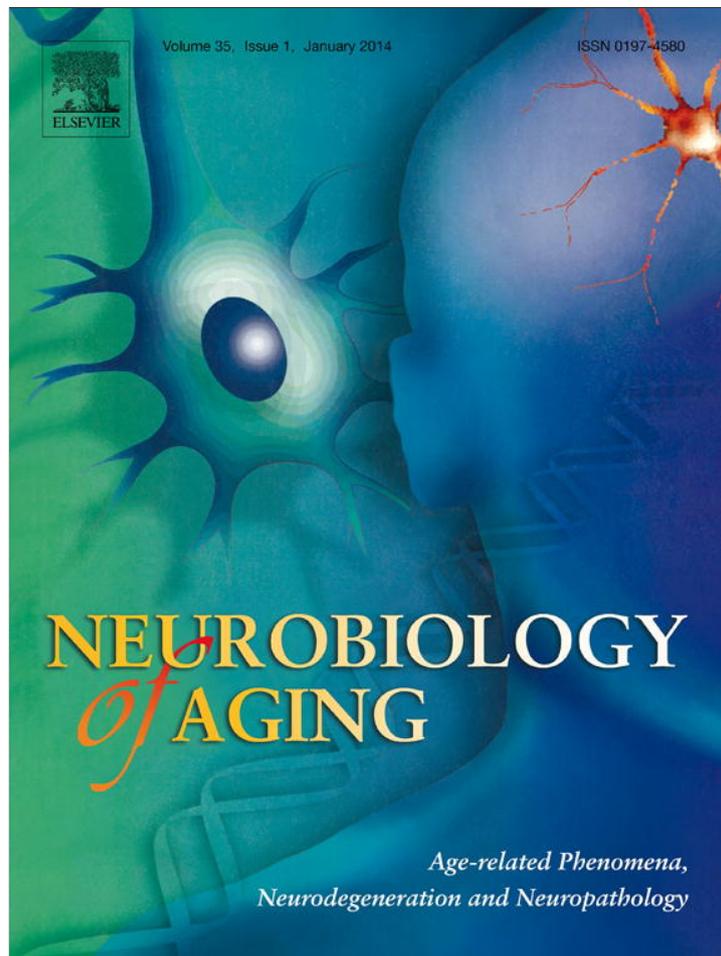


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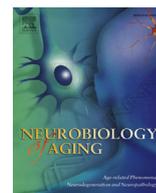
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Enhanced attention-dependent activity in the auditory cortex of older musicians

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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.

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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 et 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,

non-musician) \times 6 (pure tone frequency: 250, 500, 1000, 2000, 4000, and 8000 Hz) repeated-measures analysis of variance was calculated for the older adults. Neither the main effect of musical training ($p = 0.75$), nor the interaction between musical training and pure-tone frequency was significant ($p = 0.57$). All younger adults had pure-tone thresholds within the normal range (i.e., <25-dB HL at all frequency octaves).

2.2. Stimuli

Stimuli consisted of 6 complex sounds that were created by adding together 6 pure tones of equal intensity (i.e., 220, 440, 660, 880, 1100, and 1320 Hz). The fundamental frequency (f_0) was 220 Hz, and the third tonal element was either tuned (i.e., 660 Hz) or mistuned by 1% (666.6 Hz), 2% (673.2 Hz), 4% (686.4 Hz), 8% (712.8 Hz), or 16% (765.6 Hz) of its original value, yielding 6 complex sounds. These complex stimuli were chosen because they were physically similar to natural sound sources, but did not have a “musical” timbre. Accordingly, any differences between musicians and non-musicians in how these sounds were processed would be indicative of a musical training-related transfer of auditory processing abilities to non-musical stimuli. The pure tones were generated at a sampling rate of 22 050 Hz using Sig-Gen software (Tucker-Davis Technology, Alachua, FL), and were combined into a harmonic complex using Cubase SX (Steinberg, V.3.0, Las Vegas, NV). All 6 harmonic complex tones had durations of 150 milliseconds with 10-millisecond rise/fall times. They were presented binaurally at 80-dB sound pressure level (SPL) using a GSI 61 Clinical Audiometer via ER-3A transducers (Etymotic Research, Elk Grove, IL). The intensity of the stimuli were measured using a Larson-Davis SPL meter (Model 824, Provo, UT), which measured the amplitude of the stimuli presented from the left ER-3A transducer. The plastic tube from the transducer was attached to a 2-cc coupler on an artificial ear (model AEC1000) connected to the SPL meter.

