



## Auditory Masking and Effects of Noise on Responses of the Green Treefrog (*Hyla cinerea*) to Synthetic Mating Calls

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**Summary.** 1. Female green treefrogs (*Hyla cinerea*) are attracted to a sound source which broadcasts appropriate synthetic mating calls. Continuous noise (broad-band or band-passed) was added to these signals in order to determine masked auditory thresholds at frequencies within the two bands that are typically emphasized in the natural mating call.

2. Signal-to-noise-ratios for total masking at 900 Hz were determined in a one-speaker situation at three signal levels (55, 65, and 75 dB SPL re 20  $\mu$ Pa), and critical ratios (CR-bands) were calculated (Tables 1, 2).

3. The most reliable averaged CR-bandwidth at 900 Hz was 158 Hz ( $\pm$  22 dB). CR-bands at 3,000 Hz, measured in a two-choice situation at a signal level of 65 dB, were 141 Hz ( $\pm$  21.5 dB).

4. Thus sounds processed by both auditory organs in the treefrog (the amphibian papilla for  $f < 1,500$  Hz and the basilar papilla for higher frequencies) can be analyzed in CR-bands that are sufficiently narrow to resolve the harmonic structure of a typical mating call.

5. A super-optimal stimulus consisted of a continuous low-frequency noise (100–1,000 Hz band-pass, spectrum level = 40 dB) superimposed on 3,000 Hz tone bursts (at 65 dB) with temporal properties typical of the natural mating call.

females preferentially respond to conspecific mating calls as opposed to the calls of other, sympatric species; furthermore, females are capable of discriminating between synthetic mating calls that differ only slightly in their spectral or fine-temporal structure (Gerhardt 1974a, b, 1978; Oldham and Gerhardt 1975). However, in these studies the discriminatory behavior of the female was determined by offering her a choice between two sounds, each of which was played back from a separate speaker in a relatively quiet acoustic environment. In the natural environment many sources of sound contribute to the background noise level; there are, in addition to the calls of many conspecific males, the calls of other kinds of frogs and toads, the songs of nocturnal insects, and the noise of wind and wind-blown plants. We have thus tested the ability of female green treefrogs to detect pertinent spectral components of synthetic mating calls in the presence of continuous noise, both broad-band and band-passed. Our results not only address the biological question of pattern recognition in a noisy environment, but also provide estimates of the frequency resolving power of the treefrog auditory system. These estimates can be compared with those in other kinds of vertebrates. Finally, since the spectral properties of the mating call are of paramount importance in species recognition, the discrimination of conspecific call frequencies from other frequencies which simultaneously impinge on the animal must depend on the resolving power of its auditory system even in a quiet acoustic environment.

### Introduction

Gravid females of *Hyla cinerea* are attracted to the mating calls of conspecific males and usually initiate sexual contact by touching or moving close to the vocalizing male. Previous research established that

*Abbreviations:* SPL sound pressure level; CR-band critical ratio band

### Methods and Materials

#### *Experimental Animals*

Eighty females of *H. cinerea* were tested. Each animal was collected in amplexus, separated from the male, and refrigerated until 20

to 40 min before testing. This procedure prevented oviposition and permitted us to conduct experiments at convenient times within 24 h of the time of capture. Animals were tested at temperatures between 24 and 28 °C (see Gerhardt 1974b).

#### *Acoustic Environment and Playback System*

Experiments were conducted in a large, dimly-lit (red light) exhibit hall in the Savannah Science Museum. The sound pressure level (SPL) of the ambient background noise was less than 50 dB total level (C-weighting) in the frequency range of interest (100 to 10,000 Hz). The playback system consisted of a Revox A 77 stereophonic recorder, Crown EQ2 synergistic equalizer, Nagra DH amplifiers and Analog-Digital-Systems 200 loudspeakers (separated by 2 m). Anechoic wedges of acoustic foam (Soundcoat, Inc.) were used to minimize sound reflections in the test area. By using the equalizer in conjunction with a Brüel and Kjær 2209 or General Radio 1900 A sound level meter and a Brüel and Kjær 1621 tunable (3%) filter, we could adjust the frequency-response of the playback system at the release point (midway between the speakers) of the female. The noise spectrum was flat within  $\pm 5$  dB; the equalizer was used to adjust the sinusoidal components of synthetic signals to the same ( $\pm 1$  dB) relative amplitude.

