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Neural organization and responses to complex stimuli in the dorsal cochlear nucleus

ERIC D. YOUNG[1], GEORGE A. SPIROU[1]†, JOHN J. RICE[1] AND HERBERT F. VOIGT[2]

[1]*Department of Biomedical Engineering and Center for Hearing Sciences, The Johns Hopkins University, Baltimore, Maryland 21205, U.S.A.*

[2]*Department of Biomedical Engineering, Boston University, Boston, Massachusetts 02215, U.S.A.*

SUMMARY

The dorsal division of the cochlear nucleus (DCN) is the most complex of its subdivisions in terms of both anatomical organization and physiological response types. Hypotheses about the functional role of the DCN in hearing are as yet primitive, in part because the organizational complexity of the DCN has made development of a comprehensive and predictive model of its input–output processing difficult. The responses of DCN cells to complex stimuli, especially filtered noise, are interesting because they demonstrate properties that cannot be predicted, without further assumptions, from responses to narrow band stimuli, such as tones. In this paper, we discuss the functional organization of the DCN, i.e. the morphological organization of synaptic connections within the nucleus and the nature of synaptic interactions between its cells. We then discuss the responses of DCN principal cells to filtered noise stimuli that model the spectral sound localization cues produced by the pinna. These data imply that the DCN plays a role in interpreting sound localization cues; supporting evidence for such a role is discussed.

1. SYNAPTIC ORGANIZATION OF THE DCN

The dorsal cochlear nucleus (DCN) is a laminated structure which occupies the caudal and dorsal portion of the cochlear nuclear complex (Lorente de Nó 1981; Osen 1969). In the cat, the lamination of the DCN can be described in terms of the structure of one of the principal cell types of the nucleus, the fusiform or pyramidal cell (Blackstad *et al.* 1984); these cells have apical and basal dendritic trees. Their apical dendritic trees extend into the superficial molecular layer of the DCN. The cell bodies of the fusiform cells define the second layer of the nucleus and their basal dendrites extend into the deep DCN. The deep DCN contains the other DCN principal cell type, the giant cell, whose dendrites are mainly confined to the deep layers of the nucleus (Ryugo & Willard 1985). Axons of fusiform and giant cells project to the contralateral inferior colliculus (Adams 1979; Ryugo & Willard 1985). The DCN also contains small and mediun sized interneurons, which are distributed differently across the DCN laminae (Lorente de Nó 1981; Mugnaini *et al.* 1980; Osen *et al.* 1990). Some aspects of the relationships of the interneurons and principal cells in DCN are illustrated in the wiring diagram shown in figure 1. This figure does not show the lamination of the nucleus; instead, it shows the organization of connec-

tions as they are related to the major fibre systems that provide excitatory inputs to DCN neurons.

Auditory nerve (AN) fibres enter the DCN from the underlying posteroventral cochlear nucleus (PVCN) and project in an orderly fashion in the deep layers, preserving the monotonic sequence of best frequencies (BFS) generated in the cochlea (Osen 1970). As a result, the DCN is tonotopically organized, consisting of a stack of isofrequency sheets oriented parasaggitally (Spirou *et al.* 1989). The dendritic trees of both fusiform and giant cells are flattened and oriented in parallel with the isofrequency sheets (Blackstad *et al.* 1984; Ryugo & Willard 1985). Figure 1 shows two isofrequency sheets running from left to right. These sheets contain both fusiform (F) and giant (G) cells and are defined by the projections of AN fibres of two best frequencies (BF$_1$ and BF$_2$). Another source of excitatory input to the deep DCN comes from axon collaterals of multipolar cells in the PVCN (Oertel *et al.* 1990), and these also seem to project to isofrequency sheets.