2.3. Procedure

The same stimuli were used in active and passive listening conditions. In both listening conditions, 720 stimuli were presented (120 exemplars of each stimulus type). The stimuli were presented at an interstimulus interval (ISI) that was randomly varied according to a rectangular distribution of 1200 to 2000 milliseconds during passive trials and 2000 to 3000 milliseconds during active trials to allow time for a response. In the active listening condition, participants indicated whether the incoming stimulus was perceived as a single complex sound (i.e., a buzz) or 2 concurrently occurring sounds (i.e., a buzz plus another sound with a pure tone quality) (Alain et al., 2001; Moore et al., 1986). Responses were registered using a multi-button response box, and no feedback was given. In the passive condition, participants were instructed to ignore the sounds while they watched a muted, subtitled movie of their choice. This design allowed for the examination of the effects of age and musical training on exogenous cortical activity elicited by stimuli while minimizing the influence of top-down processes on ERPs. The use of muted subtitled movies has been shown to effectively capture attention without interfering with auditory processing (Pettigrew et al., 2004). To help control for arousal levels, all participants were monitored using a closed-circuit video camera in the EEG recording booth, and were given verbal warnings and a chance to stretch if they closed their eyes for more than a few seconds or appeared to be drowsy. All participants completed 6 blocks of trials. The first and last blocks were passive and each included 360 trials (60 exemplars of each stimulus type), the

middle 4 blocks were active, and each included 180 trials (30 exemplars of each stimulus type).

The focus of the current study was on group differences in cortical activity during active and passive listening when processing, but not perceptually segregating, a complex sound. In other words, we studied how lifelong musicianship alters endogenous and exogenous processing of auditory information. In a companion article (Zendel and Alain, 2013), we reported the effects of mistuning a harmonic component on evoked responses. Mistuning a harmonic component in an otherwise periodic stimulus engenders the perception of multiple auditory objects (Moore et al., 1986), and is a critical processes related to auditory scene analysis (Bregman, 1990). Accordingly, in our 2013 article, we explored how lifelong musicianship influences perceptual segregation of the auditory environment (i.e., auditory scene analysis). Specifically, we reported the effects of age and musicianship on cortical processing of a mistuned harmonic, and the related perception of concurrent sounds. We accomplished this by comparing ERPs evoked by the tuned stimulus to ERPs evoked by mistuned stimuli, and then comparing the amplitudes of the 2 components revealed by this comparison (i.e., ORN and P400). We found that the ORN was greatest in younger musicians, the P400 was greatest in older musicians, and the behavioral performance of the older and younger musicians was similar. Accordingly, it is likely that age-related changes in early processing of a mistuned harmonic are compensated for by enhanced attention-dependent processing of the mistuned harmonic as a separate auditory event. In Zendel and Alain (2013), participants did not perceptually segregate the tuned and 1% mistuned conditions; that is, nearly all trials were perceived as being a single “buzz.” Above 1% mistuning, participants begin to perceive a buzz plus a second sound with a pure-tone quality. In addition, there were no perceptual differences between groups for the tuned and 1% mistuned stimuli. Therefore, to further improve the signal-to-noise ratio, we averaged together the ERPs elicited by the tuned and the 1% mistuned stimuli. All behavioral results (i.e., perceptual judgment, d prime (d') and reaction time) are reported in Zendel and Alain (2013).

2.4. Recording of electrical brain activity

Neuroelectric brain activity was digitized continuously from 64 scalp locations, including those from the 10 to 20 placements, with a band-pass filter of 0.05 to 100 Hz and a sampling rate of 500 Hz per channel using SynAmps2 amplifiers (Compumedics Neuroscan, El Paso, TX). Electrodes on the outer canthi and at the superior and inferior orbit monitored ocular activity (IO1, IO2, LO1, LO2, FP9, and FP10). During recording, all electrodes were referenced to the midline central electrode (i.e., Cz); however, for data analysis, the ERPs were re-referenced to an average reference, and electrode Cz was re-instated. All averages were computed using Brain Electrical Source Analysis (BESA) software, version 5.2. The analysis epoch included 100 milliseconds of pre-stimulus activity and 1000 milliseconds of post-stimulus activity. Trials containing excessive noise ($\pm 130 \mu\text{V}$) at electrodes not adjacent to the eyes (i.e., IO1, IO2, LO1, LO2, FP1, FP2, FPz, FP9, and FP10) were rejected before averaging. ERPs were then averaged separately for each condition, stimulus type, and electrode site.

