Intracellularly Labeled Fusiform Cells in Dorsal Cochlear Nucleus of the Gerbil. II. Comparison of Physiology and Anatomy

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Hancock, Kenneth E. and Herbert F. Voigt. Intracellularly labeled fusiform cells in dorsal cochlear nucleus of the gerbil. II. Comparison of physiology and anatomy. J Neurophysiol 87: 2520 –2530, 2002; 10.1152/jn.00343.2001. Fusiform cells represent the major class of dorsal cochlear nucleus (DCN) projection neuron. Although much is understood about their physiology and anatomy, there remain unexplored issues with important functional implications. These include interspecies differences in DCN physiology and the nature of the cell-to-cell variations in fusiform cell physiology. To address these issues, a quantitative examination was made of the physiology and anatomy of 17 fusiform cells from a companion study. The results suggest that the basal dendrites of fusiform cells may be electrotonically more compact than those of the cat. This relative decrease in the filtering of excitatory inputs might account for the lower incidence of type IV units in that species. These data also suggest that the gerbil DCN lacks the high-frequency specialization described in the cat, because the tonotopic arrangement of the gerbil fusiform cells quantitatively matches the place-frequency map for the gerbil cochlea. Certain physiological properties have anatomical correlates. First, the basal dendrites of low spontaneous rate cells are directed away from the soma only in the caudal direction, while the high spontaneous rate cells have basal dendrites extending rostrally and caudally. Second, input resistance was dominated by the surface area of the apical dendrite. Third, the discharge pattern was correlated with apical dendrite orientation. Finally, there was a spatial gradient of sensitivity to broadband noise organized at least partially within an isofrequency axis. Such trends indicate that neighboring fusiform cells are endowed with different signal processing capabilities.

INTRODUCTION

The cochlear nuclei are the sole target of the auditory nerve (AN) and as such represents an obligatory processing stage in the ascending auditory pathway. The laminated dorsal cochlear nucleus (DCN) contains a variety of morphological cell types exhibiting diverse physiological responses. The outputs of the DCN arise from fusiform cells and giant cells, which project via the dorsal acoustic stria to the contralateral inferior colliculus (Adams and Warr 1976). Fusiform cells are readily identified by large cell bodies and bipolar dendritic fields (Brawer et al. 1974; Lorente de Nó 1981). In the superficial layer, spinous apical dendrites interconnect through a network of granule cells and cartwheel cells (Berrebi and Mugnaini 1991; Golding and Oertel 1997; Mugnaini et al. 1980) with somatosensory (Itoh et al. 1987; Weinberg and Rustioni 1987; Wright and Ryugo 1996), vestibular (Burian and Gstoettner 1988; Kevertier and Perachio 1989), and descending auditory inputs (Benson and Brown 1990; Weedman and Ryugo 1996). The distal portion of the basal dendrite is excited by the descending branch of the auditory nerve (Smith and Rhode 1985), while the soma and proximal dendrites are likely inhibited by vertical cells (Saint-Marie et al. 1991; Voigt and Young 1980, 1990) and possibly by stellate cells of the posteroverentral cochlear nucleus (PVCN) (Oertel et al. 1990; Zhang and Oertel 1994).

There are several theories regarding fusiform cell function. For example, strong sideband inhibition may serve to enhance the representation of spectral peaks (Rhode and Greenberg 1994) or to extend dynamic range in the presence of noise (Palmer and Evans 1982). DCN neurons better code the envelopes of amplitude-modulated stimuli than do auditory nerve fibers (Backoff et al. 1999; Kim et al. 1990), leading to the postulation of a “second axis” that codes for envelope frequency (Kim et al. 1990) or periodicity pitch (Langner and Schreiner 1996). Finally, recent evidence has led to the theory that the DCN extracts spectral cues relevant for sound localization. The head-related transfer function (HRTF) of the cat contains a prominent notch whose center frequency varies between 8 and 30 kHz according to the elevation of the sound source (Musicant et al. 1990; Rice et al. 1992). This frequency range has an enlarged representation in the cat DCN as compared with the cochlea (Spirou et al. 1993). Type IV units, an important subset of DCN projection neurons, show sensitivity to both the width and center frequency of notches in broadband stimuli (Nelken and Young 1994; Spirou and Young 1991), as do type III units in gerbils (Parsons et al. 2001).

