Linear and Nonlinear Spectral Integration in Type IV Neurons of the Dorsal Cochlear Nucleus. I. Regions of Linear Interaction

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Nelken, Israel and Eric D. Young. Linear and nonlinear spectral integration in type IV neurons of the dorsal cochlear nucleus. I. Regions of linear interaction. J. Neurophysiol. 78: 790–799, 1997. The principal neurons of the dorsal cochlear nucleus have complex response properties, many of which are classified as type IV. These units integrate energy in the acoustic signal in a nonlinear fashion; for example, at high sound levels the response to a noise of narrow bandwidth and to a band-reject filtered noise with a spectral notch of the same bandwidth may both be inhibitory. However, the sum of these two stimuli, which is broadband noise (BBN), generally gives an excitatory response. In other situations, linear interactions among stimulus components are observed. In this paper, three regimes of approximate linearity were identified. First, best-frequency (BF) tones and equal-energy narrow noise bands centered at BF evoke almost the same response, which is consistent with a stage of linear filtering followed by a nonlinearity that generates the rate responses of the neuron. Second, for sounds close to threshold (10–15 dB re threshold), energy over the full bandwidth of the unit is integrated linearly. Within this regime, responses to the narrow noiseband and the spectral notch mentioned above do sum to equal the response to BBN. Finally, two noisebands centered at different frequencies, such that their sum is a notch in a broad band of noise, sum linearly at low sound levels; the degree of linearity improves as the separation between the noisebands increases. The results are interpreted in terms of a model of type IV response generation containing two inhibitory interneurons: type II units, which are active for narrowband stimuli, including tones, and the wideband inhibitor, which is active for broadband stimuli. In most cases, the onset of nonlinearity occurs for stimuli that significantly activate the type II inhibitory interneuron.

INTRODUCTION

Most auditory neurons respond to sound in a nonlinear way, meaning that the response to the sum of two stimuli is not always equal to the sum of the responses to the individual stimuli. In the auditory nerve, the phenomena of two-tone suppression (Sachs and Kiang 1968) and combination-tone generation (Goldstein and Kiang 1968) provide examples of nonlinear processing. These and other auditory nerve nonlinearities are well described quantitatively, and models exist that are reasonably predictive of nonlinear effects in the auditory nerve representation of sounds. In the central auditory system, however, there are additional nonlinearities and more complicated models are required to reach a quantitative understanding of spectral and temporal integration processes.

The cat dorsal cochlear nucleus (DCN) is a good example of nonlinear behavior. The DCN has a complex internal circuitry, with ascending and descending inputs from other parts of the auditory system and a rich system of internal interneurons (Lorente de Nó 1981; Osen et al. 1990). DCN units have appropriately complex response characteristics (Nelken and Young 1994; Young et al. 1988). Principal cells of the DCN in de cerebrate cats most frequently have the so-called type IV response characteristic (Young 1980; Young and Brownell 1976): they are spontaneously active, and they are excited by low-level best-frequency (BF) tones but inhibited by high-level BF tones. Tone response maps of type IV units (rate of response as a function of tone frequency and sound level) typically show large inhibitory subfields both on BF and off BF. Prediction of responses to broadband noise (BBN) from tone response maps, assuming linear integration of spectral information, usually suggests that the response to noise should be inhibitory (Spirou and Young 1991). Narrowband noise is indeed inhibitory at high levels (as will be shown later), but most type IV units are excited by BBN. Even more surprisingly, it was found that type IV units are also inhibited by notch noise, meaning BBN containing a spectral notch, when the notch is centered on BF (Spirou and Young 1991). This finding illustrates dramatically the qualitative nonlinearity of type IV units: the response to a narrow band of noise centered on BF is inhibitory; the response to a notch stimulus with the same width may be also inhibitory; but the response to the sum of the stimuli, which is a BBN, is excitatory.

The nonlinearity of type IV units is an impediment to comprehensive understanding of the DCN and its role in the auditory system. There is no general method to predict the responses of a type IV unit to an arbitrary stimulus, so generating hypotheses about DCN function becomes a hit-or-miss, empirical process. This paper is part of an effort to develop general tools for characterizing nonlinear auditory neurons, in the sense of finding a set of stimuli such that, if the responses of a neuron to the stimuli in this set are known, then it is possible to predict the neuron’s responses to all other sounds. This process is straightforward when the neuron behaves in a linear fashion. In this paper, we show that DCN type IV units behave linearly for both narrowband and wideband stimuli at low sound levels. This range corresponds roughly to stimuli that evoke weak or no response in one type of inhibitory interneuron in the DCN, the type II unit.

