Excitatory/Inhibitory Response Types in the Cochlear Nucleus: Relationships to Discharge Patterns and Responses to Electrical Stimulation of the Auditory Nerve

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SUMMARY AND CONCLUSIONS

1. We have studied the response properties of single units in the cochlear nucleus of unanesthetized decerebrate cats. The purpose of the study was to compare the properties of cochlear nucleus units as described in two commonly used classification schemes. Units were first classified according to their receptive-field properties based on the relative prominence of excitatory and inhibitory responses to tones and noise. Units were then classified on the basis of their discharge patterns to short tone bursts at their best frequencies (BFs). Our results show that systematic relationships exist between the receptive-field properties and discharge patterns of cochlear nucleus units.

2. Type I units give only excitatory responses to tones and noise. They are characterized by primary-like and chopper discharge patterns. Some units in the anteroventral cochlear nucleus have prepotentials in their spike waveforms. Prepotential units most often show primary-like discharge patterns, but prepotential units characterized by nonprimary-like discharge patterns are also found. Most prepotential units lack detectable inhibitory sidebands (type I), but two of the nonprimary-like prepotential units encountered in this study had inhibitory sidebands (type III).

3. Type III units also give excitatory responses to BF tones, but they have inhibitory sidebands. Most type III units give chopper discharge patterns, and these units can be recorded throughout the cochlear nucleus. Some type III units in the dorsal cochlear nucleus give complex discharge patterns that can be described as a composite of the pauser pattern and other patterns. The complexity of these responses seems to increase as the amount of inhibition at BF increases.

4. Type I/III units give excitatory responses to tones and noise, but have little or no spontaneous activity so they cannot be tested directly for inhibitory responses. Type I/III units typically show chopper discharge patterns. One group of type I/III units have rate-level functions with sloping saturation, suggesting that these may receive a predominance of input from low spontaneous rate auditory nerve fibers.

5. Type II units are nonspontaneous and give excitatory responses to tones, but give weak or no responses to noise. While type II units are homogeneous as a group in terms of their response maps, BF rate level functions, and responses to noise, they show a variety of discharge patterns in response to short tone bursts at BF.

6. Type IV units give excitatory responses to noise. They give excitatory responses to BF tones at levels near threshold, but show inhibitory responses to tones over a wide frequency range, including BF at 30–40 dB above threshold. At levels where BF tones give inhibition, type IV units show ON-I or ON-OFF discharges.

7. Electrical current pulses delivered to the auditory nerve through round window electrodes evoke short-latency excitatory responses in auditory nerve fibers and type III units in the ventral cochlear nucleus. Presenting an
OFF-BF tone at the same time as the electrical stimulus does not significantly reduce the responses of auditory nerve fibers to the electrical stimulus. However, the electrically evoked response of type III units can be greatly inhibited by an OFF-BF tone. These results suggest that reduction of an excitatory response to the electrical shock by off-BF tones can be used as a test for inhibitory sidebands in nonspontaneous units. This method is preferable to a two-tone paradigm because an OFF-BF tone can reduce the excitatory response to a BF tone through cochlear two-tone suppression.

8. Electrical stimulation of the auditory nerve evokes inhibitory responses from both type II and type IV units. While type II and type IV units generally respond to tones and noise in a reciprocal manner, the responses to electrical shocks illustrate a situation where they respond in an identical fashion. This suggests that part of the inhibitory input to type IV units is derived from an additional source besides type II units.

INTRODUCTION

The cochlear nucleus is the first structure along the central auditory pathways where neural processing of the acoustic information encoded in the auditory nerve can occur. Physiological classification of single units in the cochlear nucleus is a first step in understanding this processing. This classification has been approached in two ways in the mammalian cochlear nucleus. One classification scheme is based on the discharge patterns of units in response to tone bursts at their best frequencies (BFs). The patterns of discharge are determined from poststimulus time histograms (PSTHs), and we refer to this method as the PSTH scheme. Response types based on the PSTH scheme were originally defined by Kiang et al. (21) and Pfeiffer (39), and this scheme has been used in a number of studies, primarily in anesthetized preparations (2, 10, 14, 16, 17, 27, 28, 33, 36, 37, 41, 48). The second classification scheme is based on the relative prominence of excitatory and inhibitory responses to tones and noise. This classification scheme was originally defined by Evans and Nelson (12), and we refer to this method as the response map scheme. Modifications of the response map scheme have been employed in both anesthetized preparations (12, 48) and unanesthetized preparations (12, 15, 20, 55, 56).

These two classification schemes emphasize different functional properties of cochlear nucleus units. The PSTH scheme emphasizes their temporal firing properties and most often concentrates on the pattern of action potentials produced by short tones bursts at their best frequencies (STBBFs). The response map scheme, on the other hand, emphasizes the receptive-field properties of units and concentrates on which frequency-intensity combinations produce excitatory or inhibitory responses. Studies concerned with information processing in the cochlear nucleus must be based on well-developed schemes for classifying units and relating physiological unit types to morphological cell types. Considerable progress has been made toward these goals using both PSTH and response map classifications. It seems important to achieve a unification of these two schemes so that classification based on the temporal discharge patterns of units can be related to classification based on their receptive-field properties.

Two studies have attempted to examine the relationships between the discharge patterns and receptive-field properties of cochlear nucleus units. Van Gisbergen et al. (48) found that units without inhibitory sidebands gave only sustained PSTHs, while units having inhibitory sidebands showed sustained or pauser patterns. However, Van Gisbergen et al. (48) did not distinguish between primary-like and chopper PSTHs, nor did they distinguish among different transient discharge patterns. Furthermore, they used anesthetized cats, and anesthesia can alter the responses of cochlear nucleus units by reducing spontaneous activity and weakening inhibition (12, 38, 55). In another study, Hui and Disterhoft (20) reported no relationship between the two schemes of classification in unanesthetized rabbits. However, Van Gisbergen et al. (48) did not distinguish between primary-like and chopper PSTHs, nor did they distinguish among different transient discharge patterns. Furthermore, they used anesthetized cats, and anesthesia can alter the responses of cochlear nucleus units by reducing spontaneous activity and weakening inhibition (12, 38, 55). In another study, Hui and Disterhoft (20) reported no relationship between the two schemes of classification in unanesthetized rabbits. However, their classification of units using the PSTH scheme was based on discharge patterns near threshold. At levels near threshold, units may not exhibit their characteristic PSTH, and in fact discharge patterns are similar for most unit types (35). In addition, Hui and Disterhoft used white noise as a search stimulus, thereby selecting against a major response type in the dorsal cochlear nucleus, which does not respond to noise and is nonspontaneous (15, 55, 56). We have reexamined this issue in un-
anesthetized decerebrate cats, and in this report we describe the systematic relationships that exist between the discharge patterns and receptive-field properties of units in the cochlear nucleus.

