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Finding a mate at a cocktail party: Spatial release from masking improves acoustic mate recognition in grey treefrogs

Mark A. Bee

Department of Ecology, Evolution, and Behavior, University of Minnesota – Twin Cities

Abstract

The ‘cocktail party problem’ refers to the difficulty that humans have in recognizing speech in noisy social environments. Many non-human animals also communicate acoustically in noisy social aggregations, and thus also encounter – and solve – cocktail-party-like problems. Relatively few studies, however, have investigated the processes by which non-human animals solve sound source segregation problems in the behaviourally relevant context of acoustic communication. In humans, ‘spatial release from masking’ contributes to sound source segregation by improving the ability of listeners to recognize speech that is spatially separated from other sources of speech or ‘speech-shaped’ masking noise. Using a phonotaxis paradigm, I tested the hypothesis that spatial release from masking improves the ability of female grey treefrogs, *Hyla chrysoscelis*, to discriminate between conspecific and heterospecific calls that were spatially separated from two sources of ‘chorus-shaped’ masking noise by either 15° or 90°. As the signal-to-noise ratio (SNR) was decreased from +3 dB to –15 dB (by decreasing the signal level in 6-dB steps), fewer females made a choice and the likelihood

Corresponding Author: Mark A. Bee, Dept. Ecology, Evolution, & Behavior, University of Minnesota, 100 Ecology, 1987 Upper Buford Circle, St. Paul, MN 55108, ph: xx-1-612-624-6749, fx: xx-1-612-624-6777, email: mbee@umn.edu.

Lay Summary Finding Your Mate at a Cocktail Party

The “cocktail party problem” refers to the difficulty we have perceiving speech in noisy social environments. Improvements in speech perception can occur when attended speech and sources of masking speech originate from different locations. Animals that acoustically communicate in large social aggregations face their own cocktail-party-like problems. For example, female frogs must detect, recognize, localize, and discriminate among calling males amid the cacophony of a noisy breeding chorus. In this study, I report experimental results showing that spatial release from masking allows female grey treefrogs to solve their own equivalent of the human cocktail party problem. Females were better able to discriminate between the mating calls of males of their own species and those of a foreign species when calls were presented in the presence of a spatially-separated noise simulating a breeding chorus. These results support the hypothesis that spatial unmasking is an important perceptual mechanism in animal acoustic communication.

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of a female choosing the heterospecific call also increased. At a SNR of -3 dB, females oriented toward and chose the conspecific call in the 90° separation condition, but not when signals and maskers were separated by 15° . These results support the hypothesis that a well-known solution to the cocktail party problem in humans – spatial release from masking – also plays a role in acoustic signal recognition in animals that communicate in biological equivalents of cocktail-party-like environments.

Keywords

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

Understanding what one person is saying in a large and noisy group of talking people is a difficult, but not impossible, perceptual challenge to overcome. Over the last several decades, one important goal of research on human hearing and speech communication has been to understand how the healthy human auditory system solves this so-called ‘cocktail party problem’ (Cherry 1953; Bronkhorst 2000; Bee & Micheyl in press). Much of the interest in the human cocktail party problem stems from the observations that both people with hearing impairments and computer algorithms for automated speech recognition have difficulties understanding target speech in the presence of masking or interfering speech or speech-like noise (Bee & Micheyl in press).

Acoustic communication in many diverse non-human animal species also occurs in large social aggregations, such as a crèche or a chorus, in which the signals of unattended signallers may be a source of auditory masking or interference (Aubin & Jouventin 1998; Gerhardt & Huber 2002; Greenfield 2002; Brumm & Slabbekoorn 2005; Langemann & Klump 2005). For these animals, perceiving acoustic signals is equivalent to the human cocktail party problem (Bee & Micheyl in press). To understand the magnitude of the computational problems that many animals encounter – and solve – in cocktail-party-like acoustic conditions, 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, in noisy social environments, 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; Hulse 2002; Brumm & Slabbekoorn 2005; Bee & Micheyl in press). In comparison to the human hearing and speech communication literature, surprisingly few studies have investigated sound source segregation in the context of animal acoustic communication (Feng & Ratnam 2000; Hulse 2002; Bee & Micheyl in press). Hence, we still know relatively little about how animals solve their own cocktail-party-like problems.

Human listeners experience stark improvements in speech recognition when a speech signal and a ‘speech-shaped’ masking noise (i.e., noise with the frequency spectrum of speech) originate from different locations (e.g., Bronkhorst & Plomp 1992; Arbogast et al. 2002; Culling et al. 2004; Hawley et al. 2004). This phenomenon, known as ‘spatial release from masking’ or ‘spatial unmasking’, contributes to human sound source segregation in noisy social environments (Bronkhorst 2000; Shinn-Cunningham et al. 2005). Non-human animals experience spatial release from masking in the detection of relatively simple signals (e.g., pure tones) that are spatially separated from sources of masking noise (reviewed in Bee & Micheyl in press). Whether spatial release from masking might function in acoustic signal recognition in behaviourally relevant contexts, such as mate choice, social recognition, or eavesdropping, has thus far received little attention in the animal behaviour literature.