METHODS

Animal preparation and unit recording

The methods have been described in detail elsewhere (Nelken and Young 1994; Spirou and Young 1991; Young and Brownell...
Acoustic stimuli and experimental protocol

Acoustic stimuli consisted of BF tones and BBN, used to determine unit type, and a variety of noiseband and notch-noise stimuli, used to test linearity of interaction of stimulus components. 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 closed acoustic system connected to a hollow ear bar inserted into the stumps of the auditory canal, cut within a few millimeters of the skull. Acoustic calibration was 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. Examples of acoustic calibrations have been shown previously (e.g., Rice et al. 1995); generally the calibration fluctuated within ±10 dB over the relevant frequency range.

During experiments, 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 (1 repetition at each level). Spontaneous rate was estimated from the interstimulus interval at levels that were clearly subthreshold.

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 (1984). Of 177 units characterized in this way, 85 were type IV, 27 were type II, and 63 were type III or I/III.

After unit characterization, a series of noiseband (e.g., S1 in Fig. 1A) and notch-noise (e.g., S2 in Fig. 1A or S3 in Fig. 1B) stimuli were presented with the use of three modes: 1) as rate-versus-level functions at fixed center frequency, bandwidth, and notch width; 2) as rate versus center frequency at fixed attenuation level, bandwidth, and notch width; and 3) as rate versus bandwidth (or notch width) at fixed level and center frequency. The fixed-level data were usually taken at the lowest spectrum level at which the response to a notch centered on BF was maximally inhibited; if a unit could be held long enough, additional data at higher levels were taken. Between each series of stimuli, BF tone and BBN rate-level functions were obtained to verify the stability of the unit. Because the design of the experiment required comparison of rate data obtained over periods of minutes to hours, unit stability was important. Recordings were not made from units unless spike isolation and triggering were clear and without artifact. Changes in unit properties over long periods of time still occurred in a minority of units (4 of 48 on which this report is based), but these occurred mostly for BBN at high levels, above the levels used for the comparisons in this paper. These units were therefore included in the sample analyzed here.

Noiseband stimuli were generated in two ways. In the early experiments, noisebands were generated by low-pass filtering two independent analog BBNs at half the required bandwidth (slope: 48 dB/octave), then modulating them in quadrature to the desired center frequency of the band and adding them. Notch-noise stimuli (e.g., S3 in Fig. 1B) were generated similarly, by modulating in quadrature two independent band-pass filtered BBNs. The resulting notches were ∼30 dB deep (see Nelken and Young 1994 for details). In later experiments, noise stimuli were generated digitally; the spectrum of the stimulus was generated in the frequency domain by filling the real and imaginary parts of the Fourier transform of the signal with independent Gaussian pseudorandom deviates (passbands) or zeros (stopbands). The resulting complex spectrum was then inverse transformed back into the time domain. The transform length was 32,768 points, giving a frequency resolution of 5 Hz at a sampling frequency of 163.8 kHz. A 16-bit D/A converter was used to transform the digital samples into an analog waveform; stimulus level was set by attenuating the analog waveform after D/A conversion. Because the Nyquist rate (81.9 kHz) was above the audible range of cats, no antialiasing filter was used. Frequency bands generated in this way had much steeper
slopes than the noisebands generated with the use of the analog modulation technique. Nevertheless, the responses to corresponding stimuli were found to be similar. In all cases, the noisebands and the notches were centered arithmetically around their nominal center frequency.

