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THE SIGNIFICANCE OF SOME SPECTRAL FEATURES IN MATING CALL RECOGNITION IN THE GREEN TREEFROG (*HYLA CINEREA*)

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SUMMARY

1. Synthetic calls with a waveform periodicity of 300/sec and a bimodal spectrum attracted female green treefrogs as effectively as natural calls.
2. Effectiveness was markedly reduced if the relative amplitude of the two spectral peaks differed by as little as 10 dB.
3. Optimal frequency bands were 900–1100 Hz in the low range and 2700–3300 Hz in the high.
4. Addition of components at 1800 and 2100 Hz rendered the call less attractive.
5. In the absence of a bimodal stimulus, most females responded to a call containing a single spectral peak in the high or low range.
6. Mating call recognition in the green treefrog is compared with that in the bullfrog.

INTRODUCTION

The recognition of species-specific signals is a prime requisite for reproductive success in many animals. Although an animal signal may be complex, behavioural studies often demonstrate that only a few, relatively invariant features of a signal are required for recognition by a conspecific individual (Marler & Hamilton, 1966). Much recent progress in understanding sensory systems has come about through the search for neurones which respond selectively to these pertinent features (Worden & Galambos, 1972).

Vocal communication is well developed in most species of frogs and toads, and the most prominent kind of acoustic signal is the mating call. In some species of hylid, bufonid and microhylid anurans the female has been shown to discriminate between conspecific mating calls and those of other species (Blair, 1964). Several investigations of call discrimination in anurans have used artificial acoustic stimuli which were similar in some respects to the call of the species being studied (Martof & Thompson, 1964; Awbrey, 1965; Loftus-Hills & Littlejohn, 1971). The effects of varying particular physical parameters of these stimuli on approach behaviour in the female suggested which features are important for recognition. In the bullfrog, *Rana catesbeiana*, the features of synthetic calls which maximized evoked calling were the same as those to which single neurones in the peripheral auditory system were most sensitive (Capranica, 1965, 1966; Frishkopf, Capranica & Goldstein, 1968). The same

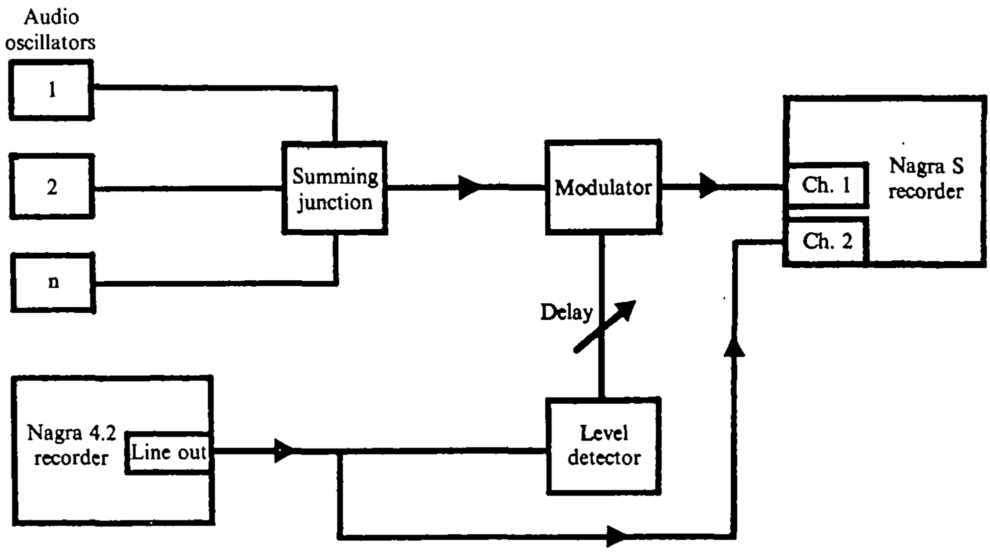

Fig. 1. Block diagram of the system used to generate the synthetic acoustic stimuli used in discrimination experiments.

features are also characteristic of the presumed mating calls of this species (Capranica, 1968).

