ULTRASTRUCTURAL ANALYSIS OF SYNAPTIC ENDINGS OF AUDITORY NERVE FIBERS IN CATS: CORRELATIONS WITH SPONTANEOUS DISCHARGE RATE

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In mammals, all known auditory information enters the brain by way of the auditory nerve. The auditory nerve is a bundle of axons whose cell bodies are located in the spiral ganglion within the cochlea. The ganglion cells send peripheral processes out to the organ of Corti to contact acoustic receptor cells and send central processes by way of the auditory nerve to terminate in the cochlear nucleus. In this way, the ganglion cells convey the output of the receptors to neurons of the brain. In turn, cells of the cochlear nucleus give rise to the ascending auditory pathways. The role of the cochlear nucleus is to receive incoming auditory nerve discharges, to preserve or transform the signals, and to distribute outgoing activity to higher brain centers. In order to understand mechanisms of stimulus coding in these early stages of the auditory system, we need to know the nature of the signals conveyed by auditory nerve fibers and structural details of their destination in the cochlear nucleus.

There are at least two different types of ganglion neurons based on cell body size, myelination, and cytoplasmic features (Kellerhals et al., '67; Spoendlin, '73; Berglund and Ryugo, '91), peripheral innervation (Kiang et al., '82; Berglund and Ryugo, '87; Brown, '87; Liberman et al., '91), and central projections (Fekete el al., '84; Brown et al., '88; Ryugo and Rouiller, '88; Ryugo et al., '91). Type I neurons constitute 95% of the ganglion population, have myelinated processes and a high somatic ribosomal content, and contact one or occasionally two inner hair cells (IHCs). In contrast, type II neurons represent 5% of the population, have unmyelinated processes, exhibit high numbers of somatic neurofilaments, and contact many outer hair cells (OHCs).

When a recording microelectrode is inserted into the auditory nerve, the physiological responses of individual fibers can be monitored (Kiang et al., '65; Liberman, '78). It is generally accepted that all single unit recordings in the auditory nerve have come from type I auditory nerve fibers and that virtually nothing is known about the response properties of type II fibers (Liberman, '82; Robertson, '84). Consequently, this report focuses on type I fibers.

It has been suggested that under a limited range of stimulus conditions, the pattern of discharges in any single auditory nerve fiber is qualitatively similar throughout the population (Pfeiffer, 1966). Quantitatively, however, single fiber responses differ along two principal

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Table I. TYPE I AUDITORY NERVE FIBERS IN CATS. QUANTITATIVE DATA SUMMARY

	Low SR Fibers	High SR Fibers
Spontaneous Discharge Rate	<18 s/s	>18 s/s
Representation in Nerve	40%	60%
Threshold at CF (dB SPL)	0-40 dB	$\approx$ 0 dB
Maximum Discharge Rate	50-200 s/s	150-250 s/s
Diameter of Peripheral Ending	<0.5 μm	$\approx$ 1.5 μm
Number of Central Endings/Fiber	$\approx$ 100	$\approx$ 55
Endbulb Form Factor (Area/Perimeter)	<0.52	>0.52

Data from Liberman, 1978, 1982; Fekete et al. 1984; Sento and Ryugo, 1989.

dimensions: frequency selectivity and spontaneous discharge rate. Frequency selectivity or characteristic frequency (CF, that frequency to which the neuron is most sensitive) refers to a fiber's tendency to be most responsive to a single frequency, and is best represented by a threshold tuning curve. A tuning curve describes the envelope of the coordinates of a neuron's response area to tonal stimuli in terms of sound level (dB SPL) and frequency, and specifies both CF and threshold at CF. Threshold at CF is correlated to spontaneous discharge rate.