Acoustic communication in frogs is a biological equivalent of the human cocktail party problem. In many frog species, males aggregate in large, multi-species choruses in which they produce loud advertisement calls that are both necessary and sufficient for species recognition by females (reviews in Ryan 2001; Gerhardt & Huber 2002; Gerhardt & Bee 2006). The high levels of background noise in a chorus can mask the perception of acoustic signals in frogs (Gerhardt & Klump 1988; Wollerman 1999; Schwartz et al. 2001; Wollerman & Wiley 2002; Bee 2007; Bee & Swanson 2007). Thus, we might expect sound source segregation to be important for communication in this taxonomic group (Feng & Ratnam 2000; Hulse 2002; Feng & Schul 2006; Bee & Micheyl in press).

In this study, I investigated the potential role of spatial release from masking in acoustic mate recognition by females of Cope's grey treefrog, *Hyla chrysoscelis*. The grey treefrog species complex is comprised of two cryptic species, *H. chrysoscelis* (a diploid) and the eastern grey treefrog (*Hyla versicolor*), which is a tetraploid (Gerhardt 1994; Ptacek et al. 1994; Holloway et al. 2006). Both species breed syntopically throughout much of their common range in North America, and a great deal is already known about the acoustic properties that mediate species recognition by females of both species (reviewed in Gerhardt 2001). Importantly, hybrid offspring can be found in syntopic breeding populations of the two species (Gerhardt et al. 1994), which suggests that females might sometimes make mistakes in choosing a conspecific male in the cocktail-party-like conditions of a mixed-species chorus. Such mistakes, while generally rare, are costly in terms of evolutionary fitness, because hybrids are infertile (Gerhardt et al. 1994). Perceptual mechanisms for sound source segregation might play some role in reducing the risk of costly mating mistakes in a mixed-species chorus. Here, I report results from a series of two-choice phonotaxis experiments that were designed to test the hypothesis that spatial release from masking improves a female's ability to discriminate between conspecific (*H. chrysoscelis*) and heterospecific (*H. versicolor*) calls in the presence of 'chorus-shaped' noise.

METHODS

Subjects and Study Sites

Nightly collections of gravid females were made between 25 May and 15 June 2007 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 a pure population of *H. chrysoscelis* (Carver Park Reserve, Carver County, MN) and two populations in which *H. chrysoscelis* breeds syntopically with *H. versicolor* (Carlos Avery Wildlife Management Area, Anoka County, MN; Tamarack Nature Center, Ramsey County, MN). For females collected from mixed-species populations, I always tested the female in an initial two-choice discrimination experiment in which I alternated broadcasts of synthetic *H. chrysoscelis* and *H. versicolor* calls (see below) to confirm the female's species identity. At the completion of all testing (typically within 1 to 3 days of collection), I released females with their mates at their original location of capture.

General Testing Procedures

I collected females in amplexus between 2130 and 0100 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. On the day of testing, the pair was transferred to a 20° C incubator until their body temperatures had reached 20±1° C. For testing, the female was separated from her mate, used as a subject in a phonotaxis test, and then returned to her mate in the incubator where they remained until the female was used in a subsequent test.

I tested females in a custom-built, hemi-anechoic sound chamber (Industrial Acoustics Company [IAC], Bronx, New York, USA; inside dimensions: $3.0 \times 2.8 \times 2.2$ m, L $\times$ W $\times$ H). The floor of the chamber was covered with dark gray carpet, and the inside walls and ceiling were constructed from acoustic insulation covered by dark gray perforated metal to reduce reverberations (IAC's Planarchoic™ panel system). The temperature inside the chamber was maintained at $20 \pm 2^\circ$ C. With the chamber ventilation unit running, the baseline sound pressure levels (SPL re 20 μ Pa) inside the chamber ranged from 2 to 12 dB SPL (LZF) over the 500-Hz to 4-kHz 1/3-octave bands, which span the frequency range of interest here. The frequency response of the playback system was flat (± 3 dB) over this same range of frequencies. I used a Larson-Davis System 834 sound level meter to measure sound levels and to calibrate the playback levels of acoustic stimuli. 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. Acoustic stimuli were calibrated at least twice daily.