METHODS

Twenty-one adult cats (1.8–3.6 kg) whose middle ears were free of infection were used. They were injected intramuscularly with atropine (0.3 mg) to suppress mucous secretions and anesthetized with an intramuscular injection of ketamine (100–120 mg). Supplemental doses of ketamine were given as needed to maintain areflexia prior to decerebration. After a tracheotomy was performed, the animal was placed in a head holder in an electrically shielded soundproof room (IAC-1204A). Its body temperature was maintained at 36–38°C. The midbrain was exposed by aspirating enough of the occipital cortex to visualize the superior colliculus, and the animal was then decerebrated by making a transection through the brain at the level of the superior colliculus. After decerebration, anesthesia was discontinued.

The external meatus was exposed and transected, and the bulla was exposed. In earlier experiments (7/11/83 to 11/1/83) the bulla was vented by drilling a small hole through its wall and cementing a length of polyethylene tubing (~60 cm) to the hole. Venting the bulla prevents negative pressure from developing, but maintains the bulla's natural resonance properties (19). In later experiments, in which the auditory nerve was electrically stimulated, the bulla was opened and the septum removed.

The animal was then placed in a Kopf stereotaxic headholder. The cochlear nucleus was exposed by removing the occipital condyle and drilling an opening in the occipital bone lateral to the foramen magnum. In three experiments, the cerebellum was partially aspirated to directly visualize the ventral cochlear nucleus (VCN). In one experiment, the auditory nerve was exposed by opening the skull at the level of the nucal ridge and gently retracting the cerebellum.

Platinum-iridium microelectrodes were used for recording single units in the cochlear nucleus. Electrodes were placed into the dorsal cochlear nucleus (DCN) and advanced along the sagittal plane into the VCN with a Kopf hydraulic microdrive. In experiments where cerebellum was aspirated, electrodes could be directly placed into the VCN, which proved to be necessary for sampling units in the rostral anteroventral cochlear nucleus (AVCN). The exposure was covered with a solution of warm 3% agar in isotonic saline to reduce brain pulsations. Glass micropipettes filled with 3 M NaCl and having resistances of 10–40 MΩ were used to record single auditory nerve fibers.

In all experiments, acoustic stimuli consisted of broadband noise and pure tones. They were delivered from an electrostatic driver (45) to the ipsilateral ear through a hollow ear bar. This system typically gave a flat frequency response of ±5 dB from 20 Hz to 20 KHz. Acoustic calibrations at the ear-drum were done with a probe tube for each animal (45). Two kinds of acoustic stimuli were used: 100- or 200-ms tone bursts or noise bursts with 10-ms rise/fall times and a period of 1 s; and 25-ms short tone bursts at the best frequency (STBBF) with 1.6-ms rise/fall times and a period of 200 ms. Acoustic search stimuli were presented while advancing the electrode in order to aid in isolating units with no spontaneous activity. Search stimuli for DCN units consisted of tone bursts at the BF of the background neural activity, while noise bursts were often used for VCN units. Noise bursts cannot be used as search stimuli for DCN units, because type II units (see below) do not respond to noise (15, 55, 56).

When a unit was isolated, it was characterized by its responses to acoustic stimuli. Its BF and excitation threshold were determined audiovisually for 200-ms tone and noise bursts. Rate versus level functions for BF tones and noise were generated over a 100-dB range in 1-dB increments. To take into account the stimulus rise time and neural delays, the driven rate was estimated as the average rate between 10–210 ms after the onset of the tone or noise burst. Spontaneous rate was estimated over a 390-ms duration before the acoustic stimulus. For units that were spontaneously active, the presence of inhibitory sidebands was determined by looking for a decrease in the spontaneous activity during tone bursts at frequencies above and/or below BF. If a unit had inhibitory sidebands, an additional rate-level function or a PSTH for an inhibitory tone was usually generated. After the responses to tones and noise were characterized, the discharge patterns of the unit were studied using PSTHs generated from STBBF at 10–40 dB above threshold. PSTHs were typically generated from 500 presentations of the STBBF. All data were displayed on-line in the form of dot displays and were processed off-line into rate-level curves and PSTHs.

The action-potential waveform of each unit was delayed, digitized at a sampling rate of 50 KHz, and averaged on-line. This averaged spike waveform was then examined for prepotentials (34). The electrode signal was always handpass filtered with a low-frequency cutoff (6 dB/octave) of 40 Hz and a high-frequency cut-off of 7 KHz (24 dB/octave) when averaging spike waveforms. Based on observations of action-potential wave shapes, these filter settings limited the low-frequency response of the electrode/amplifier combination used, but did not limit the high-frequency response.

In later experiments (11/17/83 to 7/26/84) units were also characterized by their responses to 100-
μA current pulses applied to the auditory nerve using a modification of the cottonwick technique (29). Current was passed between two stainless steel electrodes insulated with glass capillary tubing. One electrode was placed on the bone just below the round window membrane, and the second electrode was placed on the bone over the apex of the cochlea. The electrode below the round window was negative with respect to the apical electrode, and stimulating currents were 0.1–1.5 mA. Electrical shocks were delivered at a rate of 2 Hz. In order to trigger reliably on units' action potentials during electrical stimulation, the large evoked potential produced by the electrical stimulus had to be reduced. The evoked potential was digitized, inverted, and then added on-line to the electrode signal as stimuli were presented resulting in cancellation of the evoked potential. In many cases this also reduced the stimulus artifact.

