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Temporal Modulation Transfer Functions Measured From Auditory-Nerve Responses Following Sensorineural Hearing Loss

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Abstract

The ability of auditory-nerve (AN) fibers to encode modulation frequencies, as characterized by temporal modulation transfer functions (TMTFs), generally shows a low-pass shape with a cut-off frequency that increases with fiber characteristic frequency (CF). Because AN-fiber bandwidth increases with CF, this result has been interpreted to suggest that peripheral filtering has a significant effect on limiting the encoding of higher modulation frequencies. Sensorineural hearing loss (SNHL), which is typically associated with broadened tuning, is thus predicted to increase the range of modulation frequencies encoded; however, perceptual studies have generally not supported this prediction. The present study sought to determine whether the range of modulation frequencies encoded by AN fibers is affected by SNHL, and whether the effects of SNHL on envelope coding are similar at all modulation frequencies within the TMTF passband. Modulation response gain for sinusoidally amplitude modulated (SAM) tones was measured as a function of modulation frequency, with the carrier frequency placed at fiber CF. TMTFs were compared between normal-hearing chinchillas and chinchillas with a noise-induced hearing loss for which AN fibers had significantly broadened tuning. Synchrony and phase responses for individual SAM-tone components were quantified to explore a variety of factors that can influence modulation coding. Modulation gain was found to be higher than normal in noise-exposed fibers across the entire range of modulation frequencies encoded by AN fibers. The range of modulation frequencies encoded by noise-exposed AN fibers was not affected by SNHL, as quantified by TMTF 3- and 10-dB cut-off frequencies. These results suggest that physiological factors other than peripheral filtering may have a significant role in determining the range of modulation frequencies encoded in AN fibers. Furthermore, these neural data may help to explain the lack of a consistent association between perceptual measures of temporal resolution and degraded frequency selectivity.

Keywords

Auditory nerve; sensorineural hearing loss; acoustic trauma; modulation; envelope coding; chinchilla

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1. Introduction

The range of modulation frequencies (f_m) that an individual auditory-nerve (AN) fiber can encode is well characterized by the temporal modulation transfer function (TMTF). A TMTF is a trace of modulation gain as a function of modulation frequency, where modulation gain is defined as the ratio of modulation depth in the neural response to modulation depth in the input stimulus (Joris and Yin, 1992; Møller, 1972; Rees and Palmer, 1989). Auditory-nerve TMTFs generally have low-pass filter characteristics, i.e., relatively flat gain at low modulation frequencies followed by a roll off at higher modulation frequencies. The modulation frequency at which gain rolls off by 3 dB (TMTF 3-dB cut off) shows a characteristic frequency (CF) dependence in that 3-dB cutoff frequency increases with increasing CF (Joris and Yin, 1992). Since AN tuning-curve bandwidth (BW) increases with increasing CF, frequency selectivity of individual AN fibers has been suggested to influence TMTF roll off (Javel, 1980; Joris and Yin, 1992; Palmer, 1982). Given these results, one might expect that TMTF cut-off frequencies would be higher following sensorineural hearing loss (SNHL) due to broadened tuning, which is often associated with SNHL (Liberman and Dodds, 1984a). However, the effects of SNHL on neural TMTF characteristics have not previously been quantified.

Although TMTF cut-off frequencies show a CF (or bandwidth) dependence, it has been shown that TMTF 3-dB cut-off frequencies do not continue to increase with increasing CF, but rather saturate for CFs ≥ 10 kHz in cats (Joris and Yin, 1992). These results indicate a possibility that factors other than peripheral filtering may influence TMTF roll off. It has been suggested that at high CFs the temporal coding ability of individual fibers may limit TMTF roll offs in addition to cochlear filtering (Joris and Yin, 1992).

Our recent study has shown that the fundamental ability of AN fibers to phase lock to temporal envelope is not degraded following SNHL (Kale and Heinz, 2010). If temporal coding limitations of individual fibers play a major role in TMTF roll off, then it is possible that there would be no difference in TMTF cut off frequencies between normal-hearing fibers and fibers with SNHL.

Another factor that may influence TMTF roll off is the relative phases of sinusoidally amplitude modulated (SAM) tone components interacting within a single auditory filter. On the basilar membrane, if the phase of the carrier component is shifted by 90° relative to the phases of the individual sidebands then the resulting AM signal at the output of the auditory filter would be less modulated but with twice the envelope frequency. Thus, the effective basilar membrane response would resemble quasi-frequency modulated (QFM) tones with reduced modulation depth as compared to sinusoidally amplitude modulated (SAM) tones (Joris and Yin, 1992). This effective reduction in response modulation would lead to a reduction in modulation gain. It has been demonstrated that the relative phases of individual SAM response components do not contribute to TMTF roll off for normal-hearing AN fibers (Joris and Yin, 1992). However, it is not clear if such phase effects could influence TMTF roll off following SNHL given recent evidence that showed SNHL produces shallower across-CF phase transitions (Heinz et al., 2010).

Perceptual TMTFs typically measure modulation detection threshold as a function of modulation frequency. The general consensus from perceptual studies is that temporal resolution for AM stimuli is not affected by SNHL (Bacon and Gleitman, 1992; Moore and Glasberg, 2001; Moore et al., 1992). Modulation detection thresholds were slightly better in hearing-impaired listeners than in normal-hearing listeners for complex temporal patterns (Fullgrabe et al., 2003), and for amplitude-modulated tones when the carrier signal was a sine wave (Moore and Glasberg, 2001). Similar results were observed in another study that

showed significantly better than normal-hearing modulation detection thresholds in hearing-impaired listeners for very low modulation rates (He et al., 2008). Overall these results are consistent with our recent physiological study that showed that the auditory-nerve representation of the envelope is enhanced following SNHL for a low modulation rate of 50 Hz (Kale and Heinz, 2010). One question that remains unanswered is whether this enhancement in modulation coding is restricted only to low modulation rates or if it covers the complete passband of the TMTF.