**Superposition model**

The simplest means to predict the responses of a unit to an arbitrary stimulus spectrum is to assume that the unit weights energy in different frequency regions linearly; the predicted response is then the sum of the responses to an appropriately chosen set of simpler stimuli. Figure 1 shows two stimulus situations that were used to test for linearity of DCN unit responses. In each case the spectrum of stimulus S3 equals the sum of the spectra of S1 and S2. Under linear interaction, the response to S3 should equal the sum of the responses to S1 and S2. In practice, spontaneous activity must be treated separately, so the actual linear hypothesis is

\[
R_3 = R_{\text{spontaneous}} + (R_1 - R_{\text{spontaneous}}) + (R_2 - R_{\text{spontaneous}})
\]

where \(R_1, R_2,\) and \(R_3\) are the response rates to S1–3 and \(R_{\text{spontaneous}}\) is spontaneous discharge rate. That is, we assume that the driven rate to S3, defined as \((R_3 - R_{\text{spontaneous}})\), equals the sum of the driven rates to S1 and S2.

**RESULTS**

This paper is based on the responses of 48 type IV units to the stimulus paradigm described above. Data from 28 of these units were used in a previous report (Nelken and Young 1994) on related issues; additional data from 25 units are described in a related paper concerning nonlinear prediction of responses to noiseband stimuli from tone and BBN data (Nelken et al. 1997).

**Narrow noisebands produce similar responses to equal-power tones**

A simple model of type IV units would consist of a linear tuning stage, followed by a stage of nonlinear rate processing. The range within which such a model holds can be investigated by comparing responses to tones with responses to noisebands of various bandwidths; a prediction of this model is that responses to tones should be similar to responses to sufficiently narrow noisebands. Figure 2A shows the rate-level functions of a type IV unit to BF tones and to noisebands of various bandwidths. The tone level is given in dB SPL; the noiseband rate-level functions are shifted so that their energy is equal to the tone energy at each point on the abscissa. The shape of the BF tone rate-level function is typical. It is excitatory at low levels and inhibitory at high levels; this inhibition is produced by type II units (Voigt and Young 1980, 1990), whose thresholds for BF tones are \(\sim10\) dB higher than those of type IV units (Young and Brownell 1976). The narrower noisebands have rate-level functions that are similar to each other and to the tone rate level. At wider noise bandwidths, the rate functions differ from the tone function, both in shape and in threshold. Figure 2A shows an example with a relatively large discrepancy between the tone rate-level function and the narrow noiseband rate-level functions. Figure 2C shows an example where the tone and narrow noiseband data almost superimpose. Figure 2E shows an intermediate case. In most units, the BF tone rate-level function is very similar to the noiseband rate-level functions for narrow noisebands.

To justify this claim, the following measure of discrepancy was used to compare rate-level functions

\[
d = \frac{1}{2L\cdot \text{var}} \sum_{l=1}^{L} [r_1(l) - r_2(l)]^2
\]

where \(r_1(l)\) and \(r_2(l)\) are the responses to the two stimuli at sound level \(l\), var is an estimate of the variance in the responses, computed as the variance of the spontaneous rate measurements, and \(L\) is the number of sound levels at which both units were tested. Under the null hypothesis of equal responses, \(d \cdot L\) is \(\chi^2\) distributed with \(L\) degrees of freedom. The expected value for \(d\) is 1; values much larger than 1 are evidence for discrepancies between the rate-level functions that cannot be accounted for by added noise of variance var. In the text below, \(d\) is used as a measure of the amount of difference between two rate functions, and not as a statistical test for difference; in fact, most pairs of curves are significantly different in a statistical sense. For the units in Fig. 2, A and C, \(d\) is 2.38 and 1.03, respectively.

The discrepancy \(d\) between the tone rate-level function and the noiseband rate-level function at the narrowest band-
width tested (usually 200 Hz) was found to be small in the majority of units. Figure 3A shows a histogram of \( d \) values for all units tested with 200-Hz noisebands. The histogram has a peak near 1, as expected, but there are some large \( d \) values. The large \( d \) values are mainly due to discrepancies at high sound levels, usually a higher discharge rate in the noiseband response than in the tone response, as in Fig. 2A.

In addition to the differences at high levels, there is also a small systematic difference in the peak value of BF tone and narrow noiseband rate functions. This difference is illustrated in Fig. 3B, which shows a scatter plot of the maxima of the BF tone (abscissa) versus the 200-Hz noiseband (ordinate) rate-level functions. There is a high correlation between the two, but the maximum response to 200-Hz noisebands tends to be somewhat smaller than the maximum response to BF tones.

