Duration Selectivity of Neurons in the Inferior Colliculus of the Big Brown Bat: Tolerance to Changes in Sound Level

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Abstract

Duration selectivity of neurons in the inferior colliculus of the big brown bat: tolerance to changes in sound level. J Neurophysiol 94: 1869–1878, 2005. First published May 11, 2005; doi:10.1152/jn.00253.2005. At and above the level of the inferior colliculus (IC), some neurons respond maximally to a limited range of sound durations, with little or no excitatory response to durations outside of this range. Such neurons have been termed “duration tuned” or “duration selective.” In this study we examined the effects of varying signal amplitude on best duration, width of tuning, and first spike latency of duration tuned neurons in the IC of the big brown bat, Eptesicus fuscus. Response areas as a function of stimulus duration and intensity took a variety of forms, including open (V-shaped), narrow and level tolerant (U-shaped), or closed (O-shaped). The majority (82%) of duration tuned neurons had narrow U-shaped or O-shaped duration response areas. Those with narrow U-shaped response areas retained their duration tuning across a broad dynamic range, ≤50 dB above threshold, whereas those with O-shaped response areas were narrowly tuned to both stimulus duration and amplitude. For about one-half (55%) of the neurons with either a U- or O-shaped response areas, best duration (BD) changed by <1 ms across the range of suprathreshold amplitudes tested. Changes in BD most often took the form of a shift to slightly shorter durations as stimulus level increased. For the majority (65%) of U- and O-shaped neurons, 50% width of duration tuning changed by <2 ms with increasing amplitude. Latency of response at BD remained stable across changes in sound level, suggesting that the relative strengths of excitatory and inhibitory inputs to duration tuned neurons remain in balance over a wide dynamic range of sound pressure levels.

INTRODUCTION

The detection and analysis of temporal patterns of sound is crucial for a wide range of behaviors including communication, prey detection, and predator avoidance. It is therefore not surprising that the representation and analysis of temporal parameters is a fundamental property of auditory systems (e.g., Barlow and Mollon 1982; Covey et al. 1995; Faure and Hoy 2000; Roverud 1999; Schildberger 1985). Important auditory temporal parameters include the sequence of elements in a complex acoustic signal, the interval between sounds, and the duration of a sound. Although duration is a relatively simple acoustic feature, it is also one of the most salient. For example, signal duration is important for the discrimination of sounds as diverse as frog mating calls (Narins and Capranica 1980; Potter 1965) and human speech (Shannon et al. 1995). Echolocating bats emit sounds of different durations depending on behavioral context and continuously adjust the duration of their biosonar calls as they approach a target (Griffin 1958; Kalko and Schnitzler 1989; Simmons et al. 1979; Surlykke and Moss 2000).

Throughout the different levels of the vertebrate central auditory system, sound duration is represented in different ways. Below the level of the midbrain, all auditory neurons respond to sounds of any duration provided that the stimulus falls within the excitatory frequency response area of the cell. Neurons with sustained responses fire action potentials throughout the duration of a sound and provide a real-time representation of signal duration. Neurons with transient responses fire only in response to the onset and/or offset of a sound (Covey et al. 1991; Grothe et al. 2001; Rhode and Smith 1986; see also Rhode and Greenberg 1992), and thereby provide the CNS with time markers that can be used by other neurons to compute signal duration (Casseday et al. 1994; Grothe et al. 2001) and other temporal features (Casseday et al. 1997). Regardless of whether a neuron responds in a sustained or transient fashion, it responds with the same general spiking pattern for all sound durations. Thus below the auditory midbrain, it seems that specific neurons do not represent specific sound durations. Instead, signal duration is represented in the ongoing temporal pattern of neuronal firing: sustained firing for the duration of the sound and/or transient firing marking the onset, and in some cases the offset, of sounds.