The present study was designed to measure the range of modulation frequencies individual AN fibers can encode following SNHL using SAM tones. The role of several factors in the TMTF roll-off were investigated, such as cochlear filtering, temporal coding ability, and the relative phases of SAM response components. For each fiber, envelope coding for a broad range of modulation frequencies was studied and these results are discussed in relation to perceptual studies.

2. Materials and Methods

Single fiber AN recordings were made from 7 normal-hearing and 9 hearing-impaired chinchillas. All animal care and use procedures were approved by the Purdue Animal Care and Use Committee (PACUC). The protocols for acoustic overexposure and neurophysiological recordings were identical to previously described protocols (Kale and Heinz, 2010), and are only briefly summarized here.

2.1. Acoustic trauma and neurophysiological recordings

Animals anesthetized with xylazine and ketamine were exposed to a 50-Hz wide noise centered at 2 kHz, uninterrupted for four hours, in a free field environment. Noise levels were calibrated to be 114–115 dB SPL at the entrance of the ear canal. The animals were then allowed to recover for ≥ 30 days. AN-fiber recordings were made from pentobarbital-anesthetized chinchillas with 10–30 M Ω glass micropipette electrodes filled with 3 M NaCl (Kale and Heinz, 2010).

2.2. Stimuli

The system setup used for stimulus presentation and single-unit recordings was similar to the previously described setup (Kale and Heinz, 2010). A broadband noise search stimulus (about 20 dB re 20 μ Pa/ $\sqrt{\text{Hz}}$ for normal-hearing animals, and higher as needed for noise exposed animals) was used to isolate AN fibers. Isolated fibers were characterized initially by an automated tuning curve algorithm to estimate fiber CF, threshold, and Q_{10} (Chintanpalli and Heinz, 2007). For impaired fibers with very broad tuning, CF was chosen based on the bottom of the steep high-frequency tuning-curve slope, which estimates the pre-exposure cochlear CF (Liberman, 1984). Some impaired fibers had ‘w-shaped’ tuning curves with sharp tips and sensitive tails responding to a broad range of frequencies (Liberman and Dodds, 1984b). For such fibers, the broadest bandwidth was always used to compute Q_{10} values. For some severely impaired fibers, tuning was extremely broad and the low-frequency edge of the tuning curve did not rise to more than 10 dB above threshold. In such cases, an under-estimate of the 10-dB bandwidth was taken as the bandwidth between the lowest frequency for which a threshold was measured and the frequency above CF corresponding to 10 dB above threshold at CF. Computed values of Q_{10} in these cases thus represent overestimates and are labeled as such in relevant figures. Following the basic characterization, SAM tones were presented at sound levels starting from 5–10 dB below fiber’s threshold to 40–50 dB above fiber’s threshold in 5 dB steps. Carrier frequency (f_c) was equal to fiber CF, modulation frequency (f_m) was 50 Hz, and modulation depth (m) was held constant at 1.0 (full modulation). Each SAM tone was 700 ms long and a new sound

level was presented every 1000 ms until 25–30 repetitions of all levels were obtained. For each fiber, the SAM-tone best modulation level (BML) was then determined as the sound level for which the highest degree of synchrony to fm was observed. TMTFs were then measured at BML, with $f_c=CF$ and a modulation depth of 1.0. Modulation frequency was varied in 20 logarithmic steps from $(CF/100)$ to $(0.8 \times CF)$ until 25–30 repetitions of each fm were obtained.

2.3. Analysis

Synchronization index (R , or vector strength), was computed for each fm value from period histograms with 64 bins (Goldberg and Brown, 1969). A Rayleigh uniformity test ($p < 0.001$) was used to test for significant deviations of the period histogram from a uniform distribution along the unit circle, based on the Rayleigh statistics of the quantity $2nR^2$, where n is the number of spikes (Mardia and Jupp, 2000). For each significant synchronization index, modulation gain was computed as a ratio defined as $20 \cdot \log_{10}(2 \cdot R/m)$, where R was the vector strength and m was the modulation depth of the input stimulus which was always 1 (Rees and Palmer, 1989). The multiplication factor of 2 ensures 0 dB modulation gain for a half-wave rectified SAM tone with a modulation depth of 1 (Joris and Yin, 1992).

3. Results

3.1. Characterization of hearing loss

Hearing loss induced by acoustic trauma was characterized based on thresholds and Q_{10} values of individual AN fibers. Figure 1 shows the thresholds and Q_{10} values computed from the tuning curves of AN fibers obtained from normal-hearing animals (crosses) and from animals with noise induced hearing loss (NIHL, circles). The solid line in Figure 1A indicates the lowest thresholds observed in a larger normal-hearing population (Kale and Heinz, 2010). This best-threshold curve is likely to represent the behavioral audiogram better than the mean-threshold curve. Best thresholds were elevated in the NIHL population primarily between 1 and 8 kHz, with a ~35–40 dB shift for CFs between 2–3 kHz and only about a 10-dB shift for CFs below 1 kHz. This configuration of best threshold elevation is consistent with previous studies that used a similar noise-band exposure (Heinz and Young, 2004; Miller et al., 1997). Figure 1B shows Q_{10} values of individual AN fibers as a function of CF. Solid diagonal lines represent the 5th and 95th percentile regions computed for the normal-hearing Q_{10} data (as in Bruce et al., 2003). 25 of the 49 noise exposed fibers included in the present data had Q_{10} values outside the normal range (i.e., below the 5th percentile line shown in Figure 1B), indicating significantly poorer frequency selectivity. Although the remaining noise-exposed fibers had Q_{10} values within the normal range, Q_{10} values were mostly within the lower half of the normal range and they showed higher thresholds relative to normal fibers. Impaired fibers for which Q_{10} was overestimated (i.e., for which extremely broad tuning made it difficult to estimate the 10-dB bandwidth, see Methods) are shown with filled symbols in Figure 1B. Frequency selectivity in these fibers is likely to be even worse than indicated by the filled circles. Throughout this paper we have used normalized values of Q_{10} , which were normalized with reference to the 5th percentile line (Fig. 1B). Thus, normalized $Q_{10} \leq 1$ indicates tuning that is significantly broader than normal.

