Delay-Tuned Neurons in the Inferior Colliculus of the Mustached Bat: Implications for Analyses of Target Distance

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Portfors, Christine V. and Jeffrey J. Wenstrup. Response properties of delay-tuned neurons in the inferior colliculus of the mustached bat: implications for analyses of target distance. J. Neurophysiol. 82: 1326–1338, 1999. We examined response properties of delay-tuned neurons in the central nucleus of the inferior colliculus (ICC) of the mustached bat. In the mustached bat, delay-tuned neurons respond best to the combination of the first-harmonic, frequency-modulated (FM1) sweep in the emitted pulse and a higher harmonic frequency-modulated (FM2, FM3 or FM4) component in returning echoes and are referred to as FM-FM neurons. We also examined H1-CF2 neurons. H1-CF2 neurons responded to simultaneous presentation of the first harmonic (H1) in the emitted pulse and the second constant frequency (CF2) component in returning echoes. These neurons served as a comparison as they are thought to encode different features of sonar targets than FM-FM neurons. Only 7% of our neurons (14/198) displayed a single excitatory tuning curve. The rest of the neurons (184) displayed complex responses to sounds in two separate frequency bands. The majority (51%, 101) of neurons were facilitated by the combination of specific components in the mustached bat’s vocalizations. Twenty-five percent showed purely inhibitory interactions. The remaining neurons responded to two separate frequencies, without any facilitation or inhibition. FM-FM neurons (69) were facilitated by the FM1 component in the simulated pulse and a higher harmonic FM component in simulated echoes, provided the high-frequency signal was delayed the appropriate amount. The delay producing maximal facilitation (“best delay”) among FM-FM neurons ranged between 0 and 20 ms, corresponding to target distances ≤3.4 m. Sharpness of delay tuning varied among FM-FM neurons with 50% delay widths between 2 and 13 ms. On average, the facilitated responses of FM-FM neurons were 104% greater than the sum of the responses to the two signals alone. In comparing response properties of delay-tuned, FM-FM neurons in the ICC with those in the medial geniculate body (MGB) from other studies, we find that the range of best delays, sharpness of delay tuning and strength of facilitation are similar in the ICC and MGB. This suggests that by the level of the IC, the basic response properties of FM-FM neurons are established, and they do not undergo extensive transformations with ascending auditory pathways.

INTRODUCTION

Analyzing the distance to a target is an important task for many animals. Echolocating bats use the time interval (delay) between their emitted sonar vocalization and a returning echo to obtain target distance information (Simmons 1971, 1973; Simmons et al. 1979). The echolocation calls of most bats contain a brief, frequency-modulated (FM) sweep that is well suited for determining target distance information (Simmons and Stein 1980; Simmons et al. 1979). This information is encoded by neurons tuned to the delay between the FM sweep in the emitted call and the returning FM sweep in an echo (delay-tuned neurons). These delay-tuned neurons occur in the central auditory systems of several species of bats (Myotis lucifugus, Sullivan 1982a,b; Eptesicus fuscus, Dear et al. 1993; Feng et al. 1978; Rhinolophus rouxi, Schuller et al. 1988, 1991; Pteronotus parnellii, O’Neill and Suga 1979; Suga et al. 1979). In this study, we examine the basic response properties of delay-tuned neurons in the central nucleus of the inferior colliculus in the mustached bat to understand the mechanisms underlying their delay tuning.

Delay-tuned neurons in the mustached bat, P. parnellii, differ in one major respect from those in most other bat species studied. In bats like E. fuscus, delay-tuned neurons respond to the same FM harmonic in the simulated pulse and echo (Dear et al. 1993; Feng et al. 1978). However, in the mustached bat, delay-tuned neurons respond to different FM harmonics in the simulated pulse and echo, integrating information from different frequency bands (O’Neill and Suga 1979, 1982; Suga and O’Neill 1979; Suga et al. 1979, 1983). Specifically, they respond well to the combination of frequencies within the first-harmonic FM (FM1) sweep from the emitted sound and frequencies within a higher harmonic FM (FM2, FM3, or FM4) component of the echoes (O’Neill and Suga 1979, 1982; Suga and O’Neill 1979; Suga et al. 1979, 1983). These delay-tuned neurons are called FM-FM due to their responsiveness to the combination of FM sweeps in the sonar call. FM-FM neurons in the mustached bat are an example of a broader class of neurons also found in other vertebrates, called combination-sensitive, that respond to combinations of different frequencies in vocalizations (frogs, Fuzessery and Feng 1983; birds, MARGOLIASH and Fortune 1992; bats, OHLEMIller et al. 1996; SCHULLER et al. 1988, 1991; SUGA 1988; SUGA et al. 1979, 1983, MONKEYS, OLSEN 1994).

In the mustached bat, combination-sensitive neurons are found in the auditory cortex (Fitzpatrick et al. 1993; O’Neill and Suga 1979; SUGA and O’Neill 1979; SUGA et al. 1979, 1983), the medial geniculate body (MGB) (OLSEN and SUGA 1991, 1999) and the ICC (MITTEN and WENSTRUP 1995; O’Neill 1985). We address the question of whether response properties are modified within the ascending auditory pathway. The major focus here is transformations in delay-tuning properties between the ICC and MGB, the main synaptic relay between the auditory midbrain and the auditory cortex. There is some evidence that FM-FM neurons in the MGB have sharper delay tuning and stronger facilitation than FM-FM neurons in the ICC (Yan and Suga 1996). In this
paper, we compare the response properties of a large population of FM-FM neurons in the ICC with response properties of MGB neurons documented in other studies (Olsen and Suga 1991b; Yan and Suga 1996; Wenstrup 1999). We find that most basic response properties of FM-FM neurons related to delay sensitivity are similar in the ICC and MGB.

**METHODS**

**Surgical procedure**

We examined responses of single neurons in the ICC to pure tones in nine mustached bats (*P. parnellii parnellii*) from Jamaica, West Indies. Bats were anesthetized with methoxyflurane (Metofane, Mallinckrodt Veterinary, Mundelein, IL) in combination with sodium pentobarbital (5 mg/kg ip; Nembutal, Abbott Laboratories, North Chicago, IL) and acepromazine (2 mg/kg ip; Med-Tech, Buffalo, NY). The dorsal surface of the inferior colliculus was exposed by reflecting the skin and musculature overlying the skull. A tungsten reference electrode was implanted into the right cerebral cortex and cemented in place. A metal pin was cemented to the skull to secure the bat’s head during physiological recordings. A small hole was cut in the skull (usually <0.5 mm) over the appropriate region of the inferior colliculus. We applied a local anesthetic (lidocaine, Elkins-Sinns, Cherry Hill, NJ) and a topical antibiotic to the edges of the cut tissue and allowed the bat to recover from surgery for 2–3 days before electrophysiological recording. These procedures were approved by the Northeastern Ohio Universities College of Medicine Animal Care and Use Committee.