The green treefrog (*Hyla cinerea*), the barking treefrog (*H. gratiosa*) and the pine barrens treefrog (*H. andersonii*) are closely-related, genetically compatible species (Mecham, 1965; Gerhardt, 1974). The three species are sympatric in the south-eastern United States, and mating call recognition is crucial in maintaining their reproductive isolation in areas where they share the same breeding sites (Gerhardt, 1968, 1974). This paper deals with the identification of spectral features of the vocal signals of the male which are important for species recognition by females of the green treefrog. In addition to indicating how signals must be differentiated to achieve effective behavioural isolation among these three species of treefrogs, this study hopefully will relate to neurophysiological studies of the treefrog auditory system (R. R. Capranica, personal communication).

METHODS AND MATERIALS

Tape recordings

I used a Nagra 4·2 recorder and a Sennheiser 815 condenser microphone to record at 19 cm/sec the mating calls of 55 males of *H. cinerea* in three populations near Savannah, Georgia (U.S.A.). The recorded calls were analysed with the narrow band (45 Hz) filter and sectioner mode of a Kay 7029 A sound spectrograph.

Discrimination experiments

Playback system. A Nagra S (stereo) recorder drove two Nagra DH speaker-amplifiers separated by 4 m. The frequency-response of the system midway between the speakers on a cement surface was flat within ± 4 dB between 600 and 5000 Hz. For most tests, however, the frequency-response of each speaker was taken into accou