3.2. Characteristic low-pass shape of TMTFs was not affected by SNHL

The low-pass filter shape that is a characteristic of TMTFs in normal fibers (Joris and Yin, 1992) was also observed in all noise-exposed fibers. Figure 2 shows the TMTFs for a normal fiber (left column) and a noise-exposed fiber (right column) with similar CFs. The noise-exposed fiber showed broadened tuning and elevated threshold (Fig. 2B) as compared to the normal fiber (Fig. 2A). These two fibers are good representatives of their respective

populations. TMTF gain (Fig. 2C–D) initially increased slowly with increasing modulation frequency in both fibers. Such positive slope segments were present in many fibers in both the populations. Following the initial positive segment, gain reached a maximum value and then rolled off rapidly. These trends are consistent with previous data (Joris and Yin, 1992; Palmer, 1982). The modulation frequency corresponding to maximum gain was defined as the best modulation frequency (BMF). Modulation frequency at which gain rolled off by 3 and 10 dB (fm_{3dB} and fm_{10dB} , respectively) were used to quantify the range of modulation frequencies each fiber could encode. fm_{3dB} and fm_{10dB} cut off frequencies have been used previously to characterize modulation coding in cats (Joris and Yin, 1992) and in guinea-pigs (Palmer, 1982). The noise-exposed fiber shown in the example (Fig. 2D) showed slightly higher fm_{3dB} and fm_{10dB} cut off frequencies. However, this result was not consistent throughout the population, which is discussed in detail later. Cumulative phase increased linearly as a function of modulation frequency and the discharge rate was relatively constant for both fibers (Fig. 2E and 2F). Similar trends were observed for other fibers in the normal-hearing and noise-exposed populations. These trends are consistent with previous data (Joris and Yin, 1992).

Figure 3 shows the summary of TMTFs observed in both populations. Figure 3A shows the TMTFs for 20 noise-exposed fibers with broadened tuning (gray lines) superimposed on the TMTFs for 23 normal-hearing fibers (black lines). All impaired fibers had CFs between 1 and 4 kHz and significantly broadened tuning. Such a CF range was chosen because maximum impairment was observed within this CF range (Fig. 1). Overall, modulation gain was higher in noise-exposed fibers within this CF range. Since modulation in the stimulus was constant for both populations, higher modulation gain indicates that envelope coding was enhanced in the noise-exposed auditory-nerve fibers. This result is consistent with our recent data, which showed enhanced envelope coding in AN fibers for envelope frequencies of 50 and 100 Hz (Kale and Heinz, 2010). Results from the present study suggest that envelope coding is enhanced for a broad range of envelope frequencies spanning the entire passband of the TMTF.

Due to increased overall gain, noise-exposed fibers appeared to encode a broader range of modulation frequencies (i.e., broader TMTFs). To reduce the influence of increased gain on TMTF cut off frequencies, modulation gain was normalized by the maximum gain (maximum synchrony to fm) and normalized gain was plotted as a function of modulation frequency (Fig. 3B). After normalizing the gain, no distinct differences were seen in TMTF shapes across the two populations. These results indicate that TMTF cut off frequencies were not affected even for noise-exposed fibers with significantly broadened tuning. The modulation frequencies at which gain dropped to -10 dB (horizontal gray line in Fig. 3A) and the modulation frequencies at which gain dropped by 10 dB (i.e., fm_{10dB} cut off frequency) were compared across normal-hearing and noise-exposed fiber populations. These results are discussed below.

3.3. Broadened tuning following SNHL did not result in increased TMTF cut off frequencies

Figure 4(A–D) shows 3- and 10-dB TMTF cut-off frequencies for normal-hearing fibers (crosses) and noise-exposed fibers (open circles). Filled circles in the left column indicate noise-exposed fibers with broadened tuning, whereas in the right column, they indicate noise-exposed fibers with underestimated bandwidth. At least up to CFs of 2.5 kHz, both 3 and 10 dB cut off frequencies increased with increasing CF in both populations (A and C). TMTF cut off frequencies increased with increasing bandwidth up to ~ 1 –2 kHz and appeared to asymptote for larger bandwidths (B and D). In that regard, bandwidths of AN fibers influenced TMTF roll off in both populations. Some noise-exposed fibers (Fig. 4A, shaded rectangle) with CFs between 1 and 2 kHz showed slightly higher 3-dB cut off frequencies; however, a similar trend was not observed for 10-dB cut off frequencies (Fig.

4C). Many noise-exposed fibers with CFs above 2 kHz and broadened tuning had 3-dB cut off frequencies comparable to normal-hearing fibers. Secondly, noise-exposed fibers with CFs below 2 kHz, which showed slightly higher cut offs, did not show a proportional increase in 3-dB cut off frequencies as would be expected from the substantial increase in their 10-dB tuning curve bandwidth (compare 4A with 4B). This trend can also be seen in the 10-dB cut-off frequencies shown in Figures 4C and D. All the noise-exposed fibers (circles) with very broad bandwidth showed TMTF cut off frequencies comparable to normal-hearing fibers (crosses). In general, these data suggest that peripheral filtering has a limited influence on TMTF roll-off.