The present report describes the physiology and anatomy of 17 intracellularly recorded and labeled fusiform cells from the DCN of anesthetized gerbils. The fusiform cells in gerbils and cats differ in their physiological response properties in the decerebrate preparation. In particular, the incidence of type IV units in the gerbil is less than one-third that reported in the cat (Davis et al. 1996; Hofner and Young 1985). Antidromic stimulation studies in the cat indicate that at least a portion of the type IV unit population corresponds to fusiform cells (Young 1980). Direct intracellular recording and labeling studies, however, suggest that gerbil fusiform cells are not type IV...
units (Ding et al. 1999). This difference across species in the response properties of an important projection neuron motivates one aim of this study: to make a detailed quantitative comparison of gerbil fusiform cell anatomy to that of the cat. Golgi studies in the cat provide a suitable database of anatomical measurements for comparison (Blackstad et al. 1984), including the dimensions of each dendritic arbor. The anatomical analysis of this study suggests, in part, that gerbil fusiform cells may be electrotonically more compact than those of the cat, and that this difference may account for some of the observed differences in acoustic response properties.

Another issue is that fusiform cells exhibit a variety of response properties. In the decerebrate preparation, they have type III unit and type IV unit response maps (Ding et al. 1999; Young 1980). In anesthetized preparations, fusiform cells exhibit pauser/buildup, chopper, or onset discharge patterns, depending on stimulus conditions (Hancock and Voigt 2002; Rhode et al. 1983; Rhode and Smith 1986; Smith and Rhode 1985). The existence of such variations must be related to the complexity of the neural circuits with which fusiform cells interact. But are the cell-to-cell differences merely the result of random “wiring” differences, or do they reflect underlying principles of organization? This question motivates a second aim: to make a quantitative comparison of fusiform cell physiology and morphology in cats and gerbils. Certain physiological characteristics were indeed found to have specific anatomical correlates. Spontaneous rate (SR) was correlated with apical dendrite total length, and the discharge pattern at best frequency (BF) was correlated with fusiform cell orientation. It appears that neighboring fusiform cells may have different physiological properties and hence different signal processing capabilities by virtue of cell-to-cell variations in morphology.

This work represents part of the doctoral dissertation of K. E. Hancock.

METH ODS

Detailed experimental methods are provided in the companion paper (Hancock and Voigt 2002). Methods specific to the analysis of anatomical features are described below.

Position measurements

Cell location was quantified as suggested in Fig. 1. The bottom of the figure shows a series of coronal sections, one of which contains a hypothetical neuron, indicated by the dark circle. The position $\Delta z$ corresponds to the distance between the cell body and the rostral pole of the nucleus, while $L$ indicates the total length of the nucleus in the rostral-caudal direction. Near the rostral end of the nucleus, the number of layers typically decreased from three to two; the section where layering disappeared altogether was selected as the rostral pole.

The section containing the soma is shown rotated at the top of Fig. 1 and illustrates measurements made within the coronal plane. The position $\Delta y$ is the depth along a line perpendicular to the ependymal surface. The value $H$ is the length of this line extended to the bottom edge of the nucleus. The position $\Delta x$ is the length of the arc along the bottom edge measured from the ventrolateral side to the intersection with the line used to measure depth. The width $W$ is the total arc length of the bottom edge measured from ventrolateral to dorsome-

FIG. 1. Summary of position measurements.

Morphological analysis

The fusiform cells were reconstructed in three dimensions working from cameral lucida drawings using custom-designed software. The dendritic structure was analyzed quantitatively from the reconstruction data using a set of MATLAB (Mathworks) scripts. Total dendritic length was computed by approximating each dendrite as a sequence of small cylinders and summing the cylinder lengths.