The second major excitatory fibre system in the DCN is formed by the axons of granule cells which run as parallel fibres in the molecular layer (Mugnaini *et al.* 1980). Figure 1 shows that granule cell axons run perpendicular to the isofrequency sheets defined by deep layer tonotopic inputs. Granule cell axons make excitatory contacts on the apical dendritic trees of fusiform cells (Manis 1989); presumably, there are no granule cell inputs to the giant cells although there is little information on this issue. Granule cell axons also

† Present address: Department of Otolaryngology/Head and Neck Surgery, West Virginia University, Morgantown, West Virginia 26506 U.S.A.
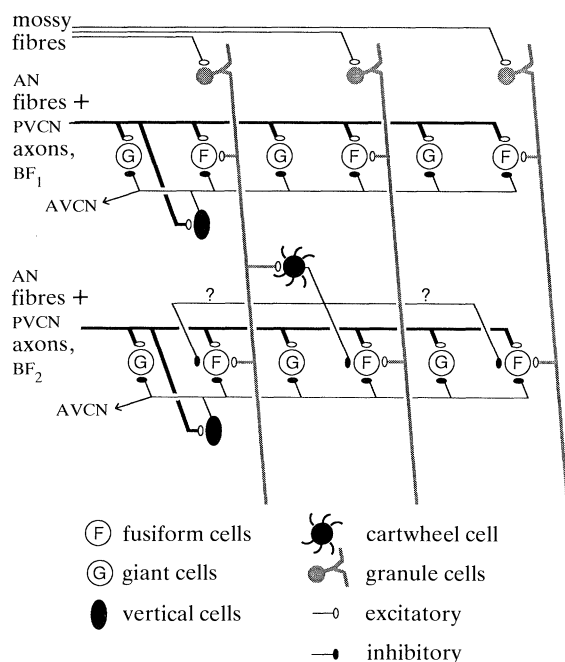
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Figure 1. Partial wiring diagram of the DCN. Cell types are represented by symbols as shown in the legend. Terminals are shown as excitatory (unfilled) or inhibitory (filled). Each isofrequency sheet is represented by a horizontal row of principal cells (F and G); two best frequencies (BF_1 and BF_2) are shown. The approximate laminar relationships of axons can be inferred from occlusions where axons cross.

terminate on three varieties of interneurones in the superficial DCN (Osen *et al.* 1990). Only one of these, the cartwheel cell, is shown in figure 1.

The mossy fibre inputs to granule cells are apparently from diverse sources which have not been identified. One source which is of interest later in this paper is a projection from the dorsal column nuclei of the somatosensory system (Itoh *et al.* 1987; Weinberg & Rustioni 1987). Because the granule cell axons run orthogonal to isofrequency sheets, and therefore contact DCN cells across a range of BFs, the granule cell system seems not to conform to traditional ideas about auditory signal processing, which depend on separation of a signal into its component frequencies. Instead, granule cell axons are positioned to coordinate processing across frequencies, perhaps by selectivity activating different sets of principal cells or by regulating overall DCN excitability.

Vertical cells are inhibitory interneurones found in the deep layers; they probably receive excitatory inputs from the fibres in deep DCN and their axons innervate fusiform cells and presumably also giant cells (Lorente de Nó 1981; Oertel & Wu 1989; Osen *et al.* 1990). Vertical cell axons terminate profusely within what appears to be an isofrequency sheet in the DCN and then project to the anteroventral division of the cochlear nucleus (AVCN), where their axons make additional contacts, also within the same isofrequency sheet (Wickesberg & Oertel 1990). Vertical cells contain inhibitory amino acids (Osen *et al.* 1990) and have been shown to inhibit AVCN principal cells (Wickesberg & Oertel 1990) and DCN principal cells (see below; Voigt & Young 1980, 1990).

Cartwheel cells of the superficial DCN are a second inhibitory interneuron; they receive excitatory input from granule cells but probably not from AN fibres (Osen *et al.* 1990; Berrebi & Mugnaini 1991; Oertel & Wu 1989). Cartwheel cell axons seem to project to an isofrequency sheet; they terminate on fusiform cell somata and basal dendritic trees. Although they are positioned to terminate on other DCN cell types, such as vertical cells, it is not known whether they do so. Less is known about two additional types of inhibitory interneurons in the superficial layer, the Golgi and stellate cells.

