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Response Growth With Sound Level in Auditory-Nerve Fibers After Noise-Induced Hearing Loss

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Abstract

People with sensorineural hearing loss are often constrained by a reduced acoustic dynamic range associated with loudness recruitment; however, the neural correlates of loudness and recruitment are still not well understood. The growth of auditory-nerve (AN) activity with sound level was compared in normal-hearing cats and in cats with a noise-induced hearing loss to test the hypothesis that AN-fiber rate-level functions are steeper in impaired ears. Stimuli included best-frequency and fixed-frequency tones, broadband noise, and a brief speech token. Three types of impaired responses were observed. 1) Fibers with rate-level functions that were similar across all stimuli typically had broad tuning, consistent with outer-hair-cell (OHC) damage. 2) Fibers with a wide dynamic range and shallow slope above threshold often retained sharp tuning, consistent with primarily inner-hair-cell (IHC) damage. 3) Fibers with very steep rate-level functions for all stimuli had thresholds above approximately 80 dB SPL and very broad tuning, consistent with severe IHC and OHC damage. Impaired rate-level slopes were on average shallower than normal for tones, and were steeper in only limited conditions. There was less variation in rate-level slopes across stimuli in impaired fibers, presumably attributable to the lack of suppression-induced reductions in slopes for complex stimuli relative to BF-tone slopes. Sloping saturation was observed less often in impaired fibers. These results illustrate that AN fibers do not provide a simple representation of the basilar-membrane I/O function and suggest that both OHC and IHC damage can affect AN response growth.

INTRODUCTION

Sensorineural hearing loss is generally accompanied by loudness recruitment, in which the perceptual loudness of stimuli grows more rapidly than normal across a narrowed dynamic range of intensities (reviewed by Moore 1995). Loudness is small near the elevated threshold, but grows to near normal at intensities around 100 dB SPL. The standard model for loudness recruitment suggests that steepened loudness growth reflects a steepening of the basilar-membrane (BM) input–output function resulting from loss of the normal compression produced by outer hair cells (OHCs; Fig. 1A; Moore 1995; Ruggero et al. 1997). However, the means by which this change in BM response is conveyed to the central auditory system is not clear. Presumably, a steeper BM slope should produce steeper auditory-nerve (AN) fiber rate versus level functions; however, the schematic examples in Fig. 1B show that not all fibers are expected to change slope. Low-threshold (high spontaneous rate) fibers normally saturate before compression sets in, so the slopes of their rate-level functions should not be changed between normal and impaired ears (light solid

and dashed lines in Fig. 1B; Sachs and Abbas 1974; Winter et al. 1990; Yates et al. 1990). Only high-threshold (low spontaneous rate) fibers should show steeper rate-level functions with cochlear damage (heavy solid and dashed lines in Fig. 1B), and then the steepening should occur only some number of dB above threshold, above the onset of BM compression.

Steepening of AN rate-level functions has been observed in some studies with ototoxic or hypoxic damage, where relatively clean OHC lesions can be expected (Evans 1975; Harrison 1981; Schmiedt and Zwislocki 1980). In contrast, another study of ototoxically damaged animals (Kiang et al. 1970) and a study in acoustically traumatized animals (Salvi et al. 1983), where mixed lesions of both inner hair cells (IHCs) and OHCs are expected (Liberman and Dodds 1984a,b), did not show a steepening of rate-level functions. IHC lesions complicate the situation because the model underlying Fig. 1 predicts that a lesion with damage only to IHCs could result in *shallower* rate-level functions, if the lesion produced threshold shifts without a loss of BM compression. In addition, previous studies mainly used tones at the best frequency (BF) of the neuron under study. For natural stimuli, such as speech, cochlear suppression in normal ears can lead to rate-level slopes that are less than those for BF tones (Schalk and Sachs 1980). In this case, damage to OHCs, with or without IHC damage, should lead to steepening of rate-level functions because of the loss of suppression.

An additional complication that may have caused confusion is the existence of so-called component 2 (C2) responses at high sound levels (Liberman and Kiang 1984; Ruggero et al. 1996; Wong et al. 1998). Component 1 (C1) responses dominate AN fibers at low and moderate sound levels and a transition to C2 is usually observed near 80–100 dB SPL. The transition is typically defined by a notch in the rate-level function and/or an abrupt change in the phase of response relative to the stimulus waveform. Acoustic trauma can reduce or eliminate C1 with little evident effect on C2 (Liberman and Kiang 1984). Because the remaining C2 response shows steep response growth, it may serve as a confounding variable in previous experiments.

These considerations make it difficult to adequately evaluate neural correlates of loudness growth in damaged ears. This issue has potential significance for understanding sensorineural hearing loss and for hearing aid design. The goal of the present study was to provide further information about intensity coding in impaired ears by comparing AN fiber rate-level functions between normal-hearing and acoustically traumatized cats. The comparisons were done for a variety of stimuli, including tones, noise, and speech. The results show diverse changes in rate-level functions, consistent with a mixture of lesions. Thus the standard model in Fig. 1 needs elaboration to account for loudness recruitment.

METHODS

Experiments were performed in healthy adult cats from Liberty Labs; cats were free of any signs of external- or middle-ear pathology and typically weighed about 3.5 kg. All animal care and use procedures were approved by the Johns Hopkins Animal Care and Use Committee (protocol number CA99M255).

Acoustic trauma

The procedure for inducing sensorineural hearing loss was the same as previously used in this laboratory (e.g., Miller et al. 1997, 1999a,b; Schilling et al. 1998) and is similar to studies that have characterized the anatomical-physiological correlates of acoustic trauma (e.g., Liberman and Dodds 1984a,b; Liberman and Kiang 1984). Cats were initially anesthetized with xylazine [2.0 mg intramuscularly (im)] and ketamine (110 mg im). Atropine (0.1 mg im) was given to control mucus secretions and eye ointment was used to

protect the eyes from drying. Additional doses of ketamine were administered as needed to maintain an anesthetized state throughout the noise exposure. The cat's head was restrained directly beneath 2 free-field speakers. The exposure was a continuous 50-Hz-wide noise band centered at 2 kHz lasting 4 h. Free-field sound levels were determined at the location of the top of the cat's head. Exposure levels ranged from 103 to 108 dB SPL. Animals were allowed to recover for ≥ 30 days because there is little to no temporary threshold shift in cat after 1 mo (Miller et al. 1963).