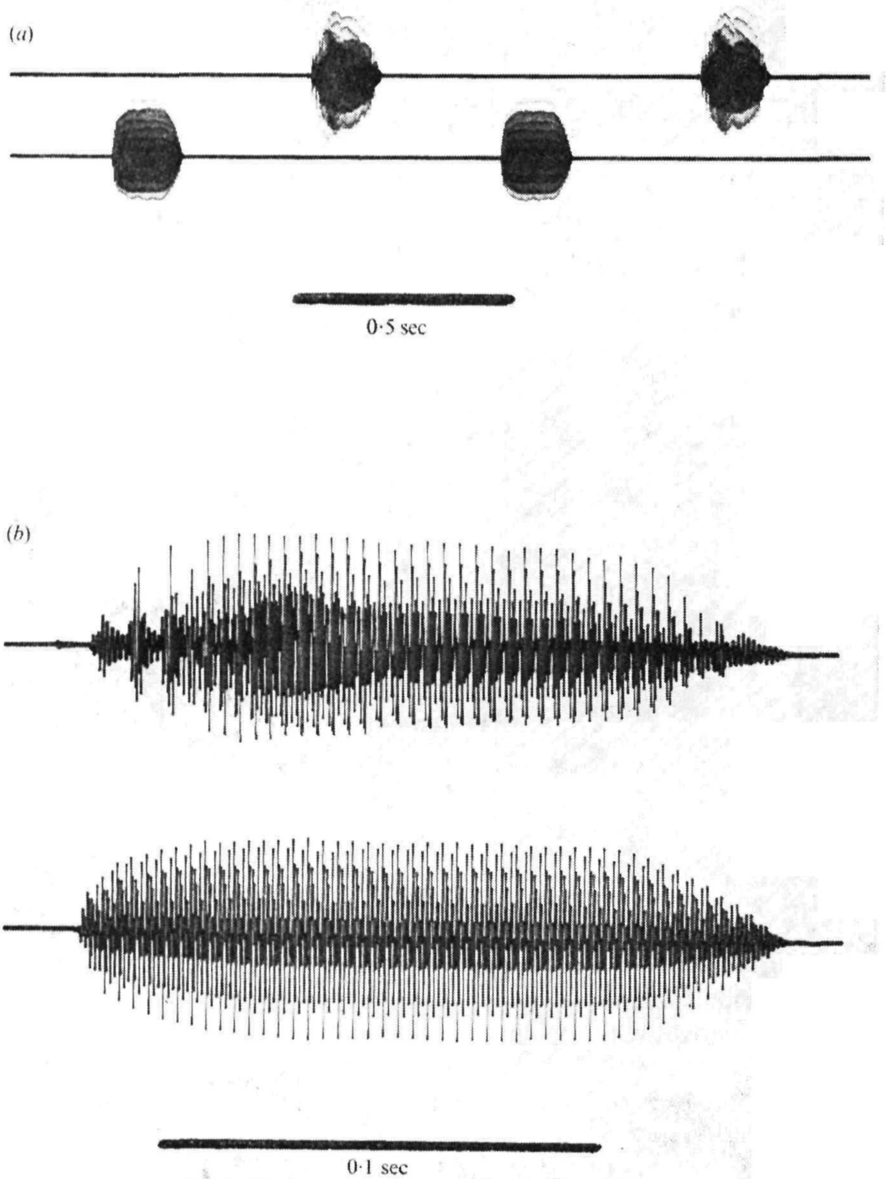

Fig. 2. (*a*) Gross temporal features and timing relationship of natural (upper trace) and synthetic (lower trace) mating calls. (*b*) Expanded oscillograms of the natural (upper trace) and synthetic (lower trace) mating calls.

during the synthesis of experimental stimuli so that, in effect, the frequency response of the system was flat within ± 2 dB at the point where each female was released.

Acoustic stimuli. A representative mating call of an *H. cinerea* from Savannah, Georgia, was the only natural stimulus used. A block diagram of the system used to generate synthetic sounds is shown in Fig. 1. The spectrum of a signal was synthesized by adding the outputs of a series of audio oscillators. The frequency of each

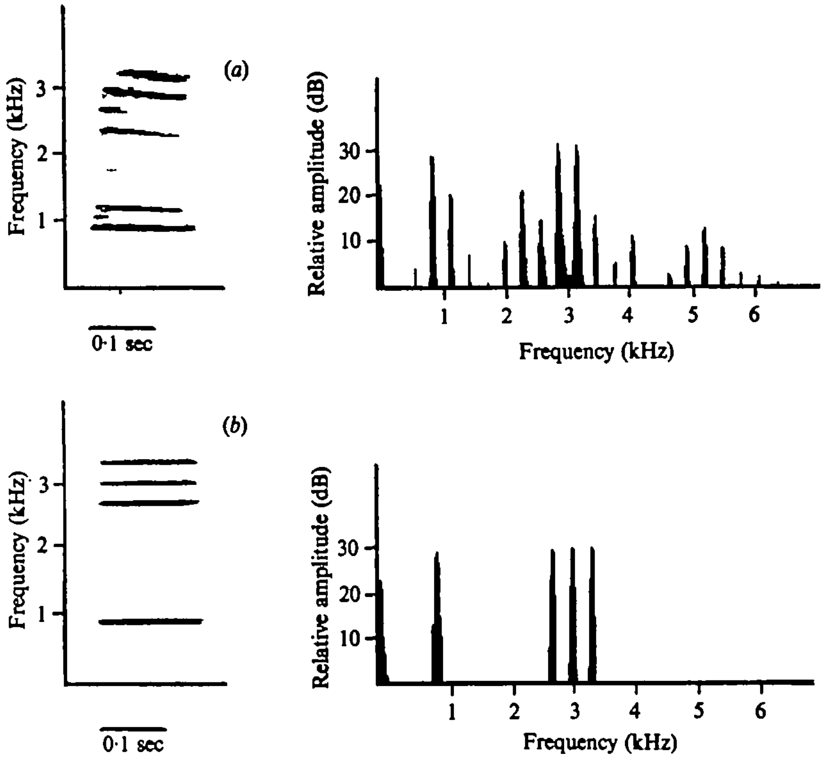

Fig. 3. Spectral features of natural and synthetic calls. Narrow band sonagrams and amplitude-frequency sections through the last one-third of (*a*) natural and (*b*) synthetic calls.