Measurements were made individually on each of the apical and basal arbors. The methods follow those detailed by Blackstad et al. (1984) and will be described briefly here. The first step was to determine the long axis of the arbor. Blackstad et al. performed this task manually, whereas in this study an automatic method was adopted that consisted of computing the line between the cell body and the center of mass of the dendritic terminals. The arbor was then rotated about its long axis in 1° steps. At each step the span of the arbor perpendicular to the long axis was computed. The arbor thickness was defined as the narrowest span, while the arbor width was defined as the widest span. The degree of planarity was quantified by computing the width to thickness ratio. The arbor height was measured as the extent of the arbor along its long axis.

RESULTS

Geometry of the dendritic arbors

The fusiform cell dendritic arbors were quantified by a series of measurements inspired by the work of Blackstad et al. (1984) in the cat and described fully in METHODS. The results serve as a basis for comparison of the gerbil to the cat and as a basis for a subsequent quantitative examination of the relationship between physiology and anatomy. It is important to note that Blackstad et al. limited their consideration to the central third of the DCN and thus avoided effects due to the significant curvature of the nucleus at its edges. It was not possible to do likewise in our case due to the sample size
The anatomical properties of the apical arbors are summarized in Table 1. Estimates were made of the total dendritic lengths by summing the lengths of the individual segments comprising each three-dimensional (3-D) reconstruction. The mean apical length was 3,359 \( \mu \text{m} \), which is very close to the mean value of 3,212 \( \mu \text{m} \) reported by Blackstad et al. (1984) in the cat. The width and thickness measurements were obtained by rotating the arbor about its long axis to find the widest and narrowest projections, respectively. Both measures are smaller in the gerbil (314 \( \mu \text{m} \)) than in the cat (392 \( \mu \text{m} \)), but the thickness is larger (112 vs. 72 \( \mu \text{m} \)). The result is that the width to thickness ratio in the gerbil (3.07) is about half that in the cat (5.70). The mean basal arbor is 250 \( \mu \text{m} \) in height as compared with 389 \( \mu \text{m} \) in the cat.

### Table 1. Properties of apical dendritic arbors

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TL, total length.

### Table 2. Properties of basal dendritic arbors

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TL, total length.

Figure 2A shows that BF increases in both the dorsomedial and caudal directions. This observation is quantified in Fig. 2B where the BF is plotted as a function of the relative X-positions (ventrolateral-to-dorsomedial location) and the relative Z-positions (rostral-to-caudal location) of the fusiform cell somata. The straight line fits to these data indicate that BF is indeed highly correlated with these two dimensions.

The tonotopic axis is described by the equation \( \log(BF) = 1.45Px + 1.01Pz \) \( (r = 0.81, P < 0.001) \), obtained by performing multiple linear regression on log BF using both the relative X- and Z-positions. A tonotopic position was determined for each neuron by projecting its location onto this axis and computing the distance from the origin \( (Px = Pz = 0) \). The resulting positions are plotted in Fig. 3 as a function of BF. For comparison, the place-frequency map for the gerbil cochlea is also plotted, where position indicates the relative distance from the base of the cochlea. In general, Fig. 3 shows that the spatial distribution of BFs in the DCN closely follows the distribution of characteristic frequencies (CFs) along the cochlea. For comparison, the place-frequency map computed for the cat DCN by Spirou et al. (1993) is also plotted.

### Fusiform cell orientation varies with location

Figure 4 summarizes a systematic shift in the orientation of the long axis as a function of rostral-caudal position. In the rostral end of the nucleus, the apical dendrites tend to be positioned on the rostral side of the soma while the basal dendrites extend in the caudal direction. Near the center of the DCN, the orientation is roughly vertical (dorsal to ventral). Toward the caudal pole, fusiform cells have caudally directed apical dendrites and rostrally directed basal dendrites.

It would appear that this trend is a consequence of the shape of the DCN itself. The DCN can be visualized as a series of thin shells, with the molecular layer wrapped around the fusiform cell layer, which in turn is wrapped around the deep layer. Thus from any position within the fusiform cell layer, the apical dendrites radiate outward to fill the molecular layer...
while the basal dendrites converge inward to occupy the deep layer. A similar finding was reported by Rhode et al. (1983), who further describe the cells in the rostral end having more numerous apical dendrites that more frequently emerge directly from the soma. Neither this study nor the previous one finds any obvious physiological sequelae to this trend, which possibly is simply a consequence of the overall curvature of the nucleus.

