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Review

Turning down the noise: The benefit of musical training on the aging auditory brain

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ABSTRACT

Age-related decline in hearing abilities is a ubiquitous part of aging, and commonly impacts speech understanding, especially when there are competing sound sources. While such age effects are partially due to changes within the cochlea, difficulties typically exist beyond measurable hearing loss, suggesting that central brain processes, as opposed to simple peripheral mechanisms (e.g., hearing sensitivity), play a critical role in governing hearing abilities late into life. Current training regimens aimed to improve central auditory processing abilities have experienced limited success in promoting listening benefits. Interestingly, recent studies suggest that in young adults, musical training positively modifies neural mechanisms, providing robust, long-lasting improvements to hearing abilities as well as to non-auditory tasks that engage cognitive control. These results offer the encouraging possibility that musical training might be used to counteract age-related changes in auditory cognition commonly observed in older adults. Here, we reviewed studies that have examined the effects of age and musical experience on auditory cognition with an emphasis on auditory scene analysis. We infer that musical training may offer potential benefits to complex listening and might be utilized as a means to delay or even attenuate declines in auditory perception and cognition that often emerge later in life.

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1. Introduction

Older adults, including those with normal hearing, often experience difficulties understanding speech in the presence of other sounds (e.g., television, music, and other people talking). Such noise-related deficits can be overwhelming, contributing to social isolation, confusion, financial insecurity, and a poor quality of life (Bettejewski, 2006; Gomez and Madey, 2001; Salomon, 1986). They also present a major challenge for hearing science and medicine because of their wide prevalence. Although recent advances in hearing aid technologies have yielded encouraging results in improving speech in noise intelligibility (Kreisman et al., 2010; Mens, 2011; Moore et al., 1999; Uziel et al., 2003), they do not

restore performance to normal levels. This may be because speech understanding is not simply a matter of delivering sound at an audible level. It also depends on how well the brain utilizes incoming acoustic information; that is cognitive abilities such as listening skills, attention, and memory are important. Consequently, the need for more effective methods to maintain or improve older adults' listening skills in noisy situations (e.g., social gatherings) becomes increasingly pressing, and further advancements on this topic can potentially improve the quality of life of aging populations worldwide.

During the last decade, there has been a surge of interest in assessing the impact of life-style choices on successful aging (for a review see, Kramer et al., 2004). For instance, older adults who engaged in physical activity demonstrated superior performance on cognitive tasks compared to those that do not exercise (Colcombe et al., 2004; Newson and Kemps, 2005). There is some evidence to suggest that increased cardiovascular fitness is related to increased brain volume, and enhanced cognitive performance (Colcombe et al., 2006; Erickson et al., 2011). Older adults can also

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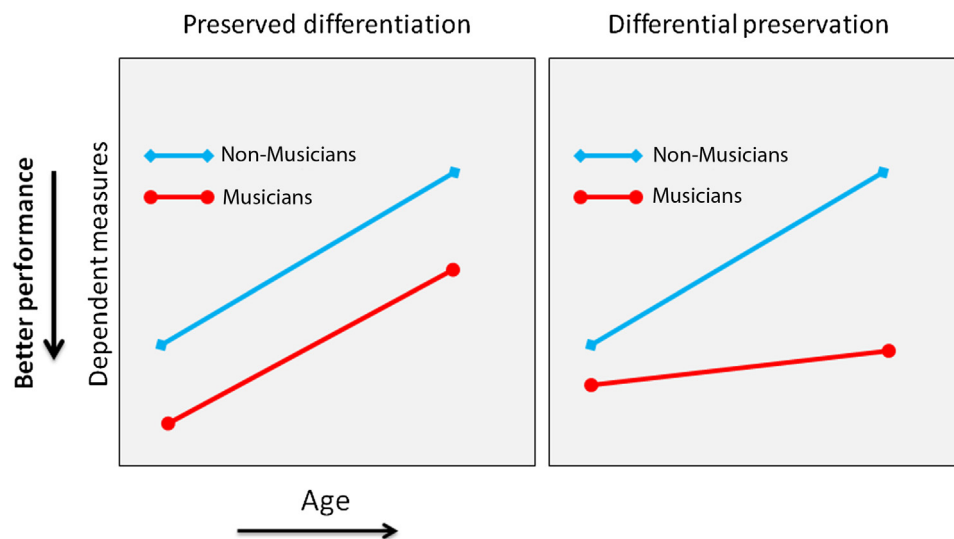


Fig. 1. Schematic illustration of preserved differentiation and differential preservation.

reduce the risk of cognitive degeneration or dementia later in life by engaging in cognitively stimulating activities (e.g., reading, learning, game playing) or being physically or socially active (Scarmeas and Stern, 2003; Stern et al., 2005). There is evidence that higher educational and occupational achievements (Qiu et al., 2001) or bilingualism attenuate the negative effects of aging on cognitive abilities (Bialystok et al., 2007). These findings suggest that enriched experiences and higher achievement engender a 'cognitive reserve'¹ that can delay age-related cognitive decline. Continued engagement in stimulating activities might act to maintain or enhance this reserve of cognitive abilities. It is therefore possible that lifestyles which demand an acute auditory system (e.g., being a musician) may enhance cognitive reserve which in turn could mitigate some of the age-related decline in auditory processing abilities (e.g., following a conversation in noisy environment such as a restaurant). Musical training not only engages the auditory system, but also involves auditory-motor coordination, audio-visual integration, and requires learning the implicit and/or explicit "rules" that govern the musical system (for a review see, Herholz and Zatorre, 2012). In children, there is ample evidence that the benefits of musical training are not limited to musical performance but can also transfer to other auditory and cognitive domains (e.g., Moreno et al., 2011; Rauscher et al., 1997; Schellenberg, 2004, 2011). Musicians may therefore be an excellent model to study cognitive reserve, especially in terms of age-related decline in processing auditory information (Wan and Schlaug, 2010).

When examining the potential benefit of musical training in mitigating age-related decline on cognitive, perceptual, or neurophysiological measures, two patterns of data may emerge (Fig. 1). The first pattern is that of a preserved differentiation which is characterized by main effects of experience (i.e., training) without interactions with age (Andrews et al., 1998; Meinz, 2000; Salthouse, 2006). Here, experts perform better than non-experts, but the difference is equal across the lifespan. The second pattern is that of differential preservation, which is characterized by interactions between age and the amount of training, where the rate

of age-related decline on a given task is slower in experts (Krampe and Ericsson, 1996; Salthouse, 2006). Importantly, only differential preservation is indicative of a protective effect of expertise because it indicates an additive benefit of experience over time (Salthouse, 2006). This differential preservation hypothesis is supported by computational models that have simulated normal aging. For instance, Mireles and Charness (2002) generated a series of neural network simulations to assess the impact of memory skills in a chess game. First, they demonstrated that aging could be simulated by progressively adding neural noise to the network. This is consistent with the neural-noise hypothesis (Welford, 1981), which posits that cognitive decline in aging is accompanied by a decrease in signal-to-noise ratio in the central nervous system. More importantly, Mireles and Charness (2002) found that increasing knowledge of the problem (in the simulated neural network) improved the performance of the network and offset age-related decline in performance (demonstrating differential preservation). This model is consistent with empirical findings showing that engagement in physically and intellectually stimulating activity can mitigate age-related decline in cognitive functions. Consequently, one would anticipate that aurally demanding activities (e.g., musical training) may also potentially offset age-related declines in auditory perception and cognition.