Figure 1 suggests that the DCN is organized into tightly bound isofrequency sheets with cross-sheet coordination only via the axons of granule cells. In fact the extent of interaction and overlap of cell processes from adjacent isofrequency sheets is likely to be larger than is implied in the figure. Although the vertical, giant and fusiform cells have flattened dendritic trees oriented parallel to the isofrequency sheets (Blackstad *et al.* 1984; Osen *et al.* 1990; Ryugo & Willard 1985), the degree of overlap of terminal fields of the various DCN axonal and dendritic systems is not known from anatomical studies. For example, it is not clear whether the axonal terminal field of a vertical cell lies in the same isofrequency sheet as its dendritic tree. Information about the interactions of DCN neurons of different types and BFs has been obtained by cross-correlation analysis of multiple simultaneous single unit recordings (Voigt & Young 1988, 1990). In the next sections, this evidence is reviewed, after the response types of DCN neurons are defined.

2. RESPONSE PROPERTIES OF DCN NEURONS

Figure 2*a, b* shows response maps of two DCN units. These maps are plots of excitatory and inhibitory response areas for tone bursts of various frequencies and sound levels. Cochlear nucleus units can be classified into five groups, types I through V, based on the relative amount of excitation and inhibition in their response maps (Evans & Nelson 1973; Young 1984). Most units in the DCN fall into types II, III, or IV; in this paper, we discuss only types II and IV. Type II responses are recorded from vertical cell interneurons and type IV responses are recorded from principal cells, both fusiform and giant cells (Young 1980).

Type II units show zero spontaneous activity, a narrowly tuned excitatory area (figure 2*a*), and weak or no response to broadband stimuli (Young & Voigt 1982). The noise response is unusual, because type II units are the only cochlear nucleus neurons that respond so weakly to broadband noise. The most straightforward explanation for their weak noise responses is that type II units have large inhibitory sidebands that are not revealed in response maps like figure 2*a* because of the lack of spontaneous activity. When a low-level BF tone is used to produce background activity in a type II unit and a response map is constructed with a second tone, the result shows a strong inhibitory sideband above BF and a weaker one
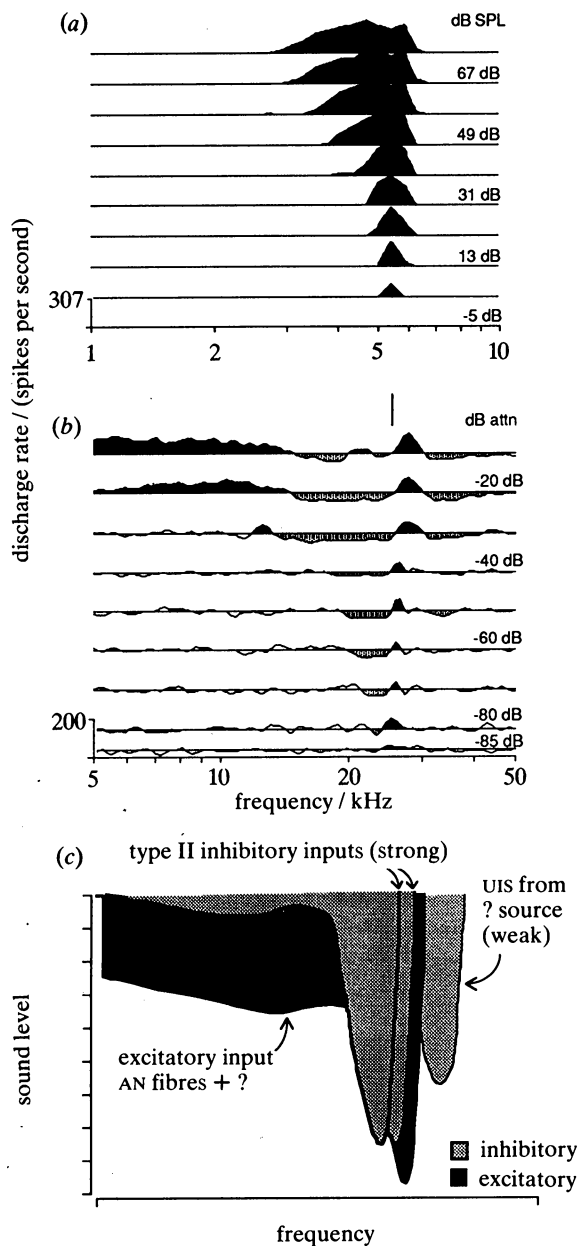
Figure 2. (*a*) Response map of DCN type II unit; map consists of ten plots, each showing discharge rate versus stimulus frequency for a sequence of 200 ms tone bursts (one per second) presented at one sound level. Sound levels given at right in dB SPL. Horizontal lines show spontaneous rate in each plot (0 spikes per second for this unit). Scale for rate plots given at lower left. Excitatory response regions (increase in discharge rate above spontaneous) filled with black. (*b*) Response map of DCN type IV unit; map constructed as in (*a*) except that this unit has spontaneous activity (≈ 50 spikes per second), so that inhibitory response areas can be seen (shaded regions where rate drops below spontaneous). Because of the way data were taken, sound levels are shown at right in dB attenuation; 0 dB is ≈ 100 dB SPL, but varies with frequency. Vertical line at top of response map is at BF. (*c*) Schematic model for generation of type IV response maps. Reproduced from Spirou & Young (1991) with permission.