Spontaneous rate depends on basal dendrite orientation

The spontaneous discharge rates of the fusiform cells in this sample range from 0 to 54 spikes/s. These can be separated into a low SR group (rate <2.5 spikes/s, 8/17 cells) and a high SR group (rate >7.5 spikes/s, 9/17 cells). The creation of two SR categories may, in fact, represent an artificial division of a continuously distributed property, but is useful here as a convenient means of visualizing a related anatomical trend. Specifically, there is a correlation between spontaneous rate group
and the disposition of the basal dendrites, as depicted in Fig. 5. The basal dendrites of the low SR cells (top row) are primarily directed caudally away from the soma. The high SR cells (bottom row) tend also to have branches oriented in the rostral direction, giving the distribution of the basal dendrites a more symmetrical appearance.

These observations were put on a more quantitative basis by computing the centroid of each basal arbor with respect to the soma. The trend is specifically captured by the rostral-caudal component, $Z_C$, as shown in Fig. 5. Note that the value of $Z_C$ is positive for positions caudal to the soma. For every low SR cell ($Z_C \approx 63.2 \mu m$), the basal arbor centroid is caudal to that of every high SR cell ($Z_C \approx 48.8 \mu m$). No correlation was found between the absolute position of the basal arbor centroid and spontaneous activity.

The nine cells shown in Fig. 5 come from the same general region of the DCN, reflected by the similarity of their best frequencies. This is an important consideration when examining the arrangement of the basal dendrites, because as described above, the orientation of the fusiform cell long axis changes as a function of position (Fig. 4).

**Input resistance is a function of total apical dendritic length**

Figure 6 shows that fusiform cell input resistance is correlated with apical dendritic length, but not with basal dendritic length. The best line fit to the apical length was computed after removing the two points indicated by triangles in Fig. 6A. The correlation with apical length is negative, so that larger lengths correspond to smaller resistances. This is consistent with a passive model in which membrane conductance is proportional to surface area, insofar as dendritic surface area is proportional to total length. Input resistance was not correlated with the sum of the apical and basal lengths ($r = -0.06$). The presence of spines, however, greatly increases the surface area per unit length of the apical dendrite and so a simple sum of total lengths probably understates the contribution of the apical dendrite to the overall passive membrane conductance. We did not consider the effects of surface area more directly because of difficulties estimating it that arose from inconsistencies in the quality of spine labeling.

**FIG. 5.** Spontaneous activity and basal dendrite arrangement. Neurons are from the 0- to 2-kHz region and are drawn in a parasagittal view. Apical dendrites are shown in gray; basal dendrites in black. Basal dendrites of low spontaneous rate (SR) cells (top row) are oriented primarily in the caudal direction. Those of the high SR cells (bottom row) have both rostrally and caudally directed branches. This difference is quantified using the parameter $Z_C$, which is the rostral-caudal component of the basal arbor’s centroid, measured with respect to the soma. The low SR units have larger $Z_C$ values (centroids located more caudally) than the high SR units.

**FIG. 6.** Relationship between input resistance and arbor length. A: input resistance is highly correlated with apical dendrite length. Regression line: $y = -10.5x + 48.2, r = -0.79, P < 0.001$. Triangles indicate data points omitted as outliers. B: input resistance is uncorrelated with basal dendrite length. Regression line: $y = 0.6x + 16.8, r = 0.08, ns.$
Regularity histogram shape depends on orientation of apical arbor

Regularity histogram shapes were quantified using three slope measurements as described in the companion paper. Briefly, the transient slope, $m_T$, most closely follows the classification scheme of Gdowski (1995). It is particularly sensitive to the change in interspike interval over the initial 5–10 ms of response and since nearly all of the cells in this study had decreasing intervals over this range, regardless of their subsequent behavior, the transient slope was not necessarily an effective means of characterizing rate trends over the entire stimulus duration. To better capture these rate trends, the slope measurements $m_1$ and $m_2$ were computed by performing a two-line fit to the interspike interval data after omitting the first bin.