I tested females under infrared (IR) illumination using two IR light sources (Noldus Information Technology Inc., Leesburg, VA, USA) that were mounted near the ceiling at the centre of opposite walls of the sound chamber. Behavioural responses were observed using an overhead, IR-sensitive video camera (Panasonic WV-BP334; Panasonic Corporation of North America, Secaucus, NJ, USA) mounted from the centre of the chamber ceiling and a video monitor located outside the chamber. Acoustic signals were broadcast through A/D/S L210 speakers (Vista, CA, USA) using a Dell Optiplex GX745 computer (Dell Computer Corporation, Round Rock, TX, USA) 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 (San Jose, CA, USA) interfaced with an M-Audio FireWire 410 multichannel soundcard (M-Audio USA, Irwindale, CA). Output from the soundcard was amplified using a Sonamp1230 multichannel amplifier (Sonance, San Clemente, CA, USA).

I conducted phonotaxis tests in a circular test arena (2 m diameter) located on the floor of the sound chamber. The walls of the arena were constructed from hardware cloth (60 cm high) and covered by visually opaque, but acoustically transparent, black cloth. The perimeter of the arena floor was divided into 24 bins of 15° (Fig. 1). Two speakers for broadcasting conspecific and heterospecific signals were positioned on the chamber floor just outside the wall of the test arena and aimed toward the centre of the arena, where females were released during a test. The signal speakers were placed 2 m and 180° apart on opposite sides of the test arena at the centre of one of the 15° bins around the edge of the arena (Fig. 1). Speakers for broadcasting masking sounds were also placed 2 m and 180° apart on the floor just outside the arena wall and centred in one of the 15° bins, but the absolute positions of the masker speakers depended on the design of a particular test (Fig. 1; see below).

At the beginning of a test, the female was placed in an acoustically-transparent release cage (9-cm diameter) located on the floor and positioned at the centre of the test arena. Females were free to move about and reorient inside the release cage and I did not quantify a female's orientation prior to her release. Following a 1-min acclimation period, I started broadcasts of the alternating signals, which were broadcast as a continuous loop during a test. After a female had heard 4 presentations of both signals, I remotely released her using a rope and pulley system that could be operated from outside the chamber. Females were given up to 5 min to make a choice, which consisted of touching the wall of the test arena inside the 15° arc directly in front of either of the two signal speakers. Responsive females typically initiate phonotaxis within seconds of their release and exhibit directed patterns of zigzag hopping or walking toward the speaker (Gerhardt 1995); they typically do not go initially to some location along the arena wall and then follow the wall to a speaker. I tested females individually and gave them a 'timeout' of at least 5 min between consecutive tests. I periodically switched the outputs from the

amplifier going to each signal speaker or switched the positions of the two signal speakers to control for any directional response bias in the chamber. No such bias was detected.

Acoustic Stimuli

I conducted two-choice discrimination tests (Gerhardt 1995; Ryan & Rand 2001) in which females were given a choice between a synthetic conspecific (*H. chrysoscelis*) call and a synthetic heterospecific (*H. versicolor*) call broadcast in an alternating fashion between the two signal speakers. Both of these signals had average temporal and spectral properties that were based on recordings of the two species at my field sites and corrected to a temperature of 20° C (M. A. Bee unpublished data; Fig. 2). The signals were comprised of a series of pulses that I synthesized using a custom-made program (courtesy J. J. Schwartz). Each pulse consisted of two harmonically-related spectral peaks that had frequencies (and relative amplitudes) of 1.3 kHz (−9 dB) and 2.6 kHz (0 dB) in the *H. chrysoscelis* call and 1.2 kHz (−5 dB) and 2.4 kHz (0 dB) in the *H. versicolor* call. The *H. chrysoscelis* call (Fig. 2a) consisted of 30 pulses (11-ms pulse duration) delivered at a pulse rate of 45.5 pulses/s (649 ms total call duration), and the *H. versicolor* call (Fig. 2b) consisted of a series of 18 pulses (30-ms pulse duration) delivered at a pulse rate of 16.7 pulses/s (1050 ms total call duration). Both calls repeated with a period of 5 s, and the two calls were presented so that there were equal intervals of silence preceding and following each call. The SPLs of the two signals were equalized at the female release site, but the absolute levels were varied in different tests to create different signal-to-noise ratios (SNRs; see below).

