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DENSITY OF MYELINATED NERVE FIBERS IN THE CHINCHILLA COCHLEA

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Spiral ganglion cell degeneration generally accompanies extensive loss of sensory cells in the cochlea (Lawrence and Johnsson, '73; Schuknecht, '74). Degeneration of afferent nerve fibers has been seen in ears damaged by excessive exposure to noise (Smith et al, '54; Johnsson and Hawkins, '76), ototoxic drugs (Kohonen, '65; Ylikoski, '74), viral infections (Lindsay et al, '60; Lindsay, '67), and is a common finding in aged humans (Bredberg, '67). Despite the prevalence of nerve fiber loss following various ototraumatic insults, the exact cause of this degeneration is unknown. Several hypotheses have been advanced in an attempt to explain this phenomenon including:

a) The nerve fibers and endings within the organ of Corti may be directly injured by the traumatic agent, eventually resulting in degeneration of the spiral ganglion cells (Smith et al, '54).

b) Neurons may undergo transneuronal degenerative changes when the sensory cells with which they synapse have disappeared (Howe, '35; Covell and Eldredge, '52; Ylikoski, '74).

c) Cochlear neurons may degenerate when there has been damage to or loss of adjacent pillar cells (Schuknecht, '74).

d) Nerve fibers within the cochlea may degenerate in areas where the reticular lamina has been damaged and endolymph has gained access to the fluid spaces of the organ of Corti (Bohne, '76).

Important information concerning the etiology of nerve fiber loss may be gained from a quantitative examination of nerve fibers in cochleae having various combinations of sensory and supporting cell loss. However, before studying damaged specimens, it is necessary to establish an adequate baseline for nerve fiber density in different

regions throughout the cochlea. In addition, since it has been found that there is a sizeable within-species variation in the length of the organ of Corti (Hardy, '38; Bredberg, '68; Bohne and Carr, '79), it is also important to determine whether or not nerve fiber density varies systematically with cochlear length.

The present study was designed to obtain baseline values for the density of myelinated nerve fibers (MNF) at eleven locations from cochlear apex to base. The results of this study will provide the groundwork for studies concerning the relation between sensory cell degeneration and spiral ganglion cell loss.

MATERIAL AND METHODS

All specimens used in this study were prepared for phase contrast microscopic examination as plastic-embedded whole mounts (Bohne, '72). The cochlear duct from each specimen was divided into quarter- or eighth-turns such that 17 - 25 pieces were obtained from each cochlea. The length (in millimeters) of the segments of the organ of Corti were measured at the junction of the heads of the inner and outer pillars as described by Bohne and Carr ('79). Subsequently, the length of the individual pieces was converted into a percentage of the total length of that particular cochlea. The number of missing sensory cells was counted and the percentage of missing sensory cells calculated.

From a large pool of non-damaged cochleae, eight were selected for the nerve fiber counts. These particular specimens were chosen so that nerve fiber data could be obtained from cochleae with widely varying lengths (i.e. 16.28 - 19.71 mm). In each specimen, outer hair cell (OHC) loss averaged less than 1.5% at any location and only 1-2 inner hair cells (IHC) were missing in the entire cochlea. Cochleae having a small degree of hair cell loss had to be used for the counts since it is virtually impossible to obtain a specimen in which the entire sensory cell population is intact. It should be noted, however, that in regions where the nerve fibers were counted, there were no missing IHC and only 1-2 missing OHC.

At eleven different percentage locations[1] from apex to base in each cochlea, a small portion (0.2-0.4 mm) of the organ of Corti was split off from the larger pieces and re-embedded in a thin layer

of plastic. The length of these samples was measured and the corresponding number of IHC was counted. From these data, the density of inner hair cells per millimeter of the organ of Corti was calculated for each sample $\left(\text{IHC/mm} = \frac{\#\text{IHC}}{\text{length (mm)}}\right)$.