At and above the level of the midbrain, however, some neurons respond preferentially to sounds within a specific range of signal durations and show little or no excitatory response to sounds of shorter and/or longer duration. Cells with these characteristics have been termed “duration tuned” or “duration selective.” Duration selective auditory neurons were first reported in the midbrain of frogs (Feng et al. 1990; Narins and Capranica 1980; Potter 1965) and have subsequently been found in the inferior colliculus (IC) of several species of bats (Casseday et al. 1994; Ehrlich et al. 1997; Fuzessery and Hall 1999; Mora and Kössl 2004; Pinheiro et al. 1991), chinchillas (Chen 1998), and mice (Brand et al. 2000), as well as in the auditory cortex of cats (He et al. 1997) and bats (Galazyuk and Feng 1997). Moreover, duration tuning may be a general feature of sensory processing (Faure et al. 2003), given that neurons tuned to sounds of any duration can represent temporal patterns in a variety of ways. Below the level of the midbrain, all auditory neurons respond to sounds of any duration provided that the stimulus falls within the excitatory frequency response area of the cell. Neurons with sustained responses fire action potentials throughout the duration of a sound and provide a real-time representation of signal duration. Neurons with transient responses fire only in response to the onset and/or offset of a sound (Covey et al. 1991; Grothe et al. 2001; Rhode and Smith 1986; see also Rhode and Greenberg 1992), and thereby provide the CNS with time markers that can be used by other neurons to compute signal duration (Casseday et al. 1994; Grothe et al. 2001) and other temporal features (Casseday et al. 1997). Regardless of whether a neuron responds in a sustained or transient fashion, it responds with the same general spiking pattern for all sound durations. Thus below the auditory midbrain, it seems that specific neurons do not represent specific sound durations. Instead, signal duration is represented in the ongoing temporal pattern of neuronal firing: sustained firing for the duration of the sound and/or transient firing marking the onset, and in some cases the offset, of sounds.

In the auditory system, duration selectivity seems to be a sensory filter property that emerges at the IC (see Casseday et al. 1994, 2000; Covey et al. 1996), and constitutes “tuning” in...
the same sense that neurons are tuned to stimulus frequency. For most neurons at all levels of the auditory system, frequency tuning broadens as sound amplitude is increased. However, some specialized neurons are tolerant to changes in sound level, maintaining a constant tuning bandwidth across a wide dynamic range (Casseday and Covey 1992; Ehret and Schreiner 2005; Suga 1969); others have upper thresholds and are amplitude tuned, responding only to a narrow range of sound levels (Casseday and Covey 1992; Ehret and Schreiner 2005). Therefore in this study, we examined duration tuning to determine the extent to which best duration and width of duration tuning remained tolerant to changes in sound level.

Echolocating bats presumably determine the distance or range to an object by measuring the time between the emission of their outgoing call and the returning echo. Although an echo’s duration will generally be the same as that of the original sound, the amplitude of the echo will be greatly attenuated compared with the original sound, which is often >100 dB SPL (Griffin 1971; Lawrence and Simmons 1982). Echo target ranging also makes requirements on neural latency. For most auditory neurons, response latency changes as a function of stimulus amplitude, typically decreasing with increased sound level, although some neurons that are greatly influenced by inhibition show “paradoxical latency shift,” in which latency increases with increasing sound level (Covey et al. 1996; Galazyuk and Feng 2001; Sullivan 1982a). Because inhibition also plays a major role in shaping the response properties of duration tuned neurons (Casseday et al. 1994; Faure et al. 2003), we examined the effects of stimulus amplitude on first spike latency for a given duration to see whether there was evidence of amplitude-related latency changes such as paradoxical latency shift or not. If there were not amplitude-related latency changes (i.e., latency remained constant across amplitude), this would mean that duration tuned neurons could provide precise and unambiguous timing information about the delay between a call and its echo, which could be relayed to other levels of the auditory system that contain neurons tuned to the interval between two sounds (Dear et al. 1993).

METHODS

All experiments and procedures were conducted at the University of Washington and were approved by the University’s Laboratory Animal Care and Use Committee.

Animals

Extracellular single unit recordings were obtained from 19 big brown bats (Eptesicus fuscus) of both sexes from a captive breeding colony. Before surgery, bats were housed in an outdoor husbandry facility in which lighting and temperature corresponded to ambient conditions. When necessary, supplemental heat was used to maintain the colony temperature above 3°C in the winter and above 21°C in the summer. Experimental bats were brought into the laboratory 1–3 days before surgical and recording procedures to allow them to acclimate to conditions of constant indoor temperature and were housed individually or with one to two other bats. Water and food were available ad libitum.