oscillator was adjusted with an electronic counter (Hewlett-Packard 532A or Tektronix 503), and the amplitude, with an a.c. voltmeter (Hewlett-Packard 400D). For stimuli used in 1972, the outputs of the oscillators were unsynchronized; in 1973, the outputs were phase-locked. The output from a summing junction was modulated to produce a series of bursts, each similar to the natural call in duration and rise-fall characteristics (Fig. 2). The modulating circuit was triggered by a pulse from a level detector which, in turn, was triggered by signal voltage available at the line output of the Nagra 4.2. The timing relationship between the two kinds of signals on each stereo tape (one kind of sound per channel) was controllable by means of a variable delay between the level detector and the modulator. Thus, a signal played back on the Nagra 4.2 was transcribed onto one channel of the Nagra S and was also used to trigger the level detector. After a delay, the level detector triggered the modulator and the resulting synthetic call was recorded on the other channel of the Nagra S. The timing relationship of the two kinds of signals on all stereo tapes was the same as that illustrated in Fig. 2.

Because the frequencies of the free-running oscillators used in 1972 drifted independently, the phase relationships of components making up the spectrum of each synthetic call changed slightly and continuously. This variation was minimized by making tape loops (67 cm long) which contained five consecutively generated calls of each of the two stimuli. The waveform remained stable throughout each call and differed only slightly from call to call. The waveforms of calls generated in 1973 w the phase-locked system were extremely stable. Thus, enough consecutively synthesized calls were recorded on a roll of magnetic tape to provide 10–15 min of playback time.

Sonagrams and amplitude-frequency sections of the natural call and a synthetic version which served as an alternative stimulus in one series of tests are shown in Fig. 3. The synthetic call consisted of 4 harmonically-related components, each evenly divisible by 300 Hz. (This was the waveform periodicity of all synthetic calls which consisted of more than one component.) During 1973 this synthetic call served as the standard call against which other synthetic calls were tested. In 1972, the standard synthetic call consisted of three components (900, 2700 and 3000 Hz).

A Bruel and Kjaer 2204/S (peak-reading) sound level meter and 4133 condenser microphone were used to adjust the sound pressure level (SPL) of each stimulus to the same value (unless otherwise stated) at a point midway between the speakers. The level chosen (86 dB peak, 75 dB fast RMS SPL *re* 0·0002 μbar) was based on measurements of call levels made in the field (Gerhardt, 1974).

Source and treatment of females. One hundred and seventy-eight females of *H. cinerea* were found in amplexus in populations within 25 km of Savannah, Georgia. Each female was separated from the male and placed in a refrigerator at about 4 °C. Refrigeration inhibited oviposition so that the animals could be tested one or two nights after the night of capture. Post-reproductive females did not respond to mating calls. This procedure was necessary because females were difficult to find until after midnight and the period of darkness remaining after collecting the animals was usually insufficient for completing the experiments. In experiments with natural calls, I found no differences in the discrimination patterns of females tested on the night of capture and those tested after 24–48 hr of refrigeration (Gerhardt, 1968).

Experimental procedure. Experiments were done at night in the field at air temperatures between 21 and 26 °C. All experiments in 1973 and most of those in 1972 were conducted on a cement surface which was sprinkled periodically with water. A few experiments in 1972 were done on short-cut grass. After the levels of the two stimuli were adjusted, a female was confined in a small covered glass dish midway between the speakers. After the sounds had been played back for 30–60 sec the animal was liberated by removing the cover of the dish. A response was tabulated when a female touched a speaker. Most females responded in several different two-stimulus situations; however, no female was exposed to the same stimulus more than once. This procedure minimized the possibility that exposure of the female to a stimulus in one test would bias her preference in a subsequent test. If the first 8 females responded to the same stimulus in a given experiment, I concluded that discrimination had been demonstrated. If all 8 females did not respond to the same stimulus of the pair, I usually tested at least 4 more females. The probability of discrimination was determined by applying the two-tailed binomial test.

