

PHYSIOLOGICAL CORRELATES OF PERCEPTUAL DEFICITS FOLLOWING SENSORINEURAL HEARING LOSS

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Introduction

Several translational issues related to sensorineural hearing loss (SNHL) have recently re-invigorated an active debate in the field of psychological and physiological acoustics regarding the perceptual role of the temporal structure of sound. Much of this recent interest over the last decade has centered on the mathematical fact that any sound can be separated into slowly-varying temporal *envelope* (ENV) and rapidly varying *temporal fine-structure* (TFS) components (Fig. 1). This dichotomy has been motivated in part from cochlear implants, which are neural prostheses that can restore the sense of hearing for patients with profound deafness through electrical stimulation of remaining cochlear neurons. Although often quite successful in understanding speech in quiet conditions, cochlear-implant patients often struggle to understand speech in noisy conditions or to appreciate music. These limitations have motivated numerous perceptual studies to understand the relative importance of ENV and TFS cues because cochlear implants currently only provide slowly varying ENV cues and are unable to provide rapidly varying TFS cues.

Envelope cues have been shown to be sufficient for understanding speech, even in a minimal number of frequency bands (Shannon *et al.*, 1995; Smith *et al.*, 2002). Fine structure has been argued to be useful for music perception, sound localization, lexical-tone perception, and source segregation (Smith *et al.*, 2002; Xu and Pfingst, 2003; Qin and Oxenham, 2005). Such findings have been given as motivation for efforts to develop cochlear-implant strategies to provide fine-structure in addition to envelope cues (e.g., Rubinstein *et al.*, 1999; Nie *et al.*, 2005). It is also believed that the use of temporal fine structure relates to the remarkable ability of normal-hearing listeners to “listen in the dips” of background sounds, e.g., in the presence of concurrent talkers (Moore and Glasberg, 1987; Schooneveldt and Moore, 1987).

In contrast, listeners with SNHL often face great difficulty in understanding speech in the presence of temporally varying backgrounds (Peters *et al.*, 1998), and this difficulty is only partially resolved with advanced amplification algorithms (Moore *et al.*, 1999). A number of recent perceptual studies suggest that listeners with SNHL have a reduced ability to use TFS cues, and that this deficit may be correlated with their inability to listen in the dips (Lorenzi

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et al., 2006; Moore *et al.*, 2006; Hopkins and Moore, 2007). 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. However, the translational implications of perceptual deficits in temporal processing with SNHL depend critically on their physiological basis, which unfortunately remains unknown. The most straightforward hypothesis is that auditory-nerve fibers, which provide all of the information at the output of

the cochlea (Fig. 2), are no longer able to encode the rapidly varying TFS information following SNHL. Prior to our recent studies, the physiological evidence regarding auditory nerve (AN) fiber phase locking with SNHL was conflicting (Harrison and Evans, 1979; Woolf *et al.*, 1981; Miller *et al.*, 1997). Thus, a number of important questions exist: (1) are TFS coding deficits peripheral or central, and (2) is it the *quantity* and/or *quality* of TFS coding that is diminished following SNHL?

This article describes recent work in our lab exploring the physiological bases for these perceptual results through a combination of neurophysiological, perceptual, and computational modeling approaches. Specifically, we have been exploring three hypotheses for the physiological bases of perceptual TFS deficits: (1) the temporal coding within individual AN fibers is degraded in quantity and/or quality following SNHL, (2) even if there is not diminished phase locking in individual fibers, the relative temporal coding across AN fibers may be degraded in ways that diminish spatio-temporal cues that have been proposed to be perceptually relevant, and (3) the perceptual TFS deficits may not actually reflect diminished TFS coding in the periphery due to “artifacts” that complicate the separation of TFS and ENV cues within the cochlea. Overall, our results suggest that the fundamental ability of fibers to phase lock to temporal fine structure is not degraded by SNHL; however, a number of other effects of SNHL have been observed that may contribute to perceptual deficits in temporal processing of complex stimuli. These results have important translational implications for auditory prostheses because they suggest that perceptual “fine-structure deficits” do not simply reflect degraded phase locking, but likely involve more complicated coding mechanisms.