below (Spirou & Young 1991). Whether these inhibitory areas are sufficient to account quantitatively for type II responses to broadband stimuli is not yet clear.

Type IV units are characterized by the response

map features shown in figure 2*b*. Usually the first response observed at low levels is excitatory, as at -80 and -85 dB. At higher levels, there is an inhibitory area (central inhibitory area or CIA) which is usually centred below BF, but which extends upward in frequency to include BF (Spirou & Young 1991). Because the CIA encroaches on BF, type IV units have a non-monotonic rate response to BF tone bursts: the response is excitatory over the first ≈ 30 dB above threshold and then becomes inhibitory. In most type IV units, there is an excitatory edge at the upper frequency limit of the CIA which separates the CIA from an upper inhibitory sideband at higher frequencies. At low frequencies, type IV units usually have a large excitatory region.

Figure 2*c* shows a model for the generation of type IV response maps based on the assumption that the CIA is produced by inhibitory inputs from type II units; the evidence for this connection has been discussed elsewhere (Young & Brownell 1976; Voigt & Young 1980, 1990) and is reviewed in the next section. The model consists of three components: (i) an excitatory input which has the characteristics of an AN tuning curve (black region), but which may be generated by both AN and PVCN inputs (Oertel *et al.* 1990); (ii) inhibitory inputs from type II units, shown by the two shaded tuning curves superimposed on the tunings curve of the excitatory input; and (iii) a second inhibitory input from an unknown source which produces the upper inhibitory sideband (UIS).

The type II inhibitory input is assumed to be strong, so that when a tone burst is within the tuning curve of the inhibitory input, the type IV unit is inhibited, producing the CIA. The BFs of the inhibitory inputs are shown slightly below the unit's excitatory BF based on two lines of evidence. First, the BFs of CIAS are generally somewhat below excitatory BFs in type IV units (Spirou & Young 1991). Second, the BFs of type II units that show inhibitory intractions with type IV units are more likely to be below than above the excitatory BFs of the type IV units (Voigt & Young 1990). The thresholds of the type II inputs are shown elevated by about 10 dB because type II units tend to have higher thresholds than type IV units (Young & Brownell 1976). These features account for the excitatory areas in type IV response maps near BF threshold and at the upper frequency edge of the CIA. The low frequency excitatory areas seen in type IV response maps result from the difference in low frequency thresholds between AN fibres (40–60 dB above threshold; Kiang 1984) and type II units (70–90 dB above threshold; figure 2*a* and Young & Voigt (1982)). There is variability in type IV response maps (Spirou & Young 1991), some of which can be accounted for by changes in the relative positions of the type II and excitatory inputs' BFs.