RESULTS

Acoustic analysis

Some features of the mating calls of *H. cinerea* from the Savannah area are given Table 1. In one mating call the amplitude of the upper peak was 9·5 dB greater

Table 1. *Spectral peaks in the mating calls of* 55 H. cinerea *from Chatham County, Georgia*

($\bar{x}$ = mean; S.D. = standard deviation.)

	Frequency of lower peak (kHz)	Frequency of upper peak (kHz)
$\bar{x}$	0·94	3·10
S.D.	0·11	0·26
Range	0·76–1·34	2·52–3·60

than that of the lower peak, and in another mating call the lower peak was 9·0 dB greater than the upper peak; however, the average difference in amplitude between the upper and lower peaks was only 3 dB. The upper peak had the greater relative amplitude in 49 % of the calls, the lower peak had the greater relative amplitude in 38 % of the calls, and the two peaks had equal amplitudes in the rest of the calls.

Discrimination experiments

In May, June and July of 1972, 42 females responded in discrimination tests; in June, July and August of 1973, 113 responded. Three of the 23 animals which failed to respond were post-reproductive.

The behaviour of a female, responding to a sound, appeared to be deliberate. The animal typically turned first her head and then her entire body toward a loudspeaker before hopping or crawling from the glass dish. The behaviour of an individual female often reflected the performance of the entire sample of females in a given experiment. When, on the one hand, all females in a sample responded to the same stimulus, each female typically oriented rapidly to the loudspeaker broadcasting the preferred stimulus. The amount of time required to leave the glass dish and touch the speaker varied, but the pathway taken was usually direct. When, on the other hand, a sample of females did not display a clear preference for one of the two stimuli, an individual female typically climbed onto the edge of the glass dish and oriented first toward one speaker and then toward the other. The direction taken initially was often perpendicular to a line connecting the two speakers. In other words, the animal tended to stay the same distance from the two sound sources for a period of time after leaving the dish and before choosing one of the sounds.

Natural call versus synthetic calls

The standard 4-component call used in 1973 was as attractive to females as a natural call (Table 2). Preliminary data also suggest that females do not discriminate between the natural call and the 3-component synthetic version used as a standard in 1972. Two females chose the synthetic call and one chose the natural call. Synthetic calls with more than 4 components were also as attractive as the natural call (Table 2).

Effects of varying the relative amplitudes of the two spectral peaks

The results of experiments in which the relative amplitudes of the two spectral peaks were varied are given in Table 3. Experiments performed in 1972 indicated th

Table 2A. *Spectral content of synthetic mating calls*

Stimulus designation	Frequency (Hz)	Relative amplitude (dB)
1973 (1), standard call	900	0
	2700	0
	3000	0
	3300	0
1973 (2)	900	0
	1200	−5
	2700	0
	3000	0
	3300	0
1972 (1)	900	0
	1200	−10
	2400	−10
	2700	0
	3000	0
	3300	0
	3600	−10

* Amplitudes of components in 1973 (1) and 1973 (2) were adjusted to compensate for nonlinearities in the frequency responses of the loudspeakers. Relative amplitudes were within 2 dB of those given above at the point where each female was released.

The spectrum of the natural call is shown in Fig. 3.

Table 2B. *Responses of* 36 *females of* H. cinerea *given a choice between natural and synthetic mating calls*

Alternatives	Responses	Probability
Natural call versus 1973 (1)	4–8	0·388
Natural call versus 1973 (2)	7–5	0·774
Natural call versus 1972 (1)	5–7	0·774

attenuation of the upper peak by 20 dB or, more critically, attenuation of the lower peak by only 10 dB rendered a synthetic sound ineffective relative to a sound in which the two peaks were of equal amplitude. The latter result was corroborated in 1973 by experiments using calls in which the frequency-responses of the speakers were taken into account in the adjustment of the relative amplitudes of each components. Other experiments in 1973 showed that a 15 dB attenuation of the upper peak was sufficient to reduce the relative attractiveness of a synthetic call.