One-micron sections of each of the samples were cut at an angle tangential to the organ of Corti. Sectioning began at the Hensen cells and continued to the lip of the limbus (Fig. 1A). Camera lucida drawings (1410x) were then made of two sections through the myelinated nerve fibers in which the lip of the limbus was visible (Fig. 1B). On each drawing, the number of MNF was counted in two or three 0.1-mm regions (total of 4-6 counts/location/ear) and the values averaged.

Because rather sizeable variations in the fiber counts were found in the eight cochleae (see Results), an attempt was made to normalize the data on the basis of inner hair cell density.

Since the mammalian cochlea is a spiral organ, a given distance along the pillar heads (where IHC are located) is not equivalent to the same distance at the lip of the limbus (where MNF were counted). In order to relate the nerve fiber counts to the IHC counts, the size of the counting window over the nerve fibers had to be reduced by a certain amount. This reduction factor was determined in the following fashion. It was assumed that the length of a given turn of the cochlea is roughly equivalent to the circumference of a circle. If the circumference of a turn is known, its radius can be calculated. Furthermore, if the distance between the pillar heads and the lip of the limbus is determined, the radius of the turn at limbus can be cal-

culated. Since the lengths (measured at the pillars) of the sectioned samples of the organ of Corti are known, the lengths of these same pieces measured at the limbus can be determined. In Figure 1C, let:

R_1 = radius of cochlear turn measured at pillar heads.

d = distance between union of pillar heads and lip of limbus.

R_2 = radius of cochlear turn measured at lip of limbus.

A_1 = length of sectioned sample measured along pillar heads.

A_2 = length of sectioned sample measured along lip of limbus.

Since: $R_2 = R_1 - d$ and $\frac{R_1}{A_1} = \frac{R_2}{A_2}$, $A_2 = \frac{A_1 R_2}{R_1}$. The reduction factor is then equal to $\frac{A_2}{A_1}$.

It was assumed that at a given location, there is a uniform distribution of nerve fibers within the osseous spiral lamina. Thus, the number of MNF in 0.1 mm was multiplied by the reduction factor and the resulting value divided by the IHC density (per 0.1 mm) at the same locus to give the number of myelinated nerve fibers per inner hair cell.

In order to determine the value of d, the distance between the union of the pillar heads and the lip of the limbus was measured on camera lucida drawings (708x) of radial sections of the organ of Corti from five cochleae ranging in length from 16.00 to 19.71 mm. These measurements were made at approximately the same percentage locations in the cochlea as used for the nerve fiber counts.

The length (and hence circumference) and hair cell density in the different cochlear turns were determined in 36 ears. These specimens were equally divided into 3 groups on the basis of the total length of the cochlea. Short cochleae ranged in length from 16.00 to 17.55 mm; average cochleae from 17.56 to 19.00 mm; and long

cochleae from 19.01 to 21.00 mm. In a previous study of the length of the chinchilla cochlea (Bohne & Carr, '79), it was found that the different cochlear turns comprise the following percentages of the total length: 21% - third turn; 26% - second turn; 32% - first turn; 21% - round window. These percentages were used to calculate the length (in millimeters) of the cochlear turns in the groups of short, average and long ears.

In each segment of the organ of Corti from all 36 cochleae, the total number of hair cells (present and absent) was counted and the density of IHC and OHC per millimeter calculated. In order to determine the density in a given turn, the densities in all segments comprising that turn were averaged.

RESULTS

There was a rather sizeable variation (e.g. 134-167 at 92.9%) in the number of MNF in 0.1 mm at all 11 percentage locations in the eight cochleae. Inspection of the data revealed that this variation was not systematically related to cochlear length. For example, at 67% of the distance from the apex, the nerve fiber count in one of the long ears was 222, that in a short ear was 220, while that in an average ear was 184.

Since the goal of this study was to provide a normal baseline to which data from damaged ears could be compared, an attempt was made to reduce this variability by expressing the data as the number of MNF per IHC. This approach seemed reasonable as it has been found that the majority of the afferent nerve fibers in the cochlea innervate

the IHC (Spoendlin, '70; Morrison et al, '75).