**Acoustic stimulation and recording procedures**

During physiological recording sessions, the awake bat was placed in a Plexiglas restraining apparatus contained in a heated and humidified acoustic chamber. The acoustic chamber was covered inside with anechoic foam to reduce echoes. Acoustic stimuli were delivered through a speaker (Technics leaf tweeter) placed 10 cm away from the bat and 25° into the sound field contralateral to the inferior colliculus under investigation. A computer running custom-made applications within the Labview environment (National Instruments) controlled the acoustic stimulation and data acquisition. Two arbitrary waveform generators (Wavetek, model 395) produced two different tone burst or frequency modulated sweep stimuli (3- to 30-ms duration, 0.5-ms rise/fall time, 3–4/s). The two sinusoids from the signal generators were shaped with switches (Tucker-Davis Technologies, model SW2), attenuated (Tucker-Davis Technologies, model PA4), added (Tucker-Davis Technologies, model SM3), fed to a power amplifier (Parasound, model HCA-800 II), and then fed to the speaker in the recording chamber.

We recorded single neurons using micropipette electrodes (5–20 MΩ resistance) filled with one of several tracers (dextran-conjugated rhodamine, dextran rhodamine green, biotin dextran amine (Molecular Probes, Eugene, OR) or Fluoro-Gold (Fluorochrome, Engleweed, CO) in 1 M NaCl (or 0.9% physiological saline when using Fluoro-Gold). The action potentials were amplified, filtered (band-pass, 500–6,000 Hz) and fed to a window discriminator (Frederick Haer, model 74–60-3), loudspeaker, and oscilloscope. The pulse output of the window discriminator was digitized at 10 kHz (National Instruments, model NB-MIO-16X) for quantitative data analysis including peri-stimulus time histograms, raster displays, and statistics on the neural responses.

The electrodes were advanced through the hole in the skull into the inferior colliculus by a hydraulic micropositioner (David Kopf Instruments, model 650). We directed the electrode penetrations to record single neurons in tonotopic regions of the ICC representing the higher frequencies of the mustached bat’s audible range (55–120 kHz). For the majority of recording sessions, we set the electrode penetration angle at 15–20° directed lateral to medial.

Most tests were conducted with tone burst stimuli (3- to 30-ms duration, 0.5-ms rise/fall time). When a single neuron was isolated, we obtained its best frequency, threshold and tuning curve audio-visually. We defined best frequency (BF) as the frequency requiring the lowest intensity to elicit stimulus-locked spikes and threshold as the lowest intensity required to elicit one or more spikes from each of five consecutive stimuli. For neurons that were responsive to two frequency bands, we refer to a best high-frequency response and a best low-frequency response.

We then tested the neuron for sensitivity to a combination of two frequencies by presenting both a low- and a high-frequency signal. Sensitivity to delay between the low- and high-frequency signals was assessed by varying the delay in steps of 1 or 2 ms and collecting neural responses to 32 presentations of the stimuli at each delay. The range of delays tested included conditions with the low-frequency signal presented first and the high-frequency signal delayed and also with the high-frequency signal presented first and the low-frequency signal delayed. All delay tests were performed using 3-ms tone bursts with 0.5-ms rise/fall times (total duration of 4 ms). The delay between the low- and high-frequency signals that elicited the greatest response (or the least response in the case of an inhibited combination-sensitive effect) was defined as the neuron’s best delay. By plotting the neural response at each delay, we quantified sharpness of delay tuning by measuring the width of the delay response curve at 50% of the maximal facilitated (or inhibited) response. We then tuned the facilitated or inhibited response. For facilitated neurons, we tuned both the low- and high-frequency sounds. To assess the low frequencies that elicited a facilitated response, the high-frequency signal was held constant, and the low frequencies elicits a facilitating response at various intensities were recorded. Then the low-frequency signal was held constant, and the responses to the high frequencies were tuned across intensities. For inhibited neurons, we determined the range of low frequencies that inhibited the high-frequency response while the high-frequency sound was held constant. For both facilitated and inhibited responses, the sound held constant was typically presented at 10 dB above threshold.

The strength of combination-sensitive facilitation or inhibition was quantified in two ways: as a percent change compared with the sum of the individual responses to the high- and low-frequency signals and as an interaction index that was defined as $(Rc - Rl - Rh)/(Rc + Rl + Rh)$ where $Rc$, $Rl$ and $Rh$ are, respectively, the neuron’s responses to the high- and low-frequency signals. A positive interaction value is referred to as a facilitation index and a negative value an inhibition index. A neuron was classified as facilitated if the facilitation index was $>0.09$, corresponding to an increase in response of 20% above the summed responses to the low- and high-frequency sounds. A neuron was inhibited if the inhibition index was $\leq -0.11$, corresponding to at least a 20% decrease in response from the summed responses to the low- and high-frequency signals. A facilitation index of 1.0 indicates the strongest possible facilitation, whereas an inhibition index of $-1.0$ indicates the strongest inhibition.

At the end of penetrations where we recorded several single neurons, we deposited the tracer that was in the recording electrode. Ionotophoretic deposits using positive current (5–10 μA, 50% duty cycle) usually were made where we documented a delay-tuned neuron and were always in the ICC.

**RESULTS**

In dorsolateral to ventromedial electrode penetrations through the ICC, we recorded 198 single neurons having best high frequencies between 54.0 and 110.0 kHz. Most neurons
were from the tonotopic representations of two frequency bands, 60–63 and 72–89 kHz. Neurons in the tonotopic representation of the 72- to 89-kHz frequency band respond to sounds within the frequency range of the third-harmonic, frequency-modulated (FM3) sweep of the sonar signal (Fig. 1). A major goal of this study was to characterize neurons responding to this frequency band, and thus the majority of neurons recorded had best frequencies between 72 and 89 kHz. The 60- to 63-kHz representation in the ICC comprises the dorsoposterior division, and its neurons respond to frequencies in the range of the second-harmonic, constant-frequency (CF2) component of the mustached bat sonar signal (Fig. 1). Neurons responsive to CF2 signals serve as a comparison to neurons responding to FM3 signals because the two types of neurons are thought to encode different features of sonar targets.