In the absence of acoustic stimulation, auditory nerve fibers manifest spontaneous, randomly-occurring spike discharges. Among units having similar CFs, SR can range from near zero to greater than 100 spikes per second (s/s). Across the entire range of CF values, SR has a bimodal distribution, and for our purposes, fibers exhibiting <18 s/s are defined as low SR fibers, whereas fibers exhibiting >18 s/s are defined as high SR fibers. Many aspects of an auditory nerve fiber response to simple stimuli can be calculated or predicted once a tuning curve and the spontaneous discharge rate (SR) are known (Kiang et al., '65; Anderson et al., '71; Sachs and Abbas, '74; Liberman, '78; Evans and Palmer, '80). For example, fibers of the different SR groups display systematic differences in their threshold at CF, dynamic range, and discharge rate properties in response to sound.

There are morphological correlates to fiber SR. In the peripheral auditory system, SR is proportional to the caliber of the unmyelinated terminal and is correlated with the location of the peripheral synapse on the IHC (Liberman, '82). Centrally, SR-related differences in fiber morphology in the anteroventral cochlear nucleus (AVCN) include the number, size, and distribution of terminal swellings (Fekete et al., '84; Rouiller et al., '86; Ryugo and Rouiller, '88; Ryugo and Sento, '91). These systematic differences in anatomical and physiological features of fibers belonging to separate SR groups (summarized in Table I) suggest that each group may represent functionally distinct components for the processing of acoustic information. The most sensitive fibers might ultimately be involved in threshold detection, whereas the least sensitive fibers might be related to the perception of loudness or contribute to the elicitation of the middle ear muscle reflex. Such a distinction between fibers of the different SR groups might be expressed at the cellular level, whereby members of each group would exhibit unique features in terms of their synaptic connections with different populations of neurons in the cochlear nucleus. We began a direct test of this hypothesis by studying synaptic relationships of intracellularly labeled auditory nerve fibers whose physiological response properties were recorded prior to staining.

In the present paper, we report on our examination of the synaptic connections formed by the ascending branches of two type I auditory nerve fibers having CFs of 1 kHz. One fiber belonged to the low SR group (0.4 spikes/sec), whereas the other belonged to the high SR group (44.8 spikes/sec). Each fiber came from the opposite nerve of the same cat, a circumstance that serves to minimize variation. The methods for surgery, sound stimulation,

Figure 1. Drawing tube reconstruction of the initial portion of an HPR-labeled ascending branch of a low SR fiber. Stippled symbols represent cell bodies in close apposition to labeled terminals which were examined with an electron microscope. The extensive branching is typical for auditory nerve fibers having low SR.

intracellular recording and horseradish peroxidase (HRP) injections, and histological procedures have been published previously (Ryugo and Sento, '91).

The light microscopic appearance of each fiber was entirely consistent with previously published descriptions (Fekete et al., '84; Ryugo and Rouiller, '88). The fiber entered the nucleus by crossing the Schwann-glia border and travelled a few hundred micrometers before bifurcation. The bifurcation gave rise to a prominent ascending branch and descending branch. In the region of the bifurcation, each ascending branch produced collaterals that ramified further, distributing swellings against cell bodies and in the neuropil (Fig. 1,2). This region, called the interstitial nucleus (Lorente de Nó, '33) or globular cell area (Osen, '69), is comprised mostly of so-called globular bushy and stellate (multipolar) cells (Osen, '69; Tolbert and Morest, '82). The low SR fiber emitted additional collaterals that ramified rather extensively and distributed themselves dorsolaterally (Fig. 1), within a region called the small cell cap (Osen, '69).

Figure 2. Drawing tube reconstruction of the initial portion of an HRP-labeled ascending branch for a high SR fiber. Stippled symbols represent cell bodies in close apposition to labeled terminals which were examined with an electron microscope. The infrequent branching is typical for auditory nerve fibers having high SR.