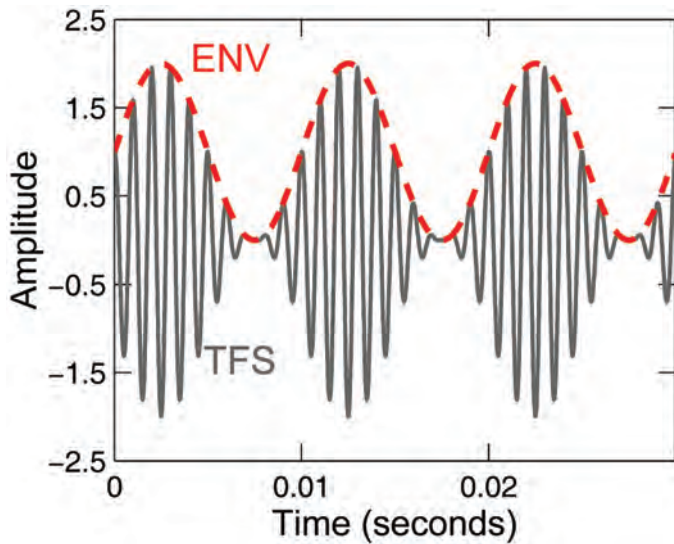


Fig. 1. Any sound can be mathematically separated into a slowly varying temporal envelope (ENV) and a rapidly varying temporal fine structure (TFS) component. Each of these temporal components of sound has been suggested to have important perceptual roles. Recent evidence suggests that many listeners with sensorineural hearing loss have a specific deficit in their ability to use TFS cues.

Temporal coding in individual AN fibers

To characterize the effects of SNHL on temporal coding in the auditory periphery, our experiments involve recording spike-train responses from chinchillas with normal hearing and from those with a noise-induced hearing loss (e.g., Kale and Heinz, 2010). Calibrated stimuli are presented via a monaural closed-field acoustic system. Glass micropipettes are used to record extracellularly from individual AN fibers as they exit the internal auditory canal, and action potential are timed with 10- μ s accuracy. The noise-induced hearing loss results in elevated thresholds of AN fibers by \sim 40 dB, along with broadened tuning that provides a good model of moderate SNHL. The excellent sensitivity and sharp tuning that benefit normal-hearing listeners are thought to relate to cochlear amplification provided to low-level sounds by outer-hair-cell (OHC) electromotility (Robles and Ruggero, 2001; Liberman *et al.*, 2002). Inner hair cells (IHCs) are the sensory transducers that convert basilar-membrane motion into neural responses. Numerous physiological studies of SNHL support a framework in which damage to both OHCs and IHCs is important for the neural coding of sound (Liberman and Dodds, 1984; Heinz and Young, 2004). Furthermore, recent studies suggest that significant synaptic degeneration can occur following noise exposure, even in cases of “temporary” hearing loss (Kujawa and Liberman, 2009).

We have characterized temporal

coding in AN fiber responses to a variety of stimuli, ranging from simple pure tones, to more complex but narrowband stimuli such as sinusoidally amplitude modulated (SAM) tones and single-formant stimuli, to complex broadband sounds such as noise and speech. The strength of temporal coding to periodic signals is most often quantified using the vector-strength metric, which ranges from 0 to 1 to indicate the degree to which spikes phase lock to a particular phase of the periodic cycle. For non-periodic stimuli, recently developed techniques that use shuffled correlograms (similar to auto- and cross-correlation functions in signal processing) provide metrics that can be used to quantify temporal coding strength to the TFS and ENV components of the sound (Joris, 2003; Louage *et al.*, 2004).

For both the simple and complex stimuli we have considered in quiet conditions, our results have not shown any decrease in the strength of TFS coding in AN fibers. We interpret these results as suggesting that the fundamental ability of individual AN fibers to encode the rapidly varying TFS components of sound is not degraded with noise-induced hearing loss. Thus, the most straightforward hypothesis based on the perceptual studies does not appear to be correct. This result could be interpreted as suggesting that a peripheral TFS coding deficit does not exist, and is perhaps created at more central levels of the auditory system. However, if we consider the fact that listeners with SNHL often do not actually have so much trouble in quiet situations, but rather struggle primarily in noisy conditions, then it is always possible that our studies of temporal coding in quiet situations have been missing something. In fact, very recent studies in our lab suggest that temporal coding of even pure tones in background noise is degraded following SNHL.

