95

SYNCHRONOUS VOCAL RESPONSE MEDIATED BY THE AMPHIBIAN PAPILLA IN A NEOTROPICAL TREEFROG: BEHAVIOURAL EVIDENCE

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SUMMARY

Acoustic playback experiments with treefrogs (*Eleutherodactylus coqui* Thomas) in their natural habitat reveal that males readily synchronize their vocalizations with synthetic calls containing frequencies equal to or lower than their own. Low-level artificial stimuli were used in order preferentially to stimulate auditory fibres originating in the amphibian papilla while avoiding excitation of basilar papillar or saccular fibres. Moreover, the synchronous vocal response persists unabated, even when the synthetic calls were simultaneously 'masked' with narrow- and wide-band noise, which strongly excited a large fraction of the basilar papillar fibres. These behavioural findings support the hypothesis that the amphibian papilla alone mediates this critical vocal behaviour.

INTRODUCTION

Anuran amphibians (frogs and toads) must often communicate in the face of high levels of ambient noise (Gerhardt, 1975; Narins, 1982*b*; Narins & Hurley, 1982). The filtering ability of anuran peripheral auditory fibres does not favour a mechanism of signal extraction from noise based purely on spectral processing (see Capranica, 1976 for review; Narins & Capranica, 1980; Shofner & Feng, 1981; Narins, 1982*b*). Recent acoustic playback experiments with calling males in their natural habitat have quantified the remarkable degree to which males can shift their call timing to avoid acoustic interference from conspecifics (Narins, 1982*a*; Zelick & Narins, 1982; R. D. Zelick & P. M. Narins, in preparation) suggesting that temporal encoding also plays a pivotal role in auditory signal processing by amphibians.

The neotropical frog, *Eleutherodactylus coqui* (Leptodactylidae) is the largest of the eight sympatric arboreal species found in the Caribbean National Forest in eastern Puerto Rico (Drewry, 1970; Rivero, 1978). Males emit a two-note advertisement call ('Co-Qui'), in which the 'Co' note is a constant-frequency tone of about 1100 Hz lasting nearly 100 ms and functions in male–male territorial interactions. The 'Co' note is followed by a pause of 150–200 ms and a second ('Qui') note which sweeps upward in frequency from 1800 to 2100 Hz in about 170 ms. The 'Qui' note serves to

attract females (Narins & Capranica, 1976, 1978). Males repeat the two-note call every 2–4 s from sunset to after midnight throughout 11 months of the year.

Large male *E. coqui* emit calls with lower fundamental frequencies than those of either smaller male *E. coqui* or males of any other eleutherodactylid frog in Puerto Rico (Drewry, 1970; P. M. Narins, unpublished data). If a 'resident' calling male is approached by a second calling male, the resident will drop the second note of his call and synchronize his 'Co' note with that of the intruder. If the calling intruder continues to approach to within about 0·6 m of the resident, the latter may initiate a biting, butting attack on the intruder in an attempt to drive him away (Reyes Campos, 1971). The synchronous vocal response preceding physical aggression may be readily elicited from a calling male by playback of natural or synthetic sounds consisting of either (a) a 'Co-Qui' call or (b) a 'Co' note alone (Narins & Capranica, 1976, 1978; Narins, 1982*a,b*).

The synchronizing of one male's call with another distant but audible call has also been observed to occur among males of several species of neotropical frogs including *E. coqui* (Loftus-Hills, 1971; Rosen & Lemon, 1974; Awbrey, 1978; Narins, 1982*b*). In this case, call synchronization by males is not necessarily a prelude to physical confrontation, but rather has been interpreted as an adaptation to minimize acoustic interference for communication in a highly noisy environment (Rosen & Lemon, 1974; Wells, 1977; Narins, 1982*a*). Synchronization of one vocalization with another ensures that the call of the follower will not be jammed by that of the leader and thus raises the probability of its detection (Littlejohn & Martin, 1969; Narins, 1982*a*).

