

Two Separate Inhibitory Mechanisms Shape the Responses of Dorsal Cochlear Nucleus Type IV Units to Narrowband and Wideband Stimuli

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SUMMARY AND CONCLUSIONS

1. The principal cells of the dorsal cochlear nucleus (DCN) are mostly inhibited by best frequency (BF) tones but are mostly excited by broadband noise (BBN), producing the so-called type IV response characteristic. The narrowband inhibitory responses can be explained by the inhibitory influence of interneurons with type II response characteristics. However, it is not clear that all the details of the type IV responses can be accounted for by this neural circuit. In particular, many type IV units are inhibited by band-reject noise (notch noise); type II units tend to be only weakly excited by these stimuli, if at all. In this paper we study the relationships between the narrowband, inhibitory and the wideband, excitatory regimes of the type IV responses and present the case for the existence of a second inhibitory source in DCN, called the wideband inhibitor (WBI) below.

2. Type IV units were studied using pure tones, noise bands arithmetically centered on BF, notch noise centered on BF, and BBN. We measured the rate-level function (response rate as function of stimulus level) for each stimulus. This paper is based on the responses of 28 type IV units.

3. Evidence for low-threshold inhibitory input to type IV units is derived from analysis of rate-level functions at sound levels just above threshold. Notch noise stimuli of the appropriate notch width produce inhibition at threshold in this regime. When BBN is presented, this inhibition appears to summate with excitation produced by energy in the band of noise centered on BF, resulting in BBN rate-level functions with decreased slope and maximum firing rate. A range of slopes and maximal firing rates is observed, but these variables are strongly correlated and they are negatively correlated with the strength of the inhibition produced by notch noise; this result supports the conclusion that a single inhibitory source is responsible for these effects.

4. By contrast, there is a weak (nonsignificant) positive correlation between the strength of the inhibitory effect of notch noise and the slope/maximal firing rate in response to narrowband stimuli, including BF tones. The contrast between this positive nonsignificant correlation and the significant negative correlation mentioned above suggests that more than one inhibitory effect operates: specifically, the type II input is responsible for inhibition by narrowband stimuli and a different inhibitory source, the WBI, produces inhibition by notch stimuli.

5. Several lines of evidence are given to show that type II units cannot produce the inhibition seen with notch noise stimuli. First, inhibitory effects are seen at notch widths well beyond estimates of the bandwidth of type II inhibitory inputs; second, the threshold of inhibition produced by notch noise stimuli is usually well below that of type II units for noise; and third, the firing rate of type II units decreases monotonically as the bandwidth of a narrow noise

band is widened, whereas the peak response rate of type IV units can increase, decrease, or vary nonmonotonically under the same conditions.

6. Type IV units can be classified along two continua, according to their responses to narrowband stimuli on the one hand and to wideband stimuli on the other. Units differ along each continuum in the strength of inhibitory effects for narrowband or wideband stimuli, respectively. There may be an inverse relationship between the two continua, although the relationship is not statistically significant in the data of this paper.

7. A qualitative model for DCN is given that is capable of explaining the known results. In the model, type IV units receive strong inhibitory inputs from type II units that dominate for narrowband stimuli and weak inhibitory inputs from the WBI that dominate only when the excitatory input to type IV units is weakened by a noise notch. For either narrow peaks or narrow notches, type IV units give inhibitory responses. We therefore hypothesize that type IV units are detectors of sharp spectral features in acoustic stimuli. In this way they may direct the attention of higher auditory centers to those parts of the spectrum that carry interesting information about natural sounds.

INTRODUCTION

The dorsal cochlear nucleus (DCN) of the cat is a layered structure, with some similarities to the cerebellum (Berrebi and Mugnaini 1991; Mugnaini and Morgan 1987). It has an intricate internal circuitry, with many interneuron types, most of which are inhibitory. Although the DCN receives auditory nerve fiber input (Ryugo 1992), it also receives input from other sources, including other divisions of the cochlear nucleus (Adams 1983; Smith and Rhode 1989; Snyder and Leake 1988), higher stations of the auditory pathways (Conlee and Kane 1982; Kane 1977; Kane and Finn 1977; Spangler et al. 1987), and nonauditory sources. One nonauditory source is a projection from the somatosensory dorsal column nuclei that reaches the granule cell domains of the DCN (Itoh et al. 1987; Weinberg and Rustioni 1987).

DCN principal cells display the so-called type IV response characteristic (Evans and Nelson 1973; Young and Brownell 1976), which is dramatically different from auditory nerve responses to sound. The principal difference is that type IV units give predominantly inhibitory responses to tones, including tones at best frequency (BF). Spirou

and Young (1991) studied the responses of type IV units to tones across a range of frequencies and sound levels (tone response map). In the face of considerable variability, they noted some common features in the arrangement of excitatory and inhibitory regions in type IV units. Some of the common features could be explained by assuming that type IV units receive excitatory auditory nerve input and inhibitory input from a DCN inhibitory interneuron. The interneuron in this model is the type II unit, which is most likely recorded from vertical or tuberculoventral cells (Young 1980), a class of glycinergic DCN interneuron (Lorente de Nò 1981; Osen et al. 1990; Saint Marie et al. 1991; Wickesberg and Oertel 1988). Type II units do not show spontaneous activity and are activated strongly by tones (Young and Brownell 1976). The hypothesis of an inhibitory type II-type IV synapse is supported by cross-correlation analysis of DCN type II and type IV units (Voigt and Young 1980, 1990). However, other parts of the tone response maps, mostly above-BF inhibitory regions, could not be explained by this mechanism.

Responses to broadband noise (BBN) stimuli have been important in studying DCN unit properties. Despite the predominance of inhibition in their tone response maps, type IV units give excitatory responses to BBN. Consistent with the model in which type II units inhibit type IV units, type II units give little or no response to BBN (Young and Voigt 1982).

Spirou and Young (1991) discovered another intriguing property of type IV units: many of them are inhibited by band-reject (notch noise) stimuli, in which a narrow band of frequencies around the unit's BF is filtered out from a BBN. This result is surprising because the tone response map suggests that a narrow band of energy overlying the type IV unit BF is inhibitory by itself; therefore subtracting such a band from a wideband stimulus should not make the wideband stimulus more inhibitory, which is the experimental result. Spirou and Young tried to explain the notch inhibition using the type II-type IV inhibitory circuit; subsequent results suggest that this explanation is insufficient (Young et al. 1992), that is, the responses of type II units are inappropriate for explaining the inhibition of type IV units by notch noise. One goal of this paper is to bring quantitative evidence to bear on this issue.

In this paper we address the apparent contradiction between the narrowband behavior of type IV units, in which narrow bands of energy overlying BF are inhibitory, and their wideband behavior, in which narrow bands of energy overlying BF are excitatory (as judged by the effect of their subtraction from a wideband stimulus). To study this transition we used many different sounds—pure tones, noise bands of various bandwidth, BBN, and notch noise with various notch widths. In this paper we concentrate on the rate-level functions to the various stimuli and the relationships among them. We conclude from the analysis that type II inhibitory input is insufficient to account for inhibitory responses to notch noise, and suggest that a recently described unit type in the ventral cochlear nucleus, the onset-C unit (Palmer and Winter 1993; Rhode and Smith 1986) serves as a wideband inhibitor (WBI) in DCN for both type II and type IV units.

METHODS

Animal preparation and unit recording

Fourteen adult cats (1.5–4 kg) selected to have clean external ears, translucent tympanic membranes, and no signs of middle ear infection were used in these experiments. The methods used here are standard and were described previously (Spirou and Young 1991). Briefly, animals were injected with atropine (0.1 mg im) to control mucus secretions. Anesthesia was induced by an injection of xylazine (0.1 mg im) followed by ketamine (75–100 mg im). After tracheotomy, each animal was placed in a head holder. Body temperature was maintained at 37–39°C with a heating pad under feedback control. An opening was made in the bone over the left parietal cortex; the cortex and caudal hippocampus were aspirated to reveal the midbrain and caudal thalamus. Decerebration was performed by aspiration through the superior colliculus under visual control. No anesthetic was given after decerebration. During the recording session, small intravenous injections of physiological saline (3–5 ml) were given every few hours to help preserve fluid volume. Some animals developed respiratory problems after decerebration. These animals were paralyzed with gallamine triethiodide (10 mg/h iv) and artificially ventilated. The expiratory CO₂ was continuously monitored (Beckman LB-1) and maintained between 4.5% and 5.5% by controlling the respiratory volume and rate.

After decerebration the animal was placed in an electrically shielded double-walled soundproof room (IAC-1204A). The left external meatus was exposed and transected and the animal was mounted in a stereotaxic frame supported by hollow ear bars and a metal plate attached to the frontal skull. To equalize pressure on the tympanic membrane, the bulla was vented by boring a small hole in it with a number 11 scalpel blade and inserting a 30-cm length of PE-90 tubing. The DCN was exposed by drilling through the bone lateral to the foramen magnum after removal of the occipital condyle (Young and Brownell 1976). No aspiration of neural tissue is needed with this approach.

Platinum-iridium microelectrodes were used to record single units. The electrodes were positioned on the surface of the DCN under visual control. They were oriented at an angle of ~35° elevation and ~10° azimuth, approximately parallel to the isofrequency planes in the DCN, and passing through the center of the DCN (Spirou and Young 1991). To achieve stability we infiltrated the exposure with agar. When the agar hardened it provided a hydraulic seal of the exposure.

Acoustic stimuli

Pure tones, BBN, noise bands, and notch noise were the stimuli used in these experiments. All stimuli were 200 ms long with 10-ms rise-fall times and a 1-s repetition period. Sound was delivered from an electrostatic driver to the left (ipsilateral) ear through a hollow ear bar (Sokolich 1977). Acoustic calibrations at the eardrum were performed for each animal by sweeping a tone between 0.04 and 40 kHz and measuring the resulting sound pressure level (SPL) with a probe tube near the tympanic membrane.

Noise band stimuli were generated by low-pass filtering two independent BBNs (from Elgenco model 3602 noise generators) at 48 dB/octave, with high cutoff f_h . The filtered noises were multiplied by quadrature tones at the desired center frequency of the band (i.e., one by $\cos 2\pi f_0 t$, the other by $\sin 2\pi f_0 t$) and the outputs of the multipliers were added, thereby creating a stationary noise band centered at frequency f_0 with a bandwidth of $2f_h$ (Fig. 1A). Quadrature modulation is necessary to ensure stationarity of the noise signal (Schalk and Sachs 1980). In fact, the signal at the output of either the $\cos 2\pi f_0 t$ or the $\sin 2\pi f_0 t$ multipliers must go identically to 0 twice per cycle, giving a temporal fluctuation in the noise variance; adding the two quad-

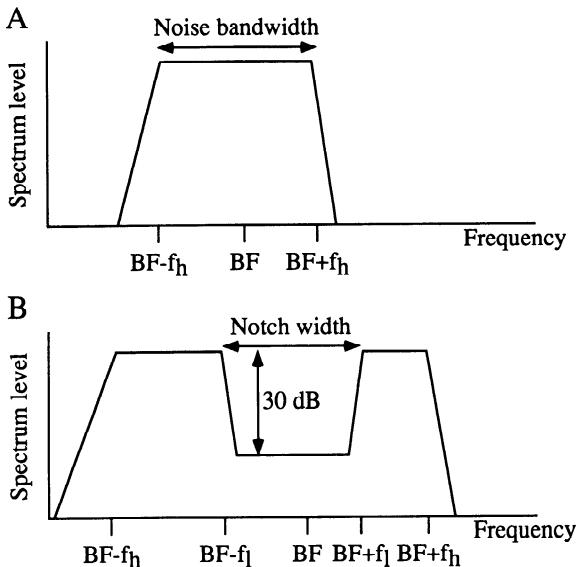


FIG. 1. A: schematic representation of a noise band spectrum. The noise band is arithmetically centered on the best frequency (BF). The top edge of the band has a slope >48 dB/octave. The bottom edge of the band is shallower and depends on BF and on the width of the band. The band half-width (f_h) could be set between 0.1 kHz and BF. B: schematic representation of a notch noise spectrum. The notch is arithmetically centered on BF and has a depth of ≥ 30 dB. It is generated within a wide noise band that is also arithmetically centered on BF. In most cases f_h was slightly smaller than BF. The notch half-width (f_1) could be set between 0.1 kHz and f_h .

nature signals gives a noise whose variance is constant in time. Notch noise stimuli were generated similarly, by band-pass filtering the two independent BBNs at 24 dB/octave, with low cutoff f_1 and high cutoff f_h , then modulating the resulting bands in quadrature to the desired center frequency of the notch. The width of the notch is $2f_1$ and the total bandwidth of the noise is $2f_h$ (Fig. 1B). The level of the carrier tone at the center of the notch was ≥ 30 dB below the spectrum level of the noise. Examples of measured spectra of notch noise are shown in Fig. 1 of Spirou and Young (1991).

