

Ultrasound sensitivity in the cricket, *Eunemobius carolinus* (Gryllidae, Nemobiinae)

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Extracellular recordings from the cervical connectives in both long- and short-winged *E. carolinus* reveal auditory units that are sensitive to frequencies >15 kHz with best sensitivity at 35 kHz (79 dB SPL threshold). Stimuli in this frequency range also elicit a startle response in long-winged individuals flying on a tether. For single-pulse stimuli, startle and neck connective thresholds decrease with increasing ultrasound duration, consistent with the operation of an exponential integrator with a ~32.5-ms time constant. There is evidence for adaptation to long duration pulses (>20 ms) in the neck connectives, however, as it is more difficult to elicit responses to the later stimuli of a series. For paired-pulse stimuli consisting of 1-ms pulses of 40 kHz, temporal integration was demonstrated for pulse separations <5 ms. For longer pulse separations, startle thresholds were elevated by 3 dB and appear to be optimally combined. Startle thresholds to 5 ms frequency modulated (FM) sweeps (60–30 kHz) and pure tone pulses (40 kHz) did not differ. The characteristics and sensitivity of this ultrasound-induced startle response did not differ between males and females. As in some other tympanate insects, ultrasound sensitivity in *E. carolinus* presumably functions in the context of predation from echolocating bats. © 2000 Acoustical Society of America. [S0001-4966(90)05502-3]

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INTRODUCTION

Numerous species in five different insect orders have independently evolved sensitivity to ultrasound, presumably as a consequence of the selective pressure from echolocating, insectivorous bats (see Hoy, 1992 for review). Although much of the behavior and neurophysiological evidence for sensitivity to ultrasound comes from experiments with tympanate moths (Roeder, 1967; Fullard, 1979), sensitivity to ultrasound in Orthopterans has been described in several families (e.g., Tettigoniidae, Libersat and Hoy, 1991; Acrididae, Robert, 1989) including Gryllidae, the family which represents the true crickets. Although this family is composed of at least nine subfamilies (Walker and Mazaki, 1989), most evidence of ultrasound sensitivity comes from members of the subfamily, Gryllinae, commonly referred to as field crickets. For example, Australian field crickets (*Teleogryllus oceanicus*) are sensitive to two spectral ranges: a low-frequency band between 3 and 9 kHz (i.e., male calling song spectrum) and a broad high-frequency band >15 kHz (i.e., the frequency range of echolocating bats; Moiseff *et al.*, 1978). When presented with ultrasound, *T. oceanicus* flying on a tether perform short-latency (~35–55 ms; Nolen and Hoy, 1986) negative phonotactic behaviors that consist in part of the lateral extension of one of the metathoracic legs. This response presumably functions to evade echolocating, insectivorous bats. Using playback experiments in the field, the repulsive effect of ultrasound was demonstrated for a North American field cricket, *Gryllus rubens*. Farris *et al.* (1998) showed that the simultaneous broadcast of batlike ultrasound with a calling song decreases that calling song's attractiveness relative to a song broadcast without ultrasound.

Few studies, however, have examined auditory sensitiv-

ity in members of another subfamily, the Nemobiinae, commonly referred to as ground crickets. Like field crickets, members of this subfamily produce species-specific calling songs that function as sexual advertisement signals and attract male and female conspecifics (Farris *et al.*, 1997). Several species of nemobiines are polymorphic for hind wing length such that individuals develop either long hind wings that are capable of flight or short hind wings that are insufficient for flying (see Harrison, 1980 for review). Presumably, nightly phonotactic flights by long-winged individuals should put them at risk from echolocating bats. To determine whether nemobiine crickets are also sensitive to ultrasound, we used both electrophysiological and behavioral assays to examine the auditory sensitivity of *Eunemobius carolinus* (Gryllidae, Nemobiinae), a species in which long-winged individuals perform nocturnal flight-phonotaxis to male calling songs (Farris *et al.*, 1997). In particular, we examined the effects of acoustic stimuli that vary in temporal and spectral structure on the response of auditory units in the cervical connectives. Furthermore, we used the hitherto undescribed ultrasound-induced startle response in flying *E. carolinus* as a behavioral assay of cricket auditory sensitivity. We show that like gryllines, the nemobiine *E. carolinus* is sensitive to ultrasound and that the ultrasound-induced startle response in flying *E. carolinus* is elicited by sounds similar to those emitted by echolocating bats. Some of these results have been previously reported in abstract form (Farris and Hoy, 1997, 1998).

I. GENERAL METHODS

A. Subject animals

The colony, started from individuals sound-trapped in Lafayette County, Mississippi (see Farris *et al.*, 1997), was

reared under a 14 L/10 D hrs light schedule and fed “cricket chow” *ad libitem*. Crickets were characterized as having one of three different wing morphologies: (1) Long-winged, possessing fully developed hind wings and thus capable of flying; (2) de-alates, long-winged crickets that have detached their hind wings at the axillary sclerites of the dorsal metathorax and are no longer flight capable; (3) short-winged, possessing undeveloped hind wings and thus never capable of flying.

B. Acoustic stimuli

Stimuli were generated using Tucker Davis Technologies (TDT) 16-bit, digital-to-analog converters and custom-written software (8- or 5- μ s sample period for pure tone and frequency modulated stimuli, respectively). Stimuli were amplified using a Harman/Kardon HK6150 integrated amplifier and broadcast from either a Radio Shack Super tweeter (Cat. No. 40-1310b) or an ESS AMT-1 tweeter located 30 cm from the cricket preparation (note that the maximum output frequency for each speaker was different). For experiments in which the carrier frequency was held constant at 40 kHz, the stimuli were broadcast through Panasonic 40-kHz transducers. Stimulus amplitude was adjusted using TDT PA4 programmable attenuators. The stimuli were calibrated at the preparation using a Bruel and Kjaer (B&K) 2608 measuring amplifier (linear weighting, fast: 125-ms integration time) with a (B&K) model 4138 1/8-inch microphone (90° angle of incidence, experiment 1 only) or with a B&K 4135 1/4-inch microphone (0° angle of incidence), B&K 2639 preamp, a B&K 5935 microphone power supply. The calibration system was checked using a B&K 4220 pistonphone calibrator. All sound-pressure levels (dB SPL) are referenced to 20 μ Pa. Depending on the speaker used, the maximum output level of the system was either 108 or 113 dB SPL. All pulse onset and offset ramps are raised cosine. Pure tone stimuli were calibrated using continuous tones, whereas the calibration signal for FM stimuli was a continuous series of 5-ms FM pulses at 100 pulses/s (50% duty cycle). The amplitude of a single FM pulse was thus corrected by 4.13 dB (the effect of the 50% duty cycle and the 1-ms ramp) to match that of the pure tone stimuli for a given SPL. This calibration signal was used to maintain the temporal relationship of the spectral components within the 5-ms FM sweep. Spectral properties of the FM sweep were analyzed at the position of the cricket preparation using a B&K 4135 1/4-inch microphone (0° angle of incidence), B&K 2639 preamp, a B&K 5935 microphone power supply, and a Hewlett-Packard 3562A signal analyzer.

