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Research paper

Age-related shifts in distortion product otoacoustic emissions peak-ratios and amplitude modulation spectra

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ABSTRACT

Amplitude modulation (AM) is an important temporal cue for precise speech and complex sound recognition. However, functional decline of the auditory periphery as well as degradation of central auditory processing due to aging can reduce the salience and resolution of temporal cues. Age-related deficits in central temporal processing have previously been observed at more rapid AM frequencies and various AM depths. These centrally observed changes result from cochlear changes compounded with changes along the ascending auditory pathway. In fact, a decrease in ability to detect temporally modulated sounds accurately could originate from changes in cochlear filtering properties and in cochlear mechanics due to aging. Nonetheless, few studies have examined cochlear mechanisms in AM detection. To assess integrity of the mechanical properties of the auditory periphery, distortion product otoacoustic emissions (DPOAEs) are a tool commonly used in clinics and in research. In this study, we measured DPOAEs to reveal age-related changes in peak f2/f1 ratio and degradation in AM detection by basilar membrane vibration. Two tones (f1 and f2, f2 > f1) at various f2/f1 ratios and simultaneous presentation of one AM and one pure tone were used as stimuli to evoke DPOAEs. In addition of observing reduced DPOAE amplitudes and steeper slopes in the input–output DPOAE functions, higher peak f2/f1 ratios and broader f2/f1 tuning were also observed in aged animals. Aged animals generally had lower distortion product (DP) and first sideband (SB 1) responses evoked by an f1 pure tone and an f2 AM tone, regardless of whether the AM frequency was 45 Hz or 128 Hz. SB 1 thresholds, which corresponds to the smallest stimulus AM depth that can induce cochlear vibrations at the DP generator locus, were higher in aged animals as well. The results suggest that age-related changes in peak f2/f1 ratio and AM detection by basilar membrane vibration are consistent with a reduction in endocochlear potential and reduced prestin activity but with preserved hair cell bundle function. SB 1 responses evoked by f2 AM/f1 pure tone with various AM depths could serve as an estimate for cochlear AM detection. The sidebands of DP could also serve as additional physiological cues for detection of AM in the presence of other tone(s), even at typical conversational levels in speech.

1. Introduction

Speech, dynamic sounds, music and animal vocalizations are complex and contain rapid modulations in amplitude and frequency over time (Rosen, 1992). Good resolution of these sounds is crucial for precise sound detection and recognition (Shannon et al., 1995; Zeng et al., 2005). With aging, functional reduction of the auditory periphery and deficits of central auditory processing (Frisina et al., 2001; Frisina, 2010; Li-Korotky, 2012) lead to a reduction of temporal resolution for speech and other complex sounds (Strouse et al., 1998). It has been reported that some older listeners with normal hearing thresholds have difficulties in understanding speech (Frisina and Frisina, 1997). This problem is even more prominent in the presence of competing sounds or when the temporal cues for speech recognition are weak (Schneider et al., 2005).

Amplitude modulations (AMs) contain important temporal cues that are extracted by the auditory system for speech recognition (Shannon et al., 1995; Snell and Frisina, 2001; Zeng et al., 2005).

Abbreviations: AM, amplitude modulation; DP, distortion product; DPOAEs, distortion product otoacoustic emissions; EP, endocochlear potential; f2/f1, stimulus-frequency ratio; I/O, input–output; OHC, outer hair cell; SB 1, first sideband

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Many psychoacoustic and physiological studies have showed that older subjects performed worse in AM detection than younger subjects (Takahashi and Bacon, 1992; Leigh-Paffenroth and Fowler, 2006; He et al., 2008; Parthasarathy et al., 2010; Parthasarathy and Bartlett, 2011; 2012). Decreased ability in detecting temporally modulated sounds accurately, e.g. difficulties in encoding small AM depth, could originate from changes in cochlear filtering properties and in cochlear mechanics due to aging (Bian and Chen, 2011). However, few studies have examined cochlear mechanisms in AM coding.

Distortion product otoacoustic emissions (DPOAEs) are commonly used as a tool in clinics and in research to assess the integrity of the mechanical properties of the auditory periphery (the cochlea), including outer hair cell (OHC) function (Shaffer et al., 2003). DPOAEs at 2f1−f2 are generated when two tones at f1 (lower tone) and f2 (higher tone) are presented simultaneously to the cochlea. The production of DPOAEs in mammals results from the dual active processes of prestin-driven electromotility (Liberman et al., 2004; Ashmore, 2008) and mechanoelectrical transduction of the hair cell bundle (Kennedy et al., 2005; Avan et al., 2013). DPOAE amplitudes are dependent upon the stimulus-frequency ratio (f2/f1) of the two tones (Abdala, 1996; Dhar et al., 2005). It has been reported that, on average, an f2/f1 ratio of 1.22 evokes the largest DPOAEs in human adults (Abdala, 1996) and in marmosets (Lasky et al., 1995; Valero et al., 2008). “Peak-ratio” used in this paper is defined as the f2/f1 ratio that evokes the largest DPOAEs. The peak f2/f1 ratio was found to be slightly larger in rodents and rabbits (1.25–1.30) (Brown, 1987; Whitehead et al., 1992). It has been demonstrated that DPOAE amplitudes show a bandpass response as a function of f2/f1 ratio (Harris et al., 1989). This indicates that there is one specific peak f2/f1 ratio which could elicit maximal DPOAEs in a tested subject.