In this review, we explore the notion that lifelong musicianship mitigates age-related decline in auditory perception and cognition. We review studies that have examined the potential benefits of musical training in auditory cognition in young and older adults with an emphasis on auditory scene analysis (i.e., the perceptual process of creating a mental representation of the auditory environment). Though auditory scene analysis itself is a specialized and somewhat circumscribed area of research, it provides a means for investigating and understanding higher auditory functions (e.g., speech and music perception) as well as natural stress to the hearing system faced in the everyday real-world. Indeed, for effective speech understanding, listeners must rely on the perceptual mechanisms that group together sound elements coming from one source (i.e., one speaker) and segregate those arising from other sources (other speakers). More importantly, auditory scene analysis allows us to transform the incoming acoustic waveform into "probable" sound objects (i.e., mental representations of these sound-emitting elements) that correspond to the events that produced them (for reviews see, Alain and Bernstein, 2008; Bregman,

¹ Here, the term "cognitive reserve" refers to the brain's ability to optimize normal performance on measures of thinking abilities (e.g., IQ test) despite neuropathological damage.

1990; Carlyon, 2004; Ciocca, 2008). The fact that listeners can focus attention on one person speaking in the presence of other talkers indicates that the perceptual system is generally successful at grouping sound elements from one source and segregating them from others. In the following sections we attempt to answer the following questions. Does aging impair auditory scene analysis? Does musical training improve auditory scene analysis and if so, does it mitigate age-related changes in auditory perception and cognition? Answering these questions will help guide further research in assessing the potential use of musical training as a means to prevent age-related decline in auditory cognition and will highlight the role music training plays in promoting and preserving healthy aging. Before beginning to answer these questions, we briefly review the literature on auditory scene analysis.

2. Auditory scene analysis

Our typical environment is acoustically complex. At any given moment, we might be surrounded by multiple sound-generating elements (e.g., a computer fan, a radio playing music, or a group of people speaking) and several of these elements might be operating simultaneously. In order to make sense of this environment, the auditory system must group and segregate components of the auditory scene into separate mental representations called auditory streams or objects (Bregman, 1990). This process is known as auditory scene analysis, and involves perceptually organizing our environment along temporal and spectral dimensions (Bregman, 1990). Organization along the temporal dimension entails sequential grouping of acoustic input over several seconds (sequential sound integration/segregation), whereas organization along the spectral dimension entails grouping and segregating acoustic input from simultaneous sound sources based on spectral analysis within hundreds of milliseconds (concurrent sound integration/segregation).

The concept of auditory scene analysis is analogous to visual scene analysis in that it seeks to explain how the incoming sensory data are perceptually organized into meaningful units (i.e., objects). Interestingly, Gestalt laws of organization such as physical similarity, temporal proximity, and good continuity (Köhler, 1947), which were introduced to explain the perceptual organization of visual objects, utilize organizational principles that can be applied in the auditory domain. That is, sounds that have similar onsets, intensities, and harmonically-related frequencies are more likely to be perceived as coming from the same source than are sounds that begin at different times, and/or differ in intensity and/or frequency. In the auditory domain, many of these processes are considered automatic or 'primitive' because they can be found in infants (Folland et al., 2012; Winkler et al., 2003) and animals such as birds (Hulse et al., 1997; Itatani and Klump, 2009; MacDougall-Shackleton et al., 1998) and monkeys (Fishman and Steinschneider, 2010; Fishman et al., 2001). The outcome of this automatic analysis may then be subjected to controlled (i.e., top-down) processes. Whereas automatic processes group sounds based on physical similarity, controlled schema-driven processes use prior knowledge to make more "informed" solutions. As such, schema-driven processes depend on a comparison of the incoming acoustic information to representations of previous acoustic experiences acquired through learning. The use of prior knowledge is particularly evident in adverse listening situations such as the cocktail party situation (i.e., listening to a single speaker in a crowded and noisy room). For example, a sentence's final word embedded in noise is more easily identified when it is contextually predictable than when it is unpredictable (Pichora-Fuller et al., 1995). Thus, schema-driven processes provide a way to resolve perceptual ambiguity in complex listening situations.

While hearing is a *sense*, listening is a *skill* that depends on additional abilities including attention and memory. To be a good listener, one must be able to parse the incoming acoustic data into separate sound objects so that attention can be allocated to the task-relevant auditory object/stream, while ignoring task-irrelevant sounds. Accordingly, higher-level processes, such as attention, play an important role in auditory scene analysis (Alain and Bernstein, 2008; Carlyon, 2004). Selective attention can be used to listen for less salient sound objects that might otherwise go unnoticed in an adverse listening situation. Moreover, selective attention may promote audio-visual integration that in turn facilitates perception of weak auditory signals (Helfer and Freyman, 2005; Sommers et al., 2005; Winkler et al., 2009). Attention to a particular set of sounds (e.g., a talker in a crowded room) also activates internalized schemata or "templates" against which incoming acoustic data can be compared to ease sound recognition and identification (Pichora-Fuller et al., 1995). These examples emphasize the dynamic nature of scene analysis and speech-in-noise (SIN) comprehension in which listeners capitalize on both data-driven (bottom-up) and top-down controlled processes to generate a coherent interpretation of their surrounding acoustic environment.

3. Aging and auditory scene analysis

Older adults have greater difficulty understanding speech in adverse listening situations such as in the presence of reverberation (Gordon-Salant and Fitzgibbons, 1993; Middelweerd et al., 1990), or when the competing signals are voices rather than homogeneous background noise (Duquesnoy, 1983a, 1983b; Helfer and Freyman, 2008; Pichora-Fuller et al., 1995; Schneider et al., 2010). The difficulties commonly observed in older individuals may be related to problems in "breaking" the acoustic wave into its various constituents (i.e., sound sources). Understanding how speech signals are translated from external acoustic energy to internal auditory "objects", and how aging affects this process, is essential for the design of more effective therapeutic interventions to improve quality of life in older listeners.