I constructed two artificial ‘chorus-shaped’ noises (i.e., noise with a spectrum approximating that of a grey treefrog chorus) using the Adobe Audition software to filter each of two separate white noises into two spectral bands, each with a bandwidth of 600 Hz (Fig. 2c). The low-frequency band had a centre frequency of 1.25 kHz and a relative amplitude that was −6 dB in relation to the high-frequency band centred at 2.5 kHz. Each spectral band, therefore, was centred at a frequency that was the arithmetic mean between the corresponding spectral peaks in the synthetic calls of the two species. These masking noises simulate the frequency spectrum of a natural, mixed-species breeding chorus of grey treefrogs (Bee 2007; Bee & Swanson 2007; Swanson et al. 2007). During phonotaxis tests that included broadcasts of the chorus-shaped noise, the level of each masker was calibrated to be 70 dB SPL (LC_{eq}) at the female release site; therefore, the overall level of both maskers together was 73 dB SPL at the female’s release site. This level falls within the range of background noise levels in natural grey treefrog choruses (Schwartz et al. 2001; Swanson et al. 2007). Note that my use of ‘chorus-shaped noise’ as a masker parallels the use of ‘speech-shaped noise’ in studies of the cocktail party problem and spatial release from masking in humans (Bronkhorst 2000).

Experimental Design

I attempted to test all females ($N = 40$) in a complete series of 10 two-choice tests. The first and last tests in this series were considered ‘reference conditions’ and they involved broadcasting the alternating conspecific and heterospecific calls at 76 dB SPL (at 1 m, LCF) with no masking noise. In the intervening eight tests, I varied the SNR and the spatial configuration between signals and maskers using a 4 (SNR) $\times$ 2 (spatial configuration) factorial design and a different random order for each subject.

I tested females at nominal SNRs of +3 dB, −3 dB, −9 dB and −15 dB, expressed as the level of each signal in relation to the overall level of both maskers at the female release site (73 dB SPL). These four SNRs, therefore, correspond, respectively, to absolute signal levels of 76 dB, 70 dB, 64 dB and 58 dB SPL (at 1 m, LCF). It is worth making explicit that these were the nominal SNRs at the female’s release site and that actual SNRs obviously varied somewhat as females moved about in the arena. Allowing subjects to move about under free-field listening

conditions is an important departure from traditional psychoacoustic studies of auditory masking, in which stimuli are typically presented over headphones, or the positions of listeners and speakers are fixed in tests conducted under free-field listening conditions. The use of traditional psychoacoustic methods is difficult and rare in studies of frog hearing and communication (Gerhardt 1995; Simmons & Moss 1995; Gerhardt & Huber 2002); therefore, most previous studies of auditory masking in frogs have used a phonotaxis paradigm (e.g., Ehret & Gerhardt 1980; Gerhardt & Klump 1988; Wollerman 1999; Schwartz et al. 2001; Wollerman & Wiley 2002; Bee 2007; Bee & Swanson 2007). Phonotaxis represents an ecologically valid behavioural measure of spatial release from masking in frogs because it takes advantage of the natural behaviour of females in response to acoustic signals.

I tested females with two spatial configurations of the signal and masker speakers (Fig. 1). In the 'grouped' conditions (Fig. 1a), masking noises were displaced 15° laterally from the signals. Approximately half of females were tested with the maskers displaced either to the left or the right of the signals. In the 'separated' conditions (Fig. 1b), the two maskers were displaced from the signals by 90°, so that each one was presented 90° from both signals on opposite sides of the arena. In both conditions, approximately half of females were tested with a particular chorus-shaped noise (i.e., noise 1 or noise 2 in Fig. 1) displaced either to the left or the right of each signal.

If a female failed to make a choice within 5 min in two consecutive tests with masking noise, then the next test of that female was another reference condition to ensure that the female was still responsive. If the female made a choice in this reference condition, then the previous two 'no-response' results were considered valid and testing with that female continued. If the female did not make a choice in this reference condition, then the data from the two previous 'no-response' tests were discarded from all analyses and the female was not tested any further. Of the 40 females tested in this study, 30 females were tested in all 10 discrimination tests; the remaining 10 females were tested in either three ($N = 1$), four ($N = 2$), five ($N = 2$), six ($N = 2$), or seven ($N = 3$) tests.

Hypotheses and Data Analysis

I made two predictions according to the hypotheses that the chorus-shaped noise would mask a female's perception of advertisement calls, and that spatial unmasking would improve a female's ability to discriminate between conspecific and heterospecific calls. First, I predicted that the proportion of females responding to one of the two signals would decrease as a function of decreasing SNR. I tested this prediction using Cochran's Q tests (Sokal & Rohlf 1995) to compare the proportion of females that chose one of the two signals across the four SNRs ($N = 30$ females that completed all tests).