We tested the neurons for tuning to multiple frequency bands and for sensitivity to combinations of signals with different frequencies. Only 7% (14/198) of the neurons had simple frequency-tuning characteristics showing only a single excitatory, V-shaped tuning curve. The rest of the neurons (n = 184) responded to two separate frequency bands, and of these, 151 showed either facilitated or inhibited combination-sensitive responses (as defined in METHODS). Most combination-sensitive neurons were FM-FM or H1-CF. FM-FM neurons responded to the combination of a low-frequency signal within the FM1 frequency band (29–24 kHz) and a signal in a frequency band associated with one of the higher harmonic FM sweeps (e.g., FM3; 89–72 kHz). H1-CF neurons responded to the combination of signals in the first-harmonic (H1) frequency band (31–24 kHz) and a frequency band associated with one of the higher harmonic CF signals e.g., H1-CF2. We recorded a third type of combination-sensitive response (“other” in Fig. 2) that was neither FM-FM nor H1-CF. These neurons responded to signals within the CF2 frequency band in combination with frequencies below (18–22 kHz) the range of the first sonar harmonic.

The majority of ICC neurons we recorded (76%, n = 151) were combination-sensitive. For both FM-FM and H1-CF combination-sensitive responses, facilitated responses (70%) were more common than inhibited responses (30%). Figure 2 summarizes the occurrence of all response types, which are described in detail in the following sections. RESULTS describes the frequency tuning, the frequency interactions, and the temporal properties of the facilitated combination-sensitive neurons, then the same for the inhibited combination-sensitive neurons. Finally, we briefly describe the response properties of another 33 neurons that displayed multiple frequency tuning without any combination-sensitive interaction.

**Facilitated combination-sensitive responses**

**FREQUENCY-TUNING PROPERTIES** Combination-sensitive facilitation was recorded in 69 FM-FM neurons and 32 H1-CF neurons. These two groups were distinguished on the basis of their high-frequency sensitivity (Fig. 3). Figure 3A shows the frequency tuning of an FM-FM neuron. This neuron showed an excitatory tuning curve centered in the FM3 sonar band (BF: 76.0 kHz), and it did not respond to low-frequency signals within the FM1 band at all intensities tested (≤100 dB SPL). However, when a low-frequency signal was presented in combination with the high-frequency signal at BF, the response was facilitated. This facilitated response was similarly tuned in frequency (- - - and ○), with a slight decrease in threshold (31 to 26 dB SPL). Among FM-FM neurons, the average threshold for the high-frequency signal presented individually was 37.8 ± 6.7 (SD) dB SPL. The average threshold for the facilitated high-frequency response was 32.4 ± 7.8 dB SPL, indicating a slight, but not significant, decrease in threshold with facilitation.

Twenty-five percent of facilitated FM-FM neurons showed two separate excitatory tuning curves to single tone bursts (Fig. 3B). Although these neurons were recorded in the tonotopic...
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**Frequency tuning curves** of combination-sensitive neurons. The frequency tuning for the single tone bursts presented alone. Facilitative frequency tuning curves were obtained by fixing the frequency and intensity of one tone burst while varying the frequency and intensity of the other to obtain threshold facilitative responses: A: FM-FM neuron with an excitatory tuning curve centered in the FM3 sonar band (BF: 76.0 kHz), and no excitatory response to signals within the FM1 frequency band. Facilitated high-frequency response was similarly tuned in frequency (−−−− and ○), with a slight decrease in threshold (31 to 26 dB SPL). Facilitating low-frequency stimulus was tuned in frequency with a BF of 29.1 kHz and a threshold of 37.8 ± 6.7 dB SPL. B: this FM-FM neuron showed a tuned excitatory response to signals within the FM3 (BF: 85.5 kHz) and the FM1 (BF: 29.1 kHz) sonar bands. Both facilitated tuning curves were more broadly tuned in frequency, and both decreased in threshold. C: H1-CF2 neuron with BF of 61.7 kHz and a threshold of 6 dB SPL. In combination with a facilitating signal within the H1 sonar band, the facilitated high-frequency tuning curve was similar in frequency and slightly decreased in threshold, ×, amplitude at which the facilitating signal was held constant to generate the facilitated tuning curves.

**Figure 3**

**A**

![Frequency tuning curve for FM-FM neuron](image)

**B**

![Frequency tuning curve for FM-FM neuron](image)

**C**

![Frequency tuning curve for H1-CF2 neuron](image)

**Frequency tuning for the single tone bursts presented alone.** ○ and - - - - - - facilitated tuning curves. Facilitative frequency tuning curves were obtained by fixing the frequency and intensity of one tone burst (×) while varying the frequency and intensity of the other to obtain threshold facilitative responses: A: FM-FM neuron with an excitatory tuning curve centered in the FM3 sonar band (BF: 76.0 kHz), and no excitatory response to signals within the FM1 frequency band. Facilitated high-frequency response was similarly tuned in frequency (−−−− and ○), with a slight decrease in threshold (31 to 26 dB SPL). Facilitating low-frequency stimulus was tuned in frequency with a BF of 29.1 kHz and a threshold of 37.8 ± 6.7 dB SPL. B: this FM-FM neuron showed a tuned excitatory response to signals within the FM3 (BF: 85.5 kHz) and the FM1 (BF: 29.1 kHz) sonar bands. Both facilitated tuning curves were more broadly tuned in frequency, and both decreased in threshold. C: H1-CF2 neuron with BF of 61.7 kHz and a threshold of 6 dB SPL. In combination with a facilitating signal within the H1 sonar band, the facilitated high-frequency tuning curve was similar in frequency and slightly decreased in threshold, ×, amplitude at which the facilitating signal was held constant to generate the facilitated tuning curves.