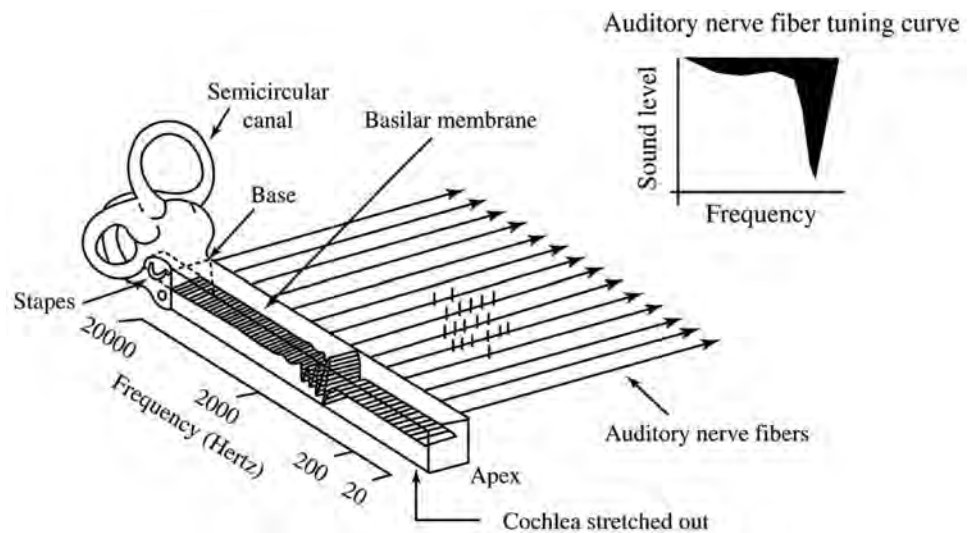


Fig. 2. The temporal structure of sound is transmitted to the central nervous system through 30,000 auditory nerve (AN) fibers, each of which is tuned to a specific characteristic frequency (CF) determined by its location along the basilar membrane. Action potentials (or spikes) occur at times that are synchronized (or “phase locked”) to the temporal fine structure and/or the temporal envelope of band-pass portions of the sound that enters the ear. Our experiments and computational modeling have been addressing three hypothesized physiological correlates for perceptual temporal fine-structure (TFS) deficits: (1) degraded TFS coding within individual AN fibers, (2) degraded spatio-temporal (across-fiber) cues in terms of reduced traveling-wave delays, and (3) whether cochlear transformations between acoustic TFS and neural envelope (ENV) complicate interpretations that perceptual TFS deficits are truly based on degraded physiological TFS coding. (Figure modified by Eric Young from Sachs *et al.* (2002), with permission from Springer and the Biomedical Engineering Society.)

Although background noise somewhat degrades phase locking in AN fibers in normal-hearing ears, the degradation is much more significant in AN fibers with noise-induced hearing loss. It is likely that this results from broadened tuning in impaired ears, which allows more noise through the auditory filter. Thus, it appears that a quantitative TFS coding deficit in the auditory periphery emerges in the presence of background noise, which may help to explain why the difficulties listeners with SNHL face are most prominent in noisy listening situations.

Beyond this quantitative TFS-coding deficit in noise, there are also qualitative degradations in TFS coding that are apparent in single AN-fiber responses to complex stimuli. Examination of the Fourier spectra of the neural correlogram functions (similar to a power-spectral density derived from an auto-correlation function), along with other system-identification approaches (e.g., reverse correlation), indicate a dramatic loss of tonotopicity that can occur following noise-induced hearing loss. Whereas the normal-hearing cochlea has systematic tonotopic representation along the basilar membrane, our neural recordings from hearing-impaired chinchillas indicate that the most-prominent frequencies for which an impaired AN fiber responds to can be up to two to three octaves below the characteristic frequency (CF) corresponding to where the fiber innervates the cochlea. This general loss of tonotopicity (i.e., listening to information at the wrong place in the cochlea), has significant implications for almost any neural coding scheme (e.g., Oxenham *et al.*, 2004). Similar effects have been seen previously in AN-fiber responses to vowel stimuli, where the neural coding of the second and third formants is degraded by a wide-spread response to the first formant following noise-induced hearing loss (Miller *et al.*, 1997). Our results indicate that these significant degradations in the quality of temporal coding following SNHL is a much more general phenomena, which is likely to affect the neural coding of any broadband sound, particularly in background noise (also see Bidelman and Heinz, 2011; Swaminathan and Heinz, 2011).

