was low (e.g.  $-12$  dB), the target signal was effectively masked at both levels of signal-masker separation. At intermediate SNRs ( $-6$  dB and  $0$  dB), masking was less pronounced, and females experienced additional release from masking at these two SNRs when the signal and masker were separated by  $90^\circ$ . At the highest SNR ( $+6$  dB), the target signal was effectively segregated from the masker in both spatial configurations of signal and masker. The pattern of phonotaxis scores in Fig. 2b allows us to estimate the magnitude of spatial release from masking (in dB) under the conditions tested in this study. Phonotaxis scores in the  $7.5^\circ$  conditions at SNRs of, for example,  $0$  dB and  $+6$  dB were lower than those in the  $90^\circ$  conditions at a SNR that was  $6$  dB lower ( $-6$  dB and  $0$  dB, respectively), but higher than those in the  $90^\circ$  conditions at a SNR that was  $12$  dB lower ( $-12$  dB and  $-6$  dB, respectively). From this pattern, we can estimate that the magnitude of spatial unmasking, measured in dB masking release, was at least  $6$  dB, but less than  $12$  dB.

## Spatial Unmasking in Other Frogs

The results reported here for *H. chrysoscelis* bear some parallels with those reported by Schwartz & Gerhardt (1989) in an earlier study of green treefrogs, *Hyla cinerea*. In that study, females experienced spatial release from masking when signals and broadband noise ( $0.1$ – $10$  kHz) were presented at an angular separation of  $90^\circ$  compared to conditions in which the signal and masker speakers were adjacent to each other. Schwartz & Gerhardt (1989) estimated that the spatial release from masking was no more than about  $3$  dB, which is somewhat lower than that reported here. In addition to possible species-level differences, several methodological differences between the present study and that of Schwartz & Gerhardt (1989) might contribute to a difference in the estimated magnitudes of spatial unmasking. For example, females in the present study were tested with a single advertisement call in the presence of a single chorus-shaped masker, whereas females in the study by Schwartz & Gerhardt (1989) were required to behaviourally discriminate between

advertisement calls and aggressive calls in the presence of two broadband noise sources.

Recent neurophysiological studies in leopard frogs, *Rana pipiens*, have revealed spatial release from masking in the detection thresholds of auditory nerve fibres (Lin & Feng 2001) and neurons in the inferior colliculus (Ratnam & Feng 1998; Lin & Feng 2003). The magnitude of spatial release from masking was about 9 dB in inferior colliculus neurons, but only about 3 dB in the auditory nerve. Since the inferior colliculus receives input from both ears, Lin & Feng (2001) concluded that binaural processing by the central auditory system was important in spatial unmasking. This result was later confirmed in a pharmacological study that showed that inhibitory interactions in the inferior colliculus are partially responsible for spatial unmasking (Lin & Feng 2003).

### Spatial Unmasking in Other Animals

In a review of the literature on the human cocktail party problem, Bronkhorst (2000) reported magnitudes of spatial release from masking between 6 and 10 dB across various types of speech maskers when the target speech and masking noise were separated by 90°. This range is similar to that reported here for grey treefrogs and by Lin & Feng (2001) for recordings of neurons from the leopard frog midbrain. Relatively few behavioural studies of spatial release from masking are available from other nonhuman animals (reviewed in Bee & Micheyl, *in press*). One notable exception is the study of budgerigars, *Melopsittacus undulatus*, by Dent et al. (1997), which reported a maximum spatial release from masking of about 10 dB when the target signal and masking noise were separated by 90°. Ronacher & Hoffmann (2003) failed to find strong evidence for spatial release from masking in a study of the grasshopper *Chorthippus biguttulus*.

A recent study by Best et al. (2005) investigated spatial unmasking in humans using zebra finch, *Taeniopygia guttata*, songs as a target signal. Participants were trained to identify five different zebra finches by their individually distinctive song motifs. On test trials, participants were asked to correctly identify the target bird whose signals were presented from a frontal position at a SNR between -40 dB and +10 dB in the presence of one of three maskers: a zebra finch chorus, a 'chorus-shaped' noise with a steady-state envelope (similar to the present study), or a chorus-shaped noise that was modulated by the amplitude envelope of a chorus. The percentage of birds correctly identified increased with increasing SNR, and subjects identified more birds correctly when the masker was displaced from a frontal position to a lateral position of 90°. Notably, the mean psychometric functions showing the percentage of songs correctly classified as a function of both SNR and signal-masker separation (their Figure 3) bear striking similarities with the grey treefrog phonotaxis scores depicted in Fig. 2b.