My second prediction was that, among the females that responded to one of the two signals at a particular SNR, a greater proportion of females would chose the conspecific call in the separated condition compared with the grouped condition. The data did not meet the requirements for using the McNemar test for significant changes (Sokal & Rohlf 1995; Zar 1999) to compare the proportions of responsive females that changed their response between the grouped and separated conditions at a particular SNR. Therefore, I used separate binomial tests for each combination of SNR and spatial configuration to test the null hypothesis that 50% of females would choose each call against the one-tailed alternative hypothesis that greater than 50% of females would choose the conspecific call. This use of binomial tests is quite common in analyses of results from two-choice discrimination experiments in frogs (Gerhardt 1992, 1995). The rationale behind these analyses was twofold. First, if females were able to discriminate between the conspecific and heterospecific calls in a particular condition, then significantly more than 50% of females should choose the conspecific call. Second, if spatial unmasking improved signal recognition at a particular SNR, then we might expect the

proportion of females choosing the conspecific call in the separated condition to be significantly greater than 50%, whereas females in the grouped condition might be expected to choose the two signals in similar proportions. These analyses were based on the number of responsive females in each test that chose one of the two signals. I used one-tailed tests based on the *a priori* expectation that females would choose conspecific calls (Gerhardt 2001) and computed power for non-significant results following Zar (1999).

As a second measure of female phonotaxis behaviour, I used the angle at which females first touched the wall of the circular test arena as a measure of directional orientation. The *H. chrysoscelis* signal was designated as originating from 0° and the *H. versicolor* call as originating from 180°. For each two-choice experiment, I used a V-test (Zar 1999) to test the null hypothesis that the angles at which females first touched the arena wall were uniformly distributed against the alternative hypothesis that females significantly oriented in the direction of the conspecific call at 0°. If, at a particular SNR, females exhibited greater orientation toward the conspecific call in the separated condition compared with the grouped condition, I interpreted this result as evidence in favour of the spatial unmasking hypothesis.

For all statistical analyses, I used a significance criterion of $\alpha = 0.05$. Descriptive and nonparametric statistics were computed either by hand or using Statistica 7.1 (Statsoft) and circular statistics were computed using Oriana 2.02 (Kovach Computing).

RESULTS

In both the first and last reference conditions, in which females were given a choice between calls of *H. chrysoscelis* and *H. versicolor* with no masking noise, 100% of responsive females chose the conspecific call (one-tailed binomial tests: first reference, $P < 0.001$, $N = 40$; second reference, $P < 0.001$, $N = 34$). In addition, females first touched the wall of the arena in the reference conditions at locations that were significantly oriented in the direction of the conspecific call (Table 1). In these conditions, the length of the mean vector (r) was near 1.0 (Table 1). Thus in my experimental setup, all females oriented toward, and chose, the conspecific call in the absence of chorus-shaped noise.

In the presence of the chorus shaped noise, the proportion of females that responded by choosing one of the two signals in both the grouped and separated conditions decreased as the SNR decreased from +3 dB to -15 dB (Fig. 3; Cochran's Q tests: grouped, $Q = 24.1$, $P < 0.001$, $N = 30$, $df = 3$; separated, $Q = 31.2$, $P < 0.001$, $N = 30$, $df = 3$). Thus, at lower SNRs, the signals were more effectively masked for a larger proportion of females. Yet even at the lowest SNRs of -9 dB and -15 dB, some females were responsive and exhibited unequivocal phonotaxis (e.g., zigzag patterns of directed walking) toward one of the two signals, thus indicating that these responsive females were clearly able to detect one or both of the signals.

As the SNR decreased from +3 dB to -15 dB, there was also a decrease in the proportion of responsive females that chose the conspecific call (Fig. 3), and a concomitant increase in the proportion of females that made a mistake by choosing the heterospecific call. For example, of the females that responded to one of the two signals when the SNR was +3 dB, 94% and 97% of females chose the conspecific call over the heterospecific call in the grouped and separated conditions, respectively (one-tailed binomial test: grouped, $P < 0.001$, $N = 35$; separated, $P < 0.001$, $N = 32$) (Fig. 3). At a SNR of -3 dB, significantly more females (92%) chose the conspecific call in the separated condition (one-tailed binomial test: $P < 0.001$, $N = 25$), but the proportion of females (68%) that chose the conspecific call in the grouped condition was not significantly greater than 50% (one-tailed binomial test: $P = 0.067$, $N = 22$, power ≥ 0.60) (Fig. 3). When the SNR was either -9 dB or -15 dB, the smaller number females that detected and responded to one of the two signals chose the conspecific and heterospecific calls

in similar proportions that did not differ significantly from the null expectation of 50:50 (Fig. 3). In the grouped conditions at SNRs of -9 dB and -15 dB, 59% and 67% of females, respectively, chose the conspecific call (one-tailed binomial test: -9 dB, $P = 0.315$, $N = 17$, power ≥ 0.60 ; -15 dB, $P = 0.194$, $N = 12$, power ≥ 0.63). In the separated conditions, 45% and 55% of females chose the conspecific call at SNRs of -9 dB and -15 dB, respectively (one-tailed binomial test: -9 dB, $P = 0.500$, $N = 11$, power ≥ 0.61 ; -15 dB, $P = 0.500$, $N = 11$, power ≥ 0.62).