3. FUNCTIONAL ORGANIZATION OF THE DCN REVEALED BY CROSS CORRELATION

A straightforward way of studying the functional organization of a nucleus is to look for signs of correlated discharge among its neurons. If neurons are

synaptically connected or receive common sources of input, then their spike trains should be correlated. Two types of correlation that are seen between pairs of neurons in the DCN are illustrated in figure 3a, b. Figure 3a shows a cross correlogram between a type II and a type IV unit. The type II unit is the reference, so the correlogram shows the average discharge rate of the type IV relative to spike times in the type II. Immediately to the right of the origin, there is a decrease in the correlogram implying that the probability of type IV spikes is reduced transiently after

type II spikes. This inhibitory trough (IT) is shaded in figure 3a. An IT is expected in the correlogram of a pair of units connected by a monosynaptic inhibitory synapse (Moore *et al.* 1970). The correlogram in figure 3b was computed from two type IV spike trains. The shaded increase in correlation near the origin, called a central mound (CM), is a sign of shared input; a CM can be produced by any effect that tends to synchronize the discharges of two neurons, including a common source of excitatory or inhibitory input (Moore *et al.* 1970).
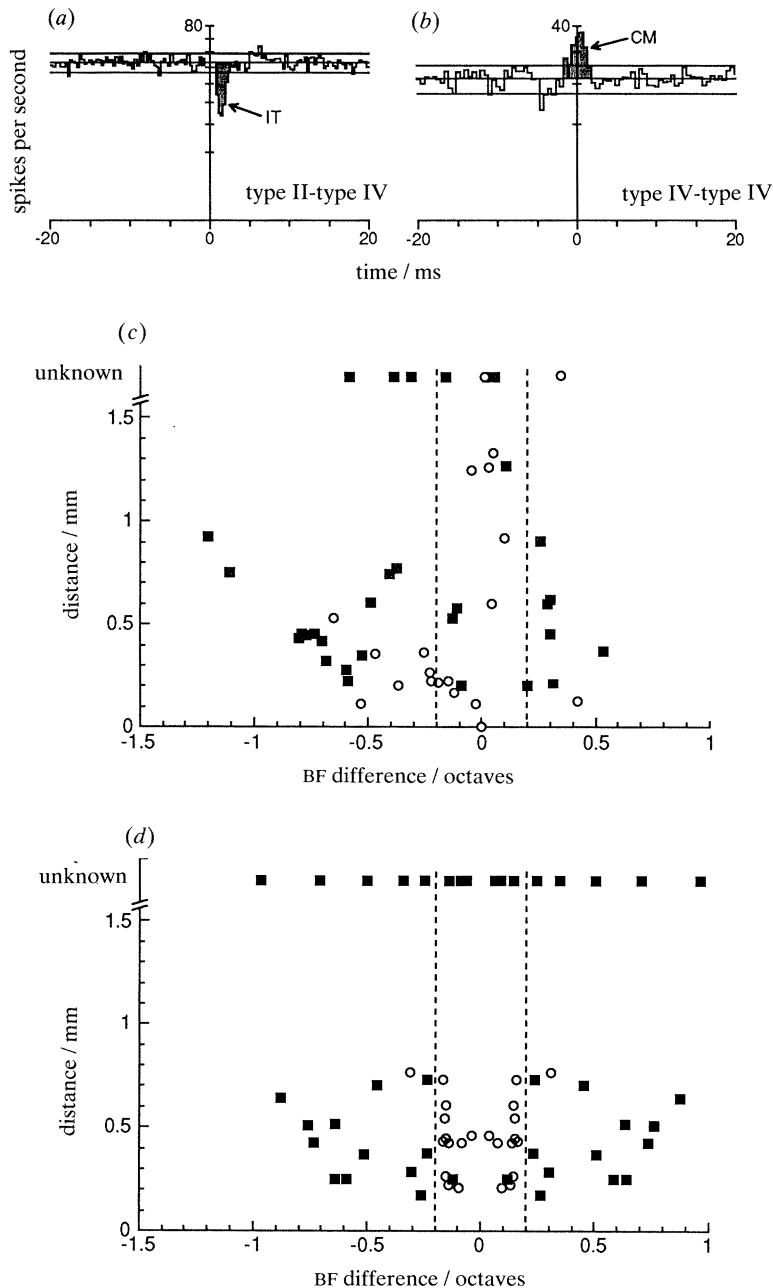

Figure 3. (a) Cross-correlogram of spike trains of simultaneously isolated DCN type II and type IV units. Horizontal lines show expected correlogram value for independently discharging neurons (centre) and ± 2 standard deviation confidence limits. Ordinate scale is square root to stabilize correlogram variance. (b) Same as (a) for type IV–type IV pair. (c) Difference in octaves between type II BF and type IV BF (abscissa) and distance apart in histological preparations (ordinate) for pairs showing and not showing an IT in their cross-correlograms. Data points at top of the figure come from pairs in which histological measure of distance is not available. (d) Same for type IV–type IV pairs showing and not showing CM correlation. Each data point plotted twice along the abscissa, at plus and minus the BF difference, because these pairs are symmetric. Redrawn from Voigt & Young (1988, 1990) with permission.