Hearing problems in the elderly are rooted in two main pathologies: (i) inner ear dysfunction that often results in bilateral sensorineural hearing loss, primarily at high frequencies with little or moderate loss at low frequencies (i.e., presbycusis) and (ii) abnormal central auditory processing in the ascending auditory pathways and primary and associative auditory areas. Central auditory processing dysfunction typically causes a speech comprehension deficit that is more severe than would be expected solely due to age-related changes in the inner ear (i.e., cochlea). For instance, impaired SIN comprehension is often present despite clinically normal audiometric thresholds (Divenyi and Haupt, 1997; Frisina and Frisina, 1997; Middelweerd et al., 1990) and hearing aids provide little benefit to SIN understanding despite restoring hearing thresholds to normal levels (Chmiel and Jerger, 1996). Hearing status does not always interact with age, suggesting that these two factors might be independent sources contributing to difficulties understanding SIN (Gordon-Salant and Fitzgibbons, 2004; Humes and Christopherson, 1991). Lastly, older adults are more impacted by informational masking compared to younger adults (Schneider et al., 2007). For example, older adults have greater difficulty when background noise is meaningful compared to meaningless speech (e.g., foreign speech or speech played backwards) (Larsby et al., 2008; Rossi-Katz and Arehart, 2009; Tun et al., 2002).

Since reduced audibility fails to adequately account for speech understanding deficits, scientific interest has progressively shifted toward identifying other contributing factors to the SIN problems observed in older adults. These findings include a failure to

segregate a mixture of sounds (Alain and McDonald, 2007; Alain et al., 2006; Snyder and Alain, 2005), deficits in filtering out task-irrelevant stimuli (Gazzaley et al., 2005; Schneider et al., 2007), deficits in working memory (Gordon-Salant and Fitzgibbons, 1997), and reduced speed of processing (Humes, 2007; Salthouse, 1996). The importance of “non-auditory” factors (e.g., attention) in SIN understanding is even more apparent when considering neuro-imaging findings. For instance, studies using functional magnetic resonance imaging (fMRI) have found correlations between activity in the brain’s attentional network (e.g., prefrontal cortex) and performance on a SIN task (Wong et al., 2009). Age-related changes in prefrontal activity appear to be partly related to changes in cortical thickness, which has also been found to be a significant predictor of performance on the SIN test in older adults (Wong et al., 2010). Even when there is no age-related difference in word recognition, there are age-related changes in brain activity in the left middle frontal gyrus (MFG) and anterior cingulate regions (Wong et al., 2010). For instance, older adults had greater activations in those brain regions when words were most intelligible. This is in contrast to younger adults who only engaged those regions when words were minimally intelligible (Kuchinsky et al., 2012). In older adults, these observations were paralleled by reduced gray matter volume within temporal lobe regions responsive to word intelligibility, which significantly predicted left MFG activity, even after controlling for total gray matter volume (Kuchinsky et al., 2012). This suggests that in older adults, declining structural integrity of brain regions responsive to speech leads to the recruitment of frontal regions when words are easily understood. Together, these findings are consistent with a decline-compensation hypothesis (Wong et al., 2009, 2010), in which deficits in sensory processing caused by normal aging can be counteracted by recruitment of more general cognitive areas as a means of compensation. That is, when the peripheral and central auditory systems cannot effectively process speech, prefrontal regions can compensate to facilitate SIN understanding.

Clinically, age-related reorganization of the relative contribution of sensory and supra-modal brain areas expands treatment possibilities for age-related decline in SIN tasks beyond peripheral hearing aids to include auditory training strategies that might target plasticity in large neural networks. In the context of music and the aging brain, one could easily imagine that musical training would provide musicians (professional and amateur alike) with strategies that may allow them to more easily tune out task-irrelevant sounds (turn down the noise). In other words, musical training may create a cognitive reserve, which would allow older musicians to maintain auditory-cognitive skills (i.e., listening abilities) in advanced age.

This cognitive reserve may help compensate for an error-prone perceptual system that leaves older adults with an impoverished representation of the auditory environment. Age-related hearing loss likely results in poor and “noisy” signals being delivered to the central nervous system, which would interfere with central auditory processing. Evidence from animal research supports a relationship between sensorineural hearing loss and increased neural excitability within the ascending auditory pathway (Willott and Lu, 1982) and primary auditory cortex (Kotak et al., 2005), which likely reflects deficits in inhibition (e.g., Kotak et al., 2005; Willott and Lu, 1982; Caspary et al., 1995, 2005). Converging evidence from human studies (e.g., Keppler et al., 2010; Kim et al., 2002; Parthasarathy, 2001; Yilmaz et al., 2007) reveal decreased otoacoustic emission amplitude as well as an age-related decline in contralateral suppression (i.e., smaller otoacoustic response when noise is presented to the contralateral ear), which suggest that aging also impairs inhibitory functions within the efferent auditory pathway. Furthermore, older adults exhibit increased variability, and reduced

phase locking and amplitude of brainstem responses to speech sounds compared to younger adults (Anderson et al., 2012). There is also evidence for age-related changes in internal neuronal noise as measured with fMRI (Garrett et al., 2011), which could potentially affect auditory processing. By extension, one can imagine that the initial distortion in neural encoding of the acoustic waveform would lead to further reductions in fidelity as the signal is submitted to subsequent stages of analyses, ultimately resulting in the disruption of higher-order processes such as speech comprehension. Specifically, the degradation or absence of certain acoustic cues would impair the perceiver’s ability to adequately separate the spectral components of the target speech event from other events occurring within the same auditory scene, thereby making speech perception more difficult.

One hypothesis put forward by our group is that older adults’ difficulty in understanding SIN is related to a failure of perceptual organization of the auditory environment (Alain et al., 2006). Given that speech perception problems arise primarily in complex listening situations where more than one sound source is active, we reasoned that aging may affect low-level automatic processes that detect, group, and/or segregate sounds that are similar in physical attributes (such as frequency, intensity, and location) as well as higher-level schema-driven processes that reflect listeners’ experience and knowledge of the auditory environment. In the subsequent sections, we examine how age affects the perceptual organization of sound elements that occur at the same time (i.e. concurrent sound segregation) and the grouping of discrete sound elements over time (e.g., syllables, words) into streams (i.e., sequential sound segregation).

3.1. Concurrent sound segregation

In social gatherings, human listeners must perceptually integrate the simultaneous sounds originating from one person’s voice (e.g., fundamental frequency (f_0) and harmonics) and segregate those of other talkers. The segregation of concurrent speech sounds is promoted by difference in spectral pattern (i.e., harmonicity), spatial location, and onset asynchrony (e.g., Alain, 2007; Carlyon, 2004; Ciocca, 2008). In the laboratory, the perception of concurrent sound objects can be induced by mistuning one spectral component (i.e., harmonic) from an otherwise periodic harmonic complex tone. Low harmonics mistuned by about 4–6% of their original value stand out from the harmonic complex so that listeners report hearing two sounds: a complex tone and another sound with a pure-tone quality (e.g., Alain et al., 2001a; Moore et al., 1986). Not surprisingly, harmonicity is an important acoustic cue for segregating concurrent speech sounds. This can be demonstrated with the double vowel paradigm where differences in f_0 cause inharmonic relationships between spectral components of the two vowels thereby easing their separation and identification (e.g., Assmann and Summerfield, 1994; Chalikia and Bregman, 1989). In addition to harmonicity, differences in vowel location (Drennan et al., 2003; Du et al., 2011; Shackleton and Meddis, 1992) and onset asynchrony also yield improvement in the identification of both vowels (Hedrick and Madix, 2009; Lentz and Marsh, 2006).