**Frequency and intensity of one tone burst:** Facilitative frequency tuning curves were obtained by fixing the threshold of 37.5 dB SPL. Low-frequency stimulus was tuned in frequency with a BF of 29.1 kHz and a low-frequency response. Facilitated high-frequency tuning curve was tuned in frequency with a BF of 76.0 kHz, and no excitatory response to signals within the FM1 frequency range, even at high intensities. Facilitating high-frequency response was similarly tuned in frequency (−−−−) while varying the frequency and intensity of the other to obtain threshold facilitative responses. FM-FM neuron showed a tuned excitatory response to signals within the FM3 frequency band (BF: 82.7 kHz) elicited a weak response (Fig. 4 A). A sound within the FM3 frequency band (BF: 85.5 kHz) elicited a weak response (Fig. 4B). Figure 4C, however, shows that the neuron was strongly facilitated by the combination of the two sounds, if the onset of the high-frequency signal was delayed 2 ms from the onset of the low-frequency signal. The facilitation index value for this neuron was 0.73. The magnitude of the facilitation can be seen both from the PST histograms and the facilitation index; this was a strongly facilitated response. The facilitated response was tuned in delay (Fig. 4D), such that there was a maximal response at 2 ms, and the response was reduced at shorter and longer delays. The delay at which the peak facilitation occurred is termed the neuron’s “best delay”. H1-CF neurons also showed tuned responses to delay. The major difference in the two populations was the distribution of best delays (Fig. 5A). FM-FM neurons had best delays ranging from 0 to 20 ms, with the greatest proportion (84%) < 10 ms. In contrast, nearly all (95%) H1-CF neurons had best delays ~ 0 ms. Thus the range of best delays is a distinguishing feature of FM-FM neurons.

**Delay sensitivity.** A characteristic feature of FM-FM and H1-CF neurons is their sensitivity to the timing between the high and low frequency signals. In Fig. 4 the responses of a facilitated FM-FM neuron to single sounds and the combination of a low- and high-frequency sound are shown. The neuron did not respond to the presentation of any low-frequency sounds within the FM1 range, even at high intensities (Fig. 4A). A sound within the FM3 frequency band (BF: 85.5 kHz) elicited a weak response (Fig. 4B). Figure 4C, however, shows that the neuron was strongly facilitated by the combination of the two sounds, if the onset of the high-frequency signal was delayed 2 ms from the onset of the low-frequency signal. The facilitation index value for this neuron was 0.73. The magnitude of the facilitation can be seen both from the PST histograms and the facilitation index; this was a strongly facilitated response. The facilitated response was tuned in delay (Fig. 4D), such that there was a maximal response at 2 ms, and the response was reduced at shorter and longer delays. The delay at which the peak facilitation occurred is termed the neuron’s “best delay”. H1-CF neurons also showed tuned responses to delay. The major difference in the two populations was the distribution of best delays (Fig. 5A). FM-FM neurons had best delays ranging from 0 to 20 ms, with the greatest proportion (84%) < 10 ms. In contrast, nearly all (95%) H1-CF neurons had best delays ~ 0 ms. Thus the range of best delays is a distinguishing feature of FM-FM neurons.

**The sharpness of delay tuning also differed among facilitated neurons.** Delay tuning sharpness was quantified as the width of the delay curve at response rates evoking 50% of the maximum facilitated response (“50% delay width”). Delay widths among FM-FM neurons varied widely, ranging from 2 to 13 ms, with a mean of 6.2 ± 3.8 ms (Fig. 5B). There was no significant correlation between best delay and 50% delay width for FM1-FM3 neurons (r = 0.3, P > 0.05). Although neurons with the sharpest delay tuning had short best delays, variability in delay width at each best delay was high. Like FM-FM neurons, H1-CF2 neurons displayed considerable variability in
Because the best delay of most H1-CF2 neurons was 0 ms, there was no correlation between 50% delay width and best delay ($r = 0.06, P > 0.05$).

In addition to variations in best delay and sharpness of delay tuning, the degree to which inhibition shaped the delay tuning curve for neurons with short (0–6 ms) and long (>4–6 ms) best delays differed. To illustrate the differences in delay tuning between short and long best delay neurons, Fig. 6A shows a neuron with a best delay of 4 ms, and Fig. 6B shows a neuron with a best delay of 10 ms. The delay tuning of the 10 ms best delay neuron (Fig. 6B) is characterized by a strong period of inhibition (100% suppression) that begins ~0-ms delay and continues up to a delay of ~8 ms. In contrast, the short best delay neuron (Fig. 6A) shows only slight inhibition preceding facilitation. The amount of any inhibition following the facilitation peak varied among all delay-tuned neurons and was not a defining characteristic for either short or long best delay neurons. For 39 facilitated FM-FM neurons, we measured the strength of response at 0-ms delay to examine the nature of an inhibitory period preceding the facilitated response. In initially assessing the delay tuning characteristics among FM-FM neurons with a broad range of best delays, it was apparent that most neurons with best delays of ≥6 ms showed a strong period of inhibition before facilitation. This characteristic was used to classify a neuron as having a long best delay. Of 26 neurons with best delays of ≥6 ms, 22 (84.6%) had responses that were suppressed by >20% at 0-ms delay. The responses decreased an average of 74 ± 23%. In contrast, of 13 neurons with short best delays, only 4 neurons showed any inhibition at 0-ms delay. The responses of the four
neurons that were suppressed however, decreased by an average of 64 ± 24%. This suggests that inhibition is involved in creating the facilitated delay tuning of FM-FM neurons with short and long best delays, but that the characteristics of the delay tuning for short and long best delay neurons are different. The delay tuning of long best delay neurons fits a postinhibitory rebound model for facilitation (Casseday et al. 1994).

STRENGTH OF FACILITATION. The strength of the facilitated response indicates the degree of selectivity for preferred delays. The strength of facilitation was measured as the facilitation index (see METHODS) to enable a comparison with previously published data on facilitated, delay-tuned neurons in the ICC and MGB. To be defined as facilitated, the response to the combination of both tone bursts had to be ≥20% (FI = 0.09) greater than the sum of the responses to the high-frequency and the low-frequency signals presented separately. Among the sample of FM-FM neurons, the mean response rate to tone bursts at best high-frequency presented 10 dB above thresholds was 0.51 ± 0.45 spikes/stimulus. The mean response rate to tone bursts at best low frequency was 0.21 ± 0.32 spikes/stimulus, and the mean facilitated response rate was 1.39 ± 0.65 spikes/stimulus. The distribution of facilitation index values (Fig. 7) shows that the majority of values were between 0.1 and 0.5 for FM-FM neurons (average 0.34 ± 0.24), corresponding to an average response increase of 104%.