### Sound Source Segregation as Receiver Psychology

A basic tenet of 'receiver psychology' is that the processing strategies used by a receiver's nervous system

influences both the evolution of communication signals and the behavioural strategies that signallers use (Guilford & Dawkins 1991, 1993; Rowe 1999; Rowe & Skelhorn 2004). Under some conditions, however, there may be constraints on the extent to which evolution can modify signals and signalling strategies to improve signal perception by receivers. Acoustic communication in dense and noisy social aggregations is probably one such condition that places demands not only on signal design and signalling strategies, but also on a receiver's perceptual system. Thus, sound source segregation and the broader concept of 'auditory scene analysis' (Bregman 1990; Feng & Ratnam 2000; Hulse 2002; Bee & Micheyl, *in press*) deserve consideration in the context of receiver psychology for animals that communicate acoustically. Anuran communication systems can serve to highlight this point.

Many previous considerations of the problem of masking in anuran choruses have focused on behavioural strategies that signallers can use to increase the probability that their signals are detected by receivers. These strategies include partitioning the frequency spectrum or the time of day by calling in locations or at times when other species with spectrally overlapping calls are not present (reviewed in Narins & Zelick 1988). Temporal separation of calling to avoid overlap with nearby neighbours (Zelick & Narins 1983; Schwartz 1993; Grafe 1996; Boatright-Horowitz et al. 2000; Greenfield & Rand 2000) and spatial separation within the available habitat (Wilczynski & Brenowitz 1988; Brenowitz 1989; Gerhardt et al. 1989; Marshall et al. 2003; Murphy & Floyd 2005) are two additional behavioural strategies that anuran signallers use to improve transmission of their signals in a chorus. But in especially dense choruses, the efficacy of these signalling strategies could break down because of unavoidable decreases in the distances between calling males (e.g. Gerhardt et al. 1989; Murphy & Floyd 2005) and increases in call overlap between neighbours (Brush & Narins 1989; Schwartz et al. 2002). Under such conditions, effective communication will depend heavily on the perceptual mechanisms of receivers.

On the receiver side, the selectivity of the anuran auditory system for temporal and spectral properties of conspecific calls is often regarded as an adaptation that improves the detection of conspecific calls by filtering out heterospecific calls (Gerhardt & Huber 2002). Indeed, receivers can evolve to become even more selective for the temporal (Gerhardt 1994) or spectral (Höbel & Gerhardt 2003; Amézquita et al. 2006) properties of conspecific calls when they breed syntopically with heterospecifics having calls with similar frequency spectra. But this selectivity for conspecific calls would contribute little towards sound source segregation in dense choruses of conspecifics. Thus, sound source segregation is likely to be an important aspect of receiver psychology in frogs.

Given that female frogs often enter a chorus from the periphery and sit and wait for several minutes while assessing different potential mates (Murphy & Gerhardt 2002; Schwartz et al. 2002, 2004), they may often encounter situations where the signals of multiple males and the general background noise of the chorus originate from different locations. Mechanisms that contribute to spatial

release from masking might be important both for segregating a male's calls from chorus background noise (Schwartz & Gerhardt 1989) and for segregating the overlapping calls of multiple individuals (Schwartz & Gerhardt 1995). The experimental approach used here and elsewhere (Schwartz & Gerhardt 1989) is admittedly artificial in that real choruses are composed of many sources located in different directions from a receiver and caution is needed when extrapolating from the laboratory to real-world listening conditions. Nevertheless, these experiments almost certainly engage perceptual mechanisms that would benefit receivers under some conditions in natural choruses. For example, as females enter the chorus from the periphery, spatial unmasking might improve the detection of males positioned near the edge of the chorus.

Investigating the mechanisms of sound source segregation is one way by which we may fundamentally improve our understanding of the perceptual mechanisms of animal acoustic communication. Such investigations also have potential to broaden our conception of receiver psychology to more explicitly include the evolution of perceptual mechanisms that allow receivers to segregate signals from noise when conditions in the real world impose constraints on signal design, behavioural signalling strategies, or both.

### Potential Applications of Studying Sound Source Segregation in Animals

Much of the interest in human sound source segregation and the cocktail party problem stems from health and technology considerations. Compared to people with healthy auditory systems, both the hearing impaired and computer algorithms for automated speech recognition have greater difficulty understanding speech under noisy conditions (Festen & Plomp 1990; Bronkhorst & Plomp 1992; Lippmann 1997; Peissig & Kollmeier 1997; Peters et al. 1998; Arbogast et al. 2005). Many of the basic sensory mechanisms for sound source segregation probably arose early in the evolution of vertebrate hearing and are shared between humans and nonhuman vertebrates (Fay & Popper 2000; Feng & Ratnam 2000; Lewis & Fay 2004). Of course, we must also remain open to the possibility that some animals might perform better than humans under some conditions. The discovery and analysis of such capabilities could uncover surprising insights into novel evolutionary solutions to problems of sound source segregation. These novel adaptations often cannot be predicted, but must be uncovered through empirical studies of an animal's sensory and communication systems. Work on sound source segregation in a diversity of animals might ultimately contribute to improvements in prosthetic hearing devices and machine-based speech recognition systems (Mason et al. 2001; Miles & Hoy 2006).

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