Surgical procedures

One to 4 days before the first recording session, a metal post was attached to the skull to immobilize the head during electrophysiological recording. The bat was anesthetized with a combination of methoxyflurane inhalation (1–5 min) and a subcutaneous injection of a neuroleptic (0.1–0.3 ml of a 1:1 mixture of fentanyl citrate 0.025 mg/ml + droperidol 1.25 mg/ml). The anesthetized bat was placed in a foam-lined restraint molded to the shape of its body to hold it firmly but comfortably while allowing access to the head. The bat’s mouth was placed in a custom bite bar attached to manipulators that allowed for precise adjustments of the animal’s head position in three dimensions. The hair overlying the skull was cropped, and the skin was swabbed with Betadine surgical scrub. Local anesthetic (0.05 ml of 2% lidocaine) was administered before making a midline incision in the scalp. The temporal muscles were reflected, and the skull was scraped clean of tissue and swabbed with 100% ethanol. The post was glued to the skull with cyanoacrylate gel adhesive. Recording began 1–4 days after surgery.

Acoustic stimuli

Sound pulses were digitally synthesized under custom software control using a digital signal processor [Tucker Davis Technologies (TDT)] at a sampling rate of 357 kHz interfaced to a D/A converter (DA3-2, TDT). The output of the D/A was fed through a low-pass anti-aliasing filter (FT5; f_c = 120 kHz; TDT), and two programmable attenuators (PA4, TDT) in series before final amplification (model 7500, Krohn-Hite). All stimuli were presented monaurally, contralateral to the IC from which we recorded, through a Bruel & Kjær type 4135 ¼-in condenser microphone modified for use as a loudspeaker with a circuit to correct for nonlinearities in the transfer function (Frederiksen 1977). The transducer was positioned with its diaphragm ~1 mm from the external auditory meatus. The output of the loudspeaker, calibrated with a B&K ¼-in condenser microphone, was flat ±5 dB from 26 to 118 kHz. Over the range of frequencies used in this study, attenuation between the two ears was ±30 dB. All signals had rise/fall times of 0.4 ms shaped with a cosine squared function. Stimuli were presented at a repetition rate of 3/s.

Neural recordings

Neural recordings from awake bats were conducted in a double-walled sound-attenuating chamber (Industrial Acoustics). Approximately 30 min before recording, each bat was tranquilized with 0.1–0.3 ml of neuroleptic (see Surgical procedures). The bat was placed in a foam-lined body holder suspended in an elastic sling attached to a stereotaxic frame. The head post was clamped to the arm of a micromanipulator (Kopf) that was attached to the stereotaxic frame. On the first daily session, a small opening was made in the skull and in the dura mater overlying the IC. Each bat was used in one to six recording sessions, with each session lasting ~6 h/day. Experiments were terminated if the bat showed any signs of discomfort. Between sessions, the opening in the skull was covered with Gelfoam (Pharmacia & Upjohn) and Neosporin (Pfizer, Morris Plains, NJ). Single unit extracellular recordings were obtained with thin-wall borosilicate glass micropipette electrodes pulled to a tip diameter of ~1.0 μm and filled with 0.15–0.5 M NaCl. Electrode impedances ranged from 8 to 50 MΩ. Micropipettes were visually aimed at the IC and advanced with a hydraulic microwire (Kopf model 650). Action potentials were amplified (model 1600, A-M Systems) and band-pass filtered (high-pass f_c = 700 Hz, low-pass f_c = 3 kHz; PC1, TDT) before passing through a spike discriminator (SD1, TDT). Spike times were collected on a computer using an event timer (ET1, TDT) and visualized on-line as dot rasters using custom software. Data were collected only when the signal-to-noise ratio was ≥4:1 (S/N ratios were typically ≥8:1).

Duration tuning and filter characteristics

Search signals consisted of variable duration pure tones or FM sweeps (bandwidth, 5–20 kHz). When a cell was isolated, we deter-
mined its approximate frequency tuning. If the cell’s responses appeared to be duration selective at 10–20 dB above threshold, we collected data by presenting blocks of 10–20 tone pulses at best excitatory frequency (BEF), with duration randomly varied and amplitude held constant. This procedure was repeated in 10 dB steps ≤50 dB above threshold. The usual range of test duration was 1–25 ms.

A neuron was classified as duration tuned if the average spike count of the cell decreased to ≤50% of the maximum spike count at stimulus durations, both longer and shorter than the peak spike count, or only at durations longer than the peak spike count. These criteria have been used previously to describe band-pass and short-pass duration tuned neurons (Casseday et al. 1994, 2000; Ehrlich et al. 1997; Faure et al. 2003).

We calculated best duration (BD) and width of duration tuning as follows. The BD was defined as the mid-point between the longer and shorter values on the duration tuning curve at 90% of the peak spike count. The 50% width was defined as the difference between the longer and shorter values on the duration tuning curve at 50% of the peak spike count. If a neuron’s response did not fall to <50% of maximum spike count at 1 ms, the shortest duration we tested, we extrapolated the spike count function to zero at a duration of 0 ms to calculate 50% width.