Experimental protocol

Tones around the BF of the unresolved neural background activity from the electrode were used to search for units. When a unit was isolated, its BF and threshold were determined manually. Rate-level series for responses to BF tones and BBN were collected, covering a 100-dB range in 1-dB increments. On the basis of these data, the unit's response type (type II, I/III, III, or IV) was determined by the criteria described by Young (Young 1984). Of 110 units characterized in this way, 57 were type IV (52%), 20 were type II (18%), and 33 were type III or I/III (30%); these proportions are similar to those previously published (Voigt and Young 1990; Young and Brownell 1976). This paper is based on 28 type IV units whose responses were measured in response to a variety of additional stimuli, including non-BF tones, BBN, noise bands, and notch noise. Data from 13 type II units whose rate-level functions to tones and BBN were measured reliably are also presented here.

The unit's response map was generated using tonal stimuli, as described in Spirou and Young (1991), except that 200-ms tone bursts (1 per second) were used here. Each attenuation-frequency combination was presented once. Response maps are plotted as discharge rate versus frequency at a succession of constant attenuations (e.g., Figs. 2C and 3C).

For the noise bands and notch noise stimuli, data were taken as rate-versus-level functions for a series of bandwidths and notch widths. Usually noise band data were taken first, starting at a bandwidth of 200 Hz, doubling the bandwidth each time, up to the maximal possible bandwidth (about twice the unit's BF, Fig. 1A). After the noise band series a notch noise series was taken, usually starting with a notch width of 250 Hz and doubling it each time, up to the maximal possible notch width; the maximal notch width was slightly smaller than the total noise bandwidth, which was set to approximately twice the BF (Fig. 1B). Between each series of stimuli, BF tone and BBN rate-level functions were obtained to verify stability of the unit. All data included here were stable as judged by informal comparisons of the BF tone and BBN rate-level functions measured during the experiment.

Stimulus levels are given in several different ways, depending on the stimulus and measurement paradigm: 1) as dB attenuation in response maps (0 dB attenuation is ~ 100 dB SPL), because the tone level was not corrected for the acoustic calibration; 2) as dB SPL (dB re 20 μ Pa) for tone rate-level functions; 3) as total stimulus power (dB re 20 μ Pa) for noise bands in some cases; or 4) as noise spectrum level in the passband for BBN, noise bands, and notch noise rate-level functions. Noise spectrum level is the energy in a 1-Hz band at unit BF and at the level of the noise passband and is specified in units of dB re 20 μ Pa/ $\sqrt{\text{Hz}}$.

RESULTS

General characteristics of type IV and type II responses

The apparent incompatibility between the responses of type IV units to tones, BBN, and notch noise is illustrated in Fig. 2. Figure 2A shows rate-level functions to BF tones and to BBN. At low levels the response to the BF tone was excitatory. However, at >15 dB re threshold the response decreased and was inhibited at levels >30 dB re threshold. The BBN rate-level function, on the other hand, was weakly excitatory at most levels tested. From the fact that BBN excited the unit, whereas BF tones inhibited it at high levels, one might conclude that off-BF tones were highly excitatory, so that they swamped the inhibitory effects of the BF tone. If this model were correct, filtering out a frequency band around BF should increase the excitatory drive of the BBN. In Fig. 2B, rate-level functions in response to notch noise stimuli are presented. The notch noise rate-level functions are inhibitory, and therefore the hypothesis that off-BF tones were excitatory is manifestly wrong. To further demonstrate this point, Fig. 2C shows the tone response map of this unit: the response of the unit to tone bursts is shown as function of frequency and level. It may be seen that the unit was inhibited by most combinations of frequency and level. Therefore a linear energy summation model predicts that the unit should be inhibited by most wideband stimuli. However, as is shown in Fig. 2A, BBN actually excited the unit. The incompatibility between type IV response maps and their responses to notch noise was studied in depth by Spirou and Young (1991).

Figure 3 is an example of another variant of the type IV response. This unit had the typical nonmonotonic rate-level function to BF tones and was excited by BBN (Fig. 3A). Whereas the unit in Fig. 2 had a relatively low firing rate in response to BBN, the unit in Fig. 3 had a robust response to BBN, about as strong as its maximal response to BF tones. It was also inhibited by notch noise, but at threshold sound levels the inhibition appeared only at wider

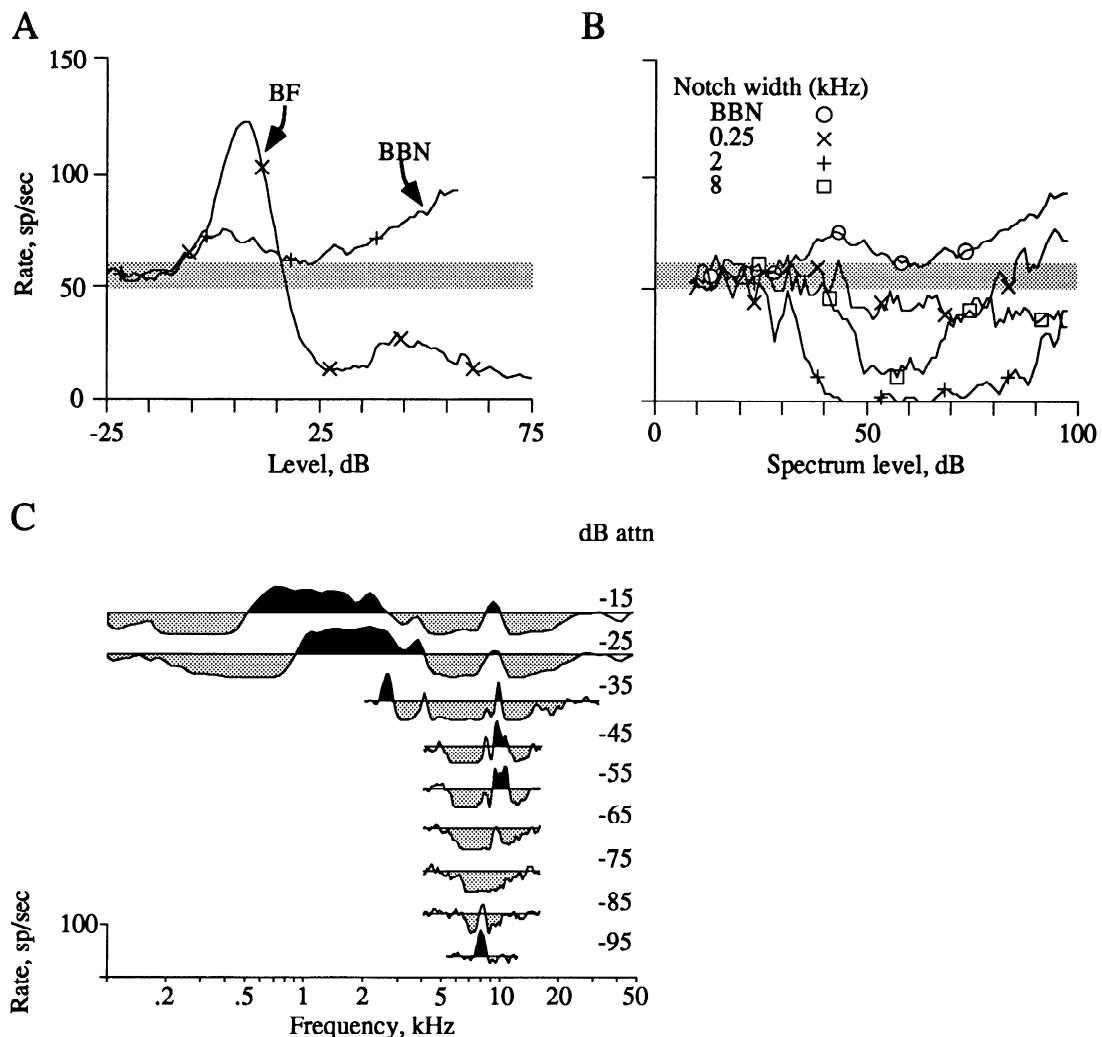


FIG. 2. *A:* BF and broadband noise (BBN) rate-level functions for a type IV unit. The unit's BF was 8.16 kHz. Gray bar: spontaneous rate range. Abscissa: dB SPL for the BF tone only; BBN curve was shifted into alignment with BF tone curve at threshold. *B:* responses of the same unit to notch noise. The bandwidth of the noise was 16 kHz, arithmetically centered on BF. The notch widths are marked on the figure. Note that the responses to all three notch widths were inhibitory at threshold. *C:* tone response map of the same unit, presented as function of frequency and level. Each line is the response rate of the unit to a series of 200-ms tone bursts at various frequencies at a fixed attenuation level; the attenuation was decreased by 10 dB between successive lines. Horizontal line in each plot: average spontaneous rate. Shaded regions: inhibitory responses. Black regions: excitatory responses. Note that the unit was inhibited by most combinations of frequency and level.

notch width (~ 4 kHz). Despite its stronger responses to noise stimuli, the tone response map of this unit (Fig. 3C) was even more inhibitory than the responses of the unit shown in Fig. 2. One result in this paper is that the noise responses of the two units in Figs. 2 and 3 are at the end points of a continuum of type IV units with correlated responses properties to all the noise stimuli used in this study. The unit in Fig. 2 is an example of those units that are weakly excited by BBN and are sensitive to the narrowest notch widths tested; the unit in Fig. 3 is an example of those units that are relatively strongly excited by BBN and are inhibited only by wider notches, if at all. We do not mean to imply here that there is a correlation between response map properties and noise responses; so far, no consistent relationships of this type have been identified.

In our sample of 28 type IV units, 26 were like the units in Figs. 2 and 3 in that they were inhibited by BF tones at the highest tested levels. The other two were excited at low

levels, inhibited at medium levels, and then excited again at high levels. All units were excited to some degree by BBN. Five units showed inhibitory components in the response to BBN: four of them were inhibited by BBN at high levels, and one unit was inhibited by BBN at threshold sound level. Tone response maps were measured for 20 of 28 type IV units. All of them showed a low-level excitatory area around BF that was transformed into an inhibitory area at higher levels [the central inhibitory area as defined by Spirou and Young (1991)—in fact, the central inhibitory area is the defining feature of the type IV units]. All units except one (the unit in Fig. 3) showed a weakening of the inhibition in a narrow frequency range above their BF at higher levels. In some cases this frequency region became excitatory again (upper excitatory region), as for the unit in Fig. 2 at ~ 10 kHz. All units except one had an upper inhibitory sideband.