For each participant, a set of ocular movements was obtained before and after the experiment (Picton et al., 2000). From this recording, averaged eye movements were calculated for both lateral and vertical eye movements as well as for eye blinks. A principal component analysis of these averaged recordings provided a set of components that best explained the eye movements. These components were then decomposed into a linear combination along with topographical components that reflect brain activity. This

linear combination allows the scalp projections of the artifact components to be subtracted from the experimental ERPs to minimize ocular contamination such as blinks, vertical, and lateral eye movements for each individual average with minimal effects on brain activity (Berg and Scherg, 1994). ERPs were then digitally low-pass filtered to attenuate frequencies greater than 30 Hz with a slope of 24 dB per octave.

2.5. Data analysis

To determine whether there were any differences in exogenous neural activity, and to make our data comparable to that of previous work with auditory evoked responses, peak amplitude and latency during the 40- to 80-millisecond (P1), 70- to 140-millisecond (N1), 140- to 240-millisecond (P2), and 220- to 400-millisecond (N2) epochs were compared separately during active and passive listening due to differences in the ISI between conditions. The effects of age, and musical status on the latency and amplitude of the auditory ERPs were quantified over 9 central electrodes (FC1, FCz, FC2, C1, Cz, C2, CP1, CPz, and CP2). The amplitude and latency for each of the waves in the auditory ERP were analyzed using a mixed-design, repeated-measures analysis of variance with age group and musical training as the between-subject factors and electrode site as the within-subject factor. When appropriate, the degrees of freedom were adjusted with the Greenhouse–Geisser epsilon (ϵ), and all reported probability estimates were based on the reduced degrees of freedom, although the original degrees of freedom are reported. The 9-electrode montage was used to ensure a stable and reliable estimate for the ERPs, and therefore the main effect of and interactions with the electrode factor are not reported.

Although the scalp distribution of exogenous auditory ERPs (i.e., P1-N1-P2-N2) is well known, the influence of endogenous neural activity on the scalp distribution of auditory ERPs is less well understood, particularly after the N2. Moreover, it is possible that the scalp distribution of endogenous activity is influenced by age or musicianship. Therefore, to avoid biasing the electrophysiological data after the N2 by selecting electrodes a priori, we used a discrete source model as a data reduction technique to reduce all the scalp data into a smaller, more manageable montage of regional sources. The analysis assumed a 4-shell ellipsoidal head model with relative conductivities of 0.33, 0.33, 0.0042, and 1 for the head, scalp, bone, and cerebrospinal fluid, respectively, and sizes of 85 mm (radius), 6 mm (thickness), 7 mm (thickness), and 1 mm (thickness). As an initial step, we used a surrogate model from BESA software, version 5.2, designed to model auditory evoked potentials. This model consisted of 11 regional sources, each containing 3 orthogonal dipoles to account for all directions of current flow at the source location (frontal pole, frontal left, frontal midline, frontal right, central midline, parietal left, parietal midline, parietal right, occipital, auditory cortex left, and auditory cortex right) (Fig. 1A). In each participant, the resulting model was held fixed and was used as a spatial filter to derive source waveforms for both active and passive listening conditions. To quantify the data, a series of pairwise permutation tests were performed using BESA statistics, version 1.0 (Maris and Oostenveld, 2007). Comparisons were made between all groups, separately during both active and passive listening. The analysis occurred in 2 stages. First, a preliminary series of *t* tests compared the amplitude of the source waveforms between 2 groups at every time point and at each source. This identified clusters of source activity that differed between the groups, wherever the *t* test revealed a difference with an alpha of