Strength of facilitation values were slightly higher for H1-CF neurons. The average response rate to signals at best high-frequency was 0.59 ± 0.52 spikes/stimulus for H1-CF neurons. The mean response rate to tone bursts at best low frequency was 0.18 ± 0.23 spikes/stimulus, and the mean facilitated response rate was 1.6 ± 0.84 spikes/stimulus. The average facilitation index of H1-CF neurons was 0.38 ± 0.18, corresponding to a response increase of 122%.

LATENCY AND DELAY-TUNED FACILITATION. Delay-tuned FM-FM neurons showed strong facilitation with a broad range of best delays. A possible mechanism for creating these response properties involves the coincidence of excitatory responses to the low- and high-frequency signals (Suga et al. 1990). This coincidence hypothesis requires that the response to the low-frequency component (simulated pulse) be neurally delayed to coincide with the response to the acoustically delayed higher frequency signal (simulated echo). The timing of the responses to the low- and high-frequency signals is likely reflected in the latencies of response to these signals presented individually. We therefore examined the latencies of FM-FM neurons in response to their best low and high frequencies. The response latencies to best high frequencies ranged from 4 to 12 ms, with a clustering ~7 ms (average latency: 6.6 ± 1.6 ms). Because not all FM-FM neurons showed an excitatory response to low-frequency signals presented alone, we could measure response latencies in only 19 (28%) of the delay-tuned neurons. Among these, latency to low-frequency sounds ranged from 6 to 30 ms (average latency: 12.8 ± 6.3 ms).

The latency-coincidence hypothesis predicts that the difference between the low- and high-frequency response latencies will be equal to the best delay of the FM-FM neuron. The delay-tuned response of an FM-FM neuron in Fig. 8 supports this hypothesis. The neuron had response latencies of 30 and 11 ms to the low- and high-frequency signals, respectively. The PST histograms show that when the high-frequency signal was delayed 20 ms, the responses coincided (Fig. 8, A and B), eliciting the strongest facilitation (Fig. 8C) in the delay curve (Fig. 8D). The full range of best delays observed among FM-FM neurons may be explained by the latency differences of the low- and high-frequency signals. For our neurons that showed excitatory responses to both the low- and high-frequency signals, we examined the correlation between latency and best delay. Figure 9A shows that the latencies of response to the low-frequency signal were strongly and positively correlated with best delay (r = 0.95, P < 0.001). In contrast, the latencies of response to high-frequency signals were not correlated with best delay (r = 0.22, P = 0.35, Fig. 9B). Figure 9C shows that the measured best delays of FM-FM neurons were highly correlated with their predicted best delay (r = 0.98, P < 0.001). These results support the latency-coincidence hypothesis and further suggest that the broad range of latencies to the low-frequency signals creates the broad range of best delays among FM-FM neurons.

Inhibited combination-sensitive responses

A second type of combination-sensitive interaction recorded in the ICC was inhibitory. In inhibited FM-FM neurons, the excitatory response to a high-frequency signal was inhibited by simultaneous presentation of a low-frequency signal. Twenty-eight FM-FM neurons and 15 H1-CF2 neurons displayed inhibited combination-sensitive responses (Fig. 2).

FREQUENCY-TUNING PROPERTIES. Inhibited combination-sensitive neurons displayed typical excitatory tuning curves in response to high-frequency stimulation. Figure 10A shows an FM-FM neuron for which the excitatory response was tuned to 79.8 kHz. There was no excitatory response to signals within the FM1 frequency range presented alone. However, the neuron’s excitatory response to the high-frequency signal was strongly inhibited by simultaneous presentation of signals within the FM1 frequency band. The shaded tuning curve in Fig. 10A shows the frequencies and intensities that produced
detectable inhibition of the high-frequency response. The best frequency of inhibition was 27.0 kHz, within the FM1 frequency band. For most inhibited combination-sensitive neurons, the low-frequency inhibition was tuned within the frequency range of the first sonar harmonic. However, seven units with best high frequencies in the CF2 frequency range were

FIG. 8. Neural responses supporting a latency coincidence model for the creation of facilitated, delay-tuned responses in the ICC. Facilitated response depends on the coincidence of the low- and high-frequency signals. Peristimulus (PST) histograms illustrate this latency coincidence model for an FM-FM neuron. A: presentation of a low-frequency tone burst elicited a weak excitatory response. Time of stimulus onset was 10 ms, and the response latency was 30 ms. B: presentation of a high-frequency signal elicited an excitatory response at a latency 11 ms from the time of the high-frequency stimulus onset. C: facilitated response occurred at 20-ms delay between the onset of the low-frequency signal and the onset of the high-frequency signal. This measured best delay is the same (within our sampling resolution) as that predicted by the latency coincidence hypothesis, where the difference between the latencies to the low and high signals is equal to best delay. D: delay tuning curve showing the strongest facilitation at 20-ms delay.

FIG. 9. Correlation of response latencies and best delay among facilitated FM-FM neurons to test the latency coincidence hypothesis. A: best delay was significantly correlated with response latency to FM1 signals. Wide range of latencies to low-frequency (FM1) sounds create the broad range of best delays among FM-FM neurons. B: best delay was not significantly correlated with response latency to high-frequency signals. C: measured best delay vs. predicted best delay. Difference between the latencies to low and high frequency signals was highly correlated with the measured best delay. For the 19 neurons in which we could measure a response latency to the low-frequency stimulus, the latency coincidence hypothesis was supported.
inhibited by a second signal in the 18- to 23-kHz frequency range, below the first sonar harmonic.

SENSITIVITY TO DELAY. As with facilitated neurons, inhibited FM-FM and H1-CF neurons were sensitive to the timing of the two signals. The characteristic feature of these neurons, however, is that the strongest inhibition occurred at simultaneous presentation of the two signals. The delay curve in Fig. 10B shows that the neuron’s response to the high-frequency signal was strongly inhibited by simultaneous presentation of a low-frequency signal. Thus the best delay of inhibition was 0 ms. The inhibited neurons had a narrow distribution of best delays of inhibition, with most (84%) at 0 ms. The sharpness of delay tuning (50% delay width) among inhibited FM-FM neurons varied between 2 and 10 ms with an average 50% delay width of 5.9 ± 1.8 ms.