Figure 2B is a plot of \( d \) against noise bandwidth for the units in Fig. 2A. The discrepancy between the tone and the noise rate-level functions is small up to 3.2 kHz, and then it increases rapidly with additional increases in bandwidth. Similar behavior can be seen in Fig. 2D (corresponding to the rate-level functions in Fig. 2C) and Fig. 2F (corresponding to Fig. 2E). The rapid increase in \( d \) occurs at a critical bandwidth above which two changes occur (these can be seen in Fig. 2, A, C, and E). 1) The threshold of the noise rate-level functions shifts as noise power moves out of the integration bandwidth of the unit. 2) The response to noise at high sound levels is disinhibited, presumably because of inhibition of the type II interneurons by the broadband stimulus (Nelken and Young 1994; Young and Brownell 1976).

The critical bandwidth was determined by finding the bandwidth at which \( d \) started to increase rapidly for all the units that were tested with the use of this paradigm. Figure 3C shows a scatter plot of the critical bandwidths against the BF of the units. There is only a weak dependence of the critical bandwidth on BF (\( r = 0.44, df = 41, P < 0.01 \)). This weak dependence is illustrated also by the examples in Figs. 2 and 3D. In Fig. 2 the three examples are ordered by decreasing BF, going from 16.9 to 9.8 kHz. The critical bandwidth does not follow the BF, however: it is 3.2 kHz for the unit with the highest BF, 1.6 kHz for the middle unit, and 6.4 kHz for the unit with the lowest BF. Figure 3D shows a population of \( d \)-versus-bandwidth curves. These are all the cases of units whose BFs lie in the octave range between 8 and 16 kHz, and for which at least five bandwidths were tested. Whereas every unit shows a critical bandwidth, the actual value of the critical bandwidth is between 0.2 and 6.4 kHz, a much wider range than the range of BFs. Even excluding the atypical extreme case of a unit whose critical bandwidth was 0.2 kHz, the range of critical bandwidths is still between 0.8 and 6.4 kHz. Note that this is not the behavior expected of the simple model mentioned at the beginning of this section, if the linear tuning stage is assumed to be peripheral auditory nerve tuning.

Further insight into the behavior of type IV units at narrow bandwidths can be gained from experiments in which noisebands with increasing bandwidth were presented at a fixed spectrum level. Figure 4 shows an example of the responses to such stimuli for one unit at three spectrum levels. The solid lines show the responses to the noisebands, and the dashed lines show predictions of the noise responses based on BF tone rate-level functions. The predictions were generated by assigning to each noise bandwidth the firing rate in response to a BF tone with the same total energy as the noiseband. At narrow bandwidths, the noiseband responses and the predictions behave similarly at the three levels. There is a close correspondence of measured and predicted values at the lowest sound level (Fig. 4A): at higher sound levels (Fig. 4, B and C) small systematic deviations between measured and predicted values appear. These deviations are similar to the ones seen in Fig. 2A: the noiseband rate is lower than the tone rate near the peak of the rate-level function (at \(-1\) dB) and the noiseband rate is higher than the tone rate in the inhibitory regime at high levels (at 9 dB).

By contrast, at wider bandwidths the responses and the predictions diverge. This is most apparent at the higher levels (Fig. 4, B and C), where the responses to the noisebands increase with bandwidth, whereas the predictions decrease. The critical bandwidth is clear in this example and in the eight other cases tested with the same stimuli. The critical bandwidths measured with the use of the paradigm in Fig. 4 are always in the expected range from the paradigm in Fig. 2, although they do not agree precisely because of the difference in coarseness of the bandwidth scale in the two determinations.

The data in Figs. 2 and 4 show that the idea of a linear integrating bandwidth has very limited application to type IV units. This model applies best to narrow bandwidths and low sound levels. An integrating bandwidth can be defined.
Responses to near-threshold stimuli add linearly

Figure 5 shows a determination of a type IV unit's region of linearity with the use of the stimulus regime of Fig. 1A (Nelken and Young 1994). Figure 5A shows the responses of a type IV unit to a BBN with a notch centered on BF (S2 in Fig. 1A), and the response to a noiseband whose bandwidth (0.8 Hz) matches the notch width, also centered on BF (S1 in Fig. 1A). The sum of these two stimuli is a BBN (S3 in Fig. 1A), so, within the linear region, the sum of the responses to the individual stimuli should equal the response to the BBN. Figure 5B shows the responses of the unit to BBN together with a linear prediction of this response, computed by adding the driven rates to the noiseband and the notch (Eq. 1).

