

Two-tone suppression in the cricket, *Eunemobius carolinus* (Gryllidae, Nemobiinae)

Hamilton E. Farris^{a)} and Ronald R. Hoy

Department of Neurobiology and Behavior, Mudd Hall, Cornell University, Ithaca, New York 14853

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Sounds with frequencies >15 kHz elicit an acoustic startle response (ASR) in flying crickets (*Eunemobius carolinus*). Although frequencies <15 kHz do not elicit the ASR when presented alone, when presented with ultrasound (40 kHz), low-frequency stimuli suppress the ultrasound-induced startle. Thus, using methods similar to those in masking experiments, we used two-tone suppression to assay sensitivity to frequencies in the audio band. Startle suppression was tuned to frequencies near 5 kHz, the frequency range of male calling songs. Similar to equal loudness contours measured in humans, however, equal suppression contours were not parallel, as the equivalent rectangular bandwidth of suppression tuning changed with increases in ultrasound intensity. Temporal integration of suppressor stimuli was measured using nonsimultaneous presentations of 5-ms pulses of 6 and 40 kHz. We found that no suppression occurs when the suppressing tone is >2 ms after and >5 ms before the ultrasound stimulus, suggesting that stimulus overlap is a requirement for suppression. When considered together with our finding that the intensity of low-frequency stimuli required for suppression is greater than that produced by singing males, the overlap requirement suggests that two-tone suppression functions to limit the ASR to sounds containing only ultrasound and not to broadband sounds that span the audio and ultrasound range. © 2002 Acoustical Society of America. [DOI: 10.1121/1.1451069]

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I. INTRODUCTION

Masking refers to the phenomenon in which the level required to detect one stimulus, the signal, is raised by the presence of another stimulus, the masker. Although the underlying mechanisms mediating the various forms of auditory masking may vary, three prominent hypotheses are [see Delgutte (1996) for review] (1) the “line-busy” mechanism, in which an excitatory masker causes a reduction in the signal-to-noise ratio in the neural code; (2) adaptive masking, in which adaptation caused by the excitatory masker reduces the excitatory response to the signal; or (3) the masker suppresses or inhibits the excitatory response elicited by the signal. The last has been studied at several different levels in auditory systems using two-tone presentations and includes examples in which one of the two tones may either reduce the excitation produced by the other tone [e.g., as demonstrated by the reduced firing rate or rate suppression in the primary auditory fibers (Kiang, 1965)] or actually inhibit the excitation produced by the first tone. Whether mediated by mechanical or neural mechanisms, this reduced response to the signal tone has been called either two-tone suppression or two-tone inhibition (Kiang, 1965; Sachs and Kiang, 1968; Arthur *et al.*, 1971; these two terms have been used synonymously whether neural inhibition is observed or not).

Two-tone suppression has been studied in a variety of taxa. For example, earlier studies of the frequency response characteristics of the auditory units in the mid and forebrains of microchiropteran bats revealed excitatory frequency bands

flanked by inhibitory side-bands (Suga, 1973), presumably sharpening the frequency resolution of these units. Unlike the two-tone rate suppression observed in the auditory afferents of cats (Kiang, 1965), Suga observed that stimulation with frequencies in the suppression side-bands in bats evokes inhibitory or polarizing responses. This class of two-tone suppression is analogous to that demonstrated in the prothoracic nervous system of crickets. In field crickets (Gryllidae, Gryllinae), ultrasound sensitivity is mediated in the CNS by a bilateral pair of ascending interneurons called Int-1 (*sensu*, Moiseff and Hoy, 1983; cf. AN2, Wohlers and Huber, 1982). Whereas the presentation of ultrasound alone elicits excitation in Int-1, the addition of a low-frequency tone (e.g., 5 kHz) can suppress this excitation. Low-frequency suppression in Int-1 is mediated by postsynaptic inhibition; the presentation of low-frequency stimuli alone evokes IPSPs and is thus capable of reducing the excitation elicited by the ultrasound (Nolen and Hoy, 1986b, 1987). Suppression of responses of auditory units in the cricket brain by low-frequency stimuli presumably reflects this ascending activity in Int-1, however, as no IPSPs are evident when excitation elicited by high-frequency stimuli (e.g., 15 kHz) is reduced by the addition of a second tone between 1 and 11 kHz (Boyan, 1981).

From a behavioral perspective, whereas the presentation of songlike (low-frequency) stimuli to field crickets flying on a tether elicits positive phonotaxis, the presentation of batlike ultrasound elicits an acoustic startle response (ASR) comprised in part of the lateral extension of the metathoracic leg, contralateral to the stimulus [response latency: 30–60 ms (Nolen and Hoy, 1986a; Moiseff *et al.*, 1978; Wyttenbach *et al.*, 1996)]. This response presumably functions in the

^{a)}Present address: Sec. of Integrative Biology, Patterson Hall, University of Texas-Austin, Austin, TX 78712. Electronic mail: hfarris@mail.utexas.edu

avoidance of echolocating insectivorous bats; the directional steering effect of the leg swing causes the cricket to steer away from the ultrasound source (Nolen and Hoy, 1986a). In experimental paradigms similar to those examining single-tone masking, the simultaneous presentation of a low-frequency stimulus (e.g., 5 kHz) with ultrasound raises the level of ultrasound required to elicit the ASR (Nolen and Hoy, 1986b). Because the experimental suppression of Int-1 using hyperpolarizing current is sufficient in suppressing startle responses to ultrasound stimuli (Nolen and Hoy, 1984, 1987), the mechanism for this type of masking (i.e., two-tone suppression using a behavioral assay) is presumably the inhibitory effect of the low-frequency stimulus on Int-1.

Sounds with frequencies ≥ 15 kHz also elicit a startle response in flying *Eunemobius carolinus* (Gryllidae, Nemo-biinae) (Farris and Hoy, 2000). In contrast to field crickets, the direct presentation of frequencies < 15 kHz to tethered *E. carolinus* does not elicit a response. These frequencies, however, can suppress the ultrasound-induced startle. Thus, because a direct assay was unavailable, we use the ultrasound-induced startle response and its suppression as an indirect test of low-frequency sensitivity in *E. carolinus*. The experimental paradigms used in this article are modeled after single-tone masking paradigms (e.g., Vogten, 1974) and are used to determine the frequency and temporal sensitivity for sounds with frequencies ≤ 15 kHz. From an ethological perspective, these tests examined whether sounds that best suppressed the ASR were similar to those typical of the *E. carolinus* male calling song [e.g., ~ 6.7 ms pulses of 5.6–6.3 kHz at ~ 75 pulses/s, these parameters vary with temperature (Alexander, 1957; Walker, 1962)] and thus might reflect specialization for song detection. Some of the results reported here have been previously reported in abstract form (Farris and Hoy, 1997, 1998).

II. MATERIALS AND METHODS

A. General methods

Except where noted, general methods are the same as those in Farris and Hoy (2000).

1. Subject animals

The colony, started from individuals sound-trapped in Lafayette County, MS (see Farris *et al.*, 1997), was reared under a 14 L/10 D h, light schedule and fed “cricket chow” *ad libitum*.