At the end of the experiment, the animal was perfused transcardially with isotonic saline, followed by 10% formalin. After fixation, the brain was removed, and the cochlear nucleus was blocked out. Frozen sagittal sections were stained with cresyl violet and Luxol fast blue. The locations of units were determined from reconstruction of the recording tracks. Recording tracks were identified by the darkly staining inflammatory response produced by the microelectrode as well as one or two electrolytic lesions along the track. Correction for tissue shrinkage was made using micrometer readings from the DCN surface, locations of lesions, and locations of sudden shifts in the BF along the track. In some cases where lesions and electrode tracks were not recovered, the location of units was estimated by the depth from the surface and the change in BF along the recording track (39).

The mammalian VCN is generally divided into a number of subregions based on cytoarchitecture (4, 31) and patterns of fibers and terminals from the auditory nerve and other sources of input (6, 8, 24, 25). In the present study, units from DCN and VCN are kept separate in the analysis, but units of the same response type from different subregions of the VCN have not been differentiated. While there is a systematic distribution of response types within the various subregions of the VCN (2, 17), it was not the goal of this study to add to the results already accumulated on this subject. However, since major differences in response types are observed between the VCN and DCN, units from these divisions of the cochlear nucleus have been analyzed separately.

**RESULTS**

Our results are based on data from 224 cochlear nucleus units and are summarized in Table 1 for VCN units and Table 2 for DCN units. Units are classified by the response map scheme according to the definitions of Evans and Nelson (12) as modified by Young (54) and Gibson et al. (15). Units are also characterized by their PSTHs as defined by Bourk (2) and Godfrey et al. (16, 17). An exception to previous PSTH categories is the composite-pauser discharge pattern. The PSTHs of the composite-pauser category show more than

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<th>TABLE 1. Summary of ventral cochlear nucleus units</th>
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<td>Primary-like</td>
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<td>Composite pauser</td>
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<td>Negative responder</td>
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<td>Unusual</td>
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<td>Total</td>
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Numbers in parentheses show the number of units with prepotentials. * These units showed 2 or 3 response peaks at stimulus onset, followed by no response. Bourk (2) called units with this discharge pattern On-A or On-P.
TABLE 2. Summary of dorsal cochlear nucleus units

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<td>ON-L</td>
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<td>ON-I</td>
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<tr>
<td>ON-OFF</td>
<td>4</td>
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<td>Pauser/buildup</td>
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<td>Composite pauser</td>
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one PSTH shape, but have pauser patterns as a predominant feature. Units that do not fit into one of the defined PSTH categories are classified as unusual. It should be emphasized that the unusual units do not represent a separate PSTH classification but show a mixture of different discharge patterns. The phase-locked category represents those low-frequency units that exhibit such strong phase locking to the stimulus that other discharge patterns cannot be distinguished.

Type I

Type I units give excitatory responses to tones and noise at all intensity levels. For units that are spontaneously active, OFF-BF tones do not result in a reduction in spontaneous rate, so Type I units do not have inhibitory sidebands. Classification of nonspontaneous units as type I is discussed below. Type I units are primarily located in the VCN (49/51). Their discharge patterns in response to STBBF fall primarily into two groups, namely primary-like and chopper (Table 1).

Figure 1, A–C, illustrates the properties of a typical type I unit having primary-like discharge patterns. The PSTH is primary-like in that it is similar to the discharge patterns of auditory nerve fibers (22). In this unit, the discharge pattern remains primary-like at higher sound levels. In other units, a brief (<2 ms) drop in firing rate called a notch appears following the initial peak in the PSTH (Fig. 8C). Units displaying a notch show otherwise primary-like characteristics and are usually grouped with primary-like units (2). The rate-level functions at BF of primary-like type I units are characterized by a monotonic increase in rate that saturates at higher levels (inset in the left column of Fig. 1).

The second group of type I units is characterized by chopper discharge patterns (Fig. 1, D–F). At 10 dB above threshold, the PSTH is a chopper in this example, but may be either primary-like or chopper. However, at levels of 20 dB and above, the chopper discharge pattern is observed. The rate-level functions at BF of these units generally are monotonic and saturate (inset in the right column of Fig. 1), but a few chopper type I units (3/12 in VCN, 1/1 in DCN) showed nonmonotonicities at higher levels.

Type III

Type III units give excitatory responses to BF tones and noise at all levels above threshold. Unlike type I units, type III units have inhibitory sidebands. In units that are spontaneously active, inhibitory sidebands can be demonstrated by the reduction in the rate of spontaneous activity in response to an OFF-BF tone (Fig. 2C). Classification of nonspontaneous units as type III is discussed below.

The discharge patterns of type III units fall into two groups. Most type III units (17/22 in VCN and 12/25 in DCN) have chopper PSTHs at intensity levels of 20 dB and above (Fig. 2, D–F). Note that the chopper discharge pattern is not observed in the PSTH for the 200-ms tone bursts where the bin width is 5
FIG. 1. Discharge patterns and BF rate-level functions for two VCN type I units. A–C: PSTHs showing primary-like discharge patterns at 3 BF levels above threshold (θ). D–F: PSTHs showing chopper discharge patterns at 3 BF levels above threshold. Insets show BF rate-level functions that are monotonic for these 2 units. In this and subsequent figures, the bin width is 100 μs for PSTHs in response to STBBF; PSTHs for STBBF are smoothed with a 3-bin triangular filter; shaded bars show the durations of tone bursts; rate-level functions show driven rates (solid lines) and spontaneous rates (dotted lines) as a function of BF tone sound pressure level; arrows on rate-level functions indicate levels at which STBBF PSTHs are made; rate-level functions are smoothed with a 5-bin triangular filter.

ms (Fig. 2B). The rate-level functions of these type III units are typically characterized by a monotonic increase in rate that saturates at higher levels (Fig. 2A).

A second family of type III units is limited to the DCN. Four of these units are classified as pauser (3/4) or buildup (1/4). An example of the pauser discharge pattern is shown in Fig. 3A. There is an initial excitatory response, followed by a pause in activity with duration ≥5 ms, followed by a gradual buildup of an excitatory response. An additional six type III
FIG. 2. Responses of a DCN type III unit characterized by chopper discharge patterns. VCN type III choppers show similar responses. A: BF rate-level function showing typical monotonic behavior. B: PSTH generated from 100 presentations of a 200-ms BF tone burst at 20 dB above threshold (6). Bin width is 5 ms, and PSTH is not smoothed. C: PSTH for a 200-ms off-BF tone demonstrating an inhibitory sideband. D-F: PSTHs for STBBF at 3 levels above threshold.

