Hearing Research 308 (2014) 84–97

Contents lists available at ScienceDirect

Hearing Research

journal homepage: www.elsevier.com/locate/heares

Review

Examining neural plasticity and cognitive benefit through the unique lens of musical training

Sylvain Moreno [a], [b], *, Gavin M. Bidelman [c], [d]

[a] Rotman Research Institute, Baycrest Centre for Geriatric Care, Toronto, ON, Canada
[b] University of Toronto, Toronto, ON, Canada
[c] Institute for Intelligent Systems, University of Memphis, Memphis, TN, USA
[d] School of Communication Sciences & Disorders, University of Memphis, Memphis, TN, USA

ARTICLE INFO

Article history:
Received 19 January 2013
Received in revised form
14 September 2013
Accepted 19 September 2013
Available online 27 September 2013

ABSTRACT

Training programs aimed to alleviate or improve auditory-cognitive abilities have either experienced mixed success or remain to be fully validated. The limited benefits of such regimens are largely attributable to our weak understanding of (i) how (and which) interventions provide the most robust and long lasting improvements to cognitive and perceptual abilities and (ii) how the neural mechanisms which underlie such abilities are positively modified by certain activities and experience. Recent studies indicate that music training provides robust, long-lasting biological benefits to auditory function. Importantly, the behavioral advantages conferred by musical experience extend beyond simple enhancements to perceptual abilities and even impact non-auditory functions necessary for higher-order aspects of cognition (e.g., working memory, intelligence). Collectively, preliminary findings indicate that alternative forms of arts engagement (e.g., visual arts training) may not yield such widespread enhancements, suggesting that music expertise uniquely taps and refines a hierarchy of brain networks subserving a variety of auditory as well as domain-general cognitive mechanisms. We infer that transfer from specific music experience to broad cognitive benefit might be mediated by the degree to which a listener's musical training tunes lower- (e.g., perceptual) and higher-order executive functions, and the coordination between these processes. Ultimately, understanding the broad impact of music on the brain will not only provide a more holistic picture of auditory processing and plasticity, but may help inform and tailor remediation and training programs designed to improve perceptual and cognitive benefits in human listeners.

This article is part of a Special Issue entitled <Music: A window into the hearing brain>.

1. Introduction

One of the modern goals of neuroscience is to understand the breadth and extent of brain plasticity. Neural plasticity is defined as the ability of the brain to modify itself or be altered by the external environment. One avenue used to study this phenomenon in human populations is the investigation of specific life experiences. Typically, training regimens induce changes in the brain specific to the area of study: auditory training changes how the brain processes specific sound stimuli (Trainor et al., 2003); juggling modifies visual-spatial brain areas (Draganski et al., 2004); and driving modifies the structures which process the spatial representations necessary to navigate busy streets (Maguire et al., 2000; Draganski & May, 2008). While these studies demonstrate that specific experience can lead to specific functional changes in the brain, it is the transfer of skill, i.e., the ability of specific experience/training to influence seemingly unrelated processes, which is of central interest to the fields of cognitive neuroscience, education, and clinical rehabilitation.

A distinction is often made between *near-* and *far-transfer* of skill. Near transfer occurs between highly similar contexts and domains, whereas far-transfer occurs between domains that have less in common (Barnett and Ceci, 2002). While tasks are usually effective in training specific skills practiced (near-transfer), most fail at generalizing to other cognitive faculties, or when applied to different skills (i.e., they lack far-transfer). Previous training programs focused on transfer have reported mixed results (Detterman and Sternberg, 1982). Nevertheless, a handful of studies have found

---

* Corresponding author. Rotman Research Institute, Baycrest, 3560 Bathurst Street, Toronto, ON M6A 2E1, Canada. Tel.: +1 416 785 2500x3642; fax: +1 901 569 4326.

E-mail address: smoreno@research.baycrest.org (S. Moreno).

0378-5955/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.heares.2013.09.012

small improvements in performance on untrained tasks (e.g., problem-solving tasks; Lovett and Anderson, 1994), whereas other studies have found no transfer to untrained tasks (Olesen et al., 2004). Unfortunately, the training paradigms in many of these previous studies lack a pedagogical foundation, and would be difficult to apply in non-laboratory settings, or toward long-term behavioral change. Finding regimens applicable to real world scenarios that can be implemented in realistic environments (e.g., at home or in the classroom) is crucial to the success of training protocols aimed to improve auditory and other cognitive functions (Craik and Rose, 2012). In the framework of training and transfer, many investigators have recently focused on the effects of musical activity and its potential benefits on both neurophysiology and behavior.

Two decades ago, the influence of music on behavior first became a topic of great interest with the publication of the so-called “Mozart effect.” Rauscher et al. (1993) investigated the effects of brief music exposure on cognition. Compared to subjects who listened to a relaxation tape or those who sat in silence, subjects who listened to 10-min of a Mozart piano sonata showed short-term improvement in spatial-reasoning abilities (subsequently dubbed the “Mozart effect” by the media). Translated into a spatial IQ-score, this benefit corresponded to approximately eight points (i.e., half a standard deviation). A popular conclusion of this work became the motto: “music makes you smarter.” This startling finding attracted considerable attention and misconceptions by the popular press, politicians, and research community alike. However, questions were subsequently raised pertaining to the validity of the findings and several alternative interpretations have been proposed including explanations based on mood or arousal effects (for reviews, see Pietschnig et al., 2010; Schellenberg, 2012). Due to these alternative interpretations and further studies investigating this finding, the Mozart effect has been largely debunked. However, this study motivated a series of empirical investigations which used more rigorous designs examining the effects of music on the human nervous system.

More recent studies that focus specifically on music training have indeed identified robust skill transfer (Schellenberg, 2004). A series of cross-sectional studies have demonstrated neuroanatomical and functional changes in a wide variety of brain regions in musically trained listeners relative to musically naïve listeners. The morphological differences in the brains of musicians also manifest in improved behaviors, auditory and non-auditory abilities alike; enhancements have been observed, for example, in musicians' perceptual, language, and high-level cognitive processing, e.g., working memory (mainly auditory) and verbal intelligence (for recent reviews, see Moreno, 2009; Kraus and Chandrasekaran, 2010; Herholz and Zatorre, 2012). It should be noted, however, that conclusions from these studies are typically drawn by comparing experts (musicians) with non-experts (nonmusicians), making it difficult to dissociate nature versus nurture influences. Nevertheless, musicians' auditory perceptual and neurophysiological enhancements are 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., Zendel and Alain, 2013; Bidelman et al., 2013a) providing some (albeit indirect) evidence for a causal relationship. These types of correspondences hint that musicians' auditory enhancements might result from neuroplastic effects that are modulated by the amount of musical exposure. It should be noted, however, that comparisons between highly proficient musicians and their age-matched nonmusician peers offer an imperfect comparison to address questions regarding the role of *experience* on brain and behavioral processing. It is entirely possible that certain individuals pursue and obtain high levels of musical proficiency based on personality traits (Corrigall et al., 2013) or some other preexisting, innate capacities rather than extensive music rehearsal. Thus, in addition to cross-sectional comparisons between expert and non-expert listeners, longitudinal studies with random subject assignment are required to truly gauge the role of musical experience on auditory processing and brain plasticity.

Here, we provide an overview of converging findings, including those from our cross-sectional, training, and longitudinal studies, which highlight the effects of musical training on a multitude of brain mechanisms, as well as cognitive transfer. Both cross-sectional and training studies are highlighted throughout this review to illustrate the known extent of musicianship on the brain as well as the more immediate effects of training intervention (i.e., long- vs. short-term plasticity). We observe that music-related plasticity ranges from low-level sensory processing specific to the auditory domain, to high-level processes supporting general cognitive functions including language and executive processes. Critically, music taps an array of multimodal mechanisms operating at different scales and time courses within the nervous system. From a neurobiological perspective, we believe that music training offers an ideal framework for studying the brain, as it offers insight into specific and general functions, robust focal and global (i.e., network-level) plasticity, and the hierarchical nature of audition not revealed by other forms of human experience. Finally, we propose a theoretical model to explain the continuum of plasticity observed with musical training that could be used as a framework to test the extent and limits of music-induced brain plasticity and cognitive transfer effects.

2. Why musical training? Music compared to other forms of intense training/learning

Throughout this review, we highlight the uniqueness and multiple advantages of using music training as a model to understand the capacity of auditory and non-auditory brain plasticity. While other models of plasticity are prevalent in the literature (e.g., motor or visual learning; reviewed by Green and Bavelier, 2010), we argue that musical training is a superior model for a number of reasons. First, in addition to auditory demands, music production contains both motor and visual components, and thus shares similar advantages with alternate models. For instance, the impact of music training on the brain can be extremely quick, with some effects resulting from only a few minutes of training (Bangert et al., 2001). However, the main advantage of music, and that which distinguishes it from the other models of plasticity, is its intricate complexity. Music recruits a rich array of brain networks subserving, among other things, auditory, visual, motor, and memory related processes (Zatorre and McGill, 2005). This likely results from the natural engagement of multiple modalities of brain processing and the interplay between perception and production during musical practice and rehearsal. Importantly, these networks also contain multiple levels of complex processing which unfold over time and at varying levels of scale. These unique properties allow one to investigate the influence of a *singular experience* on various neuroanatomical (e.g., brainstem, auditory cortices, associative areas) and functional (e.g., sensory discrimination vs. language comprehension) brain processes, ultimately providing a broader window into the connection between brain and behavior. Furthermore, music has allowed investigators to study the impact and far transfer of experience/training on higher-level cognitive skills (e.g., syntactic, semantic, emotional processing) that alternate models, like a strict motor framework, may not fully engage.

Given the breadth and permeation of music throughout the nervous system, it is difficult to identify a complementary activity exists which might share the equivalent plasticity and perceptual-cognitive benefits of musical training. It has been posited that

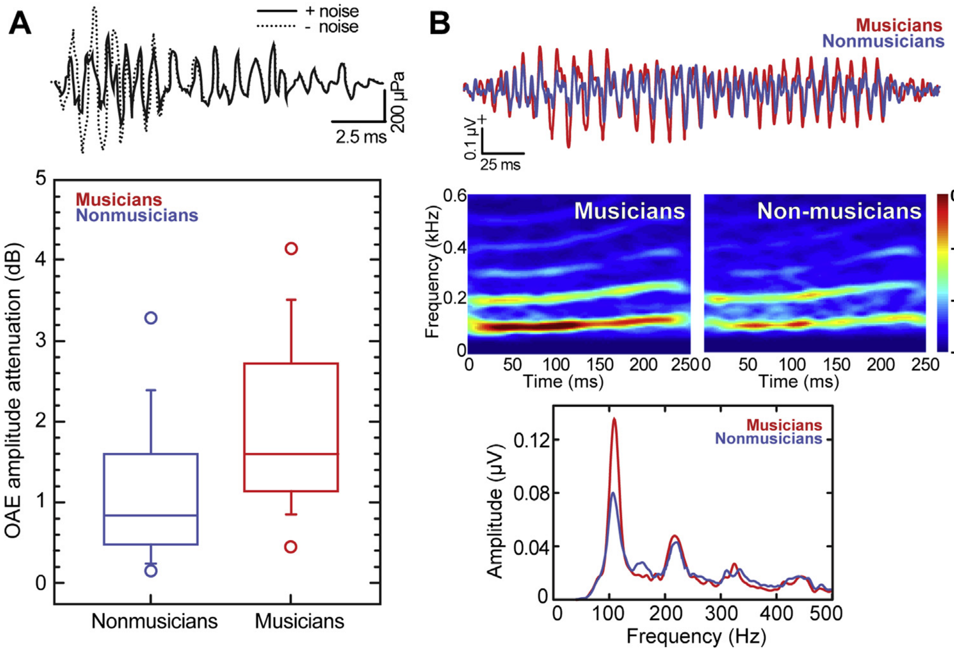

Fig. 1. Music-related auditory plasticity and transfer revealed at subcortical levels of auditory processing. (A) Otoacoustic emissions (OAEs), i.e., sound pressure waveforms, recorded from the ear canal (top) are suppressed with contralateral acoustic stimulation, providing an estimate of medial olivocochlear efferent activity and hence a proxy for top–down feedback from the caudal brainstem to the cochlea. OAE suppression is larger in musicians relative to nonmusicians (bottom panel) indicating that musical training strengthens feedback to the most peripheral stage of auditory processing. (B) Brainstem frequency-following response (FFR) waveforms recorded in musician and nonmusician listeners elicited by the 250-ms vowel token /i/ (top). FFR spectrograms (middle) and time-averaged average spectra (bottom) illustrate that musicians' brainstem evoked responses contain more salient neural representations of the time-varying properties of speech, including voice fundamental frequency (spectral band at ~100 Hz), formant-related energy (~300 Hz), acoustic cues related to voice pitch and timbre, respectively. OAE and FFR data adapted from Perrot et al. (1999) and Bidelman and Krishnan (2010), respectively; used with permission from Elsevier.