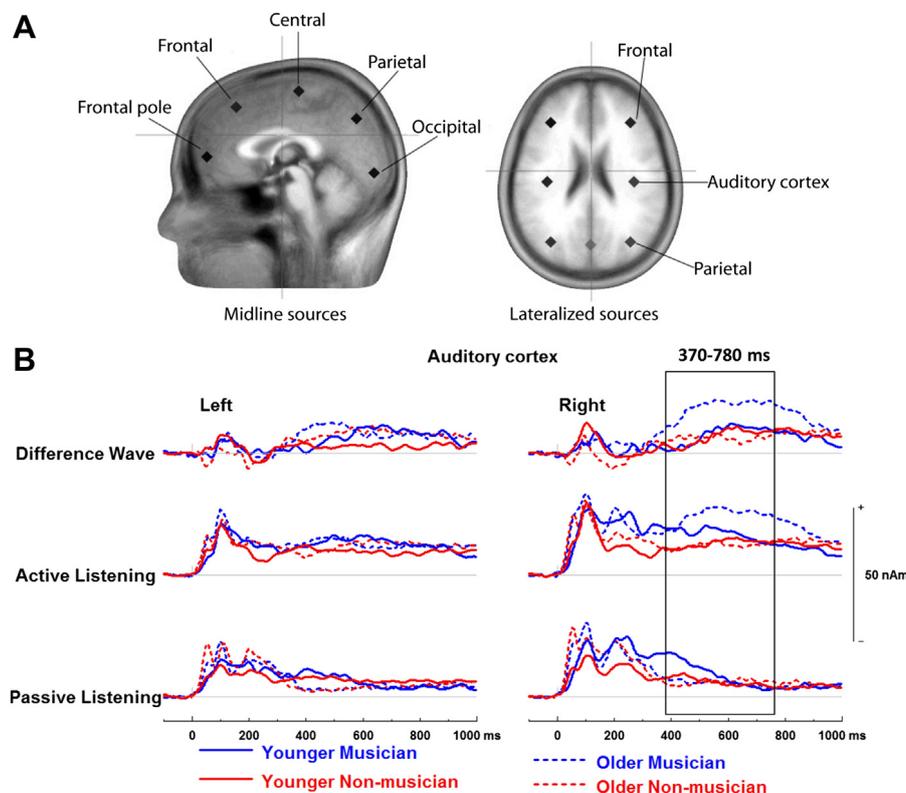


Fig. 1. (A) Auditory surrogate source model. Midline sources can be seen on the left side in the sagittal magnetic resonance image, whereas lateralized sources can be seen on the right in the transverse magnetic resonance image. (B) Source waves from the left and right auditory source. The top row shows the difference waves (active listening minus passive listening); the middle row shows the active listening condition; and the bottom row shows the passive listening condition. The 370 to 780 milliseconds is shown in a box to highlight the enhanced activity observed in older musicians.

less than 0.05. This step allowed us to further reduce our analysis to the right auditory cortex, as no other source was simultaneously influenced by both aging and musical training. Using this preliminary model, clusters in which differences between groups were observed were probed using a permutation test. A cluster was identified when statistically significant differences between the groups were found at least 2 temporally adjacent data points. Accordingly, the identification of significant clusters was entirely data driven, rather than based on an a priori assumption or a visual inspection of the data. The permutation test used a bootstrapping procedure to determine the probability values for group differences in each cluster. In the current analysis, 1000 random permutations of the data were compared. The final probability value was based on the percentage of permutations in which the identified cluster remained significant. In other words, to achieve an alpha value of 5%, 95% of the permutations tests must be significant. This process automatically corrects for multiple comparisons, and allows a more accurate determination of the exact epochs in which group differences exist. In addition, this procedure allows the identification of marginally significant clusters, by identifying clusters that were significant during the preliminary test, but in which less than 95% of the permutation test results were found to be significant.

3. Results

In all participants, the harmonic complex evoked P1, N1, P2, and N2 waves that peaked around 50, 100, 200, and 320 milliseconds, respectively. All of these deflections peaked in amplitude around central electrode sites, and reversed in polarity at mastoid sites, suggesting sources along the superior temporal plane. Figure 2A shows the auditory ERP recorded at the midline central electrode (i.e., Cz) during passive and active listening. Figures 2B and C show the group mean amplitudes for the P1, N1, P2, and N2 waves averaged across 9 fronto-central electrodes during passive and active listening, respectively.