Electrophysiology

Before physiological recording, animals were anesthetized with xylazine (2.0 mg im) followed by ketamine (120–150 mg im). Atropine (0.1 mg im) was given every 24 h to control mucus secretions. A catheter was placed in the cephalic vein to allow intravenous injections of sodium pentobarbital [about 10 mg/h intravenously (iv)] to maintain an areflexic state of anesthesia. Physiological saline (2–5 ml/h iv) and lactated Ringer's (about 40 ml/24 h iv) were given to prevent dehydration. A tracheotomy was performed to allow a low-resistance airway. The bulla was vented with a 40-cm length of polyethylene tubing to equalize the middle-ear pressure (Guinan and Peake 1967). The animal's rectal temperature was maintained near 38.5°C with a feedback-controlled heating pad.

The AN was exposed using standard techniques (e.g., Kiang et al. 1965); a craniotomy was made in the posterior fossa and the cerebellum was retracted medially. AN-fiber recordings were made by inserting a 10- to 30-M Ω glass micropipette filled with 3 M NaCl into the AN under visual control. Recordings were made in an electrically shielded, double-walled soundproofed room, and computer-controlled stimuli were presented by calibrated acoustic drivers attached to hollow ear bars. Experiments generally lasted from 24 to 48 h, and were terminated by a lethal dose of barbiturate (Euthasol). Single fibers were isolated by advancing the electrode through the AN while playing a broadband noise search stimulus (about 10 dB re 20 μ Pa/ $\sqrt{\text{Hz}}$ for normal experiments, and higher as needed in impaired experiments). The state of the cochlea was monitored by tracking thresholds as a function of BF over time and looking for abrupt increases above the minimum thresholds collected early in the experiment. None of the normal experiments had threshold elevations over time. In a few of the impaired experiments from the moderate/severe-loss population, thresholds increased significantly (about 30 dB) over time as the result of the higher sound levels used to locate and characterize impaired fibers. However, the response properties of the fibers collected after the increase were similar to those of other impaired fibers with similar thresholds collected before the increase or from other experiments, and thus these data were typically included in the impaired population.

Stimuli

Isolated fibers were characterized initially by an automated tuning-curve algorithm, which tracked the minimum level required for a 50-ms tone burst to elicit at least one more spike than a subsequent 50-ms period of silence (Kiang et al. 1970). The fiber's BF, threshold, and Q_{10} value were estimated from the tuning curves. Fibers were also classified based on spontaneous rate (high: $\text{SR} > 18$ spikes/s; medium: $0.5 < \text{SR} \leq 18$; low: $\text{SR} \leq 0.5$), as suggested by Liberman (1978).

After the tuning curve, rate-level functions were measured for a variety of stimuli. Each rate-level function was measured by presenting a single repetition of the stimulus across a range of levels, in 1-dB steps, from 10–20 dB below fiber threshold up to 80–100 dB SPL for normal AN fibers and 90–120 dB SPL for impaired fibers; stimuli were presented in ascending order of sound level. One stimulus presentation occurred every 1,000 ms and consisted of the 200- or 300-ms stimulus followed by silence. Repeat responses to stimuli

were collected for as long as the fiber was isolated. It was rarely possible to collect more than 2–3 repetitions for each stimulus, and some fibers were lost before collecting data for all of the stimuli in the protocol.

The stimuli for which rate-level functions were collected included: BF tones, 1- and 2-kHz tones, broadband noise, and a speech token (“besh”). All of the stimuli had a duration of 200 ms, except for the 300-ms speech token. The broadband noise stimulus was a frozen noise (i.e., the same noise waveform was used for all levels and for all fibers). The syllable “besh” was synthesized using a Klatt synthesizer (Klatt 1980), as described in Franck (1994) and in Miller et al. (1997). This speech token includes a steady-state vowel /ε/, for which AN responses have been studied previously (Miller et al. 1997), the consonant /b/ modeled by formant transitions, and a fricative /sh/. The power spectra of the vowel and fricative portions of “besh” are shown in Fig. 2. The steady-state portion of the vowel had a fundamental frequency of 100 Hz, and formants at 0.5, 1.7, and 2.5 kHz.

A closed acoustic system similar to that designed by Sokolich (1977) was used to deliver stimuli to the cat’s ear. An electrostatic speaker was used in normal experiments, whereas a 5-in. dynamic speaker was used in the impaired experiments so that higher sound levels (up to about 120 dB SPL) could be presented (Schilling 1995). The speakers were connected to hollow ear bars, and the acoustic system was calibrated before each experiment by a probe tube placed near the tympanic membrane. The frequency response of this system was relatively flat (± 6 dB) up to at least 5–7 kHz for both speakers, which was sufficient for the purposes of this study.

Analysis

Stimulus-driven rate at each level was based on the number of spikes that occurred within a window from 10 to 210 ms after the onset of the 200-ms stimulus. For the speech token, rate was computed separately for the steady-state vowel portion (90–170 ms after stimulus onset) and for the fricative portion (230–290 ms). Rate-level functions were averaged across all repetitions of the stimulus and were smoothed with a 5-point (5-dB) triangular window. SR was estimated from the interval between 200 ms after the stimulus offset and the end of the silent period for the lowest 20 stimulus levels for the 2-kHz tone. In the few cases in which a systematic trend was observed in these data, another stimulus was used for which the SR estimates were consistent across the lowest 20 levels.

The slopes of rate-level functions were characterized by fitting each rate-level function with a simple one- or 2-line model as shown in Fig. 3. The 2-line fit was motivated by the sloping-saturation rate-level function shape that is observed for some normal AN fibers (*example A* in Fig. 3; Sachs and Abbas 1974; Winter et al. 1990). Two least-square fits were made over the range from 10 to 90% of the maximum BF-tone driven rate (rate minus SR). The fits were done across all possible “elbow” points such that each line segment covered at least a 10-dB range and the fit with the least error was accepted. One-line fits were used when there was no evidence of sloping saturation (*example B* in Fig. 3). In some impaired cases, a steep C2 response occurred at very high levels (above 80 dB SPL). Identification of C2 responses was based on an approximately 180° phase transition and/or a notch in the rate-level function (Liberman and Kiang 1984; Wong et al. 1998). Slopes were recorded separately for the *low-level* portion of one- and 2-line fits, the *high-level* portion of 2-line fits, and C2 responses. Slopes were also characterized by fitting a regression line to the smoothed rate-level function over a series of 11-dB ranges. The 11-dB range was shifted across the range of levels presented in 1-dB steps, giving an estimate of slope versus level. The maximum slope across level was determined for each rate-level function.