Neural inhibition is a critical component of the underlying mechanism that creates duration selectivity (Casseday et al. 1994, 2000; Covey et al. 1996; Faure et al. 2003). Therefore it was of interest to determine whether duration tuned neurons possessed other response properties that might be attributed to inhibition. Nonmonotonic rate-level functions and upper thresholds are likely caused by inhibition. Rate-level functions were classified based on responses at BEF and BD, and nonmonotonicity was defined as an initial increase in spike count followed by a ≥25% decrease in spike count. Because early inhibition can cause the latency of some IC neurons to lengthen as sound level increases (Covey et al. 1996; Galazyuk and Feng 2001), we measured first spike latencies at each amplitude tested. Spike latencies are reported with respect to stimulus onset. All statistical tests employed a critical value of α ≤ 0.05 (Zar 1984).

R E S U L T S

General response characteristics

We recorded from 49 duration tuned neurons. BDs ranged from 1 to 8 ms, BEFs from 14 to 64 kHz, and thresholds at BEF from 8 to 66 dB SPL. All duration tuned neurons had transient excitatory discharge patterns. The first spike latency of 39 cells (80%) tested at 10 dB above threshold was correlated with sound offset over the range of durations to which the cell responded. The first spike latency of four cells (8%) was correlated with sound onset. Three cells (6%) had two transient responses, the first correlated with sound onset and the second with sound offset, and three (6%) could not be classified because they responded to only a single test duration. In all cases, first spike latency was greater than BD (see also Faure et al. 2003). When tested with pure tones at BD, 25 neurons (51%) had nonmonotonic rate-level functions.

The majority of neurons (40/49, 82%) remained duration tuned across all sound pressure levels tested. Figure 1, A–H, shows examples of typical duration-intensity response areas. A

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**FIG. 1.** Examples of typical duration response areas showing duration tuning across sound level. Sound duration is on the x-axis, sound level relative to threshold is on the y-axis, and spike count per stimulus is indicated by the color scale varying from dark blue (lowest) to red (highest).
few neurons that were duration tuned near threshold lost or drastically changed their tuning as stimulus amplitude was increased, resulting in V-shaped duration response areas (9/49, 18%; Fig. 1H). In no case did a neuron that lost its duration selectivity regain it at higher sound levels. For most neurons, best duration and breadth of tuning remained relatively stable across amplitude, although there were often subtle changes in the shape of the duration response area. Some of the neurons with nonmonotonic rate-intensity functions had upper intensity thresholds (Fig. 1, B and E), so that the duration response areas did not extend into the highest sound levels.

One neuron (Fig. 1I) was unusual in that it had a secondary peak at the highest intensities tested (see also Mora and Kössl 2004). At 10 dB above threshold, its BD was 3 ms, changing to 1 ms at 20 dB above threshold and higher. At >30 dB above threshold, a small weaker second peak appeared at about 6–7 ms.

Twenty neurons did not respond to a 1-ms stimulus at threshold, but at some higher sound level, their response areas broadened to include 1 ms (Fig. 1, D–G and I). As a consequence of this broadening, the tuning of some neurons appeared to be band-pass at sound levels near threshold and short-pass at higher levels. The maximal firing rate sometimes shifted slightly to shorter durations as sound level increased (Fig. 1, B–E and I). The shift to shorter durations was sometimes accompanied by a reduced response to longer durations (Fig. 1, B and I). These observations point to the arbitrary nature of using classification labels such as “short-pass” and “band-pass” to distinguish filter characteristics for duration tuning.

Figure 2 shows that, although there was a small but systematic increase in the number of neurons that lost duration tuning at higher sound levels, the majority of cells remained duration tuned even ≤50 dB above threshold.

**Effect of sound level on BD**

Figure 3 shows the mean and median BD for the population tested at each sound level. Both mean and median BD decreased slightly as sound level increased, but the changes were not statistically significant (Fig. 3, paired t-test; all P > 0.9). Thus for the population of neurons, BD remained relatively stable across a large dynamic range of sound levels.