Length of cochlear turns - The mean length (in millimeters) ± one standard deviation of the different cochlear turns in short, average and long cochleae is given in Table I. The lengths of the first, second and third turns were considered to be the circumference of a circle so that the radius is equal to circumference divided by 2 pi. The round window portion of the organ of Corti was considered to be a half circle so its length was multiplied by 2 in order to obtain the circumference. The corresponding radii of the turns (R_l) are shown in Table II.

Distance from pillars to limbus - The distance (in millimeters) from the union of the pillar heads to the lip of the limbus (d) was measured in three cochleae of average length (18.21, 18.36, 18.45 mm), one short cochlea (16.00 mm) and one long cochlea (19.71 mm).

It was found that at a particular percentage location, this distance was quite similar in all the specimens. However, there was a significant variation in this distance from apex to base. The mean values for the different percentage locations are shown in Table III. Because the values were nearly identical in the 4 locations in the second turn (21.1-47%) and the 3 locations in the first turn (47.1-79%), the respective values were averaged to obtain one figure for d for each of these turns. In the other turns, the individual values were used.

Reduction factor - Although no significant variation was found in the value of d in cochleae of different lengths, there was a significant difference in the value of R_l. Since the difference in the length of the sectioned pieces of the organ of Corti measured

at the pillar heads (A_1) and at the limbus (A_2) is dependent on the radius of the turn (R_1), the reduction factor $\frac{A_2}{A_1}$ varies with both cochlear length and cochlear turn. The reduction factors are given in Table IV.

Myelinated nerve fibers per inner hair cell - For all cochleae, the MNF counts were multiplied by the appropriate reduction factor (Table IV) and the resulting figure divided by the density of the IHC at the locations where the counts were made. The data were then plotted as a function of percentage distance from the cochlear apex (Fig. 2). At the apex, an average of 9.4 MNF/IHC was found. The number of fibers gradually rose towards the base and reached a peak of 18.8 MNF/IHC in the middle of the first turn. The number then decreased to 14.2 MNF/IHC in the round window region. In Figure 2 it can be seen that there is good agreement among the data from the different cochleae throughout the entire organ of Corti. At the different locations, the standard deviations were found to range from 0.8 to 1.5 MNF/IHC.

Hair cell density - Table V shows the average density of the inner and outer hair cells per millimeter of the organ of Corti in the various turns of short, average and long cochleae. Hair cell density was found to vary with position in the cochlea and with cochlear length. Long cochleae have lower hair cell densities than short cochleae. However, the turn-to-turn variation in density is consistent among the three groups of cochleae. For inner hair cells, density peaks in the third turn, reaches a minimum in the first turn and peaks again in the round window region. For outer hair cells, density is at a maximum in the third turn and then gradually declines

to a minimum in the round window region. A two-way analysis of variance showed that there is a significant difference (α=.05) among the densities in the different turns of the short, average and long cochleae.

DISCUSSION

Our technique for counting nerve fibers within the cochlea did not permit the inclusion of unmyelinated fibers, nor could afferent fibers be distinguished from efferents. Thus, in order to determine the validity of expressing the data as MNF/IHC, it is important to review the efferent system in the cochlea.

Efferent fibers to the cochlea originate primarily from the peri-olivary cell groups of both the ipsilateral and contralateral superior olivary complex (Warr, '75). These fibers leave the brainstem in the vestibular nerve root. Immediately distal to the saccular ganglion, the cochlear efferents join the cochlear afferents at Oort's (vestibulo-cochlear) anastomosis. Within the cochlea, the efferent fibers form the intraganglionic spiral bundle (IGSB) which is located peripherally in Rosenthal's canal. From the IGSB, the fibers turn outward to enter the osseous spiral lamina (OSL). The fibers again take a spiral course as they approach the lip of the OSL. The fibers then pass through the habenulae perforata to enter the organ of Corti.