#### *Experimental Stimuli*

Mating calls with either one (900 Hz) or two (900 and 3,000 Hz) frequency components that are characteristic of natural calls and effective synthetic ones were synthesized and recorded (19 cm/s) on magnetic tape. See Gerhardt (1974b) for details regarding the generation of the signals and for the gross temporal properties of the synthetic mating calls. When two synthetic calls were to be presented, one was recorded on one channel of the recorder and played back through one of the speakers; the other was recorded on the other channel (the timing relationship of the two calls was fixed, see Gerhardt 1974b) and played back through the other speaker. One of the recorder outputs went directly through the equalizer and DH amplifier to a speaker; the other output went separately through the equalizer but was then connected to an attenuator (Hewlett-Packard 350D) and electronic adder before going to the other DH amplifier and speaker. Noise could be added to the synthetic signals by means of the adder. First, however, the noise (from a Grason-Stadler 455C noise generator) was passed through two electronic filters (Krohn-Hite 3550, total slope: 48 dB/octave), through another attenuator (HP 350D) and an amplifier (Ithaco 255) before being added to the signals. The sound pressure levels (SPLs in dB re. 20  $\mu$ Pa) of the signals and noise were measured and adjusted independently by the sound level meter and tunable filter at the point where the female was released from a small hardware cloth cage. The noise level will always be expressed as the spectrum level, i.e., the intensity of noise in dB for every 1-Hz band within a given band-pass (see Zwicker and Feldtkeller 1967; Ehret 1977).

#### *Experimental Procedures*

Successful methods for conditioning frogs and toads to sounds are unknown. Since gravid females of *H. cinerea*, which have ovulated but not yet oviposited, are reliably attracted to a source of appropriate sounds, we used these natural responses to determine the effects of continuous noise on signal detection. Natural mating calls typically have many frequency components; however, one or two low-frequency components around 700 to 1,200 Hz and two to five high-frequency components around 2,400 to

3,600 Hz are usually emphasized (Oldham and Gerhardt 1975). Synthetic mating calls consisting of 900, 2,700, and 3,000 Hz-components of equal relative amplitude attracted females as effectively as a typical natural mating call in a two-choice situation (Gerhardt 1974b). When not given a choice, females are readily attracted to synthetic calls consisting only of a 900 Hz-component at SPLs of about 50 dB or higher; they respond to a 3,000 Hz-component only if the SPL is much higher, i.e., 90 to 95 dB (Gerhardt 1976, and in preparation). Finally, if females are given a choice between calls having only a 900 Hz-component and calls with both 900 and 3,000 Hz, they choose the two-component call when the SPL is about 55 dB and higher (up to at least 75 dB; Gerhardt, in preparation). We took these facts into consideration in designing the following experiments.

*1. Masking of Tonal Signals of 900 Hz.* A female was placed in the release cage and a series of 900 Hz calls was presented through one speaker at a predetermined SPL (see below). Normally the female oriented to the sound source; and, as soon as this occurred, we added a continuous noise (bandwidth 20 to 10,000 Hz) with a spectrum level of 20 dB. In preliminary tests, a 20 dB-spectrum level never altered the normal behavioral response to the synthetic call. When the animal began moving toward the speaker, we increased the spectrum level by 10 dB after every hop until the animal either hopped sideways or stopped moving at all for 5 min. Our assumption was that the animal was attracted to the sound source only if it detected the 900 Hz-signal within the noise; thus, hopping away or sitting motionless indicated a total masking of the tone by the respective noise level. If the female moved to within 10 cm of the speaker before masking occurred, we replaced her at the release point and ran another test starting at a higher noise level. For each animal the threshold for total masking at a given signal level was defined as the mean of the highest noise level (spectrum level) at which the animal continued its approach to the speaker and the lowest noise level at which it hopped sideways or stopped moving toward the speaker. Thresholds were determined at signal levels of 55, 65 and 75 dB SPL at the release point.

Control experiments were conducted with 19 females. As soon as a female made her first hop toward the speaker, which emitted only the signal, continuous broad-band noise at a level of 40 dB was switched on and the signal was switched off. The behavior of each animal was then observed for at least 5 min. In this way we explored the possibility that the animals, although totally masked, merely continued hopping in the same direction in which they started or were even attracted by the noise.