Figures 4E and 4F show fm values at which TMTF gain dropped to -10 dB (horizontal gray line in Figure 3A). Trend lines (see figure caption, Fig. 4E) indicated that fm values for -10 dB gain were higher in noise-exposed fibers. However, these results were influenced by overall higher gain that was observed in noise-exposed fibers (Fig. 3A). Modulation frequency values corresponding to -10 dB gain increased with increasing bandwidth (Fig. 4F) for both fiber populations. However, noise-exposed fibers (circles in Fig. 4F) with wider bandwidths than normal-hearing fibers (crosses, Fig. 4F) did not consistently show higher fm values corresponding to -10 dB TMTF gain (Fig. 4F). Thus, even for the -10 -dB gain metric, degraded peripheral filtering in noise-exposed fibers did not influence the range of modulation frequencies encoded by AN fibers.

To explore whether these results were metric specific, we also quantified envelope coding based on shuffled correlograms. Shuffled-correlogram based metrics have previously been used to quantify within-fiber envelope as well fine-structure coding (Joris, 2003; Kale and Heinz, 2010). From shuffled correlograms analysis metrics, we computed sumcor functions, where the sumcor peak height indicates the strength of phase locking to envelope. In the present study, we computed sumcor peak heights for each fm value along the TMTF curve. Sumcor peak height as a function of modulation frequency showed trends similar to the TMTF curve in that they dropped to the noise floor at high modulation frequencies. We computed the modulation frequencies at which sumcor peak height dropped to the noise floor as well as where it dropped to half the maximum value (i.e., two definitions of the TMTF passband width). Trends in TMTF passband widths computed in this manner versus CF and AN-fiber bandwidths were compared between the normal-hearing and the hearing-impaired population of fibers. These modulation cutoff frequencies computed from sumcor peak heights were similar between normal-hearing fibers and impaired fibers with similar CF and broadened tuning, which confirms that the finding of similar TMTF passband widths before and after SNHL is not metric specific.

Since a clear association between broadened tuning due to hearing loss and 3- and 10-dB TMTF cut off frequencies could not be observed, we examined TMTFs of individual noise-exposed fibers. We observed that noise-exposed fibers with CFs below 2 kHz generally showed synchrony to individual SAM components (i.e., the carrier and sidebands) better than fibers with CFs above 2 kHz. For these noise-exposed fibers, TMTF roll off corresponded well with synchrony roll off in individual sidebands. A few individual examples of noise-exposed fibers are discussed below to illustrate the variety of effects involved that create a weak association between frequency selectivity and TMTF roll-off.

3.4. For a few fibers with CFs below 2 kHz, peripheral filtering played a role in initiating roll off in gain

Figure 5 shows the TMTF gain function and synchronization index for individual SAM tone components for a normal-hearing fiber (left column) and a noise-exposed fiber (right column). Tuning curves for the two fibers are shown in the top row. The noise exposed fiber showed broader tuning (Fig. 5B) relative to the normal-hearing fiber shown with similar CF

(Fig. 5A). The 3-dB cut off frequency for the noise-exposed fiber (Fig. 5C) was slightly higher than the normal-hearing fiber (Fig. 5D). Synchrony to modulation frequency components (squares in panels E and F) showed similar trends in terms of roll off at higher fm values. Synchrony to the carrier was relatively flat over the range of modulation frequencies. This result is consistent with previous normal-hearing data (Joris and Yin, 1992). For the normal-hearing fiber, synchrony to upper sideband (upward pointing triangles) and lower sideband (downward pointing triangles) rolled-off nearly at the same modulation frequency which was roughly equal to the 3-dB cut off frequency (Fig. 5E). For the noise-exposed fiber, synchrony to upper sideband showed a more gradual decrease with increasing fm , which was initiated well before the TMTF roll off (upward pointing triangles in Fig. 5F). However, synchrony to the lower sideband showed a more gradual increase with increasing fm . The roll-off in TMTF gain in the noise-exposed fiber appeared to be initiated by the roll off in synchrony of the lower sideband (downward pointing triangles in Fig. 5F). The gradual drop in synchrony to the upper sideband appeared to have no effect on TMTF roll off in the noise-exposed fiber. Only a few such examples (all fibers with CFs ≤ 2 kHz) were observed in the noise-exposed population of fibers. However, even in these cases, the increase in TMTF cut off frequency was not proportional to the increase in tuning curve bandwidth for these noise-exposed fibers (Fig. 4).

3.5. Noise-exposed fibers with sharp tuning showed TMTF cut offs higher than normal-hearing fibers

Figure 6 shows the TMTF gain function and synchronization index for individual components of a SAM tone for a normal-hearing fiber (left column) and a noise-exposed fiber (right column). The noise-exposed fiber (Fig. 6B) showed sharp tuning but a very high threshold (62 dB SPL). Despite sharp tuning, 3- and 10-dB cut off frequencies were both higher for the noise-exposed fiber (Fig. 6D) than for the normal-hearing fiber (Fig. 6C). Synchrony to the individual sidebands (triangles) and the carrier component (circles, Fig. 6E and 6F) was much lower than synchrony to modulation frequency (squares). These data are consistent with previous data suggesting that, in chinchillas, the upper limit of phase locking is lower than in other species, such as cats that show good phase locking for CFs up to ~ 2 to 3 kHz (Johnson, 1980; Louage et al., 2004; Temchin and Ruggero, 2010). Similar trends have been observed in another but related study (see Fig. 10 in Kale and Heinz, 2010). In general, ~ 8 unique fiber pairs could be identified in which normal-hearing and noise-exposed fibers had similar CFs but the noise-exposed fiber showed a higher threshold and near-normal tuning. All of these noise-exposed fibers showed broader TMTFs than normal-hearing fibers, despite near-normal tuning. In contrast, other group of fibers showed broader than normal-tuning and yet TMTF cut off frequencies in these fibers were lower than normal. One such fiber pair is shown below.