The data in figure 3 were obtained in experiments in which two electrodes were used to isolate units (Voigt & Young 1988, 1990). By looking for correlated pairs with the electrodes placed at various distances apart and in various orientations, it is possible to map out the spread of type II inhibitory connections onto type IV units and to look for the extent and spread of shared input to DCN principal cells. Figure 3c, d shows results on the occurrence of correlation as a function of the difference in BFs of the two neurons of the pair (abscissae) and as a function of the distance apart of the two neurons (ordinates). In each plot, filled symbols represent pairs with no sign of correlation under any stimulus condition tested and open symbols show pairs that were correlated with an IT (type II–IV pairs in figure 3c) or a CM (type IV–IV pairs in figure 3d). Difference in BF, i.e. position along the abscissa, is a measure of the distance apart of the units of a pair along the tonotopic axis. The distance measure on the ordinate includes both separation along and perpendicular to the tonotopic axis.

Figure 3c shows that type II inhibitory connections spread widely within isofrequency sheets near their cell bodies. The dashed lines show BF differences of ± 0.2 octaves. Within this frequency range, 12 out of 20 (60%) of pairs are correlated; moreover, correlation is observed at all distances examined (up to 1.325 mm, more than half way across the nucleus). Correlation is less commonly observed when the type II BF is 0.2–0.6 octaves above the type IV BF (2 out of 8, 25%) or 0.2–0.6 octaves below the type IV BF (6 out of 14, 43%). The limit on the distance that inhibitory connections spread is actually more stringent than is implied by these statistics. A dimensionless measure of IT amplitude was defined by Voigt & Young (1990); this measure decreases at a rate of only -0.2 per millimetre within an isofrequency sheet (i.e. for pairs with BFs within ± 0.3 octave of each other). By contrast, it decreases at a rate of -4.32 per millimetre along the tonotopic axis, i.e. when BF differences are converted to distances in millimetres using the tonotopic map of the DCN (Spirou *et al.* 1989). Finally, type II–type IV pairs are more likely to be correlated when the type II BF is below the type IV BF, although the difference is not statistically significant. This tendency is consistent with the fact that CIAS of type IV units generally have BFs somewhat below the excitatory BF (Spirou & Young 1991) and suggests that type II axons should spread to isofrequency sheets somewhat higher in frequency than those containing their dendrites.

Figure 3d shows the cumulative effect of all sources of input on type IV units in the form of the distribution of CM occurrence. Pairs are correlated essentially only within an isofrequency sheet. Eleven out of 16 pairs (69%) with BFs within ± 0.2 octave show a CM, whereas only one pair with a larger BF difference does so. It is instructive to compare the BF differences over which CMs are observed with an anatomical estimate of the width of an isofrequency sheet. The average thickness, along the tonotopic axis, of fusiform cell dendritic fields is 80 (basal) and 115 (apical) µm (Blackstad *et al.* 1984). The largest BF difference over which correlation was observed between a pair of type IV units in the fusiform cell layer is 0.138 octaves and the smallest BF difference at which an uncorrelated pair was observed is 0.239 octaves. These BF differences correspond to 97 and 167 µm, using the tonotopic map of the DCN (Spirou *et al.* 1989; see Voigt & Young, 1988). Thus, type IV units are correlated with other type IV units only when their dendrites are adjacent or overlap, i.e. within the same or adjacent isofrequency sheets.