Figure 4 compares BD at 10 dB above threshold with BD at higher sound levels for all individual neurons. At all sound levels, more neurons were below the diagonal than above, i.e., BD decreased with increasing sound level for more than one-half the neurons. However, the proportion of neurons below the diagonal was statistically significant only at 50 dB above threshold (χ²: P < 0.04). Although there were some outliers, the majority of neurons (59–81%, depending on level) were within 1 ms of the diagonal. That is, the change in BD was typically less than the increment by which we varied stimulus duration (1-ms steps). The main exception was a small group of neurons that had BDs of 2–3 ms at 10 dB above threshold, but for which BD decreased to about 1 ms at higher sound levels.

From the examples in Fig. 1, B and E, it seems that neurons with nonmonotonic rate-level functions had a shift of BD to shorter values with increasing sound level. However, from Fig. 4, it can be seen that neurons with monotonic and nonmonotonic rate level functions differed little in this regard, with the BD of many monotonic neurons shifting to shorter values as well.

**Effect of sound level on 50% width of duration tuning**

It is obvious from Fig. 1 that the width of the duration function sometimes changed with increasing sound level. Figure 5 shows the median and mean 50% width of duration tuning at each sound level. Median 50% width increased by no more than 0.5 ms at any sound level; mean 50% width increased by 0.6 ms to 1.8 ms across levels. The mean increase in 50% width was significant at all levels (paired t-test: all P < 0.03) except at 50 dB (P < 0.1). These increases are small and
are on the order of, or only slightly greater than, the time
resolution at which stimulus duration was varied (1-ms steps).
The increase in mean 50% width was driven largely by one to
two outliers with large (>8 ms) increases in 50% width (see
Figs. 5 and 6), plus the fact that neurons with upper thresholds
and closed duration tuning response areas dropped out of our
sample at higher sound levels. There seems to be no major
difference between neurons with monotonic and nonmonotonic
rate-level functions (Fig. 6) with regard to the effect of sound
level on width of duration tuning.

Effect of sound level on first spike latency

Paradoxical latency shift, an increase in first spike latency
with increasing stimulus amplitude, has been seen in auditory
neurons of the cortex (Sullivan 1982a,b) and IC (Covey et al.
1996; Galazyuk and Feng 2001). Paradoxical latency shift
occurs when 1) a neuron receives an inhibitory input with a
latency that is equal to or shorter than the latency of its
excitatory input and 2) the strength of inhibition increases more
than the strength of excitation as stimulus amplitude is in-
creased (Galazyuk and Feng 2001). The first property is a
characteristic of duration tuned neurons (Casseday et al. 1994,
2000; Faure et al. 2003). If duration tuned neurons also
possessed the second property, they would be expected to show
consistent increases in first spike latency with increasing sound
level at any given duration. Figure 7 shows that first spike
latency of duration tuned neurons remained relatively stable
with increasing stimulus amplitude. There was no significant
difference between mean first spike latency at 10 dB above
threshold and mean first spike latency at higher sound levels
(paired t-test, all \( P < 0.1 \)). Therefore as a group, duration tuned
neurons showed neither an increase nor a decrease in spike
latency with increasing sound level, and no evidence of para-
doxical latency shift.

DISCUSSION

Our results showed that most duration tuned neurons in the
IC of the big brown bat remained tuned to sound duration
across dynamic ranges in sound pressure level as large as 50
dB. The stability of duration tuning was seen in a neuron’s BD,
50% width of duration tuning, and first spike latency. For
example, as sound level increased, BD changed by no more
than 0.5 ms for the majority of neurons. In other words, IC
neurons that encode sound duration do so reliably and rela-
tively unambiguously throughout a wide range of stimulus
amplitude. Thus duration selectivity can be thought of as a
sensory filter property in the same sense as frequency tuning.

Duration tuning compared with frequency tuning.

When considering these results, it is useful to make a
comparison with the most ubiquitous type of tuning in the
auditory system: frequency tuning. Auditory nerve fibers have
V-shaped frequency response areas: as sound level increases,
the range of frequencies eliciting a response also increases. At
higher levels of the central auditory system, more specialized
types of frequency response curves also appear. For example,
subpopulations of neurons in the dorsal cochlear nucleus, IC,
and auditory cortex of mammals have specialized frequency
tuning characteristics: some neurons stop responding entirely

**FIG. 4.** Relation between BD at 10 dB above threshold and BD at (A) 20, (B) 30, (C) 40, and (D) 50 dB above threshold for duration tuned neurons with monotonic (●) and nonmonotonic (△) rate-level functions. Solid line, 1:1 line; gray lines, ±1 ms of 1:1 line.