Evidence from scalp-recordings of event-related brain potentials (ERPs) suggests that the perception of concurrent sound objects may occur independently of attention (Alain and Izenberg, 2003; Alain et al., 2002; Dyson et al., 2005) and likely involves primary and associative auditory cortices (Dyson and Alain, 2004). Fig. 2 shows ERPs elicited by tuned and mistuned stimuli and their difference wave. This difference wave illustrates an object-related negativity (ORN) that overlaps the N1–P2 response, and is related to the presence of a second auditory object. In addition to the ORN, a second difference wave, referred to as P400, emerges only when a

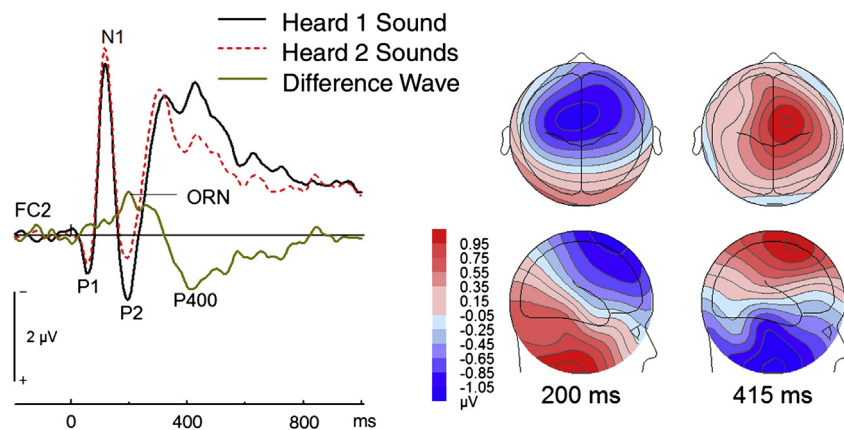


Fig. 2. Event-related potentials elicited by harmonic complex tones. The left panel shows the ERPs elicited by a 4% mistuned harmonic when participants reported hearing a single sound object (solid black) and when the same participants reported hearing two concurrent sound objects (i.e., a buzz plus another sound with a pure-tone quality; dotted red). The perception of two concurrent sound objects coincided with an object-related negativity (ORN) and a positive wave peaking at about 400 ms after sound onset, which are best illustrated in the difference wave (solid gold). The right panel shows isocontour maps for the ORN and the P400 wave. In both cases, the amplitude distribution is consistent with generators located in the auditory cortex along the superior temporal plane. Unpublished data from Alain et al. (2001a).

listener is asked to indicate whether they hear one or two sounds simultaneously. Accordingly, the P400 is likely related to attention-dependent cognitive processing of a second auditory object, while the ORN reflects automatic, attention-independent processing of the mistuned harmonic. Concurrent sound segregation may involve neurons sensitive to equal spacing between tonal elements (Roberts, 1998; Roberts and Brunstrom, 1998) which, in turn, could be used to build a harmonic sieve or template (Bidelman and Krishnan, 2009; Hartmann et al., 1990; Lin and Hartmann, 1998). That is, neurons sensitive to periodicity could act as a series of filters that allow harmonically-related partials (i.e., components sharing a common f_0) to group together into a single auditory object and the mistuned partial to form a separate representation.

Age-related decline in concurrent sound segregation may have dramatic consequences for speech understanding, particularly in complex listening environments. For instance, older adults who have difficulty understanding speech in noise also show increased thresholds for detecting a mistuned harmonic (Alain et al., 2001b). Moreover, older adults are less likely to report hearing a mistuned harmonic as a separate sound than young adults, especially if the harmonic-complex tone is short in duration (i.e., 40 ms). This age-related difference in perception coincided with a reduced ORN amplitude in older adults (Alain and McDonald, 2007). For longer duration sounds (e.g., 200 ms), the increased likelihood of reporting two concurrent sound objects as a function of mistuning was comparable for young and older adults as was the amplitude of the ORN (Alain et al., 2012). Similar to impairment in mistuned harmonic detection, older adults also have difficulty identifying simultaneously presented vowels (Snyder and Alain, 2005; Vongpaisal and Pichora-Fuller, 2007). This perceptual deficit coincides with a reduction in neural activity registering a difference in f_0 between the two vowels (Snyder and Alain, 2005).

These age-related changes in concurrent sound perception may be related to a broadening of auditory filters (Patterson et al., 1982; Peters and Moore, 1992) as well as a decrease in phase-locked neural activity (e.g., Leigh-Paffenroth and Fowler, 2006; Parthasarathy and Bartlett, 2012; Parthasarathy et al., 2010). Listeners who find it difficult to detect mistuning may assimilate one or more frequency components coming from secondary sound sources into the target signal, simply because they fail to detect or recognize frequency components that are not integer multiples of the target signal's fundamental frequency. The inclusion of extraneous frequency components into the target signal would then lead

to concomitant errors in perception. The greater age-related difference for short compared to long duration sounds may be related to a general slowing for processing acoustic information (Finkel et al., 2007; Salthouse, 1996), which could cause a broadening of the temporal integration window. In the present context, the temporal integration window of an auditory evoked response is defined as the minimal stimulus duration that produces maximal amplitude. Alternatively, independent of increased "sluggishness" in auditory processing, the system may become less efficient with advancing age due to an elevation in internal neuronal noise (Garrett et al., 2011). That is, for shorter stimulus durations there is less information to use for subsequent processing, thereby increasing uncertainty in signal detection and analysis.

3.2. Sequential sound segregation

As a real-world auditory scene unfolds over time, observers are faced with the challenge of tracking acoustic elements that belong to various sound-emitting objects. In the laboratory, stream segregation can be investigated using interleaved pure-tone patterns such as an "ABA—ABA—" pattern in which "A" and "B" are tones of different frequencies and "—" is a silent interval. Higher presentation rates, and larger frequency differences between the A and B tone results in faster segregation of the perceptual streams (i.e., one of As and one of Bs). The fusion or coherence boundary refers to the frequency separation where individuals perceive a single stream of sounds with a galloping rhythm, whereas the fission or segregation boundary refers to the point where listeners can no longer hear the galloping rhythm and report hearing the sounds as coming from two different sources (van Noorden, 1975). The perception of two streams does not occur instantly but instead *builds up* and only after several seconds does the pattern of alternating tones split into two distinct perceptual streams (Bregman, 1978). Scalp recording of ERPs in humans (Gutschalk et al., 2005, 2007; Snyder et al., 2006) and single-unit responses in mammalian auditory brainstem (Pressnitzer et al., 2008) suggest that stream segregation depend on neural activity in auditory cortices and subcortical nuclei (e.g., cochlear nucleus), which reflects the frequency difference between the A and B tones.