3.1. Effects of lifelong musicianship on the amplitude of sensory evoked responses

During passive listening the P1 wave was larger in older compared to younger adults ($F(1, 53) = 18.23, p < 0.001$), and was smaller in musicians compared to non-musicians ($F(1, 53) = 4.87, p = 0.032$). Importantly, the interaction between Age group and Musical training was not significant ($p = 0.47$). The N1 wave was larger in older adults compared to younger adults ($F(1, 53) = 6.98, p = 0.011$). The main effect of Musical training and its interaction with Age group were not significant ($p = 0.76$ and 0.24 , respectively). For the P2 amplitude, the main effect of Musical training, Age group and their interaction were not significant ($p = 0.94, 0.15$, and 0.75 , respectively). The N2 amplitude was smaller in older adults compared to younger adults ($F(1, 53) = 19.09, p < 0.001$). The main effect of Musical training and its interaction with Age group were not significant ($p = 0.5$ and 0.07).

During active listening the P1 wave was larger in older adults ($F(1, 53) = 15.47, p < 0.001$), and smaller in musicians, but unlike passive listening, the difference in amplitude between musicians and non-musicians failed to reach significance ($p = 0.17$). The Musical training by Age group interaction for P1 amplitude was not significant ($p = 0.771$). For the N1 and P2 deflections the main effects of Age group and Musical training, and their interactions were not significant (N1: $p = 0.21, 0.93$, and 0.375 , respectively; P2: $p = 0.99, 0.73$, and 0.37 , respectively). The N2 amplitude was smaller in older adults ($F(1, 53) = 7.65, p = 0.008$), but the main effect of Musical training and its interaction with Age group were not significant ($p = 0.76$ and 0.54).

3.2. Effects of lifelong musicianship on the latency of sensory evoked responses

During passive listening the P1 and N1 latency was similar between all groups. The P2 latency was longer in older adults compared to younger adults ($F_{1,53} = 20.59, p < 0.001$). The main

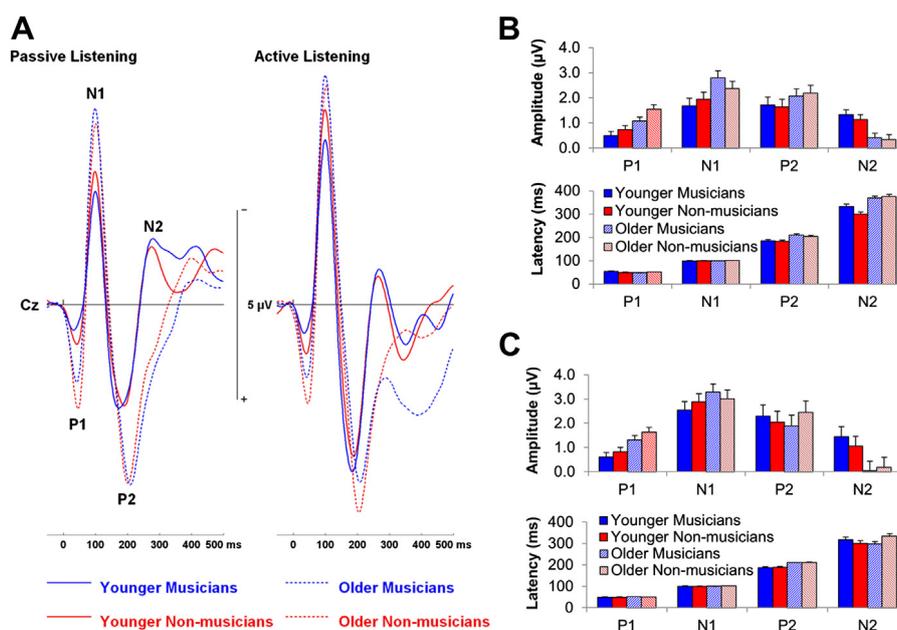


Fig. 2. (A) Auditory evoked responses from electrode Cz during passive (left) and active (right) listening. Musicians are plotted in blue, and non-musicians in red; younger adults are plotted with solid lines, and older adults with dotted lines. The P1-N1-P2-N2 waves are labeled on the left plot. (B) Passive listening: peak amplitude (top) and latency (bottom) for the P1, N1, P2, and N2 waves, separately for older and younger musicians and non-musicians. (C) Active listening: peak amplitude (top) and latency (bottom) for the P1, N1, P2, and N2 waves, separately for older and younger musicians and non-musicians. Note: Absolute values are shown for the N1 and N2 responses for ease in making comparisons between them.

effect of musical training was not significant, nor was the interaction between age group and musical training. The N2 latency was also longer in older adults compared to younger adults ($F_{1,53} = 35.63, p < 0.001$). The main effect of musical training was not significant ($p = 0.16$); however, the interaction between musical training and age group was significant ($F_{1,53} = 4.47, p = 0.039$). Follow-up t tests revealed that, in younger adults, the N2 latency was significantly shorter in non-musicians compared to musicians ($t_{27} = 2.22, p = 0.035$), whereas in older adults N2 latency was similar in musicians and non-musicians ($p = 0.57$). These results for the N2 latency should be interpreted cautiously, because although a clear N2 peak can be seen in younger adults, the N2 peak was not well defined in the older adults, which may have influenced the ability to determine a peak latency (Fig. 2A).

