



Spectral and temporal auditory processing in the superior colliculus of aged rats



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ABSTRACT

Presbycusis reflects dysfunctions present along the central auditory pathway. Given that the topographic representation of the auditory directional spatial map is deteriorated in the superior colliculus of aged animals, therefore, are spectral and temporal auditory processes altered with aging in the rat's superior colliculus? Extracellular single-unit recordings were conducted in the superior colliculus of anesthetized Sprague-Dawley adult (10 months) and aged (22 months) rats. In the spectral domain, level thresholds in aged rats were significantly increased when superior colliculus auditory neurons were stimulated with pure tones or Gaussian noise bursts. The sharpness of the frequency response tuning curve at 10 dB SPL above threshold was also significantly broader among the aged rats. Furthermore, in the temporal domain, the minimal silent gap thresholds to Gaussian noises were significantly longer in aged rats. Hence, these results highlight that spectral and temporal auditory processing in the superior colliculus are impaired during aging.

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1. Introduction

Over the past few decades, several studies (for review, see Syka, 2002) have indicated that peripheral hearing loss (presbycusis) cannot account for all speech-understanding difficulties among seniors. Recent studies (Casparly et al., 2008; Gates and Mills, 2005; Gates et al., 2008; Gold and Bajo, 2014; Walton et al., 2002) showed that presbycusis can be associated with age-related central processing deficits. Two factors that may contribute to the difficulty to precisely encode vocalizations and speech perception in a noisy environment is the decline in the ability to discriminate tone frequencies and an impoverished temporal acuity observed among the elderly listeners with good hearing (Barsz et al., 2002; Moore et al., 1992; Patterson et al., 1982) and in aged animals (mice: Barsz et al., 2002; Leong et al., 2009; Walton et al., 1998; rat: Palombi and Casparly, 1996; Suta et al., 2011; Turner et al., 2005; Walton, 2010).

A fundamental organizing principle in the auditory system is the tonotopic organization, which is maintained from the cochlea up to the auditory areas (Schnupp et al., 2011). Along the ascending auditory pathway, neurons respond to a specific frequency presented at a given threshold level, this is referred as the characteristic frequency (CF). In animal experiments, particularly in

mammalian species with a short lifespan, such as rat and mouse, spectral auditory processing deficits have been reported with age in the auditory midbrain and cortices. In this respect, Palombi and Casparly (1996) demonstrated in the inferior colliculus, a mandatory ascending auditory relay, that the CF thresholds of the auditory neurons were significantly higher and that frequency bandwidth increased among the aged rats. Furthermore, these latter authors also found, in the inferior colliculus of aged rats, an important reduction in the percentage of auditory neurons sensitive to the lowest and the highest CFs range. Walton et al. (1998) also showed that the response thresholds of the inferior colliculus auditory neurons sensitive to pure tones were more elevated among the aged mice. In addition, Turner et al. (2005) found, in aged rats, that the spectral receptive fields (RFs) in A1 layer V neurons were significantly wider relatively to those of the adult rats.

An important component of auditory processing is the ability to detect rapid temporal changes that characterizes everyday speech signals in human (Harris and Dubno, 2017; Harris et al., 2010; Langner, 1992) and species-specific vocalizations in animals (Aitkin et al., 1994). In accordance with a variety of sophisticated level of processing for complex auditory signals, the ability to encode environmental sounds under natural noisy listening conditions also depends on the temporal properties of the stimulus (Narayan et al., 2005). The gap (brief silent interval) detection paradigm is an efficient method used to assess auditory temporal resolution (Green and Forrest, 1989; Plomp, 1964). It consists of placing a silent gap in between 2 carriers which in turn mimics the

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silent intervals found in complex acoustical stimuli, such as environmental sounds and/or speech signals and animal vocalizations. After a series of different presentations of gap durations, the minimal gap threshold (MGT) in an ongoing sound or between 2 sounds is obtained. In return, this provides key indices on auditory temporal processing. Several studies conducted in the elderly listeners with normal audiograms (i.e., exempt of predominant peripheral hearing loss) demonstrated that the MGTs, the shortest duration of a silent interval in a sound that a subject is able to detect, were significantly longer in comparison with young listeners (Schneider and Hamstra, 1999; Snell, 1997; Strouse et al., 1998). Similarly, impaired auditory temporal acuity in aged animals has also been reported using the gap detection paradigm. Ison et al. (1998) showed in aged mice with no predominant sensorineural hearing loss, that behavioral MGTs were significantly increased with noise level and lead time. Moreover, Walton et al. (1998) also reported that the percentage of neurons sensitive to the gap duration was significantly reduced in the inferior colliculus of aged mice. Likewise, Suta et al. (2011) demonstrated, behaviorally and physiologically (evoked potentials in A1), that the gap detection threshold and the gap duration difference threshold, in old-age rats, increased about 2-fold in comparison with adult rats. Another study (Recanzone et al., 2011) conducted in the auditory cortex of aged monkeys also showed that the neurons recovery response to gap stimuli was much longer in older animals.

