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Neural Tuning to Sound Duration in the Inferior Colliculus of the Big Brown Bat, *Eptesicus fuscus*

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Ehrlich, Daphna, John H. Casseday, and Ellen Covey. Neural tuning to sound duration in the inferior colliculus of the big brown bat, *Eptesicus fuscus*. *J. Neurophysiol.* 77: 2360–2372, 1997. Neural tuning to different sound durations may be a useful filter for identification of certain sounds, especially those that are biologically important. The auditory midbrains of mammals and amphibians contain neurons that appear to be tuned to sound duration. In amphibians, neurons are tuned to durations of sound that are biologically important. The purpose of this study was to characterize responses of neurons in the inferior colliculus (IC) of the big brown bat, *Eptesicus fuscus*, to sounds of different durations. Our aims were to determine what percent of neurons are duration tuned and how best durations are correlated to durations of echolocation calls, and to examine response properties that may be relevant to the mechanism for duration tuning, such as latency and temporal firing pattern; we also examined frequency tuning and rate-level functions. We recorded from 136 single units in the central nucleus of the IC of unanesthetized bats. The stimuli were pure tones, frequency-modulated sweeps, and broadband noise. The criterion for duration tuning was an increase in spike count of $\geq 50\%$ at some durations compared with others. Of the total units sampled, 36% were tuned to stimulus duration. All of these units were located in the caudal half of the IC. Best duration for most units ranged from <1 to 10 ms, but a few had best durations up to ≥ 20 ms. This range is similar to the range of durations of echolocation calls used by *Eptesicus*. All duration-tuned neurons responded transiently. The minimum latency was always longer than the best duration. Duration-tuned units have best durations and best frequencies that match the temporal structure and frequency range of the echolocation calls. Thus the results raise the hypothesis that neurons in the IC of *Eptesicus*, and probably the auditory midbrain of other vertebrates, are tuned to biologically important sound durations. We suggest a model for duration tuning consisting of three components: 1) inhibitory input that is correlated with the onset of the stimulus and is sustained for the stimulus duration; 2) transient excitation that is correlated with the offset of the stimulus; and 3) transient excitation that is correlated with the onset of the stimulus but is delayed in time relative to the onset of inhibition. For the neuron to fire, the two excitatory events must coincide in time; noncoincident excitatory events are not sufficient.

INTRODUCTION

Biologically important sounds include noises made by prey or predators, communication sounds of conspecifics, and specialized sounds such as the echolocation calls of bats. Such sounds can be characterized in terms of some set of frequency, intensity, and temporal features. One of the simplest temporal features is the duration of individual sounds or their components. A biological filter for sound duration could supplement the filters for sound frequency and inten-

sity and thus aid in identification of biologically important sounds.

The echolocation calls of all bats are characterized by specific spectral and temporal patterns that are related to different stages and strategies of foraging behavior. *Eptesicus* is typical of the majority of bats in its use of a downward frequency-modulated (FM) sweep for echolocation. When searching for prey, the bat emits a relatively long signal that sweeps from ~ 28 to 23 kHz over a period of 10–20 ms. When the bat is pursuing an insect, the frequency bandwidth is broadened so that the FM initially sweeps from ~ 80 to 20 kHz. As the bat approaches its target, the upper range of the FM is progressively lowered, the interval between calls decreases, and call duration is progressively shortened so that the final calls, just before prey capture, are ≤ 1 ms in duration (Simmons 1989). Thus in any given hunting sequence there are more short than long calls, and the durations of calls range from 20 to <1 ms. Just as tuning for sound frequency and intensity is an important neural mechanism for detection of echoes from these signals, tuning to duration of sound might serve the same purpose. That is, different neurons could play a role in the different phases of hunting if they were tuned to the appropriate sound durations.

In both mammals and amphibians, the auditory midbrain is the first stage at which neurons have been found that are tuned to sound duration. At levels below the midbrain from the auditory nerve through the lower brain stem auditory nuclei, the only representation of sound duration comes from units that respond to any sound for as long it remains within an appropriate range of frequency and amplitude (e.g., Haplea et al. 1994; Møller 1972; Vater 1982). However, this one-to-one temporal transformation leaves no lasting neural representation of sound duration. For sound duration to be utilized as a sensory cue, it presumably would have to be transformed to a place code, like those for other sensory cues, so as to eventually route it to motor pathways. In the auditory midbrain of frogs and toads, some neurons are tuned to specific ranges of sound duration (Feng et al. 1990; Narins and Capranica 1980; Potter 1965). The best durations of these midbrain neurons correspond to the durations of conspecific vocalizations (Gooler and Feng 1992). In the inferior colliculus (IC) of echolocating bats, some neurons are also tuned to specific ranges of sound duration (Casseday et al. 1994; Fuzessery 1994; Pinheiro et al. 1991). Because the IC is thought to be the site of neural calculations for sound duration (Casseday et al. 1994; Covey et al. 1996), it is important to obtain information about basic response properties of duration-tuned neurons at this level and to com-

pare them with the response properties of neurons that are not tuned to sound duration.

The purpose of this study was to more fully characterize the response properties of duration-tuned neurons in the IC in terms of their location, the range of durations to which they are tuned, the width of their duration tuning, and the relation of temporal discharge patterns, especially spike latency, to duration tuning. These data are important in consideration of the neural mechanisms underlying duration tuning. Spike latency as a function of duration provides especially important clues concerning the temporal interplay of excitation and inhibition. We relate these findings on basic response properties to the vocal repertoire of *Eptesicus* as determined from behavioral observations on call durations during different stages of foraging.

METHODS

Surgical procedures

The animals used in this study were 35 big brown bats (*Eptesicus fuscus*) of both sexes, obtained from the attics of local houses. On the day before recording, the bat was anesthetized with a combination of Metofane (methoxyflurane) and Innovar-Vet (fentanyl 0.4 mg/ml + droperidol 20 mg/ml; 0.125 ml/kg). The bat's head was held in a specially designed bite bar that was attached to manipulators that allowed the head to be rotated in three dimensions. Fine adjustments were made in the orientation of the skull so that it conformed to a standard stereotaxic position, and a metal post was attached to the skull with cyanoacrylate adhesive. The post was constructed so that the placement of the bat in the stereotaxic apparatus (Kopf, modified for bats) could be replicated precisely from one day's recording session to the next. Each bat was used in one to six recording sessions on separate days. Each session was ≤ 6 h in duration. Between recording sessions, bats were housed in individual cages and given free access to food and water. The cages were located in a temperature- and humidity-controlled room.

Recording began on the day after implantation of the post. Before being placed in the stereotaxic device, the bat was tranquilized with Innovar-Vet and lightly anesthetized with Metofane (methoxyflurane). A small opening, < 1 mm diam, was made in the skull overlying the IC. Between recording sessions, the opening was covered with a coat of Vaseline. The animal was allowed to recover from the anesthesia for ≥ 30 min before recording began. This period was sufficient for recovery of neural responses to a level at which virtually all neurons could be driven by an auditory stimulus. During recording, local anesthetic was applied to the scalp incision. During the recording sessions the bat was restrained in a foam-lined holder that was molded to the shape of the body so as to hold it firmly but comfortably. The holder was suspended in an elastic sling to damp movements. If the bat showed any signs of restlessness, the recording session was terminated.

Acoustic stimulation and recording

The auditory stimuli used were pure tones, FM sweeps, or broadband noise bursts, generated by a D/A converter controlled by a digital signal processor (Tucker-Davis Technologies), controlled in turn by custom software run on a Gateway 486 computer. The waveform always started at zero phase. Stimulus duration was varied from 1 to 100 ms. The stimuli had a rise-fall time of 0.5 ms for all stimulus durations except 1.0 ms, for which the rise-fall time was set to < 0.5 ms. To the human observer, 1 ms of a low-frequency tone would sound like a click because the waveform, being shorter than the rise time, could contain an amplitude increase that is sharper than the stimulus waveform, introducing

higher frequencies that would produce a click at the loudspeaker. At the high frequencies used in our experiments, many cycles would be contained in the rise time. For example, the period of a 50-kHz tone is $20 \mu\text{s}$, so that 25 cycles would occur in an 0.5-ms rise time. At our lowest range of frequencies, 20 kHz, and rise times, 0.4 ms, there would be eight cycles. We examined on an oscilloscope the output of the waveform of the loudspeakers with the use of a 1/8-in. Brüel & Kjaer condenser microphone; we saw no evidence of waveform distortion or amplitude peak at the stimulus onset or offset.

