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Enhanced attention-dependent activity in the auditory cortex of older musicians

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ABSTRACT

Musical training improves auditory processing abilities, which correlates with neuro-plastic changes in exogenous (input-driven) and endogenous (attention-dependent) components of auditory event-related potentials (ERPs). Evidence suggests that musicians, compared to non-musicians, experience less age-related decline in auditory processing abilities. Here, we investigated whether lifelong musicianship mitigates exogenous or endogenous processing by measuring auditory ERPs in younger and older musicians and non-musicians while they either attended to auditory stimuli or watched a muted subtitled movie of their choice. Both age and musical training-related differences were observed in the exogenous components; however, the differences between musicians and non-musicians were similar across the lifespan. These results suggest that exogenous auditory ERPs are enhanced in musicians, but decline with age at the same rate. On the other hand, attention-related activity, modeled in the right auditory cortex using a discrete spatiotemporal source analysis, was selectively enhanced in older musicians. This suggests that older musicians use a compensatory strategy to overcome age-related decline in peripheral and exogenous processing of acoustic information.

1. Introduction

Musical training improves listening abilities. For musicians, this manifests as superior performance, compared to that of non-musicians, for detecting minute temporal (Rammsayer and Altenmuller, 2006) and spectral details (Micheyl et al., 2006; Schellenberg and Moreno, 2010; Zendel and Alain, 2009). Musicians are also better than non-musicians at identifying speech embedded in multi-talker babble (Parbery-Clark et al., 2009) and have been observed to have superior performance on verbal (Chan et al., 1998) and musical (Pallesen et al., 2010) memory tasks, indicating that listening skills acquired during musical training can transfer to everyday listening situations. A recent study demonstrated that lifelong musicianship preserves the benefit for detecting spectral details, and enhances the benefit for detecting temporal details in older musicians (Zendel and Alain, 2012). Most importantly, these enhancements transfer to everyday listening situations, as lifelong musicianship slows age-related decline in the ability to understand speech in the presence of background noise (Parbery-Clark et al., 2011; Zendel and Alain, 2012). One important question that remains is how lifelong musicianship mitigates functional auditory neurophysiology. For instance, lifelong musicianship may preserve low-level bottom–up auditory processes needed to solve complex listening situations. Alternatively, lifelong musicianship could enhance listening skills (i.e., top–down processes), thereby allowing older listeners to better focus their attention on task-relevant auditory stimuli.

Listening is a skill that involves bottom–up processes, in which basic features of the auditory signal are extracted, in addition to top–down processes, in which a listener can focus attention on salient aspects of the auditory scene, and match incoming acoustic information to learned schemata to extract meaning (Alain and Bernstein, 2008; Bregman, 1990). The contribution of bottom–up and top–down processes to auditory scene analysis can be examined by contrasting neural activity elicited by identical stimuli when they are either task relevant or task irrelevant. Neural activity common to both situations represents exogenous activity because its generation does not depend on a listeners' attentional focus, whereas unique neural activity evoked by the task-relevant stimuli reflects endogenous processes because it depends on goal-directed action. Exogenous activity is thought to be obligatory, in that it is driven mainly by external stimuli, whereas endogenous activity is generated internally according to an individual's intention or goal. In musicians, scalp-recorded auditory event–related potentials (ERPs, or event-related fields in the case of magnetoencephalography) revealed neuroplastic changes characterized by increased amplitude and decreased

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latency of both exogenous (Baumann et al., 2008; Kuriki et al., 2006; Pantev et al., 1998; Pantev et al., 2001; Shahin et al., 2003, 2005) and endogenous (Baumann et al., 2008; Zendel and Alain, 2009) components.

Hearing abilities diminish with age. Neurophysiologically, age-related changes in auditory processing are paralleled by changes to exogenous components of auditory ERPs. For example, the P1, N1, and P2 wave are all enlarged in older adults (Aine et al., 2005; Alain and Woods, 1999; Amenedo and Diaz, 1998; Anderer et al., 1996; Ceponiene et al., 2008; Chao and Knight, 1997; Smith et al., 1980), whereas the N2 deflection decreases with age (Anderer et al., 1996; Bertoli and Probst, 2005; Ceponiene et al., 2008). At the same time, endogenous neural activity related to the conscious/voluntary processing of a designated deviant sound (i.e., target) was little influenced by age when the detectability of the target stimuli was matched behaviorally (Alain et al., 2004). In addition, Pichora-Fuller et al. (1995) found that older adults, compared to younger adults, were better able to use sentence context when recalling the final word in an utterance. These studies support the hypothesis that older adults use compensatory strategies to overcome impoverished peripheral encoding and automatic processing of acoustic information (Schneider et al., 2010).

Although the effects of musical training and aging on the neurophysiological processing of auditory stimuli are well known, their interaction is less well understood. Brainstem responses, which are thought to reflect the exogenous encoding of acoustic information, are enhanced in older musicians compared to older non-musicians (Parbery-Clark at al., 2012), but the benefit of musical training in older adults seems smaller than that observed in younger adults (Parbery-Clark et al., 2009). Although these benefits occur at the subcortical level, these enhanced responses may represent efferent activity from the cortico-fugal pathway, and thus may reflect a top–down benefit of musical training (Kraus and Chandrasekaran, 2010).