2. Acoustic stimuli

Stimuli were generated using Tucker Davis Technologies (TDT) 16-bit, digital-to-analog converters and custom-written software (8 or 6 μ s sample period). Stimuli were amplified using a Harman/Kardon HK6150 integrated amplifier. Ultrasound stimuli (i.e., startle stimuli) were broadcast from either a Radio Shack Super tweeter (cat. no. 40-1310b) or through Panasonic 40 kHz transducers (40 kHz stimuli only). Low-frequency stimuli (i.e., suppressor stimuli, 2–15 kHz) were broadcast from either an ESS AMT-1 tweeter or Motorola piezoelectric speakers. All speakers were located 30 cm from the preparation. Stimulus amplitude was ad-

justed using TDT PA4 programmable attenuators (1 dB minimum step size). The stimuli were calibrated at the position of the test animal using online comparisons of the rms voltage of the stimuli to that generated by a B&K 4220 pistonphone calibrator (125 ms duration samples). The calibration system included a B&K 4135 $\frac{1}{4}$ -in. microphone (0 degree angle of incidence), B&K 2639 preamp, and a B&K 5935 microphone power supply. All sound pressure levels (dB SPL) are referenced to 20 μ Pa. For all speakers, the maximum output level of the system was 107 dB SPL. All pulse onset and offset ramps are raised cosine. Total harmonic distortion of the system was determined to be $< 1\%$ (-40 dB) using a Hewlett-Packard 3562A signal analyzer.

3. Startle response and suppression

Long-winged *E. carolinus* were tethered dorsally at the pronotum to a 14-cm-long piece of piano wire using low-temperature melting point wax. Flight can easily be initiated by waving the tethered cricket in the air or by giving it small puffs of air. Once flying, a tethered cricket was placed in a Faraday cage lined with acoustic foam to minimize echoes. The tethered cricket was positioned 7 cm from the floor of the cage and 30 cm from the speakers placed at 90 degrees normal to the cricket. The behavioral components of the acoustic startle response consist of an abrupt cessation of flapping, folding of the hind wings, closure of the tegmina, anterior extension of the prothoracic and mesothoracic legs, posterior extension of the metathoracic legs, and dorsal movement of the antennae (Farris and Hoy, 2000). Although flight usually resumed with the termination of the startle stimulus, reinitiating flight in some subjects became more difficult with increasing numbers of startle responses. To help ensure that most subjects would complete an experiment, we chose to measure thresholds using the adaptive procedures below.

Startle thresholds to ultrasound alone were measured using a 1/2-down, 0/2-up adaptive procedure (see Farris and Hoy, 2000). In this procedure, the amplitude of a single pulse was decreased in 6-dB steps if a startle response was observed in 1 out of 2 stimulus presentations. Stimulus step sizes were then changed to 3 and 1 dB for each reversal until a threshold was determined. This adaptive procedure converges on the stimulus level that elicits a response in 30% of the presentations (Levitt, 1971). Thresholds for two-tone suppression, however, were measured using the 2/2-suppression-down, 1/2-up adaptive procedure diagrammed in Fig. 1. In this procedure, the amplitude of the startle stimulus (ultrasound) was fixed at a level which consistently elicited a startle response (these levels are noted for each experiment; at least 5 dB above startle threshold), whereas the amplitude of the suppressor stimulus was adjusted until the minimum level for suppression was determined. As before, attenuator step sizes were 6, 3, and 1 dB for the sequence of reversals. Two procedures were used to control for any variance in response threshold over time [e.g., habituation or fatigue causing a change in threshold during some portion of the adaptive procedure, see Robert (1989)]. First, following two consecutive presentations in which a startle response was not elicited by the ultrasound+suppressor combination (i.e., 2/2 suppression), the ultrasound was presented alone to verify

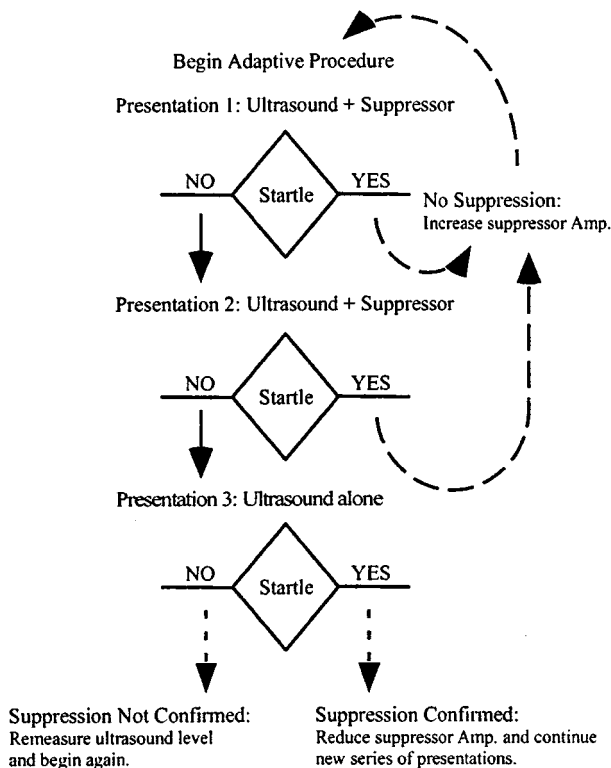


FIG. 1. Diagram of a single trial for the adaptive procedure used to determine suppression thresholds (see methods).

that the subject would still respond to the startle stimulus. If the ultrasound stimulus elicited a startle response, startle suppression for the previous two presentations of two-tone stimuli was thus confirmed, and the amplitude of the suppressor was decreased. If a startle response was not elicited by the ultrasound alone (i.e., suppression was not confirmed), then all tests with that individual were repeated and the startle threshold to ultrasound alone was remeasured to establish a stable reference (see Fig. 1). As part of a second control, the adaptive procedure stepped through the presentations of experimental stimuli in a pseudo-random order so that the same suppressor frequency was not presented in more than two consecutive trials (i.e., two sequences shown in Fig. 1). If a change in startle threshold had occurred during testing (see Sec. III), this control prevented its correlation to any suppressor frequency in particular. This adaptive procedure converges on the stimulus level that elicits suppression in 70.7% of the presentations (Levitt, 1971). The subjects were required to fly for at least 5 s prior to stimulus presentation (i.e., minimum interstimulus interval was 5 s). This interval was also chosen to reduce the probability of any habituation or sensitization. Ambient temperature for all of the experiments was 20–23°C.

4. Calling song recordings

Singing males ($N=5$) were recorded either in the field (Ithaca, NY) or in the laboratory using a Sony WM D6C Walkman Professional tape recorder (no filter), Memorex CD2 tape, and a Sony ECM 939CT microphone placed at 15 cm dorsal to the singing cricket. Temperature at the position of the male was measured using a Radioshack digital ther-

mometer. Songs were digitized (22.7 or 40 μ s sample period) using a TDT AD1 and custom-written software. The mean sound pressure level of the calling songs over all of the recorded males was calculated by comparing the rms value of 15 randomly sampled song pulses (3 pulses from the song of each male) to that generated by a B&K 4220 pistonphone calibrator.

