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Spatially mediated release from auditory masking in an anuran amphibian

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Summary. 1. The acoustic environment in which many species of frogs must communicate is characterized by high levels of background noise. Because the anuran auditory system is directionally sensitive, spatial cues should be useful in enhancing the ability of these animals to detect and localize calling conspecifics under such conditions.

2. We presented female green treefrogs, *Hyla cinerea*, with synthetic conspecific advertisement and aggressive calls in the presence of background broadband noise to assess the importance of directional information in signal detection, discrimination and localization.

3. We found that angular separation of call and noise sources facilitated a release from masking; females which failed to orient towards and approach speakers broadcasting calls positioned adjacent to a noise source did so when the noise sources were separated from the speakers by 45° or 90°. We estimate the improvement in signal-to-noise ratio with separation to be 3 dB or less. This increase was insufficient to facilitate discrimination between advertisement and aggressive calls.

Key words: Auditory masking – Directional hearing frogs

Introduction

Most frogs and toads call in dense aggregations where high levels of background noise created by both conspecific males, other organisms (anurans and acoustic insects), and abiotic sources (wind, sound of wind-blown plants) may pose a challenge to communication between individuals (Ehret and Gerhardt 1980; Gerhardt and Klump 1988; Schwartz and Wells 1983). Recent research has demonstrated that frogs employ several behavioral and neural strategies to reduce the severity of this problem (review by Narins and Zelick 1988). One potential solution that has not been previously investigated involves the use of directional cues to extract individual calls from background noise. This ability would be particularly important for female frogs that must detect the calls of individual males to identify and localize an appropriate mate in noisy choruses (Gerhardt 1982, 1989).

In humans, the ability of an individual to perform an analogous task, termed the 'cocktail party' effect (Cherry 1953), is greatly reduced when binaural sound input is eliminated by plugging one ear (Durlach and Coulburn 1978). Experiments using free-field sound presentation established that the masked thresholds of tonal signals can decrease by close to 8 dB as the angular separation of signal and noise sources increases (Ebata et al. 1968; Suchowersky 1969; Blauert 1983); experiments using earphones have shown that both interaural time and intensity differences contribute to this 'directional or space-domain filtering' (Fay and Feng 1987) or 'binaural release from masking' (Flanagan and Watson 1966).

In frogs, each ear is directionally sensitive and appears to act as a mixed pressure-gradient receiver. Because of the symmetry of the two ears, fairly large binaural discrepancies that are processed by the central auditory system, are also created at many points in acoustic space (Chung et al. 1978; Feng and Shofner 1981; Rheinlaender et al. 1981). Michelsen et al. (1986) recently presented directional sensitivity plots based on laser measurements of single tympanic membranes in the green treefrog (*Hyla cinerea*). These data provide an estimate of the upper bound of expected improvement in signal detection based on different separations of noise and signal sources. In fish, which also have a different kind of localization system than higher mammals, the behavioral experiments of Chapman and Johnstone (1974) and Hawkins and Sand (1977) showed that separation of signal and noise sources could improve signal detection in noise by as much as 7 dB.

In this study our goal was to determine whether females of the green treefrog exhibited release from mask-

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ing both with respect to the detection of attractive signals and their discrimination. In this respect our goal was analogous to that of Levitt and Rabiner (1967), who measured binaural release from masking both for speech detectability and intelligibility in humans. Males of *H. cinerea* call from dense, often multi-species, choruses in the southeastern United States, and females move close to calling males and usually initiate sexual contact. The two most common vocalizations, which have a very similar frequency spectrum, are an advertisement and aggressive call, used mainly in male-male competitive situations. Females prefer advertisement calls to aggressive calls, and experiments with synthetic calls suggest that they do so on the basis of the amplitude modulation of aggressive calls (Oldham and Gerhardt 1975; Gerhardt 1978a, b). We thus elaborated on the usual experimental paradigm used with other vertebrates by simultaneously presenting females with a choice between *two* synthetic signals in the presence of noise: an advertisement call and an aggressive call. We predicted that without separation of signal and noise sources, frogs would fail to approach a signal source, or, if signals were detected, frogs would fail to discriminate between the two kinds of calls at certain signal-to-noise ratios. With increases in angular separation of call and noise sources, we expected that the frogs would not only be able to reliably detect the signals but would also show the normal preference for the unmodulated advertisement call.