The inner ear of anurans contains two distinct and spatially separate organs which detect airborne sounds: the amphibian papilla (a.p.) and the basilar papilla (b.p.) (van Bergeijk & Witschi, 1957; Geisler, van Bergeijk & Frishkopf, 1964; Wever, 1973; Frishkopf & Flock, 1974; Lewis, 1976; Lewis, Leverenz & Koyama, 1982). Selective lesioning experiments in the bullfrog (*Rana catesbeiana*) have demonstrated the existence of three populations of fibres in the VIIIth cranial nerve of this species: the fibres most sensitive to low- and mid-frequency tones innervate hair cells of the amphibian papilla, whereas the fibres most sensitive to high-frequency tones innervate hair cells of the basilar papilla (Feng, Narins & Capranica, 1975). In *Eleutherodactylus coqui*, the two populations of auditory nerve fibres that innervate the a.p. are a low-frequency inhibitable population having best excitatory frequencies (BEFs) below 600–700 Hz, and a mid-frequency non-inhibitable group having BEFs below about 1400 Hz. A third population of fibres originates from the b.p. and has BEFs from 1800 to 3700 Hz (Narins & Capranica, 1976). The BEF of an auditory nerve fibre is that frequency to which it is most sensitive. A fibre is inhibitable if its response to an excitatory tone within its tuning curve can be totally suppressed by the simultaneous addition of a second tone of higher frequency and appropriate level (up to 30 dB above the excitatory tone) outside the fibre's excitatory tuning curve.

The goals of the present study were to determine (a) the frequency dependence of the synchronous vocal response observed during male–male interactions, and (b) the role of each of the auditory papillae in mediating this response. Evidence is presented that the number of synchronous responses evoked is indeed highly dependent on the frequency of the stimulus used to elicit them; frequencies below a calling male's 'Co' note are more effective than are frequencies an equal increment above it. Furthermore,

this vocal behaviour in anuran amphibians is very probably mediated by the amphibian papilla in the inner ear.

<center>METHODS</center>

Acoustic playback experiments with adult male *E. coqui* were conducted in the Luquillo Mountains (altitude 660–750 m) in eastern Puerto Rico during July, 1982. A relatively isolated male was located, usually calling in a vertical orientation from an elevated, partially protected perch site on a tree trunk or from within dead *Cecropia* leaves (Narins & Hurley, 1982). A directional microphone (Sennheiser ME-88) with windscreen and a portable speaker (Calrad 20-257) were placed within 1 m of the male. Synthetic 'Co' notes were generated by a portable sound synthesizer (Narins & Capranica, 1978) which was triggered by the call of the male being tested and broadcast to him after a fixed delay. The results of previous acoustic playback experiments with *E. coqui* using this delayed-trigger technique have shown that a delay of >1100 ms ensures that the synthetic stimuli will occur after the animal's absolute behavioural refractory period, during which males do not produce synchronous responses to sounds (Narins, 1982*a*). With this technique, one maximizes the number of effective stimuli, that is, those which are capable of eliciting a synchronous response from a calling male.

Experiment A: frequency-dependence of the synchronous response

A series of 50 synthetic 'Co' note mimics with a frequency (F_S) adjusted by ear to match that of the calling male's 'Co' note (F_{CO}) and a duration of 100 ms was initially presented to each test male ($N = 17$) at a low level, and the number of evoked synchronous responses was recorded. In this study, a synchronous response is defined as a vocalization which is initiated <500 ms after the onset of the acoustic stimulus used to evoke it. The playback intensity was then increased in discrete steps until a level, L_θ, was reached for which the 50 stimuli evoked 10 synchronous responses from the male under test; this was arbitrarily defined as the threshold response rate, R_θ. The threshold criterion used throughout this study (20 % synchronous responses) is conservative, but was chosen to ensure that a weak, yet consistent, vocal response was being elicited by the stimulus (Narins & Capranica, 1978; Narins, 1982*b*). Next, the stimulus level was increased to 3–4 dB > L_θ in order to evoke a reliable, vigorous synchronous response from the frog. The absolute tone levels used in the playback experiments ranged from 67–77 dB SPL at the position of the animal. With all other parameters held constant, the stimulus frequency was then increased or decreased in 20 Hz steps, and the number of synchronous responses was redetermined using the identical procedure. This experiment is thus designed to obtain the frequency-dependence of the synchronous vocal response using constant-intensity stimuli.

Experiment B: simultaneous masking

Narrow-band (NB) and wide-band (WB) noise maskers were produced by filtering broad-band noise with a 7th-order elliptical (Cauer) filter (Rockland 751A) with cut-slopes of >115 dB/octave. The resulting noise maskers were recorded on cassette

tapes (Denon DX7, $70\,\mu s$ equal.) and played back to the animal using a portable
recorder (Superscope-Marantz C 206 LP) and speaker (Calrad 20-257).