RESULTS

Characterization of hearing loss

The extent of the hearing loss caused by the acoustic trauma is illustrated in Figs. 4 and 5. Figure 4 shows the distributions of threshold and Q_{10} values across BF for the population of normal-hearing AN fibers and for 2 hearing-impaired populations. There was significant variability across cats in the amount of hearing loss created by a given noise exposure. In general, there was little correlation between the exposure level (ranging from 103 to 108 dB SPL) and the resulting hearing loss; however, many of the impaired experiments had similar hearing losses that could be pooled into one of 2 impaired populations. A *mild*-hearing-loss population from 6 cats is shown in the *middle columns* of Figs. 4 and 5. A *moderate/severe*-hearing-loss population from 4 cats is illustrated in the *right panels* of Figs. 4 and 5. The normal-hearing population from 8 unexposed cats is shown in the *left panels*. The normal data are consistent with previous results for cat (Evans and Wilson 1973; Liberman 1978; Miller et al. 1997), including the distributions of low, medium, and high SR fibers (10, 30, and 60% for BFs between 0.5 and 4.0 kHz).

The mild-loss population had elevated thresholds at BFs ranging from 0.5 to 4 kHz, with a hearing loss of 25–30 dB at 2 kHz. Most fibers had normal tuning as judged by Q_{10} , although some fibers with BFs in the 1- to 4-kHz range demonstrated broadened tuning. In several of the experiments from the mild-loss population, a few of the initial fibers recorded from had BFs in the 1- to 2-kHz region and thresholds that were elevated by only 10–20 dB. These fibers were not held long enough to record any rate-level functions, and thus only tuning curves were collected. Because these low thresholds seemed to be exceptions to the general hearing-loss configuration, which was reasonably stable throughout the rest of the experiment, these fibers were excluded from the mild-loss population. The percentages of mildly impaired fibers with BFs between 0.5 and 4.0 kHz in the 3 SR classes were 11% (low), 39% (medium), and 50% (high).

The moderate/severe-loss population had a wider BF range of elevated thresholds, with losses of 50–60 dB in the 2- to 3-kHz region. There appeared to be a reduction in the number of fibers with BFs in the range from 2 to 4 kHz, similar to previous results (Miller et al. 1997). In contrast to the mild-loss population, almost all fibers in the moderate/severe population with BFs between 1.5 and 4 kHz had broadened tuning. The percentage of impaired fibers with BFs between 0.5 and 4.0 kHz in the low, medium-, and high-SR populations were 8, 40, and 52%. Note that in both hearing-impaired populations there was a smaller percentage of high-SR fibers and a larger percentage of medium-SR fibers than in the normal-hearing population, consistent with previous studies (Liberman and Dodds 1984a).

The relation between broadened tuning and elevated thresholds is illustrated in Fig. 5 for the 3 populations of AN fibers. The normal best-threshold curve (NBTC) and Q_{10} data from Miller et al. (1997) were used to normalize the threshold and Q_{10} data from the present study. Each fiber's threshold is plotted on the abscissa as threshold relative to the NBTC and the relative sharpness of tuning is plotted on the ordinate as Q_{10} divided by the average Q_{10} at the same BF for normal fibers. The panels in Fig. 5 have been divided into 4 quadrants representing the combinations of sharp/broad tuning and small/large threshold elevations. Impaired fibers that had broadened tuning typically had large threshold elevations (lower-right quadrant). However, there are also many impaired fibers with normal tuning and large threshold elevations (upper-right quadrant), about 65% of which were low-medium SR fibers. This percentage represents a significant increase above the normal population of low-medium SR fibers [$\chi^2 = 13.3$; degrees of freedom (df) = 1, $P \ll 0.001$].

Effects of noise-induced hearing loss on rate-level functions

A number of factors were found to influence AN rate-level functions after noise-induced hearing loss. Three distinct types of impaired responses were observed that provide clear illustrations of the changes these factors can impose. However, many fibers either demonstrated a combination of these effects or did not demonstrate obvious changes (except threshold shift) from the normal variation in rate-level shapes and slopes.

IMPAIRED RESPONSE GROWTH CAN BE VERY SIMILAR ACROSS STIMULI—

One response type consisted of fibers that lacked the normal variation in rate-level slopes with stimulus type (e.g., shallower slopes for broadband noise than for tones; Schalk and Sachs 1980). These fibers typically lacked a sharp “tip” in the tuning curve, had high SR, and had rate-level slopes that were not steeper than normal when the threshold elevation was less than 85 dB.

An example of this response type is shown in Fig. 6, along with a normal AN fiber with a similar BF and SR. Note that the impaired tuning curve has a broad bowl-like shape; BF was chosen to be near the frequency at which the steep high-frequency slope ceases, rather than at the nominal best frequency in accord with Liberman (1984).

For the normal fiber, the rate-level slopes were shallower for complex stimuli than for BF tones, consistent with previous studies (e.g., Schalk and Sachs 1980). Note also the change in slope between the vowel and fricative portions of the speech token “besh.” In contrast, the rate-level slopes for the impaired fiber were similar across simple and complex stimuli.

This response type is fairly representative of the lower-right quadrant in Fig. 5. In the moderate/severe-loss population, there were 23 fibers with responses similar to Fig. 6. Of these, 21 were in the lower-right quadrant, which contained a total of 63 fibers. Fewer clear examples of this response types were observed in the mild-loss population, but those observed were also typically in the lower-right quadrant.

IMPAIRED RESPONSE GROWTH CAN BE SHALLOWER THAN NORMAL—A

second impaired response type was formed by fibers having rate-level functions with an extremely wide dynamic range and shallow rate-level slopes. Fibers with this response type often retained a sharp “tip” in the tuning curve, had low-medium SR, and had thresholds that were elevated by less than 85 dB. These fibers differ from normal fibers in cat, which almost always show some degree of saturation in rate-level functions and have limited dynamic ranges (May and Sachs 1992; Sachs and Abbas 1974).