The effects of SNHL on across-fiber temporal coding

The lack of a fundamental degradation in the ability of individual AN fibers to phase lock motivated us to also consider across-fiber temporal coding (i.e., spatio-temporal coding). Spatio-temporal cues, which are based on the sharp phase transitions that occur on the basilar membrane near the resonant place, have been hypothesized to be perceptually relevant in a number of ways (e.g., speech, pitch, and intensity coding, tone detection in noise, binaural sound localization). Furthermore, these sharp phase transitions are predicted to be degraded by broadened tuning following SNHL. Despite the hypothesized perceptual importance of spatio-temporal cues, they have been difficult to study experimentally, e.g., due to sparse CF sampling in neurophysiological experiments, across-neuron variability, and variability in CF estimates from the quick automated tuning-curve algorithms typically used (Chintanpalli and Heinz, 2007). Thus, the majority of studies on spatio-temporal coding have been computational modeling studies and there has been a lack of experimental data characterizing the effects of

SNHL on these spatio-temporal cues, which are related to the traveling-wave delays that occur near cochlear resonances.

We used an innovative data-collection procedure that avoids previous experimental limitations in the study of across-fiber temporal coding (Heinz *et al.*, 2010). The procedure uses the responses of a single AN fiber to multiple frequency-shifted stimuli to predict the responses of multiple AN fibers with differing characteristic frequencies (CFs) to a single stimulus. The experimental benefits of this approach are that it minimizes the effects of across-neuron variability, and it provides precisely known relative CFs because they are determined based on the experimenter controlled sampling rates used. These derived population data allowed us to apply shuffled cross-correlogram analyses to quantify across-fiber correlations in both fine-structure and envelope coding, and to estimate traveling-wave delays based on characteristic delays between responses at different CFs. Similar trends in across-fiber temporal coding were observed for both the broadband noise and speech sentence stimuli we used.

Two consistent effects of SNHL were seen in all individual AN fiber responses we analyzed. The cross-CF correlation for both TFS and ENV coding was higher following SNHL, with a broader range of CFs (width on the basilar membrane) providing correlated responses. The significance of this finding is that it suggests that SNHL produces fewer “independent” information channels for complex sounds, which would be expected to degrade perception. The second effect we observed was that the across-CF characteristic delays were reduced in AN fibers from chinchillas with noise-induced hearing loss. Although the absolute time scale of these reduced delays were quite small, they corresponded to a quarter cycle of the relevant stimulus frequency for two places on the basilar membrane separated by only a half octave. Thus, these “small” changes in across-fiber delays are potentially quite significant because they correspond to a difference between correlated and uncorrelated responses for any across-CF neural coincidence detection mechanism that may exist in the lower levels of the auditory system. Overall, these data suggest that SNHL reduces the traveling-wave delays on the basilar membrane, which degrades the sharp phase transitions that provide the spatio-temporal cues that have been hypothesized to be perceptually relevant. If these cues are in fact perceptually relevant, this would suggest the need for new strategies to improve hearing aids, which currently do not attempt to restore normal spatiotemporal responses.

Potential role of “recovered” envelopes in perceptual TFS deficits

The third hypothesis for the physiological basis of perceptual TFS deficits that we have been exploring relates to the open question of whether it is actually possible to separate TFS and ENV components within the cochlea. Much of the evidence to support the idea that SNHL produces a perceptual deficit in using TFS comes from vocoded speech stimuli designed to isolate acoustic TFS and ENV (Lorenzi *et al.*, 2006;