The conclusion of the previous paragraph is consistent with the wiring diagram of figure 1, in that most axons in the DCN run parallel to isofrequency sheets. The major exception are granule cell axons. Thus, the results in figure 3d imply that granule cell inputs do not produce spike discharges in type IV units which are strongly correlated over a timescale of milliseconds, i.e. like the CM in figure 3b. The effects of granule cells might be weak or sparse, so that they are not seen in cross-correlation analysis, or they might involve long-term modulation of principal cell excitability.

There is no distinction between fusiform and giant cells in terms of the functional organization revealed by cross-correlation analysis. Both cell types show IT correlation with type II units (Voigt & Young 1990) and CMs are observed between pairs of fusiform cells, between pairs of giant cells, and between mixed pairs (Voigt & Young 1988). Thus the organization of both principal cell types into a common module, implied by figure 1, is supported by the cross-correlation evidence. The major difference between fusiform and giant cells appears to be that fusiform cells are and giant cells are not innervated by the granule-cell associated circuitry in superficial DCN. Apparently, the methods which have been used to study DCN principal cells are insensitive to the effects of the inputs to fusiform cells from the superficial DCN.

4. RESPONSES OF DCN PRINCIPAL CELLS TO COMPLEX STIMULI

DCN principal cells show excitatory responses to broadband stimuli, which is surprising given their generally inhibitory responses to tones (Young & Brownell 1976). This result can be explained by the characteristics of type II units, which respond strongly to tones, but weakly to broadband noise. These type II properties force type IV units to be inhibited by tones, but allow excitation by noise. When DCN principal cells respond to band-reject filtered noise, they show an additional interesting property, a sharp sensitivity to spectral nulls or notches in the stimulus spectrum (Evans 1977; Spirou & Young 1991).

In the cat, narrow spectral notches are produced naturally by the filtering properties of the pinna (Musicant *et al.* 1990; Rice *et al.* 1992). The frequencies at which these notches occur are dependent on sound source direction and therefore provide a sound localization cue. In particular, the cat pinna produces a prominent notch (called the first notch, FN) in the 5–20 kHz range for sounds originating in the frontal
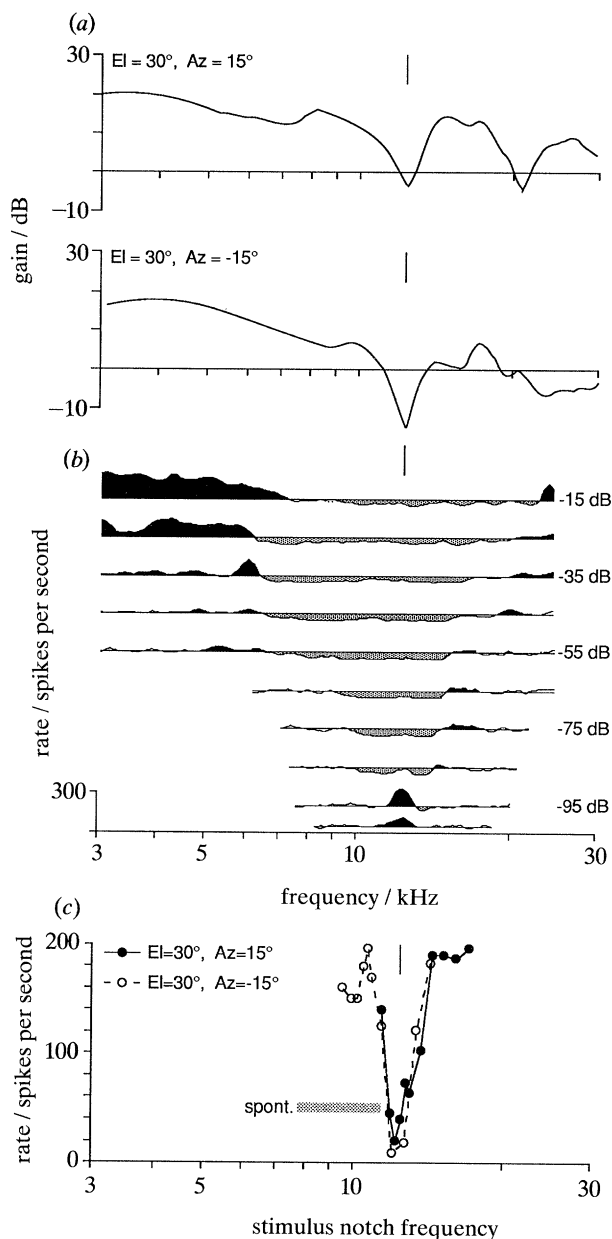
Figure 4. (*a*) Spectra at the eardrum when broad band noise is presented from two directions in space; spectra are shifted to align FN frequency with BF of unit in (*b*). (*b*) Response map of DCN type IV unit. (*c*) Discharge rate of unit as function of FN frequency for stimuli in (*a*). Fuzzy line is spontaneous rate.