It has been hypothesized that type II units are responsible

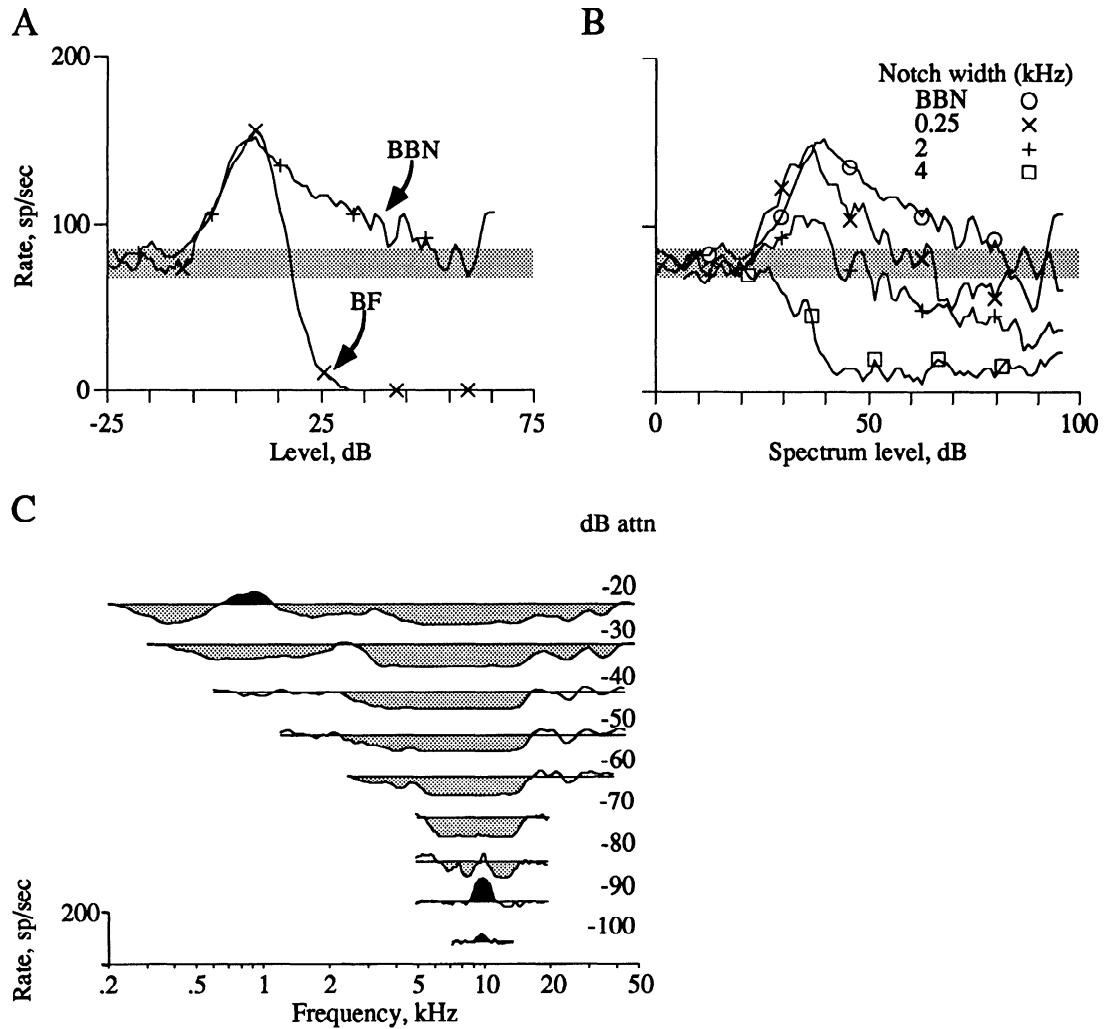


FIG. 3. *A*: BF and BBN rate-level functions for a type IV unit. The unit's BF was 9.77 kHz. The responses to tones were completely shut off at high levels. Abscissa: dB SPL for BF tone only; BBN curve was shifted into alignment with BF tone curve at threshold. *B*: responses of the same unit to notch noise. The response became inhibitory at low levels when the notch width reached 4 kHz (compare with Fig. 2*B*). *C*: tone response map of the same unit (see Fig. 2*C* for explanation). This unit did not exhibit any excitatory response components between 20 and 70 dB re threshold.

for much of the inhibitory response of type IV units to tones (Spirou and Young 1991; Voigt and Young 1990; Young and Brownell 1976). Figure 4 presents the responses of a typical DCN type II unit to BF tones, BBN, and notch stimuli. The unit does not have spontaneous activity. Its responses to BF tones are strong, with a characteristic non-monotonic rate-level function (Fig. 4*A*). The responses to noise are much weaker in comparison (Fig. 4*A*). Notch stimuli excited the unit even less than BBN when the notch was centered on the unit's BF (Fig. 4*B*).

Type II units may still be activated by notch stimuli when the notch frequency is above or below BF. Figure 4*C* shows the responses of four type II units to notches of a fixed width with varying center frequencies (these are all the type II units in our sample that were studied with this type of stimulus). The frequency axis is given as octaves re BF and the rate axis is scaled by each unit's maximal response to BF tones. The units are completely silent when the notches overlie their BF. Therefore type II units are unable to inhibit type IV units with similar BFs when stimulated by notch noise. Figure 4*D* is a concrete example of this situa-

tion. It shows the responses of a type II unit (different than the one documented in Fig. 4, *A* and *B*) and a type IV unit to a notch of a fixed width with varying center frequency. These two units were studied in the same penetration at close proximity. The type II BF (2.2 kHz) is slightly lower than the type IV BF (2.62 kHz); therefore the type II unit has the properties of units most likely to inhibit the type IV unit on the basis of cross-correlation evidence (Voigt and Young 1990). The type II unit was inactive over most of the range of notch center frequencies that inhibited the type IV unit. Comparisons of this kind suggest that type II units cannot provide the inhibitory input to type IV units to produce notch inhibition. However, a firm conclusion cannot be drawn from data like those in Fig. 4*D* without more quantitative evaluation.

Model of type II and type IV responses

In this paper we present the case for the existence of a second source of inhibition to type IV units. Figure 5 shows a hypothesis for a circuit that can explain the data in Figs. 2–4. It consists of a tonotopically organized input, repre-

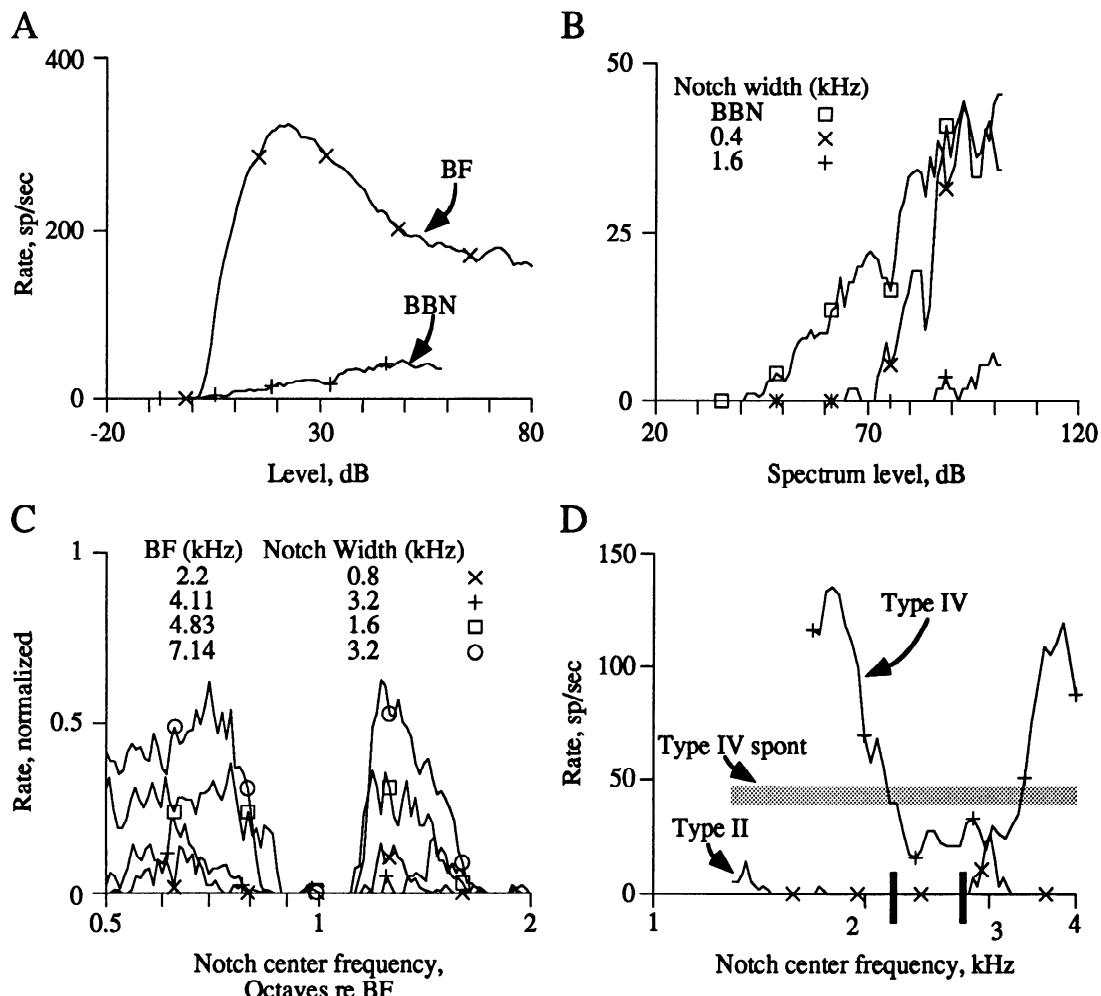


FIG. 4. *A*: responses of a type II unit to BF tone and BBN. The unit's BF was 2.2 kHz. Note the characteristic nonmonotonicity of the BF rate-level function and the relatively weak responses to BBN. Abscissa: dB SPL for BF tone only; BBN curve was shifted into alignment with BF tone curve at threshold. *B*: responses of the same unit to notch noise. Note the change in ordinate scale from *A* to *B*. As the notch widened, the unit decreased its firing rate at all levels, as expected from the decrease in the excitatory drive to the unit. *C*: responses of 4 type II units to notches of fixed width and varying center frequency at a fixed spectrum level (different for each unit). Abscissa: notch center frequency divided by the unit's BF. Ordinate: firing rate of the unit divided by the maximal firing rate of the unit to BF tones. When the notch center frequency is close to BF (normalized center frequency close to 1) the units are almost completely silent. *D*: responses of a type II unit (different from that shown in *A* and *B*) (\times) and a type IV unit (+) to a notch stimulus with varying notch center frequency at a fixed spectrum level (-18 dB in passband). Type II unit BF was 2.2 kHz, and type IV unit BF was 2.62 (heavy lines on abscissa); notch widths were 1.6 kHz in both cases. Units were recorded in the same penetration at close proximity to each other. Note that the type II unit is almost completely shut off when the notch covers its BF; the type IV unit is also inhibited when the notch covers its BF.

sented by the horizontal line at the bottom, type II and type IV units, and a WBI. The WBI inhibits both type II and type IV units. It is assumed to be weakly excited by tones and strongly excited by noise. The WBI strongly inhibits the type II units, producing their weak BBN responses. The effects of the WBI on type IV units, on the other hand, are postulated to be weaker, for reasons explained below.