*2. Masking of the 900 Hz Component in a Signal of 900+3,000 Hz.* Females were placed midway between two speakers and oriented, so that they did not face either speaker. One speaker broadcast the signal (900+3,000 Hz) only; the other, the same signal plus continuous noise. The lower band limit of the noise was 100 Hz and the upper 1,000 Hz. Thus, only the 900 Hz component of the signal was masked. The SPLs of the 900 and 3,000 Hz components were equalized ( $65 \pm 1$  dB) at the release point. Each female indicated her preference by hopping on or within 10 cm (A-criterion) or 50 cm (B-criterion) of one of the speakers. Sixteen animals were tested at a spectrum level of 30 dB, 22 animals, at 40 dB, and 17 animals at a 50 dB spectrum level. Experiments were not done at higher levels because of distortion limitations (loudspeakers).

*3. Masking of the 3,000 Hz-Component in a Signal of 900+3,000 Hz.* Tests were conducted as described above (2.). One speaker broadcast the signal alone; the other, the same signal plus noise. Here the noise band was limited to 2,000 to 10,000 Hz so that only the high-frequency component was masked. Again, signal components were equalized at 65 dB. Twenty-three animals were

tested at a spectrum level of 31 dB, 26 females at 41 dB, and 13 females at 46 dB.

**4. Control Experiments: Choice Situations.** Females were treated as before (2 and 3). One speaker broadcast the signal only, and the other noise only. The signal levels were again 65 dB for each component. Eleven animals were tested when the low-frequency noise level was 40 dB, and 22 animals at 50 dB. When high-frequency noise was used, noise spectrum levels were 31 dB (10 animals) and 41 dB (12 animals).

*Statistics*

Differences between mean thresholds were compared using a Wilcoxon rank-test. A two-tailed binomial test was used to determine the probability that a sample of females preferred one of the two stimuli in the choice experiments.

**Results**

*900 Hz Masking: One-Speaker Experiment*

The threshold for total masking (defined above) of each female at each signal level are given in Table 1. The mean ( $\bar{X}$ ) and standard deviation (SD) of all thresholds at each signal level are also presented. These data were used to calculate critical-ratio (CR) bands, which, expressed in dB, equal the difference between the SPL of the signal of a given frequency and the spectrum level of broad-band noise at which total masking occurred. This difference in level is merely a ratio of signal (tone) intensity to spectrum intensity (noise), and from this relationship we also calculated CR-bands in Hz following Fletcher (1940). The results of these calculations are also given in Table 1. Mean widths of CR-bands at 900 Hz were 158 Hz ( $\cong$ 22 dB) at a signal level of 55 dB, 316 Hz ( $\cong$ 25 dB), at 65 dB, and 1,000 Hz ( $\cong$ 30 dB) at 75 dB. Bandwidths at 55 and 75 dB were not significantly different statistically ( $P > 0.05$ ) even though the mean masked thresholds at those levels were significantly different ( $P < 0.01$ ).

In control experiments only four of the 19 animals hopped to the speaker after the signal had been switched off and the continuous broad-band noise switched on. In other words, the females were not attracted by the noise of 40 dB nor did they merely continue to hop in the same direction as their initial hop. Therefore, we are confident that we measured true masked thresholds.

*Masking of 900 or 3,000 Hz in Signals of 900+3,000 Hz*

The results of the two-choice experiments are presented in Table 2. Females consistently preferred the

**Table 1.** Masked thresholds at 900 Hz (one-speaker situation) for three signal levels. Individual thresholds, mean thresholds, and mean widths of CR-bands in dB and in Hz. Noise levels are expressed in spectrum levels