Units are classified as composite-pausers (Fig. 3, B and C). The pauser discharge pattern is the predominate feature in composite PSTHs, but it is accompanied by another superimposed discharge pattern.

Units classified as pauser/buildup show either monotonic with saturating (2/4) or nonmonotonic (2/4) BF rate-level functions. Most (5/6) type III units having composite-pauser PSTHs have strongly nonmonotonic BF rate-level functions where the driven rate at higher levels remains above the spontaneous rate.

Three examples of the rate-level functions observed in this family of units are shown in Fig. 3, A–C.

Some units with characteristics similar to type III units have nonmonotonic BF rate-level functions that approach those of type IV units (see below). An example is shown in Fig. 3D. If the driven response of a unit at 35 dB above threshold falls below a rate equal to half of the difference between the maximum rate and spontaneous rate (dashed lines in Fig. 3, C and D), and the driven does not fall below
spontaneous rate at any sound level, then the unit is classified as type IV-transitional (type IV-T). Units that fail to meet this criterion are classified as type III. Four units are classified as type IV-T based on their rate-level functions. The discharge patterns in response to STBBF of two of these units are composite-pauser with a strong off response (Fig. 3D), whereas two other type IV-T units are classified as ON-OFF (see below).

**Type I/III**

Type I/III units give excitatory responses to tones and noise at all levels above threshold. However, because they either lack spontaneous activity or have extremely low spontaneous rates, the presence of inhibitory sidebands cannot be demonstrated with single OFF-BF tones. Thus, the type I/III group is not a separate response map category, but only contains units for which the distinction between type I and type III cannot be made. Type I/III units are recorded throughout the cochlear nucleus. While a variety of PSTHs are observed, type I/III units typically show chopper discharge patterns (25/40 in VCN and 17/24 in DCN). Most type I/III chopper units (30/42) have rate-level functions similar to those already described for type I choppers and type III choppers. However, there appears to be a subgroup of type I/III choppers with different properties. Some (6/25 in VCN and 5/17 in DCN) type I/III choppers have rate-level functions that show sloping saturation (43) at higher levels (Fig. 4). One ON-I unit with a chopper onset response and one phase-locked unit also show sloping saturations. It should be noted that 7/30 type III choppers also have rate-level functions with sloping saturation. These seven units were nonspontaneous when they were first isolated and were classified as type I/III. They were subsequently shown to have inhibitory sidebands after they developed a low but sufficient rate of spontaneous activity (6/7) or were excited by electrical stimulation of the auditory nerve (1/7) (see below).

**Type II**

Type II units give excitatory responses to BF tones at all levels above threshold. Unlike type I/III units that may develop low spontaneous rates during the course of recording, type II units have no spontaneous activity and were not observed to develop any spontaneous
activity. Type II units differ from all other cochlear nucleus unit types in that they give weak or no response to broadband noise. The ratio of the maximum noise-driven response to the maximum BF tone-driven response is <0.3. Type II units are recorded only in the DCN.

Most type II units display a stereotypic nonmonotonic rate-level function (Fig. 5, A–C). The unit shown in Fig. 5D is exceptional
among type II units in that its rate declined to zero at high BF tone levels. This unit was included in the type II group because it had no spontaneous activity and no response to noise. There does not appear to be a characteristic PSTH for type II units. The PSTHs of type II units in response to STBBF show a variety of discharge patterns (Fig. 5), although

FIG. 6. A–D: PSTHs at 4 BF levels above threshold (Θ) for a DCN type IV unit characterized by ON-I discharge patterns. E–H: PSTHs at 4 BF levels above threshold for an AVCN type IV unit characterized by ON-I discharge patterns. Insets show BF rate level functions.
FIG. 7. A–D: PSTHs at 4 BF levels above threshold (Θ) for a DCN type IV unit characterized by ON-OFF discharge patterns. Notice that the ON response is as large as the OFF response. E–H: PSTHs at 4 BF levels above threshold for another DCN type IV unit characterized by ON-OFF discharge patterns. Notice that for this unit, the ON response decreases as the level increases. Insets show BF rate-level functions.
most are distributed among the chopper, ON-S and unusual PSTH categories (Table 2). Thus, while type II units form a homogeneous group with respect to their rate responses to tones and noise, they cannot be characterized as a group in terms of their PSTH discharge patterns.

**Type IV**

Type IV units give inhibitory responses to OFF-BF tones and give excitatory responses to noise, as previously described for type III units. However, type IV units are characterized by their strongly nonmonotonic BF rate-level functions (insets in Figs. 6 and 7). At intensity levels near threshold, type IV units give excitatory responses to BF tones; at levels 30–40 dB above threshold, the responses to BF tones become inhibitory. Thus, the responses of type IV units to single tones are dominated by inhibition. This inhibition is easy to demonstrate because type IV units are almost always spontaneously active.

Type IV units give similar discharge patterns at intensity levels where excitation occurs (Figs. 6 and 7). At levels between threshold and 10 dB above threshold, the PSTH shows excitation throughout the duration of the tone (Fig. 6, A and E, and Fig. 7, A and E); at levels of 10–20 dB above threshold, type IV units often but not always show pauser PSTHs (Figs. 6, B and F, and 7B).

At higher BF tone levels where type IV units give net inhibitory responses, their discharge patterns tend to fall into two groups. The first group (17/38) is characterized by an ON-I discharge pattern at levels ≥30 dB above threshold (Fig. 6, C, D, G, H). There is an initial excitatory peak followed by inhibition of activity throughout the remainder of the tone burst. The spontaneous activity of these units often remains inhibited after the tone is turned off for at least 20 ms. Four additional units gave an ON-I discharge pattern where a low level of activity was maintained during the tone burst (17). The second major group (15/38) of type IV units is characterized by ON-OFF discharge patterns (Fig. 7, C, D, F–H) at levels ≥30 dB above threshold. The PSTHs of these units have an initial excitatory peak followed by inhibition of activity throughout most of the tone with another excitatory peak.