Narrowband stimuli are assumed to excite the WBI only weakly, and the major interactions are between the excitatory input and the type II and type IV units. Type II units are known to have a somewhat higher threshold to tones than type IV units (Young and Brownell 1976); this fact is not explicitly accounted for by the model but could arise through specific input connections to type II units from high-threshold excitatory inputs or from spontaneously active inhibitory inputs. At low levels the type IV units are

excited by the tonotopic input and the type II units are silent; once the type II units are activated their strong inhibitory effect on the type IV units causes the type IV units to decrease their firing rate and eventually be shut off. This produces the central inhibitory area of type IV units, as previously described (Spirou and Young 1991).

When the circuit is excited by wideband stimuli, on the other hand, the WBI is strongly active and suppresses the type II unit. As a result the excitatory drive on the type IV units is uncovered. The WBI is assumed to affect type IV units only weakly, not enough to reverse the excitatory drive, and therefore type IV units are excited by BBN. However, when the excitatory drive is weakened, as is the case with notch noise, the WBI is strong enough to suppress the spontaneous activity of the type IV units, producing the inhibitory responses to notch noise.

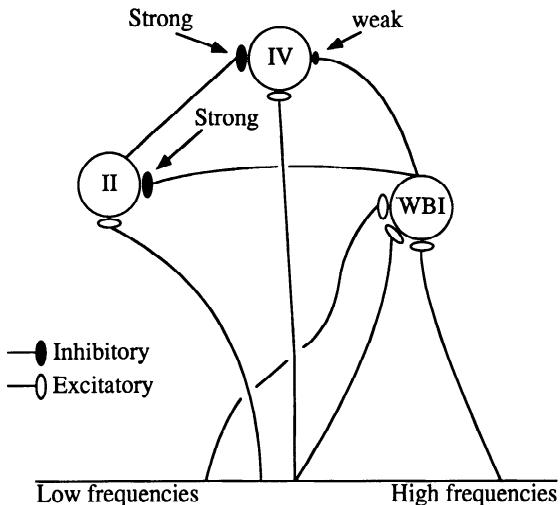


FIG. 5. Possible model of the dorsal cochlear nucleus (DCN) circuitry that explains many features of type II and type IV responses to sound. It consists of type IV units, type II units, and a hypothesized inhibitory interneuron, the wideband inhibitor (WBI). Empty ovals: excitatory connections. Filled ovals: inhibitory connections. The size of the connection is proportional to the strength of the synapse. Horizontal line at bottom: input tonotopic array, e.g., auditory nerve fibers. Auditory nerve connections to DCN units are shown originating at the point corresponding to their BF. The type II-type IV interaction is well established in the literature (Voigt and Young 1990). The WBI must have the following properties: it responds weakly to tones and strongly to wideband noise; its integration bandwidth in response to noise is wide and is distributed in a way that is consistent with Figs. 9 and 10; its threshold to BBN is low, comparable with the threshold of type IV units, and is consistent with Fig. 11A. The WBI inhibits the type II units strongly but the type IV units only weakly. In this figure the same WBI is shown to inhibit both type II and type IV units; however, there may be different populations connected to type II and type IV units. Further explanations in the text.

In the rest of the paper we will present evidence supporting the existence of the wideband inhibition on type IV units. We will show first that a low-threshold, wideband inhibition contributes significantly to the shaping of the responses of type IV units to the stimuli used in this study. Then we will show that properties of type II units are incompatible with the properties of this wideband inhibition.

Existence of the WBI

The most direct evidence for the existence of low-threshold, wideband inhibition is shown in Fig. 6. Figure 6A shows the responses of a type IV unit to an 0.8-kHz noise band centered on 5.9 kHz, the unit's BF (—), and to a 1 kHz wide notch noise, also centered on the unit's BF (---). These stimuli were chosen as a pair whose sum approximates BBN; the reason that the noise band width is slightly smaller than the notch width is the relatively shallow slope of the edges of the band and the notch. The responses to the noise band are excitatory at low levels and inhibitory at high levels, like the responses to a BF tone. The responses to the notch noise are inhibitory. The responses to the two stimuli are shown as functions of the spectrum level in their passband. The threshold of the inhibitory responses to the notch is seen to be at approximately the same spectrum level as the threshold of the excitatory responses to the noise band.

In the model of Fig. 5, the inhibitory response to the

notch noise is produced by the WBI and the inhibitory response to the noise bands at higher levels is produced by type II input. The rate-level functions in Fig. 6A suggest that BBN should activate both excitatory inputs (as for the noise bands that contain energy near the unit's BF) and inhibitory inputs (as for the notch noise that contains energy in flanking frequency regions). Assuming linearity (which is expected to hold at low stimulus levels), the response to the wide noise band should be the sum of the responses to the narrow noise band and the notch noise. Figure 6B shows a comparison between the prediction of this linear model (---) and the actually measured responses to a wide noise band (—). The fit is good up to ~20 dB above threshold, when an inhibitory component appears in the prediction that is not present in the data. This inhibitory component is probably caused by type II units responding to the narrow noise band.

Two other examples of this phenomenon from two other units are shown in Fig. 6, C and E (responses to noise band and noise notch), and D and F (linear prediction and measured responses to a wide noise band). Figure 6, C and D, is an extreme example, in which the inhibition was so strong that it caused an increase in threshold of the BBN responses (threshold approximately -40 dB in Fig. 6C but -25 dB in Fig. 6D). This type of interaction, in which excitatory narrowband responses interacted with inhibitory notch responses to generate approximately the responses to wide noise bands at low levels, was seen in 10 of the 26 units studied both with notch noise and with noise bands in this study. In the other units, the linear model was still a good approximation at low levels, but the responses to the notch stimuli were either excitatory at low levels or had a higher threshold than the noise band responses, so that summation of an excitatory noise band response and an inhibitory notch noise response could not be tested.

The examples in Fig. 6 suggest that the effect of the low-threshold inhibition on the responses to BBN is to reduce the slope of the rate-level function and also to reduce the firing rate at the turning point (the level at which the BBN rate-level function has a local maximum or an abrupt decrease in slope). To study this point quantitatively, all the repetitions of the BF tone and BBN rate-level functions from each unit were averaged. For each BF rate-level function, the maximal firing rate and the initial slope were determined. To determine the initial slope a linear regression line was fit to all the data points on the rising phase of the rate-level function between threshold and the maximal rate. To determine threshold the range of sound levels between the lowest level tested and the peak of the rate-level function was considered; threshold was defined as 1 dB louder than the highest sound level that drove the unit at <1 SD above the spontaneous rate within this range. For the two units that were excited at high levels by BF tones, the analysis was performed using the low-level peak only. The turning point of the BBN rate-level functions was determined manually and the initial slope was determined by the same algorithm as described above.

Figure 7A is a scatter plot of the slope versus maximal firing rate for BF tone rate-level functions; Fig. 7B is a scatter plot of the same variables for BBN rate-level functions.

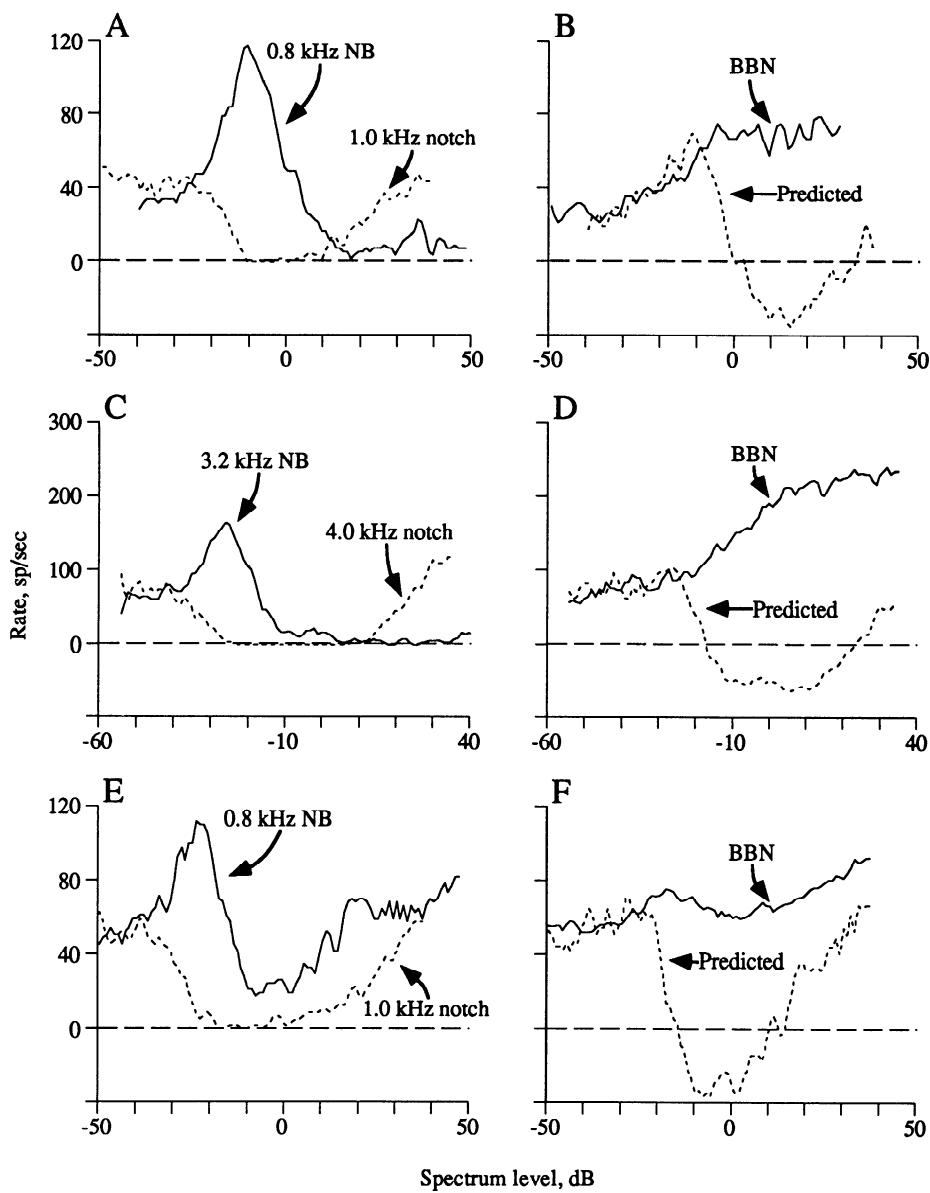


FIG. 6. Demonstration of the existence of wideband, low-threshold inhibition on type IV units. *A*: 0.8-kHz noise band rate-level function (BF 5.9 kHz, —) and a 1-kHz notch noise rate-level function (---). *B*: predicted response to wideband noise based on a linear summation of the 2 curves in *A* (—) and the actual measured responses to BBN (—). Note the good fit over the rising portion of the BBN rate-level function, with substantial difference at higher levels. *C* and *D*: same for another unit (BF 16.9 kHz, noise bandwidth 3.2 kHz, notch width 4 kHz). In this case, the low-threshold inhibition actually causes an increase in the unit's threshold to BBN. *E* and *F*: same for another unit [BF 8.16 kHz, noise bandwidth 0.8 kHz, notch width 1 kHz (same unit as in Fig. 2)].

There is a clear correlation between the two variables in both cases: the higher the slope, the higher the maximal firing or turning point rate. This correlation is also clearly illustrated by the BBN rate-level functions shown in Figs. 2*A* and 3*A*. The smallest slope of a BF rate-level function of high-spontaneous rate auditory nerve fibers measured by Sachs and Abbas (1974) is indicated in Fig. 7, *A* and *B*, by a heavy line. The slopes of both BF tone and BBN rate-level functions are significantly smaller than the slopes of the high-spontaneous rate auditory nerve fibers.