vision might represent the most complementary domain to music for studying brain plasticity and transfer. In particular, visual arts training (e.g., painting) has been explored, as it presumably requires similar demands to music in terms of practice, perceptual acuity, required motivation, and pleasurable outcomes (e.g., Gardiner et al., 1996; Moreno and Besson, 2006; Moreno et al., 2011b). However, our recent studies have begun to reveal robust advantages of music over visual arts training. In a series of studies, Moreno et al. (2009; 2011b; 2011a) contrasted the effects of music to visual art training in a group of children (4–6 yrs and 7–8 yrs) randomly assigned to either music or painting training groups. Several factors were carefully controlled using an intervention study paradigm. In this paradigm, training procedures were matched on several important criteria similar numbers of participants in each group; similar time course of the instruction; teachers held equivalent degrees and similar experience with children, etc. In terms of content, both training programs had the same number of learning goals (i.e., each lesson had a goal – music: learning and recognizing high and low pitch; VA: learning and recognizing primary color), the same number of themes (i.e., music: rhythm, melody, harmony, timbre and music reading; VA: color, line, shapes, patterns and texture) and the same number of exercises (for a full description see Moreno et al., 2009, 2011b). It was hypothesized that transfer could only be observed if cognitive activities shared the same type of sensory processing (Moreno and Besson, 2006). The data showed enhanced auditory neural and behavioral responses in musically trained children, where training auditory skills transferred to similar auditory processing required in language; no enhancements where observed in the visual arts group, confirming initial hypotheses. In a subsequent study under the same design (Moreno et al., 2009), the test battery was expanded to include the Weschler Preschool and Primary Scale of Intelligence-Third Edition (WPPSI-III), in order to further investigate the potential of transfer after visual art training; still no transfer in skill was observed in the visual art group. Finally, a more direct link between training and potential transfer was pursued (Moreno et al., 2011b). Since one of the main components of the visual art training was manipulation of shape, the study incorporated the blocks test of the WPPSI-III battery, in which participants used red and white blocks to assemble designs of different geometrical patterns. In addition, a go/no-go task using geometrical shapes (triangles and rectangles) was employed to examine visual executive processing and response inhibition. As a visual art effect may be smaller than that of music, the study also included a large number (~50) of participants to increase the sensitivity of detecting potential visual training-related benefits. Despite the visual nature of the tasks, only music students showed significant changes with training. Collectively, the results of our longitudinal training studies suggest that music (but not visual arts training) positively enhances not only auditory processing relevant to speech and language, but also impacts the visual modality and executive functions, i.e., higher-order mechanisms which regulate, control, and manage important cognitive processes like working memory, attention, and planning.

The repeated null findings of visual arts training may stem from two possible sources. First, the visual system appears to be limited in its ability to transfer skills to other cognitive activities. This interpretation is supported by a large literature on perceptual learning (for review, see Op de Beeck and Baker, 2010). Another interpretation is that human beings develop critical auditory skills early in life and are arguably auditory experts at birth. Babies, for example, recognize their mother's voice and other speech-specific stimuli *in utero* (Moon et al., 2013). In contrast, visuo-motor skills are less developed at birth and must mature into early childhood

(Kakebeeke et al., 2012). Thus, it is possible that individuals might need to reach a certain maturational stage before becoming receptive to visual training. Alternatively, a longer time course may be needed for the transfer of visuospatial skills than for the transfer of auditory skills. In other words, a longer or more intensive training period in the visual arts may be necessary to significantly influence behavioral skills; an even longer training period might be required before transfer of skill is observed (if at all). While a precise explanation remains elusive, the requirement for a longer training regimen for visual arts training may be one reason why previous work has consistently failed to observe an effect relative to musical training. Future avenues of research should investigate the impact of visual arts training on an adult population and assess the potential transfer of skills induced by longer periods of visual-based training.

Having illustrated the validity of using music training as a framework, we now turn to recent findings in the literature (mainly cross-sectional studies) which demonstrate the far-reaching plasticity afforded by musical training. Music fully engages a wide variety of brain networks well beyond the bounds of the auditory system. As such, we look beyond neurophysiological and behavioral benefits restricted only to the auditory domain to examine the time-course and multiple scales of processing tuned with musical expertise. Benefits are seen at subcortical and cortical levels of the auditory system, but also in brain regions not traditionally associated with the lemniscal hearing pathway (e.g., frontal lobes). Our goal is to describe the effects of musical training on global brain structures and highlight its influence on different levels of auditory as well non-auditory processing.

3. Neuroplastic effects of musical training on subcortical levels of brain processing

3.1. Otoacoustic emissions (OAEs)

The cochlea receives efferent feedback from the medial olivocochlear (MOC) bundle, a fiber track originating in the superior olivary complex (SOC) within the caudal brainstem and terminating on the outer hair cells in the Organ of Corti. In addition, cross-projections originating in the contralateral ear innervate SOC terminals in the medial brainstem, which project contralaterally to the opposite cochlea and hence provide an indirect connection between both ears (Guinan, 2006). Exploiting this neuroanatomical circuitry, clever experimental paradigms have been able to estimate MOC efferent activity by comparing otoacoustic emissions (OAEs)—minute acoustic signals generated by the inner ear recorded within the ear canal—with and without the presence of contralateral noise. Stimulating the opposite ear activates the crossed MOC pathway, which results in changes in cochlear gain that are measurable as a suppression of the OAEs recorded on the ipsilateral side (Collet et al., 1992; Guinan, 2006).

Cross-sectional studies examining OAE suppression in musicians and nonmusicians have shown larger contralateral suppression in musically trained ears (Micheyl et al., 1997b; Perrot et al., 1999; Brashears et al., 2003) (Fig. 1A). Musicians also show less loudness adaptation concurrent with a greater reduction in transient OAE amplitudes under contralateral acoustic stimulation (Micheyl et al., 1995; Perrot and Collet, 2013). These studies thus suggest that musical training impacts initial stages of auditory sensory processing via strengthened top–down efferent feedback from the caudal brainstem to the most peripheral sites of auditory processing. While the role of the MOC efferents in human hearing is still under investigation, they have been implicated in important aspects of "real-world" listening. MOC activity, for example, may help improve hearing in adverse listening conditions by playing an "antimasking" role (Guinan, 2006) to improve signal detection in noise (Micheyl and Collet, 1996; Giraud et al., 1997) and/or behavioral discrimination sensitivity (e.g., Micheyl et al., 1997a; Norena et al., 2002). It is plausible that certain behavioral advantages might result from enhancements to the MOC efferent system developed through rigorous musical training (See Section 5:"*Perceptual and cognitive benefits of musical training*" for potential behavioral benefits of these physiological changes). While these studies show that very initial stages of cochlear processing are tuned with musical expertise, more recent studies have extended these findings, demonstrating that early neural mechanisms at the level of the brainstem are similarly influenced with musicianship.

3.2. Brainstem auditory evoked potentials

The brainstem is an essential relay along the auditory pathway that performs significant signal processing on sensory-level information prior to cerebral cortex processing. Recent work examining human brainstem auditory evoked potentials (AEPs)—namely the frequency-following (FFR) response—have been the most revealing in probing experience-dependent plasticity at a subcortical level of the auditory system (Kraus et al., 2009; Krishnan and Gandour, 2009; Krishnan et al., 2012). The FFR is a sustained "neuromicrophonic" potential that reflects dynamic, phase-locked activity to periodic features of complex acoustic stimuli (e.g., speech and music) (for reviews, see Krishnan, 2007; Chandrasekaran and Kraus, 2010; Skoe and Kraus, 2010) (see Fig. 1B). The FFR has provided a detailed window into early, subcortical neurophysiological encoding of complex sounds not afforded by traditional auditory event-related potentials (ERPs) (e.g., click-evoked responses). As with any far-field volume-conducted potential recorded at the scalp, identifying a single neural generator for the FFR is difficult and it may reflect concomitant activity of both cortical and subcortical structures. Nevertheless, its early latency (~6–10 ms; Smith et al., 1975), high-frequency phase-locked activity (Galbraith et al., 2000), and absence with brainstem lesions (Smith et al., 1975; Sohmer et al., 1977), suggest the inferior colliculus (IC) of the rostral brainstem as its primary neural generator.

Given that the response can faithfully capture dynamic properties of an acoustic input, it has, among other things, been used to investigate the brainstem representation of perceptually salient features of sound, including linguistic pitch prosody (Krishnan and Gandour, 2009; Krishnan et al., 2009; Strait et al., 2009; Bidelman et al., 2011c), melodic and harmonic aspects of music (for review, see Bidelman, 2013), and timbral components of speech (e.g., the encoding of formant cues; Bidelman and Krishnan, 2010; Krishnan et al., 2011; Bidelman et al., 2013b). Indeed, brainstem FFRs preserve spectrotemporal properties of the eliciting acoustic stimulus with such high fidelity that when played as an auditory signal, they are intelligible to human listeners (Galbraith et al., 1995).

Recent FFR studies have demonstrated that extensive auditory experiences introduce functional reorganization in the human midbrain. First studied in the context of language, studies have shown that long-term experience with a tonal language—for which changes in pitch alter word meaning—enhances the subcortical representation of pitch-relevant information as indicated by the smoother, more robust voice fundamental frequency tracking in the FFRs of Chinese relative to English-speaking listeners (Krishnan et al., 2005, 2009). Subsequent studies extended these results by demonstrating similar effects in musically trained listeners. Indeed, musicians, in conjunction with the FFR, have proved to be an excellent model for investigating auditory plasticity at subcortical levels of audition (for review, see Kraus et al., 2009; Kraus and Chandrasekaran, 2010; Skoe and Kraus, 2012). As reflected in its response properties, recent studies demonstrate that long-term music training acts to enhance the magnitude with which the brainstem responds to musical pitch (e.g., intervals, chords) (Musacchia et al., 2007; Bidelman et al., 2011c, 2011a). Additionally, as indicated by shorter, less “jittered” neural response latencies, musicians' neural activity is also more temporally precise than that of nonmusicians, indicating that musicianship not only magnifies the “gain” of subcortical brain activity but also refines it by increasing the temporal precision of neurophysiological processing (Bidelman et al., 2011a; Parbery-Clark et al., 2012). Interestingly, these brain indices are correlated with an individual's degree of training/experience (Wong et al., 2007) and, assuming the stimuli and task are behaviorally relevant to the listener, their perceptual abilities (e.g., pitch discrimination) (Bidelman and Krishnan, 2010; Bidelman et al., 2011b). Together, the enhancements reported in FFR studies following long-term music (and language) experience indicate that experience-dependent plasticity, well-established at cortical levels of processing, also exists at *subcortical* levels of the human brain.