The first issue addressed by our serial section, electron microscopic investigation was which neurons received labeled endings (Figs. 3,4). Our objective was to determine whether low and high SR fibers contacted different sets of neurons. In fact, however, we discovered that each fiber type formed axosomatic synapses onto both globular bushy cells and stellate cells. Globular bushy cells were identified by an abundance of free cytoplasmic polysomes, an occasional small stack of rough endoplasmic reticulum, and a smooth nuclear membrane. Each globular bushy cell had more than 85% of its somatic surface apposed by synaptic endings, as determined by analyzing 3 representative sections through the cell body which included the nucleus. In contrast, stellate cells were characterized by multiple medium-to-large stacks of rough endoplasmic reticulum and an irregular nuclear membrane. Our cell type distinctions essentially confirm previously published criteria (Tolbert and Morest, '82). The stellate cell postsynaptic to the labeled high SR fiber had an average of 49.4 $\pm$ 11.2% of its somatic surface apposed to synaptic endings and that postsynaptic to the labeled low SR fiber had 41.1 $\pm$ 7.6%. These stellate cells with their well-innervated cell bodies more resembled the onset-chopper neurons than the sparsely innervated sustained-chopper neurons described in this same region of the nucleus (Smith and Rhode, '89).

We also reconstructed a number of postsynaptic targets of labeled terminals from the auditory nerve fiber having low SR in the small cell cap (see Fig. 12C of Osen, '69), but only some of these targets could be traced back to an identifiable cell body. This region contained three principal cell populations: Golgi, granule, and small cells. These cell types were distinguishable from each other by virtue of differences in their size, shape, and cytological characteristics. A thorough description of cochlear Golgi and granule cells is available in the literature (Mugnaini et al., '80). Briefly, granule cells have the smallest somata (8-10 μm in diameter) with a relatively pale-staining, thin rim of cytoplasm and a

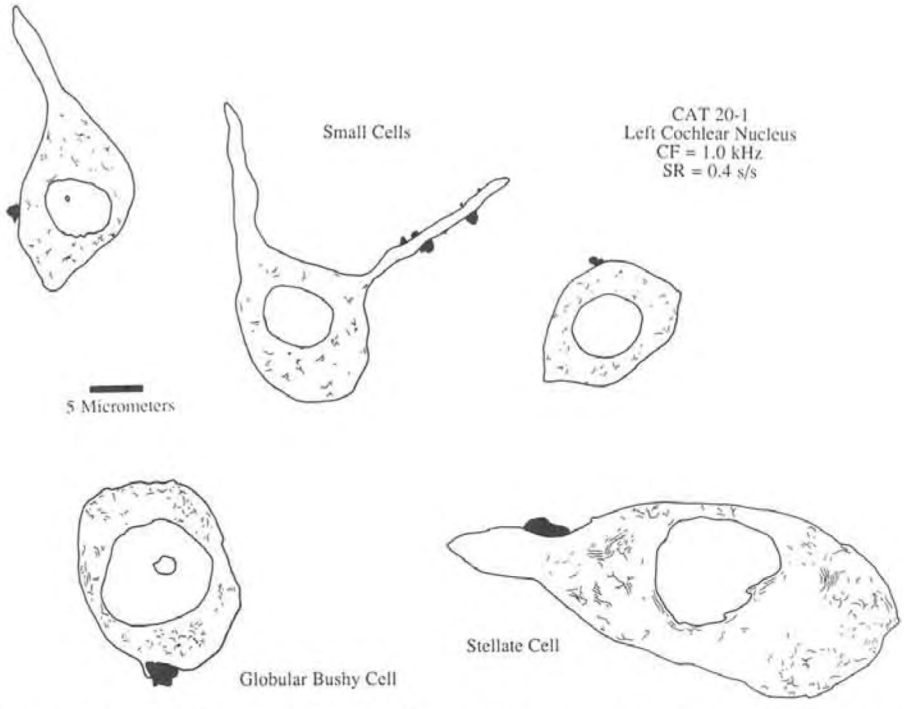

Figure 3. Tracing from low magnification (x6,000 total) electron micrograph of cells postsynaptic to labeled terminals of the low SR auditory nerve fiber. The drawings illustrate somatic shape, position and shape of nucleus, cytoplasmic pattern of endoplasmic reticulum, and locations of labeled terminals (indicated in black). Stellate cells were distinguishable from globular bushy cells by their large arrays of endoplasmic reticulum and irregular nuclear membrane.