For this experiment, the frequency of the synthetic 'Co' note stimulus, F_S, was set
equal to F_{CO} and was passively mixed with the pre-recorded narrow-band noise
masker, NB2, (bandwidth: 800 Hz; centre frequency: 1300 Hz, thus encompassing
F_S). The tones + NB2 noise masker combination was then presented to the animal at
a low level. With the tone level held constant at $3-4\,dB > L_\theta$, the spectrum level of
the NB2 noise masker was systematically increased in 3 dB steps until the animal's
synchronous response rate was reduced below R_θ. This spectrum level of the NB2
noise masker was used for each of the subsequent noise maskers presented to an
individual animal (Table 1): three NB noise maskers each with a bandwidth of 800 Hz
and with centre frequencies of 500, 2100 and 2900 Hz, respectively, and a WB masker
(bandwidth: 2000 Hz; centre frequency: 2700 Hz). For each presentation the number
of synchronous responses evoked by each tone + masker combination was recorded.
The WB masker contained frequency components which encompassed the complete
range of auditory fibre BEFs innervating the b.p. for this species (Narins &
Capranica, 1976). The total noise power, TP (in dB), in a masking signal may be
calculated by

$$TP = N_o + 10\log_{10}BW,$$

where N_o is the spectrum level of the masker in dB/Hz, and BW is the masker
bandwidth in Hz. The mean number of synchronous responses evoked by the 50 'Co'
notes in the presence of a noise masker was pairwise compared with the mean number
of synchronous responses elicited by the 50 tones presented alone (control). All
animals were tested between 21 and 24 °C.

Calibrations of the tone and noise stimuli were carried out in a $1 \cdot 5\,m \times 1 \cdot 8\,m \times
2 \cdot 1\,m$ anechoic chamber (Gilman, 1980) in which a pressure microphone (Bruel &
Kjaer 4134) was placed 1 m in front of the speaker (Calrad 20-257) used to present
sounds in the field. The microphone output was fed to a one-third octave filter (Bruel
& Kjaer 1618). The background noise level in the chamber measured with the one-
third octave filter centred at 1000 Hz was 30 dB SPL. The stimulus levels reported are
derived from the speaker calibrations in the anechoic chamber, and corrected for the
actual distance between the speaker and the frog (between $0 \cdot 5$ and $1 \cdot 5$ m) using the
inverse square law. The acoustic frequency response of the stimulus delivery system
was flat (± 6 dB) from 200 to 8200 Hz. Background sound levels at the recording site
ranged between 65–90 dB SPL (peak) measured with a precision sound level meter
(General Radio 1982) using an octave filter centred at 1000 or 2000 Hz (Narins,
1982*b*).

<div align="center">RESULTS</div>

<div align="center">*Experiment A: frequency-dependence of the synchronous response*</div>

The 'Co' note stimuli elicited two types of responses from calling males: (a) short-
latency (<500 ms – see Methods), one-note 'Co' calls and short-latency, two-note 'Co-
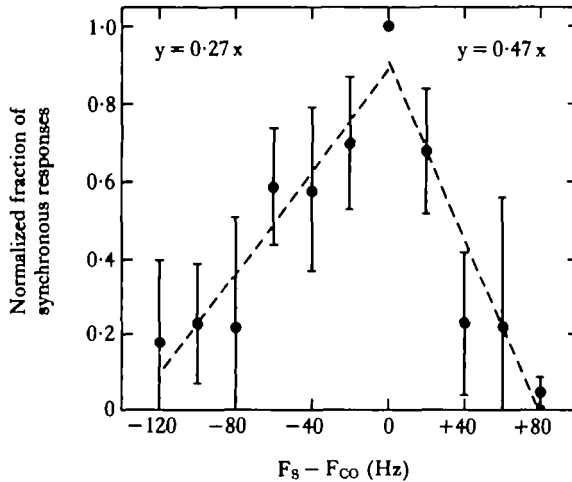Qui' calls, both time-locked to the stimulus, and (b) one-note 'Co' calls and two-n