Signal level 55 dB		Signal level 65 dB		Signal level 75 dB	
Animal	Masked threshold at noise level	Animal	Masked threshold at noise level	Animal	Masked threshold at noise level
11	25 dB	5	45 dB	2	45 dB
12	35 dB	6	55 dB	4	35 dB
14	45 dB	7	35 dB	13	45 dB
15	25 dB	8	35 dB	23	55 dB
16	35 dB	9	55 dB	24	45 dB
17	35 dB	10	35 dB	25	45 dB
18	45 dB	20	35 dB	26	35 dB
19	25 dB	22	35 dB	27	45 dB
21	35 dB	28	25 dB	31	55 dB
29	25 dB	30	45 dB	32	45 dB
$\bar{x}$	33 dB	$\bar{x}$	40 dB	$\bar{x}$	45 dB
SD	7.9	SD	9.7	SD	6.7
CR-band (dB)	22	CR-band (dB)	25	CR-band (dB)	30
CR-band (Hz)	158	CR-band (Hz)	316	CR-band (Hz)	1,000

signal (900 + 3,000 Hz) plus low-frequency noise (100–1,000 Hz) over the signal alone, provided that the noise spectrum level was 40 or 50 dB. When the high-frequency component was masked by noise of 2,000–10,000 Hz, females preferred the signal alone when the noise spectrum level was 46 dB. Thus, the threshold for total masking of 3,000 Hz is defined as the mean of 41 and 46 dB, i.e., 43.5 dB. The width of the CR-band in dB is then the difference between the signal level and noise level, i.e. 21.5 dB, and the CR-band at 3,000 Hz is 141 Hz.

*Control Experiments: Two-Speaker Tests*

The control experiments involving low-frequency noise showed that females not only preferred the signal plus low-frequency noise over the signal alone (see above), but they chose low-frequency continuous noise alone as often as they chose the unmasked signal provided that the spectrum level of the noise was 50 dB. At the spectrum level of 40 dB, they chose the signal. Control experiments involving high-frequency noise indicated that there was no attraction by the noise alone at spectrum levels of 31 and 41 dB.

**Table 2.** Number of females attracted (I) by the signal+noise or the signal in the tests with two speakers, and (II) by the noise or the tone signal in the controls to the tests. The A-values are the numbers of females which touched a speaker or came within a least 10 cm of it; B-values are numbers of females approaching a speaker at least within 50 cm thus showing clear attraction, but failing the more stringent criteria for A. Signal (tone) levels were always 65 dB

(I) Test		Signal+noise	Signal	Significance (two-tailed binomial test)
900 Hz masking	30 dB spect. level	A: 8	8	no
		B: 0	0	no
	40 dB spect. level	A: 12	3	$P \leq 0.03$
		B: 7	0	$P \leq 0.015$
		A+B: 19	3	$P \leq 0.001$
	50 dB spect. level	A: 4	1	no
		B: 12	0	$P \leq 0.001$
		A+B: 16	1	$P \leq 0.01$
	(II) Controls		Noise	Signal
40 dB spect. level	A: 0	10	$P \leq 0.002$	
	B: 1	0	no	
	A+B: 1	10	$P \leq 0.01$	
50 dB spect. level	A: 3	7	no	
	B: 8	4	no	
(I) Test		Signal+noise	Signal	
3,000 Hz masking	31 dB spect. level	A: 11	7	no
		B: 4	1	no
	41 dB spect. level	A: 7	10	no
		B: 9	0	$P \leq 0.004$
		A+B: 16	10	no
	46 dB spect. level	A: 1	8	$P \leq 0.040$
		B: 1	3	no
		A+B: 2	11	$P \leq 0.02$
	(II) Controls		Noise	Signal
31 dB spect. level	A: 0	10	$P \leq 0.002$	
	B: 0	0		
41 dB spect. level	A: 1	11	$P \leq 0.006$	
	B: 0	0		

## Discussion

### *Critical Ratios (CR-Bands) in the Green Treefrog*

Our experiments have demonstrated that the addition of continuous broad-band or band-passed noise to synthetic mating calls can alter the behavior of gravid females in both single speaker and choice experi-

ments. Furthermore, the masking patterns allow us to estimate masked thresholds at two frequencies of known pertinence to these animals. The standard deviations of masked thresholds at 900 Hz in the one-speaker tests are quite large, and this is probably attributable to at least three factors. First, the animals were unconditioned, and even in the absence of noise, they show a great deal of variability in response time and in the degree of recovery from handling from one test to the next. That is, motivational factors beyond our control could have played a role in single-stimulus trials where one criterion of masking was the absence of a response. Second, the animals were allowed to move freely towards the speaker. This meant that there was some variability in the absolute signal and noise levels at the actual points where our behavioral criteria for masking were satisfied. Third, we varied the noise levels in 10 dB steps rather than in smaller steps in order to test a wide range of noise levels in each trial. Despite the large standard deviations in 900 Hz masking, the mean masked thresholds at 55 and 65 dB signal levels differ by 7 dB, a statistically-significant ( $P < 0.01$ ) difference. The difference of 5 dB between mean masked thresholds at 65 and 75 dB signal levels is not statistically significant ( $P > 0.1$ ).