Figure 7 shows that for the 10 fusiform cells with BFs less than 2 kHz, the slope $m_1$ is correlated with the orientation of the apical dendrites. The angle $\varphi_{\text{apical}}$ corresponds to the rotation required to find the narrowest dendritic profile after making the long axis of the arbor vertical. A value of zero corresponds to an arbor oriented perpendicular to the coronal plane. The apical dendrites in Fig. 7 are drawn looking down on their tops, such that their long axes project out of the page. The values of $m_1$ have been divided into three groups: high, medium, and low, indicated in Fig. 7 by circles, triangles, and squares, respectively. The data indicate that the fusiform cells with apical arbors oriented most nearly perpendicular to the coronal plane have the most positive $m_1$ values (circles), while those oriented closest to parallel to the coronal plane have the most negative $m_1$ values (squares).

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**FIG. 7.** Relationship between regularity histogram shape and orientation of apical arbor. Top: slope $m_1$ from the regularity histogram plotted vs. the orientation of the apical arbor. The orientation $\varphi_{\text{apical}}$ is the rotation about the long axis giving the narrowest arbor profile. See text for a detailed description of how these values are measured. Regression line: $y = -1.1x + 21.8$, $r = -0.82$, $P < 0.01$. Data points indicated by circles, triangles, and squares represent high, middle, and low $m_1$ values, respectively. Bottom: each group corresponds to the data points above and shows the fusiform cell apical arbors after superimposing the somata. The view is looking down on top of apical arbors, so that the long axes project out of the page. R, rostral; M, medial.
Correlation of cell properties with location

An effort was made to identify fusiform cell characteristics that vary systematically with location. To do this, a wide variety of physiological response metrics (see companion paper) were systematically correlated with the normalized X-, Y-, and Z-position measurements (see METHODS).

Two statistically significant trends were identified, roughly orthogonal to the tonotopic axis. The relative noise index decreased in the X-direction (ventrolateral to dorsomedial), meaning that the responses to noise became progressively weaker in this direction (Fig. 8A). A gradient in wideband inhibitory strength is sufficient to account for this observation, as detailed in the DISCUSSION. The second trend was that input resistance also tended to decrease in the X-direction (Fig. 8B). This is consistent with the fact that total apical dendritic length increases in the same direction (Fig. 8C), since the inverse relationship between these two properties has already been described.

Aside from tonotopy, the only statistically significant spatial trends were found in the X-direction. Since neither trend was accompanied by a significant dependence on Z-position, it was not possible to compute an axis trajectory for quantitative comparison with the tonotopic axis computed above. It can, however, be said that while best frequency is strongly correlated with both X- and Z-position, input resistance and relative noise response are strongly correlated only with X-position. So, although these results cannot resolve the issue of an orthogonal axis per se, there is at least a qualitative suggestion that the spatial gradients of these two properties are not parallel with the frequency axis.

DISCUSSION

A detailed quantitative examination of fusiform cell physiology and anatomy was made in this study. The following findings will be discussed. 1) The basal dendrite in the gerbil is shorter than in the cat. 2) The gerbil DCN appears to lack the high-frequency specialization of the cat DCN. 3) High spontaneous firing rates are correlated with basal dendrites having both rostrally and caudally directed branches, while low spontaneous rates are correlated with basal dendrites having only caudally directed branches. 4) The inhibition reflected in the slope of the regularity histogram is related to the orientation of the apical arbor. 5) Noise response strength appears to be systematically organized within an isofrequency sheet.

Consideration of the basal arbor total length

The basal dendrites in the gerbil have about 70% the total length that they do in the cat and thus may be electrotonically more compact. The equivalent cylinder model for a dendritic arbor has a characteristic electrotonic length, which is proportional to the ratio of the physical length of the cylinder to the square root of its diameter (Rall 1977). Consider a hypothetical cat fusiform cell that has three primary basal dendrites giving rise to identical branching structures. One possibility is that the “gerbil” fusiform retains all three branches, but each branch is shortened by a third. The equivalent cylinder for such a cell would be physically shorter than its counterpart in the cat, but have the same diameter and hence a shorter electrotonic length. A gerbil fusiform cell could also be produced by removing one of the three hypothetical branches, giving the observed one-third reduction in total length. The equivalent cylinder would have the same physical length as the cat fusiform cell, but its diameter would be smaller, resulting in a longer electrotonic length.