3.6. Noise-exposed fibers with broadened tuning showed TMTF cut offs lower than normal-hearing fibers

Figure 7 shows an example of a noise-exposed fiber that showed TMTF cut off frequencies lower than a normal-hearing fiber with similar CF despite broadened tuning. The purpose of this example is to explain the overlap in TMTF cut off frequency values (see Fig 4A) between normal-hearing and noise-exposed fibers (with broad tuning). All the symbols and legends are the same as in Figure 6. Both fibers had comparable CFs but the noise-exposed fiber showed higher threshold and considerably broadened tuning (Fig. 7A and 7B). Despite broadened tuning, the TMTF of the noise-exposed fiber rolled-off much earlier than the normal-hearing fiber. Although the particular noise-exposed fiber shown here had a TMTF cut-off frequency lower than the normal-hearing fiber, the two selected fibers were towards the edges of the range of TMTF cut-offs observed in Figure 4A (CFs ≥ 2 kHz). In general, TMTF cut-offs for noise-exposed fibers were within the normal range as described

previously. In both the fibers shown in Figure 7, synchrony values for the individual sidebands and the carrier component were much lower (but still significant) than the modulation-frequency component. Due to very low synchrony values of the individual components, TMTF roll-off could not be associated with roll-off in synchrony of any of the individual SAM components. These results indicate the possibility of a greater role of temporal resolution than peripheral filtering in limiting TMTF roll-off in these fibers with CFs ≥ 2 kHz. Relatively poor phase locking to individual SAM components other than the *fm* component indicates that these fibers were more responsive to the envelope of SAM tones. These results are discussed in detail later in the discussion section.

3.7. Strength of phase locking to the modulation frequency was higher than to the carrier in noise-exposed fibers with CFs above 2 kHz

Figure 8 shows ratios of the synchrony to modulation frequency (*fm*) relative to the synchrony to individual SAM tone components (carrier and sidebands). Ratios are computed near best modulation frequency. Ratios of synchrony to *fm* relative to synchrony to carrier (Fig. 8A) show that the strength of phase locking to *fm* was at least 10 times higher in normal-hearing and noise-exposed fibers with CFs above 2 kHz. Similar results can be seen for upper (Fig. 8B) and lower (Fig. 8C) sidebands. Phase locking to the carrier component (*fc*) rolled off to the noise floor for CFs just above 2 kHz (Fig. 8D). Similar trends were observed for both the sidebands (not shown). Both the very low synchrony to the carrier and sidebands for CFs above 2 kHz and the lack of changes in TMTF cut-off frequencies despite broadened tuning suggest that beyond ~ 2 kHz temporal coding plays a greater role in initiating TMTF roll-off as compared to peripheral filtering. The reasonable synchrony observed for the *fm* component in both populations suggests that the sidebands were interacting within the pass-band of the AN fibers with CFs above 2 kHz; however, roll-off in the TMTF was not affected by broadened tuning.

3.8. Relative phases of individual SAM tone components did not play any role in TMTF roll-off

For a narrowband stimulus like a SAM tone, three components interact within the auditory filter if the modulation frequency is low relative to the carrier frequency, i.e., the two sidebands are closely spaced relative to the carrier. When these components are unresolved within a single auditory filter, the relative phases of the individual components can influence the effective envelope frequency at the output of that filter. If the carrier component is shifted in phase by 90° relative to the two sidebands, the resultant waveform would have two envelope peaks per '*fm*' period and with relatively lower modulation depth. Thus, any such phase alteration would result in less modulation in the AN-fiber responses and the TMTF would roll-off. As long as the phases of the individual sidebands relative to the phase of the carrier are symmetric around the carrier phase, i.e. the difference $[\Phi_{\text{Carrier}} - (\Phi_{\text{USB}} + \Phi_{\text{LSB}})/2]$ is constant, the phase relationship among individual SAM tone components would not influence the TMTF roll-off (Joris and Yin, 1992).

Figure 9 shows cumulative phases of individual SAM tone components for a normal-hearing fiber (left column) and a noise-exposed fiber (right column). These two fibers are good representatives of their respective populations (normal-hearing and noise-exposed). For better visualization of the trends, cumulative phase of the carrier component (circles) has been shifted by an integer number of cycles (constant shift at all *fm*) so that the phase function aligns at zero. The cumulative phase of the upper (upward pointing triangles) and lower (downward pointing triangles) side bands has also been displaced by a constant amount ($\pm n$ cycles) such that sideband phase functions are within ± 1 cycle around the phase of the carrier at the lowest *fm*. Similarly, the phase of the *fm* component (squares) has been displaced by a constant amount. The phase difference function (asterisks), i.e., the difference

in the carrier phase and the mean phase of the sidebands, has been shifted by an integer number of cycles such that it aligns at 0.5 cycles. Constant phase shifts by an integer number of cycles simply shifted the phase functions up or down without altering the shape (trends) of the individual phase functions. Phases of the individual sidebands (triangles) were symmetric around the phase of the carrier. The phase-difference function rarely exceeded the quarter-cycle shift lines (horizontal dashed lines in Fig. 9C and 9D) for modulation frequencies less than the TMTF roll-off frequency. Thus, the relative phases of individual components were not the main factor underlying TMTF roll-off. In some fibers, the phase-difference function crossed the quarter-cycle lines indicating alterations in relative phases of individual SAM components. However, in all fibers such phase alterations were always observed for fm values higher than the TMTF roll-off frequency.