stimuli in figure 4*a*. Broadband noises were filtered to have the spectra in figure 4*a* and were then presented as 200 ms bursts. In order to generate a battery of stimuli, the sampling frequency of the D/A converter was changed, which changes the frequencies of the FNS proportionally. The spectra are drawn in figure 4*a* for a sampling frequency which places the FNS at the unit's BF. Figure 4*c* shows the discharge rate of the unit as a function of the frequency of the FNS. The unit is typical of many DCN type IV units in that it undergoes a sharp change in response as a notch moves past its BF, with its response rate going from excitation to inhibition to excitation again.

The data in figure 4 show that DCN principal cells are exquisitely sensitive to spectral features of stimuli that carry sound localization information. This fact suggests that the DCN may be involved in early analysis of sound source location. Two additional findings are consistent with this hypothesis. First, Sutherland (1991) has reported that lesions of the output axons of the DCN produce deficits in localizing sound sources in elevation. Elevational sound localization, of course, depends entirely on spectral cues of the kind shown in figure 4*a*. Second, there is a projection from the dorsal column nuclei of the somatosensory system to the granule cell areas of the cochlear nucleus (Itoh *et al.* 1987; Weinberg & Rustioni 1987). The cells of origin of this projection are clustered in the lateral portion of the cuneate nucleus, where the representation of the back of the head and the pinna is located (Millar & Basbaum 1975). This correlation suggests that the somatosensory input to the DCN is providing information about the orientation of the cat's mobile pinnae and, by extension, that the DCN is integrating the pinna-position information with information about sound localization cues. Correcting for pinna orientation is essential to using spectral sound localization cues because the mapping between position in space and spectral cues changes when the pinna moves. Under this hypothesis, the orientation of the granule cell axons perpendicular to isofrequency sheets can be interpreted as providing non-auditory information about pinna position to coordinate the activity of DCN neurons of different BFS.

field. The frequency of the FN, by itself, is a sufficient cue for localizing sounds in front of the animal (Rice *et al.* 1992). Figure 4*a* shows shifted versions of the spectra at the eardrum produced when a broadband noise is presented from two locations in free field. The spectra are shifted for the reasons described below; the FNS of these spectra (vertical lines) actually occur at frequencies of 13.7 kHz (top spectrum) and 11.4 kHz (bottom spectrum). Clearly there are substantial differences in these spectra, including FN frequency, which the cat could use as sound localization cues.

Figure 4*b* shows the response map of a DCN type IV unit and figure 4*c* shows the sensitivity of this unit to the position along the frequency axis of the FNS of the

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Discussion

A. Rees (*Department of Physiological Sciences, University of Newcastle upon Tyne, U.K.*). The cytoarchitecture of the dorsal cochlear nucleus in man is different to that of the cat. What implications might this have for the operation in man of a localizing mechanism analogous to the one Professor Young has suggested for the cat?

E. D. Young. Although there are many aspects of the differences between cat and primate DCN that have not been worked out satisfactorily, it is clear from published descriptions that differences exist in the superficial layers of the nucleus, i.e. in the portions of the DCN associated with the granule cells and their associated interneurons. In apes and man, this system is small or missing. In our paper, we hypothesize that the role of the superficial granule-cell-related system in the cat is to integrate auditory information about spectral sound localization cues with somatosensory information about pinna position. If this hypothesis is correct, then animals without mobile pinnae, like apes and man, would not need the granule-cell-associated circuitry in superficial DCN. A comparative study correlating pinna mobility and DCN organization would be very interesting.