4pPP2. Modeling disrupted tonotopicity of temporal coding following sensorineural hearing loss

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Perceptual studies suggest that sensorineural hearing loss (SNHL) affects neural coding of temporal fine structure (TFS) more than envelope (ENV). Although the “quantity” of TFS coding is degraded only in background noise, Wiener-kernel analyses suggest SNHL disrupts tonotopicity (i.e., the “quality”) of TFS coding for complex sounds more than ENV coding. Specifically, auditory-nerve (AN) fibers in noise-exposed chinchillas can have their dominant TFS component located within their tuning-curve tail (i.e., the wrong place) while their ENV response remains centered at CF. Here, the ability of a AN model (Zilany and Bruce, 2007) to replicate this dissociation between TFS and ENV tonotopicity was evaluated. By varying the degree of outer- and inner-hair-cell damage, hypothesized factors such as hypersensitive tails and tip-to-tail ratio were evaluated. The model predicted the main trends in our physiological data: 1) no loss of tonotopicity for lower CFs without a clear tip/tail distinction, 2) more easily disrupted TFS tonotopicity than ENV (without requiring hypersensitive tails), and 3) disruption of both TFS and ENV tonotopicity for severely degraded tips. This computational approach allows exploration of the interaction between tip-tail ratio and phase-locking roll-off, and whether amplification strategies can restore cochlear tonotopicity. Supported by NIH grants R01-DC009838 and F32-DC012236.

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INTRODUCTION

Recent perceptual studies have suggested that people with sensorineural hearing loss (SNHL) have a reduced ability to use the rapidly varying temporal fine structure of sound for pitch and speech perception (e.g., Buss et al., 2004; Lorenzi et al., 2006; Hopkins and Moore, 2007; Strelcyk and Dau, 2009); in contrast, their ability to use the slower temporal envelope cues appears to be much less vulnerable to SNHL (e.g., Lorenzi et al., 2006). These results have fueled an active debate about the role of temporal coding in normal and impaired hearing, and have important implications for improving the ability of hearing aids and cochlear implants to restore speech perception in noise. These implications, however, depend critically on the physiological bases of these effects. Although the most straightforward hypothesis is that impaired auditory-nerve (AN) fibers simply cannot keep up with the rapid fluctuations in the temporal fine structure, early studies on the effects of SNHL on phase locking in AN fibers were contradictory (e.g., Harrison and Evans, 1979; Woolf et al., 1981). Recent recordings from AN fibers in chinchillas with noise-induced hearing loss demonstrate that the fundamental ability of fibers to phase lock to temporal fine structure in quiet conditions is not degraded by SNHL, but that degraded phase locking emerges in background noise (Kale and Heinz, 2010; Henry and Heinz, 2012).

In addition to this deficit in the “quantity” of peripheral temporal fine structure coding of tones in noise, revcor and Wiener-kernel analyses suggests a deficit in the “quality” of fine-structure coding in AN fibers for complex sounds (Kale, 2011; Henry et al., 2012). As has been reported previously for vowel-like (Miller et al., 1997) and harmonic-tone-complex stimuli (Kale et al., in press), these general system analyses demonstrate that SNHL disrupts the tonotopy of responses to complex sounds. In particular, the Wiener-kernel analyses (which extend the revcor analyses to include envelope responses) demonstrate a surprising effect where AN fibers in noise-exposed chinchillas can have their dominant fine-structure response component located within their tuning-curve tail (i.e., at the wrong place), while their envelope response remains centered at the cochlear center frequency of the fiber. These effects may be related to hypersensitive tuning-curve tails that have been reported previously based on responses to tones (Liberman and Dodds, 1984), but are likely to depend also on other factors such as the differential roll-off in phase locking to fine structure and envelope responses (Johnson, 1980; Joris and Yin, 1992). The present study used a computational model of auditory-nerve responses to evaluate whether these factors can account for the dissociation between fine-structure and envelope tonotopy.