On the surface, auditory stream segregation is a relatively simple phenomenon. However, there is increasing evidence that performance in this simple ABA paradigm may be related to dyslexia (Dole et al., 2012; Goll et al., 2010; Sutter et al., 2000) and speech

comprehension in adverse listening situations. For instance, Hong and Turner (2006) found that cochlear implant users who performed better on a streaming task also performed better on speech recognition in noise, demonstrating the important relationship between streaming and SIN understanding. Prior research has also shown that auditory stream segregation may be impeded by moderate sensorineural hearing loss (Rose and Moore, 1997, 2005; Stainsby et al., 2004) and that speech reception thresholds correlate with fusion thresholds (Mackersie et al., 2001). Hence, by studying how individuals perceptually organize sequential events, we may better understand why older individuals experience difficulties understanding target speech in the presence of other interfering talkers.

Given that older adults may have elevated (although still clinically 'normal') hearing thresholds compared to younger adults, one might expect concomitant age-related decline in auditory stream segregation. Surprisingly, older adults with normal audiometric thresholds typically have comparable fusion and fission thresholds to younger individuals (Alain et al., 1996; Snyder and Alain, 2007; Trainor and Trehub, 1989), suggesting that auditory scene analysis that relies on sequential processing is little affected by normal aging. However, when harmonic complex tones are used instead of pure tones, young adults perceive more streaming than do older adults (Grimault et al., 2001). The above studies demonstrate inconsistencies in the effects of aging on segregation of sequential sound patterns. They suggest that age-related impairment in sequential stream segregation may only become apparent when complex sounds are used instead of pure tones. Hence, it is important that future studies employ spectrally rich sounds in order to reveal age-related effects on stream segregation. Given that spoken language is complex and spectrally rich, using complex and spectrally rich signals in the laboratory will increase the ecological validity of experimental findings. Furthermore, there is evidence that the perceptual organization of speech sounds may not always follow the same grouping principles as those commonly used to account for the perceptual organization of non-verbal material (Remez et al., 1994). In fact, speech produced by a single speaker often violates grouping principles such as similarity and good continuation. This violation is due to aspects of vocal production, including vocal articulators (i.e., closures when articulating plosives and affricates) (Roberts et al., 2010). Complex sounds such as those used in spoken communication (e.g., vowels) offer a way to examine the relative influence of certain acoustic cues found in speech (e.g., f_0 and formant transitions) that play an important role in segregating speech from background noise.

Dorman et al. (1975) examined the influence of vowel formant differences on streaming using repeating four-item vowel sequences. The vowels shared the same f_0 but the order of the four vowels was manipulated to promote grouping based on the formant transitions (i.e., the formants were either continuous like in natural speech or unnatural and discontinuous). They found that the ability to perceive the items in the correct order was greater when smooth formant transitions between the vowels were preserved and that the sequence was perceived as a single auditory stream. Misjudgment of repeating vowels was explained in terms of stream segregation, triggered by the discontinuity in formant transitions of adjacent vowels (Dorman et al., 1975). Subsequent studies using repeating three- (Nooteboom et al., 1978) or six-item (Gaudrain et al., 2008) vowel sequences have also shown that increasing the f_0 difference of adjacent vowels promotes the segregation of the speech sequences into two separate streams.

The effects of age on listeners' tendency to group naturally-produced speech tokens into one or two auditory streams was recently investigated in two separate experiments by our group (Hutka et al., 2013). Younger and older adults were presented with

sequences of four vowel sounds, which were arranged with either continuous or discontinuous first-formant transitions between adjacent vowels to promote or inhibit sequential grouping. In the first experiment, participants were less accurate at identifying vowel order and more likely to report hearing two streams when the vowel transitions were discontinuous rather than continuous. Overall, older adults were less accurate than younger adults and this age difference tended to be greater for continuous than discontinuous stimuli. In a second experiment, participants indicated whether they noticed a change in the rhythm of a four-vowel pattern presented repeatedly. Young adults' thresholds for detecting changes in speech rhythm were lower when adjacent formants were continuous across consecutive vowels. This benefit was not observed in older adults whose thresholds were little affected by the type of formant transition. These two experiments provide converging evidence for an age-related deficit in exploiting first-formant information between consecutive vowels, which impedes older adults' ability to sequentially group speech sounds over time. Continuing this line of research will help to build an integrated theory of auditory scene analysis and cognitive aging as related to sequential streaming. To this aim, future studies could examine analogs between the ABA-paradigm and those involving naturalistic vowel sounds to understand the unique relationship between aging, sequential auditory streaming, and the perception of speech.

4. Benefits of musical training in young adults

The benefits of musical training on perceptual and cognitive skills have been investigated extensively in children and young adults. Not surprisingly, musical training has been shown to enhance performance in auditory tasks that require making fine-grained discrimination between auditory stimuli (Kishon-Rabin et al., 2001). For instance, musicians exhibit enhanced temporal processing as they have superior ability at detecting silent gaps in otherwise continuous sound, improved discrimination of the duration of auditory events, and superior ability to detect violations in otherwise isochronous rhythms (Rammsayer and Altenmüller, 2006). In addition, musicians have advantages in spectral processing as they have improved ability to detect violations in musical pitch patterns (Bidelman et al., 2011a; Koelsch et al., 1999; Tervaniemi et al., 2005), smaller frequency difference limens (Bidelman et al., 2011b; Kishon-Rabin et al., 2001; Michey et al., 2006), and a reduced susceptibility to timbral influences on pitch perception (Pitt, 1994). These perceptual benefits endow musicians with enhanced abilities in the perceptual organization of sounds.