4. Discussion

4.1. TMTF roll-off is influenced by physiological factors other than peripheral filtering

Overall, the range of modulation frequencies that can be encoded by noise-exposed fibers was not affected by degraded peripheral filtering. 3- and 10-dB TMTF cut-off frequencies increased with increasing CF and bandwidth in both the normal-hearing and noise-exposed fiber populations (Fig. 4A–D). The CF dependence of TMTF cut-offs indicates that the TMTF roll-off in individual fibers was influenced by peripheral filtering up to CFs of 2 kHz in chinchillas. In general, these results are consistent with previous studies (e.g., Javel, 1980; Palmer, 1982). In the present chinchilla data with CFs below 2 kHz, noise-exposed fibers with broadened tuning showed slightly higher TMTF cut-off frequencies than normal-hearing fibers with similar CFs (shaded area in Fig. 4A). However, the increase in TMTF cut-off in these fibers was not proportional to the increase in bandwidths (Fig. 4B). This poor association between increased bandwidths due to SNHL and TMTF roll-off has been reported previously for modulation detection in European Starlings with SNHL (Marean et al., 1998). Fibers above 2 kHz did not show any increase in TMTF cut-off frequency despite broadened tuning (Fig 4A and B). These results suggest that cochlear filtering of sidebands has a limited role in initiating the TMTF roll-off.

Based on the saturating trends previously observed in cat TMTF cut-off versus CF functions for CFs ≥ 10 kHz, it was argued that for high CFs, temporal coding limitations of individual fibers might influence TMTF roll-off in addition to cochlear filtering of sidebands (Joris and Yin, 1992). Although the data for fibers with CFs above 10 kHz were not collected in the present study, TMTF cut-off values at CFs above 2 kHz (Fig. 4A), or bandwidths above 2 kHz (Fig. 4B), show an asymptotic nature and more scatter. Based on this data set, it is possible that the CF region where temporal limitations dominate cochlear filtering in initiating TMTF roll-off is much lower (even in normal-hearing fibers) for chinchillas than for cats.

We observed that in normal-hearing fibers with CFs above 2 kHz, synchrony to individual sidebands and the carrier was much lower than synchrony to the modulation frequency component. These data indicate that these fibers transitioned from phase locking to the carrier (or sidebands) to phase locking to the envelope (fm) within this CF range. Similar trends have been reported in our recent study, which also showed that such a transition region was lower for noise-exposed fibers than for normal-hearing fibers (see Fig. 10 in Kale and Heinz, 2010). If noise-exposed fibers are *biased* towards encoding envelope, then it is possible that the temporal envelope coding ability of noise-exposed fibers would influence the TMTF roll off more than cochlear filtering. Considering that temporal envelope coding is not degraded by SNHL, it is possible to have TMTF cut off frequencies in noise-exposed fibers within the normal-hearing range even if sidebands interact within an

impaired auditory filter over a broader f_m range. Indirect evidence in support of this hypothesis is discussed below.

In their data, Joris and Yin (1992) found that TMTF cut-off frequencies for fibers which showed the broadest TMTFs were still lower than the upper limit of phase locking to the carrier frequency. In our data, we observed similar trends. For the CFs above 2 kHz, noise-exposed fibers with broadened tuning showed TMTF cut-off frequencies between 200 and 400 Hz (Fig. 4A and B), which is well within the range where good phase locking to the carrier is observed in normal-hearing as well as in noise-exposed fibers (see Fig. 10A in Kale and Heinz, 2010). Based on these trends, Joris and Yin (1992) argued that even at the highest CFs, the main factor influencing the TMTF roll-off might not be the same as that which influences the roll-off in phase-locking to pure tones. Considering their results with our results from the noise-exposed fibers with the broadest bandwidth (filled symbols in Fig. 4A), it is reasonable to say that for these fibers other factors might play a role in TMTF roll-off in addition to temporal coding limitations, but that peripheral filtering is the least likely candidate. It cannot be concluded what those other factors might be based on the present data, but one such factor may be developmental in nature, e.g., synaptic plasticity. During development, each cochlear nerve fiber might be programmed to encode a particular range of f_m (dependent on its BW for low CFs, and independent of its bandwidth for high CFs). Such an f_m -encoding range might be preserved following noise-induced hearing loss. If this synaptic-based f_m -limited range were preserved following SNHL, then the higher modulation frequencies available on the basilar membrane following degraded frequency selectivity would not be encoded by AN fibers in ears with SNHL. To thoroughly quantify the temporal coding ability of individual fibers and to isolate the effects of peripheral filtering from temporal limitations, future studies should measure TMTFs using broadband noise as a carrier in addition to SAM tones.

4.2. Modulation gain was enhanced following SNHL

Another important result from the present study was that the modulation gain was enhanced following SNHL. This enhancement was present not only for low modulation rates but also for higher modulation rates spanning the complete passband of the TMTF functions. These results suggest that post-cochlear ‘internal’ representations of envelope are enhanced following SNHL for a broad range of envelope frequencies. These results are consistent with perceptual studies, which suggested that lower modulation detection thresholds observed in hearing-impaired listeners as compared to normal-hearing listeners were associated with enhanced representation of ‘internal’ envelopes (e.g., Moore and Glasberg, 2001). It was suggested that the internal representation of envelope is enhanced due to the loss of basilar-membrane compression (Moore et al., 1996). However, our recent study has shown that steeper rate-level functions associated with damage to inner hair cell stereocilia were a significant factor underlying enhanced envelope coding (Kale and Heinz, 2010). Furthermore, changes in temporal dynamics of AN fibers following noise-induced hearing loss, such as enhanced onset responses and slower recovery from stimulation, may also be involved in enhanced envelope coding (Scheidt et al., 2010). Overall, the results presented here suggest that better modulation detection thresholds observed in hearing-impaired listeners compared to normal-hearing listeners, at equal sensation levels (Bacon and Gleitman, 1992; Moore and Glasberg, 2001), may be attributed to enhanced modulation gain over a broad range of envelope frequencies.