In the presence of the chorus-shaped noise presented at a SNR of $+3$ dB, female phonotaxis was significantly oriented toward the conspecific call in both the grouped and the separated conditions (Table 1) and orientation in these conditions was quite strong ($r \geq 0.89$; Table 1). At a SNR of -3 dB, females significantly oriented in the direction of the conspecific call in the separated condition (Table 1), and orientation in this condition was still fairly strong ($r = 0.57$; Table 1). In contrast, while the mean vector was also in the direction of the conspecific call in the grouped condition at a SNR of -3 dB, orientation was weaker ($r = 0.21$; Table 1) than in the separated condition at this SNR and was not directed significantly toward the conspecific call. When the SNR was -9 dB or -15 dB, female responses were not significantly directed toward the conspecific call in either the grouped or the separated conditions (Table 1).

DISCUSSION

Spatial release from masking is one important phenomenon that contributes to sound source segregation in humans, and thus functions as one solution to problems associated with speech recognition in cocktail-party-like listening conditions (Bronkhorst 2000). Noisy social environments for acoustic communication are also common among non-human animals and include many well-known examples, such as frog and insect choruses (Gerhardt & Huber 2002; Greenfield 2005), dawn choruses of songbirds (Amrhein et al. 2004; Gorissen & Eens 2004; Liu 2004), and large crèches of juvenile bats (Balcombe 1990; Balcombe & McCracken 1992) and penguins (Aubin & Jouventin 1998, 2002). Relatively few previous studies have directly investigated mechanisms of sound source segregation and solutions to cocktail-party-like problems in the context of animal acoustic communication (but see e.g., Schwartz & Gerhardt 1989; 1995; Hulse et al. 1997; Aubin & Jouventin 1998). The aim of the present study was to investigate spatial release from masking as a potential mechanism that contributes to improved sound source segregation in frogs.

Spatial Release from Masking in Grey Treefrogs

In a previous study of grey treefrogs (Bee 2007), results from single-stimulus phonotaxis tests suggested that females experienced a release from masking in the detection of a conspecific signal presented against a background of chorus-shaped noise when the signal and noise were separated by 90° compared with a separation of 7.5° . Spatial release from masking was significant at SNRs of 0 dB and -6 dB, but not at SNRs of $+6$ dB and -12 dB. The primary aim of the present study was to extend these initial findings by testing the hypothesis that spatial release from masking also plays a role in mate recognition by improving a female's ability to discriminate between conspecific and heterospecific calls under noisy conditions simulating a breeding chorus.

At SNRs of $+3$ dB, -9 dB and -15 dB, there was little evidence to suggest that females experienced spatial unmasking when the maskers were in the separated configuration. At the highest SNR of $+3$ dB, nearly all females chose the conspecific call in both the grouped and separated conditions, and the orientation of female responses was directed toward the conspecific stimulus in both conditions. At the two lowest SNRs (-9 dB and -15 dB), most females failed to make a choice and failed to exhibit any phonotaxis-related behaviors. It seems

almost certain that these unresponsive females failed to detect the signals. At these relatively low SNRs (−9 dB and −15 dB), however, some females exhibited unequivocal phonotaxis toward one of the two signals. Clearly, this subset of responsive females was able to detect one or both of the signals. Importantly, these responsive females chose the conspecific and heterospecific calls in similar proportions. In neither the grouped nor the separated conditions at SNRs of −9 dB and −15 dB was there any evidence to suggest that female phonotaxis was significantly oriented toward the conspecific call. These results are important in that they indicate that some females could still detect the signals at SNRs of −9 dB and −15 dB, but that auditory masking interfered with their ability to discriminate between conspecific and heterospecific calls.

Evidence supporting the hypothesis that spatial unmasking improved the ability of females to discriminate between conspecific and heterospecific calls was found at a SNR of −3 dB. At this SNR, females chose the conspecific call significantly more often than expected by chance in the separated condition, but in the grouped condition there was only a non-significant trend for females to more often choose the conspecific call. In the separated condition, females first touched the wall of the arena at locations that were significantly oriented in the direction of the conspecific call, but this was not the case in the grouped condition. In fact, at a SNR of −3 dB, the strength of orientation (r) was more than twice as great in the separated condition ($r = 0.57$) compared with the grouped condition ($r = 0.21$; Table 1). Thus, at a SNR of −3 dB, the ability of females to choose a conspecific call over a heterospecific call was improved when the signals and the two sources of chorus-shaped noise were spatially separated by 90° compared with a separation of just 15°. These results provide support for the hypothesis that spatial release from masking not only improves signal detection in grey treefrogs (Bee 2007), but also signal recognition.