When the signal level is increased by 10 dB, it is expected that the mean masked thresholds will also increase by 10 dB. This relationship has been found in all vertebrates tested so far and the usual interpretation is that the widths of CR-bands stay constant as the signal level increases. A further requirement, however, is that the masker spectrum level should remain below about 40 dB, which has been the usual maximum level in animal studies. In man, CR-bands for  $f > 1,000$  Hz widen at masker levels higher than 40 dB (Scharf and Meiselman 1977), and it is also possible that widening occurred in our experiments with *H. cinerea* since noise levels of more than 40 dB were required to mask the 900 Hz signal at 65 and 75 dB. If the psychoacoustic data from man and *Hyla* are comparable in this respect, then the most reliable estimate of normal CR-bandwidth for 900 Hz is that measured at the 55 dB signal level, namely 158 Hz ( $\cong 22$  dB).

Variability in motivation was minimized in the choice situations because animals showed preferences for the masked or unmasked signal. Unresponsive animals were not considered. The results of the 3,000 Hz masking experiment (Table 2) led directly to the estimation of the masked thresholds and, further, to the calculation of the width of the CR-band, namely 141 Hz or 21.5 dB. The interpretation of the 900 Hz masking in the choice situation is discussed below.

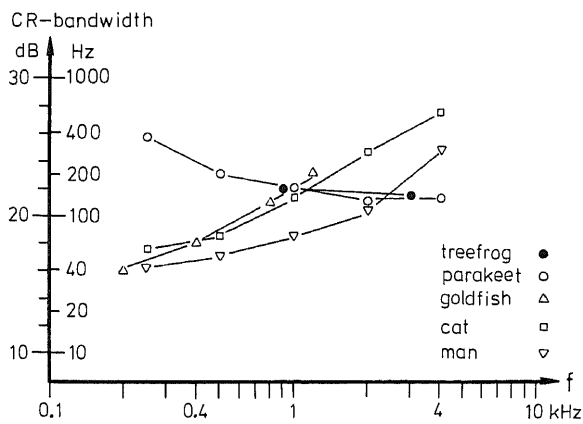


Fig. 1. CR-bandwidths of representatives of four classes of vertebrates. For goldfish, cat and man the widths of CR-bands increase with increasing frequency, for *Hyla* and parakeet CR-bands stay rather constant

In broad-band masking the signal-to-noise ratio at the masked threshold inevitably is a measure of a bandwidth in Hz. The explanation for the fact that masked thresholds are much higher as compared with absolute thresholds is that a summation of sound energy occurs in a frequency band (the CR-band) around the masked frequency (Fletcher's 1940 original assumption; Bilger 1976; Ehret 1977). Therefore, our present results, which are the first measurements in amphibians, indicate the presence of CR-bands in *H. cinerea*. This is of special interest in terms of the mechanisms of the CR-band analysis of sound. Anurans have two different hearing organs, the amphibian and basilar papillae, which probably have different mechanisms of frequency analysis (Capranica and Moffat 1977). Furthermore, Moffat and Capranica (1974) have shown that frequencies around 900 Hz are processed by 'mid-frequency' neurons and frequencies around 3,000 Hz, by 'high-frequency' fibers. In the bullfrog (Feng et al. 1975) the high-frequency neurons innervate the basilar papilla and the mid-frequency neurons the amphibian papilla. Thus, if the situation is the same in *H. cinerea*, CR-bands are involved in the analysis of sounds processed by both organs. A study of masking in single fibers of the auditory nerve of *H. cinerea* showed that CR-bands can already be extracted from the responses of single nerve fibers. The widths of CR-bands encoded in fibers with best frequencies around 900 Hz and around 3,000 Hz are comparable to the estimated widths based on our behavioral study (see Ehret and Capranica 1980). In general, our values are comparable to those reported in other vertebrates. Our estimate of 158 Hz at 900 Hz, for example, is similar to the bandwidths of cats (about 130 Hz; Watson 1963), parakeets (about 160 Hz; Dooling and