METHODS

Computational Auditory-Nerve Model

The present analyses used spike trains from a computational AN model that has been tested extensively against normal-hearing and hearing-impaired neural data (Zilany and Bruce, 2007). Model-fiber tuning curves have been well fit to the CF dependent variation in bandwidth seen in normal-hearing cats (Miller et al., 1997). Most physiological properties related to nonlinear cochlear tuning are captured in this model, including compression, suppression, and broadened tuning and shifts in best-frequency with increases in sound level. A key feature of this AN model for SNHL effects is that outer-hair-cell (OHC) and inner-hair-cell (IHC) functionality can be specified by two separate model parameters (Heinz, 2010). OHC damage is modeled by reducing cochlear-amplifier gain, thus reducing cochlear compression, frequency selectivity, and suppression (Zilany and Bruce, 2007). IHC damage is modeled by reduction in the IHC transduction slope, which increases fiber threshold without significantly changing cochlear nonlinearity, i.e., frequency selectivity is not directly degraded (Bruce et al., 2003). The AN-model input is the waveform of the sound stimulus, while the output provides a set of spike times for one high-spontaneous-rate AN fiber with a CF that can be specified.

Wiener-Kernel Analyses

Wiener kernels were computed for each model fiber by reverse correlation of the stimulus waveform and spike train response (Recio-Spinoso et al., 2005). The first-order kernel describes the tuning of the fiber based on its linear response to the temporal fine-structure. The second-order kernel is a 2-dimensional surface that describes tuning based on its nonlinear response to fine-structure and envelope. We removed the contribution of nonlinear fine-structure processing by 2-dimensional frequency-domain filtering (removal of the 1st and 3rd frequency quadrants). The filtered second-order kernel was decomposed into eigenvectors to facilitate comparison to the first-order kernel.
In order to compare the effects of SNHL on fine-structure and envelope tonotopicity, we quantified the frequency tuning of fine-structure coding from the first-order kernel and the frequency tuning of envelope coding from the second-order kernel. All responses were to broadband noise presented at 10-20 dB above fiber threshold.

RESULTS AND DISCUSSION

Wiener-kernel analyses were applied to model spike trains in the same way that they were applied to our physiological data (Henry et al., 2012). Figure 1 demonstrates a main finding that was observed in both the physiological and model results, which was that SNHL can produce a differential effect on the tonotopy of fine structure and envelope responses. The normal-hearing fiber with a well-defined tuning curve tip that is much more sensitive than its tail shows primarily envelope tuning because its center frequency (CF) is above the frequency at which AN phase locking to fine structure begins to roll off. In contrast, the same-CF model fiber with 40-db of outer-hair-cell loss shows a W-shaped tuning curve with roughly equally sensitive tip and tail. Note that in physiological responses, the fiber cochlear CF is best estimated from the upper high-frequency edge of the tuning curve (Liberman, 1984); in the model responses shown this is not an issue because the same CF can be specified for the normal-hearing and hearing-impaired fibers. The Wiener-kernel analyses of the model spike trains from this impaired fiber demonstrate that the broadband-noise responses also have a dominant envelope component near the fiber CF, but the dominant fine-structure component occurs well below the cochlear CF (i.e., in the wrong place, within the tuning-curve tail).

![Graphs showing normal hearing and 40-dB outer hair cell loss](image)

**FIGURE 1.** Computational model predictions demonstrate the dissociation between fine-structure and envelope tonotopy following SNHL. Threshold tuning curves are shown in the top row for a normal-hearing model version (left column, panel A) and a model version for which there was 40 dB of outer-hair-cell loss (right column, panel B). Frequency tuning derived from Wiener-kernel analyses is shown in the bottom row for temporal fine structure (TFS, blue) and envelope (ENV, red) responses.

Overall, the computational model predicted the main trends in our physiological data: 1) no loss of tonotopy for lower CFs without a clear tip/tail distinction, 2) more easily disrupted TFS tonotopy than ENV (Fig. 1), and 3) disruption of both TFS and ENV tonotopy for severely degraded tips. This loss of tonotopy with SNHL is likely to have many important implications for both speech perception (e.g., Young and Sachs, 1979; Shamma, 1985) and for pitch perception (e.g., Oxenham et al., 2004).

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