Hopkins *et al.*, 2008). The physiological basis for these perceptual results is difficult to evaluate because narrowband cochlear filtering limits the ability to isolate fine-structure and envelope at the output of the cochlea. Specifically, interpretation of perceptual results using these specialized acoustic stimuli (e.g., TFS speech) relies on the assumption that envelope and fine-structure can be isolated at the output of the cochlea. However, narrowband cochlear filtering imposes constraints on isolating a sound's fine-structure from its envelope (Ghitza, 2001), as predicted by several signal processing theorems (Voelcker, 1966; Rice, 1973; Logan, 1977). Thus, proper interpretation of the perceptual salience of TFS cues must include consideration of the fact that acoustic TFS not only produces true neural TFS cues, but also recovered envelope cues (see Fig. 3). In other words, acoustic TFS cues can produce useful temporal coding at the output of the cochlea in two ways: (1) AN responses synchronized to stimulus fine structure itself ("true TFS"), and (2) AN responses synchronized to stimulus envelope (i.e., "recovered envelopes," which are created by narrowband cochlear filters). These recovered neural ENV cues arise when broadband TFS signals are passed through narrowband cochlear filters, which perform an FM-to-AM conversion such that their outputs "recover" ENV patterns that are correlated with the ENV patterns from the original stimulus. It is then difficult to interpret whether observed perceptual effects related to acoustic TFS cues are truly based on neural TFS coding, or perhaps based on neural ENV cues. Of course, the answer to this question is critical for the translational implications of studies demonstrating perceptual TFS deficits.

We have been exploring this issue through a coordinated use of neurophysiological, perceptual, and computational-modeling approaches. Based on previous perceptual studies showing that recovered envelopes can contribute to the perception of TFS cues for speech in quiet conditions (Zeng *et al.*, 2004; Gilbert and Lorenzi, 2006), we collected neural data

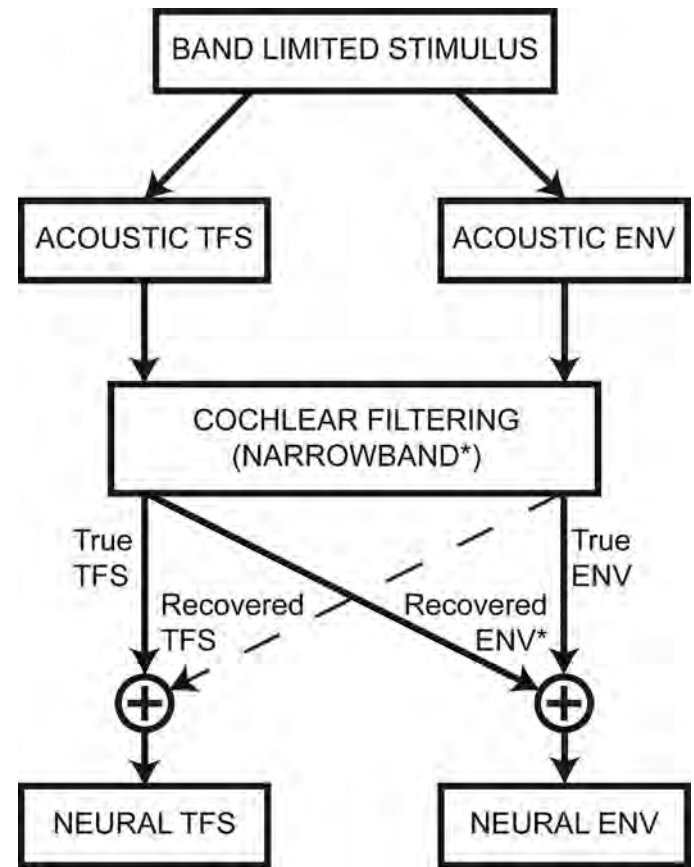


Fig. 3. Theoretical framework for evaluating the neural basis for the perceptual salience of acoustic temporal fine-structure (TFS) and envelope (ENV) cues. Acoustic TFS can produce recovered ENV cues at the output of the cochlea in addition to true neural TFS cues. Recovered envelopes arise due to narrowband cochlear filtering (*; Ghitza, 2001), and therefore are reduced or not present in listeners with sensorineural hearing loss or in cochlear-implant patients. Thus, caution is required in applying perceptual results from normal-hearing listeners to the design of auditory prostheses. (Figure is taken from Heinz and Swaminathan (2009), with permission from Springer-Verlag and the Association for Research in Otolaryngology.)