Effects of varying the frequency of the upper peak

The results of experiments in which the frequency of the upper peak was varied are given in Table 4. Synthetic calls with two or three components making up the upper peak were as effective as the standard call if at least one component had a frequency between 2700 and 3300 Hz.

Effects of varying the frequency of the lower peak

In 1972 five of five females responded readily to a synthetic call having a single quency component (900 Hz) corresponding to the lower peak in the standard

Table 3. *Effects of varying the relative amplitudes of the two spectral peaks in synthetic mating calls*

(*a*) *Spectral content of stimuli**

Stimulus designation	Relative amplitude (dB) Lower peak	Upper peak
1972 (1)	0	0
1972 (2)	0	−20
1972 (3)	0	−10
1972 (4)	−20	0
1972 (5)	−10	0
1973 (1)	0	0
1973 (2)	0	−15
1973 (3)	−10	0

(*b*) *Initial responses of 60 females of* H. cinerea *in discrimination experiments*

Alternatives	Responses	Probability (Two-tailed binomial)
1972 (1) versus 1972 (2)	8–0	0·008
1972 (1) versus 1972 (3)	7–5	0·774
1972 (1) versus 1972 (4)	8–0	0·008
1972 (1) versus 1972 (5)	8–0	0·008
1973 (1) versus 1973 (2)	11–1	0·006
1973 (1) versus 1973 (3)	10–2	0·038

* Stimuli used in 1972 had an upper peak consisting of two components of 2·7 and 3·0 kHz of equal amplitude. Stimuli used in 1973 had an upper peak consisting of three components of 2·7, 3·0 and 3·3 kHz all of equal amplitude.

synthetic call.* There was no alternative stimulus. The same animals responded to call having the upper peak alone (2700 and 3000 Hz). The females took longer to respond and stayed in the vicinity of the speaker for a shorter period of time than they did when the 900 Hz call was available. In 1973, 63 of 91 females (69 %) responded in discrimination experiments using calls having a single frequency. (Ninety of the 91 responded to bimodal calls in other experiments.) Females (13) never responded to calls having single frequencies above 1200 Hz and played back at the usual intensity (86 dB peak SPL at 2 m). One female released 1 m in front of a speaker responded to a 3000 Hz call played back at 103 dB peak SPL (1 m). There was no alternative stimulus. The results of the discrimination experiments with calls having frequencies 1200 Hz and below suggest that the optimal frequency range for the lower peak is surprisingly narrow (Table 5). Indeed, the range is narrower than the range of variation of the frequency of the lower peak in the calls of males from the same populations (Table 1). When the level of a call consisting of a 700 Hz sinusoid was increased by 15 dB relative to a call consisting of a 900 Hz sinusoid, then one of four animals responded to the 700 Hz call. The others responded to the 900 Hz call. Similarly, one of four animals responded to a 1200 Hz call after its level was increased by 15 dB relative to the 900 Hz call. One other experiment, using calls with two peaks, tends to

* A second peak (37 dB down relative to the 900 Hz component) was present at 2700 Hz in the acoustic stimulus. This peak represented third harmonic distortion by the speaker-amplifier and was determined by analysing a recording of the stimulus made 2 m in front of the speaker (General Radio 1900A wave analyser).

Table 4. *Effects of varying the frequency of the upper peak*

(*a*) *Spectral content of synthetic calls**

Stimulus designation	Frequencies of components in the upper peak (Hz)
1972 (1)	1800
	2100
1972 (2)	2400
	2700
1972 (3)	3000
	3300
1972 (4)	3300
	3600
1972 (5)	3600
	3900
1973 (1)	2700
	3000
	3300
1973 (2)	1800
	2100
	2400
1973 (3)	2100
	2400
	2700
1973 (4)	3600
	3900
	4200

(*b*) *Responses of 47 females in discrimination tests*

Alternatives	Responses	Probability (Two tailed binomial)
1972 (1) versus 1972 (2)	2–10	0·038
1972 (3) versus 1972 (4)	3–2	1·000
1972 (3) versus 1972 (5)	8–0	0·008
1973 (1) versus 1973 (2)	8–0	0·008
1973 (1) versus 1973 (3)	2–4	0·688
1973 (1) versus 1973 (4)	8–0	0·008