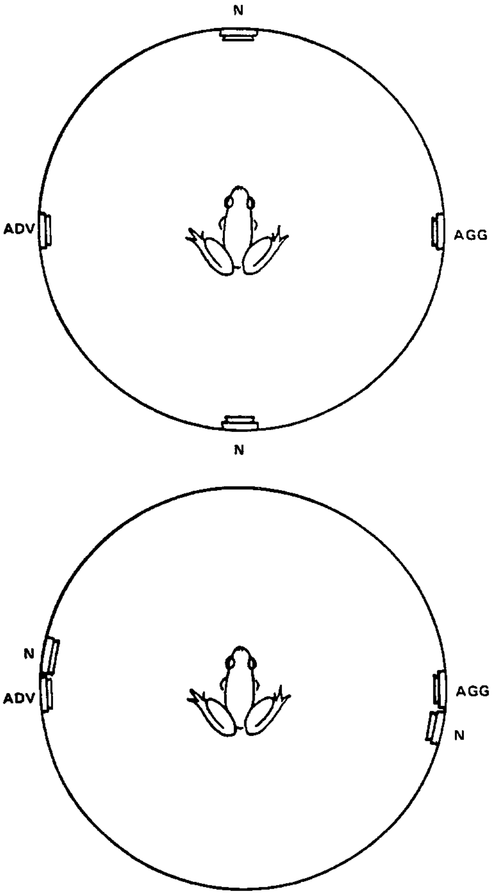

Fig. 1. Schematic diagram of the arena showing orientations of advertisement call (ADV), aggressive call (AGG), and noise (N) sources used in the two trials of the first experiment. The frog is not drawn to scale

Materials and methods

Experimental signals were produced with a custom-built analog synthesizer (Gerhardt 1974) and were composed of 3 phase-locked sinusoids of 0.9, 2.7 and 3.0 kHz lasting 160 ms. The synthetic model of the aggressive call differed from the model of the advertisement call by the imposition of 5 cycles of 50 Hz sinusoidal amplitude modulation (percent modulation$>$95%). Oscillograms of the two stimuli have been published previously (the '+5' and 'UM' calls of Fig. 1B in Gerhardt 1978a). We transcribed the original calls, which had each been recorded on a separate channel of a ReVox A77 stereophonic recorder at 19 cm/s to 2 tracks of a cassette tape using a Sony TC-D5M stereo cassette recorder. We amplified signals from the cassette recorder with a Quad 303 stereo amplifier, and broadcast them alternately every 0.4 s from Realistic Minimus-7 speakers separated by 180° on the perimeter of a 2 m diameter circle. We played back broad band noise (0.1–10 kHz), with a second Sony TC-D5M recorder from two Analog-Digital-Systems 200 speakers; each noise channel was amplified by a Nagra DH speaker-amplifier. The playback system was flat (±5 dB) from 0.1 to 10 kHz (±2 dB from 1 to 3 kHz). We equalized playback levels (72, 75 or 78 dB SPL re 20 μPa) of synthetic calls at the central release point of females with a General Radio 1933 sound level meter (C-weighting, fast RMS setting). We used the sound level meter and a Brüel and Kjaer 1621 tunable filter to equalize noise levels at a spectrum level of 52 dB/Hz at the same point.

We collected females of *H. cinerea* in amplexus in Savannah, Georgia during June and early July 1988, refrigerated them at about 4 °C to inhibit oviposition, and usually tested them the following day. Experiments took place at 25±2 °C in part of a dimly illuminated (25 W red bulb) room that was lined with acoustic foam and anechoic wedges to reduce sound reflections. After each female had warmed to room temperature, we placed her individually in a small hardware cloth cage covered with a plexiglass top in the center of the 2 m diameter circle. After the stimuli had been played back for about 30 s, we removed the top of the cage with a string and observed the movements of the female from a small opening in a black cloth curtain that covered the entrance to the testing arena.

To assess responsiveness, we usually first presented each female with the unmasked synthetic model of an advertisement call played back at 72–78 dB SPL. If the female failed to orient and move toward the speaker within 30 s, we removed her and retested her later. If she responded, we returned her to the central release point and began a trial with both signals and masking noise. We recorded a response if the female left the cage and moved to within 30 cm of a speaker within 5 min. If she failed to move during this time or wandered slowly about the arena without orienting to a speaker that broadcast a signal, we considered this to be a 'no response'. The latter criteria were the same as those used by Ehret and Gerhardt (1980) to define masking. We considered rapid hops, even if they resulted in a female's moving close to a speaker, to be escape reactions; they were not counted as either a 'response' or a 'no response'.

Each experiment consisted of two trials per female. In the first experiment, we placed the speakers emitting masking noise either adjacent to each of the speakers broadcasting the signals or at an angular separation of 90°; in either case, all speakers were positioned on the perimeter of the 2 m diameter circle (Fig. 1). We alternated the relative positions of speakers presenting signals and noise (adjacent or separated) between subjects. We also switched the sources of the two different signals periodically in order to neutralize any directional biases of the animals or minor asymmetries in the arena. None were detected. In the second experiment, we placed the speakers broadcasting masking noise either adjacent to speakers broadcasting the signals or at an angular separation of 45° (Fig. 1).