Importantly, this increased neural fidelity observed with musical training transfers to improve the neural encoding of sounds beyond the scope of music. Comparing brainstem responses elicited by speech, we have shown that musicians' FFRs contain more robust and faithful representation of the speech waveform than those of nonmusicians (Bidelman and Krishnan, 2010; Bidelman et al., 2011c) (see also, Wong et al., 2007; Parbery-Clark et al., 2009a). Increased FFR magnitude is observed in musicians for spectrotemporal components of speech including fundamental frequency (i.e., voice pitch) and formant information, cues that provide critical information for identifying who is speaking (e.g., male vs. female) and what is being said (e.g., /a/ vs. /i/ vowel) (Fig. 1B). As such, the musical brain seems to provide a more detailed snapshot of the speech waveform than found in musically naïve individuals. These finer neural representations may ultimately emerge to benefit speech listening behaviors by providing cortical and later perceptual processes a more accurate neural depiction of the input signal. Collectively, findings from brainstem FFR studies suggest that musicianship (i) tunes the early sensory encoding of auditory information to provide a more stable and detailed registration of acoustic information and (ii) transfers to provide processing advantages for non-musical sounds, including those relevant to speech communication.

4. Neuroplastic effects of musical training on cortical levels of brain processing

Beyond the brainstem, music training also induces changes at a cortical level, and several groups have employed music training as a model to study cortical plasticity and auditory processing (e.g., Munte et al., 2002; Trainor et al., 2003; Zatorre and McGill, 2005; Herholz and Zatorre, 2012). Studies utilizing ERPs and functional neuroimaging (fMRI) demonstrate enhancements in the excitability of brain circuitry within primary (lateral Heshl's gyrus) and secondary (planum temporale) auditory cortices of musicians (e.g., Schlaug et al., 1995a; Zatorre et al., 1998; Keenan et al., 2001; Pantev et al., 2001; Schneider et al., 2002; Luders et al., 2004; Schon et al., 2004; Moreno and Besson, 2005). Components of the auditory evoked potential (e.g., N1, P2 waves) shown to be sensitive to auditory training in nonmusicians are generally enhanced in musician listeners in accordance with their musical histories (Shahin et al., 2003). Further neurophysiological evidence shows enhancements in the musicians' cortical response to pitch (Fujioka et al., 2004; Krohn et al., 2007), timbre (Crummer et al., 1994; Pantev et al., 2001), and timing (Russeler et al., 2001) aspects of auditory objects. As with subcortical responses, enhancements in cortical activity transfer to benefit the processing of speech-relevant sounds; auditory ERPs (particularly later sensory components, e.g., N1–P2) are generally more robust and occur with early latency when listening to speech in musically trained listeners relative to their nonmusician counterparts (Schon et al., 2004; Besson et al., 2007; Moreno et al., 2009; Besson et al., 2011; Marie et al., 2011). These studies demonstrate that long-term music training facilitates early, sensory cortical responsiveness to speech relevant signals.

The influence of musical training on the cerebral cortex is observed in early life. Two recent examples have shown behavioral and neural influences of music activities in infants and toddlers. Gerry et al. (2012) investigated the influence of 6 months of active musical experience in children aged 6 months. In this training, parents and children attended weekly 1-h Suzuki music sessions. After training, music children showed superior prelinguistic communicative gestures and social behavior compared to infants assigned to a control group. Similarly, Putkinen et al. (2013) investigated the impact of at-home musical activities on auditory processing in toddlers. A detailed questionnaire was used to assess the amount and type of musical activity, while auditory processing was assessed via multi-feature mismatch negativity (MMN) responses, a neural signature generated in an oddball ERP paradigm that measures the pre-attentive cortical discrimination of auditory events. Results indicated a positive correlation between at-home musical activity and the magnitude of auditory change detection, as indexed by the MMN. Home-based music activity was ultimately related to more mature auditory change detection for temporal acoustic features, as well as decreased distractibility. These results show an impact of music at a very young age and provide future work the opportunity to explore the relationship between auditory processing, early music training, and neurophysiological development (e.g., Shahin et al., 2004; Hyde et al., 2009; Strait et al., 2012).

Interestingly, changes in cortical structures are also observable within relatively short periods of time. For instance, modulation in the early auditory ERPs (N1 latency: ~100 ms) have been observed during active listening tasks in as little as 3 h of music listening (Pantev et al., 1999). Furthermore, changes in neuronal responses are stimulus specific (Pantev et al., 1999), highlighting the fact that rapid plastic effects are observable only when the stimulus input carries behaviorally relevant meaning (for similar effects at subcortical levels, see Gao and Suga, 1998). Near-field recordings in animal models corroborate far-field ERP findings, demonstrating localized and dynamic facilitative changes in spatiotemporal receptive fields of auditory cortical neurons which selectively increase their responsiveness and adjust their best frequencies toward task-relevant, target stimuli (e.g., Fritz et al., 2003; Lee and Middlebrooks, 2011; for review, see Weinberger, 2011). Polley et al. (2006), for example, have shown that receptive fields in rat auditory cortex expand, selectively, along the dimension associated with learning a particular sound feature (e.g., intensity or frequency). These results suggest that map plasticity in the early auditory cortical fields can be shaped based on task-specific, top–down influences. Thus, it is conceivable that the changes in activity observed in musicians' far-field ERP recordings may reflect changes in similar microscopic neuronal tuning and response properties of underlying auditory cortical areas (e.g., Fritz et al., 2003; Polley et al., 2006; Lee and Middlebrooks, 2011; David et al., 2012). These microanatomical changes (cellular, molecular) may underlie the macroanatomical differences (e.g., volumetric and fiber tractography measures) often observed between musicians and nonmusicians in neuroimaging studies (for review, see Zatorre et al., 2012).

Rapid changes in neuronal properties may initially reflect the need to encode behaviorally relevant sounds (Fritz et al., 2003). Yet,

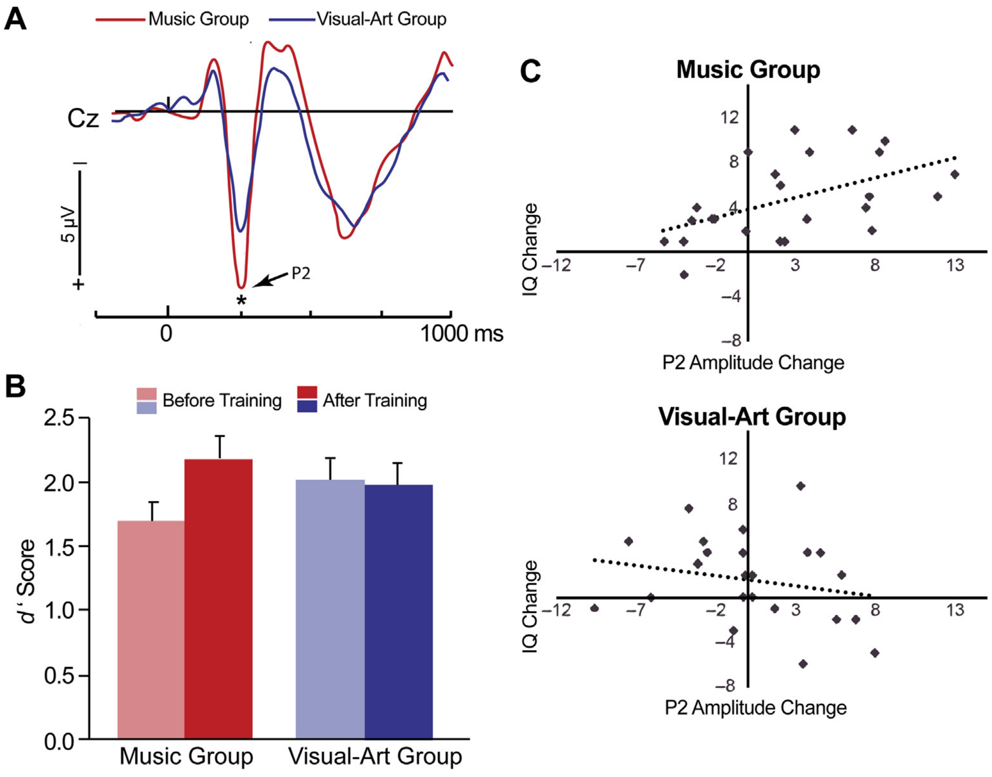

Fig. 2. Music-related plasticity and transfer revealed at a cortical level. (A) Cortical evoked potentials recorded at the vertex (Cz) elicited in a visual go/no-go task. ERPs are shown at the post-test following short-term musical or visual-arts training. Increased P2 magnitude (*) is observed for music students indicating that musical training enhances the inhibitory processing of visual information. (B) Pre/post training d' prime scores for visual go/no-go discrimination. Increased behavioral performance is observed for the music group; no change is observed with training for the visual arts group. Improvement after training in the music training group is significantly greater than in the visual art training group. (C) Correlation between change in intelligence score (i.e., post−pre test) and change in ERP signal amplitude. The change in intelligence score is positively correlated with the change in ERP amplitude in the music group (top panel) but not in the visual art group (bottom panel). Error bars = 1 s.e.m. Figure adapted from Moreno et al. (2011b), with permission from SAGE Publications.

the continued auditory demands of music practice may eventually cause persistent changes in receptive fields which may (i) establish/reinforce long-term memory for sensory events (Weinberger et al., 1993; Fritz et al., 2003; Polley et al., 2006; Bieszczad and Weinberger, 2010) and (ii) enlarge the overall responsiveness/representation of complex sounds in musician's brain (Pantev et al., 1998). It is also conceivable that long-term engagement with specific elements of music (e.g., specific instrumental timbres) may then act to further increase the selectivity for sound features required by the listener's acoustic environment (Weinberger et al., 1993; Pantev et al., 2001; Strait et al., 2012). Additionally, data from animal models indicates that top−down effects on sensory processing also depend on reward structure of the environment and valence of the stimuli (David et al., 2012). Thus, the positive valence associated with music may provide a catalyst for the aforementioned plastic changes.

Outside the auditory domain, rapid cortical plasticity has also been observed in humans under more realistic, music learning paradigms. For example, fast audio-motor coupling, as reflected by changes in the topographic orientation of slow-wave ERPs, has been demonstrated following 20-min of piano lessons (Bangert and Altenmüller, 2003). Interestingly, the coupling of this type of motor activity with auditory learning can act to increase cortical responses to auditory information (Lappe et al., 2008; Paraskevopoulos et al., 2012). That is, the inherent multi-modal nature of most musical engagement seems to induce greater functional reorganization than observed with single-auditory training alone. This may, for example, explain why studies often fail to observe skill transfer with simple auditory perceptual learning paradigms (Wright and Zhang, 2009) but find robust skill transfer in musically trained individuals (Schellenberg, 2004; Chartrand and Belin, 2006; Bidelman and Krishnan, 2010; Moreno et al., 2011b). Additionally, our recent randomized training studies (Moreno and Besson, 2006; Moreno et al., 2009, 2011b) have reported neurophysiological and related behavioral improvements in auditory (pitch) and even visual inhibitory processing after 1, 2, and 6 months of musical training in children, respectively (Fig. 2). [For behavioral implications of these neurophysiological findings see Section 6: *Perceptual and cognitive benefits of musical training*]. These plastic effects were not observed in a group that participated in an equally engaging visual arts training program, suggesting that the brain-behavior benefits that rapidly developed in the music group may have resulted from the repeated mapping of sound-to-meaning and coordination between multiple sensory modalities experienced during music training. Overall, these findings provide evidence for the exceptional speed and long-term functional reorganization that music training induces on cortical structures subserving both low- and higher-order cognitive processes.

Several studies have also revealed that the neuroanatomical differences between musicians and nonmusicians extend beyond the auditory system, reaching even non-auditory brain regions. Morphological changes have been reported, for example, in posterior band of the precentral gyrus (Amunts et al., 1997), the corpus callosum (Schlaug et al., 1995b; Schmithorst and Wilke, 2002), the anterior-medial part of the Heschl gyrus (Schneider et al., 2002), and parts of the cerebellum (Hutchinson et al., 2003). Recently, Hyde et al. (2009) reported structural changes in auditory and motor brain areas after only 15 months of musical training in children, which were found to correlate with improvements in musically relevant motor (i.e., finger dexterity) and auditory skills (i.e., melodic and rhythmic discrimination). It is important to note that these group differences were observed even when partialing out the effects of age and socioeconomic status. While this study demonstrates a relationship between the duration of music engagement and psychophysiological measures—independent of other confounding factors—the findings should be interpreted with some care given the retrospective nature of the analysis employed in the study (correlations and MANCOVA).