During active listening, the latency of the P1 and N1 was similar in all groups. The P2 latency was longer in older adults compared to younger adults ($F_{1,53} = 37.82, p < 0.001$), but the main effect of musical training and the interaction between musical training and age group were not significant ($p = 0.86$ and 0.74 , respectively). There was a significant interaction between age group and musical training for N2 latency ($F_{1,53} = 4.69, p = 0.035$); however, the main effects of both age group and musical training were not significant ($p = 0.59$ and 0.44 , respectively). Follow-up tests revealed that N2 latency in older adults was longer in non-musicians compared to musicians ($t_{26} = 2.07, p = 0.048$) but similar between musicians and non-musicians in younger adults ($t_{27} = 0.98, p = 0.33$). As with passive listening the results for N2 latency should be interpreted cautiously, because the N2 was not clear in older adults.

3.3. Effects of age and musical training on endogenous auditory evoked responses

Figure 1A shows the location of the regional sources used to extract source waveforms; the source waveforms from the active and passive listening conditions, and their difference are presented

in Fig. 1B. The source waveforms from the auditory cortex closely matched the time course of scalp-recorded ERPs, thus our analysis was focused on activity after the P1-N1-P2-N2 complex. As expected, during the active listening condition, greater activity was observed in all groups, across most sources, compared to passive listening, consistent with the proposal that attention enhances processing of acoustic information (Coles and Rugg, 1995; Hansen and Hillyard, 1980; Hillyard et al., 1973; Näätänen et al., 1978). Preliminary analysis using uncorrected t tests demonstrated the greatest and most consistent group differences in source waveform amplitude in the right auditory cortex during active listening. Small and inconsistent group differences were observed at other sources, so we chose to focus our analysis on the sources in the right auditory cortex. Tables 1 and 2 present the results of the permutation tests between each group for the source waveforms from the right auditory cortex. The amplitude of the response over the identified epoch is presented graphically. In addition, the epoch and p values are presented at the top of each graph. Fields in which “no significant clusters were identified” indicate that none of the uncorrected t tests were significant for that comparison. Permutation tests confirmed enhanced source activity during active listening starting after 370 milliseconds in older musicians compared to both older and younger non-musicians (Table 2 and Fig. 1). In the comparison between older and younger musicians, initial t tests identified enhanced source activity in older musicians, but this difference did not remain significant after permutation testing. In passive listening, no such enhancement was observed for older musicians; however, younger musicians demonstrated enhanced source activity in the right auditory cortex during passive listening (Table 1 and Fig. 1). This enhancement for younger musicians during passive listening is particularly important because the difference between older and younger musicians did not reach significance during active listening. This pattern of results suggests that there is increased exogenous activity in younger musicians (i.e., activity was present in both active and passive listening). Accordingly, the lack

Table 1
Permutation tests: Passive listening

Passive listening	Older musicians	Younger musicians	Older non-musicians
	346-440 ms, p = 0.04		
Younger musicians		XXX	XXX
Older non-musicians	No significant clusters identified		XXX
Younger non-musicians	No significant clusters identified		

Note: Y-axis on all graphs is nanoamperes (nAm). Epoch and p values determined through permutation testing are shown above each graph.

Table 2
Permutation test results: Active listening

Active listening	Older musicians	Younger musicians	Older non-musicians
Younger musicians	<p>660-720 ms, $p = 0.19$ 41.51 26.92</p>	XXX	
Older non-musicians	<p>434-636 ms, $p = 0.04$ 39.92 25.25</p>	No significant clusters identified	XXX
Younger non-musicians	<p>370-780 ms, $p = 0.02$ 38.8 22.59</p>	<p>275-450 ms, $p = 0.12$ 29.99 17.89</p>	<p>278-346 ms, $p = 0.11$ 24.99 15.93</p>

Note: Y-axis on all graphs is nanoamperes (nAm). Epoch and p values determined through permutation testing are shown above each graph.

of difference between older and younger musicians in active listening was likely due to enhanced exogenous processing in the younger musicians.