B. Experiments

1. Frequency response of two-tone suppression

Thresholds for startle suppression were measured as a function of the frequency of the suppressor stimuli. Presented simultaneously with the startle stimulus (1 pulse of 40 kHz), the suppressor stimuli had the same temporal structure as the ultrasound (5 ms duration, 1 ms ramps) but varied in frequency from 2 to 15 kHz. For each individual ($N=11$), startle threshold was first determined using the adaptive procedure described above. The startle stimulus was then fixed at 8–10 dB above startle threshold and presented simultaneously with each of the ten suppressor frequencies until the minimum suppressor level required to suppress the startle response was determined. Each individual was tested at all ten suppressor frequencies (2–10, 15 kHz).

2. Equal-suppression contours

In experiments similar to those measuring equal-loudness contours (see Plack and Carlyon, 1995), the relationship between ultrasound intensity and suppressor intensity was tested for seven different suppressor frequencies (3–9 kHz in 1-kHz steps). After determining the startle threshold (at 40 kHz) for each individual, the minimum threshold for startle suppression was measured for four ultrasound intensities above startle threshold (5, 8, 10, 12 dB *re*: startle threshold) at seven suppressor frequencies. Based on evidence from preliminary observations, this 7-dB intensity range for the ultrasound stimulus was chosen to encompass the minimum level (+5 dB *re*: startle threshold) required to consistently elicit a startle for the duration of the experiment and the maximum ultrasound intensity (+12 dB *re*: startle threshold) at which suppression was still possible. In addition to the pseudo-random order of frequency presentation mentioned above, the ultrasound level within frequency presentations was randomly chosen (i.e., 5, 8, 10, or 12 dB *re*: startle threshold). For an individual to be included in the data set, suppression thresholds had to be completed at all four ultrasound levels for at least one suppressor frequency (e.g., startle suppression thresholds at one frequency were determined at 5, 8, 10, and 12 dB above startle threshold). Unlike the frequency response for suppression measured in experiment 1 (above), no individuals flew long enough to measure all four equal suppression contours for all seven frequencies (i.e., 28 suppression thresholds).

Suppression growth (i.e., change in level of suppressor versus change in level at 40 kHz) at each suppressor frequency was calculated using a linear regression of suppression thresholds versus the level of the startle stimulus. Comparison of suppressor growth across the seven suppressor frequencies was accomplished using an analysis of covari-

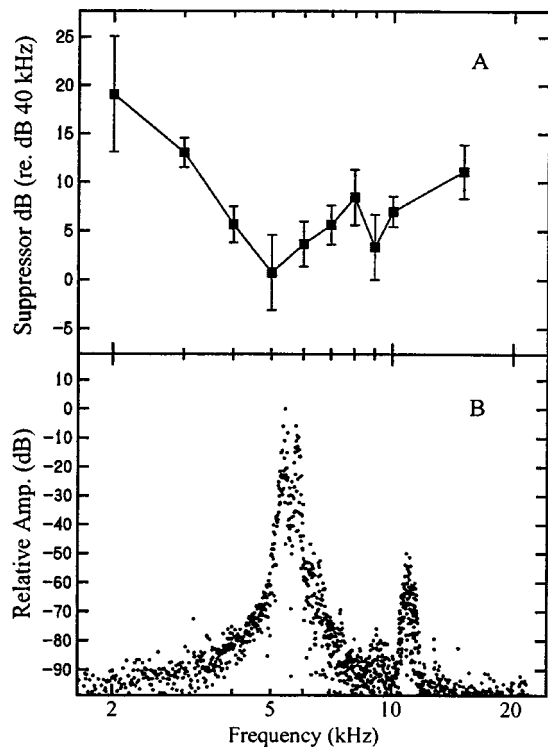


FIG. 2. Suppression tuning. (a) Symbols represent the mean (\pm SE) threshold required to suppress the ultrasound-induced startle response for ten different suppressor frequencies. Stimuli were 5-ms pulses with 1-ms ramps. The startle stimulus (40 kHz) was set at 8–10 dB above startle threshold for each individual. Individuals ($N=11$) were tested at all frequencies. (b) Amplitude spectrum of an *E. carolinus* calling song recorded at 20 °C.

ance testing for significant differences between slopes (Zar, 1984, p. 300). Comparison of the suppression slopes and intercepts between males and females at 6 kHz was done using the procedure described in Zar (1984, p. 296).

Shapes of the suppression contours were calculated from the mean suppression thresholds using a method described by Patterson *et al.* (1982; but see also Moore *et al.*, 1990). Briefly, each flank of the tuning curve (i.e., on either side of the center frequency) was modeled using the rounded exponential function $\text{roex}(p,r)$:

$$W(g) = (1-r)(1+pg)\exp(-pg) + r,$$

where g is the normalized deviation of frequency from the center frequency, fc , $g = |(f-fc)|/fc$, p is a dimensionless parameter determining the slope of the flanks of the tuning curve, and r is a constant that sets the range limitation of the roex filter. The tuning curves were assumed to be asymmetrical around the center frequency, and separate slopes (p) were calculated for the upper and lower frequency flanks; r was assumed to be the same for each side, however, and equaled the difference between the minimum and maximum thresholds on the tuning curve. After normalizing each equal suppression contour to the threshold at the center frequency (5 kHz), we used a least-squares method to solve for the slope parameter (p) of each flank of the filter. Using the slope parameters, the equivalent rectangular bandwidth (ERB) for each tuning curve was calculated (Patterson *et al.*, 1982), facilitating a comparison of tuning “sharpness.”

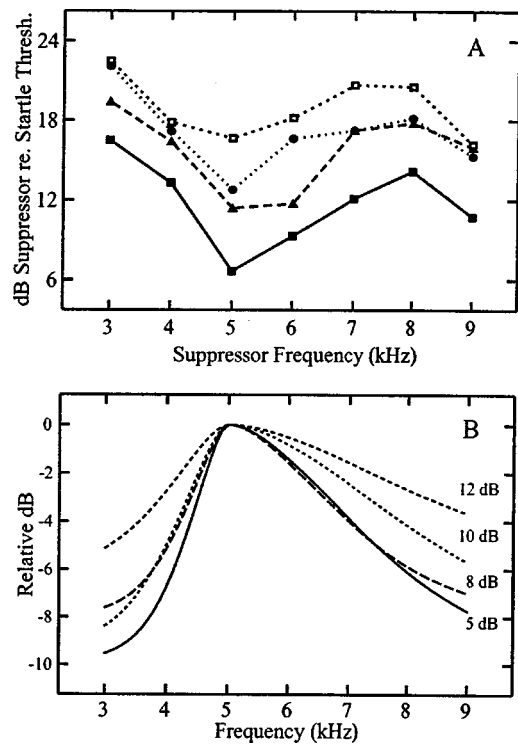


FIG. 3. Equal suppression contours. (a) Threshold to suppress a startle response as a function of frequency and startle stimulus level. Symbols: \blacksquare , \blacktriangle , \bullet , \square are the suppression thresholds for startle stimuli at 5, 8, 10, and 12 dB above startle threshold, respectively. Because the level of 40 kHz varied for these measurements, unlike in Fig. 2(a) suppression thresholds are plotted *re*: startle threshold rather than *re*: 40 kHz level. (b) Roex filter functions for each equal suppression contour above (see Table II for the parameters for each filter). Line types are the same in both panels.