sharply invaginated nuclear envelope. The granule cell somata and proximal dendrites are largely covered by glial processes. More distally, granule cell dendrites typically have a beaded appearance. Golgi cells have slightly larger somata (10-15 μm in diameter) with thick (5-8 μm), gnarled dendrites and short branches. Both the cell body and proximal dendrites are covered with numerous appendages. The somata of small cells are 15-20 μm in diameter, exhibit dispersed fragments of rough endoplasmic reticulum with no large organized arrays, and contain a centrally placed nucleus with a relatively smooth nuclear membrane. Each small cell gives rise to 4-5 primary dendrites which are characteristically slender and exhibit gentle undulations in thickness. There are few if any somatic or dendritic appendages, and 20-24% of their somata are apposed by small endings (<2 μm in diameter).

Collaterals of the low SR auditory nerve fiber formed many terminal swellings in this cap region (Fig. 1). Some of these were traceable to the somata of two small cells, whereas others made contact with the dendritic shaft of a third small cell (Fig. 3). This latter cell received seven synaptic swellings within a 12 μm length along its dendrite. There were labeled endings contacting other dendritic profiles in the neuropil but the cell body of origin could not be determined. The morphologically distinct Golgi cells and their dendrites were never in close apposition to labeled terminals. Likewise, identifiable portions of granule cells were not associated with labeled terminals. Although we could not distinguish between cross-sections of the distal dendrites of granule and small cells, the lack of labeled terminal interactions with glomerular complexes argues that small cells are the major, if not exclusive, recipient of the low SR auditory nerve fiber.

Table II. SUMMARY OF SYNAPTIC MORPHOLOGY IN THE INTERSTITIAL NUCLEUS AND SMALL CELL CAP

	Low SR Fibers	High SR Fibers	P Value
Number of Endings	13	4	-
Number of Synapses	17	18	-
Vesicle Diameter (nm)	55.9 ± 11.2	54.6 ± 8.9	n.s
Vesicles per μm^2	44.8 ± 15.3	46.5 ± 23.0	n.s
Maximum PSD Length (μm)	0.248 ± 0.12	0.246 ± 0.06	n.s
Mitochondrial Fraction (% ending volume)	15.4 ± 7.4	24.6 ± 7.5	$p<0.05$

PSD: Postsynaptic density

Within the limits of the methods, we can conclude that both low and high SR fibers make synaptic contact with the cell bodies of globular bushy cells and stellate cells in the region of the auditory nerve root. Several labeled endings made synaptic contact with dendrites of unknown origin in the neuropil, but these profiles are presumably of bushy or stellate cell origin because they are the principal cell types in the region. Since the low SR fiber made additional synaptic contact with small cells, it would appear that small cells have a synaptic relation with low SR fibers which is not shared with high SR fibers.

Our observations that primary endings terminate upon the cell bodies of globular bushy and stellate cells are directly relevant to a model of rate-place representations in the auditory nerve (Winslow et al., '87). The general idea is that at low stimulus levels, the high SR, low threshold fibers are important carriers of information into the brain, whereas at high stimulus levels or in the presence of masking noise, low SR, high threshold fibers would play a major role in sound perception. In this context, a simple neural circuit was hypothesized to account for level-dependent weighting of auditory nerve fiber rate responses. Essentially, the model assumes that high SR fibers with CFs near stimulus frequency form excitatory synapses at distal locations of the dendritic tree of a second order neuron, and that low SR fibers with similar CFs synapse closer to the soma. At low stimulus levels, the rate response of the second order neuron would be qualitatively similar to those of high SR fibers because the low SR fibers would be below threshold. At high stimulus levels, the synaptic current from the more proximal endings of low SR fibers would drive the cell. Chopper units of the ventral cochlear nucleus, known to be the physiological equivalent of stellate neurons (Rhode et al., '83; Rouiller and Ryugo, '84), are the proposed candidates for this selective weighting function (Winslow et al., '87).