Several findings show that structural differences that accompany musicianship expand beyond the sensory cortices to the inferior frontal gyrus and inferior portions of the temporal lobe (Gaser & Schlaug, 2003a,b; Luders et al., 2004). For example, Sluming et al. (2002) observed age-related volume reductions in the cerebral hemispheres, bilateral dorsolateral prefrontal cortex, and gray matter density in the left inferior frontal gyrus in nonmusicians, but not musicians, suggesting that musical expertise may provide a protective effect late into life (e.g., see Alain et al., 2013). Interestingly, musical training has also been shown to impact Broca's area, a brain region traditionally associated with speech perception, syntactic processing, and production (Maess et al., 2001; Koelsch et al., 2002). Together, these findings clearly show the large impact music training has on non-auditory brain structures. Future work should investigate the connection and possible interactions between traditional auditory structures and these non-auditory networks during the course of musical training. Such work could be used, for example, to generate a comprehensive account of neural plasticity at a global brain level and reveal the interaction between distal brain regions subserving a multitude of behavioral functions. It is often assumed that such wide and distributed changes in cortical architecture following musical training provide a key ingredient for cognitive transfer. In the subsequent sections, we address the behavioral relevance of these structural changes and focus on the perceptual and cognitive benefits of musical training observed at the behavioral level.

5. Perceptual and cognitive benefits of musical training

5.1. Lower-order perceptual benefits of musical training

5.1.1. Spectrotemporal processing and auditory scene analysis

While neuroimaging studies reveal anatomical and functional changes in brain processing resulting from musical training, behavioral work confirms that these physiological enhancements also enrich perceptual abilities. A positive functional relationship is observed, for example, between musicianship and temporal processing; musicians outperform nonmusicians in detecting and discriminating small time changes embedded in rhythmic sequences (Jones and Yee, 1997; Rammsayer and Altenmuller, 2006). Auditory fusion thresholds, a measure reflecting the minimum temporal interval required to distinguish two separate auditory events, also tend to be smaller in musicians (Rammsayer and Altenmuller, 2006), indicating a higher temporal resolving power with musical expertise. These psychophysical benefits may result from musicians developing a more acute, and possibly more adaptive, temporal integration window (Russeler et al., 2001). However, superior temporal abilities might be limited to aspects of timing derived from more immediate perceptual processing. A musician advantage is not observed, for instance, in tasks involving temporal generalization, e.g., when judging whether a final beat in a regular sequence occurred earlier or later than expected (Lim et al., 2003; Rammsayer and Altenmuller, 2006).

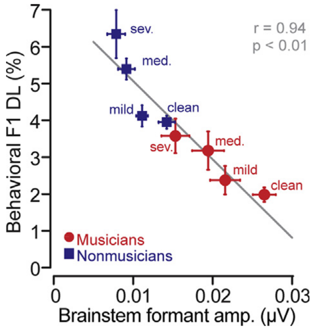

Fig. 3. Brain-behavior correlations in speech processing as a function of musical training. The magnitude of speech first-formant (F1) energy encoded in brainstem responses predicts behavioral performance for discriminating that cue in normal and adverse (reverberant) listening conditions. Across conditions, larger, more robust brain magnitudes correspond with better (i.e., lower) F1 difference limens. Higher levels of reverb (medium, severe) inhibit the encoding of formant information in both groups, as denoted by the reduced magnitudes relative to clean and mild conditions. Yet, across stimuli, musicians demonstrate more robust encoding of F1-related speech cues and superior discrimination performance, indicating that musical training strengthens not only the encoding but also the perception of speech material in clean as well as noisy listening conditions. Based on unpublished data from Bidelman and Krishnan (2010).

Increased spectral acuity has also been documented as a function of musical training. In these studies, the most widely reported measures involve pitch and frequency discrimination, where behavioral advantages are often reported in terms of difference limens (DLs), i.e., the smallest change in frequency/pitch a listener can reliably detect. In general, musically trained listeners achieve DL thresholds that are ~2–4 times smaller (i.e., better) than musically naïve listeners for both pure and complex tones (Spiegel and Watson, 1984; Kishon-Rabin et al., 2001; Micheyl et al., 2006; Bidelman et al., 2011a). Presumably, these perceptual advantages could be mediated by the higher sensitivity of musicians' cortical (Koelsch et al., 1999; Tervaniemi et al., 2005; Brattico et al., 2009) and subcortical (Bidelman et al., 2011b, 2011d) brain activity for subtle manipulations in pitch—as reviewed earlier.

In addition to basic temporal and spectral enhancements in auditory acuity, recent studies demonstrate that musicians' auditory plasticity extends and transfers to improve listening skills well outside the domain of music. Musicians parse and segregate competing signals in complex auditory scenes more effectively (Munte et al., 2001; Nager et al., 2003; van Zuijen et al., 2004; Zendel and Alain, 2009) and are less influenced by information masking (Oxenham et al., 2003) than nonmusicians. Given the importance of these factors in auditory scene analysis (e.g., "cocktail party" scenarios), these studies suggest that musical expertise improves important aspects of real-world listening required for robust communication (for a thorough treatment of this topic, see Alain et al., 2013). While these studies demonstrate perceptual enhancements in aspects of auditory processing, it is important to note that musicians' perceptual acuity might not be restricted strictly to the auditory domain. Recent studies suggest that musical expertise might enhance temporal acuity in both auditory and visual modalities (Rammsayer et al., 2012).

5.1.2. Speech processing

Intriguingly, domain specific music experience also influences faculties necessary for speech and language processing, representing far transfer of experience. Perceptually, musicians show improved language specific abilities including better performance in the identification of lexical tones (Wong et al., 2007; Lee and Hung, 2008) and a higher sensitivity in detecting timbral changes in speech (Chartrand and Belin, 2006). Interestingly, these benefits also facilitate speech processing in suboptimal acoustic conditions including speech in noise-degraded listening environments. Group comparisons reveal more robust encoding for both clean and noise-degraded speech in musicians than in nonmusicians (Parbery-Clark et al., 2009a; Bidelman and Krishnan, 2010). Bidelman and Krishnan (2010) found that these neurophysiological enhancements also manifest in improved behavioral speech discrimination performance; even in the presence of interference (reverberation), musicians' perceptual thresholds for both voice pitch and timbre discrimination were, on average, 2–3 times smaller than nonmusicians (Fig. 3). Indeed, stronger neurophysiological representation for a given speech cue was closely associated with listeners' behavioral discrimination performance. These studies highlight that brain circuitry tuned by long-term music training facilitates the psychophysiological processing of speech signals, and may even limit the deleterious effects of noise on speech recognition (Parbery-Clark et al., 2009a; Bidelman and Krishnan, 2010).

5.2. *Higher-order cognitive benefits of musical training*

5.2.1. *Phonological awareness and reading*

More recent work has begun to explore the behavioral and cognitive benefits of musical training outside the traditional scope of audition. Initial reports focused on reading, given its natural foundations in auditory skills (e.g., sound-to-word mapping). Anvari et al. (2002) conducted a large scale study with 4–5 year old children and observed a link between music skills and preliminary reading skills. Their results showed music perception was predictive of phonological awareness and reading development. This finding was confirmed by a later intervention study conducted by Dege and Schwarzer (2011) who tested preschoolers before and after three types of training: music, phonological awareness, and sport. Results indicated that a music program could improve phonological skills to a similar degree as traditional phonological training. However, this finding should be taken with caution due to the small sample size of the study (i.e., 41 children divided across three groups). Nevertheless, converging evidence from additional recent studies are beginning to show a consistent relationship between music and early reading skills (Huss et al., 2011; Tsang and Conrad, 2011).

Inevitably, the connection between music and reading might be more complex than what is currently painted in the literature. Some evidence shows a link between music and only selective aspects of reading skills. Indeed, the impact of early music training on reading skills may only manifest when the learning process consists of complex phoneme-to-grapheme mappings (Moreno et al., 2009). Subsequent longitudinal studies by our group (Moreno et al., 2011a) have also assessed phonological awareness and visual-auditory learning (i.e., the ability to map visual symbols onto words). Children receiving music and visual arts training showed similar improvement on measures of phonological awareness, but the children with music training improved significantly more than the art-trained children on measures of visual-auditory learning. These findings illustrate the complex nature of the transfer mechanisms in reading processing and the necessity of conducting more intervention studies to dissociate the specific and/or general aspects of music training's influences.

5.2.2. *Comparison between music and language experience*

Perhaps the most well studied cognitive ability that has been directly pitted against musical training is language expertise (for review see, Patel, 2013). Recent studies comparing linguistic and musical pitch experience have begun to examine whether the neural plasticity afforded by these divergent skills is domain-general or domain-specific. Our cross-domain comparisons of brainstem responses reveal overall enhancements in the FFRs (e.g., response strength, accuracy) elicited by either musical or lexical pitch patterns in musicians and tone language (Mandarin Chinese) speakers alike (Bidelman et al., 2011b, 2011c, 2013a). Similar effects have been observed at cortical levels of processing; tone language listeners and English-speaking musicians show similar enhanced mismatch responses elicited by deviations in linguistic pitch patterns (Chandrasekaran et al., 2009; Giuliano et al., 2011). Thus, both language and musical experience provide some mutual benefit to the neural extraction of linguistically relevant features of the auditory stream.

The similarities between language and music experience are not as clear cut upon closer inspection of the experience-dependent effects (Bidelman et al., 2011b, 2013a). Indeed, we find that even low-level auditory neural representations are subject to a further "tuning" according to specific acoustic features encountered in a listener's experience. For example, when presented with an identical gliding pitch stimulus, musicians show enhanced sensory encoding when the pitch pattern intersects discrete notes along the musical scale; tone language speakers, on the other hand, show enhanced sensory encoding during rapidly changing portions of tonal contour (Bidelman et al., 2011c,d). Such "cue weighting" is consistent with each group's unique listening experience and the relative importance of these dimensions to music (Burns and Ward, 1978) and lexical tone perception (Gandour, 1983), respectively. These findings collectively lead us to infer that while both language and musical experience provide some mutual benefit to the neural extraction of auditory information, specific features of the acoustic signal are highlighted in the brain depending on their perceptual salience and function within a listener's domain of expertise. They also suggest that the plasticity afforded by language and music may not be entirely isomorphic.

Differences between language and musical experience begin to further diverge when considering higher-level auditory mechanisms involving contextual processing. Tone language speakers, for example, fail to demonstrate the same benefit in musical melody discrimination, tonal memory, and even basic pitch difference limens as compared to musicians (Bidelman et al., 2011b, 2013a). In contrast, musicians consistently obtain similar levels of proficiency as Mandarin speakers in lexical tone processing tasks (Alexander et al., 2005; Lee and Hung, 2008; Bidelman et al., 2011c). Thus, as with visual arts training (see Section 2), musical training seems superior to extensive language experience, trumping its behavioral benefits. The mechanism of this differential plasticity has only recently been explored. Studies reveal that both experiences improve higher-order cognitive processing, e.g., working memory and executive functioning (Schellenberg, 2004; Bialystok and Depape, 2009; Hyde et al., 2009; Moreno et al., 2011b). Yet, our recent work suggests that musical training may enhance these general cognitive mechanisms more so than long-term language experience (Bidelman et al., 2013a). Thus, the larger perceptual and cognitive benefits of music, relative to language experience (e.g., Bidelman et al., 2011b, 2011c, 2013a), may reflect the fact that musicians develop more superior top–down mechanisms to "decode" auditory features enhanced in lower-level stages of brain processing (e.g., Section 3.2).

6. Mechanisms underlying robust music-induced brain plasticity

6.1. *The potential role of executive functions: IQ, working memory (WM), and attention*

In light of the benefits of music training on complex cognitive processes (e.g., reading, language), a natural question arises as to the origin or mechanisms that mediate this high-level cognitive transfer. Intelligence was the first domain to be explored. In a seminal intervention study, Schellenberg (2004) followed three groups of children who participated in either weekly music lessons (keyboard or voice), theater instruction, or no lessons at all for duration of one year. Compared with children in the control groups, children in the music groups exhibited greater increases in Wechsler full-scale IQ. While the effect was relatively small (a few percentage points), it nevertheless generalized across IQ subtests, index scores, and a standardized measure of academic achievement. These results were important in that they demonstrated the first causal link between music training and intelligence improvements. Subsequent larger correlational studies helped confirm the relationship between musical training and intelligence (Schellenberg, 2006).