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**FIG. 8.** A–C: spike waveforms and PSTHs showing primary-like (A, B) and primary-like with notch (C) discharge patterns for three AVCN type I prepotential units. The discharge pattern shown in A also shows phase locking. D–F: spike waveforms and PSTHs showing nonprimary-like discharge patterns for two AVCN type I prepotential units (D, E) and one AVCN type III prepotential unit (F). The discharge patterns shown in D–F are classified as unusual. Inset in F shows inhibitory response to an OFF-BF tone. Arrows indicate prepotentials.
at the end of the tone. In 7/15 of these ON-OFF units, the ON peak was at least as large as the OFF peak (Fig. 7, C and D), while in the other 8/15, the OFF peak became dominant over the ON peak as the intensity level of the STBBF increased (Fig. 7, F–H).

The characteristic discharge patterns of type IV units appear to be related to the location of the unit within the cochlear nucleus. Of the 29 DCN units which showed ON-I and ON-OFF PSTHs, the locations of 19 were determined histologically. For ON-I units, most (6/9) were located in the fusiform cell layer of the DCN, while 3/9 were found in the deep DCN layer. On the other hand, 9/10 ON-OFF units were located in the deep layer of the DCN, while 1/10 was found in the fusiform cell layer. It is interesting to note that one of the ON-I units found in the deep DCN did have an ON-OFF discharge pattern at one level, 17 dB above threshold.

Five type IV units were found in the VCN. All of these were histologically located in the caudal regions of the AVCN. Their response

![Graphs showing responses of a high-BF (A-C) and a low-BF (D-F) auditory nerve fiber to electrical stimulation of the auditory nerve through round window electrodes. A: PSTH showing the excitatory alpha (α) response to a 100 μs 0.5-mA current pulse. Arrow shows the time of delivery of the electrical pulse. The total number of spikes in the α-response is 99. B: PSTH showing the α-response to the current pulse (delivered at arrow) and an ON-BF tone of 30.9 kHz. The OFF-BF tone was turned on at time 0 and left on for 100 ms. The response between 15–40 ms is shown. The total number of spikes in the α-response is 93. The inset shows that a 100-ms, 30.9-kHz tone causes two-tone suppression of a 200-ms BF tone at 10 dB above threshold. Tone durations are indicated by bars beneath the abscissa. Hatched bars show the duration of BF tone, and stippled bars show the duration of the OFF-BF tone. C: PSTH showing the α-response to the current pulse (delivered at arrow) after the study in Fig. 9B was completed. The total number of spikes in the α-response is 89. D: PSTH showing both an excitatory α-response and a beta (β)-response to a 100-μs 0.7-mA current pulse. The total number of spikes in the α-response is 98. SA is stimulus artifact. E: PSTH showing the α-response to the current pulse and an OFF-BF tone of 1.24 kHz. Tone burst timing as in B. The total number of spikes in the α-response is 82. The α-response is only slightly reduced, but the β-response is totally suppressed. Inset shows two-tone suppression of a 200-ms BF tone at 10 dB above threshold by a 100-ms 1.24-kHz tone. F: PSTH showing the α-response and β-response to the current pulse after the OFF-BF tone was turned off. The total number of spikes in the α-response is 99. The bin width of the PSTHs is 100 μs (5 ms for insets); PSTHs have not been smoothed.

FIG. 9. Responses of a high-BF (A–C) and a low-BF (D–F) auditory nerve fiber to electrical stimulation of the auditory nerve through round window electrodes. A: PSTH showing the excitatory alpha (α)-response to a 100 μs 0.5-mA current pulse. Arrow shows the time of delivery of the electrical pulse. The total number of spikes in the α-response is 99. B: PSTH showing the α-response to the current pulse (delivered at arrow) and an ON-BF tone of 30.9 kHz. The OFF-BF tone was turned on at time 0 and left on for 100 ms. The response between 15–40 ms is shown. The total number of spikes in the α-response is 93. The inset shows that a 100-ms, 30.9-kHz tone causes two-tone suppression of a 200-ms BF tone at 10 dB above threshold. Tone durations are indicated by bars beneath the abscissa. Hatched bars show the duration of BF tone, and stippled bars show the duration of the OFF-BF tone. C: PSTH showing the α-response to the current pulse (delivered at arrow) after the study in Fig. 9B was completed. The total number of spikes in the α-response is 89. D: PSTH showing both an excitatory α-response and a beta (β)-response to a 100-μs 0.7-mA current pulse. The total number of spikes in the α-response is 98. SA is stimulus artifact. E: PSTH showing the α-response to the current pulse and an OFF-BF tone of 1.24 kHz. Tone burst timing as in B. The total number of spikes in the α-response is 82. The α-response is only slightly reduced, but the β-response is totally suppressed. Inset shows two-tone suppression of a 200-ms BF tone at 10 dB above threshold by a 100-ms 1.24-kHz tone. F: PSTH showing the α-response and β-response to the current pulse after the OFF-BF tone was turned off. The total number of spikes in the α-response is 99. The bin width of the PSTHs is 100 μs (5 ms for insets); PSTHs have not been smoothed.
characteristics to tones and noise are similar to those of DCN type IV units. Most of these units (4/5) have ON-I discharge patterns (Fig. 6, G and H), while one is characterized as an ON-OFF unit.

**Prepotential units**

A total of 25 units had prepotentials in their spike waveforms. The prepotential is a positive deflection that occurs \(\sim 0.5\) ms before the spike (arrows in Fig. 8). All prepotential units recorded had spontaneous activity. Based on their discharge patterns, prepotential units fall into two groups, namely primary-like and nonprimary-like.

Figure 8, A–C, shows typical PSTHs and spike waveforms for prepotential units with primary-like discharge patterns. These units are characterized by primary-like (11) or primary-like with a notch (4) PSTHs. The rate-level functions of these units increase monotonically and saturate at higher levels. One additional low-frequency prepotential unit was phase-locked, but had a rate-level function typical of primary-like units. None of these primary-like prepotential units (0/16) had inhibitory sidebands and thus all were type I. Units with the largest prepotentials (Fig. 8A) were located in the rostral AVCN and showed primary-like discharge patterns.

Nine additional prepotential units had nonprimary-like characteristics (Fig. 8, D–F). Most (7/9) of these are type I and show ON-L or unusual discharge patterns (Table 1; Fig. 8, D and E). Two other prepotential units have inhibitory sidebands and therefore must be classified as type III (Fig. 8F shows an example). These two type III units are classified as unusual (Fig. 8F) and ON-L, and both units have nonmonotonic BF rate-level functions. All prepotential units with nonprimary-like discharge patterns were found in the caudal AVCN.