In this case both the response to the notch and the response to the noiseband are excitatory at low levels, but both are smaller than the responses to the BBN at the same spectrum levels. Figure 5B shows that the sum of the responses to the

within this range as the critical bandwidth of Fig. 2, B, D, and F. However, its behavior is not what is expected if the tuning stage is assumed to be cochlear tuning (Fig. 3C). This point will be discussed in more detail later.

FIG. 4. Analysis of noiseband-widening experiments. Solid lines: responses of type IV unit (BF = 16.6 kHz) to noisebands at 3 spectrum levels as functions of bandwidth; spectrum level given as noise power in 1-Hz band, in units of dB re 20 μPa. Dashed lines: predicted responses, computed as BF tone response at same total stimulus energy. A: at lowest level and smallest bandwidths (<1.5 kHz), responses to noiseband are extremely well predicted by BF tone. B and C: agreement is less good; disinhibition is seen at higher bandwidths (>3 kHz), which is not predicted by responses to BF tones.

FIG. 5. Filling notch as test for linearity; each column shows data from a type IV unit. A and D: responses to narrow noiseband (S1 in Fig. 1A) and to notch of similar width (S2 in Fig. 1A). BFs of units and bandwidths/notch widths given in key. B and E: responses to BBN (S3 in Fig. 1A) and linear prediction of Eq. 1. C and F: differences between BBN responses and predictions from B and E, in terms of d (Eq. 2) plotted as function of upper limit l of summation used to produce d. Not corner level beyond which d increases rapidly. Distance between threshold of unit and this corner attenuation is linearity range of unit. In all plots, stimulus level is given as spectrum level.
notch and the noiseband fit almost perfectly the measured responses to the BBN, up to about −10 dB. Figure 5, D and E, are another demonstration of the same phenomenon in a second unit; this time the response to the notch is inhibitory at low levels, and the response to the BBN is smaller than the response to the narrow noiseband by exactly the inhibition supplied by the notch; the prediction superimposes on the BBN data up to about −25 dB. In both examples, at higher levels the prediction is much smaller than the actual measured response. The high-level behavior of the prediction reflects the strong inhibitory response to noisebands at high levels. Presumably the inhibition is due to type II inhibition of type IV units; with broadband stimuli, like BBN and the notch noise, type II units are not active or only weakly activated (Nelken and Young 1994; Young and Brownell 1976; Young and Voigt 1982), and the inhibition is not seen. Thus the predicted and measured data diverge when the type II inputs become dominant.

To estimate the range of levels over which this type of linearity holds, \( d \) (Eq. 2) was used to measure the discrepancy between the linear prediction and the measured responses to the BBN; in this case, \( d \) was computed as a function of the upper limit of the summation \( L \). That is, the summation in Eq. 2 was taken over a range of levels extending from below threshold to a variable upper limit \( L \). As long as \( L \) is within the linearity range, \( d \) is expected to remain near 1; when \( L \) increases beyond the linearity range, \( d \) should increase rapidly. This is indeed the case, as is demonstrated in Fig. 5, C and F, which show \( d \) as function of \( L \) for the two examples.

The linearity range for a unit was estimated as the decibel range between threshold and the value of \( L \) at which \( d \) increases rapidly. This value was determined with the use of an automatic fitting procedure that found the threshold of the unit (the value at which firing rate increased by 1 SD above the spontaneous rate) and the value at which \( d \) increased by >1 SD above its value in the region of the unit threshold; the results were then inspected and corrected manually for gross errors. Figure 6 shows a histogram of the linearity ranges for 34 type IV units; for each unit, the median value of linearity range across all bandwidths tested is shown. The median was used rather than the mean to avoid biasing the linearity range toward large values; high values of linearity range could arise when the notch was very wide and the response to the noiseband was essentially equal to the response to BBN. The median of the linearity ranges is 15 dB, which is approximately equal to the range of levels from threshold to the rate maximum for type IV unit BF rate-level functions (for the sample of units here, the median distance from threshold to the maximum of the rate-level function is 13 dB). The linearity range was not correlated with BF (\( r = 0.04, \text{df} = 34, \text{not significant} \)), but depended strongly on the unit: some units had wide linearity ranges at all notch widths, whereas others had narrow linearity ranges at all notch widths [1-way analysis of variance (ANOVA), \( F(3,138) = 3.57, P \approx 0 \)]. The maximum of a type IV unit’s rate-level function, of course, occurs at the threshold of the type II inhibitory input to the type IV unit (Young and Voigt 1981), so the region of linearity corresponds roughly to sound levels below the threshold of type II inhibitory input.