**FIG. 5.** Relation between 50% width of duration tuning and sound level relative to threshold. Box extends from 25th to 75th percentiles. Bars above and below box, 10th and 90th percentiles; dotted line, mean with offset error bars indicating ±SE; solid line, median; dots, individual data points. Mean 50% width was significantly greater at 20, 30, and 40 dB above threshold than at 10 dB above threshold (all \( P < 0.03 \)), and there was a trend at 50 dB above threshold \( (P < 0.1) \).

\[ \text{AMPLITUDE TOLERANCE OF DURATION TUNING} \]

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at high sound levels and have closed or O-shaped frequency response areas. Other neurons have level tolerant or U-shaped frequency response areas in which the width of tuning remains relatively unchanged as sound level increases (e.g., Casseday and Covey 1992; Ehret and Schreiner 1997; Spirou and Young 1991; Suga and Tsuzuki 1985; Sutter 2000). Because the balance between excitation and inhibition may change as a function of duration (e.g., Covey et al. 1996), it does not necessarily follow that a neuron that has an O-shaped frequency response area for tones at one duration would maintain it across all of the durations to which it responds. For example, a neuron with a tilted duration-response area might appear to have an O-shaped frequency response area if only one duration were tested. In this study, we found that most duration selective neurons have duration response areas that resemble the more specialized classes of frequency tuning (i.e., O-shaped or U-shaped): only 18% of duration tuned neurons had V-shaped duration response areas and were not level tolerant. Thus there appears to be a subpopulation of neurons that are level tolerant for duration as there are for frequency. Given these results and that duration sensitive neurons make up about one-third of all IC neurons in the big brown bat (Ehrlich et al. 1997), it seems that >25% of IC neurons are both duration sensitive and level tuned or level tolerant.

Level tolerant response areas may be an important neural mechanism underlying a hallmark feature of much auditory perception: its robust independence of sound level, at least over biologically relevant ranges (Comalli and Altshuler 1976; Seaton 1979; see also Eggermont 2001). For example, our own experience tells us that a sentence can generally be understood regardless of whether it is shouted or whispered, and that a familiar song is usually recognized whether its volume is high or low. Suga and Tsuzuki 1985 proposed that level-tolerant response curves are one neural mechanism by which intensity independent auditory perception can arise (see also Ehret and Merzenich 1985; Suga 1997). Consistent with this idea, there

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**FIG. 6.** Relation between 50% width of duration tuning at 10 dB above threshold and 50% width of duration tuning at (A) 20, (B) 30, (C) 40, and (D) 50 dB above threshold for duration tuned neurons with monotonic (●) and nonmonotonic (△) rate-level functions. Sold line, 1:1 line.

**FIG. 7.** Relation between mean first spike latency for a BD tone at 10 dB above threshold and first spike latency for a BD tone at (A) 20, (B) 30, (C) 40, and (D) 50 dB above threshold. Sold line, 1:1 line. Sample size decreased by 1 or 2 neurons compared with the corresponding panels in Figs. 3 and 5 because we did not have latency measures for 2 cells.
seems to be a strong relation between level-tolerant frequency-response curves and critical band perception (Ehret and Merzenich 1985; Ehret and Schreiner 1997, 2005; although see Eggermont 2001). Level-tolerant duration selective neurons may play a similar role in auditory perception.

The finding of duration selective cells with closed (O-shaped) duration response areas indicates that a subpopulation of duration tuned neurons are specialized to respond to signals of specific amplitudes. For echolocating bats, this specialization could be important for orientation and hunting. The echoes returning to a bat's ear are greatly attenuated relative to the emitted vocalization. This is because the amplitude of the echo varies with target size relative to the signal wavelength used to ensonify the target and with the propagation distance from the bat to the target and back (Lawrence and Simmons 1982). Neurons that are tuned to both stimulus duration and amplitude could provide a means to segregate calls and echoes into different processing streams and allow comparison of pulses and echoes of the same duration (Casseday et al. 2005). This hypothesis is bolstered by the fact that duration selective neurons appear to be more concentrated within a frequency range that corresponds to the lower frequency end of the echolocation calls: 20–30 kHz in Eptesicus (Faure et al. 2003) and 30–40 kHz in Molossus (Mora and Kössl 2004). In Eptesicus, this range corresponds to the frequencies of the “quasi-CF” calls used when searching for prey, and occupies an expanded representation in the IC (Casseday and Covey 1992; Faure et al. 2003).