C. Neurophysiological recordings

The experimental procedure used in this study is the same as that used by Farris *et al.* (1998). Briefly, cold-anesthetized, colony-reared crickets were mounted ventral side up on a platform in a foam-lined Faraday cage that reduced acoustic reflections and electrical noise. The prothoracic legs of the crickets were extended laterally and the tarsi were fixed to small bars using low melting point wax. The acoustic stimuli were presented from loudspeakers 30 cm

from the preparation, positioned 0° normal to the longitudinal axis of the cricket. Extracellular recordings were made using a sharpened tungsten electrode inserted ventrally through an opening in the cervical membrane and hooked under the left or right cervical connection between the prothoracic and subesophageal ganglia. When recording ascending information only, the neck connectives were cut anterior to the placement of the hook electrode. The electrode was insulated using a mixture of mineral oil and Vaseline jelly applied around the connective. The indifferent electrode was inserted into the abdomen. Recordings from the cervical connectives were amplified using a model 1700 AM Systems differential amplifier and bandpass filtered between 10 and 10 000 Hz. The stimuli and neural responses were recorded simultaneously onto tape using a 400-PCM recorder or digitally captured using a TDT AD1 analog-to-digital converter (sampling period: 40 μ s) for later analysis. We also monitored the recordings visually using a Tektronix R5030 oscilloscope and aurally using an Archer amplified speaker.

The threshold for eliciting a response in the neck connectives was determined as the minimum sound-pressure level necessary to elicit at least three responses to a series of five pulses. Stimuli were presented at 0.5 pulses/s. In addition to this 3/5 threshold criteria, for experiments that tested the effects of stimulus duration on threshold, we used a 1-out-of-2-down, 0-out-of-2-up adaptive procedure. For this adaptive rule, the amplitude of a single pulse was decreased in 6-dB steps if a response was detected in one out of two presentations. Stimulus step sizes were then changed to 3 and 1 dB for each reversal until a threshold was determined. The minimum interstimulus interval in this procedure was 5 s.

D. Startle response

Long-winged *E. carolinus* were tethered dorsally at the pronotum to a 14-cm-long piece of piano wire using low melting point wax. Flight can easily be initiated by waving the tethered cricket in the air or by giving it small puffs of wind. Once flying, a tethered cricket was positioned in the foam-lined Faraday cage 7 cm from the cage floor and 30 cm from the speakers placed at 90° normal to the cricket. The behavioral components of the startle response consist of an abrupt cessation of flapping, folding of the hind wings, closure of the fore wings, anterior extension of the prothoracic and mesothoracic legs, posterior extension of the metathoracic legs, and dorsal flexion of the head and antennae. Flight usually resumed with the termination of the stimulus. Restarting flight became more difficult with increasing numbers of startle responses in some subjects, however. Thus to help ensure that most subjects would complete the test, we measured the startle threshold using the 1/2-down, 0/2-up adaptive procedure described above. Note that thresholds are statistical constructs and that this adaptive procedure converges on the stimulus level that elicits a response in 30% of the presentations (Levitt, 1971). Without measurement of a second point on each individual's psychometric function (i.e., using a 2-down, 1-up method), it is impossible to know the function's slope and thus extrapolate what change in stimulus level will induce a certain change in the probability of

response. Individuals were required to fly for at least 5 s prior to stimulus presentation (i.e., minimum interstimulus interval was 5 s). This interval was chosen to reduce the probability of any habituation or sensitization.

The hind wings of long-winged crickets were removed for morphometric measurement following an experiment by simply squeezing the wings with a pair of forceps and allowing the cricket to reflexively detach the wings (de-alation). With each detached wing in its folded position, their proximo-distal lengths (along the length of the costal vein) were measured using vernier calipers (0.05-mm resolution). Wing size for an individual was then determined as the average wing length measured for both hind wings.

II. EXPERIMENTS

A. Frequency sensitivity

To determine the effect of stimulus carrier frequency on responses in the neck connectives of long-winged individuals ($N=7$), we measured the threshold for eliciting a detectable neural response to pure tone pulses of 18 frequencies ranging from 2–55 kHz. Pulses were 5 ms in duration with 1-ms ramps and presented at 0.5 pulses/s. The threshold for eliciting a startle response was determined by presenting individual flying crickets ($N=8$) a single 5-ms pulse with 1-ms ramps for 20 frequencies ranging from 2–65 kHz and visually noting whether a startle response occurred. Stimulus frequencies were presented in a pseudorandom order.

B. Wing morph and frequency sensitivity

The frequency responses (2–60 kHz) in the neck connectives of flightless crickets (6 short-winged and 9 long-winged de-alated individuals) were examined using the same protocol as in experiment 1. Wing-morph was determined after the prep was completed by examining the axillary sclerites of the dorsal metathorax for the presence of undeveloped hind wings in short-winged individuals or “stumps” from the de-alated wings.

C. Frequency sensitivity of ascending units

Following the measurement of the frequency sensitivity in the neck connectives of six individuals (all de-alates), we examined the tuning of just the ascending units by cutting both connectives anterior to the hook electrode and repeating the measurements for frequencies ranging from 2–60 kHz.

D. Temporal integration: Single pulse

Startle response and neck connective thresholds were measured for stimuli that varied in duration (i.e., duration versus intensity paradigm). A stimulus consisted of a single pulse of 40 kHz with 1-ms ramps that varied in duration from 2–80 ms. The threshold for eliciting a response in the neck connectives was measured using both the 1/2-down, 0/2-up adaptive procedure ($N=10$) and the 3/5-down criteria ($N=10$). Ten different individuals were used in each test. The effect of duration on the startle response was measured for 14 individuals using the 1/2-down, 0/2-up procedure only.

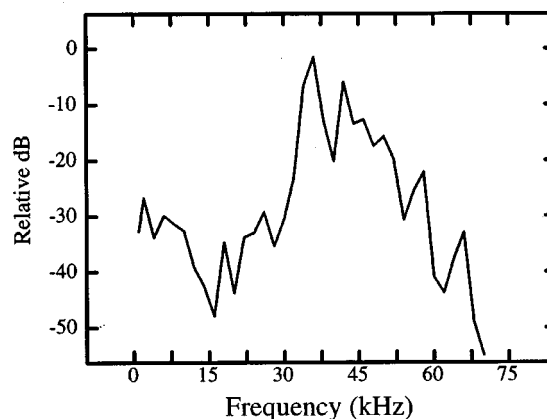


FIG. 1. Amplitude spectrum of a single pulse of the FM sweep used in Sec. II E. Each pulse was 5 ms in duration with 1-ms ramps and consisted of a 60- to 30-kHz linear sweep.