4.3. Relationship with perceptual studies

Several perceptual studies have used the task of modulation detection as a measure of temporal resolution of the auditory system. These perceptual studies measuring TMTFs using noise-band carriers have reported worse modulation detection thresholds especially at

modulation frequencies higher than 100 Hz (Bacon and Viemeister, 1985, Formby, 1987). These results have been interpreted as a consequence of loss of audibility at high frequencies rather than as a limitation in temporal resolvability of the system following hearing loss. Listeners with relatively flat hearing loss have been reported to show modulation detection thresholds comparable to normal hearing listeners at equal SPLs (Bacon and Gleitman, 1992). Although these studies used a broadband noise carrier in contrast to the sinusoidal carriers used in the present study, and hence are not directly comparable, a rather tenuous link across these studies is that the general TMTF shape was not affected by SNHL and that peripheral filtering seemed to play a limited role in initiating TMTF roll-off. A more recent perceptual study that used sinusoidal carriers (e.g., Moore and Glasberg, 2001) has shown that at equal SPLs temporal resolution is not affected by SNHL, but at equal SLs modulation detection thresholds tend to be better than those for normal-hearing listeners. Similar results have been reported in listeners with flat hearing losses when a broadband noise carrier was presented at equal SLs to normal-hearing and hearing-impaired listeners (Bacon and Gleitman, 1992). These results are consistent with our data (Fig. 3) that suggest that enhanced modulation gain can aide listeners to detect amplitude modulation as explained previously.

One caveat in directly comparing the present (and most) neurophysiological data to perceptual data is that 100% modulation depth is often used in neural studies, whereas perceptual studies track modulation-depth thresholds that are often well less than 100%. However, it has been reported previously that overall TMTF shape is unaffected by changes in stimulus modulation depth, whereas the TMTF gain increases with decreasing modulation depth (Joris and Yin, 1992). Given that we observed no effects of SNHL on TMTF shape and enhanced modulation gain for 100% modulated stimulus, we would expect to see similar trends for the 10–30% modulated stimuli more typically used in perceptual studies. One possibility is that the increase in TMTF gain would not be proportional to the decrease in stimulus modulation. However, the data would have similar implications for perceptual studies, i.e., no effect of degraded frequency selectivity on TMTF roll-off and higher TMTF gain aiding modulation detection in impaired ears when sinusoidal carriers were used.

A recent perceptual study in aged hearing-impaired listeners suggested that for a low carrier frequency region, where both spectral and temporal cues were available, modulation detection was based primarily on temporal cues (He et al., 2008). While the hearing-impaired listeners in their study showed age-related deficits in temporal processing, TMTF cut-offs where listeners transition from using primarily temporal cues to spectral cues were similar across aged and young listeners. These results suggest that despite broadened tuning associated with aging (Ruggero and Rich, 1991; Schmiedt et al., 2002; Sewell, 1984), TMTF cut-offs were influenced by the ability of aged listeners to use temporal cues. These results are consistent with a more recent electrophysiological study in rats, which showed that TMTF cut-offs derived from non-invasively measured amplitude modulation following responses were similar across young and aged rats (see Fig. 2 in Parthasarathy et al., 2010). Thus, it is possible that broadened tuning does not influence TMTF cut-off given the recent evidence that phase locking ability of AN fibers is not affected by SNHL (Kale and Heinz, 2010).

The present study used sinusoidal carriers located at CF. As discussed previously, with a sinusoidal carrier, the spectrum of the amplitude-modulated stimuli changes with modulation frequency. In contrast, the spectrum of the amplitude-modulated stimuli is invariant with changes in modulation frequency if a broadband noise is used as the carrier. Such stimuli could provide a more thorough characterization of the ability of individual fibers to follow rapid envelope fluctuations irrespective of fiber CF. Although data with broadband-noise carriers were not collected in the present study, based on previous work we

hypothesize that similar trends would be observed with a broadband-noise carrier. It has been shown that noise-exposed impaired AN fibers show slower recovery from adaptation compared to normal-hearing fibers (Scheidt et al., 2010), and slower recovery has been shown to enhance modulation coding (Zilany et al., 2009). Thus, slower recovery could be another factor that leads to enhanced TMTF gain. Phase locking to envelope has been shown to be unaffected by SNHL (Kale and Heinz, 2010), and the present data show that the TMTF cut-off frequencies were comparable between the population of normal fibers and impaired fibers. Together these results suggest that even with a broadband-noise carrier it is likely that TMTF gain would be enhanced and TMTF cut-off frequencies would be unaffected by SNHL.

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Abbreviations

AN	auditory nerve
BMF	best modulation frequency
BML	best modulation level
BW	bandwidth
CF	characteristic frequency
NIHL	noise-induced hearing loss
SAM	sinusoidally amplitude modulated
SNHL	sensorineural hearing loss
TMTF	temporal modulation transfer function

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Highlights

TMTFs were measured from AN fibers in chinchillas using SAM tones following SNHL.

SNHL was induced by acoustic over-exposure.

The range of modulation frequencies encoded by AN fibers was not affected by SNHL.

Higher than normal modulation gain was observed along the TMTF passband after SNHL.

Factors other than peripheral filtering play some role in TMTF roll-off.

FIG. 1.

Tuning-curve characteristics as a function of characteristic frequency (CF) for the normal-hearing (crosses) and noise-induced hearing loss (circles) populations. A: Fiber thresholds at CF. Solid lines represent the distribution of best thresholds across CF for a larger normal-hearing population (Kale and Heinz, 2010). B: Tuning-curve sharpness as represented by Q_{10} (ratio of CF to bandwidth 10 dB above threshold). Solid lines represent the 5th and 95th percentiles of the larger normal-hearing population. Filled symbols indicate AN fibers for which Q_{10} was overestimated (see text).

FIG. 2.