As with brainstem responses, scalp-recording of cortical auditory ERPs has revealed an age-related interaction between musicians and non-musicians. An interaction between age and musical training was found for neural activity related to perceptual segregation of auditory stimuli (Zendel and Alain, 2013). To isolate the neural activity related to perceptual segregation, we subtracted auditory ERPs elicited by stimuli perceived as a single sound object (i.e., harmonic complex) from those generated by stimuli perceived as two sound objects (i.e., harmonic complex with a mistuned component; see Alain et al., 2001). This comparison revealed enhancements to an attention-independent component (i.e., object-related negativity [ORN]) in younger musicians and an attention-dependent component (i.e., P400) in older musicians, which demonstrates that musicians have an enhanced ability to use spectral details during concurrent sound segregation. Critically, the benefits of musical training to concurrent sound segregation were different in younger and older musicians. Whereas younger musicians had an enhanced attention-independent response to a spectral cue that promotes concurrent sound segregation (i.e., the ORN), older musicians appear to rely more on top–down cognitive processes (i.e., the P400) to achieve the same performance on a perceptual judgment task. In the study by Zendel and Alain (2013), the effects of age and musical training were not examined separately for stimuli perceived as a single sound object, making it difficult to parse the contribution of age and musical training to exogenous and endogenous components of auditory processing independent of concurrent sound segregation. Hence, it remains to be determined whether musical training enhanced exogenous and/or endogenous auditory processing in older musicians. The distinction between endogenous and exogenous processing is particularly important because of the differential influence of age on these two types of auditory processing (e.g., Alain et al., 2004). Specifically, exogenous processing declines with age, and endogenous processing compensates for this decline; thus, understanding how training influences these two stages of auditory processing is of the utmost importance.

In the present study, we re-analyzed electroencephalographic (EEG) data from an existing database (Zendel and Alain, 2013) to determine the influence of aging and musical training on endogenous and exogenous activity that was not related to perceptual segregation. We hypothesized that exogenous aspects of auditory processing would be enhanced in both younger and older musicians compared to age-matched non-musicians, but we did not have a clear hypothesis regarding the interaction between age and musical training. One could argue that exogenous processing in musicians and non-musicians should be similarly affected by age as long as the groups are matched for hearing sensitivity, because exogenous components of auditory ERPs primarily reflect low-level acoustic encoding. Alternatively, it is possible that continued musical activity through adulthood promotes neuroplastic changes in the ascending pathways that strengthen exogenous processing. For the endogenous components of auditory ERPs, we hypothesized that musicians would exhibit a pattern of differential preservation (i.e., a difference between musicians and non-musicians that becomes more pronounced with age), because older adults increasingly rely on cognitive strategies to process complex auditory information, and that musical training appears to mitigate age-related decline in tasks that place high demand on attention, such as understanding speech in noisy environments (Zendel and Alain, 2012).

2. Methods

2.1. Participants

Fifty-seven participants were recruited for the study and provided formal informed consent in accordance with the joint Baycrest Centre–University of Toronto Research Ethics Committee. These participants were divided into 4 groups: older musicians ($n = 15$, 3 female, age 58–91 years, mean = 69 years, standard deviation [SD] = 9.24 years); older non-musicians ($n = 13$, 5 female, age 61–84 years, mean = 69.2 years, SD = 6.69 years); younger musicians ($n = 14$, 8 female, age 23–33 years, mean = 28.1 years, SD = 3.17 years); and younger non-musicians ($n = 15$, 7 female, age 23–39 years, mean = 29.9 years, SD = 5.97 years). Musicians were defined as having advanced musical training (e.g., university degree, Royal Conservatory grade 8, college diploma, or equivalent) and continued to practice on a regular basis until the day of testing, whereas non-musicians had no more than 2 years of formal training throughout life, and did not currently play a musical instrument. All participants reported that they were right-handed. The musicians played a variety of musical instruments; the most common primary instruments played were piano ($n = 8$) and clarinet ($n = 4$). Two participants each played violin, trumpet, trombone, saxophone, percussion, or voice. Finally, the French horn, guitar, bassoon, tuba, and euphonium were each played by one participant. All participants were screened for neurological or psychiatric illness and for hearing loss. Noise-induced hearing loss is a common problem for many older musicians because of life-long exposure to high-amplitude sounds (Jansen et al., 2009). Not surprisingly, some participants in the older musician group met the threshold for mild hearing loss, based on a pure-tone threshold audiometric assessment (i.e., 25–35-decibel (dB) hearing level [HL] for octave frequencies from 250 to 8000 Hz). To compensate for this, older non-musicians with mild-hearing loss were recruited so that pure-tone thresholds in older non-musicians did not differ from those in older musicians. To confirm this, a 2 (musical training: musician,