Another domain that has received particular attention is the link between music and executive functions (EF). EF is an umbrella term which defines cognitive processes that regulate, organize and control other cognitive processes including working memory, attention, planning, problem solving, inhibition, mental flexibility, and task switching. We will focus here on one of these processes, namely, working memory (WM), given that it is predictive of general intelligence and other complex cognitive behaviors (Kane et al., 2004). Current lines of thinking suggest that improvements in WM may lead to transfer effects and a general enhancement of cognitive abilities. Indeed, WM improvements due to musical training have been observed, e.g., musicians are able to hold and manipulate information in a short-term memory buffer longer than their nonmusician peers (Chan et al., 1998). Neuroimaging work corroborates these behavioral data, demonstrating increased cortical activation in musicians relative to nonmusicians during WM tasks (Pallesen et al., 2010). Interestingly, recent training studies have demonstrated similar WM improvements in older adults following short-term (6 months) individualized piano instruction (Bugos et al., 2007). Thus, repeated musical practice may act to stimulate and reinforce multiple integrated brain networks, including those subserving more general cognitive functions (WM, EF). Bugos et al. (2007) posit that the enhanced engagement of such networks late into life may serve as an effective cognitive intervention to offset age-related cognitive declines. [For a more thorough discussion of the potential impact of musical training on the aging brain, see Alain et al. (2013) and Strait and Kraus (2014), this issue.]

While these studies offer provocative evidence for music WM benefits, the exact nature of this benefit is still unclear; some reports show improvements in verbal (i.e., auditory), but not visual aspects of WM following formal music training (Brandler and Rammsayer, 2003; Ho et al., 2003; Tierney et al., 2008; Parbery-Clark et al., 2009b; Strait et al., 2010; Hansen et al., 2012), while others show increased WM performance for musicians independent of modality (George and Coch, 2011; Bidelman et al., 2013a). These equivocal results imply that the cognitive benefits of musical experience—at least onto WM—might be stronger in the auditory than non-auditory domain. Conversely, these inconsistencies might also be explained by subtle differences in musicians' listening histories. For example, instruments like the piano require a continuous mapping and recall of spatial location along the keyboard to execute the correct order of notes. Indeed, an association between musicianship and visuospatial WM has been observed in trained pianists, who commonly exercise abstract visual rules in their music practice (Bidelman et al., 2013b). Nevertheless, the equivocality of these findings highlights the necessity to further examine the role of WM in mediating the broader plastic effects of musical training.

Recent findings have begun to further examine the relationship between music and another prominent component of EF, namely, attention. Bialystok and Depape (2009) used a modified Stroop task to investigate whether extensive musical experience leads to enhancements in executive processing. The stimuli involved auditory and linguistic conflict between a word and its pitch (e.g., the word *high* spoken with a low pitch). The authors showed that musicians performed better than the control group on this task, revealing an influence of music expertise on inhibition processing. Recently, our group conducted an intervention study looking at intelligence and inhibition in young children (Moreno et al., 2011b). After one month of music training, the results indicated an improvement in verbal IQ and visual inhibition, as indexed by a go/no-go task. Results also showed a positive correlation between improvement in IQ and functional changes at the cortical level during the go/no-go task (i.e., increased P2 magnitude in the ERP), demonstrating a correspondence between brain and behavior changes (Fig. 2B–C). The degree of neurophysiological enhancement following training corresponded with an increase in the children's verbal intelligence. The benefits in this study were relatively strong (effect size = 0.33). Moreover, these improvements were five times larger for those who participated in music lessons relative to those in a similarly engaging visual arts course. These results identified a plausible potentiating brain mechanism that mediates music-induced plasticity. Recent studies extend these results and support the notion that certain aspects of EF, particularly the regulation of attentional resources, may play a mediating role between music training, auditory sensory plasticity, and the observed higher-order cognitive skills in musicians (e.g., intelligence; Degé et al., 2011).

Unfortunately, the neural generators of the P2 are difficult to ascertain from scalp recordings which in turn makes it difficult to characterize the functional relationship between this ERP wave and abstract measures like IQ. The visual P2 is thought to include both frontal and inferior occipital generators including visual cortex (Talsma and Kok, 2001); the analogous component in the auditory modality likely arises from primary and secondary auditory cortices (Scherg et al., 1989; Picton et al., 1999). While the functional role of P2 is still unclear, in both sensory modalities the component likely reflects higher-order auditory/visual processing and the analysis of sensory input against stored memories or meaning (Luck and Hillyard, 1994; Freunberger et al., 2007; Alain and Snyder, 2008; Bidelman et al., 2013b). Several studies have even reported associations between P2 and higher-level processes such as memory (Dunn et al., 1998; Lefebvre et al., 2005) and semantic processing (Federmeier and Kutas, 2002). Parieto-occipital brain regions contributing to the response are also implicated in aspects of intelligence (Jung and Haier, 2007). It is conceivable then, that the correspondence between P2 plasticity and verbal intelligence (Moreno et al., 2011b) might reflect a general enhancement in the brain's ability to execute and organize the mapping between auditory-visual information and meaning—a requisite of verbal understanding and reasoning.

It is plausible that at least some of the myriad of neural and behavioral benefits observed in musically trained individuals—including those related to lower-level sensory enhancements (see Section 3)—might result from an augmentation of these more general, and perhaps singular, top–down mechanisms. The notion of top–down, attentional/executive regulation of sensory processes has also been highlighted in recent animal (Fritz et al., 2003) and human studies (Myers and Swan, 2012). Increased "feedback" could act to enhance or inhibit the activity in stimulus-selective sensory cortices, driven by the engagement of prefrontal and parietal control regions. Distributing attention across a wider variety of sensory modalities has also been shown to enhance perceptual performance in complex audio-visual tasks (Mishra and Gazzaley, 2012).

Thus, it is conceivable that if musical training increases and enables one to deploy attentional resources more effectively (e.g., Strait et al., 2010; Strait and Kraus, 2011)—and possibly across modalities—this could account for at least some of the perceptual and cognitive abilities reviewed herein. While findings collectively suggest a potential link between EF (i.e., attention) and transfer mechanisms induced by musical training, more studies are needed to fully understand the underlying mechanism(s) of high-level skill transfer.

6.2. *Cognitive transfer effects as a multidimensional continuum*

The aforementioned studies illustrate that musical training provides transfer to benefit both sensory and cognitive levels of brain processing. To account for such widespread neuroplasticity, we propose a more global landscape of music-induced transfer effects conceptualized as a multidimensional phenomenon, and characterized by a *continuum* along two orthogonal dimensions (Fig. 4). We characterize the extent to which the trained activity (musical training) influences seemingly unrelated abilities along a *transfer dimension*, where "near transfer" represents benefits to untrained activities directly related to music (e.g., violinists showing enhanced perception of piano tones) and "far transfer" represents benefits to activities unrelated to the domain of music (e.g., speech and language processing). An orthogonal but complementary dimension describes the affected *processing level*, where "sensory processing" represents benefits to basic perceptual feature extraction (e.g., enhanced neural representation of auditory stimuli) and "cognitive processing" represents benefits to higher-order aspects of cognition (e.g., working memory, intelligence). While we acknowledge that these dimensions may not be mutually exclusive, they parsimoniously account for a wide range of studies demonstrating music-related transfer.

In this framework, initial plasticity afforded by musical training enhances auditory sensory processing specific to the domain of study. Thus, the neural encoding of musically-relevant sound is improved both within and perhaps outside the direct instrument of training (sensory/near) (Chartrand and Belin, 2006; Bidelman et al., 2011a, 2011b). Repeated exposure and experience with manipulating auditory patterns subsequently develops analytic listening skills necessary for robust auditory stream segregation (Zendel and Alain, 2009), complex sound manipulation (e.g., musical transposition: Foster and Zatorre, 2010), and "cocktail party listening" (Parbery-Clark et al., 2009a; Bidelman and Krishnan, 2010), representing near transfer and benefits to cognitive levels of audition (cognitive/near). Eventually, the auditory precision demanded by music begins to benefit auditory sensory encoding in unrelated domains like speech/language (Wong et al., 2007; Moreno et al., 2009; Bidelman and Krishnan, 2010; Schlaug et al., 2010; Bidelman et al., 2011c), representing more remote transfer outside the immediate scope of music or basic audition (sensory/far). The combination of improved auditory pattern recognition and sensory processing eventually influences the hearing of higher-order cognitive constructs, including the phonological characteristics of speech and language (cognitive/far) (Anvari et al., 2002; Dege and Schwarzer, 2011; Moreno et al., 2011a). Ultimately, the specific amount of benefit and the extent of transfer from music to unrelated skills (represented by the location within the pyramidal model) might be governed by an umbrella effect: the degree to which general cognitive abilities (e.g., executive processing, intelligence, working memory) are tuned by musical training itself (Schellenberg, 2004; Pallesen et al., 2010; Moreno et al., 2011b). We note that this simplistic framework may not account for all transfer observed in the literature, however, it nevertheless offers a viable framework to empirically test the extent and limitations of music-related plasticity. Based on the model, it is plausible, for example, that the amount of far transfer (and hence benefit) from music to linguistic processing is mediated by an individual's general cognitive capacity (e.g., EF). These and other features in the model, e.g., the true independence of the dimensions, await future research.

7. Conclusions, caveats, and future directions

Music training influences the brain quickly, effectively, and does so across the lifespan. Importantly, music's impact on the brain is unique in that it offers distinct perceptual and cognitive benefits not observed with other forms of intense training or experience. Perhaps more significantly, music training is a rare activity that modifies a hierarchy of brain structures ranging from the cochlea to multimodal, non-auditory cortices. At the cochlear level, studies indicate that music training strengthens top–down efferent feedback from the caudal brainstem to enhance signal detection at the most peripheral sites of auditory processing. At a subcortical level, brainstem FFR responses have shown that music experience introduces functional reorganization in the human midbrain that acts to enhance the neural transcription of complex sounds, including

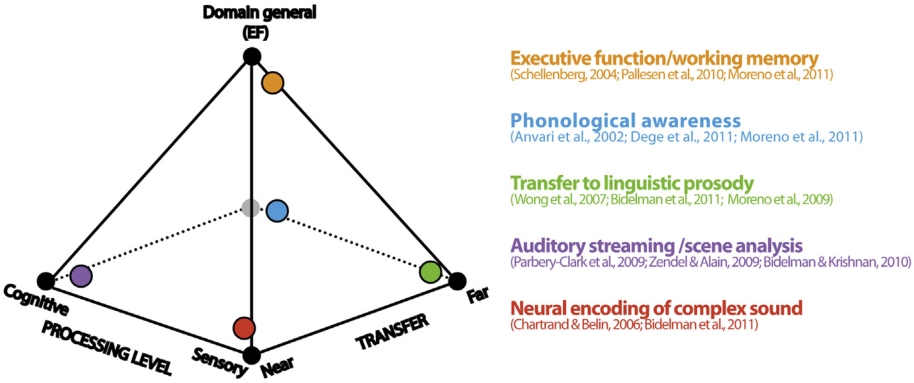

Fig. 4. Musical training and cognitive transfer effects conceptualized as a multidimensional continuum. The extent of a transfer effect from one activity to another can be characterized by two continuous, orthogonal dimensions: (i) the level of affected processing (low-level sensory ↔ high-level cognitive) and (ii) the "distance" of transfer from the domain of training (near ↔ far). These complementary dimensions explain a wide range of transfer and cognitive benefit observed across many studies examining music-related plasticity (denoted by the colored orbs). Ultimately, the specific amount of benefit and extent of transfer from music to unrelated skills (represented by the location within the pyramidal model) might be governed by an umbrella effect: the degree to which general cognitive abilities (e.g., executive processing, intelligence, working memory) are tuned by musical training itself.

those relevant for speech and language. At a cortical level, music impacts auditory, motor, frontal, and prefrontal brain areas, suggesting a broad involvement of cerebral structures in music training.