Both normal-hearing and hearing-impaired TMTFs had low-pass shapes, with linear cumulative phase growth and relatively constant discharge rate as a function of modulation frequency. A–B: Tuning curves for a normal-hearing (A) and noise-exposed (B) fiber. Arrow indicates CF chosen based on Liberman (1984). C–D: TMTFs: modulation gain as a function of modulation frequency (fm). Dashed vertical lines: fm values at which gain rolled off by 3 dB (fm_{3dB}). Solid vertical line: gain roll off of 10 dB (fm_{10dB}). Best modulation frequency (BMF) is shown with the downward arrow. E–F: Cumulative phase for fm component (circles) and discharge rate (asterisks) plotted versus modulation frequency.

FIG. 3.

Overall modulation gain was higher in noise-exposed fibers, but 3- and 10-dB cut off values remained unchanged. A: TMTFs superimposed for 23 normal-hearing fibers (black lines) and 20 noise-exposed fibers (gray lines). Single horizontal gray line indicates the modulation frequency at which gain decreased to -10 dB in individual fibers. Modulation frequency (f_m) values corresponding to this line are shown in Figure 4E–F. B: Normalized gain (see text) as a function of modulation frequency superimposed for all fibers shown in panel A. After normalizing the gain, there were not any distinct differences in TMTF shapes between normal-hearing and noise-exposed populations of fibers. All fibers shown had CFs between 1 and 4 kHz and all noise-exposed fibers showed significantly broadened tuning

(normalized $Q_{10} < 1$). Noise-exposed fibers that showed high thresholds but narrow tuning are excluded from this population.

FIG. 4.

Broadened tuning following SNHL did not result in increased TMTF cut off frequencies. A and C: Modulation frequency (f_m) at which TMTF gain rolled off by 3 dB (A) and 10 dB (C) in individual fibers is plotted versus CF. Crosses: Normal-hearing fibers. Open circles: Noise-exposed fibers. Filled circles: Noise-exposed fibers with normalized Q_{10} less than 1 indicating significantly broadened tuning. Shaded area in panel A shows a few noise-exposed fibers with broadened tuning that showed higher 3-dB cut offs. B and D: Same as A and C, except f_m values are plotted versus 10 dB tuning curve bandwidth. E and F: f_m at which TMTF gain dropped to -10 dB plotted versus CF (E) and tuning-curve 10-dB bandwidth (F). Solid lines in panels A, C and E (thin: normal hearing; thick: noise-exposed) are triangular weighted averages across 0.7-octave wide windows (0.35-octave steps, at least 4 points in each window).

FIG. 5.

Peripheral filtering of the sidebands initiated the roll off in TMTF for fibers with CFs below 2 kHz. Normal-hearing fiber (left column) and noise-exposed fiber (right column). A–B: Tuning curves, C–D: Temporal modulation transfer functions (TMTFs). Vertical dashed and solid lines are the same as in Fig. 2. E–F: Synchrony to individual SAM tone components. Squares: modulation frequency (*fm*) component, Circles: Carrier component (*fc*), Upward pointing triangles: Upper sideband (*usb*), Downward pointing triangles: Lower sideband (*lsb*). It can be seen that roll off in TMTF occurs approximately when one of the sidebands rolls off in synchrony. Filled symbols indicate synchrony values that failed to reach statistical significance as per Rayleigh statistics (Mardia and Jupp, 2000).

FIG. 6.

The TMTF of a noise-exposed fiber showed a higher 3-dB cut off than a normal-hearing fiber with similar CF, despite relatively sharper tuning. Normal-hearing fiber (left column) and noise-exposed fiber (right column). A–B: Tuning curves, C–D: TMTFs, E–F: Synchrony to individual SAM components. Symbols are same as in Fig. 5. Synchrony to the individual sidebands and the carrier was very low compared to synchrony to the modulation frequency.

FIG. 7.

The TMTF of a noise-exposed fiber showed a lower 3-dB cut-off than a normal-hearing fiber with similar CF, despite broadened tuning. All the symbols and legends are the same as in Fig 6. Normal-hearing Fiber: CF=2.35 kHz, Threshold=21 dB SPL, Normalized Q_{10} =1.15. Noise-exposed fiber: CF=2.31 kHz, Threshold=80 dB SPL, Normalized Q_{10} =0.51.

FIG. 8.

Above CFs of 2 kHz, synchrony to individual sidebands and the carrier was much less than synchrony to the modulation frequency (fm). This figure shows the ratio of synchrony to modulation frequency over synchrony to individual SAM components computed at best modulation frequency (BMF, see Fig. 2). A ratio of 1 indicates that synchrony to individual SAM components was the same as synchrony to fm . A ratio less than 1 indicates that synchrony to individual SAM components was higher than synchrony to fm . At CFs above 2 kHz, synchrony to fm was nearly 10 times higher than synchrony to the individual SAM components. A: synchrony to fm /synchrony to carrier fc . B: synchrony to fm /synchrony to upper side band, USB. C: synchrony to fm /synchrony to lower side band, LSB. D: Synchrony to the carrier as a function characteristic frequency (similar trends were seen for USB and LSB, data not shown).

FIG. 9.

Relative phases of individual SAM tone components did not influence the TMTF roll-off. A: Normal-hearing fiber, CF=1.31 kHz, Normalized Q_{10} =2.41 and Threshold=15 dB SPL. B: Noise-exposed fiber, CF=1.30 kHz, Normalized Q_{10} =0.80 and Threshold=65 dB SPL. Symbols for individual SAM components are the same as in Fig. 5. Asterisks: difference between phase of the carrier and mean phase of the sidebands. Horizontal dashed lines are half way between carrier phase and the phase-difference curve (asterisks) and indicate a phase shift of 0.25 cycles (90°) relative to the phase-difference function. Phase functions have been displaced by ± 1 cycle for sidebands and +1.5 cycles for modulation frequency for

better visualization. Similarly, the phase-difference function (asterisks) has been displaced by 0.5 cycles.