On the basis of our data, however, it seems that a differential distribution of primary endings onto separate compartments of the same cell does not occur with respect to fiber SR. That is, endings from both high and low SR fibers synapse upon the cell body of the stellate cell. On the other hand, because we have examined only one low SR fiber and one high SR fiber from a single cat, it is premature to draw strict conclusions. If one considers the differential distribution of SR related inputs onto second order neurons to be a probability function rather than an absolute function, then the model of Winslow et al. ('87) may still be valid. Certainly, the cells postsynaptic to our labeled endings also received input from unlabeled endings exhibiting the morphologic features of primary fibers. Unfortunately, it could not be determined whether such endings arose from high or low SR fibers.

The ability to identify primary endings with respect to fiber SR group, without having to first intracellularly record from and stain them, would be very useful in determining the complement of primary endings onto postsynaptic cell classes, especially with respect to the issues posed above. Such information would also be useful in answering questions such as whether some cell classes in the cochlear nucleus receive little or no input from endings of a particular SR group, and whether some other cell classes receive a relatively equal amount

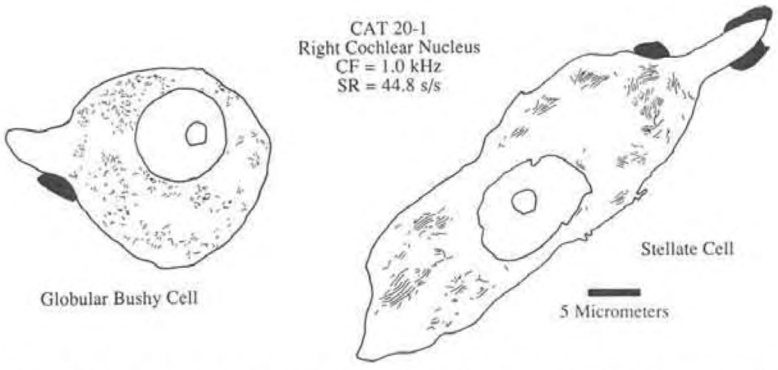

Figure 4. Tracing from low magnification(x6,000 total) electron micrograph of cells postsynaptic to labeled terminals of the high SR auditory nerve fiber. The drawings illustrate the locations of labeled endings (indicated in black) and structural differences between the somata of stellate and globular bushy cells.

of input from both SR groups. Because answers to these kinds of questions are of interest to us, we sought distinctive morphologic markers for the endings of different SR fibers by examining the fine structure of labeled endings.

Assessing the fine structure of endings for the separate SR groups using electron microscopy is not trivial because of the often large distances between swellings and because within any single swelling the density of synapses, synaptic vesicles, and mitochondria is not uniform. For example, some swellings were filled with synaptic vesicles, but there were no mitochondria and no apposing postsynaptic densities. Others, however, contained mitochondria and synaptic vesicles, and apposed one or several postsynaptic densities. Morphometric analysis was conducted on coded micrographs and was restricted to endings containing at least one synapse.

The synaptic endings of primary fibers are qualitatively similar to each other, irrespective of fiber SR or location (Table II). Endings contained numerous clear, round synaptic vesicles and mitochondria, and formed asymmetric synapses which were characterized by a prominent postsynaptic density and one or more synaptic vesicles located within a distance of their diameters to the membrane specialization (Fig. 5). The endings of high SR fibers contained vesicles having an average ($\pm$ SD) diameter of 54.6 $\pm$ 8.9 nm (n=505), compared to 55.9 $\pm$ 11.2 nm (n=420) for endings of low SR fibers. These vesicles had a similar packing density where the average number of synaptic vesicles per μm^2 was 46.5 $\pm$ 23.0 for the high SR fiber and 44.8 $\pm$ 15.3 for the low SR fiber. There was no statistical difference between the two groups of endings with respect to the length of the postsynaptic densities: 0.246 $\pm$ 0.06 μm for the high SR fiber and 0.248 $\pm$ 0.12 μm for the low SR fiber.