STRENGTH OF INHIBITION. The neuron in Fig. 10B illustrates a strongly inhibited combination-sensitive response. At simultaneous presentation of the low- and high-frequency signals, the response of the neuron was suppressed by 85%. For the population of inhibited FM-FM neurons, there was a broad distribution of inhibition strengths (Fig. 7). The average response rate to the best high-frequency signal presented 10 dB above threshold was 1.23 ± 0.67 spikes/stimulus. The mean inhibited response rate was 0.52 ± 0.53 spikes/stimulus. Corresponding values for H1-CF neurons were 1.7 ± 0.84 and 1.04 ± 1.02 spikes/stimulus, respectively.

Multiply tuned complex interactions

Eighteen neurons in the FM3 representation and 15 neurons in CF2 representation of the ICC showed complex response properties without any facilitated or inhibited response. These neurons displayed two separate excitatory tuning curves with best frequencies separated by an octave or more. The responses to low-frequency signals were clearly separate from the high-frequency responses and were not the flanks of the high-frequency excitatory tuning curves. Seven of the CF2 multiply tuned neurons had best low frequencies of 18–23 kHz, below the range of the first sonar harmonic.

DISCUSSION

This study describes the physiological response properties of combination-sensitive neurons in the mustached bat’s ICC with the main objective of understanding the mechanisms underlying delay tuning. A variety of combination-sensitive responses occur in the mustached bat’s ICC, and we found that these responses are abundant in the tonotopic regions representing the frequencies in the higher harmonics of the sonar signal. In contrast, Leroy and Wenstrup (1996) did not find combination-sensitive responses in the tonotopic regions representing the first harmonic of the sonar signal. In our sample of neurons, 76% showed a combination-sensitive interaction. Fifty-one percent of the neurons were facilitated and 25% were inhibited combination-sensitive responses. A smaller percentage (17%) of neurons were tuned to two separate frequency bands without any facilitation or inhibition. The smallest proportion (7%) of ICC neurons we recorded were tuned to a single frequency band. The abundance of combination-sensitive neurons tuned to frequencies occurring in vocalizations indicates the importance of combination-sensitive neurons in processing species-specific vocalizations.

FM-FM neurons show specializations of basic response properties related to selectivity for delay. FM-FM neurons in the ICC show relatively strong facilitation when the low (FM1)- and high-frequency signals are combined at the appropriate delay. In our sample, FM-FM neurons had a range of best delays between 0 and 20 ms. Our data bear on two mechanistic issues for creating combination-sensitive responses. First, the data suggest that coincidence of excitatory responses to the low- and high-frequency signals generates the facilitated response. Second, the range of response latencies to the low-frequency signal creates the range of best delays seen among FM-FM neurons.

Response properties of combination-sensitive neurons

Combination-sensitive responses are common throughout the tonotopic high-frequency regions of the ICC. Recent evidence suggests that these responses, in particular facilitated responses (Leroy and Wenstrup 1998; Wenstrup et al., 1999), are created in the ICC. If this is the case, it is important to understand how response properties at this early stage of processing compare with response properties at higher levels. As combination-sensitive neurons are found in the ICC, MGB, and auditory cortex, we examine how the basic response properties of combination-sensitive neurons are transformed with ascending processing. The major focus here is a comparison between
response properties of delay-tuned, FM-FM neurons in the ICC and MGB. There is some evidence that sharpness of delay tuning and strength of facilitation of FM-FM neurons is greater in the MGB (Yan and Suga 1996) than in the ICC. Our data suggest that basic response properties related to coding delay are similar between the ICC and MGB.

FACILITATED RESPONSE PROPERTIES. Basic response properties of FM-FM neurons related to coding delay include the strength of facilitation, best delay, and the sharpness of delay tuning. The strength of facilitation provides a measure of how well the neuron responds to the combination of the two signals, compared with the responses to each signal separately. Most (95%) of the neurons in the high-frequency tonotopic representations (FM3 and FM4) responded to high-frequency tone bursts, whereas only ~25% of these same neurons responded to low-frequency tone bursts. The average response rate of neurons to best frequency tone bursts was 0.52 ± 0.45 spikes/stimulus when the best high-frequency signal was presented 10 dB above threshold. However, when both the high- and low-frequency signals were combined at the appropriate delay, the responses of FM-FM neurons were facilitated with an average frequency index of 0.34 is similar to Wenstrup's results obtained in our laboratory from a companion study (Wenstrup 1999). This may be due to the clustering of observable in multiple-unit responses (Wenstrup and Grose 1991b; Yan and Suga 1996; Wenstrup 1999). The functional significance of this range of best delays is discussed later.

A second feature of delay-tuned, facilitated neurons is the distribution of delay sensitivities among the population of neurons. Best delays among our sample of FM-FM neurons in the ICC ranged between 0 and 20 ms. H1-CF neurons, in contrast, showed a narrow range of best delays with most at 0 ms. Thus the range of best delays among FM-FM neurons distinguishes them from H1-CF neurons. The broad range of best delays among FM-FM neurons in the ICC is similar to the range among FM-FM neurons in the MGB (Fig. 11B) (Olsen and Suga 1991b; Yan and Suga 1996; Wenstrup 1999). The functional significance of this range of best delays is discussed later.

Not only does best delay among FM-FM neurons vary, so does the sharpness of delay tuning. Sharpness of delay tuning provides an indication of the selectivity of the neuron for preferred delays. A sharply tuned neuron will only respond over a narrow range of delays, whereas a more broadly tuned neuron will respond to a broad range of delays. The variability of sharpness of delay tuning among FM-FM neurons was high. We quantified the sharpness of delay tuning as the 50% delay width and found a range of delay widths between 2 and 13 ms with no significant correlation between delay width and best delay.