**Responses to electrical stimulation of the auditory nerve**

In order to provide a method of testing for inhibitory sidebands in units without spontaneous activity, we have studied the responses to electrical shocks delivered to the auditory nerve through round window electrodes (see METHODS). The responses of cochlear nucleus units to electrical shocks are best considered by comparison with responses of auditory nerve fibers. Responses to electrical stimuli alone were compared with responses to combined electrical stimuli and tone bursts. The tone bursts had frequencies outside of the excitatory tuning curves and were chosen to have frequencies and intensities that produced two-tone suppression in auditory nerve fibers (insets of Fig. 9, B and E).

The responses of 10 auditory nerve fibers and one type I VCN unit with a prepotential were studied with current pulses applied to the auditory nerve. Type I units in the cochlear nucleus were difficult to study, because triggering on the relatively small action potentials was often unreliable, even when the evoked potential and stimulus artifact were reduced. All 10 auditory nerve fibers showed an excit-
Responses of Cochlear Nucleus Units

A monosynaptic excitatory \( \alpha \)-response (29) with a median latency of 0.7 ms to the electrical shock (Fig. 9). Three low-frequency units with BF < 1.0 kHz showed additional long-latency excitatory \( \beta \)-responses (29) with latencies > 5 ms (Fig. 9, D and F). While the long-latency \( \beta \)-responses could be suppressed (Fig. 9E), the short-latency \( \alpha \)-responses were only slightly reduced by tones that were demonstrated to produce two-tone suppression of BF tones (Fig. 9, B and E). The electrically evoked response of the type I VCN unit had a latency of 1.1 ms and was only slightly reduced by an \( \text{OFF-BF} \) tone, whereas the response of this unit to an acoustic click could be suppressed by the same \( \text{OFF-BF} \) tone. The responses of the auditory nerve fibers and the VCN type I unit to the combined electrical shock and \( \text{OFF-BF} \) tones were at least 80% of the responses to the shock alone (unshaded and black boxes in Fig. 10A). This reduction appears to be within the test/retest reliability of this determination (Fig. 10B).

Electrical stimulation of the auditory nerve evoked a single excitatory response from nine VCN type III units that were studied. The latency of this excitatory response ranged from 1.6–4.4 ms with a tendency for high-frequency units to have shorter latencies than low-frequency units. The median latency was 2.4 ms.

![Graphs showing responses to electrical stimulation](image)

**FIG. 11.** Responses of a spontaneous type III unit (A–C) and a nonspontaneous type III unit (D–F) to electrical stimulation of the auditory nerve. SA is stimulus artifact. A: PSTH showing the excitatory response (spike) to a 100-\( \mu \)s, 0.4-mA current pulse. B: reduction of the excitatory response to the current pulse by a 100-ms \( \text{OFF-BF} \) tone. Note the inhibition of spontaneous activity during the tone. C: PSTH showing the return of the excitatory response after the tone was turned off. D: PSTH showing the excitatory response to a 1.0-mA current pulse. E: reduction of the excitatory response by an \( \text{OFF-BF} \) tone. F: PSTH showing the excitatory response after the inhibitory tone was turned off. Bin width is 200-\( \mu \)s, and PSTHs were not smoothed. The stimulus artifact (SA) and evoked potential (EP) were triggered on. The stimulus artifact has been truncated at 1,000 spikes/s.
The BF of these 9 VCN units are >2 kHz. Because β-responses were not observed in high-BF auditory nerve fibers, the responses of the VCN cells to electrical shocks were almost certainly mediated by the α-responses of auditory nerve fibers. The responses to the combined electrical stimulus and an OFF-BF tone were at most 50% of the responses to the shock alone with most units falling below 30% (shaded boxes in Fig. 10A). Figure 11, A–C, shows data from a type III unit in which the excitation response to the electrical stimulus and the spontaneous activity are reduced by an OFF-BF tone. The excitation response returns after the tone is turned off (Fig. 11C). This behavior was typical of type III units (shaded boxes in Fig. 10B).

The fact that tones capable of two-tone suppression do not reduce the electrical response of type I units (including auditory nerve fibers) suggests that the reduction by OFF-BF tones of the short-latency, electrically evoked excitatory responses can be used as a test for inhibitory sidebands in nonspontaneous cochlear nucleus units. Four type I/III units were classified as type III by this method. An example is shown in Fig. 11, D–F. OFF-BF tones reduced the electrically evoked response to at least 30% of the response to the current pulse alone in these 4 units (hatched boxes in Fig. 10A). Three type I/III units were classified as type I when no OFF-BF tone could be found that reduced the excitatory response to the electrical shock.

Responses to electrical shocks to the auditory nerve were also studied for units in the DCN. Type II units could not be excited by electrical stimulation of the auditory nerve. However, in 5/5 cases, the excitatory responses of type II units to BF tones were inhibited following a single shock to the auditory nerve (Fig. 12). The spontaneous activity of type IV
FIG. 13. PSTHs showing the response of a type IV unit to electrical stimulation of the auditory nerve. A: response to a 100-μs, 0.2-mA current pulse showing spontaneous activity only. B: response to a 0.6-mA pulse showing inhibition of spontaneous activity lasting 45 ms. Note that no tone was presented. The stimulus artifact (SA) and evoked potential (EP) were triggered on. Bin width is 400 μs, and histograms were not smoothed.

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inhibitory areas overlap. This mechanism has been proposed to explain the stereotypic non-monotonic behavior of rate-level functions of type II units (56). The methods used in the present study do not allow us to distinguish between the inhibitory mechanisms described above. However, with the exception of four type I chopper units, all units having non-monotonicities in their BF rate-level functions had inhibitory responses at some frequencies. This suggests that the nonmonotonicities we observed arise from inhibitory inputs to the neurons.

Type I units show the simplest response maps in the cochlear nucleus in that they exhibit only excitatory responses to tones. Auditory nerve fibers show type I response maps. The simplicity of type I units is also observed in their discharge patterns. Type I units show primary-like and chopper discharge patterns. A few type I units having chopper PSTHs do show some nonmonotonicities in their rate-level functions, suggesting they may receive weak inhibitory influences at BF. Because we could not detect inhibitory responses to OFF-BF tones in type I units, it is unlikely that the nonmonotonicities we observed result from strong V-shaped inhibitory sidebands. These results are similar to those of Van Gisbergen et al. (48) in anesthetized cats where units showing only excitatory responses to tones gave sustained discharge patterns. The sustained patterns described by van Gisbergen et al. consisted of both primary-like and chopper patterns, although they make no distinction between the two patterns.