Indeed, there is evidence that musical training provides a significant advantage in complex listening situations that require listeners to parse a complex auditory scene comprised of multiple sound objects. Consequently, it has been suggested that musical training influences both sequential and concurrent sound segregation processes. Previous work has shown that younger musicians are able to perceptually maintain auditory streams longer (Beauvois and Meddis, 1997), showed a greater tendency to group sounds based on good continuation than non-musicians (van Zuijen et al., 2004), and have enhanced abilities to separate simultaneously occurring sounds (Zendel and Alain, 2009). Zendel and Alain (2009) presented participants with complex sounds that had either all the harmonics in-tune or the second harmonic mistuned; the probability of hearing two sounds simultaneously increased with mistuning. This effect was greater in musicians than non-musicians, and was paralleled by an ORN that was larger and peaked earlier in musicians. Segregation of the mistuned harmonic from the harmonic series also coincided with a late-positive wave (P400), whose amplitude was larger in musicians than in non-

musicians. In a related study, Vliegen and Oxenham (1999) investigated sequential stream segregation in the absence of spectral cues. Participants were either musicians (greater than four years of formal, instrumental training) or non-musicians. All participants experienced three spectral conditions: pure tones; harmonic complexes with rich spectral information (filtered with a bandpass region between 500 and 2000 Hz); and “unresolved” harmonic complexes with severely limited spectral information (filtered with a bandpass region chosen so that only harmonics above the tenth would be passed by the filter). As compared to non-musicians, Vliegen and Oxenham (1999) found that musicians had less variable performance in all spectral conditions, segregating two tones into two separate, perceptual streams when the f_0 interval exceeded four semitones. Vliegen and Oxenham (1999) posited that the musically-trained participants may have had less difficulty than non-musicians when relating the f_0 of a harmonic-complex tone to the pure tone corresponding to that frequency. This may be due to the extensive practice musicians have in analyzing incoming acoustic information (Vliegen and Oxenham, 1999). Indeed, musical training may act to provide a more robust internalized harmonic template which allows musicians to more successfully match sparse spectral information to a corresponding f_0 pitch (e.g., Bidelman and Krishnan, 2009; McDermott et al., 2010). Together, these findings thus suggest that musical training affects the processing necessary for sequential stream segregation.

More importantly, recent studies demonstrate that these music-induced benefits to auditory scene analysis transfer to improve listening performance in real-world situations (e.g., cocktail party scenarios). Indeed, amateur musicians with about 10 years of expertise show enhanced ability in identifying and discriminating target speech in the face of acoustic interferences including reverberation (Bidelman and Krishnan, 2010) and noise babble (Parbery-Clark et al., 2009). Bidelman and Krishnan (2010) found that perceptual discrimination for voice pitch and formant cues was roughly 2–4 times better (i.e., smaller difference limens) in musically-trained listeners than non-musician controls for vowel sounds presented in both quiet and in the presence of reverberation. These behavioral findings were corroborated by auditory brainstem recordings to clean and degraded speech, which revealed more robust and faithful neural responses in musicians relative to non-musicians. Complementary effects have been reported by Parbery-Clark et al. (2009) who observed that musicians could tolerate ~1 dB more noise than their non-musician counterparts in speech recognition. While the significance of this benefit may not be readily apparent, a 1 dB change in signal-to-noise ratio (SNR) can equate to an improvement in speech recognition performance by as much as 10–15% (Middelweerd et al., 1990). Although benefits for SIN comprehension are well-documented in younger adults with decades of musical training, demonstrating listening advantages in older adult musicians would be particularly germane to understanding the ubiquitous declines in speech recognition that often emerge with age (Crandell, 1991; Humes, 1996). Indeed, older adults often experience perceptual deficits in many aspects of auditory processing including frequency/intensity discrimination (He et al., 1998) and temporal resolution (e.g., gap detection, Strouse et al., 1998), both important psychophysical factors that relate to speech perception abilities (Gordon-Salant and Fitzgibbons, 1993; Moore, 2008).

In addition to changes in perceptual performance, musical training has also been shown to yield neuro-plastic change. For instance, cross-sectional studies using neuro-imaging techniques have shown that musicianship is associated with neuro-plastic changes in the auditory brainstem responses (Musacchia et al., 2007; Wong et al., 2007), auditory cortex (Gaser and Schlaug, 2003; Hyde et al., 2009b; Koelsch et al., 1999; Schlaug et al.,

1995; Schneider et al., 2002), motor cortex (Gaser and Schlaug, 2003), visuo-spatial brain areas (Gaser and Schlaug, 2003), as well as in higher-order brain areas involved in working memory and executive functions (Peretz and Zatorre, 2005). Longitudinal studies have yielded similar findings, suggesting that the differences between musicians and non-musicians are due to training rather than genetic differences (Fujioka et al., 2006; Hyde et al., 2009b). While musical training has been well-studied in young adults, few studies have examined its effects in older adults and even fewer have looked at the corresponding changes in neural activity. Given that musical training seems to strengthen acuity for basic auditory features (Bidelman et al., 2011c; Micheyl et al., 2006), and affects performance on some complex auditory processes (Vliegen and Oxenham, 1999; Zendel and Alain, 2009), it stands to reason that music engagement may prove to be an effective regimen to maintain or even improve listening skills in older adults. Hence, an intriguing question is whether playing a musical instrument during adulthood (or even perhaps only in childhood) can reduce the detrimental effects of normal aging on auditory perception and cognition (e.g., impaired speech perception in a noisy environment). In the next section, we turn to studies that have begun to tackle this research question.

5. Musical training as a means to mitigate age-related changes in auditory cognition

During the past decade, there has been a steady increase in research assessing the potential benefits of musical activities in improving various aspects of life including cognitive reserve in older adults (Dowling et al., 2008; Hirokawa, 2004; Koyama et al., 2009). This is due in part to studies suggesting that musical training (i.e., piano lessons) can enhance executive functioning and working memory in older adults (Bugos et al., 2007) and that expert musicians, compared to amateur musicians, experienced less age-related decline on speeded motor tasks related to music performance (Krampe and Ericsson, 1996). Moreover, evidence from cross-sectional studies suggests that continued engagement in music performance over a lifetime may slow age-related declines in auditory processing abilities including SIN perception (Parbery-Clark et al., 2011; Zendel and Alain, 2012). However, not all cognitive domains appear to be sensitive to musical training. For instance, the ability to recognize speeded or slowed melodies declined similarly with age in musicians and non-musicians (Andrews et al., 1998). Meinz (2000) found that memory and perceptual speed in musical situations declined with age in pianists, and that more experienced pianists performed better than non-musicians, but that all levels of pianists declined at the same rate. Although musical training does not always result in differential preservation for all cognitive (or even auditory) domains, musicians are nonetheless an excellent population to investigate whether musical training creates a cognitive reserve that helps older adults cope with age-related auditory deficits.