Fig. 1. Normalized mean number of synchronous responses (± 1 s.d.) as a function of the synthetic 'Co' note stimulus frequency, F_S minus the animal's 'Co' note frequency, F_{CO}. For each male tested ($N = 14$), the greatest number of synchronous responses occurred for $F_S = F_{CO}$. The function is asymmetrical about its maximum indicating that a stimulus with a given frequency difference from a male's 'Co' note frequency, will evoke a greater number of synchronous responses for negative rather than positive deviations. The dashed lines are the best-fit least-squares regression lines through the mean response rates for each frequency tested.
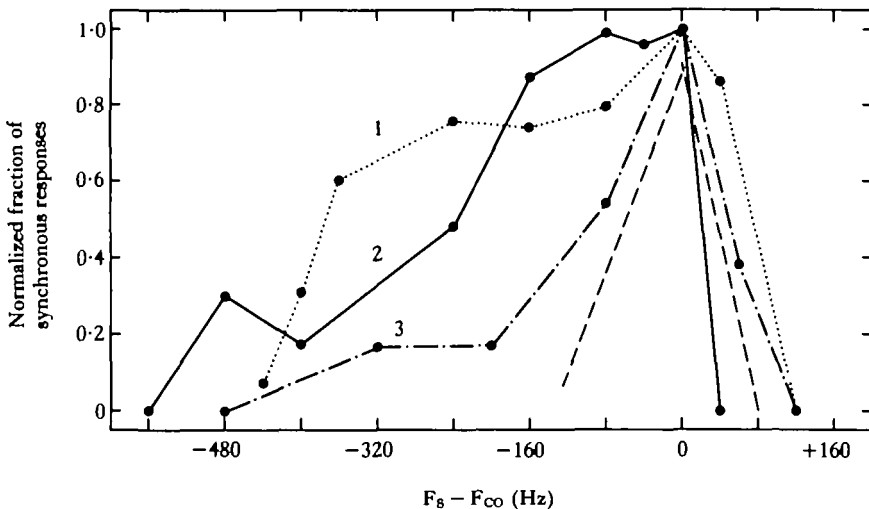

Fig. 2. Normalized number of synchronous responses as a function of frequency for three males (1, 2 and 3). Although the general form of the function is similar to that indicated in Fig. 1, the extended low frequency range over which synchronous responses could be evoked in these males is probably due to simultaneous vocal interactions with adjacent calling males. The dashed lines are the regression lines from Fig. 1 replotted for comparison.

'Co-Qui' calls which appeared to alternate with the stimulus, but with no obvious fixed time relationship to it. In this study all one-note and two-note time-locked responses were pooled and treated as synchronous responses.

Fig. 1 shows the mean fraction of synchronous responses given by 14 males as a function of stimulus frequency, F_S, normalized such that the maximum number of

synchronous responses (always evoked by a 'Co' note stimulus with a frequency $F_S = F_{CO}$) was set equal to 1. Two least-squares regression lines were fitted through the mean response levels: one for stimulus frequencies below F_{CO} ($r = 0.95$) and the other for stimulus frequencies above F_{CO} ($r = 0.95$). The absolute values of the slopes of the regression lines through the mean response rates for $F_S < F_{CO}$ ($|m| = 0.27$) and $F_S > F_{CO}$ ($|m| = 0.47$) are significantly different [analysis of covariance: $F = 5.45$, $P < 0.05$, $d.f. = 1.8$ (Snedecor & Cochran, 1974)], suggesting that *E. coqui* synchronize their vocalizations more readily with call notes differing in frequency by Δf Hz below their own call rather than with call notes of Δf Hz higher than their call. The number of synchronous responses as a function of frequency for three males differed from the others (Fig. 2). For these individuals, the response was much more robust, being evoked by stimuli over a much wider range of (low) frequencies than for the other males tested.