Stimuli were presented at a rate of three per second. For specific experiments, stimulus parameters were varied as described in RESULTS. For most measurements, stimuli were presented monaurally to the contralateral ear. To determine binaural characteristics, stimuli were presented to both ears simultaneously. Sounds were delivered via Brüel & Kjaer 1/4-in. condenser microphones, modified for use as loudspeakers and placed as close as possible to the external ear, at a distance of ≤ 1 mm. The output of the loudspeakers was measured with a 1/8-in. Brüel & Kjaer microphone and found to be flat ± 5 dB between 20 and 100 kHz. With the use of these measurements, the sound levels used during the experiments were converted from attenuator settings to sound pressure levels (SPL re $20 \mu\text{Pa}$). Cross talk between the two ears was measured by presenting sound at one ear and measuring the sound at that ear and at the opposite ear. The results indicated that, over the frequency range used, the SPL at the ear opposite the source was > 30 dB below that at the ear next to the source.

Neural response properties were recorded with glass micropipettes filled with 2 M KCl, a 5% solution of horseradish peroxidase in physiological saline, or a 2% solution of Chicago sky blue in 0.5 M sodium acetate. The recording electrodes were mounted on a multibarrel assembly for microiontophoresis of pharmacological agents (Havey and Caspary 1980). The recording micropipettes had tip diameters of $\sim 1.0 \mu\text{m}$ and impedances ranging from 10 to 40 M Ω . The electrode was aimed visually or stereotaxically and advanced with the use of a Kopf stepping hydraulic microdrive. Data were only collected from single units (signal-to-noise ratio $> 3:1$) that could be identified as cell bodies with reasonable certainty in that the waveform of their action potentials was biphasic. Data were collected on a Gateway computer with the use of custom software for data collection and storage, and viewed on-line as dot raster displays. Whenever a unit was isolated, certain routine tests were conducted. First, it was determined whether the unit responded best to pure tones, FM sweeps, or noise. For units that responded to pure tones, the best frequency (BF), i.e., the frequency at which threshold was lowest, was determined. For units that responded best or exclusively to FM sweeps, the optimal frequency range for the sweep was determined. Stimuli were then presented at the unit's BF or best sweep range. Duration was then varied in 1-ms increments up to 10 ms, and usually in 2- or 5-ms increments thereafter. The data set at each duration consisted of the responses to 20 stimulus presentations. These data were used to construct poststimulus time histograms (PSTHs) and to determine sound-evoked spike count, latency of the first spike, latency of subsequent spikes, variability of first-spike latency, distribution of spikes over time, and rate-level functions. In addition, a data set with no stimulus present was collected to measure the rate of spontaneous discharge. For most units, the spike times were recorded at each duration increment. For a few units, the spike times were only recorded at some increments, but spike counts were always obtained at all increments.

Histological procedures

Multiple electrode penetrations were made in each animal, and selected recording sites were marked with small iontophoretic injections of Chicago sky blue, ~ 50 – $100 \mu\text{m}$ diam. These injections

marked the locations of neurons with specific response properties and served as reference points in the reconstruction of electrode penetrations. One to four injections were made in a single animal, at dorsal-ventral levels separated by $\geq 400 \mu\text{m}$. The injections were made with the use of a pulsed (7 s on, 7 s off) current of 0.75–0.9 μA , positive at the electrode, applied for 2.0–3.5 min. After the final recording session, animals were administered a lethal dose of Nembutal (pentobarbital) and perfused through the heart with phosphate-buffered saline followed by a fixation solution of 4% glutaraldehyde in phosphate buffer. The brain was removed and refrigerated overnight in a solution of 30% sucrose in phosphate buffer. Sections 40 μm thick were cut on a freezing microtome, mounted on glass slides, dehydrated, and coverslipped without staining. Injection sites were plotted on drawings of individual sections with the use of a camera lucida and then transferred to a standard set of sections stored in a computer program (Cadkey). These sections were then pooled to create a three-dimensional reconstruction of the IC with recording sites from all animals.

RESULTS

We recorded responses to sound from 136 single units in the IC of 35 big brown bats. A neuron was classified as duration tuned if the spike count reached a peak at some sound duration, and the peak was $\geq 50\%$ greater than the spike count elicited by sounds of longer or shorter durations. By this criterion, 49 neurons (36%) were tuned to stimulus duration. Of these duration-tuned neurons, 31 (63%) responded best to pure tones and 18 responded best or exclusively to downward FM sweeps. For 36 of the duration-tuned neurons, we obtained PSTHs at a sufficient number of durations to analyze spike latency as a function of duration. For the remainder, duration tuning was determined by spike counts, but PSTHs were saved only at some durations.

Location in IC

All of the neurons were located in the central nucleus of the IC. Figure 1 compares the locations of recording sites at which duration-tuned neurons were encountered with the locations of sites in which we found neurons insensitive to sound duration. Duration-tuned neurons were confined within the boundaries of the central nucleus of the IC (see Casseday and Covey 1992 for a description of the cytoarchitecture of the IC). All of the duration-tuned units from which we recorded were located in the caudal half of the IC, whereas neurons not tuned to duration were more widely

distributed (Fig. 1B). However, most of the non-duration-tuned units from which we recorded were also localized in the caudal part of the IC. This sampling bias is partly due to a related observation that fewer units in the rostral part of the IC responded to pure tones or to single FM sweeps than in the caudal part (Casseday et al. 1997; Grothe et al. 1996). Furthermore, in this study we usually did not mark penetrations that did not contain duration-tuned neurons. Therefore further evidence is needed to determine whether or not there is an expanded representation of duration-tuned neurons in the caudal part of the IC.

Spontaneous activity

The responses of most IC neurons occurred against a background of low spontaneous activity. The range of spontaneous activity for duration-tuned neurons ($n = 45$) was 0–12 spikes/s, with a mean of 1.6 ± 2.7 (SD) spikes/s. Most of these (31) had no spontaneous activity, 14 had a spontaneous rate between 1 and 5 spikes/s, and 4 had spontaneous rates >5 spikes/s. For neurons that were not tuned to sound duration ($n = 31$), the mean spontaneous discharge rate was nearly identical, 1.7 ± 2.8 (SD) spikes/s. Thus there does not seem to be any difference in spontaneous activity between the two populations.

Duration tuning

Figure 2 shows PSTHs of typical responses of a duration-tuned neuron to sounds of different durations. All duration-tuned neurons responded transiently with one or a few spikes. There was a tendency for duration-tuned neurons to respond at sound offset, at least at durations near best duration. These observations are important in the analysis of mechanisms for duration tuning, because they are properties that may be produced by inhibition. Latency characteristics will be described more fully below. For some units that responded at nonoptimal durations, it was possible to see that the transient property was not altered when sound duration changed. For example, in Fig. 2 the responses were spread over a period of ~ 10 ms regardless of stimulus duration and total spike count. We distinguish between neurons that were tested with pure tones and those that were tested with FM sweeps. Some neurons in the IC of *Eptesicus* respond to FM sweeps but do not respond to pure tone bursts or noise bursts.

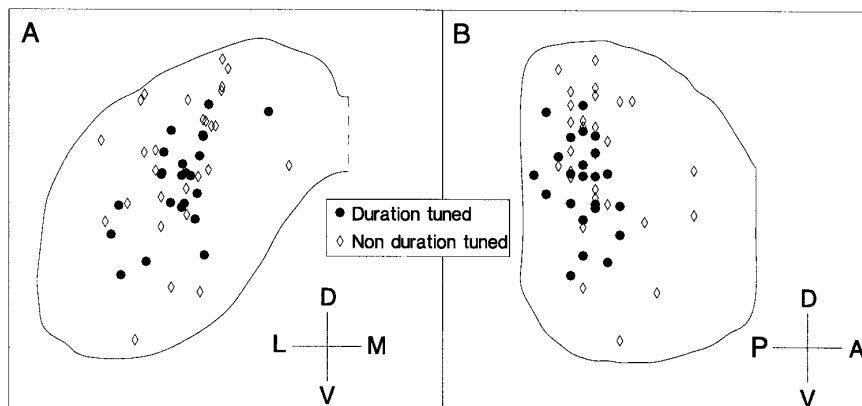


FIG. 1. Locations of duration-tuned units (●) compared with the locations of units insensitive to sound duration (◇). A: composite reconstruction of a frontal view of the inferior colliculus (IC). B: composite reconstruction of a parasagittal view through the IC. D, dorsal; V, ventral; L, lateral; M, medial; P, posterior; A, anterior.