Which case best represents the actual situation? Blackstad et al. did not report branch order statistics for the cat, so it is not possible to make a comparison in this regard. But, as shown in Table 2, the height of the basal arbor is about one-third smaller in the gerbil than in the cat. This would seem to reject the second scenario above, since the pruning of one branch would not affect the size of the remaining branches and hence the
arbor height should remain about the same. This leaves the first scenario as the most viable and suggests that the effect of dendritic shortening in the gerbil is to make the basal arbor electrotonically more compact than in the cat.

Assuming that inputs from the auditory nerve are distributed toward the distal ends of the basal dendrites (Smith and Rhode 1985), a possible effect of this electrotonic shortening would be to decrease the attenuation of excitatory synaptic potentials. To the extent that inhibitory inputs are received at more proximal locations (Berrebi and Mugnaini 1991; Saint-Marie et al. 1991), they are relatively unaffected by the overall length of the dendrite. Hence, an electrotonically more compact basal dendrite might preferentially enhance excitatory drive relative to inhibition. Indeed, previous results suggest that the proportion of type III units having type IV unit properties is smaller in the gerbil than in the cat (11% vs. 32–45%) and the proportion of type III units is larger (62% vs. 23%) (Davis et al. 1996). Ding et al. (1999) reported on 13 labeled fusiform cells from the decerebrate gerbil, none of which had classic type IV unit response properties. Interestingly, the type IV unit incidence in rabbit (23%) and chinchilla (25%) appears to follow the same size-related trend (Davis et al. 1996; Hui and Disterhoft 1980; Kaltenbach and Saunders 1987).

This species-related difference in unit incidence was considered by Davis and Voigt (1996) using a point neuron model. Their hypothesis was that a weakened contingent of type II unit inhibition onto DCN projection neurons was responsible for the lack of type IV units found in the gerbil relative to the cat. They showed that a 40–50% reduction in the number of type II unit inputs was sufficient to turn a model type IV unit into a type IV-T or type III unit. A hypothesis based on the present finding in regard to basal dendrite length, in contrast, suggests that the balance is shifted toward excitation by an enhancement of the excitatory inputs, rather than by a reduction of the inhibitory inputs. These issues might effectively be explored using a compartmental model of a fusiform cell.

**Tonotopic organization of the gerbil DCN**

The qualitative picture of tonotopy presented in Fig. 2 agrees well with the description of frequency organization in gerbil DCN obtained using measurements of 2-deoxyglucose uptake (Ryan et al. 1982). On a more quantitative basis, the fusiform cell BFs were plotted in Fig. 3 as a function of the cell position along the tonotopic axis. The data plotted in this manner correspond well with the cochlea place-frequency map determined by Müller (1996) in the Mongolian gerbil (Fig. 3). Such quantitative correspondence between frequency representation in the cochlea and tonotopic organization in central auditory structures is frequently observed (Müller 1990).

A notable exception is the cat DCN, whose representation of the 8- to 30-kHz range is disproportionately larger than the representation of the same frequency range in the cochlea (Spiro et al. 1993). The head-related transfer function (HRTF) in the cat contains spectral notches that may serve as cues for determining sound source elevation (Rice et al. 1992). These notches fall in the 8- to 30-kHz range, suggesting that the enhanced representation of these frequencies in the cat DCN is a functional specialization related to coding those particular spectral features (Spiro et al. 1993).

The place-frequency analysis shown in Fig. 3 is limited to the extent that it is a one-dimensional description of the tonotopy; it does not consider variations in cell density or the possibility of a two-dimensional frequency gradient. The comparison with the cat data of Spirou et al. (1993) is appropriate insofar as the cat data are also based on a one-dimensional frequency axis. That study, however, was based on BF estimates made at finely spaced locations from a large number of electrode tracks. Furthermore, Spirou et al. (1993) accounted for variations in fusiform cell density when drawing conclusions about BF representation in the DCN.