Two examples of AN fibers with this second response type are shown in Figs. 7 and 8, each with a fiber of similar BF and SR from a normal-hearing cat. The impaired fiber in Fig. 7 had a BF-tone rate-level function with a “straight” shape, a shallow slope, and a wide dynamic range. Impaired fibers with straight rate-level functions like this one were primarily observed in the BF region above 4 kHz.

The example in Fig. 8 shows very shallow slopes for all stimuli over at least a 20-dB range above threshold, similar to the example in Fig. 7. In contrast, this fiber’s rate-level functions became extremely steep at high levels. This steeply sloping portion at high sound levels is probably a C2 response, as suggested by the sharp phase transition in the BF-tone response.

Fibers with this response type tended to occur in the upper-right quadrant of Fig. 5; however, this response type was not generally representative of this region. In the moderate/severe-loss population, there were 8 fibers like the examples in Figs. 7 and 8, 6 of which were in the upper-right quadrant (the other 2 had slightly broadened tuning). A similar

representation was observed for the mild-loss population. The remaining fibers in the upper-right quadrant generally had responses that were not obviously different from normal.

RESPONSE GROWTH CAN BE VERY STEEP FOR SEVERE IMPAIRMENT—A third impaired response type that was observed in the moderate/severe-loss population was AN fibers with extremely steep rate-level functions for all stimuli. Fibers with this response type always had BF thresholds that were elevated by at least 85 dB, always had very broad tuning, and typically had medium SR (i.e., all examples of this type were in the extreme lower-right quadrant of Fig. 5).

An example of a fiber with this response type is shown in Fig. 9. The rate-level functions for all stimuli to which the fiber responded were very steep, with slopes above 15 spikes/s/dB. The dynamic ranges for these rate-level functions were generally much smaller than the typical dynamic ranges of normal AN fibers. This type of response is similar to some of the severe-impairment responses that were described by Liberman and Kiang (1984), and is likely to be associated with the C2 response they described. However, strict identification of C2 responses is difficult for fibers with this response type because there is not a sharp phase transition in cases where the C1 response is eliminated. Note in this case that there is a small increase and then decrease in rate below 80 dB SPL for the BF-tone rate-level function of the impaired fiber. This small response below 80 dB SPL may be a remnant of a C1 response, which has been almost entirely eliminated.

Effects of noise-induced hearing loss on AN activity growth rates with sound level

Rate-level slopes from the 2-line fitting procedure were compared between the normal-hearing, mild-loss, and moderate/severe-loss populations for each stimulus. Low-level slopes are compared in Fig. 10 for the responses to 4 stimuli. A summary of the low-level slopes from the normal-hearing and hearing-impaired populations is shown in Table 1, including statistically significant differences between normal and impaired populations.

The distributions of normal and impaired slopes in Fig. 10 show a large amount of overlap, but some trends are evident from the moving averages in Fig. 10, *A* and *B*, the distributions in Fig. 10, *C–F*, and the mean slopes in Table 1. For BF tones, the impaired low-level slopes were significantly shallower than normal at BFs with the most elevated thresholds (0.5–4 kHz; Fig. 10, *A* and *C*). A similar effect was also seen for the populations of 1- and 2-kHz-tone responses (Fig. 10*E* and Table 1). For broadband noise responses (Fig. 10, *B* and *D*), there was no significant effect of noise-induced hearing loss on low-level slopes within the elevated-threshold region (Table 1), although slopes were shallower between 1 and 2 kHz in both impaired populations. For the vowel responses (Fig. 10*F*), the low-level slopes were steeper than normal within the elevated-threshold region, significantly so for the moderate/severe-loss population, the only case with significantly steeper slopes. Fricative responses did not show significantly changed slopes in the elevated-threshold region (Table 1). Overall, the low-level slopes did not suggest that AN rate-level functions from impaired ears are consistently steeper than normal rate-level functions.

There were systematic differences in slopes across the SR classes, which account for some of the variability seen in Fig. 10. High-SR fibers typically had lower slopes than medium- and low-SR fibers; however, this effect can be accounted for in terms of the reduced range of driven rate (rate minus SR) for high-SR fibers. When slopes were normalized by the maximum driven rate for each fiber, the across-SR differences disappeared without changing the main effects described above.

A consistent effect in normal fibers is that rate-level slopes are less steep for complex stimuli than for tones (as in the examples of Figs. 6–9). This effect is presumably caused by

rate suppression in the complex stimulus response and is weaker in impaired fibers. Figure 11 shows population plots of the relative slopes for broadband noise and the vowel, defined as slope to the complex stimulus divided by slope for the BF tone. In normal fibers, the moving averages of the relative slope are significantly below one (averages of 0.7 and 0.5 for the noise and the vowel). For both impaired populations, the ratios are closer to one for fibers in some BF ranges. The BF ranges are within the region of largest threshold shift, but tend to be at higher frequencies and, for the vowel, at BFs above the threshold shift region as well.

Table 2 presents a detailed analysis of the rate-level slopes. Averages are shown for low-level, high-level, and relative slopes and the impaired populations are divided into groups of fibers with sharp and broad tuning. Fibers are placed in the sharply or broadly tuned groups according to whether their Q_{10} values are above or below the heavy horizontal line in Fig. 5. In each case, the average slope is computed from fibers with BFs between 0.5 and 4 kHz. Slopes that differ significantly from normal values are indicated by asterisks (decrease in slope) or daggers (increase in slope). Significant slope decreases are seen in the broadly tuned fibers for BF tones, as in Table 1. Significant slope increases are seen only for broadly tuned fibers at high levels for noise and low levels for vowels. The relative slope changes shown in Fig. 11 are also significant, except in one case. Thus when fibers that probably have significant OHC damage are separated (the broadly tuned fibers), slope increases are not always seen.