Type III units are more complex than type I in that type III units have easily detectable inhibitory sidebands. Our results suggest that two groups of type III units exist. The simplest type III units have only inhibitory sidebands with no apparent inhibitory influences at BF as suggested by their monotonic rate-level functions. These units have chopper discharge patterns and are found throughout the cochlear nucleus. Van Gisbergen et al. (48) showed that units having inhibitory sidebands and sustained discharge patterns were found in both the VCN and DCN. Nonchopper type III units are confined to the DCN and these units show PSTHs in which the pauser pattern is a dominant feature. These results are consistent with those of Van Gisbergen et al. (48) who found units having inhibitory sidebands and pauser discharge patterns only in the DCN of anesthetized cats.

Type II units appear to be homogeneous when considered in terms of their response maps, spontaneous rates, rate-level functions, and responses to noise. However, type II units are diverse in terms of their PSTHs and therefore cannot be classified as a group based on their discharge patterns. Thus, for type II units the PSTH scheme does not seem to be particularly useful. Several lines of evidence summarized below suggest that type II units receive strong inhibitory inputs as well as excitatory inputs. The variability in type II discharge patterns seems to reflect minor quantitative differences in strength between excitatory and inhibitory inputs rather than fundamental differences in response properties.

The diversity in type II and type III PSTHs illustrates the point that when one classification scheme is used alone, valuable information may be lost. Using the PSTH scheme alone, one cannot distinguish among type I, type II, and type III units that have chopper discharge patterns. Similarly, using the response map scheme alone, distinctions cannot be made between chopper type III units and pauser type III units. However, when both schemes are used in conjunction, subtle differences concerning the balance of excitatory and inhibitory inputs can be seen. For example, as the inhibitory responses of cochlear nucleus units become dominant over excitatory responses, the temporal discharge patterns of units reflect the interplay between the excitatory and inhibitory inputs of the unit by becoming more complex and variable (Fig. 3). These conclusions are consistent with those of Greenwood and Maruyama (18).

Inhibition in the DCN

Several lines of evidence suggest that type II units receive substantial inhibitory sideband inputs. Type II units generally have sharper excitatory areas than auditory nerve fibers, show weak or no responses to broadband noise, and have nonmonotonic rate level functions (Ref. 56; Fig. 5, above). All of these properties can be explained by inhibitory sidebands (56). Further evidence of inhibitory inputs comes from electrical stimulation of the auditory nerve (Fig. 12). Electrical stimulation of the auditory nerve does not excite type II units, but can inhibit the excitatory response
RESPONSES OF COCHLEAR NUCLEUS UNITS

935

to a BF tone. In contrast, VCN chopper type III units give excitatory responses to electrical stimulation of the auditory nerve. Type III chopper units have inhibitory sidebands, but show less evidence of inhibition at BF in that they have monotonic BF rate-level functions. The difference in the behavior of type II and VCN chopper type III units most likely results from stronger inhibitory sideband inputs to type II units.

Previous studies have shown that in most stimulus situations, type II and type IV units respond in a reciprocal fashion (49, 55-57). For instance, type II units are nonspontaneous, whereas type IV units are highly spontaneous. While type II units give weak or no responses to noise, type IV units show strong excitatory responses to noise. At moderate to high BF levels, type II units give excitatory responses, while type IV units are inhibited. However, our results show a situation in which type II and type IV units respond in the same way. Both type II and type IV units give inhibitory responses to electrical stimulation of the auditory nerve. Evidence indicates that type II units provide some of the inhibitory input to type IV units (49, 53, 57), but the findings with electrical stimulation of the auditory nerve imply that part of the inhibitory input to type IV cells must also be derived from another source because type II units do not give excitatory responses to electrical shocks. It is noteworthy that the long lasting inhibition observed in type IV units following electrical stimulation of the auditory nerve is similar to that observed following electrical stimulation of the AVCN (11).

Nonspontaneous units and sloping saturation

Many units in the present study lacked spontaneous activity in the absence of any controlled acoustic stimuli. These are type II and type I/III units. In earlier studies, no distinctions were made among response types on the basis of spontaneous activity (12, 55). The type II/III category of Young and Brownell (55) contains type II, type III, and type I/III units by the present definitions. In a later study, Young and Voigt (56) separated response types on the basis of spontaneous rates, resulting in type II and type III categories. However, some type II units in their study had values > 0.3 for the maximum noise response relative to the maximum BF tone response (see Fig. 5 of Ref. 56); these units correspond to type I/III units in the present study.

Some type I/III units have rate-level functions with sloping saturation, similar to those observed in auditory nerve fibers with low spontaneous rates (32, 43, 44). It is therefore possible that auditory nerve inputs to at least some nonspontaneous units in the cochlear nucleus may be predominately from low spontaneous rate auditory nerve fibers. It is interesting to note that low spontaneous rate auditory nerve fibers have a greater number of bouton terminals and en passant swellings (40) and have more complex branching patterns (13) in the cochlear nucleus than do high spontaneous rate fibers. This greater number of central terminations may provide a morphological substrate by which some cochlear nucleus cells could receive afferent inputs predominantly from low spontaneous rate auditory nerve fibers.

Morphological correlates

Morphological cell types have most often been correlated with unit response types based on the PSTII scheme (2, 16, 17, 36, 37, 41). A few studies have attempted to make correlations between cell morphologies and unit response types in the response map scheme (38, 53, 55, 56). Based on the results of the present study, some morphological correlates of response map types can be proposed.

Bourk (2) proposed that stellate cells in the VCN give chopper discharge patterns, and this was directly verified by Rhode et al. (36) and Roullier and Ryugo (41). Stellate cells are found throughout the cochlear nucleus (4) as are chopper responses (2, 16, 17, 33, 51, Tables 1 and 2). Because type III and type I/III units with chopper discharge patterns are recorded throughout the cochlear nucleus, it seems likely that these units correspond to stellate cells. Stellate cells in the AVCN have been divided morphologically into two groups based on the fine structure of their inputs (7). Noncochlear inputs terminate on the proximal dendrites in one group of stellate cells, but are found to synapse on the soma in the second group. These noncochlear inputs should have a stronger influence on the cells when they terminate on the soma rather than on the dendrites. If these inputs are inhibitory, then stellate cells with noncochlear inputs on the soma may correspond to type III units, while stellate
cells with noncochlear inputs only on the dendrites may correspond to type I units. Chopper units have not been previously observed in the DCN of decerebrate cats (55), but this is due to the large bin width used to construct their PSTHs (e.g., see Fig. 2B).