In a recent report from our group (Zendel and Alain, 2012), musicians and non-musicians participated in a series of auditory assessments including SIN testing (Fig. 3). Musicians were defined as individuals who began musical training prior to age 16, continued practicing music until the time of testing, and had an equivalent of at least six years of formal music lessons; non-musicians in the study did not play a musical instrument. Audiometric thresholds were comparable across age-matched participants thus ruling out the possibility that differences in hearing sensitivity might cloud the interpretation of our findings. Results showed that older musicians had a clear advantage over non-musicians in SIN performance. Parallel enhancements were seen in gap-detection thresholds. Importantly, the positive benefits of

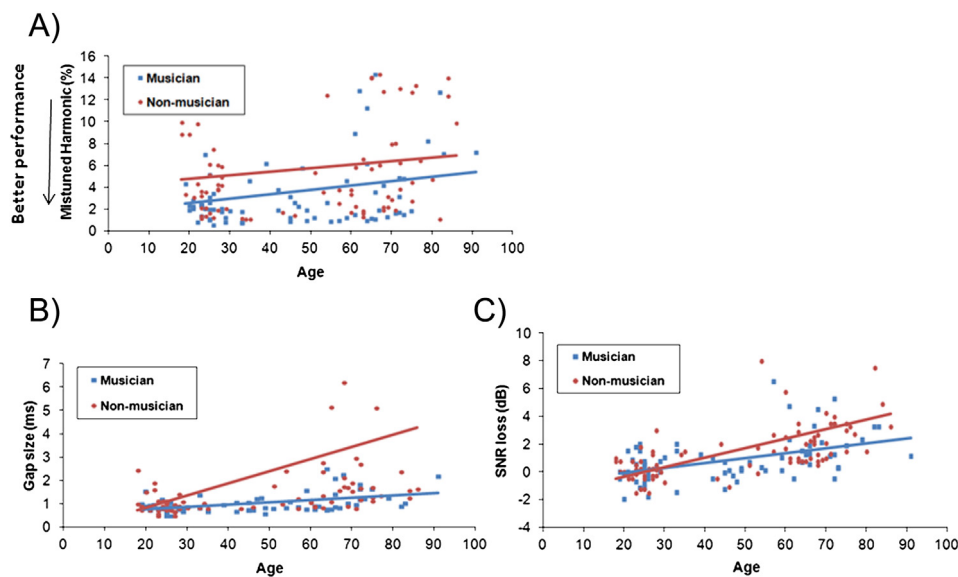


Fig. 3. Effects of musical training on auditory perceptual abilities. Data reported by Zendel and Alain (2012) consisting of 163 participants (73 musicians) with age ranging from 18 to 91 years. A) Thresholds for detecting inharmonicity in a complex sound using a two-alternative forced-choice procedure. Thresholds increased with age, and musicians had lower thresholds that remained constant throughout the lifespan. This is an example of preserved differentiation. B) Thresholds for detecting a silent gap embedded in the middle of a short duration sound (20 ms 1 kHz tone) using a two-alternative forced-choice procedure. The thresholds increased with age, but the effect of age on gap detection was greater in non-musicians. This is an example of differential preservation. C) Performance in the Quick SIN (standardized measure of the ability to understand speech in noisy environments). Thresholds for understanding speech in noise increase with age, but the effect of age was greater in non-musicians, revealing a differential preservation in listening skills needed to segregate and identify speech tokens embedded in multi-talker babble.

musical experience became more pronounced in older individuals, such that at age 70, older musicians were able to understand speech in a noisy environment as well as an average 50-year old non-musician. In addition, we also found older musicians to have better (i.e., lower) mistuned harmonic detection thresholds, indicating that musical training also influences the ability to segregate concurrent sound objects – a task which is often difficult for older listeners (Alain et al., 2001b; Grube et al., 2003). Because hearing sensitivity was controlled between groups, we posited that lifelong musicianship tunes *central auditory mechanisms* to yield positive functional benefits in auditory processing. Ultimately, our findings suggest that lifelong musicianship may delay and/or mitigate some age-related speech listening deficits including those necessary for robust auditory scene analysis. While the neurological underpinnings of these findings were not investigated at the time, recent work suggests that behavioral SIN benefits might be mediated by improved efficiency and/or precision in which musicians' brains transcribe the elements of speech within the early auditory pathway. For example, auditory brainstem responses to consonant-vowel speech sounds revealed less age-related neural delay in older musicians relative to older non-musicians (Parbery-Clark et al., 2012).

To further understand the benefits of lifelong musicianship to central auditory processing, we investigated the influence of lifelong musicianship on concurrent sound segregation and its underlying cortical neural correlates (Zendel and Alain, 2013). Again, we found behavioral advantages in musicians (both older and younger), who were better able to segregate a mistuned harmonic as a separate auditory object compared to their non-musician counterparts. Paralleling this perceptual improvement, neurophysiological data revealed enhanced P400 amplitudes in older musicians relative to age-matched controls, while no differences were observed in ORN amplitude. In contrast, younger musicians showed more robust magnitudes for both ORN and P400 components. Yet, perceptually, older and younger musicians did not differ with respect to their behavioral performance in mistuned harmonic

detection (Zendel and Alain, 2009, 2013). Together, these findings suggest that the lifelong benefit of musical training to auditory scene analysis may be related more to volitional, attention-dependent cognitive processing of acoustic information (as indexed by the P400) and not necessarily to pre-attentive, automatic processing of those features (as indexed by the ORN).

Evidence from neuropsychological studies shows that musical training and lifelong musicianship also enhance cognitive abilities not directly related to auditory processing. For instance, musicians aged between 45 and 65 also performed better than age-matched controls on an auditory working memory task (Parbery-Clark et al., 2011), a benefit that was not observed for a comparable visual working memory task (Parbery-Clark et al., 2011). Older adults (aged 60–83) with at least 10 years of musical experience performed better on a nonverbal memory task, the Boston naming test, and measures of speeded visual information processing (i.e., Trails A and B) (Hanna-Pladdy and MacKay, 2011). In a subsequent study, that controlled for general activity level, Hanna-Pladdy and Gajewski (2012) demonstrated that older musicians scored higher on tests of phonemic fluency, verbal working memory, verbal immediate recall, visuospatial judgment, and motor dexterity than older non-musicians. Interestingly, Sluming et al. (2002) found differential preservation of gray matter density in left inferior frontal gyrus, with non-musicians showing an age-related volume reduction while professional (orchestral) musicians showed no significant age-related changes in gray matter density. Using structural equation modeling, Anderson et al. (2013) showed that central processing and cognitive function predicted a significant proportion of variance in the ability to understand SIN. More importantly, past musical experience modulated the relative contributions of cognitive ability and lifestyle factors (e.g., physically and intellectually engaging activity) in the ability to understand SIN for older adults (aged 55–79). These findings suggest that musical training might create a cognitive reserve, which can delay age-related cognitive decline even in non-musical tasks (Amer et al., in press). This highlights the uniqueness of musical training in

enhancing perceptual and cognitive abilities beyond musical performance.

6. The necessity of causality and longevity for music-based remediation

Empirical work cited in the preceding sections demonstrates that musical training enhances auditory abilities in complex listening situations, and that these enhancements persist across the lifespan. While these studies are no doubt encouraging to promote music-based remediation programs, they have focused exclusively on highly-trained musicians with decades of musical expertise. Ultimately, the efficacy of music to effectively improve listening strategies and perceptual performance will depend on demonstrating a causal relationship between music training and auditory perceptual benefits over short-term periods.