3. Temporal sensitivity: Suppressor duration

Thresholds for startle suppression were measured as a function of suppressor duration. Presented with simultaneous onsets, the startle and suppressor stimuli consisted of single pulses of 40 and 6 kHz, respectively. In part 1 the startle stimulus had a 5-ms duration and suppressor duration varied from 2 to 80 ms, whereas in part 2, the startle stimulus had a 20-ms duration and suppressor duration varied from 2 to 200 ms. The amplitude of the ultrasound stimulus was set 8–10 dB above startle threshold.

4. Temporal sensitivity: Nonsimultaneous suppression

Similar to forward and backward masking, startle suppression was measured while varying the relative onset times of the suppressor (5-ms duration, 1-ms ramps, 6 kHz) and startle (5-ms duration, 1-ms ramps, 40 kHz) stimuli from 3 to –6 ms (*re*: startle onset). The amplitude of the ultrasound stimulus was set 8–10 dB above startle threshold, whereas the amplitude of the suppressor pulse was adjusted until the minimum suppressor level required to suppress the startle was determined for each of eight different relative onset times.

III. RESULTS

A. Frequency response of two-tone suppression

Suppression was tuned to frequencies near 5 kHz, overlapping components in the male calling song (Fig. 2). Whereas a gradual increase in suppression thresholds was measured for frequencies >5 kHz (although a secondary sensitivity peak can be seen at 9 kHz), for frequencies <5 kHz there was a steeper decline in suppression sensitivity [Fig. 2(a)]. Thresholds were measured for at least 10 of the 11 individuals tested for all frequencies except 2 kHz, in which suppression was effective in only three individuals.

B. Equal suppression contours

As in experiment 1, suppression thresholds were lowest for frequencies near 5 kHz with a second sensitivity peak at 9 kHz [Fig. 3(a)]. The equal suppression contours were not parallel, however, as suppressor growth (change in level of suppressor versus change in level at 40 kHz) differed significantly across the seven suppressor frequencies (ANCOVA, $N=236$, $F=3.99$, $P<0.002$; Zar, 1984, p. 300). Because suppressor growth was >1 for 5–7 kHz and <1 for 3–4 and 8–9 kHz (Table I), the equal suppression curves appear to flatten at the higher ultrasound levels. Furthermore, significant positive slopes for suppressor growth (i.e., at five of seven frequencies, Table I) suggests that each individual's startle threshold was stable throughout the procedure, as no relationship would be expected if startle threshold varied.

Although analysis of the equal suppression contours using the roex model did suggest a decrease in the slope parameter for frequencies >5 kHz (and increase in ERB) with increasing ultrasound levels, the model's predictions were not significantly correlated with the data for the highest ultrasound level (i.e., 12 dB *re*: startle threshold) [Fig. 3(b), Table II]. The failure of the roex model for the 12-dB contour is presumably due to the suppression thresholds at 9 kHz. Although the model assumes a center frequency of 5 kHz, at the 12-dB contour, lowest suppression thresholds shifted from 5 to 9 kHz, reducing the amount of variance explained by the model. Indeed, when the thresholds at 9 kHz were removed from the contours, the fit of the roex

TABLE I. Relationship between suppression threshold and ultrasound level for each suppressor frequency. Although threshold means are shown in Fig. 3, slopes are calculated from the entire data set using linear regression analysis. Suppressor growth varies significantly across suppressor frequency (ANCOVA, $N=236$, $F=3.99$, $P<0.002$; Zar, 1984, p. 300). Significant positive slopes for five of seven frequencies suggests that reference thresholds (i.e., startle threshold) were stable throughout the experiments.

Suppressor frequency (kHz)	<i>N</i>	Suppressor growth (Δ Suppressor dB/ Δ 40 kHz dB)	R^2	<i>P</i> value
3	36	0.903	0.312	0.0004
4	36	0.648	0.070	0.1189
5	32	1.370	0.158	0.0243
6	36	1.354	0.210	0.0049
7	28	1.140	0.192	0.0195
8	32	0.859	0.129	0.0437
9	36	0.728	0.045	0.2145

TABLE II. Filter dimensions and correlations for the least-squares fit of roex(p, r) to the equal suppression contours. Columns are the roex slope parameters (p) for frequencies above and below the center frequency (5 kHz), the equivalent rectangular bandwidth (ERB) of the filter, Q_{3dB} of the filter, and the R^2 and P values of the least-squares fit to the threshold means for the four different startle stimulus amplitudes (*re*: startle threshold).

40 kHz level (dB)	Upper slope p	Lower slope p	ERB (kHz)	Q_{3dB}	R^2	<i>P</i> value
5	4.437	14.802	2.93	2.33	0.737	0.013
8	5.181	13.275	2.683	2.284	0.799	0.007
10	3.245	11.367	3.959	1.676	0.570	0.05
12	2.876	8.746	4.621	1.136	0.218	0.291

model was significant at each contour, revealing an increase in ERB with increasing ultrasound levels (Table III).

C. Temporal sensitivity: Suppressor duration

As suppressor duration increased, suppression threshold did not decrease like that of a simple exponential integrator (Fig. 4). Temporal integration of the low-frequency suppressor was analyzed using a least-squares-fit of the following equation proposed by Plomp and Bouman (1959) for the change in threshold as a function of stimulus duration:

$$\text{Threshold shift } (T) = -10 * \log \left(1 - \exp \left(\frac{-T}{\tau} \right) \right),$$

where τ represents the temporal integration (i.e., summation) time constant that describes the rate at which the threshold reaches an asymptote as a function of T , the duration of the suppressor stimulus. (Note that for the 20-ms ultrasound treatment, because no suppression was measured for suppressor durations <10 ms, these durations were not included in the model.) Correlations between the data and the model were not significant for either the 5 ms ($\tau=12.2$ ms, $r^2=0.25$, $P=0.18$) or 20 ms ($\tau=17.3$ ms, $r^2=0.51$, $P=0.13$) ultrasound treatments and, thus, estimates for the temporal integration time of the suppressor (6 kHz) using a duration versus intensity paradigm were inconclusive. In addition, there was no evidence for tuning to any particular suppressor duration (i.e., similar to pulse durations of the male calling song). For both ultrasound durations (5 and 20 ms), suppression thresholds decreased up to the duration of the startle

TABLE III. Filter dimensions and correlations for the least-squares fit of roex(p, r) to the equal suppression contours not including thresholds at 9 kHz. Columns are the roex slope parameters (p) for frequencies above and below the center frequency (5 kHz), the equivalent rectangular bandwidth (ERB) of the filter, Q_{3dB} of the filter, and the R^2 and P values of the least-squares fit to the threshold means for the four different startle stimulus amplitudes (*re*: startle threshold). Although all upper slopes are affected by the removal of the data at 9 kHz, the lower slope at 12 dB is also changed due to a change in the dynamic range (roex parameter r) of the entire 12-dB filter (see Table II).