Fusiform cells in the DCN have been shown to give pauser PSTHs and type III responses in anesthetized cats (37). Anesthesia has been shown to alter the response properties of DCN type IV units so that they become type III pausers (12, 55). In unanesthetized decerebrate cats type IV units can be antidromically activated from the dorsal acoustic stria (53). All of this evidence suggests that fusiform and giant cells give type IV responses. Two groups of type IV units appear to exist in the DCN based on their discharge patterns. ON-I type IV units are primarily located in the fusiform cell layer, while ON-OFF type IV units are found in the deep layer. Thus, ON-I units may correspond to fusiform cells, whereas the giant cells of the deep DCN may be the correlate of ON-OFF units. Responses other than type IV may also be recorded from fusiform and giant cells. There appears to be a continuum of discharge patterns from type III pausers to type IV ON-OFF or ON-I units, corresponding to an increase in inhibition at BF. Thus, pauser type III, composite pauser type III and type IV T units may represent fusiform and giant cells with weaker inhibitory inputs. It is consistent with this notion that some DCN type III units can be antidromically stimulated from the dorsal acoustic stria (53).

A few type IV units were histologically located in the posterior regions of the AVCN, and these units typically showed ON-I discharge patterns. Bourk (2) recorded a few pauser units in the AVCN in anesthetized cat, which may correspond to the type IV units in our decerebrate cats. These units may correspond morphologically to the giant cells in the AVCN (4). However, it was argued above that giant cells in the DCN give ON-OFF type IV responses. Thus, the question arises as to why AVCN giant cells might be ON-I. The characteristic inhibition at BF of DCN type IV units is thought to arise from interneuronal input of type II units (49, 55, 57). One interneuron in the DCN is the vertical or corn cell (24, 25), which appears to give type II responses (53). These cells are in the deep layer of the DCN and send axon collaterals to the AVCN (24, 25). Thus, they could serve as the type II input to the AVCN giant cells. There presumably would be some conduction delay of the type II response associated with the length of the corn cell axon from the deep DCN to the caudal AVCN. This conduction delay, if it were long enough, could explain ON-I discharge patterns in AVCN giant cells.

Prepotential units

The prepotential is thought to arise as an action potential discharge in the end bulbs of Held (23, 34), which synapse on bushy cells in the AVCN (3, 25, 42). Bourk (2) concluded that prepotential units gave only primary-like and primary-like with notch PSTHs, although he did report 4/201 prepotential units characterized by nonprimary-like PSTHs. However, Martin and Adams (27) reported finding 10/36 prepotential units with chopper discharge patterns. Our results also show that prepotential units are not uniquely correlated with strictly primary-like discharge patterns.

We have recorded from 9/25 prepotential units characterized by nonprimary-like discharge patterns. The PSTHs of these nonprimary-like units were generally difficult to classify. While four units were classified as ON-L, it should be noted that the distinction between ON-L and primary-like with notch discharge patterns can be difficult, because at high sound levels the steady state discharge of primary-like with notch units is small compared to the transient rate in the onset burst. Five other nonprimary-like prepotential units were classified as unusual, because their discharge patterns did not easily fit into any of the defined PSTH categories. Despite the obvious differences between the unusual PSTHs and primary-like or primary-like with notch PSTHs, all prepotential units, primary-like and nonprimary-like, share a characteristic strong onset response followed by an irregular steady-state discharge of spikes. Primary-like and nonprimary-like prepotential units differ in their behavior during the transient phase from onset to steady state. The strong onset response is seen as the initial peak in the PSTH and represents the precise firing of the first spike to the onset of the tone burst. The discharge of all prepotential units during the steady-state portion of their response is irregular compared with chopper units (2, unpublished results). Moreover, all but two of our nonprimary-like
prepotential units have monotonic BF rate-level functions and type I response maps, which are the same as the response properties of primary-like units. Therefore, we conclude that the prepotential units characterized by nonprimary-like discharge patterns are not a separate category of units, but are in the same class as primary-like units. The subtle differences in discharge patterns among primary-like, primary-like with notch, and nonprimary-like prepotential units may reflect variations in the strengths or positions of their bouton synaptic inputs or differences in membrane channels leading to different refractory properties.

In our study, nonprimary-like prepotential units were located in the caudal regions of the AVCN. Based on intracellularly stained, physiologically classified units, Rouiller and Ryugo (41) have found that bushy cells in the caudal AVCN can give rise to nonprimary-like discharge patterns. Thus, our prepotential units with nonprimary-like discharge characteristics probably have been recorded from globular bushy cells. It is interesting to note that the end bulbs in the caudal AVCN are smaller than those in the rostral AVCN (3), thus providing a possible morphological substrate for the subtle differences in discharge patterns among prepotential units discussed above.

All but two of our prepotential units with nonprimary-like characteristics were type I. Two prepotential units had inhibitory sidebands and thus were type III. These two units also had nonmonotonic rate-level functions. Recording from the large-diameter trapezoid body axons which presumably come from the globular bushy cells (47, 50), Brownell (5) found that these units had inhibitory sidebands. It is unclear why only two of our prepotential units had inhibitory sidebands if we were recording from the same units as Brownell. However, Brownell constructed response maps from PSTHs by systematically varying the stimulus frequency and intensity. In some cases, the inhibitory sidebands were small and weak, and therefore, may have gone undetected using our manual methods. In brain slice preparations, intracellular recordings from bushy cells show that the excitatory postsynaptic potential produced by electrical stimulation of the auditory nerve is followed by a later inhibitory postsynaptic potential (30, 52). These physiological findings are consistent with anatomical observations that bushy cells receive inputs other than those of auditory nerve fibers (9, 46). Some of these noncochlear inputs appear to be GABAergic (1). Thus, physiological and anatomical evidence suggests that at least some bushy cells may be more complex than previously thought.

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