The data for high-level slopes in Table 2 show some changes. However, the major change in rate functions at high sound levels is that sloping saturation occurred less often in the moderate/severe-loss population. For BF tones, 43% of the normal fibers with BFs between 0.5 and 4 kHz had sloping saturation, in contrast to 34 and 19% of the mild-loss and moderate/severe-loss populations ($\chi^2 = 6.7$, $df = 2$, $P < 0.05$). A similar trend was observed for all other stimuli (e.g., broadband noise: 50, 49, and 13% sloping saturations for the normal, mild, and moderate/severe populations; $\chi^2 = 17$, $df = 2$, $P < 0.001$).

Steeper than normal rate-level functions have been shown in cases of severe impairment after acoustic trauma, presumably associated with the invulnerability of the C2 response (Fig. 9; Liberman and Kiang 1984). The prevalence of this effect is illustrated in Fig. 12, where distributions of maximum rate-level slopes for BF tones are compared between the normal and impaired populations of AN fibers. The maximum slope described in the methods was taken from slope estimates computed from 11-dB ranges centered at every point in the rate-level function. To separate the effects of presumed C2 responses, maximum slopes were determined over 2 level ranges: excluding very high levels (<80 dB SPL, Fig. 12A) and across all levels (Fig. 12B). The results of this analysis are consistent with those in Fig. 10 in that maximum slopes were not steeper in impaired fibers compared with normal fibers when the C2 slopes were excluded. Maximum slopes for impaired fibers were steeper than normal only when the high levels were considered, and this effect was observed in only a small percentage of the impaired fibers. Similar effects were observed for all other stimuli. Thus the results from this objective test are consistent with the basic findings from the more intuitive 2-line model (i.e., that impaired AN rate-level functions are steeper than normal only in limited conditions).

DISCUSSION

Interpretation of response types after noise-induced hearing loss

Acoustic trauma has been shown to produce a mixture of IHC and OHC damage. Liberman and Dodds (1984a,b) used single-fiber labeling studies to demonstrate consistent correlations between structural damage to the stereocilia of IHCs and/or OHCs and changes

in AN tuning-curve properties and spontaneous rate. Although histological examinations of the cochleae from the present study were not performed, the current acoustic-trauma paradigm was very similar to that used by Liberman and his colleagues (e.g., Liberman and Dodds 1984a,b; Liberman and Kiang 1984). Thus it is reasonable to apply the correlations between changes in tuning-curve properties and underlying structural hair-cell damage established by Liberman and Dodds (1984a,b) to the results from the present study. The 3 response types illustrated in Figs. 6-9 can be interpreted with these results.

The response type in Fig. 6 was typically observed in AN fibers that had broad tuning curves that lacked a sharp “tip” region. These fibers had low-level slopes that were not steeper than normal and lacked the normal sloping saturation and shallower slopes for broadband stimuli. These characteristics are consistent with an OHC lesion, which should produce broad tuning (Liberman and Dodds 1984b) and a loss of suppression (Miller et al. 1997; Ruggero and Rich 1991; Salvi et al. 1982; Schmiedt et al. 1980). Behavior like this was observed in the population measures by the increase in relative slopes (Fig. 11) for broadband noise and the vowel, especially among impaired fibers with broad tuning (Table 2).

Fibers like those in Figs. 7 and 8 typically retained a sharp tuning-curve “tip,” had low-medium SR, and had thresholds that were elevated by less than 85 dB. These fibers had very wide dynamic ranges and shallow slopes above threshold. These properties are consistent with primarily IHC damage (Liberman and Dodds 1984b). The sharp tuning curves suggest that there is remaining OHC function. Thresholds elevated by less than 85 dB and low-medium SR were interpreted by Liberman and Dodds (1984b) as suggesting that there was damage to the tallest row of IHC stereocilia. The shallow slopes are expected if BM compression were present as a result of remaining OHC function; the elevated AN threshold resulting from IHC damage would shift the rate-level function such that the entire dynamic range would overlap with the compressive region. The shallower slopes could also be attributed to reduction in the saturated rate of AN responses. Liberman and Kiang (1984) reported a reduction in the maximum rate of the C1 response (i.e., below about 80 dB SPL) after IHC damage. Reduced C1 rate was often observed in our data in association with shallow low-level slopes (e.g., Fig. 8). Liberman and Kiang (1984) suggested that the reduction in maximum rate was produced by a reduction in the number of transduction channels resulting from stereocilia damage. This explanation is consistent with the observation that administering furosemide at doses that reduce the endocochlear potential, and thus the maximal transduction current, also selectively reduces the maximal rate in the C1 response (Sewell 1984). Although the examples in Figs. 7 and 8 suggest several ways that isolated IHC damage can produce shallower slopes, low-level slopes were not significantly shallower for the populations of impaired fibers with sharp tuning (Table 2) because of the large number of such fibers with essentially normal rate-level slopes.

Fibers like the one in Fig. 9 show severe threshold shifts with very steep rate-level functions for all stimuli that elicit a response. These fibers always had thresholds elevated by at least 85 dB, broad tuning, and typically had medium SR. The severe threshold shifts and broad tuning suggest that these steep responses are associated with the C2 response described by Liberman and Kiang (1984) and that the C1 response has been entirely eliminated. Liberman and Kiang (1984) observed large portions of the cochlea with only short IHC stereocilia that appeared normal, despite severe damage to both the OHC stereocilia and to the tallest row of IHC stereocilia. Presumably the loss of the tallest stereocilia accounts for the loss of C1 and the C2 response is produced by the short cilia. Such responses were observed for both tones and complex stimuli, as expected (Wong et al. 1998).

Although the distinct response types illustrated in Figs. 6-9 can be accounted for primarily in terms of isolated OHC or IHC lesions, most impaired fibers did not fall into one of these

distinct response types. Rather, many fibers demonstrated a mixture of the effects illustrated by these examples (e.g., fibers with broadened tuning had shallower BF-tone slopes on average, Table 2), which suggests that most of the impaired fibers had a mixed hair-cell lesion. This observation is consistent with the typical overlap in frequency regions over which IHC and OHC stereocilia are damaged after acoustic trauma (Liberman and Dodds 1984a,b; Liberman and Kiang 1984).

Are auditory-nerve rate-level functions steeper in impaired ears?