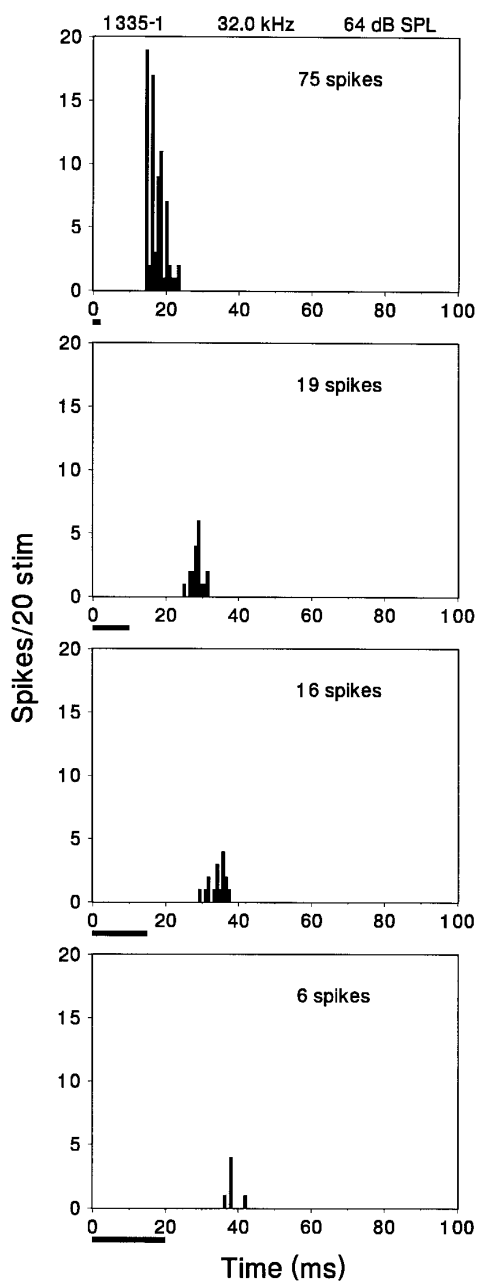


FIG. 2. Poststimulus time histograms (PSTHs) illustrating the discharge pattern of a duration-tuned neuron as a function of sound duration. This neuron continued to fire a few spikes correlated in time with the offset of the tone even at relatively long stimulus durations. Binwidth = 0.8 ms.

These neurons, which we refer to as FM-selective neurons, are treated separately below.

Figure 3 shows examples of duration tuning in neurons that responded either to pure tones or to FM sweeps. Of 36 duration-tuned neurons in which we recorded PSTHs at each increment in sound duration, 12 (33%) discharged within a specific range of sound durations and did not respond at all to sounds outside this range (Fig. 3, *E* and *G*). The remaining 24 units (67%) discharged at low levels even when presented with sounds much longer than their best duration (e.g., Figs. 2 and 3*B*); for some of these the spike count was not above their spontaneous rate of activity (Fig. 3, *A*

and *F*). For the neuron shown in Fig. 3*B*, only the response to the shortest (1-ms) tone is below spontaneous level, suggesting that spontaneous activity was inhibited at this duration.

We determined a “best duration” for each neuron. For neurons that had band-pass characteristics (Fig. 3, *B–H*), the best duration was defined as the duration that elicited the most spikes. Neurons that responded best to 1 ms (Fig. 3*A*) were assigned a best duration of 1 ms. This assignment is necessarily somewhat arbitrary because we did not test with sounds <1 ms. Similarly, because we seldom measured responses to sounds >50 ms and never tested stimuli >100 ms (Fig. 3*D*), we did not determine whether the few neurons with very long best duration (>30 ms) had an upper duration at which they ceased responding (Fig. 3, *D* and *H*).

The finding that many FM-selective units also appear to be duration tuned raises the question of whether the observed duration tuning in FM-sensitive units is actually due to tuning of some other FM parameter such as sweep rate. For example, in testing FM-selective units, the FM depth (frequency range) was held constant with the result that when stimulus duration lengthened, the FM sweep rate decreased. We cannot rule out the possibility that FM-selective neurons were tuned to the sweep rate rather than to the stimulus duration. However, one observation argues against this interpretation. Two units that responded both to pure tones and to FM stimuli were tested for duration tuning with the use of both types of stimuli (Fig. 4). Both units were tuned to longer durations for FM sweeps (5 and 8 ms) than for tones (1 and 3 ms), suggesting that they were sensitive to the duration of a restricted frequency range within the sweep. Further studies that vary FM range as well as sweep rate and sound duration will be necessary to establish whether the response is determined by FM rate or by the duration of a specific frequency range in the FM sounds.

The distribution of best durations is of interest for comparison with the durations of the bat’s echolocation pulses. For IC neurons, the largest proportion of best durations is <8 ms (Fig. 5). Units that responded best to pure tones had best durations that ranged from 1 to 7 ms, with a few >20 ms; most (80%) were tuned to durations of ≤ 5 ms. Units that responded best to FM had slightly longer best durations, ranging from 2 to 20 ms with most (83%) tuned to durations between 3 and 10 ms. In a typical hunting sequence, the duration of echolocation pulses range from <1 to ~ 20 ms; the largest proportion of echolocation sounds is <6 ms in duration, and of these, most are ~ 1 ms (Simmons 1989). Thus the durations of echolocation pulses have approximately the same range as the best durations of IC neurons.

Neurons with short best durations were more narrowly tuned to duration than neurons with long best durations. This relationship, illustrated in Fig. 6, was more systematic for neurons that responded to pure tones than for neurons tuned to FM sweeps, especially at long sound durations. In part, the relationship between best duration and width of duration tuning might be expected: the tuning of neurons with short best durations cannot expand much in the short direction, whereas the tuning of neurons with long best durations can expand in both directions. However, the reverse is not true; there is no logical necessity for neurons with long best durations to be broadly tuned.