40 kHz level (dB)	Upper slope p	Lower slope p	ERB (kHz)	Q_{3dB}	R^2	<i>P</i> value
5	5.963	14.802	2.353	2.902	0.995	0.0001
8	6.068	13.275	2.401	2.552	0.936	0.0016
10	5.066	11.367	2.853	2.325	0.857	0.0081
12	5.706	8.278	2.961	1.678	0.839	0.01

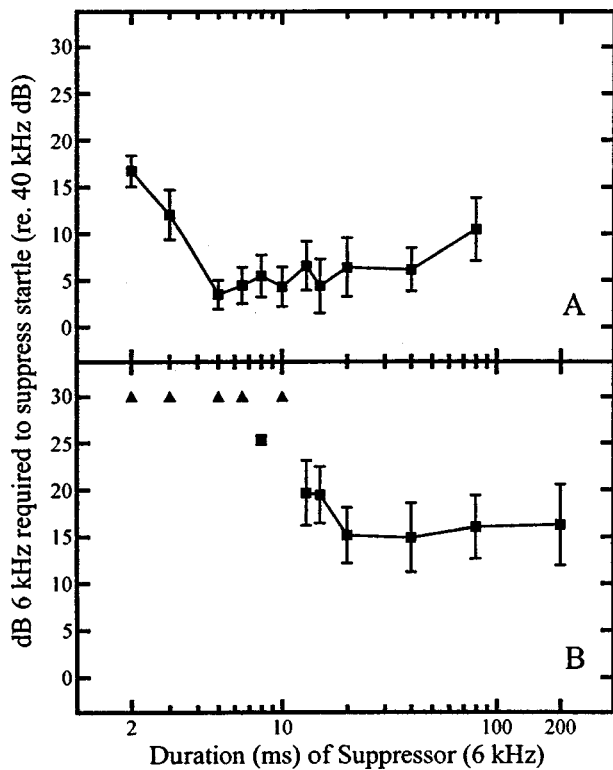


FIG. 4. Suppression threshold (*re*: startle stimulus dB) as a function of suppressor duration. Suppressor and startle stimuli have simultaneous onsets. Durations of the startle stimulus (40 kHz) were 5 and 20 ms for (a) and (b), respectively. Triangles mark suppressor durations in which <2 individuals exhibited suppression.

stimulus, but varied for greater suppressor durations. Because suppression threshold depended on the duration of the startle stimulus, these results are inconsistent with a hypothetical filter that band-passes durations near 7 ms (i.e., the duration of a typical calling song pulse).

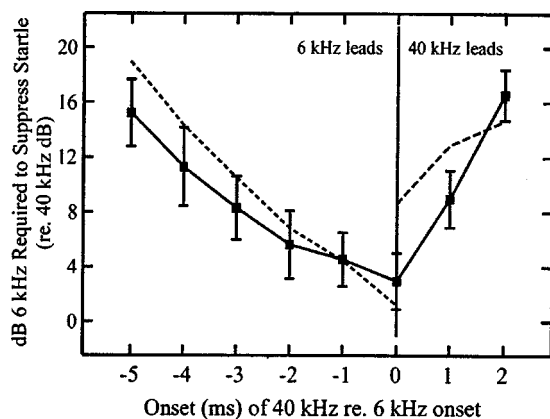


FIG. 5. Suppression threshold (*re*: startle stimulus dB) as a function of the relative onset times of the suppressor (6 kHz) and startle (40 kHz) stimuli. Both stimuli were 5-ms duration pulses with 1-ms ramps. No suppression occurs when the onset of the suppressing tone is >2 ms after and >5 ms before that the ultrasound stimulus. Dashed curves represent the thresholds predicted by the simple summation model (see results, Fig. 6) when the integration time is 9.395 ms ($r^2=0.987$, $P=0.00006$) in the forward suppression condition (6 kHz leads) and 47.07 ms ($r^2=0.914$, $P=0.19$) in the backward suppression condition (40 kHz leads).

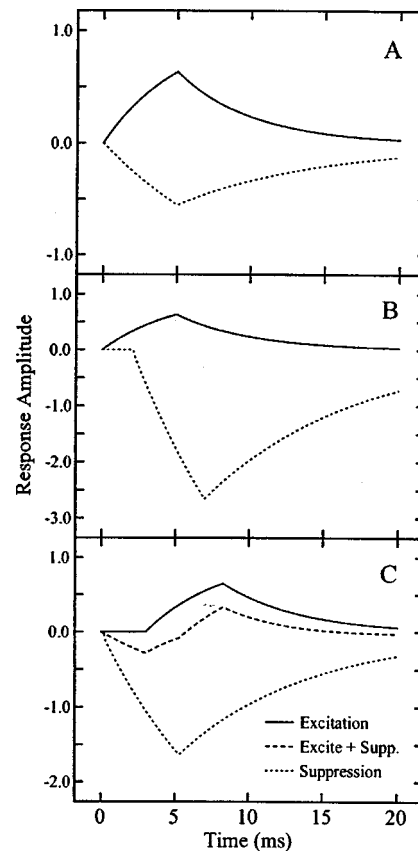


FIG. 6. Diagram of the suppressor and startle stimuli in the nonsimultaneous suppression paradigm when modeled as the interaction of an IPSP (dotted curve) and EPSP (solid curve), respectively. In each condition, the amplitude of the IPSP is multiplied by that (*re*: EPSP amplitude) required to suppress the startle (Fig. 5). The model assumed that suppression occurred when the sum of the two integrals was -8 dB *re*: EPSP peak amplitude: (a) simultaneous onset, (b) backward suppression (suppressor trails by 2 ms), and (c) forward suppression (suppressor leads by 3 ms). In (c) the dashed curve represents the sum of the excitation and suppression responses. In this case, because the peak of the summed response is -8 dB (*re*: the excitatory response), the model deemed that suppression had occurred.

D. Temporal sensitivity: Nonsimultaneous suppression

No suppression could be measured when the onset of the suppressing tone was >2 ms after or >5 ms before that of the ultrasound stimulus (Fig. 5). In both backward and forward suppression, increasing levels of 6 kHz were required to suppress the startle response for greater temporal separations between the two stimuli. Because these data presumably reflect the relative temporal integration times for the two frequencies, we constructed a simple summation model to estimate the integration time of the low-frequency suppressor, which we were unable to measure sufficiently in the previous experiment.

Both the excitatory (40 kHz) and suppression (6 kHz) integrals were modeled as simple exponential integrators that change as

$$1 - \exp(-T/\tau)$$

when the stimulus is on, and decay as

$$\exp(-T/\tau)$$

when the stimulus is turned off (Fig. 6). The suppression integral is negative, however, and its amplitude is scaled like that measured at suppression threshold for each of the different relative onset times (e.g., when 40 kHz leads 6 kHz by 2 ms, the amplitude of the 6-kHz pulse is 16.2 dB *re*: 40 kHz at suppression threshold; see Fig. 5) [Fig. 6(b)].