Although two-tone stimuli and the evoked DPOAEs can provide much information about cochlear mechanics, sinusoidal AM tones can also be utilized to explore cochlear AM coding and motions for more complex sounds. Recently, Bian and Chen (2011) used simultaneous presentation of an AM tone and a pure tone as stimuli to study indirectly how OHCs respond to AM signals by measuring DPOAEs in normal-hearing human subjects. They systematically investigated the behavior of DPOAEs when either the f1 or the f2 was the AM tone. Their results showed that the dependence of DPOAE amplitudes on the AM stimulus was linear when the f1 was modulated but it was nonlinear and more complex when the f2 was an AM tone.

Although central deficits can also result in degradation of temporal processing during aging (Walton et al., 1998; Walton et al., 2002; Simon et al., 2004; Frisina and Walton, 2006; Parthasarathy et al., 2010; Parthasarathy and Bartlett, 2011), this paper focuses on how aging could alter peak-ratio and cochlear mechanics in detecting temporally modulated sounds, e.g. AM signals, particularly in the presence of another sound. According to some studies, cochlear responses may then be coded by central auditory neurons in some cases (Smoorenburg et al., 1976; Fahey and Allen, 1985; McAlpine, 2004; Abel and Kössl, 2009). To our knowledge, no study has been carried out to compare AM spectra and the potential for AM coding via a cochlear mechanism in aging using DPOAEs. In this study, we first examined if peak f2/f1 ratio would be different in young and aged animals, and then assessed cochlear AM coding using AM tone evoked DPOAEs. We hypothesize that there are age-related changes in peak-ratio and degradation in AM coding by basilar membrane vibration measured by DPOAEs. We aim to test the hypothesis by performing two experiments. In experiment 1, we investigated age-related differences of peak-ratio using two pure tones with various stimulus-frequency ratios to elicit DPOAEs (Harris et al., 1989; Dhar et al., 2005; Valero et al., 2008). In experiment 2, we assessed AM detectability of basilar membrane vibration in young and aged rats using a few combinations of one pure tone and one AM tone, in which the AM depth of the AM tone was varied systematically at different degrees.

2. Methods

2.1. Subjects

Depending on the protocol, 8 to11 young (3–6 months, 250–300 g) and 8 to14 aged (21–24 months, 400–450 g) male Fischer-344 rats (Taconic and Charles River laboratories) were used in each experiment in this study. All the animals were kept and raised in relatively quiet, standard laboratory conditions. All protocols were approved by the Purdue Animal Care and Use Committee (PACUC 1111000167).

2.2. Distortion product otoacoustic emissions (DPOAEs)

All DPOAE measurements were performed in a 9′X9′, double walled acoustic chamber (Industrial Acoustics Corporation). Animals were anaesthetized initially by inhaling 4% isoflurane in an induction chamber. They were then transferred to the manifold and maintained with 1.8% isoflurane (for young rats) or 1.5% isoflurane (for aged rats) on a water circulated warming blanket (Kent Scientific) set to 37 °C during the whole recording session of 30–60 min (Cederholm et al., 2012). Stimulus presentation and DPOAE recordings were performed using BioSig (Tucker Davis Technologies, TDT) in the acoustic chamber. An earpiece (Etymotic-10B), containing a miniature low noise microphone and two sound delivery tubes, was placed in the right ear canal of animals. Two multifunction closed field speakers (TDT), which delivered f1 and f2 tones to the ear canal, were connected to the earpiece via flexible tubes. While the speakers played sounds, the microphone recorded DPOAEs from ear canal simultaneously. The output of the microphone was delivered as an input to a TDT RZ 5 system which converted the responses from analog to digital. Each response is an averaged response of 100 stimulus sweeps presented continuously to the animals.

The DPOAE input/output (I/O) functions, with f1 and f2 centering at 8 kHz and f2/f1 ratio of 1.2, were tested in all animals. The intensity of f1 was varied from 50 dB to 75 dB SPL in 5-dB steps while the intensity of f2 was 10 dB lower than that of f1. This enabled us to estimate the integrity of OHCs around 8 kHz in each animal. Stimuli were set close to 8 kHz because the most sensitive hearing region of rats falls in the region of 6–16 kHz (Parthasarathy et al., 2014).

2.3. Auditory brainstem responses (ABRs)

Hearing threshold of 8 kHz was measured in each animal using ABRs. Similar to DPOAEs, ABRs were performed in an acoustic chamber. The experimental procedures were similar to those described in detail in Parthasarathy and Bartlett (2012); Parthasarathy et al. (2014). Subdermal needle electrodes (Ambu) were positioned at two different configurations on the scalp. In the first configuration, i.e. channel 1, a positive electrode was placed along the midline of the head in the Fz to Cz position. Meanwhile, a negative electrode was placed under the mastoid of the ear ipsilateral to the inserted earpiece. A ground electrode was placed in the nape of the neck. In channel 2, another positive electrode was positioned horizontally along the interaural line and above the location of the inferior colliculus. Electrode impedances were ensured to be always less than 1 kHz using the low-impedance amplifier (RA4LI, TDT). After electrode placement, animals were