E. Temporal integration: Multipulse

Two different experimental methods were used to assess the temporal integration of multiple pulse stimuli. First, 5-ms pulses consisting of a linear FM sweep from 60 to 30 kHz (Fig. 1) were presented at varying pulse rates to flying crickets to determine the effect of repetition rate (and pulse separation) on startle threshold. The duration and spectral characteristics of the pulses in these stimuli were chosen to model the characteristic search phase pulses of some bats (Simmons, 1987). In trial 1 ($N=10$), the total stimulus duration was 1 s (pulse number varied), whereas in trial 2 ($N=12$) only a pair of pulses was presented. Thresholds were determined for pulse repetition rates ranging from 1 to 181 pulses/s. Each pulse had 1-ms ramps. To assess whether the FM structure of the stimulus had an effect on startle threshold relative to that for a pure tone stimulus, startle threshold to a single 5-ms pulse of 40 kHz (1 ms raised cosine ramps) was also measured for each individual in trial 1 and compared to that for a single FM pulse using a paired t -test (Zar, 1989).

Second, the threshold for eliciting a startle response to a pair of 1-ms pulses (0.1-ms ramps) of 40 kHz was measured as a function of pulse separation ($N=20$). For both the duration versus intensity (i.e., single-pulse stimuli in Sec. II D) and paired-pulse paradigms, the response functions were described analytically using a least-squares fit to the means.

F. Effects of sex and wing length on startle threshold

A sample population across several experiments was used to assess the effects of wing size and sex on startle threshold. The threshold for eliciting a startle response to a single 5-ms pulse of 40 kHz with 1-ms ramps was compared between males and females using a Mann–Whitney test of ranks (Zar, 1989). This test was also used to compare male wing length to female wing length (i.e., long-winged). The relationship between wing length and startle threshold was analyzed using linear regression in which wing length and startle threshold were the independent and dependent variables, respectively.

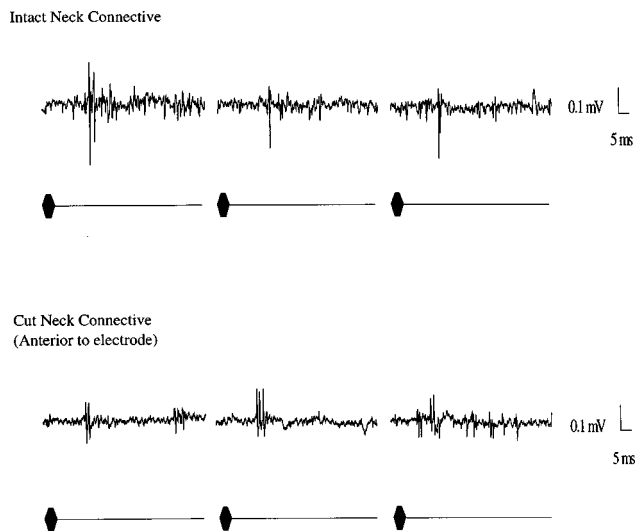


FIG. 2. Responses recorded in the neck connective of a female *E. carolinus* presented with three 5-ms pulses of 40 kHz at 82.3 dB SPL at 0.5 pulses/s. Upper and lower panels are the responses of the same connective in the intact and cut conditions, respectively. Relative to recordings in the intact preps, spike amplitudes were commonly reduced in the cut-connective recordings.

III. RESULTS

A. Frequency sensitivity

Extracellular recordings from the cervical connectives in long-winged *E. carolinus* show recognizable auditory units that are sensitive to frequencies higher than 15 kHz with best sensitivity at 35 kHz (79 dB SPL threshold) (Figs. 2 and 3). This range of frequencies also elicits a startle response in individuals flying on a tether (Fig. 3). The components of the startle response in *E. carolinus* (see Sec. I) do not appear to be directional, which is different from the ultrasound-induced directional steering response in field crickets (*Gryllinae*) (May and Hoy, 1990).

B. Wing morph and frequency sensitivity

The frequency response curves of neural activity in the neck connectives of both de-alate and short-winged individuals (i.e., both flightless morphs) were similar to those of long-winged individuals. Comparison of the audiograms of the two short-winged groups to that for long-winged crickets shows that best sensitivity occurs at frequencies >20 kHz (Fig. 3). Ultrasound sensitivity was not uniform across the three wing-morphs, however, as long-winged individuals were 5–7 dB more sensitive from 20–30 kHz and 5–7 dB less sensitive above 45 kHz than the two short-winged morphs.

C. Frequency sensitivity of ascending units

The exclusion of any descending information by cutting the neck connective did not change the frequency response in the neck connectives. Figure 4 shows the average tuning in the same preparations prior to and after cutting the connective in six de-alates. Like those for experiments 1 and 2, frequency sensitivity increased for frequencies above 15 kHz. One notable difference between the cut and intact volt-

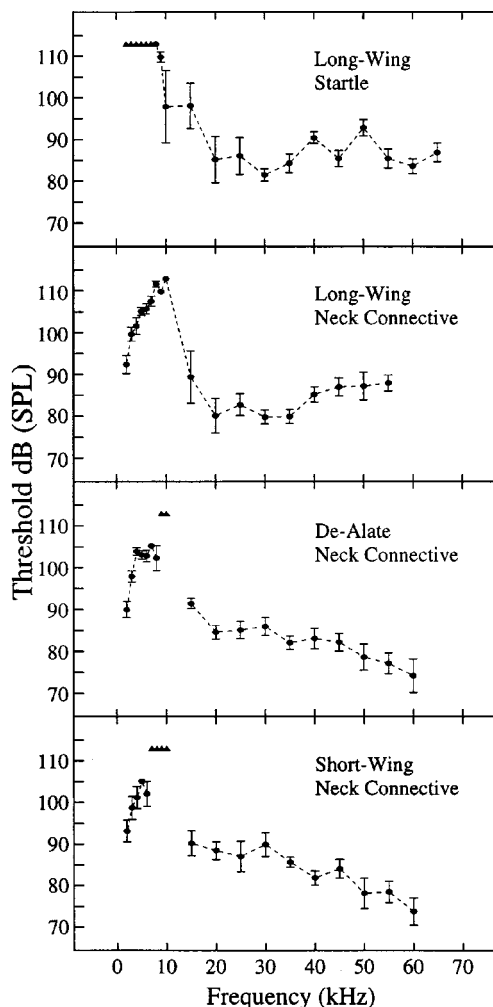


FIG. 3. Frequency tuning curves for the startle response of long-winged individuals flying on a tether and the neural activity recorded in the neck connectives for the three-wing morphs. Circles are the mean thresholds (\pm SE) necessary to elicit a response in 1/2 stimulus presentations for the startle response ($N=8$) and 3/5 stimulus presentations for the neck connectives. Sample sizes for the three-wing morphs were: $N=7, 9,$ and 6 for the long-winged, de-alates, and short-winged crickets, respectively. Triangles mark frequencies to which <2 individuals responded to stimuli below 113 dB SPL.

age records was that the evoked potentials in the intact connective showed a tri-phasic change in potential, whereas those in the cut connective appeared to be bi-phasic (Fig. 2).