The decreased slope might be explained in two ways: first, it could be interpreted as a result of low-threshold inhibition, as suggested by Fig. 6; second, it could be a sign of a low gain in the transmission between the auditory nerve

fibers and the type IV units. If low synapse gain were the only mechanism altering slopes, the slopes of type IV units' rate-level functions in responses to BF tones and to BBN should be highly correlated, because these slopes are essentially the same for high-spontaneous rate auditory nerve fibers (Schalk and Sachs 1980). However, Fig. 7*C*, which is a scatter plot of the two slopes for type IV units, shows that the two are clearly uncorrelated ($r = 0.04$, $df = 26$, not significant). In fact, the slopes of the BBN rate-level functions are generally smaller than the slopes of the BF tone rate-level functions, supporting the hypothesis that there is an inhibitory input specifically activated by wideband stimuli, as predicted by the WBI model. Units for which the slope of the BBN rate-level function is larger than the slope

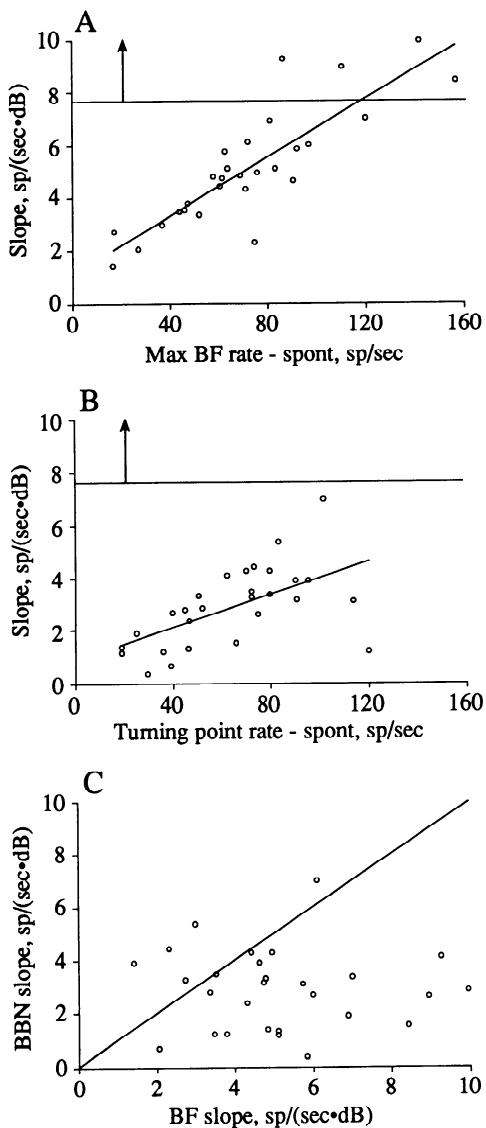


FIG. 7. *A*: scatter plot of the maximum response to BF tones (spontaneous rate subtracted) vs. the initial slope of the same rate-level function. Note the positive correlation between the 2 variables (regression line: $y = 1.124 + 0.0554x$, $r = 0.848$, $df = 36$, $P \ll 0.01$). Horizontal line: smallest slope for high-spontaneous rate auditory nerve fibers (Sachs and Abbas 1974). Note that most type IV unit slopes are significantly smaller than the slopes from auditory nerve fibers. *B*: scatter plot of the turning point rate (spontaneous rate subtracted) of the BBN rate-level function vs. the initial slope of the same rate-level function, for type IV units. The horizontal line is the same as in *A*. Note the positive correlation between the 2 variables (regression line: $y = 0.886 + 0.0313x$, $r = 0.574$, $df = 26$, $P < 0.01$). *C*: scatter plot of the initial slope of BF tone rate-level functions vs. the initial slope of the BBN rate-level functions. Continuous line: 2 slopes are equal. Note the lack of correlation between the 2 variables ($r = 0.04$, $df = 16$, not significant). Note also that the BBN slopes are significantly smaller than the BF slopes, although these slopes are close to each other for high-spontaneous rate auditory nerve fibers (Schalk and Sachs 1980).

of the BF tone rate-level function require a different explanation. One possibility is that this is the effect of very low-threshold type II inhibition (although rare, such type II units can be found, e.g., Young and Brownell 1976), which causes a reduction in firing rate and rate-level function slope for BF tones in a manner that is analogous to the way the WBI affects the BBN rate-level functions.

Two manifestations of the WBI have been described:

first, the inhibition in response to notch noise, and second, the low turning point firing rates (and slopes) of the BBN rate-level functions. If these are really two effects of the same mechanism, they should be correlated. The examples of rate-level functions shown in Figs. 2*B* and 3*B* suggest that such a correlation exists. One possible measure of the notch sensitivity is the minimal inhibitory notch width, the narrowest notch width at which the responses at threshold are inhibitory. To check the generality of the correlation between notch sensitivity and BBN rate-level function shape, a scatter plot of the minimal inhibitory notch width against the turning point rate of the BBN rate-level function is shown in Fig. 8*A*. There is a clear positive correlation between the two variables ($r = 0.522$, $df = 23$, $P < 0.01$), which supports the interpretation that they are caused by a common mechanism, the hypothetical WBI.

Figure 8*B* presents a scatter plot of the maximum rate of the BF rate-level function against the minimum inhibitory notch width. The correlation is negative in this case, although it just misses significance ($r = -0.360$, $df = 23$, not significant). The existence of no or negative correlation in this case argues that the minimum notch width and the maximum rate in response to BF tones reflect different processes; we suggest that the WBI determines the minimum notch width and the BBN rate-level function shape, whereas type II inhibitory input determines the maximum BF tone rate.

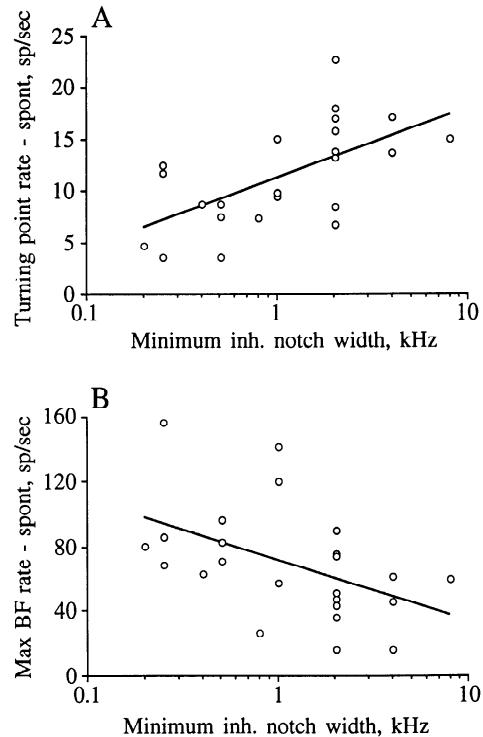


FIG. 8. *A*: scatter plot of the turning-point rate of the BBN rate-level function (spontaneous subtracted) vs. the minimal inhibitory notch width. There is a positive correlation between the 2 variables (regression line: $y = 11.2 + 6.76\log(x)$, $r = 0.522$, $df = 23$, $P < 0.01$). *B*: scatter plot of the maximal response to BF tones vs. the minimal inhibitory notch width. There is a negative but nonsignificant correlation between the 2 variables (regression line: $y = 71.8 - 37.4\log(x)$, $r = -0.360$, $df = 23$, not significant).

Properties of the WBI

The inhibitory source that causes the suppression of the spontaneous activity in response to notch stimuli has not been identified. To get some hints as to its properties, the bandwidth and the threshold of the wideband inhibition were studied.

Type II units are the best studied source of inhibition to the type IV units. They are sharply tuned in frequency, and their threshold to tones tend to be somewhat higher than type IV thresholds (Young and Brownell 1976). The central inhibitory area of the tone map of type IV units is thought to be the effect of type II inhibition (Spirou and Young 1991). The center of the central inhibitory area tends to lie below the unit's BF, and its width is often wider than a single type II tuning curve, suggesting that more than one type II unit inhibits each type IV unit (Spirou and Young 1991; Voigt and Young 1980, 1990). We use the central inhibitory area as a measure of the frequency range over which type II inputs to a particular type IV unit are tuned. Therefore, if a notch that is wider than the central inhibitory area causes a suppression of type IV activity, it must be concluded that the inhibitory drive does not originate exclusively from type II activity, because such a notch would not activate the type II units that have direct inhibitory connection on the type IV unit (e.g., Fig. 4, C and D).

In 16 cases, both the tone response map and the responses to the full range of notch widths were measured. In these cases the maximal inhibitory notch width can be determined as a function of level. This width can then be compared with the width of the central inhibitory area of the same unit at the corresponding tone level. There is some uncertainty in the choice of the spectrum level that is equivalent to a given tone in dB SPL, because such correspondence is based on a somewhat arbitrary choice of an integration bandwidth for the type IV unit. Two ways of choosing the integration bandwidth were used here. One way is to find the thresholds for BF tones and BBN. Under the assumption of linearity near threshold, and assuming that there are no inhibitory interactions strong enough to overwhelm the excitatory effects at low levels, the difference between the thresholds can be translated immediately into an integration bandwidth. In practice, the difference between the two thresholds is used to shift the notch rate-level functions to an equivalent dB SPL scale by equating spectrum levels of the BBN and notch noise passband. The other way to choose the integration bandwidth is to assume that it is fixed at 200 Hz. This assumption is based on the finding that 200-Hz noise bands centered on BF evoke essentially the same responses as BF tones when the response is plotted as a function of stimulus energy instead of stimulus spectrum level (e.g., Fig. 12B). The two estimates deviated in most cases by <10 dB from each other. The integration bandwidth at threshold as measured from the thresholds of the BF tone and BBN rate-level functions was somewhat <200 Hz in most cases. For the following comparison, the more conservative of the two estimates (the one producing smaller shifts) was always used.

Figure 9A shows an example of such a comparison. The widest notch that caused inhibitory responses at each level is superimposed on the unit tone response map (—); the central inhibitory area is also indicated in the figure

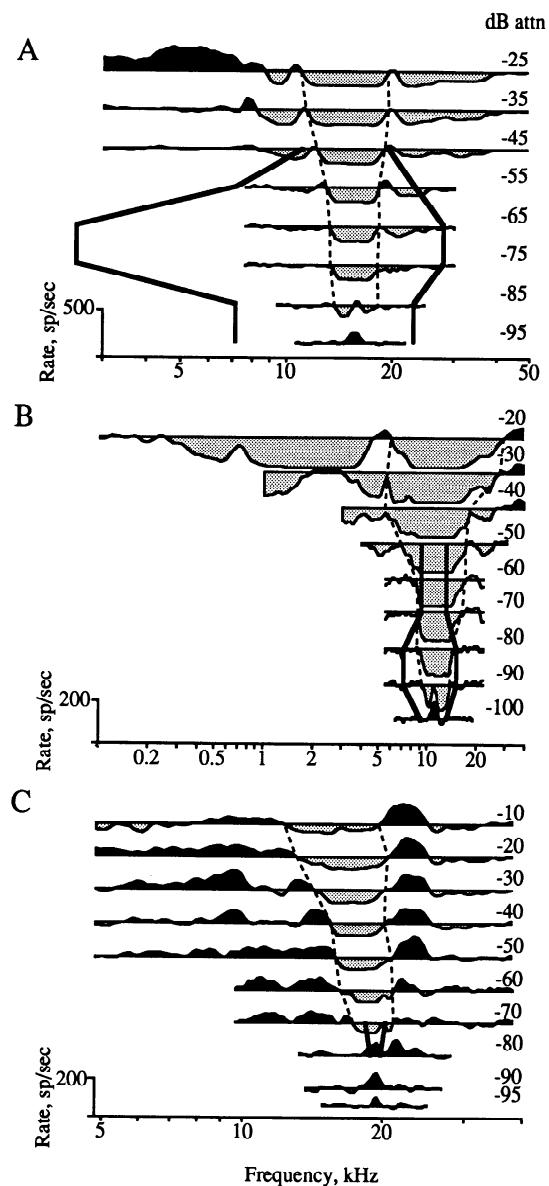


FIG. 9. *A:* tone response map of a type IV unit, with the widest inhibitory notch as function of level. The *bottom* and *top shoulders* of the widest inhibitory notch are marked by the 2 heavy lines plotted as function of level. Dashed lines: boundaries of central inhibitory area. Note that the widest inhibitory notch is wider than the central inhibitory area at all levels (in fact it is wider than any single-tone feature at most levels). At the highest levels, no notch width tested caused any inhibition. Nine of 16 units showed this relationship between widest inhibitory notch and central inhibitory area. *B:* same for another unit. Note that the maximal inhibitory notch is wider than the central inhibitory area at -90 and -80 dB attenuation, but is narrower than the central inhibitory area at higher levels. Five of 16 cases had these features. *C:* same for another unit. Note that this unit is inhibited by notches only over a very small range of levels and bandwidths. The widest inhibitory notches for this unit are within the central inhibitory area. This is one of the 2 of 16 cases that showed such an effect.