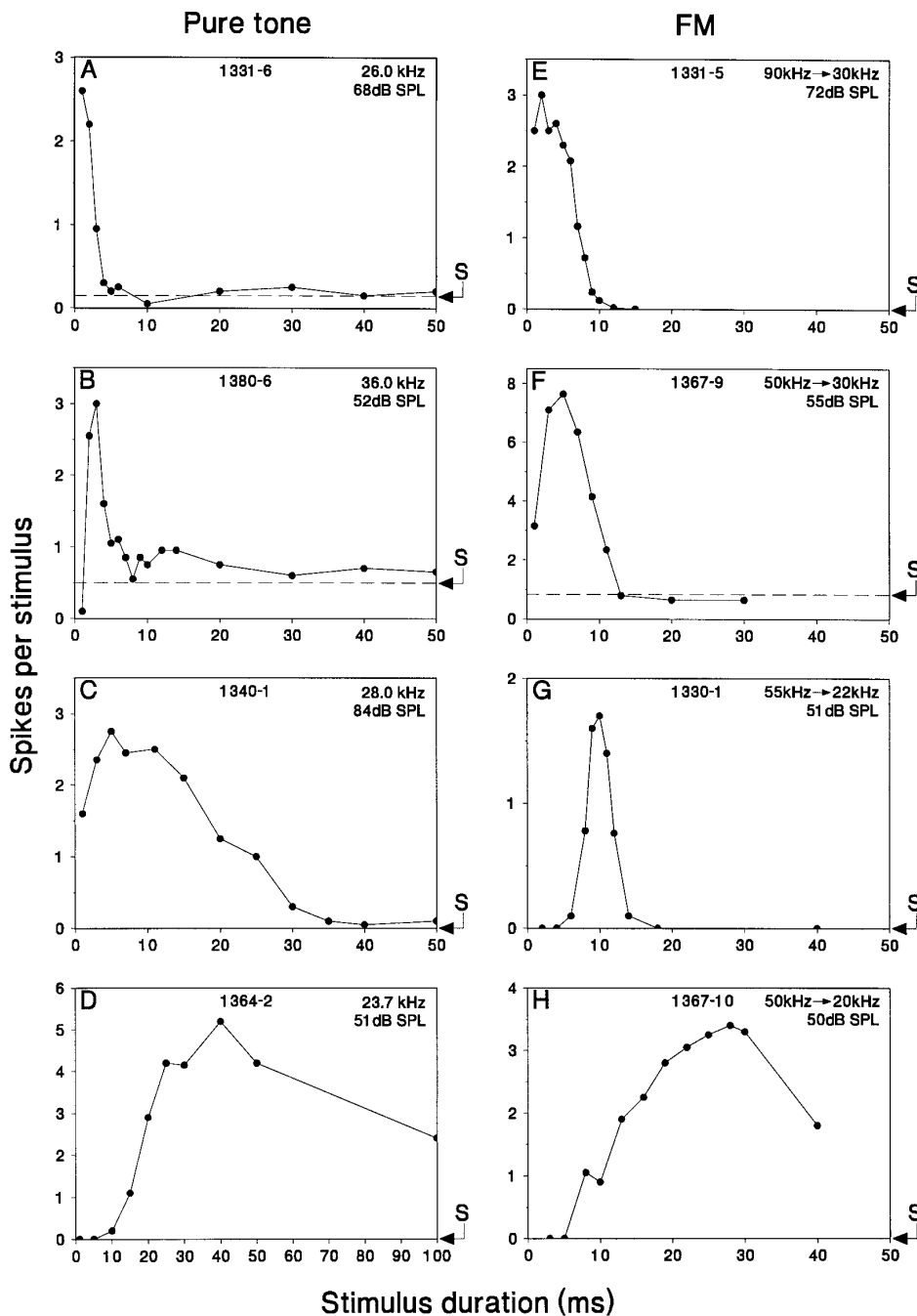


FIG. 3. Spike count as a function of sound duration for a sample of duration-tuned neurons. *A–D*: responses of neurons tuned to the duration of fixed-frequency tones. *E–H*: responses of duration-tuned neurons that only responded to downward frequency-modulated (FM) sweeps. Number of spikes per stimulus, averaged over 20 trials, is plotted on the vertical axis of each graph. Stimulus duration is plotted on the horizontal axis. Spontaneous discharge rate is indicated by arrows, and by a dashed line in cases where it was >0 . Numbers at *top middle of each graph*: unit numbers. Numbers at *right corner of each graph*: stimulus frequency and sound pressure level.

Frequency tuning

For 26 duration-tuned neurons that responded to pure tones, BFs ranged from 19 to 64 kHz. The relationship between best duration and BF is shown in Fig. 7. There is a hint that units with BFs between 20 and 30 kHz had the widest range of best durations, because this frequency range included longer best durations than were found in other frequency ranges. That is, 6 of 10 units with BFs between 20 and 30 kHz had best durations >4 ms, whereas only 2 of 15 units with BFs >30 kHz had best durations >3 ms. During echolocation, the longest sounds, emitted while the bat is searching for prey, have fundamental frequencies in the low-frequency range, between

20 and 30 kHz (Simmons 1989). It would be of interest to explore further the relationship between BF and best duration for its behavioral implications.

For 16 duration-tuned units that responded only to FM sweeps, the sweep parameters that elicited the highest spike count were estimated by audiovisual inspection. The sweep depths that elicited the best response varied from 15 to 40 kHz, and the upper, starting frequencies ranged from 90 to 45 kHz. Most neurons had starting frequencies <60 kHz and ending frequencies >20 kHz. The FM-selective neurons with starting frequencies >60 kHz all had relatively short best durations. During echolocation, the sounds emitted while the bat pursues prey are brief (0.5–5.0 ms) FM sounds

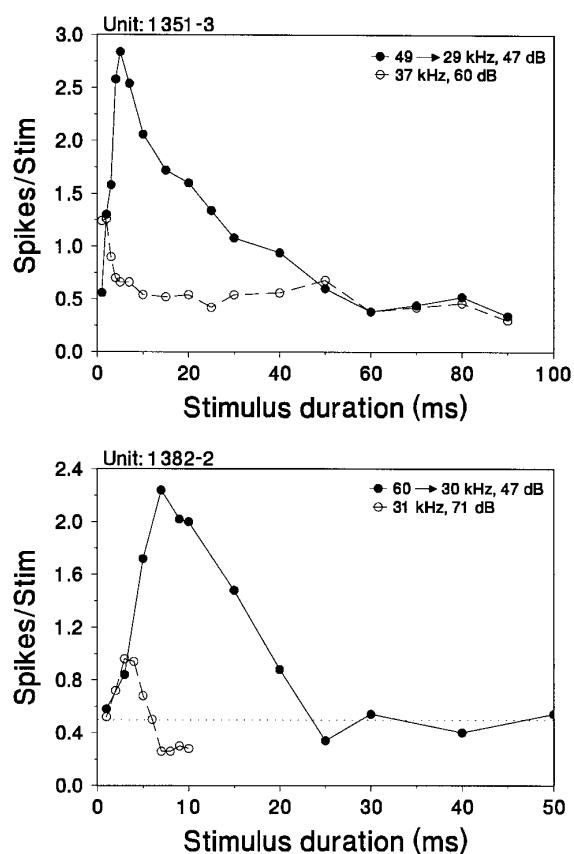


FIG. 4. Examples of duration tuning to FM sweeps and pure tones. The few neurons that responded to pure tones and to sweeps had a shorter best duration to tones than to FM sweeps.

whose fundamental sweeps from ~ 60 to 23 kHz (Simmons 1989).

Latency

There are two reasons why it is important to present a detailed analysis of latency. First, any device that measures stimulus duration must operate on information about the onset and offset of the stimulus, although the measurement is not complete until the offset. Thus a neural system for calculating sound duration should have a response latency that is no less than the durations to which it is tuned. The following results show that the latency of duration-tuned neurons is always greater than the best duration. Second, information on the timing of evoked spikes relative to the onset or the offset of the stimulus is relevant to hypotheses concerning the inhibitory and excitatory mechanisms underlying duration tuning. The latency data are used in a model of duration tuning as an ongoing process involving sub-threshold responses to onset, duration, and offset of sound.

Discharge pattern and latency, at best duration, as a function of duration were analyzed for 26 duration-tuned neurons that responded to pure tones. All of these neurons responded transiently with a burst of several spikes (e.g., Fig. 2). Latencies, as measured from sound onset at best duration, were always greater than the unit's best duration. Figure 8 shows the distribution of average first spike latencies relative to the offset of pure tones at the neurons' BFs and best durations.

This figure makes two points. First, most neurons have a latency of ~ 5 ms or more after the offset of the sound. Second, for each best duration there is a wide range of latencies.

It might be argued that the spread in latencies among neurons was simply due to testing some neurons under stimulus conditions at which response magnitude was not optimal. However, in measuring we were careful to place sound duration, level, and frequency at values that produced the maximal spike count. Further, the spread is much greater than would be expected by changes in sound level, for example.

Models for duration tuning contain excitatory components that are locked to the onset and offset of sound (Casseday and Covey 1995; Narins and Capranica 1980). We therefore examined latency at different durations to see how it was related to the onset or offset of the stimulus. The results indicate that the responses of most duration-tuned neurons followed the offset of pure tones for most sound durations; however, there were two kinds of exceptions. First, the response latency of some neurons was locked to sound offset only up to some maximum duration, beyond which it appeared to be locked to sound onset. Second, the response latency of a very few neurons appeared to be locked at all durations to the onset of sound. These exceptions provide useful insight concerning the underlying mechanisms. We plotted latency and variability of the first spike as a function of duration for 21 duration-tuned neurons that responded to pure tones and 16 that responded to FM sweeps (Figs. 9–12). Of course, this analysis is limited to neurons that had at least a small spike count at durations longer than their optimal duration. Some units, especially those with short best durations, fired action potentials over such a limited range of durations that it was difficult to determine whether the latency was correlated with the onset or the offset of the stimulus. The latency of most pure tone responders was longer than any sound duration presented (Fig. 9), so that the spikes appeared to be clearly locked to the offset of pure tones (Fig. 2). For nine of these units, responses always occurred at a fixed latency after stimulus offset, regardless of sound duration. Three examples are shown in Fig. 9. *A*, *C*, and *E* show the latency from sound onset; *B*, *D*, and *F* show latency from offset. Even at durations well beyond

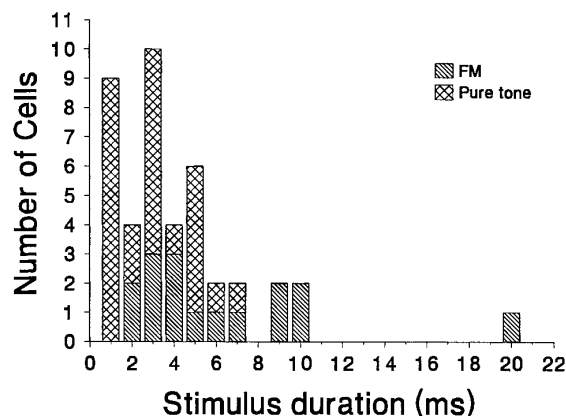


FIG. 5. Distribution of best durations. Best durations of IC neurons that responded best to pure tones or FM sweeps. A few neurons with best durations > 26 ms have been omitted from this graph.