D. Temporal integration: Single pulse

Startle response thresholds to single 40-kHz pulses decrease exponentially with increasing pulse duration (Fig. 5). The individual data were normalized to their minima prior to the analysis of the effect stimulus duration on threshold. The dashed curve in each panel of Fig. 5 represents 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,

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

where τ represents the temporal integration (i.e., summation) time constant that describes the rate at which the threshold

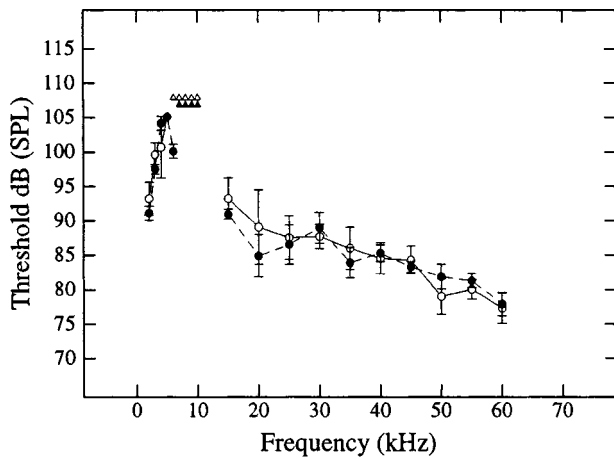


FIG. 4. Frequency tuning curves for intact (●) and cut (○) neck connectives. Values are the mean thresholds (\pm SE) necessary to elicit a response in 3/5 stimulus presentations ($N=6$, all de-alates). After measuring the frequency response in intact preparations, both connectives were cut anterior to the electrode and measurement of the frequency response was repeated. Triangles mark frequencies in which <2 individuals responded to stimuli below 108 dB SPL. Examples of the responses recorded in the two conditions are shown in Fig. 2.

reaches an asymptote as a function of T , the duration of the stimulus. For the two experiments that used a 1/2-down, 0/2-up procedure, the time constants were virtually the same: 32.36 ms ($r^2=0.726$) and 33.08 ms ($r^2=0.624$) for the startle response and neck connectives, respectively. For the response in the neck connectives measured using a 3/5 threshold criteria, however, there appears to be some evidence for adaptation to pulses longer than 20 ms. During these presentations it was common for a response to be elicited to the first pulse in the five-pulse train, with little response after that (Fig. 6). Thus the thresholds measured at these longer durations are higher (to meet the 3/5 criteria) and there is an apparent increase in τ to 45.04 ms ($r^2=0.421$). Linear regression analysis of the mean threshold versus the logarithm of stimulus duration showed that the slopes for the time-intensity tradeoff for the three data sets in Fig. 5: A, B, and C are: -10.9 dB ($r^2=0.72$), -11.3 dB ($r^2=0.62$), and -7.8 dB ($r^2=0.33$) per decade duration, respectively.

E. Temporal integration: Multipulse

For stimuli consisting of 5-ms FM pulses, there was no salient effect of pulse rate on the startle threshold (Fig. 7). Although the data show a slight increase in sensitivity to pulse rates near 20 pulses/s, this peak is only ~ 4 dB lower than that for a single pulse in the 1-s pulse train tests [Fig. 7(a)] and at the most 1.5 dB better in the paired-pulse test [Fig. 7(b)]. These thresholds are thus indistinguishable from the rest of the response function, and there does not appear to be any clear multiple pulse integration revealed by this paradigm. These stimuli were chosen to more closely simulate bat biosonar (Simmons, 1987; see discussion). Using a pairwise comparison for each individual in trial 1, we found no significant difference between the startle threshold for a

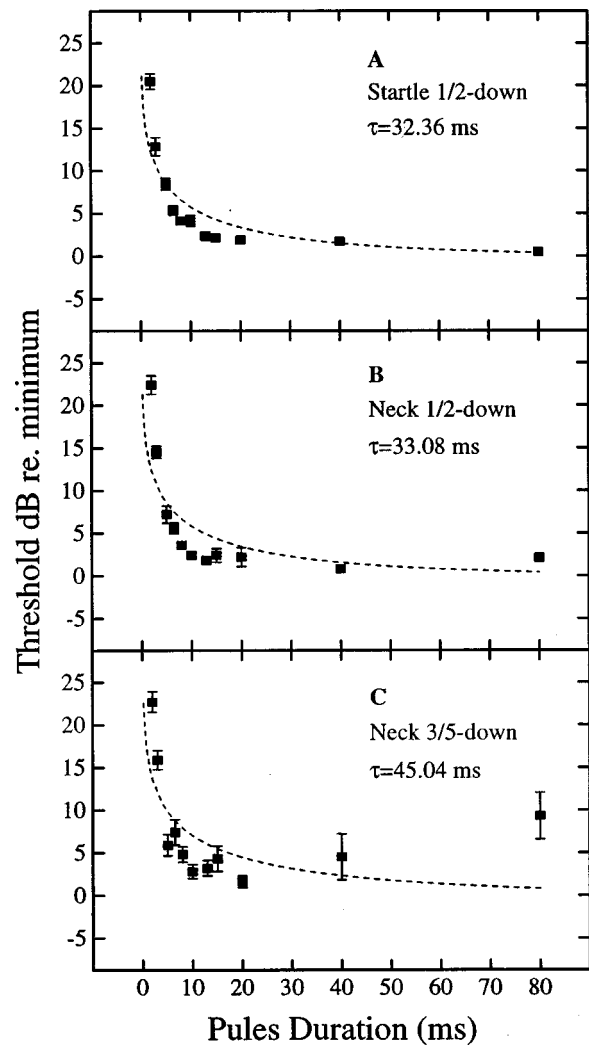


FIG. 5. Relationship between stimulus duration and threshold for eliciting: (A) a startle response ($N=14$), (B) a response in the neck connectives using a 1/2-down adaptive procedure ($N=10$), and (C) a response in the neck connectives using a 3/5-down adaptive procedure ($N=10$). Data were normalized to their minima prior to averaging. Filled squares are the mean thresholds (\pm SE; in some cases SE is smaller than the symbol) for eliciting a response to 40-kHz pulses with 1-ms ramps at varying durations. The dashed curves represent the least-squares fit to the data using the equation proposed by Plomp and Bouman (1959) for the change in threshold as a function of duration (T) (see text). The time constants (τ) for each fit are noted in each panel.

single FM pulse and that for a pure tone 40-kHz pulse ($t=0.34$, $N=10$, $P=0.741$; absolute mean difference $=0.469 \pm 4.21$ dB).