4. Discussion

The main finding from this study was that endogenous source activity from the right auditory cortex of older musicians in response to a complex sound was enhanced relative to the other three groups. These results suggest that lifelong musicianship enhances attention-related processing of an auditory input. This effect appears to be limited to endogenous processing as the latency and amplitude of sensory evoked responses showed comparable changes as a function of age or musical training. The lack of interaction between age and musical training suggest that in musicians and non-musicians, exogenous evoked responses are similarly affected by age. This pattern of results further suggests that musical training can improve early exogenous processing of acoustic information, but that this stage of processing continues to decline with age. On the other hand, later endogenous processing of acoustic information was further enhanced in lifelong musicians, perhaps to compensate for age-related decline in the peripheral encoding and exogenous processing of acoustic information.

The first analysis focused on the scalp-recorded auditory ERPs. This was done to ensure that the current data set was consistent with previous research that has reported age or music-training related changes to the auditory ERPs. During passive listening, the P1 and N1 were larger in older adults compared to younger adults, whereas the P2 was delayed and the N2 was smaller. During active listening, the effect of age on ERPs was similar, although the age-related increase in P1 and N1 amplitude did not reach statistical significance, which suggests that older adults may compensate for age-related decline in exogenous processing of acoustic

information by focusing attention toward the auditory environment. Our findings are consistent with previous research that demonstrated age-related increases in P1 amplitude (Aine et al., 2005; Alain et al., 2012; Ross et al., 2009; Smith et al., 1980) and N1 amplitude (Alain and Woods, 1999; Anderer et al., 1996; Chao and Knight, 1997; Ross et al., 2009). In addition, previous research has demonstrated a delayed P2 and a smaller N2 in older adults (Anderer et al., 1996; Bertoli and Probst, 2005; Ceponiene et al., 2008). This pattern of results has been attributed to a failure to inhibit irrelevant auditory information as a result of age-related changes in prefrontal functions (Bertoli and Probst, 2005; Knight et al., 1999; Kok, 1999). Evidence for this hypothesis comes from neurological studies showing that patients with lesions in the dorsolateral prefrontal cortex have an enhanced P1 (Alho et al., 1994) and N1 (Knight et al., 1980; Woods and Knight, 1986) amplitude relative to age-matched controls. Hence, the dorsolateral prefrontal cortex appears to play an important role in gating sensory input to the auditory cortex, although the exact mechanisms by which this is achieved remain to be determined. Moreover, the age-related difference in P1 and N1 amplitude was smaller during active compared to passive listening, which suggests that focused attention may mitigate some of the age-related changes in inhibitory function. Finally, it is possible that age-related decline in N2 amplitude was also related to deficits in inhibitory functions (Ceponiene et al., 2008). Alternatively, the reduced N2 amplitude may be related to an age-related decrease in the off set response to the harmonic complex, as the stimuli were 150 milliseconds long, which would result in an offset response that overlaps the N2.

In musicians, enhanced automatic inhibitory function may explain their reduced P1 amplitude. The reduction in P1 amplitude in musicians did not interact with age, which suggests that musical training may enhance automatic inhibition of irrelevant incoming acoustic information, and that this ability declines equally with age

in both musicians and non-musicians. Interestingly, there was little effect of musical training on the other deflections of the auditory ERPs. Previous research has shown that the N1 (Baumann et al., 2008; Pantev et al., 1998, 2001), and P2 (Kuriki et al., 2006; Shahin et al., 2003, 2005) waves were enhanced in musicians. The N1 enhancements may be specific to using musical stimuli (Pantev et al., 1998), or stimuli specific to the instrument on which the musician trained (Pantev et al., 2001). At the same time, P2 enhancement in musicians was related to the spectral complexity of the sounds, with the difference in P2 amplitude increasing as the spectral complexity (i.e., more harmonics) of the evoking stimulus increased (Baumann et al., 2008; Shahin et al., 2005). Stimuli in the current study were not musical, which may explain a lack of effect on N1 amplitude. Also, the stimuli contained only 6 harmonics, which may not be enough spectral complexity to observe differences between musicians and non-musicians for P2 amplitude.