(dashed lines). Clearly, at each level the maximum inhibitory notch is wider than the central inhibitory area. This conclusion is not changed by shifts of 10 dB up or down in the equivalence between spectrum level and decibels SPL. It may be concluded that in this case, at all levels, the inhibitory source that suppresses the activity of the unit in response to notch stimuli cannot be exclusively type II units.

Figure 9B shows another example of such a comparison. Here the maximal inhibitory notch width is wider than the central inhibitory area at some levels and narrower at other, higher levels. In this case, as in the previous case, shifts of 10 dB up or down in the equivalent level would not change this conclusion. Therefore in this case also it can be concluded that at least part of the inhibition in response to notches originates from a source other than type II units. Note that in these two examples, in addition to the fact that the maximal inhibitory notch width is wider than the central inhibitory area at least at some levels, there is also a clear qualitative difference in the behavior of the two: whereas the width of the central inhibitory area increases with level, the maximal inhibitory notch tends to decrease at high levels. This is related to the fact that at high levels the notch responses often become excitatory again (Spirou and Young 1991).

Figure 9C is an example in which the maximal inhibitory notch width is smaller than the width of the central inhibitory area of the same unit. This unit was very weakly affected by notches. In fact, the response to notches at threshold was always excitatory, and only the 1- and 2-kHz notches caused some weak inhibition at medium levels.

Of 16 cases in which such an analysis could be made, 9 of 16 were of the type shown in Fig. 9A, 5 of 16 were of the type shown in Fig. 9B, and only 2 of 16 were of the type shown in Fig. 9C. We conclude that for the majority of type IV units type II inputs as expressed in the central inhibitory area are insufficient to explain the inhibition by notch stimuli.

Another way of studying the width of the notch effect is by estimating the effective integration bandwidth of the wideband inhibition and comparing it with an estimate of the maximal bandwidth over which type II units effectively inhibit type IV units. This comparison is weaker than the one in Fig. 9 because it involves comparison of population data, but it could be performed for a larger sample of units. The effective inhibitory bandwidth was estimated by the notch width at which the inhibitory effects started to weaken. In Fig. 2B, for example, this width would be between 2 and 8 kHz; using data at additional notch widths, the inhibition appeared to weaken at ~ 4 kHz. In Fig. 3B it would be >4 kHz. Figure 10 shows a scatter plot of the upper and lower boundaries of the effective inhibitory bandwidth in octaves re BF; because the notches are arithmetically centered on BF, the upper boundary of the notch uniquely determines its lower boundary, causing all the points to fall along a single curved line. The extent of the effective inhibitory bandwidth can be compared with the known extent of the type II inhibition. Voigt and Young (1990) found that type II units showed inhibitory interactions with type IV units whose BFs were ≤ 0.64 octaves above and ≤ 0.4 octaves below their own BF. Spirou and Young (1991) estimated the width of the central inhibitory area from the type IV responses to tones and used this as another estimate of the frequency range over which type II units inhibit type IV units; these bounds can be read from their Fig. 8 to be approximately from 0.5 octaves above BF to 0.8 octaves below BF. These last bounds, which are somewhat larger than the boundaries in Voigt and Young (1990), are shown in Fig. 10. Half the population (10 of 20

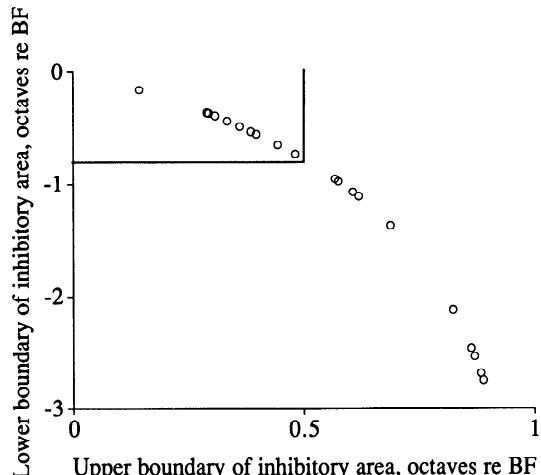


FIG. 10. Scatter plot of the lower and upper boundaries of the effective inhibitory area, measured in octaves re the unit's BF. The effective inhibitory bandwidth is the notch width above which the inhibition started to weaken. These data are derived from notches arithmetically centered on BF, so the upper boundary of a notch determines uniquely its lower boundary, causing all the points to fall on a single curved line. Lines at the *top left corner*: largest measured values of central inhibitory areas (from Spirou and Young 1991). Note that half of the population (10 of 20 cases) has an effective inhibitory area that is wider than the widest measured central inhibitory area. For these units the notch inhibition cannot be explained by type II responses.

cases) has a wider effective inhibitory bandwidth for notch noise than any measure of the bandwidth of type II inhibition.

A second parameter of WBI that can be estimated is threshold. WBI threshold was defined as the minimal inhibitory threshold spectrum level of notch noise. It was determined from the notch rate-level function that showed the deepest inhibition for each unit. In Fig. 2B, for example, the threshold would be estimated from the 2-kHz notch rate-level function; in Fig. 3B it would be estimated from the responses to the 4-kHz notch. The threshold estimation was done by determining the spontaneous rate and its standard deviation, then following the rate-level function from its minimum toward lower levels until the rate became >1 SD below spontaneous rate. This estimate is an upper bound on the actual threshold of the inhibitory source for BBN. The reason for this is that the estimate is made from a notch stimulus, where the notch may also cover the inhibitory source's BF. Therefore the actual excitatory drive on the inhibitory source is lower than when using BBN. However, in all cases the threshold was estimated from a notch that was at least twice as narrow as the estimated inhibitory bandwidth. Therefore, in the worst case, the effective noise components in the stimulus from which the threshold was estimated were half as wide as the full inhibitory bandwidth, which would give a threshold shift of ≤ 3 dB.

Figure 11A is a histogram of the estimated WBI thresholds. For comparison, Fig. 11B is a histogram of the BBN excitation thresholds of 13 type-II units studied in these experiments. It can be seen that, on average, the estimated WBI thresholds (Fig. 11A) are lower than the type-II BBN thresholds (Fig. 11B); in fact, almost all type-IV units for which a WBI threshold could be determined (20 of 22) had inhibitory thresholds that are lower than the median type-II BBN threshold.

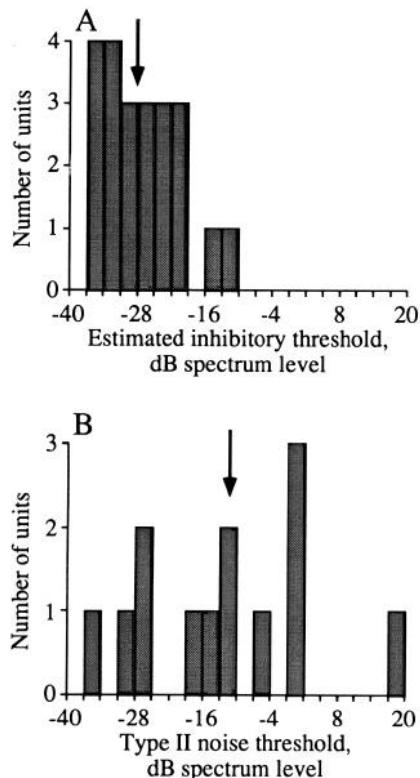


FIG. 11. *A*: histogram of the thresholds of wideband inhibition as judged from the notch noise stimuli. These are given in decibels spectrum level in the passband and are upper bounds on the real threshold of the wideband inhibition, as explained in the text. Arrow: median of the distribution. *B*: histogram of the thresholds to BBN of type II units measured in the same experiments. Arrow: median of the distribution.

More information about the properties of the WBI can be gained by considering the transition between the narrow-band (in which BF is inhibitory, as for tones) and the wide-band (in which BF is excitatory, as for notch noise) regimes of type IV activity. In the model, this transition occurs when the WBI inhibits the type II units. This transition was studied using noise bands arithmetically centered over BF with increasing bandwidths.

Figure 12*A* shows the rate-level functions in response to 0.2-, 0.8- and 5.0-kHz noise bands centered on 2.62 kHz, the BF of this unit. The responses are shown as functions of the spectrum level of the stimulus. The shape of the response to the narrowest noise band was similar to that of the BF rate-level function. As the bandwidth increased, three effects were seen. First, the threshold of the responses decreased with increasing bandwidth. Second, at high levels the response became disinhibited, approaching the response to BBN. Third, the peak response rate decreased with increasing bandwidth. Below, we argue that the first effect has nothing to do with inhibitory inputs, the second is largely produced by type II inputs, and the third reflects activity of the WBI and possibly also type II inputs.

The decrease of threshold with bandwidth is expected if the unit integrates stimulus energy over some finite bandwidth near threshold, because the energy of noise bands with the same spectrum level is proportional to their bandwidth. To test this prediction, the rate-level functions are replotted in Fig. 12*B* as functions of the stimulus energy

instead of the stimulus spectrum level. The BF rate-level function is displayed on the same figure, also as a function of the tone energy. It can be seen that the 0.2-kHz noise band evokes responses that are practically the same as those evoked by tones at all levels. The 0.8-kHz noise band has the same threshold as the tone and the 0.2-kHz noise band in terms of energy.

The disinhibition occurring for the 5-kHz bandwidth in Fig. 12, *A* and *B*, is typical of all type IV units studied. Typically, the discharge rate at 50 dB re threshold remains approximately constant at a low, inhibited level up to a critical bandwidth and then increases rapidly. This effect is most likely due to decreased activity of the type II inhibitory interneuron as noise bandwidth is increased. Figure 13 shows rate-level functions for a type II unit responding to noise bands of various bandwidth. The behavior of this unit is typical of all type II units in that as noise bandwidth increases discharge rate decreases; this point is illustrated in Fig. 14*B*, which shows the maximal discharge rate as function of the noise bandwidth for all type II units studied with noise bands.

For type IV units, the bandwidth at which rapid disinhibition starts is only weakly correlated with BF (data not shown). Some units with high BFs were disinhibited at relatively low bandwidths, whereas other units with low BFs remained inhibited almost up to the highest possible bandwidth (twice the unit's BF). In fact, 7 of 25 type IV units were not completely disinhibited (meaning that the response of the unit was suppressed below spontaneous activity at high enough sound levels) at the highest possible bandwidth. Four of those seven units were inhibited also by BBN at high levels, but three were excited by BBN. It can be concluded that in these last three units the energy region >1 octave above BF contributed to the disinhibition of the responses. This fact suggests that type II units may have very wide inhibitory sidebands; such bands were actually measured in some cases (Spirou and Young 1991).