Startle threshold did depend on pulse separation for the shorter duration, pure tone pulses (1-ms duration, 40 kHz), however (Fig. 8). Thresholds relative to that for a single 1-ms pulse decreased for pulse pairs separated by <10 ms (i.e., 0- to 5-ms interpulse intervals). As in the duration versus intensity tradeoff above, the change in startle threshold as a function of pulse separation can be modeled as a leaky integrator (Zwislocki, 1960) using the following equation:

$$\text{Threshold Shift } (T) = -10 \cdot \log \left(1 + \exp \left(\frac{-\Delta T}{\tau} \right) \right) + C,$$

where C is a constant that describes the asymptote of the

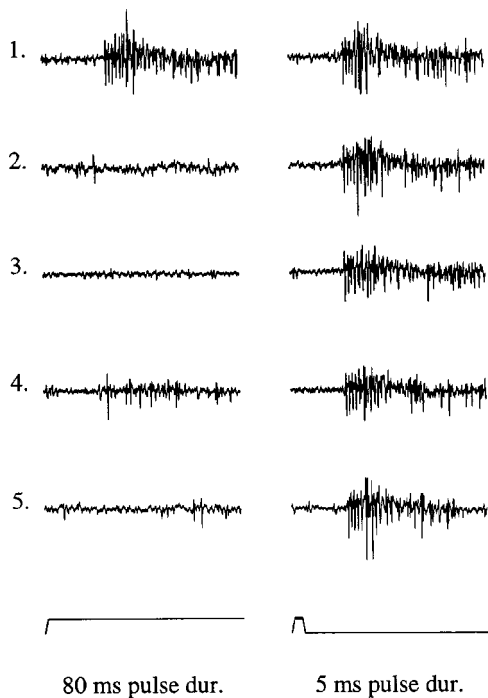


FIG. 6. Demonstration of reduced response to five presentations of pulses with long durations. Traces are the responses recorded in the neck connectives for two different pulse durations (40 kHz, 1 ms-ramps, 90 dB SPL, 2-s pulse period). For the 80-ms stimulus (left column), a response was noted for sweep 1 only (note that trace 4 may contain a response of the same unit that responds in sweep 1). Whereas for the 5-ms stimulus, a response was noted in all five presentations.

function and ΔT is the time interval between pulses. A least-squares solution for τ and C showed that the startle threshold changed like that of a leaky integrator with a time constant (τ) of 5.30 ms that reaches an asymptote (C) at -1.30 dB ($r^2=0.803$).

F. Effects of sex and wing length on startle threshold

There was no significant difference between male and female startle thresholds ($U=50$; $N=11$ female, 13 male; $P>0.2$). Startle threshold (i.e., long-winged individuals) did not vary significantly with wing length ($r^2=0.006$, $N=24$; male and female wing sizes were not significantly different, $U=58$, $P>0.2$). Because wing lengths in our study population only ranged from 10.95–12.78 mm, we would expect only a 1.34-dB range in startle thresholds (Forrest *et al.*, 1995; see discussion). It is thus not surprising that regression analysis showed no correlation between *E. carolinus* size and startle threshold.

IV. DISCUSSION

A. Frequency tuning

Without doubt, *E. carolinus* is sensitive to frequencies below 15 kHz, especially those contained in the calling song (see Farris *et al.*, 1997). It was the focus of this study, however, to examine the more salient auditory capabilities in the ultrasound band. Extracellular recordings of neural activity in the neck connectives of *E. carolinus* demonstrate recognizable auditory units that are excited by ultrasound. This physiological tuning is similar to that found in other insects

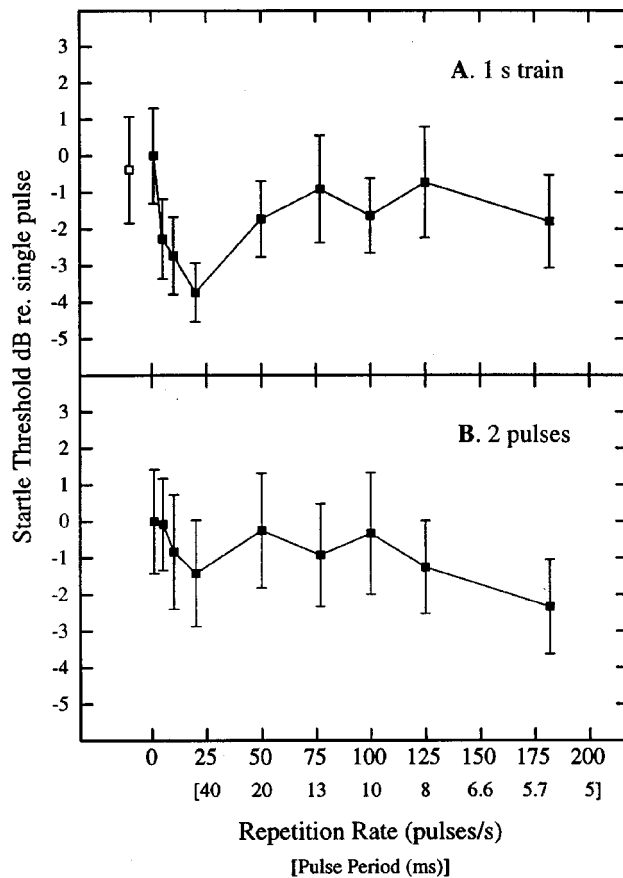


FIG. 7. Relationship between FM pulse repetition rate and startle threshold. Filled squares are the mean thresholds (\pm SE, re 1 FM pulse) necessary to elicit a startle response. (a) Stimuli consisted of a 1-s train of 5-ms pulses (1-ms ramps) of a linear 60–30 kHz FM sweep presented at variable pulse rates ($N=10$). The open square is the mean threshold for eliciting a startle response to a single 5-ms pulse (1-ms ramps) of 40 kHz for the same 11 crickets. There was no difference in pairwise comparison of startle threshold to single pulses of FM and pure tone (40 kHz) ($t=0.34$, $N=10$, $P=0.741$; absolute mean difference $=0.469\pm 4.21$ dB). (b) Stimuli consisted of a pair of 5-ms pulses (1-ms ramps) of a linear 60–30 kHz FM sweep presented at variable pulse rates. Corresponding pulse periods (time between the beginning of two successive pulses) are noted on the x-axis in brackets.