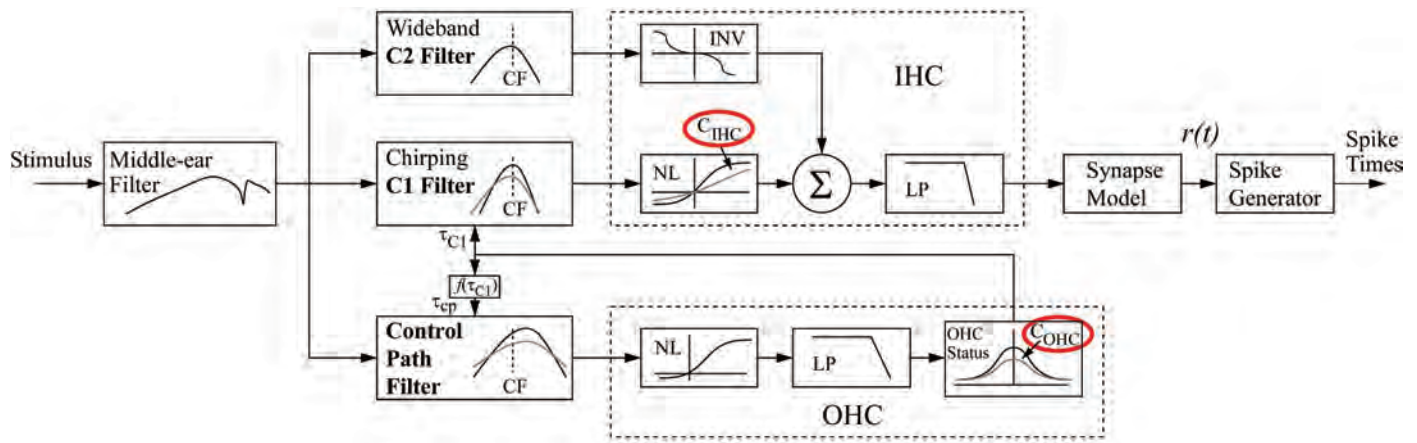


Fig. 4. A computational auditory-nerve (AN) model predicts spike-train responses of a single AN fiber to an acoustic stimulus. The characteristic frequency (CF) of the fiber, as well as the degree of inner-hair-cell (C_{IHC}) and outer-hair-cell (C_{OHC}) dysfunction can be specified. This model has been tested against physiological data from animals with normal hearing or with noise-induced hearing loss. We used this model to predict neural temporal fine-structure TFS and ENV coding in response to the same vocoded speech stimuli for which consonant identification was measured in human listeners. Results suggest that recovered neural ENV cues from acoustic TFS cues provide important information for speech perception in noise. Predictions with OHC dysfunction suggest that these recovered ENV cues are reduced following sensorineural hearing loss (SNHL). (Figure modified with permission from Zilany and Bruce (2006). Copyright 2006, American Institute of Physics.)

from chinchillas to demonstrate that recovered envelopes do in fact occur in actual AN responses (Heinz and Swaminathan, 2009). We used correlogram based neural cross-correlation metrics that we developed to quantify the fidelity of TFS and ENV coding in AN responses to the same types of vocoded speech stimuli that have been used in the perceptual studies. Although these data provided physiological evidence that recovered ENV cues do occur at the output of the cochlea, these data alone did not allow us to evaluate the perceptual relevance of these recovered ENV cues directly.

Jayaganesh Swaminathan addressed this issue directly in his PhD dissertation through a coordinated neural modeling and perceptual study, which allowed him to evaluate quantitatively the relative perceptual salience of neural TFS and ENV cues for speech perception in noise (Swaminathan, 2010). His psycho-physiological approach involved (1) the measurement of consonant identification in normal-hearing listeners, and (2) the prediction of neural TFS and ENV coding based on a physiological auditory-nerve model (Swaminathan and Heinz, 2012). By comparing the effects of signal-to-noise ratio on the measured perception and predicted neural coding using the same set of vocoder speech stimuli, he was able to quantify the relative contributions of neural ENV and TFS to the perception of noise-degraded speech. A range of five different vocoder types were used to represent 16 consonants spoken by four speakers in the presence of speech-shaped background noise. This range of vocoders provided a range of stimulus conditions for which true TFS, true ENV, and recovered ENV cues were present (Fig. 3). The computational AN model used (Fig. 4) has been validated against neurophysiological single-unit responses to stimuli ranging from simple tones to broadband noise to speech stimuli (Zilany and Bruce, 2006; 2007), and has been used in a number of applications related to SNHL (Heinz, 2010).