* The lower peak was 900 Hz in all stimuli.

corroborate these results. All six females responded to a synthetic call composed of 800, 2700 and 3000 Hz in preference to a call composed of 700, 2700 and 3000 Hz.*

Effect of adding frequency components between the two spectral peaks

The results of experiments in which the standard call was tested against calls having two additional components at 1800 and 2100 Hz are given in Table 6. Addition of energy in this region of the spectrum clearly had an adverse effect on the relative attractiveness of a synthetic call.

* The standard call was not tested against calls in which the lower peak was varied because, except at 600 and 1200 Hz the waveform periodicity would be different as well. For example, the periodicity of a call composed of 800, 2700, 3000 Hz tones is 100/sec as opposed to the 300/sec periodicity of the standard call.

Table 5. *Effects of varying the frequency of the single-component synthetic calls*

(*a*) *Spectral content of synthetic calls*

Stimulus designation	Frequency (Hz)
1973 (1)	900
1973 (2)	800
1973 (3)	700
1973 (4)	600
1973 (5)	1000
1973 (6)	1200
1973 (7)	3000

(*b*) *Responses of* 51 *females in discrimination tests*

Alternatives	Responses	Probability (two-tailed binomial)
1973 (1) versus 1973 (2)	11–1	0·006
1973 (1) versus 1973 (3)	8–0	0·008
1973 (1) versus 1973 (4)	8–0	0·008
1973 (1) versus 1973 (5)	4–3	1·000
1973 (1) versus 1973 (6)	8–0	0·008
1973 (1) versus 1973 (7)	8–0	0·008

Table 6. *Effects of adding components with frequencies between the two spectral peaks*

(*a*) *Spectral content of synthetic calls*

Stimulus designation	Frequency (Hz)	Relative amplitude (dB)
1973 (1)	900	0
	2700	0
	3000	0
	3300	0
1973 (2)	900	0
	1800	+5
	2100	+5
	2700	0
	3000	0
	3300	0
1973 (3)	900	0
	1800	0
	2100	0
	2700	0
	3000	0
	3300	0

(*b*) *Responses of* 34 *females of* H. cinerea *in discrimination tests*

Alternatives	Responses	Probability
1973 (1) versus 1973 (2)	19–3	< 0·001
1973 (1) versus 1973 (3)	11–1	0·006

DISCUSSION AND CONCLUSIONS

The standard synthetic signals differed in four principal ways from a typical mating call of *H. cinerea*. First, the waveform periodicity of a synthetic call was constant. The natural call had a short distinctly pulsatile, aperiodic initial part; the waveform became periodic during the rest of the call. Secondly, the amplitude-time envelope of a synthetic call was much smoother than that of the natural call. This was true because the synthetic call lacked the pulsatile initial part and because its decay pattern was only an approximation of the decay pattern of the natural call. Thirdly, the spectrum of a synthetic call stayed constant. In the natural call the relative amplitudes and frequencies of components changed slightly during the call. Fourthly, the synthetic call lacked some components found in the natural call. These components in the natural call occurred in three regions of spectrum: (1) below 900 Hz; (2) between the two peaks; and (3) above 3300 Hz. Since synthetic calls were as attractive as the natural one, these differences must be relatively insignificant in mating call discrimination in the green treefrog.

In addition to having similar gross temporal features, natural calls and equally attractive synthetic calls shared two features: (1) a waveform periodicity (or quasi-periodicity) of about 300/sec; and (2) a bimodal spectrum with a lower peak around 850–900 Hz and an upper peak consisting of two or three components between 2700 and 3300 Hz. A study of the significance of waveform periodicity is underway. The results presented herein show clearly that a bimodal spectrum is very important. Indeed, a stimulus was most effective when the amplitudes of the two peaks were approximately the same.