The present data therefore should be regarded as preliminary but appear to underscore the fact that the tonotopy of the gerbil DCN (and cochlea) is largely devoted to a lower frequency range. Frequencies below 10 kHz occupy about 60% of the length of both structures, and no specialized frequency representation in the gerbil DCN is apparent. It is currently unknown whether or not the gerbil HRTF contains spectral elevation cues similar to those identified in the cat HRTF. Measurements of the HRTF in gerbil and a more detailed examination of frequency representation in the DCN are essential to a comparative evaluation of DCN function in the two species.

**Spontaneous rate**

The results indicate that the disposition of the basal dendrites is correlated with spontaneous rate for the fusiform cells with best frequencies less than 2 kHz. The basal dendrites of low SR cells are directed away from the soma only in the caudal direction, while the high SR cells have basal dendrite branches extending both rostrally and caudally. The basal arbors of the low SR units, relative to those of the high SR units, have more caudally located centroids. It is important to note that this observation is based on relative comparisons of basal arbor structure among cells having similar orientations. No absolute metric was found to allow for a global quantification of the relationship between SR and basal dendrite position. It was thus necessary to limit consideration to this BF range because of the general shift in long axis orientation with rostral-caudal position (and hence BF) and because there were not sufficient numbers in any other frequency band for cell-to-cell comparisons to be made.

It is not immediately clear how the orientation of the basal dendrites may influence spontaneous activity. Liberman (1993) suggested that auditory nerve inputs to the cat DCN may be segregated based on spontaneous rate, with the high SR fibers terminating deeper in the nucleus than the low SR fibers. This appears to be inconsistent with our results, since the rostrally directed basal dendrites of the high SR fusiform cells tend to be more shallow in depth than the caudally directed branches common to both SR groups.

Another possibility is that the rostrally directed branches access some other set of inputs that modulate spontaneous activity. It also may be that the orientation characteristic of the high SR cells has electrotonic consequences that emphasize excitatory inputs over inhibitory inputs. Regardless of the mechanism, the results suggest that the distribution of fusiform cell spontaneous activities is not entirely due to happenstance.

It is difficult to say what functional consequences may arise from having a subset of the fusiform cell population preferentially receive low SR input. It has been suggested that low SR
auditory nerve fibers are recruited to improve intensity discrimination at high sound levels or are useful for signal in noise problems (Vieille 1983). Extending such interpretations to the DCN is problematic, because they are based on the fact that low SR AN fibers typically have high acoustic thresholds (Liberman 1978), a trend not generally characteristic of DCN units. It has been shown that low SR AN fibers better synchronize to AM tones (Joris and Yin 1992), but there remains disagreement over the general suitability of DCN projection neurons for encoding such stimuli (Joris and Smith 1998).

**Shape of regularity histogram**

For the fusiform cells in the 0- to 2-kHz band, a correlation was observed between the orientation of the apical dendritic arbor, quantified by the rotation, \( \phi_{apical} \), about the long axis yielding the narrowest projection of the arbor, and the shape of the regularity histogram, as quantified by the slope, \( m_1 \) (Fig. 7). The slope values \( m_1 \) and \( m_2 \) are obtained by simultaneously fitting two lines to the interspike interval plot after omitting the first bin. For the data of this study, the value of \( m_1 \) appears to be a more useful measure of inhibition than the monotonicity of the BF rate-level curve, because the \( m_1 \) values are more evenly distributed over a wider interval. A positive value of \( m_1 \) reflects a rate trend similar to the underlying excitatory drive from auditory nerve fibers and hence suggests relatively weak inhibitory input. Negative values are taken as an indication of a relatively stronger inhibitory contribution.

One interpretation of this result is that the apical dendrite orientation determines the cross-sectional area of the arbor perpendicular to the trajectory of the parallel fibers and hence affects the pattern of activity in the apical arbor. For example, those presenting a narrow face to the parallel fiber network may be more strongly influenced by inhibitory inputs from the cartwheel cell population. Although cartwheel cells are known to be acoustically responsive, their activity is relatively weak and of high threshold (Ding et al. 1999; Parham and Kim 1995) and would not be expected to account for the relatively strong inhibition represented by negative values of \( m_1 \).