Could Spatial Unmasking Contribute to Sound Source Segregation in the Cocktail-Party-Like Conditions of a Frog Chorus?

Previous studies of the problem of auditory masking in frog choruses have elucidated various behavioural strategies that signallers use to increase the likelihood that their signals are detected by receivers (reviewed in Narins & Zelick 1988; Gerhardt & Huber 2002; Wells & Schwartz 2006). These strategies include (i) 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 calling, (ii) precise call timing interactions to avoid call overlap with nearby males in the chorus, (iii) spacing out within the available breeding habitat to avoid calling too closely to other signalling males, and (iv) increasing calling effort in dense social conditions by calling more frequently or producing longer calls. While these strategies clearly function to improve signal transmission in a chorus, the efficacy of these behavioural strategies might be diminished in particularly dense choruses, for example because of unavoidable increases in call overlap (e.g., Brush & Narins 1989; Schwartz et al. 2002) and decreases in inter-male distances (e.g., Gerhardt et al. 1989; Murphy & Floyd 2005). Effective communication under such listening conditions, therefore, should depend at least in part on the perceptual mechanisms of receivers.

Historically, the selectivity of the frog auditory system for the spectral and temporal properties of conspecific calls has often been viewed as analogous to a template-matching process for call detection and recognition that could ameliorate masking interference, at least by heterospecifics (e.g., the 'matched filter' hypothesis; Capranica & Moffat 1983; reviewed in Gerhardt & Huber 2002). For the two grey treefrog species, spectral selectivity for conspecific calls might provide little such benefit in syntopic breeding populations because the calls of both species are spectrally quite similar (Gerhardt 2001, 2005). More generally, template-matching processes alone might contribute little toward separating the overlapping calls of conspecific males from each other or from the general din of background noise in a dense

chorus. This follows because all conspecific males in a chorus would have signals approximating a receiver's spectro-temporal template. Moreover, as the results of this and other laboratory studies show, background noise can impair a female frog's ability to detect and discriminate among calls (Ehret & Gerhardt 1980; Gerhardt & Klump 1988; Wollerman 1999; Schwartz et al. 2001; Wollerman & Wiley 2002; Bee 2007; Bee & Swanson 2007). Hence, in addition to auditory selectivity for conspecific calls, we might expect the operation of other perceptual mechanisms that also contribute to signal detection and recognition under the noisy conditions of a breeding chorus. Spatial release from masking is likely one such mechanism.

In an earlier study of green treefrogs, *Hyla cinerea*, females were given the choice between an attractive conspecific advertisement call and a less attractive conspecific aggressive call (Schwartz & Gerhardt 1989). Females experienced spatial release from masking in signal detection when the signals and two sources of broadband noise (0.1–10 kHz) were presented at angular separations of either 45° or 90° compared with conditions in which the signal and masker speakers were adjacent to each other. In that study, however, there was little evidence that spatial release from masking improved the ability of females to discriminate between the two types of conspecific calls. Neurophysiological studies of Northern leopard frogs (*Rana pipiens*) have also revealed spatial release from masking in the signal detection thresholds of auditory nerve fibres (Lin & Feng 2001) and neurons in the auditory midbrain (torus semicircularis; Ratnam & Feng 1998; Lin & Feng 2003). Together with these earlier studies, the results of the present study suggest that in frogs, the auditory system may exploit spatial separation between signals and noise to improve not only the detection of mating signals (Schwartz & Gerhardt 1989; Bee 2007), but also the ability to recognize the signals of appropriate mates.

The contribution of spatial release from masking to mate recognition might be important under the listening conditions of natural breeding choruses. In this study, the manipulations of SNR and spatial configuration simulated males signalling at different distances and locations in relation to fixed sources of masking noise, with lower SNRs simulating more distant males. Female treefrogs typically enter a chorus from the periphery and spend several minutes assessing different nearby males as potential mates (Murphy & Gerhardt 2002; Schwartz et al. 2002, 2004). It is not unreasonable to expect that females may often encounter situations during mate assessment in which the signals of multiple conspecific and heterospecific males and the general background noise of the chorus originate from different locations and distances. Under such listening conditions, spatial release from masking might improve a female's ability to detect and recognize the calls of conspecific males, such as those calling near the edge of a breeding pond. In real breeding choruses, of course, the acoustic scene is composed of many sound sources located in different locations and directions from a receiver. Therefore, some caution is necessary in extending to the real world the findings from controlled laboratory experiments like the one reported here and elsewhere (Schwartz & Gerhardt 1989; Bee in press). Nevertheless, experiments on spatial release from masking in frogs almost certainly engage perceptual mechanisms that benefit receivers under some listening conditions in natural choruses.