Importantly, the neural plasticity garnered via music experience offers important functional changes to human behavior. Neurophysiological enhancements in the auditory system produce benefits in basic sound processing (e.g., sound discrimination) which interestingly, also confer benefits to listening skills required for speech comprehension. Larger brain networks tuned by musical exposure produce benefits that extend well beyond the scope of music to influence the high-level cognitive functions of language, intelligence, attention, and memory. Given the spectrum of effects observed, we propose that music-induced plasticity is best conceptualized as a multidimensional continuum where transfer effects are defined by the level of processing (sensory to cognitive) and distance of transfer from the auditory domain [near (specific) to far (general)].

Several limitations and caveats should be considered for some of the findings presented herein. First, we note that a majority of the findings in this field of study are correlational (expert versus non-expert) which hinders causal inference and interpretation. As such, care should be taken in distinguishing correlational and causal findings and delineating the effects of music expertise (i.e., correlational) from music training (i.e., causal). Of the few longitudinal or intervention studies that have been conducted, most suffer from having small sample sizes, preexisting differences between groups, high attrition, and large variability in the sample. All these factors must be considered when interpreting training studies and the magnitude of the resulting effects. Furthermore, few studies have investigated the interaction and influence of other factors which may influence an individual to pursue or achieve in music or creative activities. For example, certain genetic markers may endow a listener with enhanced auditory recognition abilities (Drayna et al., 2001), ultimately increasing one's aptitude for musical activities (Ukkola et al., 2009; Park et al., 2012). Alternatively, it is possible that musically savvy individuals differ in behavioral traits such as personality (Corrigall et al., 2013) and/or motivation (McAuley and Tuft, 2011). In this regard, the purported cognitive benefits of music may be partially epiphenomenal in that cognitive benefits may be governed not by musical training per se, but by certain genetic and/or behavioral predispositions.

Finally, studies have yet to address potential limitations or even detriments caused by the transfer effects induced by music training. The thousands of hours required to become musically proficient are undoubtedly accompanied by both neural and opportunity costs. Neural tradeoffs are evident, for example, in the taxi-driver effect (Maguire et al., 2000) which showed that enhanced spatial memory in taxi drivers was also accompanied by reduced associative memory. Assuming some capacity limit to cognitive functions, the extensive practice needed to acquire musical expertise could actually lessen the enhancement and refinement of other traits such as athleticism or social skills. The pure quantity of hours devoted solely to musical practice also limits an individual's time in becoming proficient in other activities (e.g., becoming versed in literature, sports, etc.). It is unlikely that the neurocognitive benefits of musicianship are garnered without some cost to other behaviors. Further studies are needed to explore and understand these potential limits.

While studies suggest many positive effects of music on the human experience, future work is also needed to validate the efficacy of music-based training for improving cognitive deficits. For children with cognitive impairments, an important question to be addressed is at what age will music training be the most beneficial? Currently, there are several studies that seem to suggest greater benefit the earlier one starts musical lessons, including measures of brainstem electrophysiology (Wong et al., 2007; Skoe and Kraus, 2012) and white-matter fiber connectivity (Steele et al., 2013). However, several factors are confounded in these studies (e.g., parental style, personality, social class, etc.), and these factors, in turn, are all involved in the decision to start music training at an early age. The conduction of carefully controlled, randomized training studies is necessary to better understand the potential benefits of early musicianship (e.g., Schellenberg, 2004; Moreno et al., 2009, 2011b). Furthermore, the use of musical training as an intervention for certain pathologies or in older adults is a matter of great interest (Strait and Kraus, 2013). Yet, only a few studies have examined the effect of music training on the aging brain (Bugos et al., 2007; Hanna-Pladdy and MacKay, 2011; Parbery-Clark et al., 2012). While initial findings show a general positive effect in highly experienced older musicians, it remains to be determined whether training programs can truly mitigate cognitive declines in musically naïve older adults. Future work must demonstrate a clear, causal benefit of music on these populations with reliable longevity (i.e., lasting power). Ultimately, understanding the influence and extent of musical training on important facets of human cognition will provide a more comprehensive account of brain function, neural plasticity, and cognitive transfer.

Acknowledgments

The authors thank Madeline Lee Harris, Courtney Smith, Dr. Yunjo Lee, and Dr. Sean Hutchins for their helpful comments on early versions of this manuscript. The preparation of this work was supported by a grant from the FedDev for Ontario awarded to S. M. and grant-in-aid from the GRAMMY Foundation awarded to G.M.B.

References

Alain, C., Snyder, J.S., 2008. Age-related differences in auditory evoked responses during rapid perceptual learning. Clin. Neurophysiol. 119, 356–366.

Alain, C., Zendel, B.R., Hutka, S., Bidelman, G.M., 2014. Turning down the noise: the benefit of musical training on the aging auditory brain. Hear. Res. 308, 162–173.

Alexander, A., Wong, P., Bradlow, A., 2005. Lexical tone perception in musicians and nonmusicians. In: 9th European Conference on Speech Communication and Technology, Lisbon.

Amunts, K., Schlaug, G., Jäncke, L., Steinmetz, H., Schleicher, A., Dabringhaus, A., Zilles, K., 1997. Motor cortex and hand motor skills: structural compliance in the human brain. Hum. Brain Mapp. 5, 206–215.

Anvari, S.H., Trainor, L.J., Woodside, J., Levy, B.A., 2002. Relations among musical skills, phonological processing and early reading ability in preschool children. J. Exp. Child Psychol. 83, 111–130.

Bangert, M., Altenmüller, E., 2003. Mapping perception to action in piano practice: a longitudinal DC-EEG-study. BMC Neurosci. 4, 26–36.

Bangert, M., Haeusler, U., Altenmuller, E., 2001. On practice: how the brain connects piano keys and piano sounds. Ann. N. Y. Acad. Sci. 930, 425–434.

Barnett, S.M., Ceci, S.J., 2002. When and where do we apply what we learn?: a taxonomy for transfer. Psychol. Bull. 128, 612–637.

Besson, M., Chobert, J., Marie, C., 2011. Transfer of training between music and speech: common processing, attention, and memory. Front. Psychol. 2, 94.

Besson, M., Schon, D., Moreno, S., Santos, A., Magne, C., 2007. Influence of musical expertise and musical training on pitch processing in music and language. Restor. Neurol. Neurosci. 25, 399–410.

Bialystok, E., Depape, A.M., 2009. Musical expertise, bilingualism, and executive functioning. J. Exp. Psychol. Hum. Percept. Perform. 35, 565–574.

Bidelman, G.M., 2013. The role of the auditory brainstem in processing musically-relevant pitch. Front. Psychol. 4, 1–13.

Bidelman, G.M., Krishnan, A., 2010. Effects of reverberation on brainstem representation of speech in musicians and non-musicians. Brain Res. 1355, 112–125.

Bidelman, G.M., Krishnan, A., Gandour, J.T., 2011a. Enhanced brainstem encoding predicts musicians' perceptual advantages with pitch. Eur. J. Neurosci. 33, 530–538.

Bidelman, G.M., Gandour, J.T., Krishnan, A., 2011b. Musicians and tone-language speakers share enhanced brainstem encoding but not perceptual benefits for musical pitch. Brain Cogn. 77, 1–10.

Bidelman, G.M., Gandour, J.T., Krishnan, A., 2011c. Cross-domain effects of music and language experience on the representation of pitch in the human auditory brainstem. J. Cogn. Neurosci. 23, 425–434.

Bidelman, G.M., Gandour, J.T., Krishnan, A., 2011d. Musicians demonstrate experience-dependent brainstem enhancement of musical scale features within continuously gliding pitch. Neurosci. Lett. 503, 203–207.

Bidelman, G.M., Hutka, S., Moreno, S., 2013a. Tone language speakers and musicians share enhanced perceptual and cognitive abilities for musical pitch: evidence for bidirectionality between the domains of language and music. PloS One 8, e60676.

Bidelman, G.M., Moreno, S., Alain, C., 2013b. Tracing the emergence of categorical speech perception in the human auditory system. Neuroimage 79, 201–212.

Bieszczad, K.M., Weinberger, N.M., 2010. Representational gain in cortical area underlies increase of memory strength. Proc. Natl. Acad. Sci. U. S. A. 107, 3793–3798.

Brandler, S., Rammsayer, T.H., 2003. Differences in mental abilities between musicians and nonmusicians. Psychol. Music 31, 123–138.

Brashears, S.M., Morlet, T.G., Berlin, C.I., Hood, L.J., 2003. Olivocochlear efferent suppression in classical musicians. J. Am. Acad. Audiol. 14, 314–324.

Brattico, E., Pallesen, K.J., Varyagina, O., Bailey, C., Anourova, I., Jarvenpaa, M., Eerola, T., Tervaniemi, M., 2009. Neural discrimination of nonprototypical chords in music experts and laymen: an MEG study. J. Cogn. Neurosci. 21, 2230–2244.

Bugos, J.A., Perlstein, W.M., McCrae, C.S., Brophy, T.S., Bedenbaugh, P.H., 2007. Individualized piano instruction enhances executive functioning and working memory in older adults. Aging Ment. Health 11, 464–471.

Burns, E.M., Ward, W.D., 1978. Categorical perception – phenomenon or epiphenomenon: evidence from experiments in the perception of melodic musical intervals. J. Acoust. Soc. Am. 63, 456–468.

Chan, A.S., Ho, Y.C., Cheung, M.C., 1998. Music training improves verbal memory. Nature 396, 128.

Chandrasekaran, B., Kraus, N., 2010. The scalp-recorded brainstem response to speech: neural origins and plasticity. Psychophysiology 47, 236–246.

Chandrasekaran, B., Krishnan, A., Gandour, J.T., 2009. Relative influence of musical and linguistic experience on early cortical processing of pitch contours. Brain Lang. 108, 1–9.

Chartrand, J.P., Belin, P., 2006. Superior voice timbre processing in musicians. Neurosci. Lett. 405, 164–167.

Collet, L., Veuillet, E., Bene, J., Morgon, A., 1992. Effects of contralateral white noise on click-evoked emissions in normal and sensorineural ears: towards an exploration of the medial olivocochlear system. Audiology 31, 1–7.

Corrigall, K.A., Schellenberg, E.G., Misura, N.M., 2013. Music training, cognition, and personality. Front. Psychol. 4, 222. http://dx.doi.org/10.3389/fpsyg.2013.00222.

Craik, F.I.M., Rose, N.S., 2012. Training cognition: parallels with physical fitness? J. Appl. Res. Mem. Cogn. 1, 51–52.

Crummer, G.C., Walton, J.P., Wayman, J.W., Hantz, E.C., Frisina, R.D., 1994. Neural processing of musical timbre by musicians, nonmusicians, and musicians possessing absolute pitch. J. Acoust. Soc. Am. 95, 2720–2727.

David, S.V., Fritz, J.B., Shamma, S.A., 2012. Task reward structure shapes rapid receptive field plasticity in auditory cortex. Proc. Natl. Acad. Sci. U. S. A. 109, 2144–2149.

Dege, F., Schwarzer, G., 2011. The effect of a music program on phonological awareness in preschoolers. Front. Psychol. 2, 124.

Degé, F., Kubicek, C., Schwarzer, G., 2011. Music lessons and intelligence: a relation mediated by executive functions. Music Percept. 29, 195–201.

Detterman, D.K., Sternberg, R.J.E., 1982. How and How Much Can Intelligence Be Increased? Ablex, Norwood, NJ.

Draganski, B., May, A., 2008. Training-induced structural changes in the adult human brain. Behav. Brain Res. 192, 137–142.

Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U., May, A., 2004. Neuroplasticity: changes in grey matter induced by training. Nature 427, 311–312.

Drayna, D., Manichaikul, A., de Lange, M., Snieder, H., Spector, T., 2001. Genetic correlates of musical pitch recognition in humans. Science 291, 1969–1972.