In addition to type II rate changes with noise bandwidth, there should also be changes in rate of the WBI. Evidence that not all the effects in Fig. 12 can be explained by changes in type II rate is provided by considering the behavior of maximum discharge rate as a function of bandwidth (Fig. 12*C*, —). Figure 14*A* is a population plot of the maximum rate as a function of bandwidth for all 28 type IV units in the sample. Clearly there is considerable variability in the behavior of this parameter. In 5 cases maximum firing rate decreased with bandwidth (as for the unit in Fig. 12), in 9 others the rate increased with bandwidth, and in the remaining 14 it was nonmonotonic. In contrast to the type IV units in Fig. 14*A*, type II units show a monotonic decreasing relationship between any measure of discharge rate and bandwidth (Figs. 13 and 14*B*, already discussed). If type II units were the only inhibitory source on type IV units, then the data in Fig. 14*B* clearly imply that there should be a monotonic increase in maximum discharge rate in the type IV unit data in Fig. 14*A* [see also simulation studies by Pont and Damper (1991)].

Even in some of the nine cases in which the type IV unit maximum firing rate increased as a function of bandwidth, other response properties could be used to exclude type II units as the only inhibitory source. For seven of these nine units, the inhibitory bandwidth could be determined from

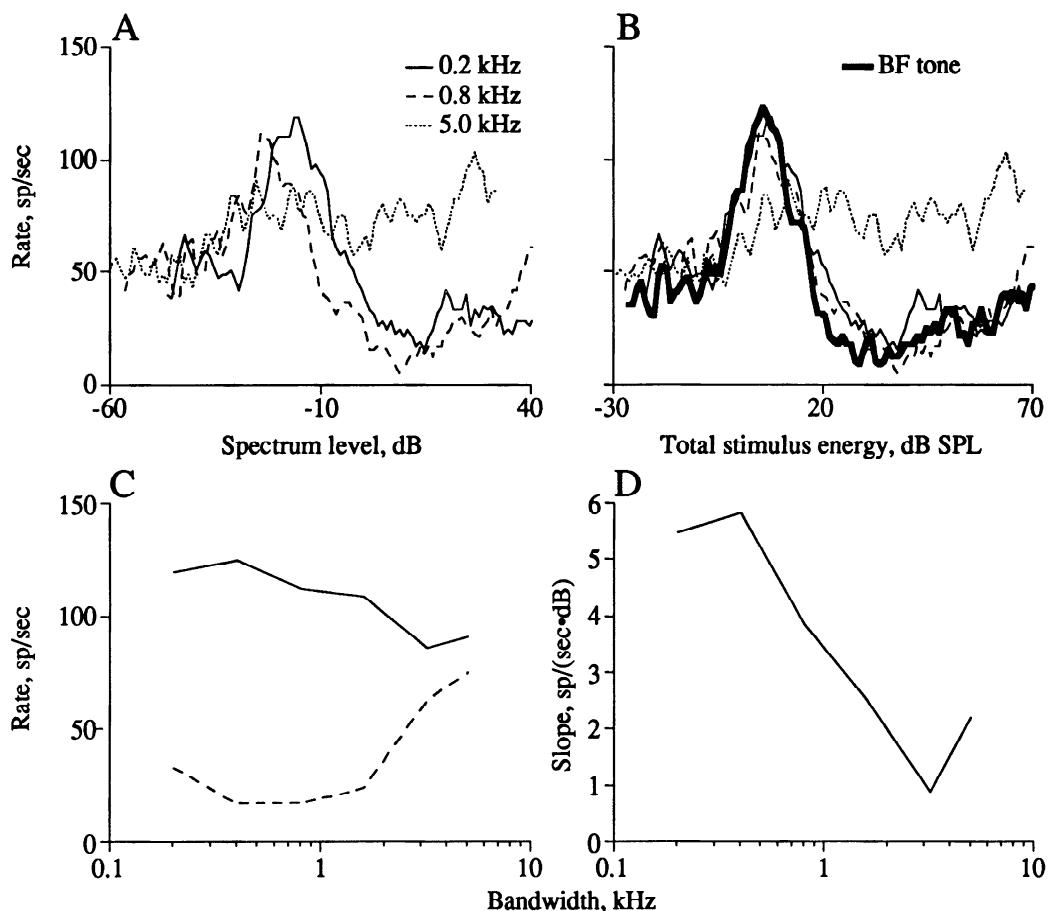


FIG. 12. Analysis of noise band widening experiment. *A*: rate-level functions in response to 3 noise bands arithmetically centered on the unit's BF. Note the decrease in threshold and in maximal firing rate with increase in bandwidth. *B*: same rate-level functions plotted as function of the total stimulus energy. Thick line: responses to a BF tone in the same unit. Note that the 0.2-kHz and 0.8-kHz noise bands have approximately the same threshold. *C*: maximum rate (—) and the rate 50 dB above threshold (---) as functions of bandwidth. *D*: initial slope of the rate-level functions as function of bandwidth.

the notch noise data. Five of the seven units had inhibitory boundaries that were wider than the maximum central inhibitory area, as in Fig. 10. For the remaining two units, one had an inhibitory threshold that was lower than the BBN threshold of any of the type II units measured here and the other one had a threshold that was somewhat higher, but still below that of 70% of the type II population.

The initial slope of the noise band rate-level function was highly correlated with the maximum rate, replicating the result in Fig. 7 for BF and BBN rate-level functions. This is clearly seen in the example in Fig. 12, *C* and *D*, where the two variables increase and decrease together as functions of bandwidth. To demonstrate this for the whole sample, the correlation coefficient between the initial slope as a function of bandwidth and the maximum rate as a function of bandwidth was computed for each unit. The correlation coefficients range from -0.627 to 0.961 ; their mean is 0.399 , which is significantly larger than 0 ($t = 4.36$, $df = 26$, $P \ll 0.001$).

DISCUSSION

General features of type IV responses

The data shown in this paper indicate that type IV responses can be classified along two continua, one related to

their responses to narrowband stimuli and the other to wideband stimuli.

The responses to wideband stimuli (wide noise bands, BBN, and notch noise) show a cluster of properties. Units with strong responses to BBN (high turning point rates and initial slopes of the rate-level functions) show relatively weak notch noise inhibition (they are inhibited only at wider notch widths) and conversely, units with weak responses to BBN show stronger notch inhibition. Moreover, the initial slopes of the BBN rate-level functions are usually smaller than the slopes of high-spontaneous rate auditory nerve fibers, which are a likely source of excitatory input to DCN type IV units. The argument given in connection with Fig. 6 suggests that one probable mechanism for the slope change from input to output in DCN is the existence of inhibitory influences on type IV units, even near threshold. In fact, such an inhibitory mechanism, with variable threshold and strength, can explain the whole cluster of wideband stimulus properties. This inhibitory source would reduce the turning point rate and the slope of the BBN rate-level function; when the unit is presented with notches, the excitatory input is weakened and this inhibitory source would inhibit the unit's activity. Finally, when this source is strong and low threshold, its effect would be manifested at narrower notch widths. On the other hand, when it is

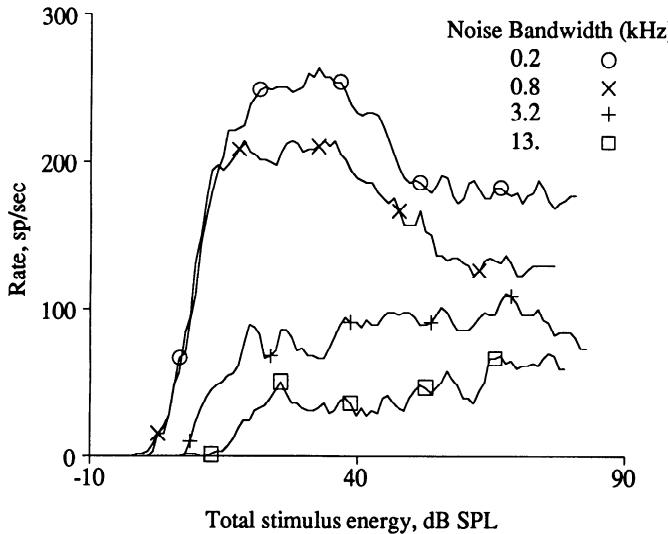


FIG. 13: Rate-level functions from a band-widening experiment on a type II unit (BF 6.88 kHz). Note that the firing rate is a monotonic decreasing function of bandwidth at all levels.

weaker, the unit would respond more vigorously to BBN, and removing narrow noise bands centered on BF from the stimulus would have a smaller effect on its firing rate.

The responses of type IV units to narrowband stimuli, including tones, also show a correlation between initial slope and maximal rate and also show lower initial slopes than are seen in high-spontaneous rate auditory nerve fibers responding to the same stimuli. In the case of narrowband stimuli, evidence like that in Fig. 6 is lacking as to the mechanism of the slope changes. Nevertheless, a similar mechanism, variability in the threshold and strength of an inhibitory input, is a sufficient explanation. In this case the inhibitory source is most probably the type II unit, so the slope variability in type IV BF tone rate-level functions can be explained by the observed variability in type II properties (Young and Brownell 1976; Young and Voigt 1982). However, for narrowband stimuli, the argument against the existence of other effects, such as a variation in the excitatory input, cannot be ruled out. One explanation that can be ruled out, however, is that an excitatory input gain that is <1 is the only mechanism causing the reduction in slopes. Such a low gain should affect responses to both narrowband and wideband stimuli and should produce correlation between the slopes and maximal rates for the two stimulus classes; this correlation is, if anything, negative (Fig. 7C).

The two clusters of properties, in response to wideband and narrowband stimuli, seem to be negatively correlated, but rather weakly (Fig. 8B). If this correlation were real, then DCN type IV units would show a single continuum of properties: on one side are the units that have a robust response to low-level tones and weak response to BBN. These units are also highly notch sensitive. On the other side are units that have weak responses to low-level tones but robust responses to BBN. These units are inhibited only by wider notches. Even if this correlation does exist, however, it is weak and at any given place on the wideband continuum there is a large variability in the responses to narrowband stimuli.

Young et al. (1992) showed a bimodal distribution in the

response of type IV units to one specific notch that was derived from a natural stimulus (BBN filtered through a pinna transfer function). Units were either inhibited by the notch or responded to the notch by shifting their rate-level function to higher levels without inhibition. This result may be related to the phenomena described here; there is a range of minimum inhibitory notch width, which spans the notch width used by Young et al. However, the units in the present study are distributed along a continuum of notch sensitivity so it is not clear why the units of Young et al. (1992) formed two distinct clusters. It may be that the maximal inhibition by a notch is a sensitive function of the notch width so the measure used by Young et al. (1992) would generate bimodal distribution even when the population has actually a continuum of sensitivities.