Conclusion

The mechanisms underlying spatial release from masking contribute to sound source segregation in humans and to our ability to solve the cocktail party problem (Bronkhorst 2000). Compared to the large number of studies of spatial release from masking in humans, however, only a few studies have investigated spatial unmasking in animals. In addition to frogs, behavioural studies have reported spatial release from masking in signal detection tasks in fish (Chapman & Johnstone 1974; Hawkins & Sand 1977), birds (Dent et al. 1997), ferrets

(Hine et al. 1994), mice (Ison & Agrawal 1998), harbor seals (Turnbull 1994; Holt & Schusterman 2007) and California sea lions (Holt & Schusterman 2007). Ronacher and Hoffmann (2003) failed to find strong evidence for spatial release from masking in a study of a grasshopper. Together, these studies indicate that spatial release from masking might be a general and taxonomically widespread phenomenon that contributes to sound source segregation in a diversity of animals, at least among vertebrates. Our understanding of the perceptual mechanisms of sound source segregation, and their potentially important roles in animal acoustic communication in noisy social environments, would be greatly improved by investigating these processes in a greater diversity of animals and behavioural contexts. Such investigations have considerable potential to increase our understanding of the evolved sensory mechanisms that allow humans and other animals to perceptually organize the complex acoustic scenes associated with noisy social aggregations (Feng & Ratnam 2000; Hulse 2002; Bee & Micheyl in press).

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Figure 1.

Schematic diagram illustrating the circular test arena divided into 15° bins along the perimeter and the positions of speakers broadcasting signals and chorus-shaped noises in (a) the grouped condition and (b) the separated condition. Note that the frog and speakers are not drawn to scale.

Figure 2.

(a–b) Oscillograms of the (a) conspecific (*H. chrysoscelis*) signal and (b) the heterospecific (*H. versicolor*) signal depicting a temporal window of 1.5 s around each call. Insets in (a) and (b) depict a single pulse from the corresponding call. The pulses in the *H. chrysoscelis* call (a) were 11 ms in duration and separated by 11 ms inter-pulse intervals (pulse period = 22 ms; pulse duty cycle = 50%) and were shaped with onsets (4 ms) and offsets (7 ms) that had half-amplitude times that were 43% and 53% of the duration of the onset and offset times, respectively. The pulses in the *H. versicolor* call (b) were 30 ms in duration and separated by 30 ms inter-pulse intervals (pulse period = 60 ms; pulse duty cycle = 50%) and were shaped with onsets (20 ms) and offsets (10 ms) that had half-amplitude times that were both 55% of

the duration of the respective envelope ramp. Note that this *H. versicolor* call was effective at eliciting phonotaxis from females of *H. versicolor* (M. A. Bee unpublished data). (c) Power spectrum of the chorus-shaped noise.

Figure 3.

Histograms showing the proportion of responsive females making a choice that chose the conspecific call as a function of SNR. Results are shown separately for the grouped (grey bars) and separated (white bars) conditions. The numbers associated with each bar depict the ratio of the number of females that chose the conspecific call to the number of females that actually made a choice in that condition; N represents the total number of females that were tested in that condition. The error bars depict either the upper or lower 95% confidence interval around the proportion of females choosing and the horizontal dashed lines depict the expected proportion according to the null hypothesis that females would choose the conspecific and heterospecific calls in a 50:50 ratio. Asterisks indicate that significantly more females than expected by chance chose the conspecific call (one-tailed binomial $P < 0.05$).

Table 1

Results from circular statistical analyses of orientation angles for females that touched the arena wall in each condition. V-tests were used to test the null hypothesis that female responses were randomly distributed against the alternative hypothesis that responses were oriented in the direction of the conspecific call (0o).

parameter	reference condition		grouped conditions				separated conditions			
	first	last	+3 dB	-3 dB	-9 dB	-15 dB	+3 dB	-3 dB	-9 dB	-15 dB
number of females	40	34	36	28	29	26	33	29	22	30
mean vector (μ)	0.0°	0.9°	0.4°	5.5°	46.9°	283.0°	2.6°	12.3°	319.4°	227.9°
length of mean vector (r)	0.99	0.99	0.90	0.21	0.17	0.29	0.89	0.57	0.13	0.17
circular standard deviation	7.5°	8.1°	26.2°	101.1°	107.5°	90.6°	27.2°	60.4°	116.8°	107.5°
V test (u)	8.9	8.2	7.6	1.6	0.9	0.5	7.3	4.3	0.6	-0.9
V test (P)	<0.001	<0.001	<0.001	0.058	0.187	0.323	<0.001	<0.001	0.266	0.813