Experiment B: simultaneous masking

The results of the noise-masking experiments for 16 males are shown in Fig. 3. The spectrum level of NB2 was set in each case to suppress the synchronous response from the male under test. A comparison between the mean number of synchronous responses elicited by the tones masked by NB2 *vs* the unmasked tones revealed that they differed significantly ($t = 10.41$, $P < 0.001$, $d.f. = 32$). In contrast, the mean number of synchronous responses evoked by the 50 'Co' notes in the presence of the NB
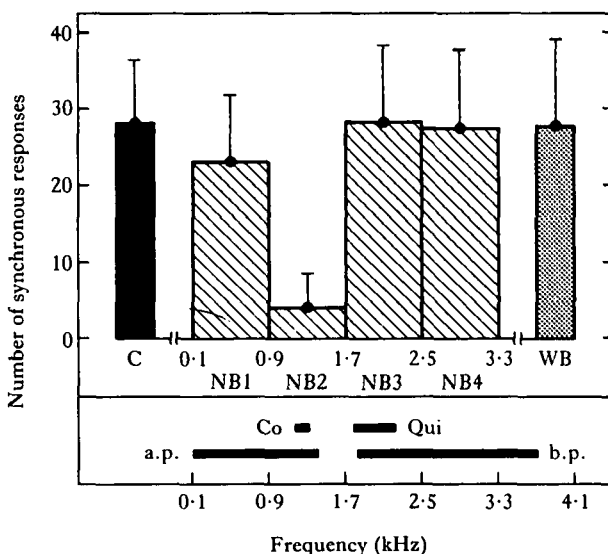

Fig. 3. Mean $+1$ S.D. number of synchronous vocal responses to 50 stimulus tones at $F_S = F_{CO}$ presented at a spectrum level 3 dB above that level which elicited a threshold response, i.e. 10 synchronous responses (control, C). Also shown are the responses to tones simultaneously masked by various narrow-band maskers (NB1, NB2, NB3, NB4) and a wide-band masker (WB). Each of the noise maskers was presented to a given male at the same spectrum level, i.e., the spectrum level of NB2 which reduced the number of synchronous responses below threshold. Also indicated are the ranges of the 'Co' note frequencies (1150–1285 Hz) and 'Qui' note frequencies (1800–2200 Hz) for the 16 males tested. In addition, the ranges of auditory nerve fibre BEFs originating from the a.p. (100–1380 Hz) and b.p. (1800–3700 Hz) of male *E. coqui* are shown (Narins & Capranica, 1976).
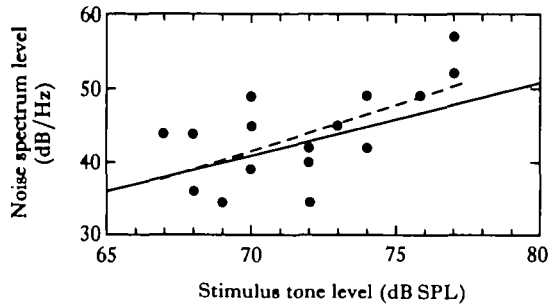
Fig. 4. Stimulus tone levels used to evoke a vigorous synchronous response (see text) from a calling male *E. coqui vs* the spectrum level of a narrow-band noise masker (bandwidth; 800 Hz; centre frequency; 1300 Hz) required to reduce this response below threshold (<20 % synchronous responses). Dashed line is best-fit least-squares regression line ($r = 0.63$) and solid line represents the locus of points for which the stimulus tone power equals the total power in the noise masker.

Table 1. *Stimulus and response parameters for simultaneous masking experiments*

Frog No.	F_{CO} (kHz)	Stimulus tone level (dB SPL)	Masker spectrum level (dB/Hz)	Control	No. of synchronized vocal responses/50 calls				
							Masker		
					NB1	NB2	NB3	NB4	WB
4	1·26	68	44	10	16	0	20	9	10
5	1·28	76	49	27	27	3	24	25	27
8	1·12	70	49	34	11	4	22	19	13
11	1·20	70	39	30	27	9	33	36	36
12	1·18	77	57	33	23	0	32	43	41
13	1·26	73	45	24	25	4	30	31	33
15	1·24	69	34·5	18	14	3	14	13	14
16	1·28	72	40	41	37	8	42	45	38
18	1·16	67	44	30	22	1	19	28	25
20	1·20	70	45	32	22	1	41	30	37
21	1·18	74	49	31	29	8	17	25	25
22	1·20	72	34·5	25	6	1	14	22	12
23	1·28	68	36	34	32	2	37	30	40
24	1·22	72	42	45	45	2	47	44	48
25	1·20	74	42	22	14	2	23	21	25
26	1·24	77	52	23	21	2	36	25	28

maskers NB1, NB3 and NB4, as well as the WB masker, was not significantly different from the mean number evoked by the 'Co' notes presented alone (t-test, $P > 0.05$ see Table 1). Fig. 4 shows the tone levels used to evoke the synchronous response from each male tested and the corresponding NB2 noise masker spectrum level necessary to reduce the number of synchronous responses below R_θ. The NB2 spectrum level required varied from frog to frog, and ranged between 34·5 dB/Hz and 57 dB/Hz. This corresponds to a total noise power between 63·5–86 dB SPL for the NB maskers and 67·5–90 dB SPL for the WB masker.