We first equalized the signal levels to 75 dB SPL; the spectrum level of the noise level was always 52 dB/Hz. This signal-to-noise ratio approximates the masked threshold at about 0.9 kHz as estimated in *H. cinerea* by both Ehret and Gerhardt (1980) and Moss and Simmons (1986). If the female responded positively in both orientations of signal and noise speakers, then we reduced the signal-to-noise ratio by lowering the signal SPL by 3 dB and retested the female. If the female did not respond in either orientation, then we increased the signal-to-noise ratio by 3 dB and retested her.

Results

Signal detection

We tested a total of 38 different females in the two experiments; 27 of these were used in the first experiment and 20 in the second experiment. Twenty-eight of the females we tested responded at least once. In the first experiment, ten females, which failed to respond when signal and noise sources were adjacent, responded to one of the signals when signal and noise sources were separated by 90°. Two females responded to a signal when signal and noise sources were not separated, but failed to do so when the sources were separated ($P=0.019$, one-tailed binomial test). In the second experiment, seven females were released from masking when signal and noise sources were separated by 45°; one female responded to a signal when the noise source was adjacent but not at the 45° separation ($P=0.035$, one-tailed binomial test). Details of all tests are in Table 1.

In many tests in both experiments females either failed to respond to the signals in both adjacent and separated conditions, or they responded to a signal in both conditions. Eight females, 4 in each experiment, failed to respond at one signal-to-noise ratio in both conditions; each of the same animals then responded to a signal in both conditions when the signal-to-noise ratio was increased by 3 dB. The data indicated that the masked thresholds were between 72 and 75 dB SPL in 6 of these animals, and between 75 and 78 dB SPL in the other two. These results also suggest that the improved signal-to-noise ratio for detecting signals in the situations where the sources of signals and noise were spatially separated is very small, i.e. 3 dB or less.

Table 1. Responses of female *Hyla cinerea* in 4 speaker experiments. Data above are the choices of females in tests in which only one of the speaker orientations elicited a positive response. Also shown are the total number of frogs tested and the number of individual tests (including retests), each consisting of two trials. Data below are the choices of females in tests in which both speaker orientations elicited a positive response. The number of switches in preference of call type is also shown. Call source and noise source speakers adjacent (ADJ); call source and noise speakers separated (SEP); responses to the unmodulated (U) and modulated (M) calls; α = angular separation between call and noise speakers; *P* levels are for a one-tailed binomial test of the null hypothesis that the number of females responding with speakers separated was not greater than the number responding with speakers adjacent.

Responses to one orientation

α	ADJ		SEP		Frogs	Tests	*P*
	U	M	U	M			
90	2	0	6	4	27	35	0.019
45	1	0	7	0	20	31	0.035

Responses to both orientations

	ADJ		SEP		Switch	
	U	M	U	M	U>M	M>U
90	5	2	5	2	0	0
45	2	4	2	4	1	1

Selectivity

Considering all trials, there were 30 responses to the advertisement call model and 16 to the aggressive call model. Among the 10 females released from masking at the 90° separation of signal and noise sources 6 chose the advertisement call, and 4 chose the aggressive call. The 2 frogs that responded when signal and noise sources were adjacent but not when separated both chose the advertisement call. Among the frogs released from masking at the 45° separation, all 7 chose the advertisement call; the female that responded in the adjacent situation but not when the sources were separated also chose the advertisement call. Taken together, these results indicated a preference for the advertisement call (16 vs. 4, $P=0.006$, one-tailed binomial), although there was certainly no preference among females released from masking at the 90° separation. Moreover, considering the females that responded in both the adjacent and separated conditions, there was little evidence for a preference in either situation.

Discussion

Our results indicate that the spatial separation (45° and 90°) of the sources of broad band noise and signals improved the detectability of signals in noise by female green treefrogs compared to the situation in which signals and noise were broadcast from the adjacent positions. The effect was not observed in every female, however. We believe this is a reflection of the only small improvement in the signal-to-noise ratio with angular separation which we estimate to be 3 dB or less. In fact, females of this species failed to choose consistently the more intense of two otherwise identical signals that differed by 3 dB at 80 dB (80 vs. 83 dB SPL) under quiet conditions, although they did so at lower playback levels (60 vs. 63 dB and 70 vs. 73 dB SPL; Gerhardt 1987).