Regression models were used to predict consonant identification based on the neural coding of TFS and ENV (quantified using our neural cross-correlation coefficients). Separate models were used for positive and negative SNRs to evaluate the commonly held hypothesis that the relative salience of ENV and TFS differs in quiet and noisy conditions. The significance of the individual model terms, along with the TFS x ENV interaction term, allowed us to evaluate the perceptual salience of the different types of neural coding. Overall, our psycho-physiological analyses suggested that TFS cues play a less important role than has been suggested from acoustical and psychoacoustical studies. Psychoacoustic analyses alone (present and previous) suggest that speech perception in noise is primarily supported by TFS cues. In contrast, relating neural coding to measured speech identification demonstrated that (1) neural ENV is a primary cue for speech perception, even in degraded listening conditions, and (2) neural TFS does contribute in degraded listening conditions (less by itself and more through an interaction with ENV), but rarely as the primary cue. Differences in conclusions between psycho-acoustical and psycho-physiological analyses are likely due to cochlear signal processing that transforms TFS and ENV coding (e.g., recovered envelopes, Fig. 3) in normal-hearing ears. Interestingly, our computational modeling has also predicted that recovered

envelope coding is degraded with OHC damage (Heinz and Swaminathan, 2009), and thus these cochlear transformations are likely to be different in impaired ears.

Translational significance for hearing aids and cochlear implants

In summary, although it is always difficult to relate physiological and perceptual effects in a quantitative manner, this article illustrates several approaches that we have been taking to address the currently active debate regarding the role of TFS cues in perception, particularly for listeners with SNHL. By evaluating the physiological bases for perceptual effects, the translational implications of the observed perceptual TFS deficits can be better understood. Although the recent perceptual studies suggesting a reduced ability to use TFS cues following SNHL could be taken to suggest AN-fiber phase locking is reduced following SNHL, our results suggest that the fundamental ability of AN fibers to encode TFS is not degraded following SNHL for either simple or complex sounds. Thus, a straightforward interpretation from perceptual studies that hearing aids simply need to overcome degraded TFS coding strength in AN fibers would appear to be misguided. However, other “TFS coding” deficits were observed in impaired AN responses (e.g., degraded TFS quantity in noise, as well as degraded TFS quality in terms of loss of tonotopicity, degraded spatio-temporal (across-CF) coding, and reduction of recovered ENV cues). Each of these effects provides alternative interpretations of the perceptual TFS deficits, and provide insights into the limitations of current hearing aids as well as potential strategies for improving hearing aids.

Our findings on the relative perceptual importance of ENV and TFS cues for speech perception in noise also have important potential implications for the development of improved strategies for cochlear implant (CI) signal processing. These implications can be understood by considering each of the regression-model terms (ENV, TFS, and ENV x TFS) with respect to current CI technology. The finding that neural ENV was a primary contributor to speech perception in quiet and in noise is actually quite promising because CIs are currently able to provide ENV directly to the AN. However, an important distinction is that CIs currently provide *acoustic ENV*, rather than *neural ENV*. The finding that neural TFS alone was rarely the primary cue for speech perception, even in noise is also encouraging since CIs are currently unable to provide neural TFS. In fact, our results suggest that if neural TFS alone could be provided, speech perception in steady noise would likely be no better than a CI providing neural ENV alone. The last finding, that the interaction term (ENV x TFS) was also significant for speech perception in noise, implies that when TFS does contribute it does so primarily in the presence of neural ENV cues. This suggests that if TFS were able to be provided in future technology, an important design constraint must be that TFS be provided in a way that does not disrupt neural ENV coding.

Our hope is that this work as a whole will contribute to the long-term goal of improving the daily lives of people with hearing loss through the application of physiological

knowledge to the diagnosis and rehabilitation of sensorineural hearing loss.[AT](#)

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