Dunn, B.R., Dunn, D.A., Languis, M., Andrews, D., 1998. The relation of erp components to complex memory processing. Brain Cogn. 36, 355–376.

Federmeier, K.D., Kutas, M., 2002. Picture the difference: electrophysiological investigations of picture processing in the two cerebral hemispheres. Neuropsychologia 40, 730–747.

Foster, N.E., Zatorre, R.J., 2010. Cortical structure predicts success in performing musical transformation judgments. Neuroimage 53, 26–36.

Freunberger, R., Klimiesch, W., Doppelmayr, M., Holler, Y., 2007. Visual P2 component is related to theta phase-locking. Neurosci. Lett. 426, 181–186.

Fritz, J., Shamma, S., Elhilali, M., Klein, D., 2003. Rapid task-related plasticity of spectrotemporal receptive fields in primary auditory cortex. Nat. Neurosci. 6, 1216–1223.

Fujioka, T., Trainor, L.J., Ross, B., Kakigi, R., Pantev, C., 2004. Musical training enhances automatic encoding of melodic contour and interval structure. J. Cogn. Neurosci. 16, 1010–1021.

Galbraith, G., Arbagey, P.W., Branski, R., Comerci, N., Rector, P.M., 1995. Intelligible speech encoded in the human brain stem frequency-following response. Neuroreport 6, 2363–2367.

Galbraith, G., Threadgill, M., Hemsley, J., Salour, K., Songdej, N., Ton, J., Cheung, L., 2000. Putative measure of peripheral and brainstem frequency-following in humans. Neurosci. Lett. 292, 123–127.

Gandour, J.T., 1983. Tone perception in Far Eastern languages. J. Phon. 11, 149–175.

Gao, E., Suga, N., 1998. Experience-dependent corticofugal adjustment of midbrain frequency map in bat auditory system. Proc. Natl. Acad. Sci. U. S. A. 95, 12663–12670.

Gardiner, M.F., Fox, A., Knowles, F., Jeffrey, D., 1996. Learning improved by arts training. Nature 381, 284.

Gaser, C., Schlaug, G., 2003a. Brain structures differ between musicians and non-musicians. J. Neurosci. 23, 9240–9245.

Gaser, C., Schlaug, G., 2003b. Gray matter differences between musicians and nonmusicians. Ann. N. Y. Acad. Sci. 999, 514–517.

George, E.M., Coch, D., 2011. Music training and working memory: an ERP study. Neuropsychologia 49, 1083–1094.

Gerry, D., Unrau, A., Trainor, L.J., 2012. Active music classes in infancy enhance musical, communicative and social development. Dev. Sci. 15, 398–407.

Giraud, A.L., Garnier, S., Micheyl, C., Lina, G., Chays, A., Chery-Croze, S., 1997. Auditory efferents involved in speech-in-noise intelligibility. Neuroreport 8, 1779–1783.

Giuliano, R.J., Pfordresher, P.Q., Stanley, E.M., Narayana, S., Wicha, N.Y., 2011. Native experience with a tone language enhances pitch discrimination and the timing of neural responses to pitch change. Front. Psychol. 2, 146.

Green, C.S., Bavelier, D., 2010. Exercising your brain: a review of human brain plasticity and training-induced learning. Psychol. Aging 23, 692–701.

Guinan Jr., J.J., 2006. Olivocochlear efferents: anatomy, physiology, function, and the measurement of efferent effects in humans. Ear Hear. 27, 589–607.

Hanna-Pladdy, B., MacKay, A., 2011. The relation between instrumental musical activity and cognitive aging. Neuropsychology 25, 378.

Hansen, M., Wallentin, M., Vuust, P., 2012. Working memory and musical competence of musicians and non-musicians. Pyschol. Music. http://dx.doi.org/10.1177/0305735612452186.

Herholz, S.C., Zatorre, R.J., 2012. Musical training as a framework for brain plasticity: behavior, function, and structure. Neuron 76, 486–502.

Ho, Y., Cheung, M., Chan, A., 2003. Music training improves verbal but not visual memory: cross sectional and longitudinal explorations in children. Neuropsychology 17, 439–450.

Huss, M., Verney, J.P., Fosker, T., Mead, N., Goswami, U., 2011. Music, rhythm, rise time perception and developmental dyslexia: perception of musical meter predicts reading and phonology. Cortex 47, 674–689.

Hutchinson, S., Lee, L.H.L., Gaab, N., Schlaug, G., 2003. Cerebellar volume of musicians. Cereb. Cortex 13, 943–949.

Hyde, K.L., Lerch, J., Norton, A., Forgeard, M., Winner, E., Evans, A.C., Schlaug, G., 2009. Musical training shapes structural brain development. J. Neurosci. 29, 3019–3025.

Jones, M.R., Yee, W., 1997. Sensitivity to time change: the role of context and skill. J. Exp. Psychol. Hum. Percept. Perform. 23, 693–709.

Jung, R.E., Haier, R.J., 2007. The parieto-frontal integration theory (P-fit) of intelligence: converging neuroimaging evidence. Behav. Brain Sci. 30, 135–154.

Kakebeeke, T.H., Caflisch, J., Locatelli, I., Rousson, V., Jenni, O.G., 2012. Improvement in gross motor performance between 3 and 5 years of age. Percept. Mot. Skills 114, 795–806.

Kane, M.J., Hambrick, D.Z., Tuholski, S.W., Wilhelm, O., Payne, T.W., Engle, R.W., 2004. The generality of working memory capacity: a latent-variable approach to verbal and visuospatial memory span and reasoning. J. Exp. Psychol. Gen. 133, 189–217.

Keenan, J.P., Thangaraj, V., Halpern, A.R., Schlaug, G., 2001. Absolute pitch and planum temporale. NeuroImage 14, 1402–1408.

Kishon-Rabin, L., Amir, O., Vexler, Y., Zaltz, Y., 2001. Pitch discrimination: are professional musicians better than non-musicians? J. Basic Clin. Physiol. Pharmacol. 12, 125–143.

Koelsch, S., Schroger, E., Tervaniemi, M., 1999. Superior pre-attentive auditory processing in musicians. Neuroreport 10, 1309–1313.

Koelsch, S., Gunter, T.C., v Cramon, D.Y., Zysset, S., Lohmann, G., Friederici, A.D., 2002. Bach speaks: a cortical "language-network" serves the processing of music. Neuroimage 17, 956–966.

Kraus, N., Chandrasekaran, B., 2010. Music training for the development of auditory skills. Nat. Rev. Neurosci. 11, 599–605.

Kraus, N., Skoe, E., Parbery-Clark, A., Ashley, R., 2009. Experience-induced malleability in neural encoding of pitch, timbre, and timing. Ann. N. Y. Acad. Sci. 1169, 543–557.

Krishnan, A., 2007. Human frequency following response. In: Burkard, R.F., Don, M., Eggermont, J.J. (Eds.), Auditory Evoked Potentials: Basic Principles and Clinical Application. Lippincott Williams & Wilkins, Baltimore, pp. 313–335.

Krishnan, A., Gandour, J.T., 2009. The role of the auditory brainstem in processing linguistically-relevant pitch patterns. Brain Lang. 110, 135–148.

Krishnan, A., Gandour, J.T., Bidelman, G.M., 2012. Experience-dependent plasticity in pitch encoding: from brainstem to auditory cortex. Neuroreport 23, 498–502.

Krishnan, A., Xu, Y., Gandour, J., Cariani, P., 2005. Encoding of pitch in the human brainstem is sensitive to language experience. Brain Res. Cogn. Brain Res. 25, 161–168.

Krishnan, A., Gandour, J.T., Bidelman, G.M., Swaminathan, J., 2009. Experience-dependent neural representation of dynamic pitch in the brainstem. Neuroreport 20, 408–413.

Krishnan, A., Gandour, J.T., Ananthakrishnan, S., Bidelman, G.M., Smalt, C.J., 2011. Linguistic status of timbre influences pitch encoding in the brainstem. Neuroreport 22, 801–803.

Krohn, K.I., Brattico, E., Valimaki, V., Tervaniemi, M., 2007. Neural representations of the hierarchical scale pitch structure. Music Percept. 24, 281–296.

Lappe, C., Herholz, S.C., Trainor, L.J., Pantev, C., 2008. Cortical plasticity induced by short-term unimodal and multimodal musical training. J. Neurosci. 28, 9632–9639.

Lee, C.C., Middlebrooks, J.C., 2011. Auditory cortex spatial sensitivity sharpens during task performance. Nat. Neurosci. 14, 108–114.

Lee, C.Y., Hung, T.H., 2008. Identification of Mandarin tones by English-speaking musicians and nonmusicians. J. Acoust. Soc. Am. 124, 3235–3248.

Lefebvre, C.D., Marchand, Y., Eskes, G.A., Connolly, J.F., 2005. Assessment of working memory abilities using an event-related brain potential (ERP)-compatible digit span backward task. Clin. Neurophysiol. 116, 1665–1680.

Lim, V.K., Bradshaw, J.L., nicholls, M., Altenmuller, E., 2003. Perceptual differences in sequential stimuli across patients with musician's and writer's cramp. Mov. Disord. 11, 1286–1293.

Lovett, M.C., Anderson, J.R., 1994. Effects of solving related proofs on memory and transfer in geometry problem solving. J. Exp. Psychol. Learn. Mem. Cogn. 20, 366–378.

Luck, S.J., Hillyard, S.A., 1994. Electrophysiological correlates of feature analysis during visual search. Psychophysiology 31, 291–308.

Luders, E., Gaser, C., Jancke, L., Schlaug, G., 2004. A voxel-based approach to gray matter asymmetries. Neuroimage 22, 656–664.

Maess, B., Koelsch, S., Gunter, T.C., Friederici, A.D., 2001. Musical syntax is processed in Broca's area: an MEG study. Nat. Neurosci. 4, 540–545.

Maguire, E.A., Gadian, D.G., Johnsrude, I.S., Good, C.D., Ashburner, J., Frackowiak, R.S., Frith, C.D., 2000. Navigation-related structural change in the hippocampi of taxi drivers. Proc. Natl. Acad. Sci. U. S. A. 97, 4398–4403.

Marie, C., Delogu, F., Lampis, G., Belardinelli, M.O., Besson, M., 2011. Influence of musical expertise on segmental and tonal processing in Mandarin Chinese. J. Cogn. Neurosci. 23, 2701–2715.

McAuley, J.D., Tuft, S., 2011. Musician advantages in music perception: an issue of motivation, not just ability. Music Percept. 28, 505–518.

Micheyl, C., Collet, L., 1996. Involvement of the olivocochlear bundle in the detection of tones in noise. J. Acoust. Soc. Am. 99, 1604–1610.

Micheyl, C., Carbonnel, O., Collet, L., 1995. Medial olivocochlear system and loudness adaptation: differences between musicians and non-musicians. Brain Cogn. 29, 127–136.

Micheyl, C., Perrot, X., Collet, L., 1997a. Relationship between auditory intensity discrimination in noise and olivocochlear efferent system activity in humans. Behav. Neurosci. 111, 801–807.

Micheyl, C., Khalfa, S., Perrot, X., Collet, L., 1997b. Difference in cochlear efferent activity between musicians and non-musicians. Neuroreport 8, 1047–1050.

Micheyl, C., Delhommeau, K., Perrot, X., Oxenham, A.J., 2006. Influence of musical and psychoacoustical training on pitch discrimination. Hear. Res. 219, 36–47.

Mishra, J., Gazzaley, A., 2012. Attention distributed across sensory modalities enhances perceptual performance. J. Neurosci. 32, 12294–12302.

Moon, C., Lagercrantz, H., Kuhl, P.K., 2013. Language experienced in utero affects vowel perception after birth: a two-country study. Acta Paediatr. 102, 156–160.

Moreno, S., 2009. Can music influence language and cognition? Contemp. Music Rev. 28, 329–345.

Moreno, S., Besson, M., 2005. Influence of musical training on pitch processing: event-related brain potential studies of adults and children. Ann. N. Y. Acad. Sci. 1060, 93–97.

Moreno, S., Besson, M., 2006. Musical training and language-related brain electrical activity in children. Psychophysiology 43, 287–291.