We assumed that the addition of the two integrals was linear [Fig. 6(c)] and that there was no latency difference between the two responses. We also assumed that $\tau=5.30$ ms for the excitatory integral (Farris and Hoy, 2000) and that suppression occurred when the amplitude of the excitatory integral was reduced by 8 dB (i.e., 40 kHz startle stimulus was set at 8–10 dB above startle threshold) as a result of its addition to the suppression integral. Using a least-squares method, we solved for the integration time (τ) of the suppression stimulus (6 kHz) that produced an 8-dB reduction in excitatory amplitude for each of the relative onset times shown in Fig. 5. Although separate time constants were calculated for both the forward and backward suppression conditions, data for the simultaneous presentation of the two stimuli (0 ms relative onset time) were included in both analyses.

The time constant (τ) for the integration of 6 kHz differed for forward and backward suppression (Fig. 5). In forward suppression (e.g., 6 kHz leads 40 kHz), suppression thresholds were best modeled when the 6-kHz stimuli were integrated over 9.395 ms ($r^2=0.987$, $P=0.00006$). In backward suppression, however, integration appeared to occur over a much longer time, as suppression thresholds were best modeled when the integration of 6 kHz lasted 47.07 ms ($r^2=0.914$, $P=0.19$) (Fig. 5). The model for backward suppression was not significantly correlated to the data, however. Potential causes for this difference between the two measurements are addressed below.

IV. DISCUSSION

A. Frequency sensitivity

Because the behavioral context and stimulus structures required to elicit responses to calling songlike stimuli vary (e.g., Loher *et al.*, 1993), it is not clear why tethered *E. carolinus* do not respond to such stimuli when presented alone. Although this lack of a response prevents any direct measure of low-frequency (i.e., <20 kHz) sensitivity (sound trapping notwithstanding, Farris *et al.*, 1997), its measurement is still facilitated by low-frequency suppression of the ultrasound-induced startle. Thus, in experimental paradigms similar to those examining single-tone masking in humans (Vogten, 1974), we used the increase in startle threshold produced by low-frequency sounds to indirectly measure aspects of sensitivity below 20 kHz. Similar to two-tone suppression in field crickets, suppression sensitivity was best at 5 kHz with a secondary peak at 9 kHz (Moiseff and Hoy, 1983). Sensitivity to frequencies across this band overlaps much of the spectrum of male calling songs (Fig. 2) and thus could function in the context of song detection.

Tuning sharpness or the frequency biases of auditory systems are known to change with the amplitude of the stimuli, however. For example, in single-tone masking ex-

periments with humans, the frequency that produces the most masking varies with the intensity of the probe (Vogten, 1974). Furthermore, masking experiments using various broadband maskers show that the shapes of critical bands centered at the same frequency vary with the amount of input or stimulus level (Shailer *et al.*, 1990; Moore *et al.*, 1990). Generally, this change is measured as an increase in critical band ERB as stimulus intensity increases. With respect to tuning across multiple critical bands, a well-known example of such a change is the “flattening” of equal loudness contours in humans as a function of the amplitude of the standard [usually 1 kHz; see Plack and Carlyon (1995) for review]. From a physiological perspective, Capranica (1992) pointed out that the frequency tuning of units in the VIIIth nerve of frogs is not maintained at stimulus levels above threshold. Indeed, iso-intensity measures of spike rate at various frequencies are not necessarily parallel and can reveal either an increased or decreased frequency bias in the unit (Capranica, 1992; Rose *et al.*, 1971). Imaizumi and Pollack (1999) measured the analogous response in the auditory afferents of crickets (*Teleogryllus oceanicus*) and demonstrated that for a 15-dB change in stimulus intensity, the bandwidth of the iso-intensity response curves for one afferent changed from ~ 2 to ~ 12 kHz. With respect to physiological measures of two-tone suppression, the tuning of low-frequency (~ 4 kHz) suppression of ultrasound-induced excitation in an ascending unit in *T. oceanicus* broadened with increases in suppressor intensity (Hutchings and Lewis, 1984).

Similar to the iso-intensity measures above, two-tone suppression tuning in *E. carolinus* varied with the sensation level of the ultrasound stimulus. Because the slopes for suppression growth (change in level of suppressor versus change in level at 40 kHz) were not the same for the seven frequencies (Table I), the suppression contours were not parallel. If these equal suppression contours do reflect the frequency response of the calling song channel in *E. carolinus*, the results suggest that comparisons of songs at various frequencies may vary with intensity. Furthermore, the data suggest that there may be greater dynamic range for frequencies near 5 kHz than those near 3 and 9 kHz (i.e., the intensity range between threshold and apparent saturation appears smaller for 3 kHz than for 5 kHz).

The rounded exponential (roex) filter with its rounded peak and exponentially decaying skirts is one of the most widely used methods for describing the shape of auditory filters (see Moore, 1995). Because it describes filter selectivity, we find it surprising that it has been so rarely employed in studies of comparative audition. Indeed, use of the roex model would facilitate the quantitative comparison of tuning curves within and between studies. We used the roex model to compare the shape of suppression tuning at four different intensities of the startle stimulus. When including the data at 9 kHz, the model explained a significant proportion of the variance in the threshold means for the 5-, 8-, and 10-dB suppression curves (Table II; Fig. 3). There was, however, too little selectivity in suppression tuning for the 12-dB startle stimulus to adequately fit the model. For the lower three contours, however, the change in both the upper slope parameter and the ERBs do suggest a decrease in filter tun-

ing (Table II; Fig. 3). Comparison of the 5- and 10-dB parameters suggests a decrease and an increase in the upper slope and ERB, respectively. Although 9 kHz is clearly part of the suppression channel, we explored the filter shape around 5 kHz after removing the 9-kHz thresholds from the data set. Without 9 kHz, the model can be significantly fit to all of the curves (Table III) and reveals a ~ 600 Hz increase in ERB over the 7-dB change in startle stimulus.

Although our results do suggest that the relative weighting of frequencies by *E. carolinus* varies at intensities above threshold, certain concerns do exist in analyzing the equal suppression contours as exact analogs of equal loudness (or masking) contours. First, because each individual is not represented in every point on the curves (individuals were included only if their thresholds were measured at the four levels for at least one frequency), there is a potential that one individual could bias the results at one frequency. This concern is mitigated, however, by the similarity between the suppression tuning curve in Fig. 2 (in which each individual was tested at all ten frequencies) and the 8- and 10-dB equal suppression contours in Fig. 3. In addition to the tuning being centered at 5 kHz, both experiments revealed a secondary sensitivity peak at 9 kHz. This suggests that the frequency response of the equal suppression contours was not affected by limited replication across frequencies. A second concern arises from the variance around each suppression contour. The mean standard error over all thresholds on the equal suppression contours (Fig. 3) is 2.3 dB (this variance was not presented in Fig. 3 for clarity). Although the variances for some thresholds do overlap, a statistically significant correlation between suppressor level (dB) and startle level (i.e., when regressed against the entire data set to include all of the variance) can still be resolved for all suppressor frequencies except 4 and 9 kHz (Table I).