The inferior colliculus and other auditory regions of the brainstem and cortex send substantial projections to a multimodal center known as the superior colliculus (SC), to enable reflexive eye and head movements toward sound directions (Cadusseau and Roger, 1985; Druga and Syka, 1984; King et al., 1998; Oliver and Huerta, 1992). The SC is of particular interest, because, contrary to the primary auditory cortex, the majority of the auditory neurons found there exhibit a clear preference for sound source directions, which vary systematically with anatomic position within the nucleus to form an auditory directional space map (Champoux et al., 2008; Costa et al., 2016a; Gaese and Johnen, 2000; King and Palmer, 1983; Middlebrooks and Knudsen, 1984). Consistent with the relationship between the auditory localization cue values and directions in space, the auditory directional space map has to be computed by tuning the neurons to the combinations of localization cues that correspond to specific sound directions (King, 1999). Particularly, in mammals, SC auditory neurons are sensitive to interaural level differences and to monaural spectral cues, which seems to provide the acoustic basis for the auditory directional space map (King and Carlile, 1995; Wise and Irvine, 1985). Thus, age-related frequency tuning deficits of central auditory neurons are also likely to alter the spatial response characteristics of the SC neurons. In this respect, Ingham et al. (1998) showed, in aged guinea pigs, that the SC multi-unit auditory RFs on the azimuthal plane were rather broadly tuned and that the topographical organization of the auditory directional map was severely disrupted. Likewise, our previous study (Costa et al., 2016a) also highlighted that no systematic directional spatial arrangement was present among the SC auditory neurons of aged rats.

In light of this, since the SC auditory directional spatial map also depends on spectral cues (King, 1999), this raises the question of whether spectral central auditory processing with aging is also present at the level of the SC of the rat. Furthermore, given that the SC receives numerous auditory inputs from the inferior colliculus, which neurons are known to be sensitive to time-varying stimuli, such as amplitude modulation (Langner, 1992; Rees and Møller, 1987), envelope detection (Barsz et al., 1998) and gap detection (Walton et al., 1997); features often found in environmental sounds under natural noisy listening conditions. This raises the question of whether central auditory senescent alterations in temporal acuity

seen at the level of the inferior colliculus and the auditory cortex were also passed onto the auditory neurons in the deeper SC layers of old-age rats. This question is particularly noteworthy given that the SC is believed to act as a multimodal interface, which superimposed maps give rise to enhanced responses to acoustic stimuli that are presented in close temporal and spatial proximity.

To further investigate potential central underlying mechanisms involving in presbycusis, this study aims specifically to gain insights on how aging affects the frequency tuning as well as the auditory level thresholds of neurons in the rat SC deep layers. Second, we also address the question of whether SC auditory neuronal responses to gap stimuli are impaired with aging.

2. Material and methods

2.1. Animals

Fifteen Sprague-Dawley rats (7 adults: 10 month old; 8 aged: 22 month old) of either sex were used in the present study. Following the initial ages of the rats, Zhao et al. (2015) showed that adult Sprague-Dawley rats ranging from 8 to 30 weeks of age have similar gap detection abilities. According to Ingvar et al. (1985), Sprague-Dawley rats of 6 months are considered as young-adults. This animal strain loses its hearing gradually at a much slower pace than the Fisher 344 rats. The aged time window, 22–23 months, is considered to be late enough within the Sprague-Dawley rat lifespan to qualify as aged (Ingvar et al., 1985). In addition, 22–23-month-old Sprague-Dawley rats exhibit moderate age-related loss of 8 nerve fibers, whereas very old rats show a much greater (as high as 20%) loss (Hoeffding and Feldman, 1987; Keithley and Feldman, 1979). Adult rats were obtained from Charles River (Saint-Constant, QC, Canada), and the aged rats were supplied by Harlan Laboratories Inc (Indianapolis, IN, USA). In all important respects, all rats had similar environmental and nonototoxic history. They were housed in our facilities, where a 14/10 hours light-dark cycle was maintained in an isolated quiet room. To verify hearing function, every rat was subjected to distortion product of otoacoustic emissions (DPOAEs) testing. Only animals which the DPOAE amplitude levels were present and within the normal range were utilized. Prior experimentation, all procedures were performed in accordance with approved protocols by the Université de Montréal Animal Care Committee. All efforts were made to diminish the number of animals used and to alleviate any discomfort during surgical and experimental procedures.

2.2. Functional physiological status of the cochlea

To understand age-related effects on central auditory processing, it was important to minimize the contribution of peripheral hearing loss; therefore, all rats underwent DPOAE testing (Intelligent Hearing System 4630, Miami, FL, USA; SmartDPOAE version 4.60) to evaluate the integrity of the outer hair cells (OHCs). Briefly, as described in Costa et al. (2016a), sedation was induced with an i.m. injection of ketamine (50 mg/kg, Ketaset, Ayer Veterinary Laboratories, Guelph, ON, Canada) and xylazine (5 mg/kg, Rompun, Bayer, Toronto, ON, Canada). In mammals, the amplitude of the distortion product at the frequency defined by $2f_1-f_2$ is the most robust and reliable indicator of the OHCs function (Lonsbury-Martin and Martin, 1990). Thus, cubic difference tone ($2f_1-f_2$) DPOAEs were acquired (4.5 frequencies/octave; sampling rate: 128 kHz, 32-bit A/D) using 2 calibrated primary tones, f_1 and f_2 (ratio $f_2/f_1 = 1.22$), set to the same sound pressure level (65 dB SPL). Since the rat's auditory sensitivity is at its highest between 4 and 16 kHz (Polak et al., 2004), pure tones were presented from 2 to 24 kHz systemically, starting at the lowest frequencies and

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