The optimal frequency band for the upper peak extended from about 2700 to 3300 Hz. The optimal band for the lower peak was narrower: 900–1100 Hz. (The range may be even narrower since a call with a frequency of 1100 Hz was not used.) The mating calls of the barking (*H. gratiosa*) and the pine barrens (*H. andersonii*) treefrogs also have bimodal spectra. The frequencies of the two peaks in the calls of *H. gratiosa* fall completely outside the optimal ranges for *H. cinerea* and at least one peak in the calls of most *H. andersonii* lies outside these optimal bands. Thus, although there are other differences between the calls of the green treefrog and these other species, the differences in their spectral structures alone may be sufficient to account for mating call discrimination (Gerhardt, 1968, 1974). However, it is important to note that the frequencies of the lower peaks in the calls of a substantial proportion of conspecific males also fall outside optimal range for the lower peak. Seven (12·7 %) males had lower peaks below 825 Hz, and three (5·1 %) had lower peaks above 1100 Hz.

Attenuation of components having frequencies between the two peaks is another important property of an effective stimulus. In *cinerea* calls, components in this region of the spectrum were at least 5 dB down from the amplitude of the lesser of the two peaks. The upper peak in the calls of *H. gratiosa* and some *H. andersonii*, however, occur in this region of the spectrum.

The results of experiments with the green treefrog parallel in several ways those of Capranica (1965, 1966) with the bullfrog. Evoked calling in the latter species was maximized by presentation of a periodic stimulus having a bimodal spectrum. Addition of energy between the peaks inhibited calling. A striking difference between the behaviour of the bullfrog and treefrog was the responsiveness of the treefrog to a wide variety of less than optimal stimuli when these were presented one at a time. For example, calling was elicited in the bullfrog only by the playback of calls of other adult bullfrogs from among the calls of 34 different species of frogs and toads. Not only did males of the green treefrog readily call back in response to the calls of certain other species (*H. andersonii* and *H. gratiosa*), but, more significantly, many females made vigorous responses to these heterospecific signals in experiments from which conspecific calls were excluded (Gerhardt, 1968, 1974). With respect to synthetic sounds, Capranica found that at low to moderate levels only stimuli which possessed both spectral peaks were capable of evoking the calls of the bullfrog.* By contrast, about 70% of the treefrogs tested responded readily to a synthetic call consisting of a tone between 800 and 1000 Hz. Responses of 5 females to signals having only the upper of the two peaks were less vigorous but unmistakable. The difference between the bullfrog and the green treefrog is probably based mainly on species differences in the auditory system. If, for example, the two peaks in the mating call of the treefrog reflect at least partially the spectral sensitivities of its two inner ear organs (amphibian and basilar papillae) as in the bullfrog (Frishkopf *et al.* 1968), then the lack of selectivity of the treefrog in single-stimulus experiments might be explained by assuming that excitation of either one of the two organs will elicit approach behaviour.† Capranica's experiments clearly suggest that evoked calling in the bullfrog depends on simultaneous excitation of both organs. Another possibility is that the artificial conditions in which Capranica maintained his animals rendered them unresponsive to less than optimal stimuli (Paillette, 1970; Schmidt, 1973).

The performance of the female treefrog in discrimination (two-stimulus) experiments is another matter. Even though stimulus filtering by the peripheral auditory system is not selective enough to exclude responses to some heterospecific signals, the central auditory system is capable of discriminating between sounds having very subtle differences.

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* A call with a low frequency peak alone was effective if there was also sufficient sound energy, but not necessarily a peak, in the high frequency region.

† One could argue that energy present at 2700 Hz due to third harmonic distortion of the 900 Hz call is sufficient to excite neurones tuned to this part of the spectrum, but this argument does not apply to experiments with the call having only the upper peak. Alternatively, auditory neurones in the periphery, although optimally tuned to one of the spectral peaks, nevertheless may be sensitive enough to respond to energy in the other peak as well. Neurophysiological studies and behavioural experiments using sounds played back at very low levels should resolve these questions.

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