By examining myelin-stained sections of the olivocochlear bundle in the cat, Rasmussen ('46) determined that there are about 500 cochlear efferent fibers. Warr ('75) studied the efferent system in cats using the techniques of retrograde axonal transport of horseradish peroxidase (HRP) and acetylcholinesterase staining. Following injection of HRP into the cochlea, labelled neurons were counted in the

brainstem. On the basis of this study, Warr estimated that there are 1700-1800 cochlear efferents in the cat. The discrepancy between Warr's estimate and that of Rasmussen was explained by noting that the cochlea contains numerous unmyelinated efferent fibers which could not be counted in Rasmussen's preparations (Terayama et al, '69; Terayama and Yamamoto, '71; Paradiesgarten and Spoendlin, '76). Also, in the cat, some cochlear efferents leave the brain by way of the cochlear nerve rather than the vestibular root (Gacek et al, '65). These fibers would not have been counted by Rasmussen either.

Recently, Strutz ('81) studied the efferent system in the guinea pig. Following unilateral injection of HRP into the cochlea, up to 500 labelled neurons were identified in the ipsilateral and contralateral superior olivary complex and ventral nucleus of the lateral lemniscus.

Terayama et al ('69) and Kimura (as cited by Warr '75) have found that only 58-60% of the fibers within the vestibulocochlear anastomosis of the guinea pig are myelinated. In the intraganglionic spiral bundle of the cat, Paradiesgarten and Spoendlin ('76) reported that the myelinated efferent fibers are in the minority, ranging from 34% of the total at the base to 13% at the apex.

In a study involving acetylcholinesterase staining in the cat cochlea, Nomura and Schuknecht ('65) found one or more efferent fibers in each habenula perforata. Spoendlin ('66) reported that the number of habenulae in the cat cochlea is approximately equal to the number of IHC and therefore estimates that there are 2500-3000 habenulae and a corresponding number of efferent fibers at the level of the habenula.

The increase in the number of efferent fibers between the brainstem and the habenulae can be explained by noting that some of the myelinated efferents branch within the internal auditory meatus whereas many of unmyelinated fibers branch in the osseous spiral lamina (Terayama et al, '69).

Spoendlin ('70) studied the effect of elimination of the olivocochlear bundle on nerve fiber density in the cat and guinea pig cochleae. In both species, Spoendlin found only a slight reduction in the number of fibers per habenular opening in the nerve-sectioned animals as compared to controls. In contrast, Morrison et al ('75) reported a 25-30% reduction in myelinated nerve fibers in the OSL following vestibular nerve section in guinea pigs. Since the nerve was sectioned within the internal auditory meatus, it is possible that the cochlear afferents were inadvertently damaged. However, all ears included in the Morrison et al study were reported to have a normal complement of spiral ganglion cells and typical afferent synapses on the hair cells.

Except for the results from the Morrison et al study, data from the studies just cited indicate that the number of efferent fibers within the osseous spiral lamina is considerably smaller than the number of afferent fibers. In addition, only a certain percentage of these fibers is myelinated. Although more data are needed, the percentage of myelinated efferents appears to decrease when moving peripherally (i.e. 60% in vestibulocochlear anastomosis and 13-34% in IGSB).

The percentage of myelinated fibers within the OSL which are efferent can be roughly estimated in the following fashion. In the cat, there are approximately 1800 efferent fibers in the olivocochlear bundle

(Warr, '75). Assuming that only 60% are myelinated, there would be 1080 myelinated efferents. Howe ('35) counted spiral ganglion cells in four normal cats and found an average of 50,271. Spoendlin ('72) has found that the number of nerve fibers within the OSL remains nearly constant from the ganglion cell bodies to the habenulae. Thus, it is assumed that there are 50,271 plus 1080 myelinated nerve fibers in the OSL. Therefore, approximately 2.1% (1080 ÷ 51,351) of the myelinated fibers are efferent.