DISCUSSION

Evidence from the present experiment and other recent studies supports the hypothesis that *the synchronous vocal response in E. coqui is mediated by the amphibian papilla*. A summary of that evidence follows.

(1) The frequency dependence of the synchronous response in $E.$ $coqui$ is clearly revealed in the results of experiment A (Fig. 1). A synthetic 'Co' note evoked a greater synchronous response from a calling male if its frequency was below that of the male under test rather than an equal frequency increment above it. The form of this function is consistent with the known tonotopic organization of the a.p. in anuran amphibians (Lewis et $al.$ 1982). The low- and mid-frequency fibres presumably innervating the a.p. of males of this species have BEFs ranging from 100 to 1380 Hz (Feng et $al.$ 1975; Narins & Capranica, 1976). Since the 'Co' note frequencies for the frogs studied ranged from 1150 to 1285 Hz (Table 1), the stimuli most effective in evoking the synchronous response (those for which $F_S = F_{CO}$) will preferentially excite the fibres innervating hair cells located at the caudalmost extreme of the recurved extension of the a.p. (Lewis et $al.$ 1982). Decreasing F_S should result in excitation of auditory fibres innervating hair cells in the central region of the a.p.; further decreases in F_S should lead to stimulation of those hair cells in the rostralmost region of this organ. In contrast, increasing F_S should result in a rather rapid reduction of a.p. hair cell excitation and thus a decreased total output from the a.p. fibre array. It is precisely this pattern that is reflected in the asymmetric synchronous response function determined in the present study (Figs 1, 2).

The behavioural significance of this finding is of interest. A negative linear correlation between calling male size and call note fundamental frequency has been reported for another neotropical frog, $Physalaemus$ $pustulosus$ (Ryan, 1980). Within a given population of $E.$ $coqui$ in the Luquillo Mountains of Puerto Rico, large males have lower call note fundamental frequencies than small males (A. S. Rand & G. E. Drewry, in preparation; P. M. Narins, unpublished data). This implies that the number of synchronous responses depends on the size of the animal evoking them; animals of similar size elicit the highest number of synchronous responses from each other, whereas for a given size discrepancy, the larger animal will evoke a greater number of synchronous responses than the smaller animal. This suggests that an animal's temporal position in a chorus may be a function of its size (and therefore call note fundamental frequencies); however, further studies are needed to clarify amphibian chorus structure (Foster, 1967; Wickler & Seibt, 1974; Paillette, 1976; M. J. Ryan, M. D. Tuttle & L. K. Taft, in preparation). $E.$ $coqui$ is the largest of the eight sympatric arboreal frog species in the Caribbean National Forest, and produces the lowest call note frequency. Based on the results of the present study, therefore, one might predict that $E.$ $coqui$ would synchronize its calls less readily with those of $E.$ $portoricensis$ [a smaller sibling species with which $E.$ $coqui$ is known to interact vocally (Drewry, 1970)], than $E.$ $portoricensis$ would synchronize its calls with those of $E.$ $coqui$. Experiments to test this hypothesis are currently planned.

In a previous study with $E.$ $coqui$ it was demonstrated, using a constant-threshold response criterion (e.g. 10 synchronous responses/50 calls), that the intensity of a stimulus at F_{CO} required to evoke the threshold response was as much as 30 dB below the level needed at $F_{CO} \pm 200$ Hz (Narins & Capranica, 1978). This result is consistent with the idea that frequencies near F_{CO} are most effective at evoking a vocal response from a male.

Although 14 of the 17 males responded synchronously to synthetic 'Co' notes over a frequency range limited to 200 Hz about F_{CO} (Fig. 1), three males continued to

roduce synchronous responses for F_S as much as 440 Hz (in one case 560 Hz) below F_{CO} (Fig. 2). A possible explanation for this observation is that despite removing several nearby calling males, these three frogs were simultaneously interacting vocally with one or more neighbours. Thus, an animal's 'susceptibility' to acoustic stimuli might be heightened (or suppressed) under various ambient acoustic conditions. Results obtained from previous masking experiments with *E. coqui* in their natural habitat also support this notion (Narins, 1982*b*). This intriguing phenomenon has yet to be experimentally verified under field conditions.

