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Research paper

Sensorineural hearing loss amplifies neural coding of envelope information in the central auditory system of chinchillas

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ABSTRACT

People with sensorineural hearing loss often have substantial difficulty understanding speech under challenging listening conditions. Behavioral studies suggest that reduced sensitivity to the temporal structure of sound may be responsible, but underlying neurophysiological pathologies are incompletely understood. Here, we investigate the effects of noise-induced hearing loss on coding of envelope (ENV) structure in the central auditory system of anesthetized chinchillas. ENV coding was evaluated non-invasively using auditory evoked potentials recorded from the scalp surface in response to sinusoidally amplitude modulated tones with carrier frequencies of 1, 2, 4, and 8 kHz and a modulation frequency of 140 Hz. Stimuli were presented in quiet and in three levels of white background noise. The latency of scalp-recorded ENV responses was consistent with generation in the auditory midbrain. Hearing loss amplified neural coding of ENV at carrier frequencies of 2 kHz and above. This result may reflect enhanced ENV coding from the periphery and/or an increase in the gain of central auditory neurons. In contrast to expectations, hearing loss was not associated with a stronger adverse effect of increasing masker intensity on ENV coding. The exaggerated neural representation of ENV information shown here at the level of the auditory midbrain helps to explain previous findings of enhanced sensitivity to amplitude modulation in people with hearing loss under some conditions. Furthermore, amplified ENV coding may potentially contribute to speech perception problems in people with cochlear hearing loss by acting as a distraction from more salient acoustic cues, particularly in fluctuating backgrounds.

1. Introduction

People with sensorineural hearing loss (SNHL) often have substantial difficulty understanding speech in their daily lives, even with amplification from a hearing aid. The severity of the problem typically depends on the listening environment, with many individuals reporting great difficulty understanding speech in noisy or reverberant environments with more than one source of sound.

Degraded speech perception in people with SNHL may be caused by diminished sensitivity to the temporal structure of sound. Acoustic signals contain two types of temporal information: rapidly varying temporal fine structure (TFS) and slower changes in the overall amplitude envelope (ENV). Recent studies have shown that with SNHL, the ability to use ENV cues remains intact while the ability to use TFS information is drastically reduced (Lorenzi et al., 2006; Moore et al., 2006). Moreover, listeners with high frequency hearing loss and normal-hearing thresholds at low frequencies still appear to experience deficits in TFS sensitivity (Lorenzi et al., 2009). While information from the ENV alone may be enough to discern speech in quiet conditions, the inability to use TFS information in people with SNHL could underlie their degraded ability to perceive speech in fluctuating background noise (Hopkins et al., 2008; Zeng et al., 2005).

The physiological contributors to this phenomenon have not yet been elucidated. One theory is that in cases of SNHL, neurons in the peripheral auditory system lose their ability to phase lock, or to discharge synchronously with the stimulus TFS. However, studies of phase locking to pure tones in animals with SNHL have provided

Abbreviations: ABR, auditory brainstem response; AEP, auditory evoked potential; ENV, envelope; SAM, sinusoidally amplitude modulated; SNHL, sensorineural hearing loss; TFS, temporal fine structure

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conflicting results. One study found that the loss of outer hair cells, a major component of SNHL, does not affect the ability of auditory nerve fibers to encode pure tone signals in guinea pigs (Harrison and Evans, 1979). Similarly, noise induced hearing loss in cats does not affect phase locking to tones (Miller et al., 1997). However, another study in chinchillas showed that outer hair cell loss decreases both the strength of phase locking and the range of frequencies over which phase locking occurs (Woolf et al., 1981). More recent attempts to clarify these conflicting results suggest that individual auditory nerve fibers do not lose the ability to encode TFS information of narrowband sounds, at least in quiet conditions (Kale and Heinz, 2010; Henry and Heinz, 2012). A second theory, on which we focus here, is that amplified coding of ENV information in the cochlea with SNHL leads to a "relative" deficit in TFS coding. Enhanced ENV coding, which is expected with reduced compression of the basilar membrane input–output function (Sellick et al., 1982; Ruggero and Rich, 1991; Glasberg and Moore, 1992; Moore et al., 1996), has been observed in auditory-nerve fiber responses to amplitude modulated tones in chinchillas with SNHL (Kale and Heinz, 2010, 2012).

Previous studies of temporal coding in animals with SNHL are limited in several regards. Most studies were conducted in quiet settings while deficits in speech perception in people with SNHL are most prominent in noisy environments. A recent study of chinchillas illustrated the importance of this difference by demonstrating that phase locking in auditory nerve fibers to tones degrades more rapidly with the addition of background noise in animals with noise-induced SNHL than in normal-hearing control animals (Henry and Heinz, 2012). Second, most studies have examined temporal coding of auditory-nerve fibers at the level of the peripheral auditory system. It has recently been proposed that the degradation of speech perception may be due to deficits in more central processing (Moore, 2008), which suggests a need for studies of the central auditory processing system.