It is tempting to hypothesize that at least one of the two continua, or both in case they are correlated, is mapped along the isofrequency direction of the DCN. This hypothesis is especially attractive in the case of wideband stimuli,

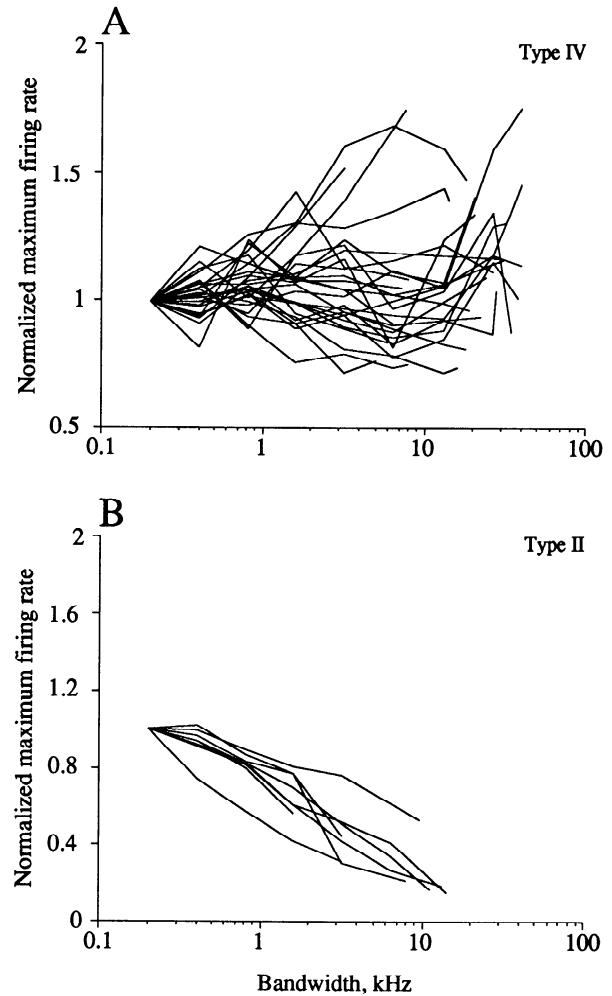


FIG. 14: Maximum firing rate as function of noise bandwidth, normalized by the maximum rate at the 0.2-kHz noise band, for the type IV and type II populations measured in these experiments. A: population data for type IV units. Note the variability in the behavior of the maximal firing rate in the type IV population. Some units lower their rate with increase in bandwidth; other units increase their firing rate with increase in bandwidth. B: population data for type II units. Note that all the type II units decrease their firing rate by large amounts with increase in noise bandwidth.

because it would create a map of notch width sensitivity on the DCN. The functional importance of such a map will be discussed later.

Insufficiency of type II units to explain type IV responses

It has been proposed that the type II interneurons are responsible for the inhibitory responses of type IV units to narrowband stimuli (Voigt and Young 1980, 1990). In a paper that described the inhibition of type IV units by notch stimuli, Spirou and Young (1991) hypothesized that type II interneurons are also sufficient to explain the wideband inhibition of type IV units. However, four arguments can be made against the hypothesis of Spirou and Young.

1) It is assumed here that the low slope and poor responses of some type IV units to BBN are caused by the wideband inhibitory source (Fig. 6). Therefore the WBI should have a threshold as low as the excitatory effects of BBN on type IV units, or even lower, in the case of the one unit that was inhibited by low-level BBN. However, type II responses to noise are weak and have a relatively high threshold (Fig. 11).

2) The inhibitory bandwidth that affects the type IV units can be >2 octaves re BF (Fig. 10); however, type II units show inhibitory interactions with type IV units over a smaller frequency range (≤ 0.8 octaves, Spirou and Young 1991; ≤ 0.65 octaves, Voigt and Young 1990). This point was even more strongly demonstrated in individual cases (Fig. 9, A and B). In fact, only in 2 of 16 cases was the notch inhibitory bandwidth contained within the central inhibitory area when the widest inhibitory notch was superimposed on the tone response map.

3) Type II responses to noise bands are a monotonic decreasing function of the bandwidth (Figs. 13 and 14B). Therefore it is expected that an increase in bandwidth would result in a monotonic increase in the maximal firing rates of type IV units. Such behavior was seen in some cases; however, in a larger number of cases the maximal firing rate showed some nonmonotonicity as a function of bandwidth, indicating an increase in net inhibitory input with increasing bandwidth (Figs. 12C and 14A).

4) A somewhat weaker argument can be made from the weak correlation between the narrowband and wideband properties. Weak responses to narrowband stimuli are interpreted here as a sign of strong type II inhibition on type IV units. If type II units were also the source of the wideband inhibition, then type IV units with weak tone responses should give weak BBN responses also and should be highly notch sensitive. In practice, the opposite seems to occur.

The arguments against the role of type II units in the responses to wideband stimuli are not definitive; nevertheless, taken together they form a strong case that is based on the responses to all the stimuli used here. We hypothesize therefore that the inhibitory drive during wideband stimulation is provided by a new, as yet unidentified inhibitory source. This inhibitor must be strongly excited by wideband stimuli but weakly activated by tones (and, by inference, by narrowband stimuli). Spirou and Young (1991) hypothesized that the above-BF upper inhibitory sideband (their UIS) comes from a weak inhibitory source. It may well be

that the UIS is in fact a manifestation of the WBI. The WBI is also weaker than the type II inhibition: type II units completely reverse the effect of the excitatory inputs onto the type IV units but the WBI does not inhibit type IV units below their spontaneous level unless their excitatory drive is weakened by using notch stimuli. Another reason to believe that the WBI is relatively weak is the fact that it interacts linearly with the excitation at low levels, as shown in Fig. 6.

On the basis of the results shown here we can predict some of the response properties of the WBI. First, as mentioned above, it should be relatively weakly activated by tones but strongly activated by noise. Second, its noise threshold should be very low—about as low as the excitatory responses of type IV units, as shown in Figs. 6 and 11A. Finally, its effective integration region may be from 2.5 octaves below the type IV BF to ~ 1 octave above the type IV BF, and it should reach at least one of these two boundaries.

There is one class of units that is a possible candidate: these are the onset-C units described by Palmer and Winter (1993). These may be the same as the onset-C units of Rhode and Smith (1986) and the stellate-D units of Oertel et al. (1990), although definitive evidence for this is lacking. The onset-C units of Palmer and Winter are weakly activated by tones, strongly activated by noise, and show two-tone facilitation. They may well be both the WBI of type IV units, as we suggest here, and the WBI of the type II units, as originally suggested by Palmer and Winter (1993). As long as there is no evidence to the contrary, this is the most parsimonious model. However, it may be that different populations act as WBIs on type II units and on type IV units. Currently, there is neither anatomic nor physiological evidence that onset-C units inhibit type IV units.

There is no role in the model of Fig. 5 for the intricate neural machinery of the superficial layer of the DCN (Lorente de Nò 1981; Osen and Mugnaini 1981; Osen et al. 1990). This layer contains presumed granule cell interneurons (Manis 1989) as well as three or more varieties of inhibitory interneurons. It seems unlikely that the WBI could be located in the superficial DCN for two reasons: first, effects of the WBI are apparent in type IV units located in both the fusiform cell layer and the deep layer of DCN, but the axons of superficial layer interneurons do not seem to extend to the deep DCN (Berrebi and Mugnaini 1991); second, auditory nerve fiber inputs do not seem to extend to the superficial layer (Jones and Casseday 1979; Osen 1970; Ryugo and May 1993), so it is not clear what source of auditory input would serve to generate responses to sound in the WBI if it were located superficially.

Mechanisms of type IV responses

The data presented in this paper support the model presented in Fig. 5 as a possible circuit to explain the seemingly contradictory responses of type IV units to narrowband and wideband stimuli. One peculiarity of the model presented here is that it cannot be identified either by probing it with pure tones alone or by probing it with white noise methods (Eggermont and Smith 1990). The reason is that pure tones activate the WBI only weakly, and therefore this part of the circuitry is downplayed when probed with tones; white

noise, on the other hand, activates the type II units only weakly, and therefore white noise methods downplay that part of the circuitry. This situation is in fact the basis of the apparent inconsistency in the type IV responses to narrowband and wideband stimuli.

Recently two computational models of type IV responses have been proposed in the literature (Arle and Kim 1991; Pont and Damper 1991). Both models assume that type II units are responsible for the inhibition of type IV units by narrowband stimuli. The two models differ in the way the type II responses to noise are reduced, and neither of them tested the responses to notch noise. Pont and Damper (1991) assume the existence of an interneuron (their type III?) that inhibits the type II units. This interneuron has the required properties of the WBI. Their type IV units do not get direct input from this neuron. Their model nevertheless shows relatively weak responses to noise stimuli. This was achieved by wiring a very large number of type II units, distributed over an unphysiologically large BF range, to each type IV unit. Although noise excites very weakly each type II unit, the total activity of the large ensemble of type II units is sufficient to reduce type IV unit responses. Such a model may show inhibitory responses to notch noise, although the paper does not report any such tests. Pont and Damper also tested their model on noise band stimuli and report that type IV responses are a monotonic increasing function of the bandwidth. This result is, as mentioned above, inconsistent with the data shown in Fig. 14A. It seems, however, that the model could be salvaged by decreasing the number of type II units connected to each type IV unit and connecting their type III(?) interneuron directly to the type IV units. Such a change in wiring would give rise to a model that is essentially the same as the one shown in Fig. 5.

The model of Arle and Kim (1991) is much more physiologically oriented at the single-cell level. They generate type II responses not by directly inhibiting them but rather by adjusting their parameters in such a way that their auditory nerve inputs in response to BBN are close to their threshold. The large difference in input rates for tone and for noise in their model also explains the relatively weak responses of their type IV units to noise. They did not test their model with noise bands or notch noise. Their model does not contain any mechanism that would explain inhibition by notch noise.

The two models are therefore unable to describe the responses of type IV units to all the stimuli used in this study. On the other hand, the model proposed here (Fig. 5) is at least qualitatively able to explain all the results and is physiologically plausible. The type II-type IV inhibitory circuit was studied using cross-correlation techniques by Voigt and Young (1980, 1990). The excitatory input and the type II inhibition were shown by Spirou and Young (1991) to explain most of the response properties of type IV units to tones. A WBI of type II units has been postulated in the past (Palmer and Winter 1993) and it is known that type II units show very wide suppressive sidebands when tested with a weak BF excitor (Spirou and Young 1991; Spirou et al. 1992). Therefore the only new element in this circuit is the interaction between the WBI and the type IV unit. Simulation studies of the circuit shown in Fig. 5 are needed to

show that the model can also quantitatively explain type IV responses.

Function of type IV units

What is the function of type IV units? We suggest here two possible answers. First, type IV units are extremely sensitive to low-level stimuli (Young and Brownell 1976). They also have excellent masking properties: their rate-level functions to BF tones shift by 1 dB for each increase of 1 dB in the level of a continuous noise masker (Gibson et al. 1985). These properties may make them useful for detecting near-threshold stimuli, both in silence and in background noise.

The second function is a rewording of the fact that type IV units tend to be inhibited both by narrowband stimuli, or spectral maxima and by notch noise, or spectral minima. In other words, they are inhibited by narrow features in the spectrum, depending on their frequency location. Therefore we suggest that type IV units are detectors of interesting features in the stimulus spectrum, features that may carry important information about the external world. For example, many natural sounds are defined by their spectral peaks [human speech as well as many animal communication sounds (Suga 1992)]. Spectral notches are thought to be important in sound source direction estimation (Blauert 1983; Rice et al. 1992). In this interpretation the information carried by type IV units is not specifically or exclusively used for direction estimation; rather, it may be that type IV units became sensitive to notches because of the importance of notches in direction estimation, which made them "interesting features" in the spectrum.

In the model presented above, the strength and threshold of the type II inhibition determine what is a narrow spectral peak by determining the bandwidth at which the type IV unit's responses are disinhibited at high stimulus levels. As mentioned above, the disinhibition bandwidth is variable and is uncorrelated with BF. Therefore the type IV units present an array of sensitivities to spectral peaks. The same is true for their notch sensitivity: it is only weakly correlated with BF, so that at the same BF, different type IV units show different notch sensitivity. Finally, the disinhibition bandwidth and the notch sensitivity (as measured by the minimal inhibitory notch width) are uncorrelated or only weakly correlated. Therefore type IV units present an array of sensitivities to spectral maxima of varying widths and spectral minima of varying widths. In this way type IV units can support a multiresolution analysis of the information-bearing regions (Suga 1992) in the spectral envelope to help in extracting meaning from the external auditory world.

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