In experiments with fish (cod and haddock), the threshold for detection of a low frequency pure tone in broad band noise improved by about 7 dB at an angular separation of 45° and greater (Chapman and Johnstone 1974; Hawkins and Sand 1977). In the fish experiments, subjects had been conditioned to respond to tones and the experimental setup was simpler than ours in that there was one source of signals and one of noise. We do not, however, think that these differences account for the weaker release from masking for signal detection in the treefrog. Rather, the monaural directional sensitivity data provided by Michelsen et al. (1986) for green treefrogs indicate that only a 3 to 4 dB improvement in threshold sensitivity would be expected for two signals separated by 90°. Moreover, although we are unaware of any study in which frogs have been conditioned to respond to sound, we are nevertheless confident that the failure of gravid females to move or to approach a source of an attractive signal in the presence of noise is a reliable criterion for masking. Both the study of Ehret and Gerhardt (1980), who first used this criterion, and this study yielded estimates of masked thresholds that were very similar to those provided by Moss and Simmons (1986), who used a reflex modification technique. The reflex modification procedure does not depend on a frog's reproductive state nor its motivation to respond phonotactically.

How do our results pertain to the task of call detection by anurans in nature? Treefrogs typically call in multi-species choruses. Moreover, as females enter a pond at the periphery, they are often in situations where multiple signals and background noise arrive from different directions. While the natural background noise is certainly not the same as broad band noise, there is usually acoustic energy in the natural environment over a wide range (0.4 to 6 kHz), which is contributed by other species of frogs, acoustic insects and abiotic sources. It is also true that natural background noise tends to fluctuate in intensity, and female anurans could take advantage of these changes as they approach calling conspecifics (Schwartz and Wells 1983). Our use of constant intensity broad band noise represents a test of what anurans can do under particularly adverse acoustic conditions and enables us to compare our results with those of other psychophysical studies.

We chose to use two signals, each representative of one of the most common calls in the species' repertoire, in order to ascertain the effect of signal and noise separation on the selectivity of the frogs. The main reason for this particular choice, rather than one offering a heterospecific call, was that the advertisement and aggressive calls have very similar spectra. As Moss and Simmons (1986) showed, females of *H. cinerea* are not only most sensitive to frequencies in the range of the two spectral peaks characteristic of conspecific calls, but they are also more capable of detecting these same frequencies against a broad band background than other frequencies within their range of hearing. We speculate that at the noise level we used, the frogs would have failed to respond to signals with spectra very different from that typical of the conspecific call under all conditions because of a failure to detect the signals rather than because of a failure to discriminate them from a conspecific model. At noise levels at which they could detect both signals, we think that a choice between calls with different spectra would provide too easy a task in order to gain insight into the effects of spatial filtering on female selectivity. In behavioral experiments in quiet conditions, for example, females of *H. cinerea* chose synthetic calls with a typical conspecific spectrum that were played back at 12 dB less than those of an alternative stimulus with a spectrum typical of a sympatric congener, *H. gratiosa* (Gerhardt 1987).

There are two explanations, not mutually exclusive, for the failure of females to show a clear cut preference for the synthetic advertisement call over the aggressive signal. First, the discrimination task is almost certainly more difficult than the detection task. In analogous experiments with humans, for example, Levitt and Rabiner (1967) showed that the binaural release from masking for the detection of single words in broad band noise (13 dB) was about twice to four times the magnitude (3 to 6 dB) of the gain in intelligibility (ability to correctly identify the words) and that the two phenomena depended on different factors. Thus, we find it hardly surprising that the selectivity of the female treefrogs was not clearly superior in the separated conditions given that the improvement in detectability of signals was so small. Second, the difference by which females differentiate between advertisement and aggressive calls is particularly subject to degradation by high levels of background noise. Gerhardt (1978b), using synthetic calls, showed that females reliably discriminated between calls with different depths of 50-Hz amplitude modulation only when the difference in depth exceeded about 40%. The effect of background noise is to reduce effectively the amplitude minima in the synthetic aggressive calls, and thus the improvement in signal-to-noise ratio under the separated conditions was apparently insufficient to restore the requisite perceived depth of modulation to consistently identify the aggressive signal.

Both our data and those from studies of the directional sensitivity of the frog's peripheral auditory system suggest that spatial filtering will result in only a slight improvement in detection and possibly in discrimination of signals with similar spectra. We predict, however, that there should be a much stronger effect when signals with the typical conspecific spectrum are compared with signals of different spectra. Indeed, a mixed pressure gradient system is especially sensitive to the stimulus frequency. While the large spectral differences between conspecific calls and those of other species would almost certainly result in large effects on both detection and discrimination, a more interesting biological question for future research concerns the effectiveness of spatial filtering in sharpening the preferences of females for conspecific advertisement calls that differ in frequency. The low-frequency spectral peak in *H. cinerea*, for example, may vary by nearly an octave (0.7 to 1.3 kHz) within a single population (Gerhardt et al. 1987).

In future empirical work, it also would be particularly interesting to incorporate more of the complexity present in real choruses. Since frogs communicate in a three-dimensional environment, it is important to learn whether spatially-mediated release from masking can occur in the vertical in addition to the horizontal plane. Moreover, we should determine whether anurans can utilize directional information to facilitate pattern recognition when calls overlap and assess the impact of multiple discrete sources of interference on call detection and localization.

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