In the guinea pig, there are about 500 cochlear efferents (Strutz, '81), 300 of which are estimated to be myelinated. Gacek and Ramussen ('61) found an average of 24,011 fibers in the cochlear nerve of the guinea pig (N=4). Thus, approximately 1.2% (300 ÷ 24,311) of the myelinated fibers within the OSL are efferent. These estimates probably represent an upper limit since the percentage of myelinated efferents within the IGSB is considerably less than 60%.

There are no data available on the number of efferent fibers in the chinchilla cochlea. However, in view of the similarities between the chinchilla and guinea pig cochlea in regard to length of the organ of Corti, density of the inner and outer hair cells and number of fibers in the cochlear nerve, it seems reasonable to assume that the number of efferents would also be similar in the two species. Boord and Rasmussen ('58) found an average of 23,554 fibers in the cochlear nerve of the chinchilla (N=5). Assuming that the chinchilla has 300 myelinated efferents in Oort's anastomosis, approximately 1.3% of the myelinated fibers in the OSL would be efferent.

For the eight cochleae used in the present study, the individual data on inner hair cell density and number of MNF/IHC were used to

obtain an estimate of the total number of MNF within the osseous spiral lamina. Assuming that 1.3% of these fibers are efferent, the number of afferent fibers per cochlea ranged from 23,768 to 31,356 and averaged 26,771 ± 2607. In the same specimens, the length of the organ of Corti ranged from 16.28 to 19.71 mm and averaged 18.57 ± 1.11 mm. Our estimated number of cochlear afferents is somewhat larger than the average number of fibers in the chinchilla cochlear nerve (23,554) found by Boord and Rasmussen ('58). Since Boord and Rasmussen did not report a range or a standard deviation for their counts, the cause of this discrepancy cannot be determined. Part of the discrepancy could be due to a sampling error. Also, it should be noted that the average length of the cochleae in this study is 0.25 mm greater than the average found in a very large sample (Bohne and Carr, '79).

Using methods similar to those employed in the present study, Ehret ('79) calculated the number of myelinated nerve fibers per inner hair cell in the house mouse. Despite the large difference between the average length of the house mouse cochlea (6.84 ± 0.16 mm) (Ehret and Frankenreiter, '77) and the chinchilla cochlea (18.32 ± 0.89 mm) (Bohne and Carr, '79), striking similarities are seen in the number of myelinated nerve fibers per inner hair cell in the two species. Ehret found a maximum of 18-19 MNF/IHC at 3.5-4 mm or 51-58% distance from apex. This compares with a value of 18.8 MNF/IHC at 67% distance from the apex in the chinchilla. At the apex, Ehret found 8-9 MNF/IHC whereas 9.4 MNF/IHC was found in this study. In the round window region, the data from the two species are more divergent, averaging 14.2 MNF/IHC in the chinchilla and 7 MNF/IHC in

the house mouse.

In other studies, nerve fiber density has been determined at a few discrete regions in the organ of Corti. Spoendlin ('72) determined the number of MNF in 200 μm regions at 6 different locations in the cat cochlea. A maximum number of fibers was found in the middle and upper basal turns whereas the lowest number occurred in the apical turn. The data from the chinchilla and cat cannot be compared quantitatively, however, since in the cat, the exact locations (millimeter or percent) where the fibers were counted were not reported nor were the counts related to the density of the inner hair cells.

It is of interest to note that a maximum inneration ratio can be achieved by having an increased number of nerve fibers or a decreased number of hair cells in a particular area. In the chinchilla, the ratio of MNF to IHC is at a maximum (Fig. 2) in the region where IHC density is at a minimum (Table V). This contrasts with the situation in the house mouse where the innervation ratio is the greatest in the region with the highest density of hair cells. (Ehret, '77).