B. Temporal integration and suppression

Using a duration versus intensity experimental paradigm, Farris and Hoy (2000) found that power integration of single pulses of 40 kHz by *E. carolinus* occurred over ~ 32 ms. Simple duration versus intensity experiments in which the duration of the suppressor stimulus was varied were insufficient, however, in measuring the integration time of low-frequency stimuli. In trials using a 5-ms ultrasound stimulus, suppression thresholds decreased as the duration of the suppressor increased to 5 ms, but became less effective for longer durations (Fig. 4). From an ethological perspective, these results are interesting as they suggest that there might be some “duration tuning” to 6-kHz stimuli. At temperatures near 23 °C, male calling songs consist of 6.7-ms pulses of 6 kHz at 75 pulses/s. Best suppression to 5-ms duration pulses of 6 kHz could thus reflect the response of a temporal bandpass filter applied to frequencies characteristic of male calling songs. Although evidence for such a filter has been found for certain amplitude modulation rates (Schildberger, 1984), there is no prior evidence for a filter that bandpasses certain pulse durations in crickets. In subsequent experiments using a 20-ms ultrasound stimulus, however, we found that suppression thresholds decreased as suppressor duration increased up to 20 ms, with thresholds becoming more variable

for longer durations (Fig. 4). Thus, these data suggest that best suppression durations appear to be the result of stimulus overlap rather than the result of a bandpass duration filter. In other words, even though integration of the ultrasound stimulus is known to continue for up to ~ 32 ms [i.e., 27 ms beyond the end of the 5-ms pulse of 40 kHz (Farris and Hoy, 2000)], we found little evidence for any backward suppression effects produced by increasing the duration of the suppressor stimuli into this time window trailing the startle stimulus. Thus, in order to examine this effect of overlap more closely, we used a nonsimultaneous suppression paradigm to measure the temporal window in which suppression of the ultrasound-induced startle could be elicited.

With the exception of the forward suppression condition in which the startle stimulus started at the offset of the suppressor, stimulus overlap was required for startle suppression. For the 5-ms duration stimuli, no suppression could be measured when the onset of the suppressor was >5 ms before or >2 ms after the ultrasound pulse (Fig. 5). As in human psychoacoustics, nonsimultaneous masking experiments effectively probe the limits of auditory inertia or the time over which the summation of masker and signal occurs. Figure 5 can be thought of as showing the shape of such a temporal window centered at the onset of the 6-kHz pulse. A variety of models have been proposed for describing the characteristics of temporal integration including the temporal analog of the roex filter used above for spectral analysis (Moore *et al.*, 1988). Solutions to this model in humans maximized the signal-to-noise ratio for a signal temporally centered between forward and backward maskers. We chose a different method for analyzing this temporal window, however.

Nolen and Hoy (1986b) found that two-tone suppression in *T. oceanicus* was mediated by low-frequency-induced postsynaptic inhibition in a pair of bilaterally symmetric auditory interneurons called Int-1. Summation of IPSPs effectively reduced excitation below that required to elicit a startle. Central auditory processing of ultrasound in *E. carolinus* appears similar to that in *T. oceanicus*, as extracellular recordings in the neck connectives of *E. carolinus* reveal at least one identifiable auditory unit that responds like Int-1 in *T. oceanicus* (Farris and Hoy, 2000). Thus, the interaction of the suppressor and startle stimulus in the nonsimultaneous paradigm was modeled as the hypothetical summation of inhibitory and excitatory post-synaptic potentials (Fig. 6). Because the time over which nonsimultaneous suppression could be measured was an order of magnitude less than that for temporal integration of a single pulse of ultrasound (32 ms), the model solved for the inhibitory time constant using an excitatory time constant of 5.3 ms, the time constant for paired-pulse integration of ultrasound (Farris and Hoy, 2000). For forward suppression, the data were best modeled when the inhibitory time constant equaled 9.17 ms. In the backward suppression condition the model failed to significantly explain the change in suppression threshold. If the model does represent the underlying neural mechanism of suppression, then at least one hypothesis for the model's failure when the suppressor follows the startle stimulus is related to the production of action potentials. The model only

takes into account graded potentials. If the onset of the suppressor stimulus follows or overlaps with the production of action potentials, the inhibitory effect of the suppressor will be quite different from interactions with only EPSPs.

C. Two-tone suppression and masking in other tympanate orthoptera

Two-tone suppression of the ultrasound-induced startle response is a phenomenon common to both ensiferan and caeliferan orthopterans. For the locust *Locusta migratoria*, Robert (1989) showed that the negative steering behaviors elicited by pulses of 15 kHz are suppressed by the simultaneous presentation of pulses of 5 kHz at 10–15 dB greater amplitude. With respect to crickets, Nolen and Hoy (1986b) found similar suppression tuning in *T. oceanicus*, with best suppression measured between 4 and 5 kHz. Different from *E. carolinus*, however, frequencies >8 kHz were not effective in suppressing the startle response in *T. oceanicus*. Unlike our study, the measurements of suppression threshold in *T. oceanicus* were not normalized to startle threshold, however, as the startle stimulus was presented at 70 dB SPL. The mean startle threshold to 30 kHz in *T. oceanicus* is ~55 dB SPL (Nolen and Hoy, 1986a). Given the limits of their broadcast system, it is likely that the 70 dB SPL startle stimulus used by Nolen and Hoy (1986b; ~15 dB above startle threshold) was too great for any suppression by stimuli with frequencies >8 kHz. Thus, it is not clear if the suppression tuning curves for the higher frequencies (>8 kHz) in the two studies are comparable. Like *E. carolinus*, *T. oceanicus* showed linear suppression growth when tested in a two-tone paradigm. Estimates from Nolen and Hoy's (1986b) study, however, suggest that the slope of suppression growth at 5 kHz for *T. oceanicus* is <1. For *E. carolinus*, when suppression thresholds are normalized to the startle threshold, such low growth rates were measured only for frequencies outside the most sensitive region (Table I). Moreover, we found the greatest suppression growth at the best suppression frequency, 5 kHz (Table I). When the 5-kHz data for *E. carolinus* are not normalized to startle threshold, however, and are plotted as sound pressure levels (as in Nolen and Hoy, 1986b), suppression growth is <1 (slope=0.95; $P=0.007$) and thus comparable to that in *T. oceanicus*.