It has often been stated or hypothesized that rate-level functions of AN fibers are steeper in hearing-impaired ears than in normal-hearing ears (e.g., Harrison 1981; Moore 1991, 1995; Pickles 1988; Schroder et al. 1994), and this idea has been used to interpret psychophysical performance of hearing-impaired listeners (e.g., Moore 1991; Schroder et al. 1994). The justification for this idea has come from several physiological studies that reported steeper rate-level functions after impairment for certain conditions (e.g., Harrison 1981; Liberman and Kiang 1984). The results from the present study confirm that impaired rate-level functions can be steeper than normal, but only in limited conditions. Rate-level functions in impaired ears are not consistently steeper than normal after noise-induced hearing loss, especially for tones, the stimulus most often used in psychophysical studies.

The finding that impaired rate-level functions are steeper than normal only in limited conditions is consistent with the predictions from the commonly accepted model for the effect of BM compression on the shapes of AN-fiber rate-level functions (Fig. 1; Sachs and Abbas 1974; Yates et al. 1990). For example, the reduction in sloping saturation is consistent with the predictions from this model. There are 2 probable reasons for the reduced occurrence of sloping saturation in impaired fibers. First, reduced compression (resulting from OHC damage) eliminates sloping saturation by making the shallow portion of the rate-level function (above the elbow) steeper. This effect is consistent with the results of Harrison (1981), who showed that AN-fiber rate-level functions tended to have similar slopes for tones at all frequencies after ototoxic damage, in contrast to normal fibers. Second, an elevated threshold with remaining compression (resulting from IHC damage) produces a straight, shallow rate-level function (e.g., Fig. 7).

The results from Harrison (1981) have often been interpreted as indicating that rate-level functions are steeper in impaired ears. However, the primary steepening in Harrison's data occurred for tone frequencies above BF or for high-threshold fibers, both of which represent a relatively small fraction of the AN population response. Also, the effects demonstrated by Harrison (1981) were for the limited case in which only OHCs were damaged. The results from the present and previous studies suggest that isolated OHC damage may not occur very frequently in cases of noise-induced hearing loss (e.g., Liberman and Dodds 1984a,b; Liberman and Kiang 1984; Miller et al. 1997, 1999a,b).

It was not surprising that impaired rate-level functions for complex stimuli could be steeper than normal in some conditions (Figs. 10 and 11), because suppression is typically reduced with impairment (e.g., Miller et al. 1997; Salvi et al. 1982). Steeper relative slopes appear to be primarily associated with broadened tuning (Fig. 11, Table 2), but could result from either steeper slopes for complex stimuli or from shallower BF-tone slopes. The rate-level slopes shown in Fig. 10 suggest that the main effect producing increased relative slopes for broadband noise was reduced BF-tone slopes. For vowels, the effect appears to result from a combination of both shallower BF-tone slopes and steeper vowel slopes (Fig. 10). The overall consequence of both of these effects is that there is less variation in the slopes of rate-level functions across different stimuli in impaired fibers than in normal fibers.

The debate over the effects of sensorineural hearing loss on the slopes of AN-fiber rate-level functions has typically focused on whether slopes become steeper after impairment. The present study suggests that impaired rate-level functions are often shallower than normal after noise-induced hearing loss. As discussed above, these cases are likely to be associated with IHC damage. Some of the cases with narrow tuning may result from elevated thresholds and remaining compression, as predicted by the Sachs and Abbas (1974) model. Surprisingly though, impaired AN fibers with broadened tuning had significantly shallower slopes for BF tones, whereas those with narrow tuning did not (Table 2). This observation suggests that many of the broadly tuned fibers had substantial IHC, as well as OHC, damage. It appears then, that a change in the IHC transduction function, associated with the reduction in C1 responses (Liberman and Kiang 1984), is necessary in some cases for the Sachs and Abbas (1974) model to fully account for the effects of acoustic trauma on AN rate-level functions.

Thus although the effects of sensorineural hearing loss on AN rate-level functions have typically been interpreted entirely in terms of OHC loss, IHC damage can also have significant effects. This result is consistent with a recent modeling study by Bruce et al. (2003) in which it was shown that IHC damage could have a significant effect on the encoding of speech in AN responses, in addition to OHC damage. Further, although the effects of sensorineural hearing loss on psychophysical performance have typically been interpreted based on the effects of OHC loss (e.g., Moore 1995; Moore and Oxenham 1998; Plack and Oxenham 1998), it appears to be important to consider the effects of IHC damage as well, especially in cases of noise-induced hearing loss.

Implications for loudness recruitment

It has long been assumed that the percept of loudness is closely related to the total activity within the AN population (e.g., Goldstein 1974; Moore 1995; Wever 1949); however, the details of this relation remain unclear (e.g., Pickles 1983; Relkin and Doucet 1997). This assumption has led many researchers to look for neural correlates of loudness recruitment in the AN. The simplest and most common hypothesis has been that steeper AN rate-level functions in impaired ears are likely to form the neural basis for the steeper growth of loudness associated with loudness recruitment (e.g., Harrison 1981; Moore 1991, 1995; Pickles 1988; Schroder et al. 1994). This assumption appears to be untenable from our results; however, alternative hypotheses exist.

First, recruitment could result from a more rapid growth in the spread of excitation caused by reduced frequency selectivity (e.g., Evans 1975; Kiang et al. 1970). However, preliminary analyses of the current data do not suggest that broadened tuning has a major effect on total AN activity growth with sound level, which is consistent with predictions from psychophysical loudness models (Moore 1995). Second, there is evidence of recruitment-like effects in the response growth of central auditory neurons with sound level, presumably because of changes in synaptic gains after cochlear damage (Popelar et al. 1987; Salvi et al. 1990; Saunders et al. 1972; Syka et al. 1994; Szczepaniak and Møller 1996). Finally, it is possible that there are neural correlates of recruitment other than those directly related to average discharge rate. It has been hypothesized that sound level may be encoded in the temporal patterns of AN discharges (Carney 1994), meaning that cochlear nonlinearities associated with OHCs produce systematic level-dependent changes in phase that could be used to code stimulus intensity (Heinz et al. 2001).

In addition, recent psychophysical data have challenged several aspects of the classical view of loudness recruitment (Buus and Florentine 2002). Those data imply that loudness in impaired listeners is elevated at threshold, grows at normal rates near threshold, grows faster than normal at suprathreshold levels, and is near normal at high levels. These results are

consistent with our data in that low-level slopes were not steeper than normal, and there was some evidence for steeper slopes at high levels (increased high-level slopes and steeper C2 responses at very high levels). Liberman and Kiang (1984) noted that the invulnerability of the C2 response provides a possible correlate for normal loudness at high levels. However, the neural basis for elevated loudness at threshold is not clear from our data.