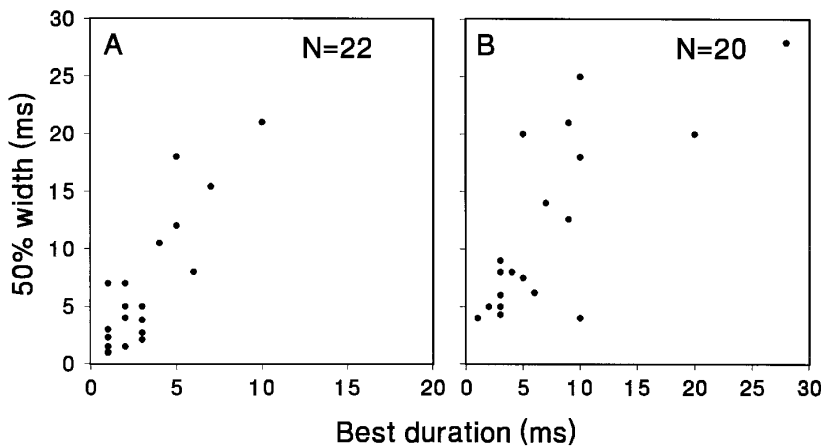


FIG. 6. Width of duration tuning, expressed as the range of sound durations over which spike count was 50% of maximum, plotted as a function of best duration at 10 dB above threshold. *A*: for units that responded best to pure tones, tuning width increased as best duration increased. *B*: for units that responded best to FM sweeps, the relationship between tuning width and best duration was not as systematic as it was for units that responded to pure tones.

their best durations, these three examples respond at no less than 10 ms after the end of the stimulus.

However, for some units, latencies appeared to be locked to sound offset at short durations but not at long durations. In these cases latencies increased as duration increased up to some maximum; then, as duration increased further, a point was reached at which the response occurred before the stimulus ended. In the example in Fig. 10, *A* and *B*, the latency followed the end of the stimulus by ~ 9 ms up to a duration of 15 ms. Then, at durations of ≥ 20 ms, latency occurred at and before the end of the sound. The latency of one neuron quite clearly followed the onset of sound (Fig. 10, *C* and *D*). These exceptions to the main population of duration-tuned neurons illustrate that their response latency can sometimes or even always be linked to the onset of sound.

To illustrate further that some neurons may be responding to both the onset and the offset of sound, Fig. 11 shows PSTHs for the neuron shown in Fig. 10, *A* and *B*, at three sound durations. When sound duration was increased from 4 to 10 ms, latency increased from 9 to 14 ms. However, at a 50-ms sound duration, there was no further increase in latency of the first spike, and the spikes were considerably dispersed in time, most occurring before sound offset. Thus it appears that this neuron has both an offset excitatory component to short sounds and an onset excitatory component to long sounds.

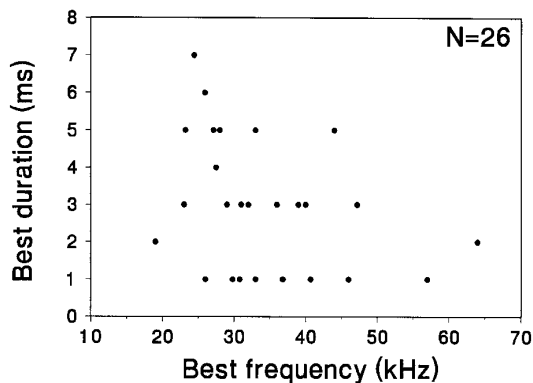


FIG. 7. Frequency tuning of duration-tuned neurons that responded best or exclusively to pure tones. Relationship between best duration and best frequency for neurons shows the widest distribution of best durations at low best frequencies.

For most neurons that responded to FM sweeps, latency increased as sweep duration increased (Fig. 12, *A–F*). However, for some neurons the increase in latency was not in proportion to the increase in sweep duration, so that above optimal durations, latency was shorter than total sweep duration (Fig. 12, *A–D*). The response of these neurons may be locked to the onset or offset of some frequency component within the FM sweep. For other neurons (Fig. 12, *E* and *F*), latency was clearly locked to the offset of the sweep.

Figures 9–12 also illustrate the tendency for the variability of the first spike latency to increase at durations longer than those to which the neuron responded best.

Given the above data, it would be an oversimplification to characterize these units as responding to the onset or to the offset of sound. However, it is possible to describe their latency behavior over their maximal response range. Taking the duration range over which response was $\geq 50\%$ of maximal, we determined whether latencies in this range were directly proportional to sound duration. For cells that responded to pure tones, 17 of 21 neurons showed this relationship, as in Figs. 9 or 10, *A* and *B*. For neurons that responded to FM sweeps, 11 of 16 neurons showed this relationship, as in Fig. 12, *E* and *F*. The remainder had

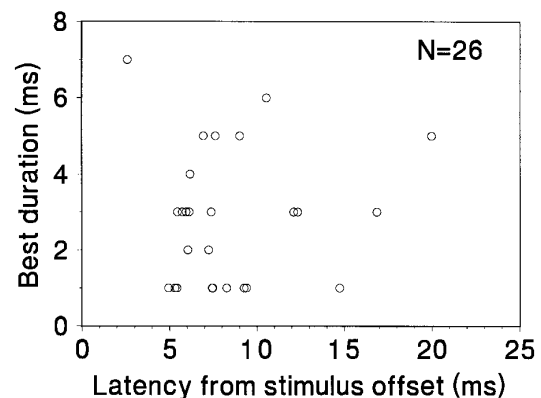


FIG. 8. First-spike latency as a function of best duration for neurons that responded best to pure tones. The latencies were measured from the offset of the sound with the sound set at best duration, best sound level, and best frequency. Latency for all but 1 neuron was ~ 5 ms or more after sound offset. At each best duration there was a spread of latency values.

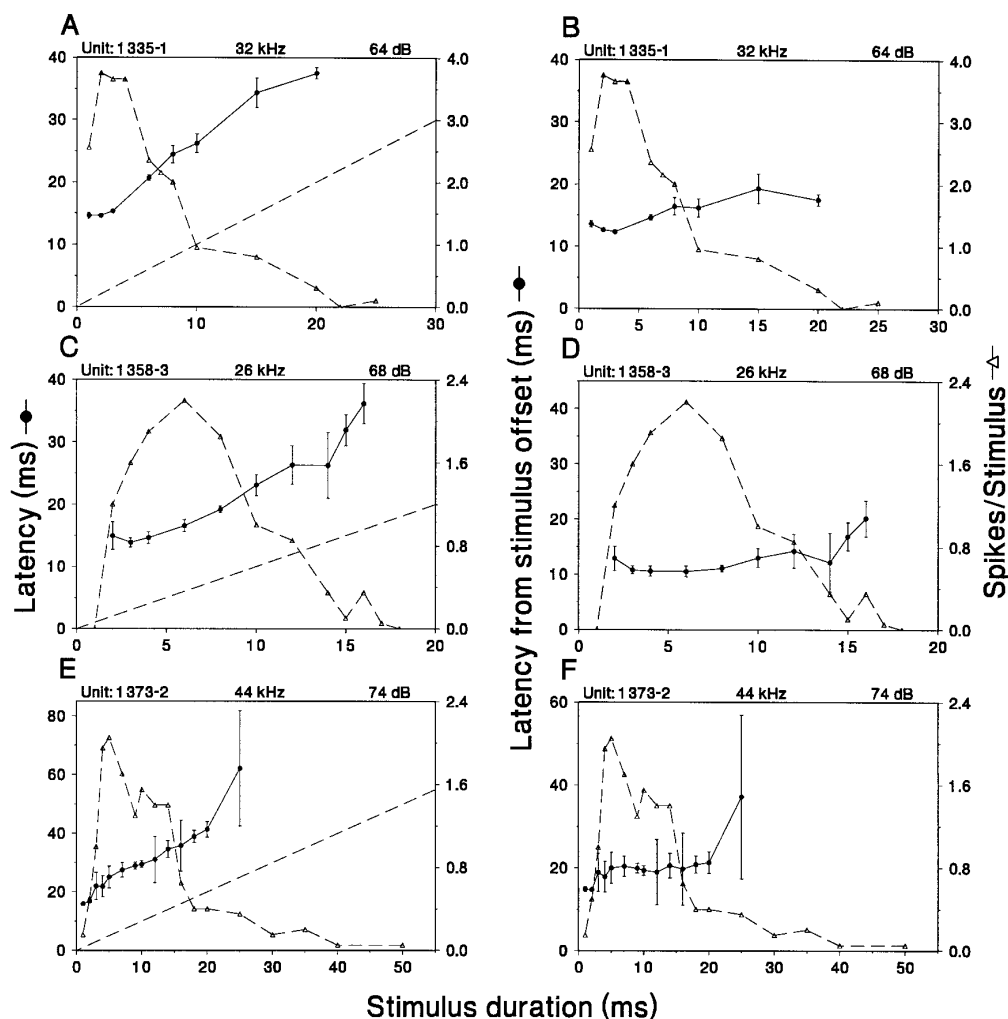


FIG. 9. Three examples of neurons whose latency followed the duration of sound for neurons that responded best or exclusively to pure tones. For each neuron latency is plotted from onset (A, C, and E) and from offset (B, D, and F). Solid curves with filled circles: 1st spike latency relative to stimulus onset or offset. Bars: SD. For comparison, dashed curves with open triangles indicate spike count as a function of stimulus duration. Dashed diagonal lines in A, C, and E: stimulus offset. Unit numbers and stimulus conditions are given at the top of each graph. Note that the spike times were always greater than the sound duration (dashed lines in A, C, and E; 0 on ordinates in B, D, and F).

latency functions like those shown in Figs. 10, C and D, or 12, A and B.