(2) The 'Co' note stimulus intensities used throughout this study ranged from 67–77 dB SPL at the animal. It is reasonable to ask if these levels are sufficient to excite fibres from the b.p. In a previous neurophysiological investigation of the peripheral auditory sensitivity of *E. coqui*, single units were recorded from the b.p. of immobilized adult males (Narins, 1976; Narins & Capranica, 1976). The 49 units studied had BEFs from 1800 to 3700 Hz and thresholds at their BEFs (best thresholds) ranging from 59 to 120 dB SPL ($\bar{x} = 87$ dB SPL). Of this sample, only one unit had a threshold below 77 dB SPL (74 dB SPL) at a frequency corresponding to the highest 'Co' note frequency tested (1285 Hz). The significance of the output of such a high threshold neurone for the vocal synchronization behaviour is dubious for two reasons; (a) because the particular test conditions used represent extremes in the normal range of values tested and (b) because most synchronous responses were readily evoked by stimuli presented at levels far below the lowest unit threshold for any b.p. fibre encountered.

(3) The total power of the NB noise maskers used in this study corresponds to tone levels of 63·5–86 dB SPL. These tone intensities are sufficient to excite a large fraction of the high-frequency fibres recorded from male *E. coqui* (Narins, 1976). Linear dynamic ranges for high-frequency fibres innervating the b.p. of anuran amphibians range from 20–30 dB (Capranica & Moffat, 1975; Narins, 1976; Feng, 1982). Thus, the noise masker levels used in the present study were sufficiently high to excite a large fraction of the b.p. fibres. Narrow-band noise maskers with a spectral content limited to frequencies above the frog's 'Co' note frequency (NB3, NB4, see Fig. 3) would selectively excite most of the b.p. fibres, thereby reducing their ability to respond to other stimuli. Moreover, results from tests with WB masking noise of the same spectrum level (total power between 67·5–90 dB SPL) and containing all the frequency components in the range of BEFs for b.p. fibres were not different from results using NB noise. Under all these masking conditions, the synchronous response persisted unabated, suggesting that the b.p. fibres do not play a role in mediating the synchronous vocal response. In addition, noise masker NB1 was ineffective in reducing the percentage of synchronous responses. This is not surprising in view of the fact that although this masker would excite the fibres innervating the rostralmost portion of the a.p., the stimulus tones preferentially stimulate the unexcited caudalmost region of the a.p. The frequency dependence of the synchronous response in the presence of simultaneous NB noise masking has not been investigated.

The power of the NB2 noise masker necessary to reduce the number of synchronous responses below threshold is very nearly equal, over the range of tones used, to the power of the tone (at 3 dB > L_θ) that evoked the synchronous responses (Fig. 4). It would be instructive to determine if this relationship is level-independent, and to

P. M. NARINS

characterize the linear range of the frog's auditory 'filter' under field conditions.

(4) The saccule has been reported to respond to airborne sounds in the American toad, *Bufo americanus* (Moffat & Capranica, 1976). However, the best thresholds for the non-inhibitable units with BEFs from 700 to 1100 Hz ranged from 93–115 dB SPL ($N = 13$). Moffat & Capranica (1976) speculated that the saccule in the amphibian has evolved to enable recognition of the species-specific mating call '. . . even though the fibers from the auditory papillae are saturated'. But it is unlikely that the stimulus tones used in this study (67–77 dB SPL) would stimulate the relatively high threshold fibres innervating the saccule.

The peripheral auditory system of anuran amphibians is specialized to detect sounds of biological significance (Capranica, 1976). The amphibian papilla in *E. coqui* plays a critical role in mediating the synchronous vocal response during male–male interactions. To which ecologically relevant sounds does the basilar papilla respond? It has been suggested that this organ is tuned to detect (a) the male's 'Qui' note frequency, (b) frequencies produced by prey species, and (c) harmonics of the 'Co' note (Narins & Capranica, 1976, 1980). Further field experiments under natural conditions are needed to distinguish between the relative importance of these factors and to elucidate the function of the basilar papilla in the life of these fascinating animals.

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