Auditory evoked potentials (AEPs) recorded from the scalp surface can be used to non-invasively study central processing of acoustic stimuli. AEPs reflect the summed neural response generated by populations of neurons along the auditory pathway. AEP waveforms can exhibit phase locked components to both the ENV and low frequency TFS of sustained acoustic stimuli (Krishnan, 2006). Using latency calculations, previous studies suggest that AEPs originate primarily from the auditory brainstem and midbrain (Galbraith, 1994; Galbraith et al., 2000; Glaser et al., 1976; Smith et al., 1975). Furthermore, AEPs are absent in human subjects with upper brainstem lesions (Sohmer et al., 1977) and in cats when the inferior colliculus is cooled (Smith et al., 1975). The non-invasive nature of AEPs allows for assessment of central auditory processing in humans and for comparisons of auditory processing before and after induction of hearing loss in the same animal subject.

In the present study, we used AEPs evoked by sinusoidally amplitude-modulated (SAM) tones to examine the effects of noise-induced SNHL on neural coding of the ENV structure in the central auditory system of chinchillas. Previous studies of amplitude modulation evoked AEPs in another rodent, the Mongolian gerbil, show that ENV responses to modulation frequencies from 50 to 200 Hz have a group delay of approximately 6 ms, consistent with generation in the auditory midbrain or brainstem (Dolphin and Mountain, 1992). In a more direct study in cats, lesions were used to demonstrate that the inferior colliculus is the major contributor to responses to amplitude-modulation frequencies from 20 to 200 Hz (Kiren et al., 1994). ENV responses recorded in the current study of chinchillas were consistent with generation in the auditory midbrain. Responses to TFS were also typically observed but not examined further because they had short latency consistent with

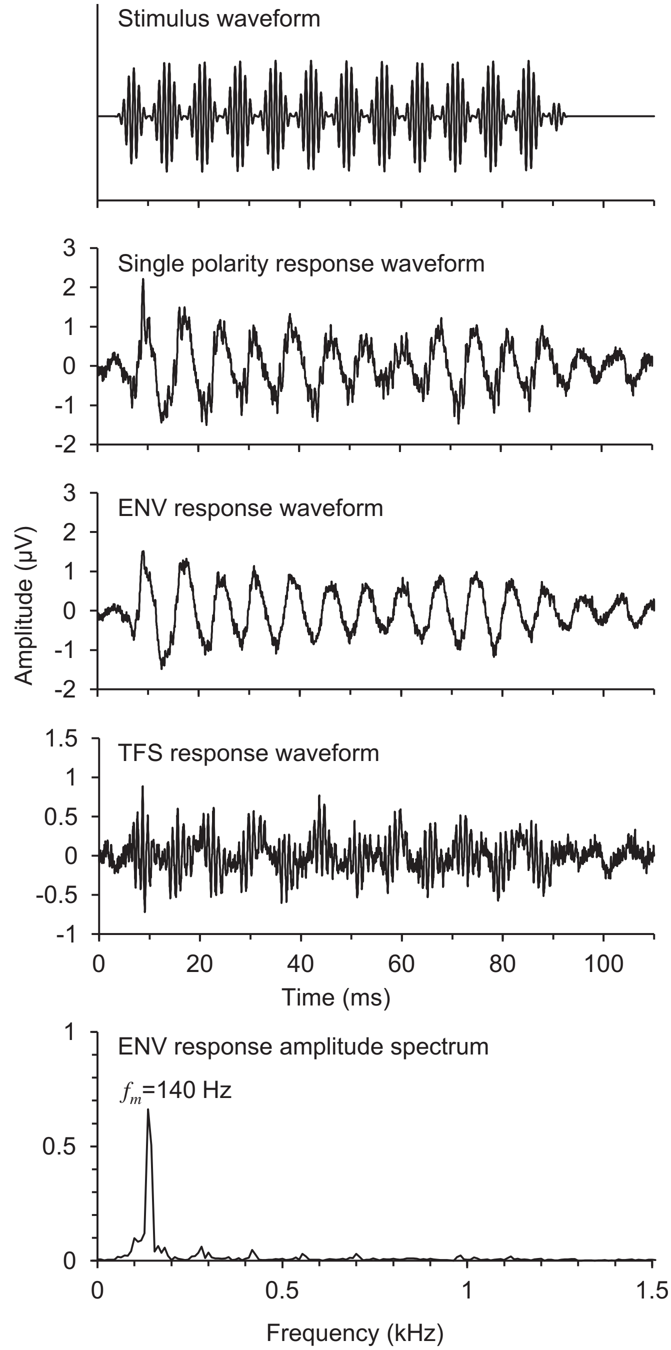

Fig. 1. SAM tone stimulus waveform and representative AEP responses from a normal hearing chinchilla. The stimulus carrier and modulation frequencies were 1 kHz and 140 Hz, respectively, presented at 52 dB SPL. AEP responses to stimuli of opposite polarity (e.g. second trace from top) were halved and then added to yield the ENV response (third trace) and subtracted to yield the TFS response (fourth trace). The amplitude of the ENV response at f_m = 140 Hz was measured from its Fourier transform (bottom panel).

generation by outer hair cells of the cochlea (i.e. the cochlear microphonic; Chimento and Schreiner, 1990) rather than neurons of the central auditory pathway. Responses to SAM tones were recorded under both quiet and noisy conditions to determine if changes in processing of ENV information with SNHL depend on the listening environment. We predicted that noise-induced SNHL would (1) amplify coding of ENV information in the central auditory system, at least under quiet conditions, and (2) lead to a