Implications for hearing aids

Whereas loudness recruitment has often been assumed to result from steeper BM responses associated with OHC damage, the present study illustrates that AN fibers do not provide a simple representation of the BM I/O function. Indeed, AN fibers can show either steeper or shallower rate-level functions after sensorineural hearing loss. Thus compression algorithms that are designed to overcome a reduced dynamic range may need to account for more than reduced BM compression. This is particularly true in cases of mixed IHC and OHC damage (e.g., noise-induced hearing loss), where IHC and OHC damage may interact to produce different effects on AN responses.

Another potential implication for hearing aids is the observation that noise-induced hearing loss can produce very steep AN growth at high levels associated with C2 responses. Although the C1/C2 transition has often been ignored in normal hearing because it occurs at such high levels, these are often the levels at which hearing aids operate. In normal AN fibers, the C2 response produces a steep rate-level function only over a few dB (if at all) because the maximum response to C1 is typically the same as that to C2 (Liberman and Kiang 1984). In contrast, the selective vulnerability of the C1 response to cochlear insult can lead to an accentuation of the C1/C2 transition, resulting in very steep AN responses between 80 and 100 dB SPL (e.g., Figs. 8 and 9). Thus the high levels at which hearing aids often operate can have abnormally steep AN growth rates, which may adversely affect perception. A similar suggestion was made by Wong et al. (1998), who demonstrated that the neural representation of speech in normal ears is degraded at these high sound levels (i.e., above the C2 threshold).

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Figure 1.

Schematic growth of basilar-membrane (BM) velocity (A; after Ruggero et al. 1997) and auditory-nerve (AN) fiber discharge rate (B; after Sachs and Abbas 1974) for normal ears (solid) and in the presence of substantial outer hair-cell damage (dashed). A. For tones at best frequency, BM velocity in normal ears grows linearly with sound level at low sound levels, but then shows compression over a broad range of levels as the cochlear-amplifier gain is reduced (solid line). With OHC loss, the cochlear amplifier is gone and BM velocity grows linearly with sound level (dashed line). Loudness functions in normal and hearing-impaired listeners show a general correspondence to these data (Buus and Florentine 2002; Moore 1995; Schlauch et al. 1998), suggesting that loudness recruitment reflects the steepened BM response. Note that both axes are logarithmic so linear growth corresponds to a slope of 1 dB/dB, which is the slope of the dashed line. B. AN-fiber discharge rates for two theoretical fibers, a low-threshold high spontaneous-rate fiber (light solid line) and a high-threshold low spontaneous-rate fiber (heavy solid line). The low threshold fiber is saturated at the sound level at which the BM becomes compressive (vertical dotted line), so its discharge rate does not reflect the compression. By contrast, the high threshold fiber has a knee in its rate-level function at the threshold for BM compression. In the impaired ear (dashed lines), the low-threshold fiber's rate-level function is shifted without a change of slope, but the high-threshold fiber's is steepened at suprathreshold levels.

Figure 2. Power spectra for the vowel (top) and fricative (bottom) portions of the speech token (“besh”). Magnitude is shown relative to the first formant (F1=500 Hz) of the vowel.

Figure 3.

The slopes of rate-level functions were characterized using one- or two-line models. Two-line fits were made in cases of sloping saturation (fiber A, triangles). One-line fits were used in cases of sharp saturation (fiber B, +’s). Estimated slopes (shown in parentheses) are in units of spikes/s/dB. Data are BF-tone responses of two fibers from one normal-hearing cat.

Figure 4.

Distributions of tuning-curve characteristics across best frequency (BF) illustrate the extent of the hearing loss for three populations of fibers. The top panels show the distributions of threshold as a function of BF. Three spontaneous-rate (SR) classes are identified by symbols. The solid line is the NBTC curve from Miller et al. (1997), which summarizes the BF dependency of the lowest thresholds observed in their normal-hearing data. The bottom panels show the distributions of Q_{10} values, where Q_{10} is a measure of sharpness of tuning (the ratio of tuning-curve BF to the bandwidth 10 dB above threshold). The solid lines indicate the 5th and 95th percentiles of the normal Q_{10} values from Miller et al. (1997).

Figure 5.

The relation between broadened tuning and threshold elevation for the three populations of AN fibers. Relative sharpness of tuning (Q_{10} normalized by the mean from normal AN fibers of the same BF) is plotted as a function of threshold elevation (fiber threshold relative to the best-threshold curve, NBTC). The dotted and dashed lines indicate the 50th (mean) and 95th percentiles of normal tuning from Miller et al. (1997). The solid horizontal line (5th percentile) is used throughout to separate sharp and broad tuning. The solid vertical line represents an arbitrary division between small and large threshold elevations. The three SR classes of AN fibers are identified by symbols.

Figure 6.

An example of an impaired AN fiber for which rate-level functions were similar for all stimuli. The impaired fiber (right column) is compared to a fiber from a normal-hearing cat (left column) with similar BF and SR. Tuning curves for each fiber are shown in the top row. Discharge rate in response to a BF tone (2nd row) and broadband noise (3rd row) is plotted as a function of tone level or noise spectral level, respectively. Thick lines show the regression fits, with slopes in parentheses (spikes/s/dB). Rate-level functions for the vowel (solid regression line) and fricative (dotted regression line) portions of “besh” are shown in the bottom row as a function of overall vowel level. Normal fiber: BF=2.0 kHz; threshold=15 dB SPL; SR=68.6 spikes/s; Q_{10} =3.4. Impaired fiber: BF=2.3 kHz; threshold=79 dB SPL (84 dB re: NBTC); SR=68.0 spikes/s; Q_{10} =1.0 (0.23 re: normal, see Fig. 5).

Figure 7.

An example of an impaired AN fiber with a very wide dynamic range and shallow rate-level slope at all levels. Same format as Fig. 6. Normal fiber: BF=6.5 kHz; threshold=25 dB SPL; SR=0.4 spikes/s; Q_{10} =7.5. Impaired fiber: BF=6.3 kHz; threshold=57 dB SPL (61 dB re: NBT); SR=0.3 spikes/s; Q_{10} =7.6 (1.10 re: normal).