Response at different sound levels

A potential issue is raised by the fact that the overall signal level is a function of signal duration. The issue is whether or not duration-tuned neurons were in any sense energy detectors that responded only over a specific and narrow range of signal amplitudes. If they were, they should have nonmonotonic rate-level functions. That is, their response should be limited either by increasing sound duration or by increasing sound intensity, both of which increase stimulus magnitude. We obtained rate-level functions at best duration for 39 duration-tuned units to examine their tolerance to intensity changes and for comparison with the rate-level functions of neurons not tuned to duration. Functions were classified as monotonic or nonmonotonic. Monotonic functions were characterized by a regular increase in firing rate with increased intensity. Some monotonic functions

reached a plateau at high sound levels. A nonmonotonic function was one in which the spike-count first increased with intensity and then decreased by 10% or more with further intensity increments. Of the duration-tuned neurons that responded to pure tones, only 33% had a nonmonotonic rate-level function or an upper threshold. This percentage is relatively low compared with that observed in neurons not tuned to duration, more than two thirds (79%) of which had nonmonotonic rate-level functions. Some units (7 of 28, 25%) with nonmonotonic functions failed to respond at high intensities and so had upper thresholds. In the 28 non-duration-tuned neurons tested, 13 (46%) had upper thresholds. Nonmonotonic rate-level functions, with or without upper thresholds, were seen more commonly in duration-tuned units that responded best to FM sweeps (8 of 12 cells) than in duration-tuned units that responded best or exclusively to pure tones (7 of 24 cells). These data indicate that the responsiveness of most duration-tuned neurons is maintained even at high stimulus levels. Thus, for the neurons with monotonic rate-level functions, inhibition appears to limit

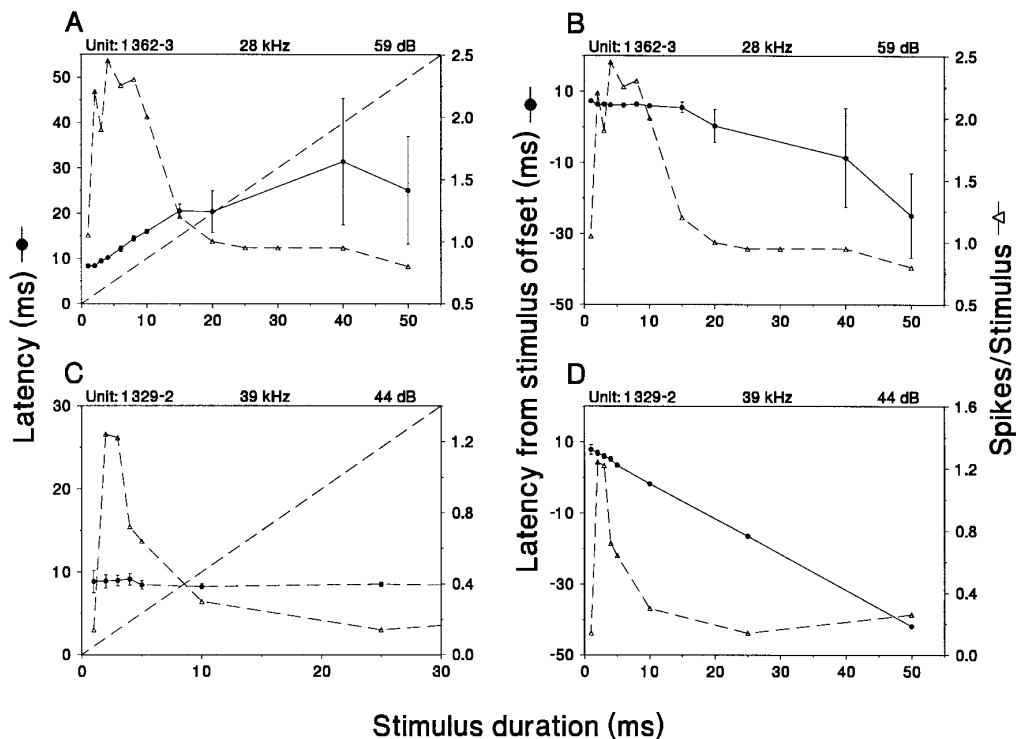


FIG. 10. Examples of neurons whose latency was not consistently correlated with sound duration. *A* and *B*: spike latency of this neuron increased as duration increased and followed the offset of sound until ~ 20 ms. At durations >20 ms, 1st spike occurred before sound offset. *C* and *D*: spike latency of this neuron remained nearly constant regardless of duration; latency from onset was longer than the durations to which it responded best and was always longer than best duration. Conventions as in Fig. 9.

response to sound duration, but it does not appear to limit response over wide changes in sound level. It seems safe to conclude that these neurons are not simply energy detectors. However, further studies, varying intensity at different sound durations, are needed to clearly determine whether sound level alters duration tuning.

DISCUSSION

The creation of duration tuning results in a population of neurons that provide an additional filter besides those for frequency and intensity of sound. The neural computation for sound duration is a transformation from the temporal domain at lower levels in the auditory pathway to a place code in the IC. In other words, at lower levels, sound duration is measured by the "ON time" of neurons whose firing is sustained for the duration of sound, with each neuron responding in the same way to sounds of any duration. However, in the IC, specialized neurons appear that are tuned to sound duration. Because different neurons have different best durations, a place code for sound duration is established.

What is the prevalence of duration-tuned neurons in the vertebrate midbrain? In the present sample of neurons in the IC of *Eptesicus*, over one third were tuned to sound duration. Neurons tuned to sound duration were first found in the auditory midbrain or torus semicircularis of amphibians (Gooler and Feng 1992; Narins and Capranica 1980; Potter 1965). The earliest report of duration tuning in mammalian IC neurons was in the big brown bat (Pinheiro et al. 1991). In the pallid bat, *Antrozous pallidus*, Fuzessery (1994) found

that 58% of neurons tuned to frequencies in echolocation signals were duration tuned, and 20% of neurons tuned to frequencies below those in echolocation signals were duration tuned. The fact that tuning of midbrain neurons to sound duration is found in two species of bats and in more than one vertebrate order suggests that it is a general characteristic of the vertebrate midbrain.

The fact that duration tuning has not been found at lower levels of the auditory system, in either amphibians (Condon et al. 1991; Hall and Feng 1991) or mammals (Casseday and Covey 1995, 1996) suggests that tuning for this temporal parameter of sound is created by mechanisms operating within the vertebrate midbrain. This conclusion is supported by experiments in which duration tuning of IC units was eliminated by antagonists of inhibitory transmitters as well as by intracellular recordings of the time course of inhibition and excitation in a duration-tuned cell (Casseday et al. 1994; Covey et al. 1996).

Location in IC and relation to frequency organization

In the pallid bat, *A. pallidus* (Fuzessery 1994), the percentage of IC neurons that was duration-tuned varied according to frequency range. Duration-tuned neurons constituted 58% of high-frequency (>30 kHz) neurons and 20% of low-frequency (<30 kHz) neurons. This frequency-specific distribution is somewhat different from the distribution in *Eptesicus*, where most (73%) of the duration-tuned neurons had BFs <40 kHz. Despite this expanded representation of low BFs, there were few duration-tuned neurons in the