Responses to separate noisebands can be used to define a region of linearity

Figure 7 shows examples of the range of goodness of fit that can be achieved in the linearity analyses with the use of the stimuli of Fig. 1B. The responses to noisebands (S1 and S2 in Fig. 1B) have been used to predict the responses to a stimulus composed of two flanking bands with a notch between them (S3 in Fig. 1B): the width of the noisebands was chosen to be the same as the width of a flanking band in the notch stimulus. The width of the band into which the notch was introduced was usually slightly narrower than 2 \( \times \) BF, so the width of the flanking bands was BF-NW/2, where NW is the notch width. Usually, the notch widths started at 250 Hz and were tested in octave steps. Figure 7A shows the responses of a type IV unit to a noiseband of fixed spectrum level (−22 dB SPL) and bandwidth (1.5 kHz), as a function of the center frequency of the band. The response shows an excitatory region when the noiseband is centered at BF (arrow at 6.3 kHz). Figure 7B shows the response to a dual noiseband stimulus (S3 in Fig. 1B) consisting of two bands, each of the same bandwidth and spectrum level as the band in Fig. 7A (——); the two bands were separated by 3.2 kHz in center frequency (NW in key). This figure shows response versus the center frequency of the whole complex as it is moved in frequency; the abscissa is the center frequency of the notch between the two noisebands. The dashed line shows the linear prediction of the response to the two-band stimulus computed by adding the driven rates to the single-band stimuli (Eq. 1). The similarity between the predicted and the measured responses is clear. Cases with very close fits like Fig. 7B were rare. In many cases, however, there was good correspondence between the measured responses and the prediction in terms of the width of the central dip in the two-band response and in the width of the excitatory areas caused by the individual bands. Cases from different units, ordered by decreasing goodness of fit, are shown in the rest of Fig. 7. In Fig. 7D, the response to the lower band of the stimulus is consistently larger than the linear prediction. In Fig. 7F, the responses to the two bands

![Fig. 6. Distribution of median linearity ranges for 34 type IV units, equal to range from threshold to rapid increase in \( d \) in plots such as Fig. 5, C and F. Median of this distribution: 15 dB.](image-url)
whereas the unit almost did not change its mean firing rate in response to the two-band stimuli at most frequencies.

The quality of the fit was quantified again by the distance measure. Using $d$ was somewhat problematic, because it is highly sensitive to small departures between prediction and measurement. For example, the $d$ value for Fig. 7F is larger than for Fig. 7H, although subjectively the two cases were judged in the inverse order. There was, however, a correlation between $d$ and a subjective rating of the fit (not shown), and so $d$ is used here.

Figure 8A shows $d$ for the two-band comparison as a function of the passband spectrum level of the noisebands. Spectrum level is plotted as dB re a reference level, which are appreciably larger than the prediction, although the qualitative features of the response, including the central dip, are still predicted rather well.

Figure 7, I and J, are cases in which the prediction failed to account for even the qualitative features of the response. In Fig. 7H, the responses to the flanking bands are rather good, but the central dip is not predicted at all. Finally, in Fig. 7J, the prediction does not fit the actually measured response at all—the prediction is dominated by inhibition,
is the spectrum level at which the rate-level function in response to the 200-Hz noiseband reached its maximum. Note that below 5 dB re reference, most fits are reasonably good (52 of 76 cases have $d < 6.2$, the median value of the population), whereas above 5 dB, most fits are above the median value (40 of 51 have $d > 6.2$). Once again, the range of linearity is confined to the region below and slightly above the rate maximum of the rate-level function, that is, at a range in which type II units are inactive or only weakly active. The fit between the predicted and the measured responses tended to improve with increasing notch width, corresponding to increasing separation between the two bands. Because of a very large interunit variability in $d$ values [1-way ANOVA, $F(31, 94) = 16.71$, $P ≈ 0$], this effect was lost when plotting $d$ as a function of notch width for the whole population. To demonstrate the effect despite this large variability, the $d$ values for each unit were normalized by using ranks. For each unit tested with the use of this paradigm, the $d$ value at each notch width was ranked (there were between 2 and 6 notch widths tested for each unit) and the ranks were normalized between 0 and 1; notch widths were also ranked, and the ranks were compared (Fig. 8B). The decrease of the rank of $d$ with increase in bandwidth is readily apparent in this figure. There was a significant effect of the notch width on the rank of $d$ [1-way ANOVA, $F(5, 120) = 11.9$, $P ≈ 0.001$].