There were, however, some potentially important differences between the endings of the separate SR groups. On average, the mitochondria within terminals of the high SR fiber occupied a greater proportion of the terminal (24.6 $\pm$ 7.5%) than did those of the low SR fiber (15.4 $\pm$ 7.4%; $p<0.05$). There was also a difference in the number of synapses formed by individual endings: 4.5 synapses per ending for the high SR fiber and 1.3 per ending for the low SR fiber. These morphologic distinctions would suggest that the increased mitochondria provide energy for the higher levels of activity in high SR fibers, and that a key feature of the endings is in the number and not the appearance of synapses.

More data are needed in order to confirm these morphometric values, and there are certain limitations inherent to the methods that serve to temper the conclusions. For example,

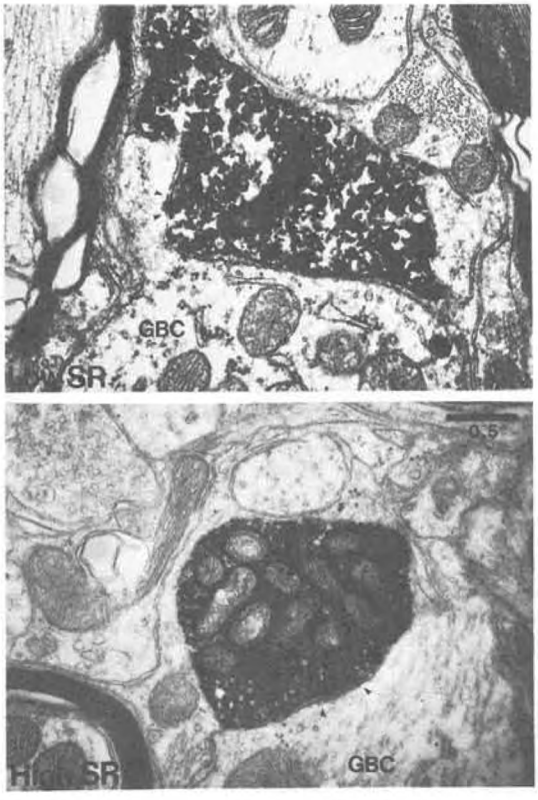

Figure 5. Electron micrographs through representative sections of labeled endings contacting the somata of globular bushy cells (GBC). The ending in the upper panel is from the low SR fiber which is synapsing on a somatic spine (arrowheads). The ending in the lower panel is from the high SR fiber which forms a synapse at the junction between the cell body and primary dendrite (arrowheads). Mitochondria, postsynaptic densities, and the lumina of synaptic vesicles are visible. Note the uniform diameter of the synaptic vesicles in both endings and the higher density of mitochondria in the ending of the high SR fiber.

due to the difficult nature of intracellular recording and staining techniques coupled to the labor-intensive serial section electron microscopy, the sample size is relatively small. Furthermore, this sample represents only a fraction of the total complement of endings generated by each fiber. Second, the HRP method can itself introduce a problem when on occasion, the reaction product is so dense that the entire ending is opaque and organelles are obscured. Finally, due to the small size of some of the endings, curvature of the ending membranes within the tissue section often smears the postsynaptic densities, thereby diminishing their visibility. Despite these challenges, our data nevertheless represent an important beginning for morphometric inquiry into the synaptic organization of auditory nerve projections to the cochlear nucleus. These kinds of quantitative studies are necessary if we are to understand further the intricate relationship between structure and function in the biology of hearing.

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