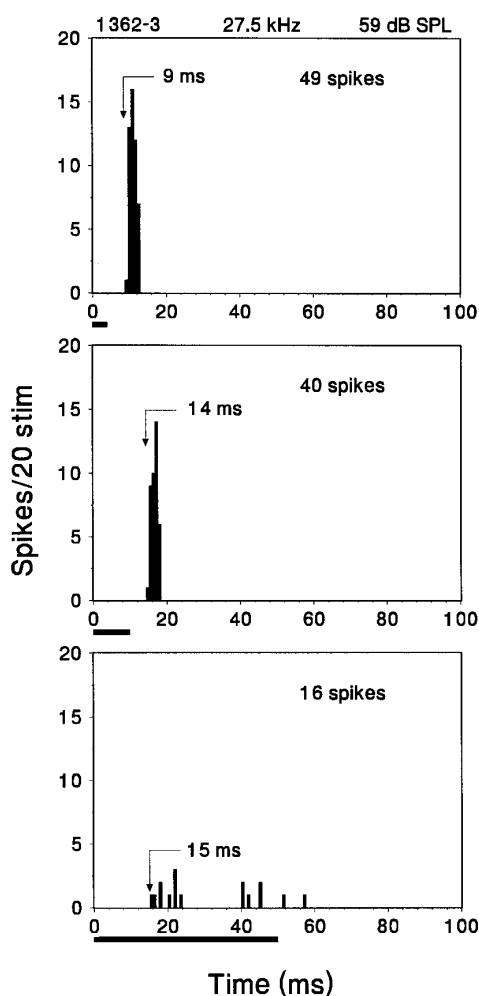


FIG. 11. PSTHs to show latency of spikes to 3 different stimulus durations. At best duration of 4 ms (*top*) the neuron responded with a latency of ~ 9 ms. Arrows: latency of spikes in 1st bin. Bars below X-axis: sound duration. Note the large increase in latency when sound duration was increased from 2 ms (*top*) to 10 ms (*middle*) but little further latency change at 50-ms sound duration (*bottom*). Binwidth = 0.8 ms.

rostral portion of the IC, a region that has a greater proportion of frequencies ≤ 40 kHz than does the caudal part of the IC (Casseday and Covey 1992). The observation that most duration-tuned neurons were located in the posterior part of the IC, together with the fact that the anterior part of the IC contains a high proportion of neurons that are selective for periodic FMs (Casseday and Covey 1995; Casseday et al. 1997), raises the possibility that some functional difference in the processing of temporal features of signals is organized along the anterior-posterior plane.

The frequency-tuning curves, spontaneous activity levels, and rate-intensity functions of duration-tuned neurons are similar to those of other IC neurons. However, unlike other IC neurons, which typically respond at the onset of sound, most duration-tuned neurons appear to respond at the offset of sound, at least over their range of optimal durations.

Model for producing duration tuning

We have proposed a three-component model to explain the creation of duration tuning (Casseday and Covey 1995;

Casseday et al. 1994; Covey et al. 1996). The model is similar to those proposed for duration tuning by Narins and Capranica (1980) and for delay tuning by Suga et al. (1995). The principal difference among the models is that ours adds an inhibitory component that is sustained for the duration of the stimulus. According to this model, the first component is sustained inhibitory input to the neuron [Fig. 13, A and B, Input a (Inh)]. The second component is transient excitation that occurs at the offset of sound (Fig. 13, A and B, Input a (E_{OFF})). Because we cannot distinguish between offset excitation and rebound from inhibition, we simply use the term “offset excitation” to refer to both possibilities. The third component is transient excitation correlated with the onset of the stimulus but delayed in time relative to the onset of the inhibition [Fig. 13, A and B, Input b (E_{ON})]. By themselves, neither of the excitatory components are usually sufficient to elicit a spike. The duration of the first component, sustained inhibition, and the timing of the second component, offset excitation, vary with the duration of the stimulus. However, the timing of the third component does not vary with sound duration, but it does vary from neuron to neuron. When the duration of the sound is such that the delayed onset excitation and the offset excitation coincide, the neuron fires action potentials (Fig. 13A, Output). However, when the duration is longer, the inhibition overlaps with the onset excitation, the offset and onset excitation do not overlap, and a spike is not initiated (Fig. 13B, Output). The inhibitory component is introduced for two reasons. First, it ensures a temporal band-pass filter even at short durations at which onset and offset excitations might summate to produce a short-pass duration filter, i.e., responses to all sound durations below some minimum. Second, we know from intracellular recordings (Covey et al. 1996) and from application of antagonists to γ -aminobutyric acid or glycine (Casseday et al. 1994) that inhibition plays an important role in creating duration tuning. Given the evidence of inhibition, it may turn out that the most parsimonious model will be one in which the offset excitation is a “rebound” from the sustained inhibition, leaving a two-component model. Inhibition may also be necessary to make the tuning “level tolerant,” that is, to prevent spikes to noncoincident excitatory inputs even at high sound levels.

Previous data on duration-tuned neurons in the IC of the pallid bat support the proposal of offset excitation. Fuzessery (1994) found that latencies were always longer than best duration. Moreover, that study also provided indirect evidence for a fast inhibitory pathway that precedes excitatory input.

In unaltered form the model will account for only some of our results. The fact that most duration-tuned neurons responded at the offset of sound at least throughout their range of maximal responsiveness is predicted by the model. In the case of neurons that continued to respond at low levels outside their range of maximal duration tuning, it was often possible to see that latency increased as a function of stimulus duration up to the point at which responsiveness started to decrease, and at longer durations, latency changed very little.

How does the model account for this continued response, even though small, and how does it account for the failure to follow signal offset? In other words, how can we modify

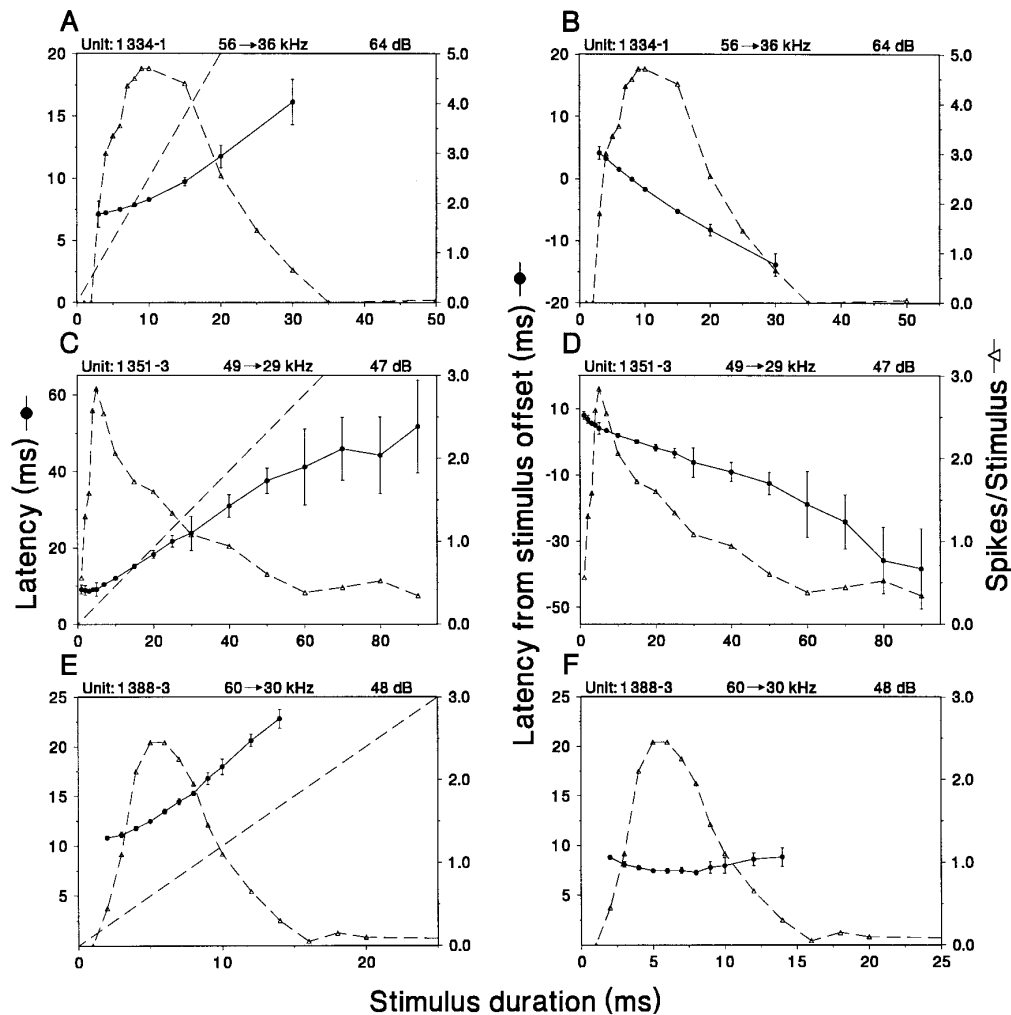


FIG. 12. Three examples of latency measurements as a function of the duration of an FM sweep. For each neuron latency is plotted from FM onset (A, C, and E) and from FM offset (B, D, and F). A and B: latency of this neuron was greater than sweep duration only at the shortest sweep durations, up to ~ 8 ms. C and D: latency of this neuron was greater than sweep duration over the range of durations to which the neuron was most responsive, < 15 ms. E and F: latency of this neuron was always greater than the sweep duration. Data in A–D suggest that these 2 neurons were responsive to the duration of frequency components in the early part of the sweep. Data in E and F suggest that this neuron was responsive either to the duration of frequency components in the last part of the sweep or to overall sweep duration regardless of specific frequency components.