One issue in a majority of the aforementioned studies, for example, is the difficulty to infer causality using quasi-experimental, cross-sectional designs. The degree of a musician's auditory perceptual and neurophysiological enhancements is often positively associated with the number of years of his/her musical training and negatively associated with the age at which training initiated (e.g., Parbery-Clark et al., 2009; Zendel and Alain, 2012). These types of correspondence hint that the benefits observed in these studies stem from neuro-plastic effects that are modulated by the amount of musical training and/or a sensitive period in childhood. Yet, current evidence is largely correlational; it remains possible that individuals who pursue music do so because they have natural enhancements in auditory perception. While care must be exercised when drawing causation from correlational data, these findings are corroborated by recent randomized, longitudinal training studies which demonstrate causal, experience-dependent effects of musical training at both behavioral and neurophysiological levels (for a review see, Herholz and Zatorre, 2012). Indeed, changes in brain morphology and physiology subserving auditory processing have been observed following even relatively short-term music lessons (1 year: Fujioka et al., 2006; 15 months: Hyde et al., 2009b; 2 weeks: Lappe et al., 2008; 9 months: Moreno et al., 2009). Importantly, these effects remain intact even after controlling for confounding factors (e.g., age, socioeconomic background, or music listening). Thus, true experimental manipulations have helped isolate musical training as the key ingredient which mediates these auditory benefits as opposed to other confounding or latent explanations involving self-selection or genetic predispositions (e.g., Ellis et al., 2012; Hyde et al., 2009b). These studies also demonstrate clear psychophysiological improvements in audition with relatively short-term musical training (i.e., <1 year).

Unfortunately, these studies typically do not involve a long-term follow-up, and thus, the longevity (i.e., “sticking power”) of these training regimens is unknown. Nevertheless, recent work suggests that the auditory neuroplasticity afforded by music training in childhood might be retained into adulthood, even when the music lessons are interrupted in early adolescence (Skoe and Kraus, 2012). Thus, even short-term musical lessons may promote positive functional changes in auditory processing that persist well beyond the termination of training. While these results are promising, future work is needed to fully validate short-term music-based training programs aimed to counteract age-related declines in auditory scene analysis and other complex listening abilities.

Critical questions also arise as to what intensity, duration, and exact content of a music-based instruction might provide the greatest auditory benefits. For example, it is likely that successful music-induced brain and behavioral effects documented for young adults and children (e.g., Fujioka et al., 2006; Hyde et al., 2009a; Moreno et al., 2011) may not yield the same degree of benefit in

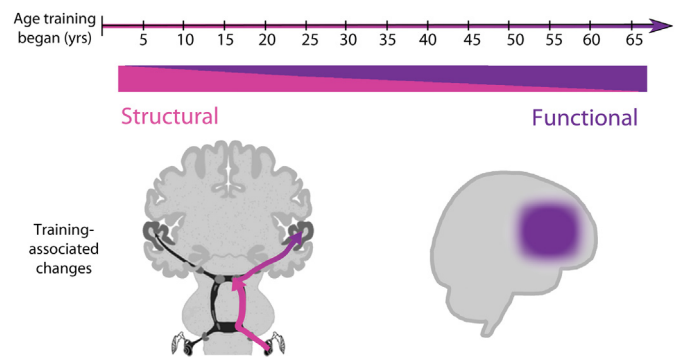


Fig. 4. Schematic showing how musical training might mitigate age-related changes in auditory perception and cognition. The model posits that musical training enhances perceptual and cognitive functioning via structural and functional changes in the brain. In this model, we assume a shift between the role of structural and functional changes in mitigating age-related changes in cognition. The earlier the onset of musical training the greater the structural changes and their potential impact in enhancing auditory processing early in life and maintaining these faculties later in life. After a “sensitive period” musical training is thought to enhance performance via functional changes that improve listening skills. The top shows a time scale for the onset of musical training. The earlier the training the greater the structural changes, the later the onset of musical training the greater the reliance on higher order brain areas and strategic listening skills. The bottom left shows a schematic of the ascending auditory pathway. The change in the color gradient indicates the putative impact of age-of-training onset on neurophysiological changes. The bottom right shows a lateral view of the brain. The Frontal areas are highlighted in purple to demonstrate that as age increase, musical training primarily mitigates age-related decline in auditory perception and cognition by recruitment of higher order brain areas (i.e., prefrontal cortex).

the older “less plastic” brain (Stiles, 2000). One might expect musical training in childhood to induce long-lasting neurophysiological changes that will provide older adults with an advantage in noisy listening environments. At the same time, we can also posit that if the musical training begins later in life, the balance will shift toward enhancing listening skills, which can then be used to segregate and attend to a conversation in noisy settings (Fig. 4). Moreover, while leisurely music listening may promote health and well-being in older individuals (e.g., mediating stress, reducing heart and respiratory activity, Bernardi et al., 2006), it is unlikely to have an efficacious impact on real-world auditory abilities. For musical training to transfer and benefit non-musical functions (e.g., SIN listening, auditory scene analysis), it is likely that an individual must be engaged with fairly intense instruction so as to promote both perceptual and cognitive forms of hierarchical processing. Indeed, the beneficial effects of musicianship have been attributed to the fact that musical training exerts plastic effects at both micro-(localized) and macro-scopic (network) levels of the brain (Wan and Schlaug, 2010) engaging a wide variety of multimodal functions. Such distributed plasticity may be responsible for musicians’ enhanced cognitive abilities observed in some reports, e.g., working memory, attention, and executive processes (Bialystok and Depape, 2009; Bidelman et al., 2013; Pallesen et al., 2010; Strait et al., 2010). Such a “global tuning” is unlikely to occur without active engagement under repetitive, intensified training. Thus, in addition to examining the long-term retention of music-related benefits and providing cognitive reserve, future work will need to assess the duration for which music regimens must be applied before yielding a lasting change in behavior. It is of course entirely plausible that the benefit of music training might vary in an age-dependent manner.

7. Concluding remarks

Older adults have difficulty processing rapid temporal fluctuations and segregating concurrent objects in the auditory environment. These perceptual deficits are thought to contribute to their

difficulties in auditory scene analysis, including perceiving speech-in-noise and parsing acoustic information into multiple streams. The presence of these deficits in the absence of measurable hearing loss indicates that the perceptual issues faced by older adults probably emerge as a result of changes to central (i.e., non-cochlear) auditory mechanisms. Studies indicate that musical training positively modifies central brain and behavioral mechanisms to provide robust, long-lasting improvements to auditory abilities across the lifespan. Intense and engaging short-term musical training programs may offer potential benefit to improve or at least offset the difficulties in complex listening experienced by older adults.

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