Saunders 1975; Saunders et al. 1978) and goldfish (about 200 Hz, Fay 1974) at this frequency (Fig. 1). The 141 Hz-bandwidth at 3,000 Hz is comparable only to the respective ones of man (about 180 Hz; Hawkins and Stevens 1950) and the parakeet (Dooling and Saunders 1975; Saunders et al. 1978). The bandwidths of the CR-bands of the treefrog apparently remain stable and do not increase with increasing frequency as in goldfish, cats and man. In this respect our results are similar to those in the parakeet, where the widths of CR-bands tended to stay constant or even decrease over the range between 500 and 4,000 Hz. In the frog, however, we know that this may reflect the fact that the two frequencies at which we measured CR-bands are processed by different auditory organs.

#### *Attraction of Females by Low-Frequency Noise (100–1,000 Hz)*

The results of the choice experiments involving low-frequency noise (masking the 900 Hz component in the two-component synthetic call) were surprising and cannot be interpreted in terms of masking as such. When the spectrum level of the low-frequency noise (100–1,000 Hz) exceeded 30 dB, females more often responded to the signal plus noise than to the signal alone. This is especially astonishing when the results of the one-speaker experiment are considered: here the attraction by a 900 Hz signal of 65 dB was negated by the addition of *broad-band noise* (20–10,000 Hz) with an average spectrum level of 40 dB. Females not only preferred a stimulus consisting of 3,000 Hz tone bursts and continuous low-frequency noise over the unmasked signal (900 + 3,000 Hz), but also continuous low-frequency noise without the 3,000 Hz-signal was as attractive as the unmasked synthetic call when the noise spectrum level was 50 dB (Table 2, controls). A particular pattern was, however, evident in the behavior of the females. Although clearly attracted by the noise plus signal or noise alone at the release point, females seldom completed their initial approaches to the speaker as indicated by the prevalences of type-B responses. Possibly this behavior reflects a saturation of the auditory system or disorientation in the near field of such a high intense continuous noise. Since the low-frequency peaks in the mating calls of *H. cinerea* vary between about 700 and 1,300 Hz in the southeastern U.S. and since there are typically many males calling at the same time and place, we can assume confidently that females are exposed to continuous acoustic stimulation within this frequency band. However, before speculating about a possible chorus effect we need to answer

three important questions. First, do females use the sound of the chorus for orientation to the breeding site? Second, if so, where are they when they begin to approach the chorus? Third, what is the spectrum of the chorus sound and background noise at these beginning points?

#### *CR-Bands and Mating Call Detection*

Females of *H. cinerea* not only discriminate against the similar calls of other sympatric species in two-speaker experiments, but they also prefer synthetic calls with low-frequency spectral peaks between about 800 and 1,100 Hz; the low-frequency peaks in the calls of conspecifics range from around 700 to 1,300 Hz (Gerhardt 1974a, and unpublished). Since the signals were presented alternately, without temporal overlap, these experiments are comparable to frequency discrimination tasks in mammals (mammalian psychoacoustics, e.g. Ehret 1977). However, in nature, many conspecific males and frogs of other species typically aggregate and form immense choruses. In this situation the female must choose a mating call from among an array of simultaneously produced signals that impinge upon her auditory system. The animal must 'recognize' the appropriate sound pattern on the basis of the relative amplitudes of frequency components and of the temporal pattern of occurrence of these components. The discrimination of simultaneously heard signals is based upon the frequency resolution of the auditory system, a measure of which is the width of CR-bands. The waveform of the typical mating call of *H. cinerea* is quasi-periodic and repeats at about 300/s (Oldham and Gerhardt 1975). Experiments have suggested that females can discriminate among synthetic signals with different waveform periodicities on the basis of time-domain processing (Gerhardt 1978). However, the 300/s periodicity is also reflected in the frequency domain by the spacing of frequency components at intervals of about 300 Hz. Our estimates of CF-bandwidths (158 and 141 Hz) suggest that the frogs can also resolve this structure in the frequency domain.

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