the model to account for the presence of a small remaining onset response? One possibility is to adjust the magnitude of any of the three components in the model: sustained inhibition, offset excitation, or delayed onset excitation. For example, if we assume that the relative contribution of the two excitatory components varies among neurons and that the strongest of these is sufficient to elicit spikes occasionally even when the other excitatory input is not coincident, then the different response patterns can be explained: the neurons in which the second component, offset excitation, is stronger than the delayed onset excitation would have spike latencies correlated with sound offset at all durations. The neurons in which the third component, delayed onset excitation, is stronger than offset excitation would have predominantly an onset pattern because the leading inhibition is insufficient to completely suppress the delayed onset excitatory input. This pattern could also be achieved by reducing the inhibitory component. An intermediate response type in which latency

is correlated with offset near best duration but correlated with onset at longer durations could also be explained. Here, the leading inhibition is strongest at sound onset and gradually decays throughout the duration of a sound. Therefore the leading inhibition would progressively encroach on the first part of the excitatory input, increasing spike latency as sound duration increases. However, as sound duration further increases, the early inhibition would decay to the point that it could not totally suppress spikes, so that for sounds of this duration and longer, the number of spikes would be low, but spike latency would remain constant or would not increase in proportion to sound duration. Of course, in each variation of the model the maximum spike output would still occur when the two excitatory inputs coincide.

Duration tuning was not only observed in cells that responded to pure tones, it was also present in cells that responded exclusively to FM sweeps, as previously reported by Fuzessery (1994). Because a change in the duration of

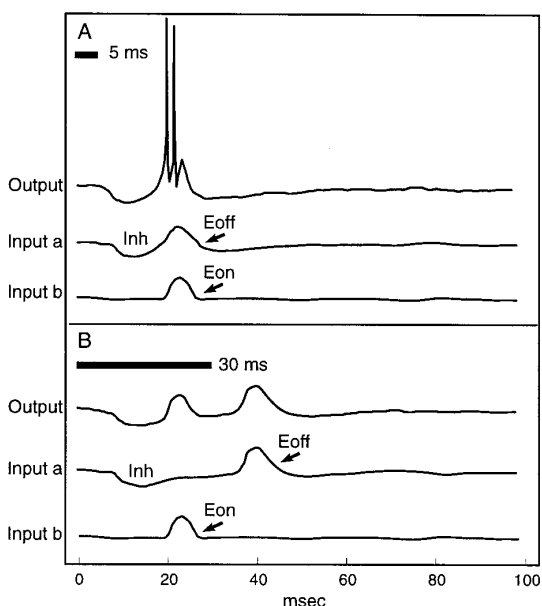


FIG. 13. Model of the mechanism for duration tuning. In this example the neuron responds to a 5-ms tone (A, Output) but does not respond to a 30-ms pulse (B, Output). To create duration tuning, 2 kinds of input are hypothesized to underlie the initiation of a spike (Input a and Input b). Input a has 2 components. The 1st is inhibition that lasts for the duration of the stimulus (Inh). The 2nd is transient excitation that follows the inhibition and is correlated in time with the offset of the stimulus (E_{OFF}). Input b is transient excitation that is correlated in time with the onset of the stimulus but is delayed in time relative to the onset of inhibition (E_{ON}). A: neuron fires because the 2 excitatory events coincide in time. B: neuron does not fire because the 2 excitatory events do not coincide. In this model the inhibitory component of Input a is always sufficient to prevent the excitation of Input b from initiating a spike, and the neuron's latency is always locked to sound offset. If the magnitude of inhibition in Input a was slightly decreased or the magnitude of excitation in Input b was increased, the neuron would become more poorly tuned to duration, and a spike would sometimes occur at durations in which the offset excitation occurs later than the onset excitation.

an FM sweep must necessarily change either the range or the slope of the sweep, there is a problem in characterizing duration tuning for FM cells. Without additional testing, we cannot say for certain whether their response depended on the duration of a specific frequency or frequency band within the sweep, or on the rate of frequency change. In neurons that responded to both pure tones and FM sweeps, the fact that the best durations for FM stimuli were somewhat longer than for pure tones suggests that these neurons were responding to the duration of a frequency band or bands in the FM, and further, that the mechanism for duration tuning to pure tones and FM may be the same. Fuzessery (1994) presented evidence that IC neurons respond to sweep duration independently of sweep depth. However, to fully resolve this question, further experiments are needed in which parameters of the FM are systematically manipulated so that sweep rate is changed while depth is kept constant, and sweep depth is changed while rate is kept constant.

Latency and the question of onset versus offset responses

In this study most units that responded to the offset of sound were also duration tuned, and the latency of nearly all duration-tuned neurons was correlated with the offset of

sound over some range of durations. For some neurons, a systematic analysis of the relation of latency to sound duration revealed a duration at which the neuron's latency stayed constant as duration further increased. These findings reveal a methodological issue in characterizing a neuron as responding to the onset or offset of sound if only a few durations are tested. If the neurons in this study had only been tested with sounds of durations near their best duration, most would have been characterized as offset responders, and the onset component would have been missed. If the same neurons had only been tested with sounds >20 ms, a high proportion would have been characterized as onset responders, and their offset component would have been missed.

Level tolerance

When tested at best duration, duration-tuned neurons were much less likely to have closed tuning curves or nonmonotonic rate-level functions than were neurons not sensitive to sound duration. This observation means that most duration-tuned neurons are capable of responding to both loud and soft sounds, such as the bat's echolocation pulse and an attenuated echo.

Biological importance

Finally, what is the significance of duration tuning for the bat? The finding by Fuzessery (1994) that the distribution of best durations corresponds to the range of call durations used by the pallid bat during different stages of hunting suggests that duration tuning plays an important role in echolocation and foraging behavior. The present results on a different species support this conclusion. *Eptesicus*, like other echolocating bats, uses its longest signals during stages of foraging in which it searches for prey. These signals tend to be very shallow frequency sweeps, called quasi-constant-frequency signals to distinguish them from the pure constant-frequency signals that some bats emit (Schnitzler et al. 1987). The longest best durations were found in cells with BFs in the range of 20–30 kHz. The quasi-constant-frequency calls last up to 20 ms and contain frequencies within the 20- to 30-kHz range. Bats use short signals as they approach and capture prey (Griffin 1958; Schnitzler et al. 1987; Simmons 1989). Neurons tuned to durations of ~ 20 ms may provide temporal filters for these sounds. Of course, duration tuning would be useful for hearing sounds other than echolocation sounds or their echoes. The few neurons that were tuned to longer-duration sounds might be specialized to respond to communication sounds, which may have longer durations than echolocation sounds (Gould 1971; Kanwal et al. 1994).

The finding of a large range of latencies at each best duration could have special significance for processing at higher levels. For sounds at any given duration, the population of duration-tuned neurons will fire over a span of several milliseconds. Therefore the targets of these neurons will receive a series of inputs with short, intermediate, and long delays, possibly providing timing information for another coincidence mechanism based on some other sound parameter (Dear et al. 1993). We have argued elsewhere that this kind of delay line could be the basis for auditory depth

perception (Casseday and Covey 1996). Echoes from one pulse, reflected from a target or targets at the same distance, would all have the same delay. However, echoes returning from multiple targets at different distances would have multiple delays. If at a higher level short-latency neurons converge with long-latency neurons, then there is a possibility for coincidence detection of similar-duration echoes from different distance targets. Another possibility is that these neurons serve some streaming purpose (Bregman 1990). The output of a set of duration-tuned cells with similar best durations but different latencies could perceptually connect the echoes from one pulse to the echoes from the next. That is, long-latency activation by the echoes from one pulse would coincide in neural time with short-latency activation by echoes from the next pulse. By coincidence at a higher level, this delay mechanism could provide temporal stability in the reflections from a single target. The time limit of the integrated stream—perhaps corresponding to the perception of one target—would be determined by the range of latencies. The longer the spread of latencies, the greater the number of sequential echoes that could be connected into one perceptual stream. This sort of temporal stability could provide the perception of a single target that in turn may be necessary for the bat to have a continuous image of its prey.

We thank B. Fubara and C. O'Connor for technical assistance and two anonymous reviewers for useful comments.

This research was supported by National Institute of Deafness and Other Communications Disorders Grants DC-00287 and DC-00607 and National Science Foundation Grant IBN-9210299.

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Received 19 March 1996; accepted in final form 18 January 1997.

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