known to use acoustic cues to avoid echolocating bats (Hoy, 1992). For example, general physiological sensitivity to ultrasound in tympanate moths is tuned to frequencies between 20 and 120 kHz and best sensitivity is found near 30 kHz at ~ 50 dB SPL (e.g., Faure *et al.*, 1993; Waters and Jones, 1996). Sensitivity to this spectrum in noctuid moths reflects the parallel tuning of a pair of peripheral auditory neurons with staggered thresholds called A1 and A2 (Coro and Perez, 1984). In addition to moths, mantids (Dictyoptera), lacewings (Neuroptera), and beetles (Coleoptera) all possess similar ultrasound sensitivity. Although independently evolved (Fullard and Yack, 1993), these convergent auditory systems all mediate ultrasound-induced startle responses that presumably function in the avoidance of echolocating bats.

More closely related to the ground cricket, *E. carolinus* (Gryllidae: Nemobiinae) are the field crickets (Gryllidae: Gryllinae). Sensitivity to ultrasound in the central nervous system (CNS) of gryllines is carried out by a bilateral pair of ascending interneurons called INT-1 (Moiseff and Hoy, 1983; cf. AN2 Wohlers and Huber, 1982), and its tuning

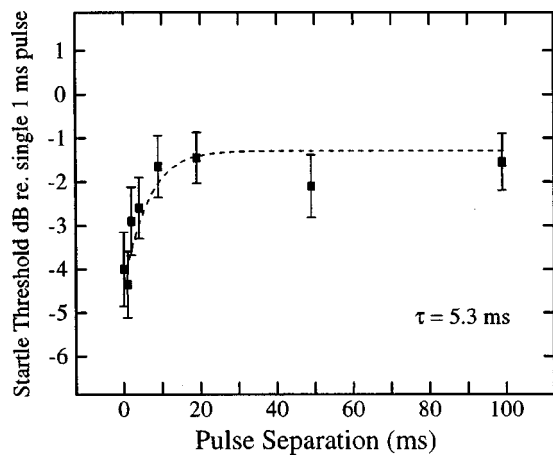


FIG. 8. Relationship between pulse separation and startle threshold. A stimulus consisted of a pair of 1-ms pulses of 40 kHz (0.1-ms ramps) that varied in separation from 0–99 ms. Squares (■) are the mean (\pm SE) threshold necessary to elicit a startle response relative to the threshold for a single pulse ($N=20$). Dashed curve represents the expected threshold for an integrator with a 5.3-ms time constant (τ) (Zwislocki, 1960).

closely matches the tuning of evasive startle behavior in flying field crickets (Nolen and Hoy, 1986). Similarly, the frequency tuning and temporal integration properties of recognizable auditory units in the neck connective recordings of *E. carolinus* closely match those for the startle response (Figs. 3 and 5). Although we have not yet identified these auditory units by intracellular recording and dye injection, potentials recorded in the neck connectives of *E. carolinus* appeared to be associated with ascending units (Figs. 2 and 4) and may represent the activity of an INT-1 homologue.

Comparison of startle tuning in *E. carolinus* with that of the steering response in field crickets (Gryllidae: Gryllinae) is shown in Fig. 9 (to normalize the energy of stimuli with different durations, thresholds are dB energy *re* a 125-ms,

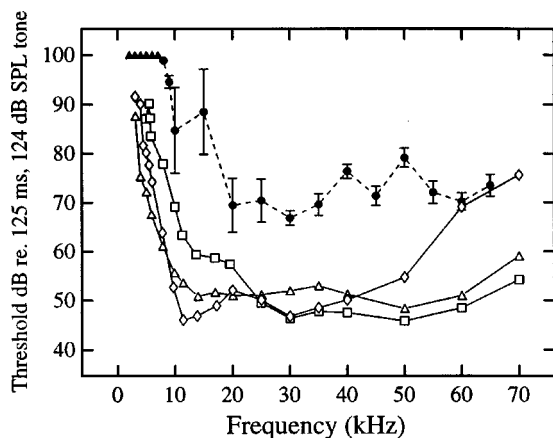


FIG. 9. Frequency tuning of the startle response in *E. carolinus* and the negative steering response in three species of field crickets (Gryllidae: Gryllinae). Circles (●) represent the mean thresholds (\pm SE) necessary to elicit a startle response in *E. carolinus* ($N=8$ cf. Fig. 3). Squares (□), triangles (Δ), and diamonds (\diamond) represent the mean thresholds for eliciting negative phonotaxis in flying *Teleogryllus oceanicus*, *T. commodus*, and *Gryllus bimaculatus*, respectively (Nolen and Hoy, 1986). To accommodate the different duration stimuli, all thresholds are normalized for stimulus energy relative to a 125-ms, 124-dB (*re* 20 μ Pa) tone, the calibration tone in both studies. Closed triangles mark frequencies in which <2 individuals (*E. carolinus*) responded to stimuli below 99 dB.

124-dB SPL tone). Although the broad tuning is similar for all four species, the startle response in *E. carolinus* is elicited by more energy than is field cricket steering. From a proximate point of view, because larger insects can be echolocated with lower levels of sonar (and therefore at greater distances; see Dusenbery, 1992, pp. 284–291 for discussion), Forrest *et al.* (1995) proposed a negative relationship between insect size and startle threshold. Although flying field crickets have \sim nine times the cross-sectional area of *E. carolinus* which predicts \sim 9.5 dB more sensitivity (i.e., the wing lengths of *G. bimaculatus* and *T. oceanicus* are \sim three times longer than *E. carolinus*, translating into nine times the cross-sectional area when modeled as sphere), Fig. 9 shows that in the 25–40 kHz range, the thresholds for the field cricket steering response are \sim 15 dB more sensitive than that for the startle response in *E. carolinus*. The steering response in gryllines and the startle response in *E. carolinus* may not be analogous behaviors, however. Whereas the steering response only changes a cricket's flight direction, the startle response of *E. carolinus* consists of an abrupt stop in flight and a dive to the ground (50-ms latency, Farris, unpublished data). Like the steering response in moths presented with low intensity ultrasound (Roeder, 1967), the steering response in field crickets may thus be more adaptive in avoiding echolocating bats at earlier stages in the attack and is therefore tuned to lower levels of ultrasound.