**Discussion**

Recently, Nelken and Young (1994) suggested a model of DCN type IV units that accounts qualitatively for most of the known response characteristics of these cells (Fig. 9). In the model, two sources of inhibition differentially affect the responses of type IV units for narrowband and broadband stimuli. Inhibition caused by type II units is dominant for narrowband stimuli at high levels, whereas for broadband stimuli a wideband inhibitor (WBI) inhibits type II units strongly and type IV units weakly. In the following discussion, we interpret the results of this paper in terms of this model.

**Linear regime of type IV units**

We describe three regimes in which type IV units behave linearly. First, type IV units give essentially identical responses to narrow noisebands and to tones with the same energy. This behavior is consistent with a model in which a linear filter integrates energy over a certain bandwidth and then the energy at the output of that filter drives a nonlinear system that produces the rate-level functions of the neuron. Two small differences were noted: at low levels the maxima of the rate-level functions for narrow noisebands were somewhat lower than for tones (Fig. 3B), and at high levels narrow noisebands inhibited the units somewhat less than equal-energy tones (Fig. 2, A, C, and E). Both effects can be interpreted in terms of the WBI model. We assume that the WBI responds weakly to the narrow noisebands, but that the noiseband response is stronger than the response to equal-energy tones; this behavior is observed for onset units of the type that are likely to be the WBI (Palmer et al. 1996). At low levels, around the maximum of the BF rate-level function, type II units are minimally active. As a result, the weak inhibition of type IV units by the WBI is revealed, so that the type IV units have higher thresholds than excitatory inputs to type IV units (Young and Brownell 1976; Young and Voigt 1981). WBI responds preferentially to broadband stimuli; it strongly inhibits type II units, preventing them from responding to broadband stimuli, and weakly inhibits type IV units, producing their inhibitory responses to noise (Nelken and Young 1994). Characteristics inferred for WBI match those of onset-C units of ventral cochlear nucleus (Winter and Palmer 1995), which are known to project inhibitory terminals to DCN (Smith and Rhode 1989).
subtle. The main effect is that responses to narrowband stimuli are essentially the same as the responses to equal-level tones. The implication is that some energy integration is done before the nonlinear stage of type IV units. However, the bandwidth over which this integration is valid is only weakly correlated with the BF (Fig. 3C). It is interesting, therefore, to consider whether this integration is a property of the input to DCN or is a result of DCN mechanisms. The critical bandwidths of auditory nerve fibers were measured by Pickles and Comis (1976) with the use of noiseband-widening methods similar to those of Figs. 2 and 4. The resulting bandwidths were highly correlated with BF. Thus the critical bandwidths of DCN type IV units, as measured in Fig. 2, must be determined by factors in addition to peripheral tuning. These factors might include variation in the BF range over which auditory nerve fibers converge on DCN type IV units and variation in the integration bandwidths and thresholds of DCN inhibitory interneurons.

The second and third linear regimes are related. They were demonstrated in tests in which the responses to two stimuli are used to predict the response to their sum. At low levels, a noiseband can be used to fill a notch of similar width: the sum of the responses to the two stimuli adds up to the response of the unit to BBN at the same spectrum level (Fig. 5). Similar properties hold for the sum of two noisebands (Fig. 7); in this case, the degree of linearity is improved at low levels (Fig. 8A) and if the bands are separated in frequency (Fig. 8B).