Figure 8.

A second example of an impaired AN fiber with a very wide dynamic range and shallow ratelevel slope above threshold, but with steep responses at very high levels. Same format as Fig. 6, except a phase raster plot is shown for the impaired fiber's BF-tone response to illustrate the C1/C2 transition associated with the steep high-level response. For each sound level, a dot is plotted at the stimulus phase (in cycles) of each action potential. A phase transition of approximately $\frac{1}{2}$ cycle occurred at ~90 dB SPL. Normal fiber: BF=1.6 kHz; threshold=11 dB SPL; SR=5.2 spikes/s; Q_{10} =3.7. Impaired fiber: BF=1.5 kHz; threshold=62 dB SPL (67 dB re: NBTC); SR=4.8 spikes/s; Q_{10} =4.8 (1.38 re: normal).

Figure 9.

An example of an impaired AN fiber with severe threshold elevation and very steep responses for all stimuli. Same format as Fig. 8. Normal fiber: BF=1.6 kHz; threshold=21 dB SPL; SR=8.1 spikes/s; Q_{10} =2.6. Impaired fiber: BF=1.3 kHz; threshold=83 dB SPL (88 dB re: NBTC); SR=17.1 spikes/s; Q_{10} was undefined.

Figure 10.

Rate-level slopes from the three populations of AN fibers indicate that neural activity growth in impaired ears is not steeper than normal except in limited conditions. A,B. Low-level slopes from the two-line fitting procedure are plotted as a function of BF for the normal (solid triangles), mild-loss (circles), and moderate/severe-loss (x's) populations. Slopes are shown for BF tones (A) and broadband noise (B). The solid lines in panels A and B represent weighted moving averages calculated using an octave-wide triangular window in steps of 0.5 octaves. All fibers were included in the weighted averages (i.e., no separation based on SR), and a minimum of three fibers was required in each window. Steep slopes at very high levels that appeared to be C2 responses were not included (see text). C-F. Distributions of low-level slopes are shown for BF tones (C), broadband noise (D), 1-kHz tones (E), and the vowel (F) portion of the speech token "besh". Only fibers with BFs between 0.5-4 kHz were included. Statistical comparisons between the normal and impaired populations are summarized in Table 1 for all stimuli.

Figure 11.

Relative rate-level slopes illustrate how activity growth in AN fibers varies across stimuli. Low-level slopes for broadband-noise (left) and vowel (right) responses were normalized to the low-level slope for a BF tone for each fiber. Triangular weighted moving averages (using geometric means) are also shown (solid lines). Relative slopes were on average less than one (shallower for complex stimuli) for the normal-hearing population (thick line), but were closer to one in some frequency regions for both hearing-impaired populations (thinner lines). Vertical dotted lines (right) indicate the first three formant frequencies of the vowel.

Figure 12.

The distributions of maximum rate-level slopes provide an alternative indication that impaired AN-fiber rate-level functions are not consistently steeper than normal. Maximum rate-level slope across level was determined (see text) for each AN fiber within the elevated-threshold region (BFs between 0.5 and 4 kHz). Maximum slopes from impaired AN fibers were equal to or less than normal maximum slopes when high sound levels were excluded (A: maximum taken up to 80 dB SPL). Only when the maximum was taken over all levels (B) did some impaired AN fibers have steeper maximum slopes than normal. Note that, although data from normal fibers were not typically collected above 80-100 dB SPL to avoid inducing cochlear damage, the only significant slopes at high levels in normal ratelevel functions are associated with occasional narrow (a few dB) notches (e.g., Kiang 1984,1990).

TABLE 1

Summary of low-level slopes from the normal-hearing and hearing-impaired populations

Stimulus	Normal	Mild Loss	Moderate/Severe Loss
BF tone	7.3	6.1 *	5.9 *
1-kHz tone	7.1	5.2 *	5.8 *
2-kHz tone	5.6	4.2 *	5.6
Broadband noise	5.1	4.8	4.8
Vowel	3.7	4.2	4.8 †
Fricative	5.4	4.5	5.7

Mean low-level slopes (in spikes/s/dB) were calculated for all fibers with BFs within the elevated-threshold region ($0.5 \leq \text{BF} \leq 4.0$ kHz). The statistical significance of differences between each hearing-impaired population and the corresponding normal-hearing population was evaluated using two-sided *t*-tests.

* significantly shallower than normal ($P < 0.05$);

† significantly steeper than normal.

TABLE 2

Summary of the effects of broadened tuning on mean slopes

Stimulus	Slope	Mild Loss		Moderate/Severe Loss	
		Normal Sharp	Sharp	Broad	Broad
BF tone	Low-level	7.1 (56)	6.5 (68)	5.3* (34)	6.5 (23)
	High-level	2.2 (23)	3.0 (25)	2.2 (10)	2.1 (4)
Broadband noise	Low-level	5.0 (47)	4.8 (60)	4.7 (29)	5.1 (20)
	High-level	1.6 (23)	1.8 (31)	2.5 [†] (13)	1.8 (4)
Vowel	Relative	0.7 (47)	0.7 (59)	0.9 [†] (29)	0.8 (19)
	Low-level	3.6 (40)	4.5 (53)	3.6 (28)	4.6 (15)
	High-level	1.6 (7)	2.8 (9)	2.6 (7)	—
	Relative	0.5 (40)	0.6 [†] (52)	0.7 [†] (28)	0.9 [†] (17)

Fibers were separated into 2 groups based on tuning-curve width; sharp: Q10 above the 5th percentile of normal fibers, broad: Q10 below the 5th percentile (see Figs. 4 and 5). Mean slopes are shown for all fibers with BF's within the elevated-threshold region ($0.5 \leq \text{BF} \leq 4.0$ kHz). Low- and high-level slopes from the 2-line fitting procedure are in spikes/s/dB (Fig. 3). Relative slopes represent low-level slopes for the complex stimuli normalized to the low-level BF tone slopes for each fiber (Fig. 11). Number of fibers in each category is shown in parentheses.

* significantly shallower than normal ($P < 0.05$);

[†] significantly steeper than normal. Mean slopes are not shown when fewer than 4 slopes were in the group.