Sharpness of delay tuning among FM-FM neurons in the MGB is also variable (Yan and Suga 1996; Wenstrup 1999). Olsen and Suga (1991b) reported that delay widths were strongly correlated with best delay, but Yan and Suga (1996) and Wenstrup (1999) found only weak correlations. To compare the sharpness of delay tuning among our ICC data and MGB data from our other study (Wenstrup 1999), we calculated Q50% values, defined as best delay divided by 50% delay width. This measure also allows us to compare our data with Yan and Suga’s (1996) ICC and MGB data. The average Q50% of our ICC neurons was 1.0 ± 0.68. This value, indicating relatively sharp tuning, differs from the average Q50% of 0.38 in the ICC reported by Yan and Suga (1996). Our results show that FM-FM neurons in the ICC are sharply tuned in delay, whereas Yan and Suga’s data indicate that delay tuning is fairly broad among FM-FM neurons in the ICC. We are unsure why their neurons are more broadly tuned in delay, but it may be related to the differences in the degree of facilitation due to multunit recordings as discussed previously. Sharpness of delay tuning is more difficult to measure when facilitation is weak. The delay tuning sharpness among our
FM-FM neurons in the ICC is similar to delay tuning in MGB (Yan and Suga 1996; Wenstrup 1999). Figure 11 displays delay tuning sharpness of the ICC neurons from this study and the MGB neurons from the companion study (Wenstrup 1999). The average Q50% of our ICC neurons (1.0 ± 0.68) is similar to our MGB values (1.1 ± 0.8) and also to Yan and Suga’s MGB values (0.82 ± 0.45). Again, the discrepancy in results arises mostly from differences between the ICC data in the two studies and not from results in the MGB. Our results suggest that delay tuning among FM-FM neurons in the ICC is, on average, as sharp as delay tuning among FM-FM neurons in MGB.

The similarities in the range of best delays, strength of facilitation and sharpness of delay tuning between FM-FM neurons in the ICC and MGB (Fig. 11) suggest that basic response properties of delay-tuned neurons are established at the ICC and do not undergo extensive processing transformations between the ICC and MGB. Furthermore, these data provide additional evidence that combination-sensitive responses are created in the ICC (Wenstrup and Grose 1995; Wenstrup et al. 1999).

**INHIBITED COMBINATION-SENSITIVE RESPONSE PROPERTIES.** The ICC also contains FM-FM inhibited neurons. Among these neurons, the low-frequency signal inhibits the excitatory response to the higher frequency signal, around a best delay of 0 ms. Inhibited FM-FM neurons are common in the tonotopic regions representing the higher frequencies of the sonar signal. In this study, they comprised 25% of all acoustically responding neurons. This percentage is similar to that reported by Mittmann and Wenstrup (1995). Inhibited FM-FM neurons in the ICC first were reported by O’Neill (1985), but an understanding of their functional significance is lacking. A comparison between the ICC and MGB may provide an indication of their significance. The most striking change in combination-sensitive response properties between the ICC and MGB is the proportion of inhibited FM-FM neurons; the MGB contains very few (Olsen and Suga 1991a,b; Yan and Suga 1996; Wenstrup 1999). Only one report documents the proportion of inhibited FM-FM neurons in MGB. Wenstrup reported that inhibited FM-FM neurons comprised 9% of acoustically responsive neurons, whereas facilitated FM-FM neurons comprised 49%. In contrast, we found that 25% of neurons were inhibited and 51% were facilitated in the ICC.

**Neural mechanisms underlying delay tuning**

Because recent evidence suggests that most facilitated, delay-tuned responses are created in the inferior colliculus (Leroy and Wenstrup 1998; Wenstrup et al. 1999), the neural mechanisms underlying delay-tuned facilitation probably occur at the ICC. One goal of the present study was to examine whether the response properties of delay-tuned, FM-FM neurons in the ICC provide evidence in support of particular mechanisms for creating delay sensitivity.

The present results strongly support several aspects of the coincidence hypothesis proposed by Suga and co-workers (Olsen and Suga 1991b; Suga et al. 1990). Under this hypothesis, the delay-tuned response of an FM-FM neuron requires the coincidence of excitatory postsynaptic responses to both a low- and a high-frequency signal. To create delay-tuned facilitation at nonzero delays, responses to the low-frequency signal...
must be neurally delayed to coincide with the acoustically delayed response to the high-frequency signal. Among MGB neurons, the coincidence mechanism is supported by the finding that the difference in the latencies of a neuron’s excitatory responses to the low- and high-frequency signals is highly correlated with the neuron’s best delay (Olsen and Suga 1991b). Among our ICC neurons in which this could be tested (27%), there was an even stronger correlation with a nearly one-to-one relationship between the latency difference and a neuron’s best delay.

A second feature of the coincidence mechanism proposed by Olsen and Suga (1991b) was that the latency of the low-frequency response was most closely related to a neuron’s best delay and, therefore, the mechanisms underlying it. Among MGB neurons, there was a strong correlation between the latency of the low-frequency response and the best delay, whereas there was no correlation between the high-frequency latency and the best delay. This is also true of our ICC neurons. These ICC data, obtained at the probable site of construction of delay-tuned neurons, emphasize that understanding the mechanism for the broad distributions of latencies among low-frequency responses is fundamental to understanding the mechanism that creates the delay-tuned response. At present, it is unclear whether the low latency response to the low frequency is created by delay lines present in the low frequency input to delay-tuned neurons in the ICC or by the postsynaptic response of these ICC neurons.

The delay tuning properties of FM-FM neurons in the ICC suggest that inhibition plays a role in eliciting a facilitated combination-sensitive response (Fig. 6B). This role may be different for neurons with shorter and longer best delays. For most FM-FM neurons with best delays >4–6 ms, whether in the ICC (this study) or MGB (Olsen and Suga 1991b), there is a pronounced inhibitory period before the facilitation peak. This inhibitory period may be related to a mechanism that creates a postinhibitory rebound excitation at the neuron’s best delay. In contrast, there is not as consistent or strong an inhibitory period preceding facilitation among neurons with best delays <4–6 ms. However, inhibition does play a role in short best delay neurons because the application of the glycine antagonist, strychnine, eliminates the facilitated response among both long and short best-delay neurons (Leroy and Wenstrup 1998). These several observations suggest that there may be more than one role of inhibition in creating delay tuning and facilitation.