SUMMARY

Baseline values for the density of myelinated nerve fibers at 11 locations in the chinchilla cochlea were obtained as a prerequisite for studying the relationship between sensory cell degeneration and spiral ganglion cell loss. Myelinated nerve fibers were counted within the osseous spiral lamina near the habenulae perforata. The data were expressed as myelinated nerve fibers per inner hair cell (MNF/IHC). Since the vast majority of the afferent fibers innervate the inner hair cells and since the percentage of myelinated efferent

fibers at the level of the osseous spiral lamina is estimated to be quite small, MNF/IHC is a useful statistic which allows one to compare data from normal and damaged specimens. An average density of 9.4 MNF/IHC was found at the apex. This rose to a peak of 18.8 MNF/IHC in the first turn and then decreased to 14.2 MNF/IHC in the round window region. The standard deviations at the different locations ranged from 0.8 to 1.5 MNF/IHC.

FOOTNOTES

1. Percentage distance from cochlear apex at which nerve fiber counts were made: 5.3, 15.8, 21.9, 30.4, 39.3, 46.5, 57.2, 67.0, 77.1, 87.3 and 92.9.

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TABLE I: LENGTH OF COCHLEAR TURNS (mm)

Cochlear Length	% Distance from Apex 0-21 (3rd T)	21.1-47 (2nd T)	47.1-79 (1st T)	79.1-100 (Round window)
Short	3.53 ± .11	4.37 ± .13	5.38 ± .16	3.53 ± .11
Average	3.85 ± .10	4.76 ± .13	5.86 ± .16	3.85 ± .10
Long	4.15 ± .15	5.14 ± .18	6.32 ± .23	4.15 ± .15

TABLE II: RADIUS (R_1) OF COCHLEAR TURNS (mm)

Cochlear Length	3rd T	2nd T	1st T	RW
Short	.56	.70	.86	1.12
Average	.61	.76	.93	1.23
Long	.66	.82	1.01	1.32

TABLE III: DISTANCE FROM PILLARS TO LIP OF LIMBUS

	% Distance from Apex 3rd T		2nd T				1st T			RW	
% dist	4.9	15.1	22.6	29.3	39.6	46.2	56.4	67.2	76.9	87.0	92.8
d (mm)	.120	.112	.109	.108	.110	.109	.106	.104	.104	.082	.072

TABLE IV: REDUCTION FACTOR

Cochlear Length	% Distance from Apex 0-10	10.1-21	21.1-47	47.1-79	79.1-90	90.1-100
Short	.786	.800	.844	.878	.927	.936
Average	.803	.816	.857	.887	.933	.941
Long	.818	.830	.867	.896	.938	.945

TABLE V: DENSITY OF HAIR CELLS IN CHINCHILLA COCHLEA

Cochlear Length		3rd T	2nd T	1st T	RW
Short	I	106	102	99	106
	O	444	417	410	394
Average	I	102	100	98	102
	O	428	412	401	386
Long	I	98	95	93	98
	O	410	395	383	375