A second possible explanation for the age-related increase in P1 amplitude is that it reflects a deficit in stimulus adaptation. It has been shown that the P1 decreases in amplitude to sequentially presented stimuli; however, this decrease in amplitude was smaller when the subsequent stimulus differed from the initial stimulus (Chakalov et al., 2012; Snyder et al., 2006). Accordingly, the reduction in P1 amplitude in musicians may be due to stronger adaptation to the stimulus. This further suggests that the encoding of acoustic properties in the brainstem should be enhanced in musicians, because this hypothesis requires the signal reaching the auditory cortex to be more consistent on a trial-by-trial basis. In other words, each stimulus presentation may be encoded more accurately in musicians, and therefore, the neural signal reaching the cortex would be more similar on a trial-by-trial basis. This similarity would increase the level of adaptation in the P1 response, thus making P1 smaller in musicians. In support of this idea, it has been shown that brainstem encoding of harmonic information is enhanced in younger musicians (Bidelman and Krishnan, 2010; Parbery-Clark et al., 2009; Wong et al., 2005). In addition, enhanced brainstem responses to speech sounds have been observed in older musicians (Parbery-Clark et al., 2012). Critically, none of these findings point to the moderating factor that slows age-related changes in processing acoustic information for lifelong musicians, as observed by Zendel and Alain (2012), because none of the exogenous processes demonstrated age by musical training interactions.

In the present study, we found an age by musical training interaction for endogenous activity, which was caused by increased attention-related activity in the right auditory cortex that began approximately 370 milliseconds after sound onset and lasted for over 400 milliseconds. It has been shown that older adults engage in compensatory strategies to overcome age-related decline in peripheral encoding and exogenous processing of acoustic information (Alain et al., 2004). It is therefore likely that these compensatory mechanisms are further enhanced in older musicians. Interestingly, the enhancement was focalized in the right auditory cortex. The right auditory cortex is more sensitive to processing spectral aspects of the acoustic stimulus (Warrier et al., 2009; Zatorre, 1988), and the current experimental task required the listener to make a judgment about the spectral relationships in the acoustic stimulus. This specialization for spectral processing in the right auditory cortex is in contrast to the left auditory cortex, which has been shown to be more sensitive to rapid temporal changes within an acoustic stimulus (Liegeois-Chauvel et al., 1999; Warrier et al., 2009). It is therefore likely that lifelong musicianship contributes to plastic changes in auditory regions that are more important for music, and these benefits generalize to other, non-musical, auditory inputs that rely on the same neural architecture, such as separating speech sounds based on spectral cues (Reinke et al., 2003). Critically, the enhanced neural activity

observed in older musicians was observed only during active listening, suggesting enhanced endogenous processing of spectral information. This enhanced endogenous processing of a complex sound may explain why the rate of age-related decline is slower on auditory processing tasks in musicians (Zendel and Alain, 2012).

Data from the current study suggest that being a musician influences age-related changes in auditory processing. Exogenous processing of acoustic information was enhanced in musicians, but declined at an equal rate in musicians and non-musicians, demonstrating a pattern of preserved differentiation (Salthouse, 2006). A pattern of preserved differentiation may be indicative of neural plasticity, but could also reflect pre-existing enhancements. Although some endogenous processes were enhanced in age, activity in the right auditory cortex was further enhanced in older musicians, suggesting a pattern of differential preservation (or enhancement) (Salthouse, 2006). The enhancement of endogenous processes in older non-musicians compared to younger non-musicians supports the idea that older adults use compensatory strategies to overcome impoverished peripheral encoding and automatic processing of acoustic information. Further enhancement in older musicians suggests that lifelong musicianship accumulates, and may enhance, these compensatory mechanisms. Nevertheless, it is possible that people who continue to play a musical instrument throughout their lives do so because of predispositions to experience less age-related decline in auditory processing abilities. Unfortunately, the current study was not designed to test this possibility; however, another study found that individuals who took music lessons as children but were not currently musicians exhibited similar, but less robust, auditory processing benefits when compared to lifelong musicians (Skoe and Kraus, 2012). This suggests that the advantages in older musicians are not entirely due to predispositions. It is therefore reasonable to assume that continuous lifelong musicianship enhances endogenous processes related to processing auditory stimuli, perhaps to compensate for age-related decline in exogenous processing of acoustic information.

Disclosure statement

The authors declare no competing interests.

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