Different response criteria used in different studies could account for differences in thresholds. To determine the steering threshold in field crickets, Nolen and Hoy (1986) used a 10/15 response criteria. This method converges on the stimulus level that elicits a 63% response rate (Levitt, 1971). If the three species of field crickets mentioned above had the same psychometric function as *E. carolinus*, then we would expect the stimulus level required to elicit the 63% response rate to be higher than that for the 30% response rate (i.e., 63% steering threshold in the field crickets is higher than the 30% startle threshold in *E. carolinus*). The opposite is true (Fig. 9), however, eliminating this methodological explanation for these comparative differences in behavioral thresholds.

There is evidence that the auditory systems of some insects differ for short- and long-winged individuals. For example, Yager (1990) found that both auditory sensitivity and ear anatomy were associated with wing morphology in mantids; long-winged males were sensitive to ultrasound whereas short-winged (flightless) females were not. Such a correlation between flight capability and ultrasound sensitivity is consistent with the hypothesis that ultrasound sensitivity in mantids functions in the context of avoiding echolocating, aerial-hawking bats.

A similar correlation between macroptery and auditory development has been found in crickets (Ingrisch, 1977). In *Trigonidium cicindeloides* (Gryllidae: Trigoniniinae), for example, the development of a tympanic membrane in long-winged individuals only, suggests that like mantids, the acoustic ecology of the two-wing morphs differs and that the development of an ear is more costly for short-winged individuals. Evidence for such tradeoffs associated with the maintenance of flight have also been measured in nemobiine crickets. In *Allonemobius fasciatus*, for example, mainte-

nance of the flight muscles is correlated with the presence of fully developed hind-wings (Tanaka, 1986). Whereas individuals with intact hind-wings maintain the dorso-longitudinal flight muscles (DLFM), individuals with at least one wing de-alated histolyze the DLFM. For females in particular, flight muscle maintenance is negatively correlated with oocyte production. Because ultrasound sensitivity appears to function at least in the context of flight (i.e., detecting aerial hawking bats) and also may be costly to maintain in flightless individuals, we tested whether short-winged and de-alated crickets possessed the same sensitivity as long-winged crickets (hind-wings still attached). Tuning of the responses in the neck connectives of de-alated and short-winged individuals is similar to that in long-winged crickets (Fig. 3). From a functional point of view, these results are interesting and may mean that ultrasound sensitivity still plays a role in the behavioral ecology of flightless crickets. Conversely, the economics of flight muscle maintenance and the maintenance of ultrasound sensitivity may not be analogous. Resources devoted to auditory maintenance presumably are small relative to that for flight muscles and its cost in terms of oocyte (and hypothetically spermatophore) production may not be so significant that selection has produced a noticeable reduction in the sensitivity of flightless morphs. Such traits are of course under the influence of a number of factors such as nutrition, and more study is required to argue this conclusively.

B. Temporal sensitivity

Commonly described as a “time-intensity tradeoff,” the decrease in threshold for detecting a signal as its duration increases is usually modeled as an integration process that effectively integrates (or sums) signal energy over a short period of time called the temporal integration time constant (τ). The limits of temporal processing (including integration) in auditory systems are known to vary relative to the specific processing tasks; however, as different experimental procedures testing various aspects of temporal resolution and integration reveal different time constants (Tougaard, 1996; but see Eddins and Green, 1995 for review). In humans, for example, although duration versus intensity experiments suggest integration occurs over ~ 200 ms, paired-pulse tests reveal a much shorter time constant on the order of 5 ms (Viemeister and Wakefield, 1991). Furthermore, no simple long-term integration seems to occur and the behavior of the human subjects is consistent with a multiple-short-term-look model. In other mammalian taxa, differences between the time constants measured in duration versus intensity and paired-pulse paradigms are comparable to those in humans. In bottle-noise dolphins for example (*Tursiops truncatus*) duration versus intensity integration times range from ~ 10 – 200 ms (Johnson, 1968), whereas paired-pulse time constants are as short as $264 \mu\text{s}$ (Au *et al.*, 1988).

Physiological assays of temporal integration in insects also reveal disparities in τ , reflecting differences in the experimental tasks. For example, in a duration versus intensity paradigm using pure tone ultrasound stimuli, Surlykke *et al.* (1988) found that the A1 receptor in noctuid moths integrates over ~ 25 ms. A slightly larger time constant (69 ms) was

estimated for the peripheral receptors of noctuids; however, when the rise and fall times of the stimuli were also varied with duration (Waters and Jones, 1996). As in humans, paired-pulse paradigms with moths reveal a much shorter temporal integration time constant. Tougaard (1996) showed that the threshold for a response in the A1 cell of noctuids decreases for pairs of clicks separated by < 5 ms. This interval is comparable to the 2–3-ms temporal resolution time constant (acuity) also measured for the A1 cell using gap detection and amplitude modulation tests (Surlykke *et al.*, 1988).

Experiments testing the temporal sensitivity of tympanate moths are not limited to the physiological assays of the auditory periphery, however. In addition to evasive flight, the behavioral repertoire of some moths (Arctiidae) presented with ultrasound includes the production of a series of high-frequency clicks. Fullard (1984; Fullard *et al.*, 1994) used this phonoresponse as a behavioral assay of the effects of stimulus temporal structure (i.e., amplitude modulation rate) on the auditory sensitivity of *Cynia tenera* (Arctiidae). For pulses of pure tone stimuli presented at varying repetition rates, *C. tenera* are most sensitive to rates from 30–50 pulses/s. The response to the playback of actual echolocation attack sequences, however, shows that the *C. tenera* phonoresponse is best tuned to the faster rates of the terminal phase of the echolocation sequence. Thus this defensive behavior appears to function as a jamming signal that decreases the ability of the bat to locate the target moth (Fullard *et al.*, 1994). These experiments do not explore the limits of temporal power integration, however, and it is unclear how to best compare these results to the physiological experiments above.

From a comparative point of view, ultrasound sensitivity presumably functions in similar contexts for *E. carolinus* and many tympanate moths, the detection of insectivorous, echolocating bats. In this study, we examined the temporal integration characteristics of the startle response and responses in the CNS of *E. carolinus* using both the duration versus intensity and multipulse experimental paradigms. For the duration versus intensity paradigm, the time constants estimated for the startle and neck connective responses are nearly the same when using the same adaptive experimental procedure [$\tau \approx 32.5$ ms; Fig. 5(a) and (b)]. Although this integration time is comparatively longer than that for the negative steering response in *T. oceanicus* ($\tau \approx 15.6$ ms; calculated from data in Nolen and Hoy, 1986), the time-intensity slopes for the two responses are similar. The time-intensity slope measured for the startle response in *E. carolinus* and the steering response of *T. oceanicus* are 10.9 and 9.5 dB/decade, respectively, slightly steeper than that for humans (7.5 dB/decade; Florentine *et al.*, 1988). Using the 3/5 adaptive procedure, the multiple presentation of longer pulse durations appears to cause adaptation (Fig. 6) and thus, raise the threshold for longer pulse duration stimuli. As described above, while testing durations > 40 ms at levels above the threshold previously determined in the 1/2-down procedure, it was common to observe a larger response to the first pulse in the series of five pulses and then little or no response thereafter. Thus greater levels were required to

meet the threshold criteria at the longer durations which resulted in a greater τ ($\tau=45.04$ ms).