Comparison with other studies

Zhou and Jen (2001) examined the responses of duration selective neurons in Eptesicus across a wide range of sound intensities (≤50 dB above threshold); however, their study did not report whether there were changes in BD or first spike latency as a function of sound level. Insofar as comparisons can be made, their results seem consistent with ours. Their Table 1 suggests that the majority of neurons with short-pass and band-pass filter characteristics for sound duration at 10 dB above threshold remained duration selective with progressive increases in sound level, and their Table 3 suggests that width of duration tuning did not increase markedly in the majority of short-pass and band-pass neurons examined.

It is less clear if our results are consistent with those found by Mora and Kössl (2004), who examined the stability of duration tuning across a wide range of amplitudes, ≤90 dB SPL, in a bat species from a different family (family Molossidae, Molossus molossus). Mora and Kössl (2004) found that of the 36 duration tuned neurons that were tested over multiple stimulus intensities, only 9 (25%) retained their duration function characteristic across stimulus intensity. However, they did not differentiate between neurons that completely lost duration tuning and neurons that remained duration selective, but changed filter type (i.e., from band-pass to short-pass etc.). We found few duration selective neurons that completely lost their selectivity (9/49, 18%) but many that changed filter type. For example, in our study, 20 duration selective neurons changed from band-pass to short-pass as stimulus intensity increased. Mora and Kössl (2004) did not report median or mean changes in BD or 50% width. Thus their study and ours have few common measures that would allow us to determine whether duration tuned cells in the IC of Molossus were any less stable in response to changes in stimulus intensity than those in Eptesicus. However, data from some of the individual neurons presented in their data set suggest that duration selectivity may not be as stable in M. molossus as in E. fuscus. For example, one of their neurons was duration selective at low sound pressures, became unselective at a higher amplitude, and became duration selective again at an even higher SPLs. Another neuron was unselective for duration, became selective at a higher signal amplitude, and became unselective again at an even higher intensity. None of our neurons displayed such drastic changes in selectivity or filter type: if a neuron was unselective at a given amplitude it remained so at all higher amplitudes.

A clear difference between our results and those in Molossus is in the percentage of duration selective neurons that had multiple duration selectivity peaks. Mora and Kössl (2004) found that 30% of their duration selective neurons had double-peaked response areas, whereas we found only one such neuron (see Fig. 1f). This comparison suggests that there are species-specific differences in duration tuning between Molossus and Eptesicus. However, there was a major methodological difference between our study and the study of Mora and Kössl (2004). On isolating a neuron, we tested it for duration selectivity at 10 dB above threshold. If the cell was selective for duration, we tested its selectivity at higher SPLs. If it was not duration selective at 10 dB above threshold, we did not test its selectivity at higher intensities. In contrast, after Mora and Kössl (2004) isolated a neuron, they tested its duration selectivity over a range of intensities regardless of its duration selectivity at 10 dB above threshold. Thus our search strategy selected for neurons that were duration selective at low sound levels, and the search strategy of Mora and Kössl (2004) selected for neurons that were duration selective at any sound level. It is possible that there are multiple populations of duration selective neurons and that they differ depending on whether or not a neuron is duration selective at low sound levels.

Duration tuned neurons have also been found in the IC of nonecholocating mammals, including rodents and chinchillas (Brand et al. 2000; Chen 1998). However, in these species, long-pass duration sensitivity is more common than band-pass sensitivity (e.g., Brand et al. 2000), suggesting that tuning to a restricted range of duration may be especially important for echolocation. For example, Brand et al. (2000) found only 13 band-pass duration selective neurons in the IC of the mouse of a total of 107 neurons. Nevertheless, when these authors tested four band-pass neurons across a range of sound amplitudes, the four band-pass neurons retained their duration tuning not only across amplitude, but also for tones of different frequencies, under different binaural conditions, and when stimulated with noise bursts.

In summary, these results, in combination with previous studies, suggest that there is at least a subpopulation of duration selective neurons in various mammalian species whose responses are relatively intensity independent.

Stability of first spike latency

Most duration selective neurons respond at sound offset (Brand et al. 2000; Chen 1998; Ehrlich et al. 1997; Faure et al.
originally proposed a model of duration tuning composed of tuned neurons has a number of implications. The finding of constant latency responses in duration selective neurons is more constant than the latency average remained quite stable as sound level increased, at least over the 50 dB range that we tested. The response latency of duration selective neurons is more constant than the latency response in the IC as a whole, where on average, first spike latency decreases as sound intensity increases (Klug et al. 2000). The finding of constant latency responses in duration tuned neurons has a number of implications.