As in *E. carolinus*, suppression of the ultrasound-induced startle in *T. oceanicus* is most easily elicited when the low-frequency suppressor precedes or overlaps the startle stimulus (Nolen and Hoy, 1986b). Although Nolen and Hoy (1986b) used 30-ms duration pulses to measure suppression in the nonsimultaneous presentation paradigm, their measurements are consistent with ours when normalized to pulse duration. In the backward suppression condition, we were unable to measure suppression in *E. carolinus* when the suppressor followed the startle stimulus by >0.4 pulse durations (2 ms). For the similar presentation sequence to *T. oceanicus*, suppression could not be elicited when the suppressor followed the startle stimulus by >0.66 pulse durations (20 ms). In the forward suppression condition (suppressor leads), we were unable to measure any suppression when the startle stimulus followed the suppressor by >1 pulse duration (5 ms). Although the relationship is similar in *T. oceanicus*, the

separations in which suppression could be measured are somewhat longer. When the suppressor leads the ultrasound pulse there is a decrease in suppression at a separation of 1 pulse duration (30 ms), but suppression can still be measured when the two stimuli are separated by up to 3 pulse durations (Nolen and Hoy, 1986b).

An alternative method to the two-tone suppression paradigm used here to measure frequency selectivity at different intensities is the classic masking paradigm in which thresholds for the detection of single tones at different intensities are measured as a function of the bandwidth of simultaneously presented maskers [Fletcher, 1940; but see Moore (1995) for review]. While quite common in human psychoacoustics, Ehret *et al.* (1982) uniquely employed this experimental method to measure the critical bands centered at frequencies in the calling song and ultrasound channels of *T. oceanicus*. By measuring the spectrum level of a noise band required to mask either positive or negative phonotaxis to an amplitude modulated tone, critical bands were calculated using the critical ratio formula. Similar to our results using the two-tone suppression paradigm, Ehret *et al.* (1982) found that the critical bandwidth centered around 4.5 kHz (near the calling song carrier frequency) increased with increases in the probe stimulus intensity (model calling song). Although the conclusion that auditory filter bandwidth increases at higher intensities is similar between the two studies, the experiments presumably probe two different underlying mechanisms. Whereas the two-tone suppression paradigm affects threshold using stimuli outside the excitatory band, the masking paradigm used by Ehret *et al.* (1982) presumably changes the signal-to-noise ratio using stimuli within the excitatory band.

D. Function of two-tone suppression in *E. carolinus*

Although two-tone suppression is common across disparate taxa and is mediated by a variety of different mechanisms, most hypotheses for its function are based on the benefits generated from increases in frequency resolution. Indeed, feature extraction in the spectral domain that is important to foraging bats and sexual signaling frogs, for example, is mediated at least in part by nonlinear inhibitory/suppression mechanisms (Capranica, 1965; Suga, 1973; Fuzessery, 1988). With respect to orthopteran insects, the resulting nonlinear response to the coupling of a variety of auditory stimuli has also been shown to modulate the auditory system in a variety of behavioral contexts. For example, the acoustic components of wind modulate the responses of certain auditory units in *Locusta migratoria* to stimulation with other sounds (Boyan, 1986). This modulation effectively shifts the frequency response of the auditory system to higher frequencies when the animal is in flight. The adaptive significance proposed for this shift is one of a contextual filter where noise produced by the wingbeat is prevented from eliciting a startle response (Boyan, 1986; Robert, 1989). In crickets, however, the most likely source of the characteristic sounds that best suppress the ultrasound-induced startle is not the wingbeat, but presumably singing conspecifics. Indeed, our finding that there is some evidence for sexual dimorphism in two-tone suppression sensitivity

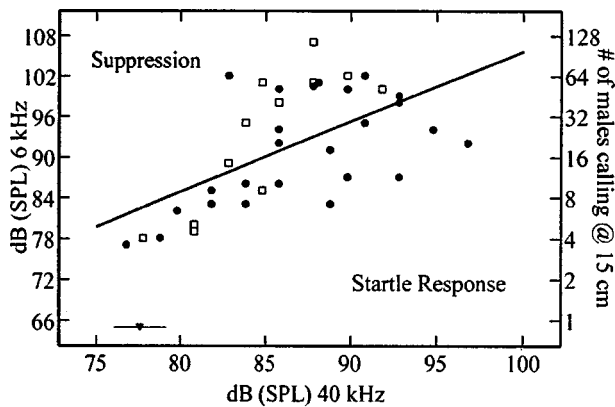


FIG. 7. Plot of suppression thresholds for a 6-kHz suppressor when measured in dB SPL (*re*: 20 μ Pa) rather than *re*: threshold (Fig. 3). Data are the same as those presented in Fig. 3. Based on the mean power output measured for five males calling in the field (@ 15 cm), the right axis is the number of males required to produce an aggregate song with the corresponding sound pressure level. The right axis scale assumes ideal summation of the songs. Circles and squares are the suppression thresholds for females and males, respectively. The triangle represents the mean startle threshold (\pm S.E.) to 40 kHz alone for these individuals. Thus, these data suggest that in the field \sim 8 singing males (@ 15 cm) would be necessary to suppress the startle response, presumably making two-tone suppression unlikely. Note that when measured in SPL the slope for the suppression growth of 6 kHz is 1.04 ($r^2=0.352$, $P<0.001$), whereas in Fig. 3, where suppression thresholds are measured *re*: startle threshold, the slope is 1.35. This change in scale also reveals a significant difference between suppression growth in males and females ($\text{slope}_{\text{males}}=2.15$, $\text{slope}_{\text{females}}=0.85$, $t=4.518$, $P<0.001$) not found when measured *re*: startle threshold ($t=0.051$, $P=0.609$).

(see Fig. 7) suggests that the trait may play a role in calling song assessment. There are few data, however, supporting the initial hypothesis that two-tone suppression in crickets functions in the relative comparison of conspecific and predatory signals. As in *T. oceanicus* (Nolen and Hoy, 1986a), we found that relatively high levels of low-frequency (songlike) sounds were required to suppress the ultrasound-induced startle. Based on the average power output of males singing in the field, Fig. 7 shows that under ideal conditions an unrealistically high density of singing males (Farris, personal observation) would be necessary to produce suppressor stimuli. An alternative hypothesis for the function of two-tone suppression is that it could prevent negative phonotaxis to the harmonics of a calling song. Indeed, Nolen and Hoy (1986b) showed that there is enough power in the harmonics of the calling song of *T. oceanicus* to elicit negative phonotaxis. The addition of the low-frequency fundamental was sufficient to prevent negative steering and elicit a positive response. In *E. carolinus*, however, there is relatively little power in the harmonics. The second harmonic of the calling song fundamental is already 50 dB down [Fig. 2; harmonics are not required for effective song attraction (Farris *et al.*, 1997)]. Based on the songs recorded in this study, an aversive song would have to be unrealistically powerful and at close proximity. An alternative context from long-range mate attraction in which two-tone suppression could function is courtship in which aversive behavior in response to a courtship song rich in high frequencies is suppressed. In *E. carolinus*, however, not only is the courtship song similar in spectrum to the calling song (Alexander, 1957; Farris, un-

published observation), but suppression is elicited in the context of flight and, thus, an unlikely adaptation to the close-range communication during courtship. Thus, left without an obvious conclusion for its function, we can only speculate that two-tone suppression of the ultrasound-induced startle responses to sounds containing *only* ultrasound. Broadband sounds that span the audio and ultrasound bands (potentially produced by tettigoniids) would thus be prevented from eliciting any antipredator behavior. Further research is needed to elucidate the behavioral ecology of this trait.

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