The stimuli within the linear range are at low levels and activate type II units only minimally, which was deduced by assuming that the type II threshold corresponds to the peak point or turnover point of type IV rate functions for narrowband stimuli. This assumption is justified by the results of simultaneous recordings from type II and type IV units; in cases where cross-correlation analysis of the spike trains of a type II/type IV pair suggests that the type II makes inhibitory terminals on the type IV, the type II threshold is found to correspond closely to the turnover point of type IV rate-level function (Young and Voigt 1981). Therefore both linearity regimes probably reflect mostly interactions between the excitatory input on type IV units and the WBI. In fact, whenever type II units are activated, the linearity prediction fails in such a way that the prediction does not include the effects of the type II inhibition of type IV units. This was discussed in Results for the case shown in Fig. 5. In cases such as that in Fig. 7, most failures in the prediction of notch-noise responses by the sum of the responses to noisebands were caused by the predicted rates being too small. A likely cause is the bandwidth behavior of the WBI. The WBI is postulated to respond more strongly to wideband than narrowband stimuli and the onset-C neurons show this behavior over a very wide bandwidth (Palmer et al. 1996). Because the notch is embedded in a noiseband with bandwidth more than twice the width of the single bands used in the prediction, the notch noise should activate the WBI more strongly and the type II units less strongly than the single bands; the net effect should be larger responses to the notch noise than to the single noisebands.

The fact that the prediction is better for frequency components that are more widely separated could be explained with the use of the same argument. As the component noisebands move farther apart in frequency, they tend more and more to activate separate populations of type II and WBI interneurons. When two widely separated bands are combined, their interactions in type II and WBI interneurons will thus be minimal, and the degree of nonlinearity will be minimized.

**Implications for DCN models**

The results presented here can all be at least qualitatively understood in terms of the model in which type IV units receive inhibition from both type II units and WBI (Fig. 9). Recently it has been argued that the WBI connection to type IV units is not necessary for explaining type IV responses (Blum et al. 1995; Reed and Blum 1994). The argument is based on modeling studies in which much of the variability in type IV unit properties is explained by variations in the connectivity between type II and type IV units. However, this model does not explain either the bandwidth of the effects of notch noise on type IV units or the low threshold of the broadband inhibition, as discussed by Nelken and Young (1994). The decrease in rate at the peak of BF rate-level functions, shown in Figs. 2A and 3B, is also difficult to explain with the model of Blum et al. In our model, it is explained by activation of the WBI; in the model of Blum et al., it would have to be explained by type II units responding more strongly to narrow noisebands than to tones at levels near threshold; such a difference is not observed (e.g., Fig. 13 of Nelken and Young 1994).

The current results nevertheless require some modifications to the model. First, the bandwidth of the excitatory and inhibitory inputs to type IV units is much more variable than has been thought (Fig. 3C). Although it is easy to develop explanations for this with the use of the model, the implications of this behavior for type IV synaptic organization need to be defined further. In particular, it is important to know whether type IV units vary systematically in the bandwidth of their excitatory input and what effect these bandwidth variations have on other properties of the neurons. Second, the dependence of linearity of interaction on the separation of noisebands (Fig. 8B) has an uncertain correlation in the model. A possible explanation is discussed above, but this phenomenon is quantitative in nature. Thus a convincing explanation must be based on a quantitative model, which captures the details of interactions of different inputs.

Our approach to the DCN up to now has been to build a working model of its synaptic organization, as in Fig. 9. Although this process holds the promise of ultimately resulting in a complete understanding of this structure, it is not a general method and it is doubtful that this process can be successfully applied to more central auditory nuclei, where the anatomic organization is less well known and there are more inputs that are less well understood. A desirable alternative would be to develop a general modeling approach to auditory nuclei that does not require detailed knowledge of their internal synaptic mechanisms. The results of this paper are a first step in the direction of building a formal model of type IV DCN units, in the sense that these results delimit the range over which linear models are valid. Nonlinear corrections are then necessary outside this range (Nelken et al. 1997), and should decrease to zero as the linear range
is approached. In this sense, this paper imposes boundary conditions on any realistic model of DCN type IV units.

The comments of our colleagues in the Hearing Sciences Center were helpful in preparing this manuscript. This work was supported by National Institute of Deafness and Other Communications Disorders Grant DC-00115 and by a grant from the Israeli Science Foundation.

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Received 30 August 1996; accepted in final form 15 April 1997.

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