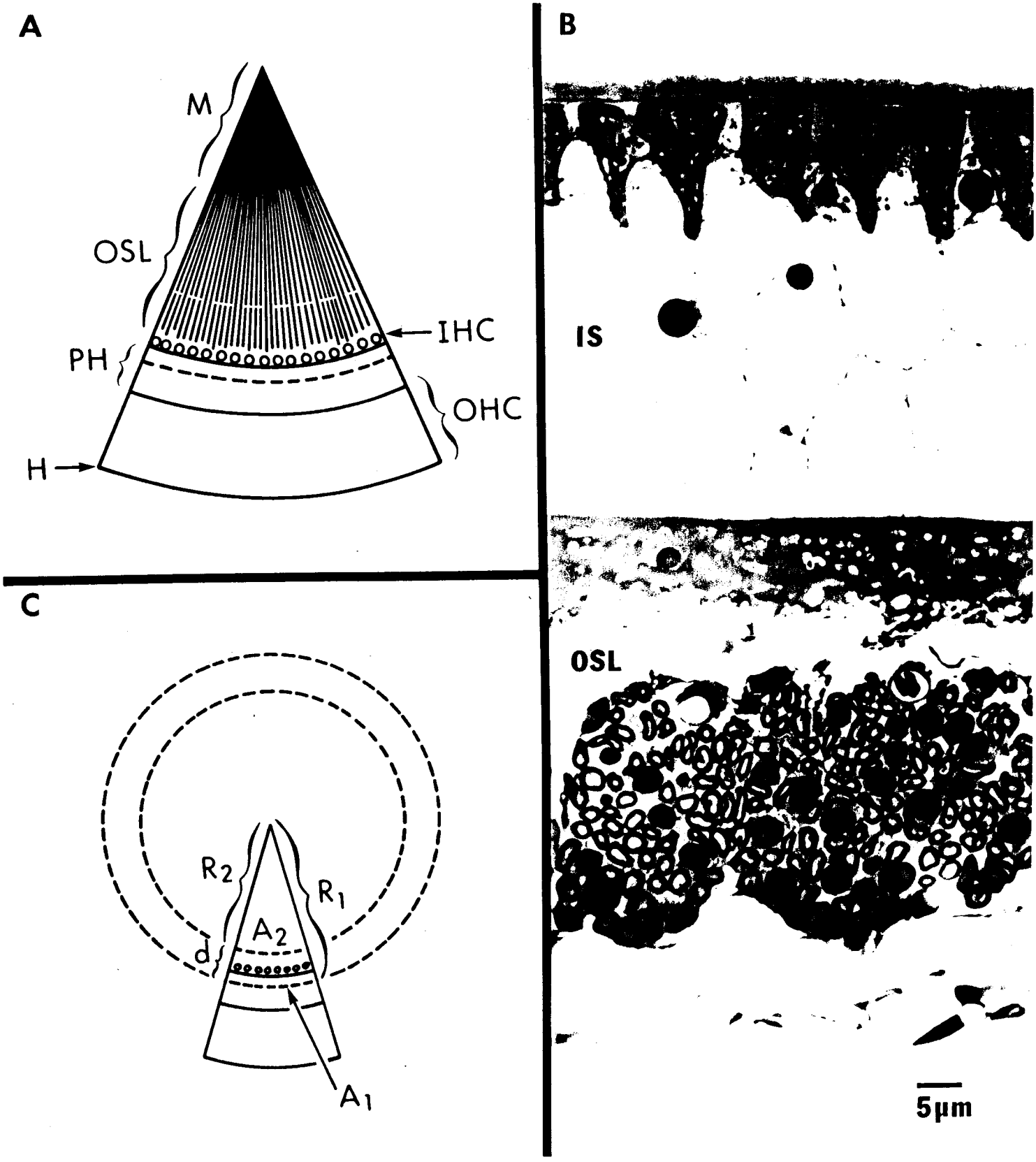
I - IHC/mm of organ of Corti
O - OHC/mm of organ of Corti

LIST OF LEGENDS

Figure 1: a) Drawing of portion of organ of Corti used for nerve fiber counts. Sectioning angle was perpendicular to plane of drawing. Organ was sectioned from Hensen's cells (H) to lip of limbus (white dashed line). IHC - inner hair cells; M - modiolus; OHC - outer hair cells and Deiters' cells; PH - heads of inner and outer pillars; b) Photomicrograph of stained, one-micron section through myelinated nerve fibers in osseous spiral lamina. A drawing of the section at 1410x was made to facilitate counting of fibers. OSL - osseous spiral lamina; IS - inner sulcus cells; L - lip of limbus; c) Drawing of idealized cochlear turn. Outer dashed line indicates position of union of pillar heads and inner dashed line indicates position of lip of limbus. See text for explanation of labels.

Figure 2: Number of MNF per IHC as function of percentage distance from cochlear apex. Different symbols depict cochleae with following lengths: ♦ - 16.28; ◊ - 18.06 mm; ○ - 18.13 mm; △ - 18.72 mm; □ - 18.79 mm; ● - 19.33 ; ▲ - 19.52 mm; ■ - 19.71 mm.