A second possibility is that since the neurons represented in Fig. 7 come from the ventrolateral third of the nucleus, the change in apical arbor orientation may result from curvature of the strial axis in this region (Blackstad et al. 1984). In this case, the variations in orientation and in slope \( m_1 \) may, in fact, be functions of position. That no such dependence was apparent in our position data may indicate limitations in the accuracy of mapping position across different tissue samples.

**Possible significance of physiology-morphology correlations**

Figures 5–7 demonstrate that certain morphological features are correlated with specific physiological properties. The geometries of the apical and basal arbors influence input resistance and spontaneous activity, respectively, while some aspect of cell orientation apparently contributes to the inhibition measured in the regularity histogram. It is thus possible that fusiform cells along the isofrequency axis have graded physiological properties, and hence different signal processing characteristics. In this way, the fusiform cell population might be capable of performing different operations on the same set of inputs.

A chance example from the present study illustrates that significant morphological differences may indeed exist between nearby cells. Figure 9 is a sagittal view of two fusiform cells, labeled in a single electrode track, their cell bodies separated by less than 10 \( \mu m \). They were located in the caudal DCN, and hence, as described earlier, their long axes have a rostral-to-caudal orientation. The apical arbor of the black-colored neuron is sparser than that of the gray-colored neuron. Furthermore, the two basal arbors do not overlap completely, but follow slightly different trajectories. The results of Fig. 9 support the notion that neighboring fusiform cells might have markedly different morphologies.

**Organization of sensitivity to broadband noise**

The notion that the DCN contains a functional axis orthogonal to the frequency axis is suggested by anatomical features. First, there is the network of parallel fibers oriented perpendicular to the underlying auditory nerve fibers. If systematic variations in activity within the parallel fiber network contribute to the variations in fusiform cell physiology, then fusiform cell properties might vary in a spatially dependent manner. Another anatomical substrate for a second axis in the DCN is a progressive decrease in the number of vertical cells in the dorso-medial direction within the coronal plane (Lorente de Nó 1981). Since vertical cells presumably inhibit fusiform cells, the magnitude of inhibitory response features (tone slope, interspike interval slope, etc.) should also decrease in the dorso-medial direction.

The results show that the relative noise index is negatively
correlated with position in the ventrolateral to dorsomedial direction (Fig. 8A). In other words, fusiform cell responses to noise tend to become weaker in the same general direction in which Lorente de Nó (1981) reported the vertical cell layer becoming thinner. A decrease in the number of vertical cells, however, represents a loss of inhibition and so cannot account for the diminishing noise responses. The noise sensitivity of DCN principal cells is thought to be shaped by a source of wideband inhibition, possibly originating in the PVCN (Nelken and Young 1994). The observed noise responses in the current study might be accounted for by an increasing contribution of this inhibitory source in the dorsomedial direction.

Earlier studies have identified two inhibitory components to the response maps of type IV units, as schematized in Fig. 10. The first arises from a band of type II units, centered below the BF of the type IV unit (Voigt and Young 1990), while the second component, wideband inhibition, possibly arises from the PVCN and is centered above the type IV unit BF (Nelken and Young 1994; SpiroU and Young 1991). This organization might be consistent with wideband inhibitory input strengthening in the dorsomedial direction, as suggested by the present results, and the vertical cell layer thinning in the same direction, as described by Lorente de Nó. If, for example, each type IV unit receives input from a band of type II units (presumably vertical cells) centered spatially on BF, then the resulting inhibitory band would have a lower BF because the vertical cells are more dense in that direction. Similarly, if the wideband inhibition is stronger in the dorsomedial direction, inhibition from a band spatially centered on BF will itself have a higher BF. The idea that these two inhibitory sources might trade for one another across the width of the DCN is consistent with data presented by Nelken and Young (1994). Their Fig. 8B suggests that the influence of inhibition by type II units, as measured by the maximum driven BF rate, is negatively correlated with the influence of wideband inhibition, as measured by the minimum inhibitory notch width.

Conclusion

This report has described differences between cats and gerbils in the anatomical properties of DCN fusiform cells and in their tonotopic arrangement. The report also described systematic distributions of functional properties within the fusiform cell population. How such variations contribute to DCN function is yet to be understood.

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