First, latency stability can provide some insight into the mechanisms that create duration tuning. Casseday et al. (1994) originally proposed a model of duration tuning composed of three synaptic events: 1) a transient, onset-evoked excitatory postsynaptic potential (EPSP); 2) a sustained, onset-evoked inhibitory postsynaptic potential (IPSP) with a latency shorter than or equal to that of the EPSP; and 3) a transient, offset-evoked excitation, possibly the result of rebound from sustained inhibition. According to this model, duration tuned cells fire only when there is overlap between the onset- and offset-evoked excitatory events and do not fire when there is overlap between the IPSP and the onset-evoked EPSP. For some duration selective neurons, particularly those with long pass duration filter characteristics, offset-evoked excitation may not be necessary (Faure et al. 2003). For these neurons, duration tuning is probably created through an initial inhibitory event that precedes excitation (Casseday et al. 1994, 2000; Covey et al. 1996; Faure et al. 2003; Fuzessery and Hall 1999; Mora and Kössl 2004).

The latency stability we observed in band-pass duration tuned neurons suggests that, in the initial part of the response, inhibition and excitation remain in balance as sound level changes. If the inputs were such that inhibition grew at a slower rate than excitation with increases in sound amplitude, first spike latency might decrease; if inhibition grew at a faster rate than excitation, latency might increase, producing paradoxical latency shift. With the exception of a few cells (Fig. 7), neither happened.

The changes in BD and 50% width of duration tuning are likely caused by small changes in the timing or balance between the inhibitory and excitatory events that create duration tuning. However, for most cells, these changes were small, with the most common effect being a shift of BD to shorter durations. This observation suggests that, for these neurons, the latency of the onset-evoked EPSP shortened and/or that it became stronger than the early part of the IPSP with increasing sound level. Nevertheless, the neuron remained duration tuned, indicating that the balance and relative timing of excitation and inhibition changed only slightly. In summary, our results on changing sound level indicate that the onset-evoked IPSP and the onset-evoked EPSP remain in balance as sound level changes, producing a wide dynamic range over which duration tuning remains stable.

Second, latency stability in duration selective neurons suggests that constant latency neurons at earlier levels of the auditory system may contribute to duration selectivity. It further suggests that cells that do not respond with a fairly constant latency are unlikely to be a major source of input to duration selective neurons in the IC. There are several possible sources of constant latency input to the IC from the lower brain stem. These include OC-type onset responders in the ventral cochlear nucleus (e.g., Haplea et al. 1994; Oertel 1999; Rhode and Smith 1986), constant latency onset responders in the columnar division of the ventral nucleus of the lateral lemniscus (VNLLc) (e.g., Covey 1993b; Covey and Casseday 1991, 1995), and onset and/or offset responders in the medial superior olive (MSO) (Grothe et al. 2001; Klug et al. 2000). Other subdivisions of the nuclei of the lateral lemniscus, the dorsal nucleus (DNLL) intermediate nucleus (INLL), and the multi-polar cell division of the ventral nucleus (VNLLm), also contain at least some constant latency neurons in bats, and may provide sustained constant latency inhibition and excitation (Covey 1993a; Covey and Casseday 1991, 1995).

Third, it has been suggested that duration selective neurons in bats may feed into delay lines that converge on other neurons at the thalamus and cortex that show selectivity to more complex patterns of sound, perform auditory stream segregation, and/or compute the distance to a target during echolocation (e.g., Ehrlich et al. 1997; Faure et al. 2003). If the outputs of duration selective neurons are used in delay lines, the finding that they respond with a constant latency rules out one commonly proposed delay mechanism in bats: paradoxical latency shift (e.g., Hattori and Suga 1997; Sullivan 1982b). Instead, delay lines would have to be created by some other means, possibly the large latency differences that exist among different neurons that all have the same best duration (Ehrlich et al. 1997; Faure et al. 2003). Assuming that the emitted call and its echo have the same duration, both sounds would activate the duration selective neurons within the population tuned to that particular duration. This selective pattern of activation within the population of duration tuned neurons could help segregate echolocation signals from other ambient sounds. Because duration tuned neurons also have a wide range of lower and upper amplitude thresholds, those with relatively low sensitivity and high thresholds might fire only to the call, whereas those with high sensitivity and upper thresholds might fire only to the echo. If these neurons converged on a neuron at a higher level that acts as a coincidence detector, they could provide a system for detecting a call and echo of matched duration, separated by a specific delay.

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