Figure 1



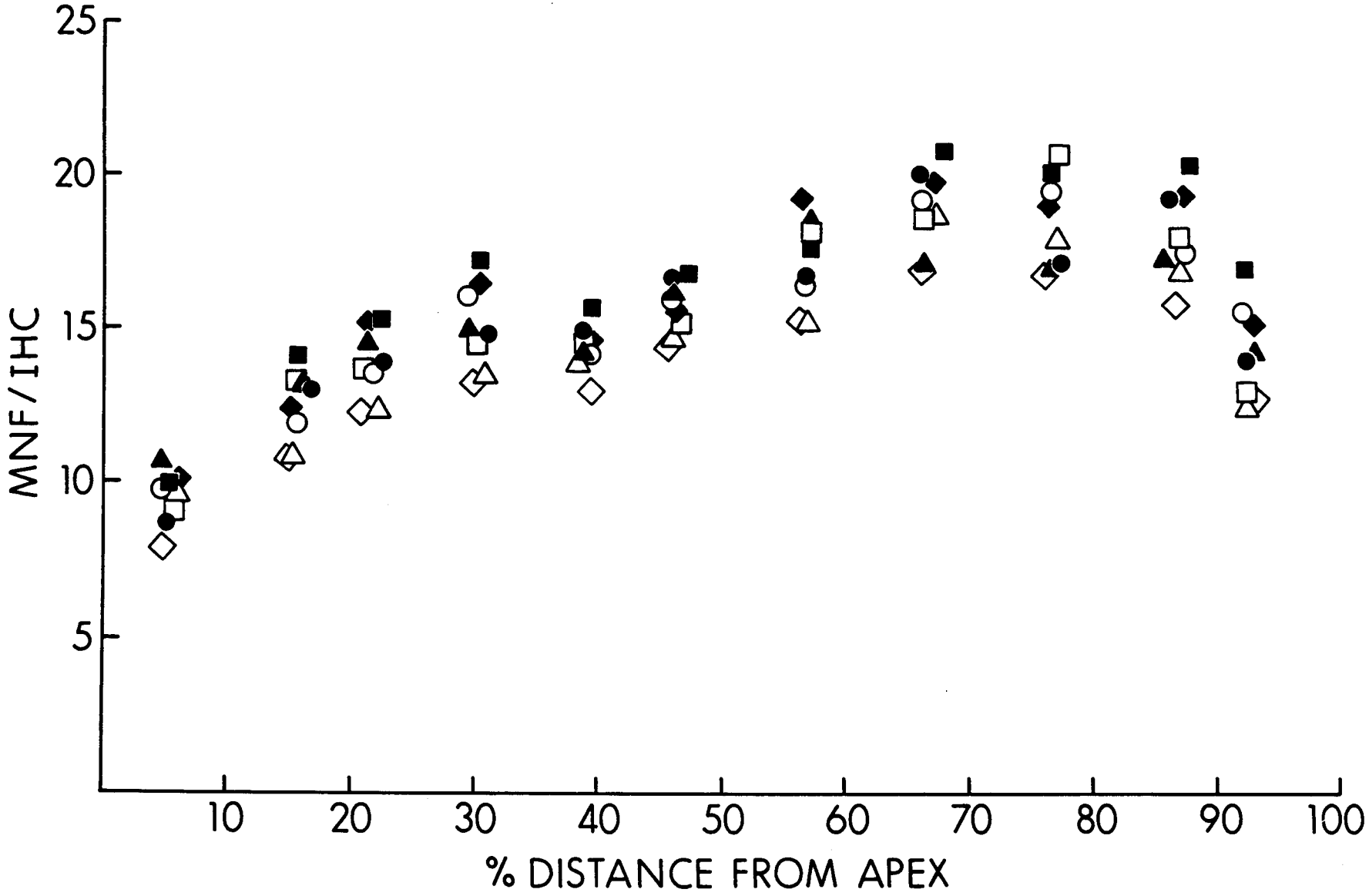

25
20
15
10
5
MNF/IHC
10
20
30
40
50
60
70
80
90
100
% DISTANCE FROM APEX

Figure 2