Functional properties of combination-sensitive neurons

NEURAL ANALYSIS OF TARGET DISTANCE. The main difference between the response properties of FM-FM and H1-CF neurons is the broad distribution of best delays among facilitated FM-FM neurons. While H1-CF neurons are tuned to delays ~0 ms (simultaneous presentation of the low- and high-frequency sounds), the population of FM-FM neurons are tuned to best delays between 0 and 20 ms. This suggests that FM-FM neurons are involved in coding distance information. That these neurons have best delays between 0 and 20 ms indicates that target information at distances up to 3.4 ms could be coded by these neurons. Although best delays among FM-FM neurons in the mustached bat ranged between 0 and 20 ms, most (84%) neurons were tuned to delays of <10 ms. These delays correspond to target ranges up to 170 cm. A similar distribution of best delays is found in the MGB (Olsen and Suga 1991b; Wenstrup 1999) and in the FM-FM area in the auditory cortex of the mustached bat (O’Neill and Suga 1979). Neurons tuned to shorter delays also are emphasized in the auditory cortex of other bat species. In Rhinolophus rouxi, delays between 2 and 4 ms predominate (Schuller et al. 1991), and in Myotis lucifugus, delays <10 ms are overrepresented (Wong and Shannon 1988). However, in the auditory cortex of Eptesicus fuscus, the big brown bat, there are more neurons with best delays between 10 and 20 ms, representing target distances between 170 and 340 cm (Dear et al. 1993). This is also the case for delay-tuned neurons in the superior colliculus (Valentine and Moss 1997) and other midbrain regions (Dear and Suga 1995) in the big brown bat. The greater number of neurons that are delay-tuned to longer delays in the big brown bat compared with the mustached bat suggests that the former has a longer operating range for echolocation. This agrees with the range of distances over which big brown bats detect insect-sized objects (Kick 1982). There may be a greater emphasis on neurons with short best delays in the mustached bat because it forages in more cluttered environments and may have a shorter operational range for echolocation.

An important response property of facilitated, FM-FM neurons related to coding distance information is sharpness of delay tuning. These delay-tuned neurons can be thought of as filters, and the sharpness of the delay filter describes the precision of delay coding. However, even a neuron with sharp delay tuning will respond to more than one specific delay. For instance, the most sharply tuned neurons in our sample had 50% delay widths of 2 ms. If the role of these neurons is to specifically code target distance information, they would respond well to targets within a 34-cm range. Thus it is apparent that the response of one neuron is not sharp enough to encode a particular target distance precisely. The neural mechanisms underlying precise target localization are not well understood but may involve a population of neurons with the same best delay. Fairly broad delay tuning may explain the necessity for the large populations of FM-FM neurons found in the ICC, MGB, and auditory cortex.

MULTIDIMENSIONAL ANALYSIS OF SONAR TARGETS. On the other hand, delay-tuned neurons may have a function that is broader than specifically encoding the distance to a target, and the broad delay tuning of some neurons may play a different role. Delay-tuned neurons may function as filters to encode aspects of the target when it is within a particular extent of space, instead of encoding the specific distance to the target. While a target is at a particular distance, delay-tuned neurons that are facilitated by that delay may encode several aspects of the target important for prey localization and identification, such as horizontal and vertical location, texture, or wingbeat frequency. In other words, delay-tuned neurons are involved in multidimensional analyses of targets when the targets are within a particular extent of space. Evidence from the auditory cortex of Myotis lucifugus supports the hypothesis that delay-tuned neurons are involved in multi-dimensional analyses of targets (Maekawa et al. 1992; Paschal and Wong 1994; Sullivan 1982a). As yet, we do not know whether delay-tuned neurons in the ICC of the mustached bat are selective for other stimulus attributes such as interaural intensity differences or...
amplitude modulations. However, as a large number of ICC neurons are delay tuned (>50%), and more than one-third of the neurons in the ICC are sensitive to interaural intensity differences (IID), encoding horizontal location (Fuzessery and Pollak 1985; Wenstrup et al. 1986), it seems likely that a sizable number of neurons are both delay tuned and IID sensitive, for example. In the superior colliculus of the big brown bat, *E. fuscus*, delay-tuned neurons are directionally selective, encoding azimuth, elevation, and distance (Valentine and Moss 1997). These neurons may represent the convergence of target spatial information necessary to guide the motor behavior of the bat. It seems unlikely that the only functional role of delay-tuned neurons in any bat species is to encode target distance.

**INHIBITED COMBINATION-SENSITIVE NEURONS.** Combination-sensitive inhibited responses in the high-frequency representations of the ICC comprised 25% of acoustically responsive neurons. The key feature of these neurons is that their inhibition prevents a response to certain spectrally complex stimuli that may be either communication or echolocation sounds. For example, some neurons that respond to frequencies in the CF2 (~60 kHz) are inhibited by simultaneous presentation of low frequencies (18–23 kHz) outside the sonar range. The mustached bat has a rich repertoire of social communication calls (Kanwal et al. 1994) that contain frequencies both within and outside the sonar range. The inhibition evoked by simultaneous presentation of a nonsonar low-frequency signal and a CF2 signal may inhibit these neurons from responding to communication calls within these frequency bands, but they still would respond to CF2 sonar echoes provided the nonsonar signals are not present.

Inhibited FM-FM neurons also could function to inhibit a response to the bat’s own sonar pulse. When the bat emits a sonar vocalization, the neural response to the pulse may be inhibited because the emitted signal usually has sufficient energy in the first harmonic FM to activate the inhibitory mechanism of inhibited FM-FM neurons. In contrast, these neurons would respond well to echoes because the pulse FM-evoked inhibition decays very rapidly, and there is insufficient energy in the first FM harmonic of the echo to re-activate the inhibitory mechanism. As a result, these neurons could respond to high-frequency echoes that arrive shortly after pulse emission and extract information contained within the echo.

While these inhibited FM-FM neurons may analyze echo features on their own, they also may contribute to the creation or modification of facilitated FM-FM responses. Here we consider the hypothesis that an inhibited FM-FM neuron provides significant high-frequency excitatory input onto a facilitated FM-FM neuron. A major feature of its input is that it is inactive during pulse emission; thus the facilitated FM-FM neuron will not respond during pulse emission. However, the inhibition due to the low-frequency signal decays very rapidly, within 1–3 ms, after which the previously inhibited FM-FM neuron becomes active. The facilitated neuron then will respond maximally to the coincidence of a neurally delayed low-frequency input (FM1), arriving from a separate neuron, and an acoustically delayed high-frequency input carried by the inhibited FM-FM neuron. By suppressing a response to the emitted pulse, this mechanism creates a facilitated neural response highly selective for pulse-echo delay. This proposed mechanism is consistent with the finding that inhibited FM-FM neurons are common in the ICC but not in the MGB, suggesting that these neurons converge with others in the ICC or MGB. Hence, facilitated combination-sensitive responses may not only be created in the ICC from the convergence of low- and high-frequency inputs from lower brain stem nuclei but also may be created or modified in the ICC by inhibitory combination-sensitive responses.

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