Two sets of experiments examined temporal integration of multipulse stimuli. One set of experiments measured startle threshold as a function of FM repetition rate (i.e., pulse separation). These tests were designed to test temporal sensitivity while more closely simulating the detection task presented by echolocating bats. The results from the FM experiments are similar for the two types of stimuli (1-s trains of FM pulses or a pair of FM pulses). In both cases, startle threshold did not decrease like that of an energy detector with a time constant similar to those measured in the duration versus intensity tests (Fig. 7). For example, for an integrator with a time constant (τ) of 32 ms, thresholds are expected to change by ~ -8 dB as the 1-s pulse train changes rates from 1 to 181 pulses/s (Zwislocki, 1960). In the paired-pulse FM tests, the expected change in threshold is only -3 dB as the energy within the integration interval (τ) is doubled when the separation between the two pulses decreases to less than τ (Zwislocki, 1960). Because these reductions in threshold were not observed in the two stimulus paradigms, the data suggest that: multiple-pulse stimuli are not integrated over the same time as single-pulse stimuli and the 5-ms duration of the FM pulses is longer than the multipulse integration time constant.

Temporal integration of multipulse stimuli was thus examined by measuring the change in startle threshold as a function of the separation of a pair of 1-ms duration pulses of 40 kHz. This stimulus design facilitated the measurement of a shorter multipulse τ , while at the same time controlling for any effect due to FM bandwidth. For pulse separations <5 ms, startle threshold decreases by 3 dB (Fig. 8), suggesting a combination of the two pulses. Because the repetition rate of typical bat sonar does not exceed 200 pulses/s (5–6 ms interpulse interval; see Fullard *et al.*, 1994) such temporal resolution ($\tau=5.3$ ms) appears adequate for processing even the fastest sonar rates of the attack sequence.

It is interesting to note that the startle threshold for two pulses separated by >5 ms remains ~ 1.7 dB below that for a single pulse. These results are quite similar to those in humans (Viemeister and Wakefield, 1991) and may be explained in part by the optimal combination of two independent samples, the two pulses. Thus the normalized difference between the signal-and-noise and the noise distributions (d') for the two-pulse stimulus increases by a factor of $\sqrt{2}$ relative to that for a single pulse and reduces the threshold. For the human subjects tested by Viemeister and Wakefield (1991), this change translated into an expected decrease in threshold of 1.3 dB, slightly worse than the 1.6 dB they observed. Modeling the expected decrease in threshold for two pulses in *E. carolinus* would require the measurement of more than one point on the startle threshold psychometric function (i.e., probability of a startle response as a function of stimulus intensity), which we did not do.

C. FM versus pure-tone threshold

Although the temporal structure (i.e., amplitude modulation) and intensity of bat biosonar appear to be the most

reliable cues of the proximity of aerial-hawking bats, the capacity for frequency analysis in tympanate insects could also contribute to the assessment of predation risk from echolocating bats. For example, the bandwidth of the sonar pulses of the big brown bat, *Eptesicus fuscus*, changes with the stages of the echolocation attack sequence. During the search phase, longer duration (15–20 ms) sonar pulses may have bandwidths <10 kHz, whereas during the approach phase, the bandwidth of the first harmonic may be as large as 40 kHz (60 to 20 kHz FM, 5–10 ms) (Simmons, 1987).

There is no conclusive evidence in tympanate insects for frequency analysis in the ultrasound band, however. In some moths (e.g., noctuids), the auditory receptors show parallel frequency tuning (Surlykke and Miller, 1982; Waters and Jones, 1996), presumably preventing any spectral processing of the signal. In crickets, although behavioral assays and recordings in the CNS have shown sensitivity to frequencies up to 100 kHz (Moiseff *et al.*, 1978; Moiseff and Hoy, 1983), there is unfortunately little information regarding ultrasound sensitivity in the primary auditory units (i.e., the most distal cells of the crista acoustica). In the most extensive such study in crickets, Imaizumi and Pollack (1999) found that across individuals, frequency selectivity in primary units sensitive to ultrasound (≤ 40 kHz) varied from broad-banded (>20 kHz) to more narrow-banded selectivity (<5 kHz). Unlike moths, the latter type of unit in crickets could provide the neural substrate necessary for frequency analysis in the ultrasound band. As in the physiological assay, the results of behavioral tests of frequency sensitivity to ultrasound also vary, as critical bandwidths centered at 40 kHz range from ~ 28 –50 kHz wide (in direct measurement and critical-ratio calculation) to only 3.55 kHz (using the ratio of the absolute thresholds of broadband noise and single tones) (see Ehret *et al.*, 1982). Consistent with the wider critical bandwidth measure (e.g., 28–50 kHz), Wytenbach *et al.* (1996) found that habituation of the ultrasound- (20 kHz) induced steering response in flying *T. oceanicus* could only be dishabituated by frequencies <16 kHz. Thus in their experimental paradigm, because frequencies >16 kHz were not distinguished from the 20-kHz habituating stimulus, it appears that the critical band around 20 kHz covers at least the range of ultrasound frequencies tested (16–40 kHz).

We found no difference in startle thresholds for a single 5-ms pulse of 40 kHz (1-ms ramps) and a 5-ms FM sweep (60–30 kHz, 1-ms ramps). Like moths and field crickets, it appears that for *E. carolinus*, frequency tuning in the ultrasound range is broad and that the FM sweep did not probe multiple frequency channels (i.e., critical bands) or spectral regions of a single channel that differed in sensitivity from that of 40 kHz (i.e., an effect of intensity rather than frequency). Unlike humans, for example, where the psychophysical tuning from 0.05–20 kHz is effectively modeled as a bank of overlapping frequency filters (i.e., critical bands) (see Moore, 1995 for review), our results suggest that the broad tuning of the startle response and the response in the neck connectives is representative of a single ultrasound filter with little variation in threshold from 60 to 30 kHz.

In conclusion, this study adds a new taxon to the growing list of insects that are sensitive to ultrasound. Relative to

that in gryllines (field crickets), however, the nemobiine startle response appears comparable in spectral sensitivity only. In addition to the differences in the motor components between the nemobiine and grylline startle responses, salient differences in absolute threshold as well as temporal sensitivity also appear evident. From a comparative point of view, the auditory behavior of *E. carolinus* is not unlike that across a variety of disparate taxa (e.g., mammals).

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