Moreno, S., Friesen, D., Bialystok, E., 2011a. Effect of music training on promoting preliteracy skills: preliminary causal evidence. Music Percept. 29, 165–172.

Moreno, S., Marques, C., Santos, A., Santos, M., Castro, S.L., Besson, M., 2009. Musical training influences linguistic abilities in 8-year-old children: more evidence for brain plasticity. Cereb. Cortex 19, 712–723.

Moreno, S., Bialystok, E., Barac, R., Schellenberg, E.G., Cepeda, N.J., Chau, T., 2011b. Short-term music training enhances verbal intelligence and executive function. Psychol. Sci. 22, 1425–1433.

Munte, T.F., Altenmuller, E., Jancke, L., 2002. The musician's brain as a model of neuroplasticity. Nat. Rev. Neurosci. 3, 473–478.

Munte, T.F., Kohlmetz, C., Nager, W., Altenmuller, E., 2001. Superior auditory spatial tuning in conductors. Nature 409, 580.

Musacchia, G., Sams, M., Skoe, E., Kraus, N., 2007. Musicians have enhanced subcortical auditory and audiovisual processing of speech and music. Proc. Natl. Acad. Sci. U. S. A. 104, 15894–15898.

Myers, E.B., Swan, K., 2012. Effects of category learning on neural sensitivity to non-native phonetic categories. J. Cogn. Neurosci. 24, 1695–1708.

Nager, W., Kohlmetz, C., Altenmuller, E., Rodriguez-Fornells, A., Munte, T.F., 2003. The fate of sounds in conductors' brains: an ERP study. Brain Res. Cogn. Brain Res. 17, 83–93.

Norena, A., Micheyl, C., Durrant, J., Chery-Croze, S., Collet, L., 2002. Perceptual correlates of neural plasticity related to spontaneous otoacoustic emissions? Hear. Res. 171, 66–71.

Olesen, P.J., Westerberg, H., Klingberg, T., 2004. Increased prefrontal and parietal activity after training of working memory. Nat. Neurosci. 7, 75–79.

Op de Beeck, H.P., Baker, C.I., 2010. The neural basis of visual object learning. Trends Cogn. Sci. 14, 22–30.

Oxenham, A.J., Fligor, B.J., Mason, C.R., Kidd Jr., G., 2003. Informational masking and musical training. J. Acoust. Soc. Am. 114, 1543–1549.

Pallesen, K.J., Brattico, E., Bailey, C.J., Korvenoja, A., Koivisto, J., Gjedde, A., Carlson, S., 2010. Cognitive control in auditory working memory is enhanced in musicians. PLoS One 5, e11120.

Pantev, C., Wollbrink, A., Roberts, L.E., Engelien, A., Lütkenhöner, B., 1999. Short-term plasticity of the human auditory cortex. Brain Res. 842, 192–199.

Pantev, C., Roberts, L.E., Schulz, M., Engelien, A., Ross, B., 2001. Timbre-specific enhancement of auditory cortical representations in musicians. Neuroreport 12, 169–174.

Pantev, C., Oostenveld, R., Engelien, A., Ross, B., Roberts, L.E., Hoke, M., 1998. Increased auditory cortical representation in musicians. Nature 392, 811–814.

Paraskevopoulos, E., Kuchenbuch, A., Herholz, S.C., Pantev, C., 2012. Evidence for training-induced plasticity in multisensory brain structures: an MEG stud. PLoS One 7, e36534.

Parbery-Clark, A., Skoe, E., Kraus, N., 2009a. Musical experience limits the degradative effects of background noise on the neural processing of sound. J. Neurosci. 29, 14100–14107.

Parbery-Clark, A., Skoe, E., Lam, C., Kraus, N., 2009b. Musician enhancement for speech-in-noise. Ear Hear. 30, 653–661.

Parbery-Clark, A., Anderson, S., Hittner, E., Kraus, N., 2012. Musical experience offsets age-related delays in neural timing. Neurobiol. Aging 33, 1483 e1–1483 e4.

Park, H., Lee, S., Kim, H.J., Ju, Y.S., Shin, J.Y., Hong, D., von Grotthuss, M., Lee, D.S., Park, C., Kim, J.H., Kim, B., Yoo, Y.J., Cho, S.I., Sung, J., Lee, C., Kim, J.I., Seo, J.S., 2012. Comprehensive genomic analyses associate UGT8 variants with musical ability in a Mongolian population. J. Med. Genet. 49, 747–752.

Patel, A.D., 2014. Can nonlinguistic musical training change the way the brain processes speech? The expanded OPERA hypothesis. Hear. Res. 308, 98–108.

Perrot, X., Collet, L., 2014. Function and plasticity of the medial olivocochlear system in musicians: a review. Hear. Res. 308, 27–40.

Perrot, X., Micheyl, C., Khalfa, S., Collet, L., 1999. Stronger bilateral efferent influences on cochlear biomechanical activity in musicians than in non-musicians. Neurosci. Lett. 262, 167–170.

Picton, T.W., Alain, C., Woods, D.L., John, M.S., Scherg, M., Valdes-Sosa, P., Bosch-Bayard, J., Trujillo, N.J., 1999. Intracerebral sources of human auditory-evoked potentials. Audiol. Neurootol. 4, 64–79.

Pietschnig, J., Voracek, M., Formann, A.K., 2010. Mozart effect–Shmozart effect: a meta-analysis. Intelligence, 314–323.

Polley, D.B., Steinberg, E.E., Merzenich, M.M., 2006. Perceptual learning directs auditory cortical map reorganization through top-down influences. J. Neurosci. 26, 4970–4982.

Putkinen, V., Tervaniemi, M., Huotilainen, M., 2013. Informal musical activities are linked to auditory discrimination and attention in 2–3-year-old children: an event-related potential study. Eur. J. Neurosci. 37, 654–661.

Rammsayer, T., Altenmuller, E., 2006. Temporal information processing in musicians and nonmusicians. Music Percept. 24, 37–48.

Rammsayer, T., Buttkus, F., Altenmüller, E., 2012. Musicians do better than nonmusicians in both auditory and visual timing tasks. Music Percept. 30, 85–96.

Rauscher, F.H., Shaw, G.L., Ky, K.N., 1993. Music and spatial task performance. Nature 365, 611.

Russeler, J., Altenmuller, E., Nager, W., Kohlmetz, C., Munte, T.F., 2001. Event-related brain potentials to sound omissions differ in musicians and non-musicians. Neurosci. Lett. 308, 33–36.

Schellenberg, E.G., 2004. Music lessons enhance IQ. Psychol. Sci. 15, 511–514.

Schellenberg, E.G., 2006. Long-term positive associations between music lessons and IQ. J. Educ. Psychol. 98, 457–468.

Schellenberg, E.G., 2012. Cognitive performance after music listening: a review of the Mozart effect. In: MacDonald, R.A.R., Kreutz, G., Mitchel, L. (Eds.), Music, Health and Wellbeing. Oxford University Press, Oxford, UK.

Scherg, M., Vajsar, J., Picton, T.W., 1989. A source analysis of the late human auditory evoked potentials. J. Cogn. Neurosci. 1, 336–355.

Schlaug, G., Jancke, L., Huang, Y., Steinmetz, H., 1995a. In vivo evidence of structural brain asymmetry in musicians. Science 267, 699–701.

Schlaug, G., Jancke, L., Huang, Y., Staiger, J.F., Steinmetz, H., 1995b. Increased corpus callosum size in musicians. Neuropsychologia 33, 1047–1055.

Schlaug, G., Norton, A., Marchina, S., Zipse, L., Wan, C.Y., 2010. From singing to speaking: facilitating recovery from nonfluent aphasia. Future Neurol. 5, 657–665.

Schmithorst, V.J., Wilke, M., 2002. Differences in white matter architecture between musicians and non-musicians: a diffusion tensor imaging study. Neurosci. Lett. 321, 57–60.

Schneider, P., Scherg, M., Dosch, H.G., Specht, H.J., Gutschalk, A., Rupp, A., 2002. Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. Nat. Neurosci. 5, 688–694.

Schon, D., Magne, C., Besson, M., 2004. The music of speech: music training facilitates pitch processing in both music and language. Psychophysiology 41, 341–349.

Shahin, A., Roberts, L.E., Trainor, L.J., 2004. Enhancement of auditory cortical development by musical experience in children. Neuroreport 15, 1917–1921.

Shahin, A., Bosnyak, D.J., Trainor, L.J., Roberts, L.E., 2003. Enhancement of neuroplastic P2 and N1c auditory evoked potentials in musicians. J. Neurosci. 23, 5545–5552.

Skoe, E., Kraus, N., 2010. Auditory brain stem response to complex sounds: a tutorial. Ear Hear. 31, 302–324.

Skoe, E., Kraus, N., 2012. A little goes a long way: how the adult brain is shaped by musical training in childhood. J. Neurosci. 32, 11507–11510.

Sluming, V., Barrick, T., Howard, M., Cezayirli, E., Mayes, A., Roberts, N., 2002. Voxel-based morphometry reveals increased gray matter density in Broca's area in male symphony orchestra musicians. Neuroimage 17, 1613–1622.

Smith, J.C., Marsh, J.T., Brown, W.S., 1975. Far-field recorded frequency-following responses: evidence for the locus of brainstem sources. Electroencephalogr. Clin. Neurophysiol. 39, 465–472.

Sohmer, H., Pratt, H., Kinarti, R., 1977. Sources of frequency-following responses (FFR) in man. Electroencephalogr. Clin. Neurophysiol. 42, 656–664.

Spiegel, M.F., Watson, C.S., 1984. Performance on frequency-discrimination tasks by musicians and nonmusicians. J. Acoust. Soc. Am. 766, 1690–1695.

Steele, C.J., Bailey, J.A., Zatorre, R.J., Penhune, V.B., 2013. Early musical training and white-matter plasticity in the corpus callosum: evidence for a sensitive period. J. Neurosci. 33, 1282–1290.

Strait, D.L., Kraus, N., 2011. Can you hear me now? Musical training shapes functional brain networks for selective auditory attention and hearing speech in noise. Front. Psychol. 2, 113.

Strait, D.L., Kraus, N., 2014. Biological impact of auditory expertise across the life span: musicians as a model of auditory learning. Hear. Res. 308, 109–121.

Strait, D.L., Kraus, N., Skoe, E., Ashley, R., 2009. Musical experience and neural efficiency: effects of training on subcortical processing of vocal expressions of emotion. Eur. J. Neurosci. 29, 661–668.

Strait, D.L., Kraus, N., Parbery-Clark, A., Ashley, R., 2010. Musical experience shapes top-down auditory mechanisms: evidence from masking and auditory attention performance. Hear. Res. 261, 22–29.

Strait, D.L., Chan, K., Ashley, R., Kraus, N., 2012. Specialization among the specialized: auditory brainstem function is tuned in to timbre. Cortex 48, 360–362.

Talsma, D., Kok, A., 2001. Nonspatial intermodal selective attention is mediated by sensory brain areas: evidence from event related potentials. Psychophysiology 38, 736–751.

Tervaniemi, M., Just, V., Koelsch, S., Widmann, A., Schroger, E., 2005. Pitch discrimination accuracy in musicians vs nonmusicians: an event-related potential and behavioral study. Exp. Brain Res. 161, 1–10.

Tierney, A.T., Bergeson, T.R., Pisoni, D.B., 2008. Effects of early musical experience on auditory sequence memory. Empir. Music. Rev. 3, 178–186.

Trainor, L.J., Shahin, A., Roberts, L.E., 2003. Effects of musical training on the auditory cortex in children. Ann. N. Y. Acad. Sci. 999, 506–513.

Tsang, C.D., Conrad, N.J., 2011. Music training and reading readiness. Music Percept. 29, 157–163.

Ukkola, L.T., Onkamo, P., Raijas, P., Karma, K., Jarvela, I., 2009. Musical aptitude is associated with AVPR1A-haplotypes. PLoS One 4, e5534.

van Zuijen, T.L., Sussman, E., Winkler, I., Naatanen, R., Tervaniemi, M., 2004. Grouping of sequential sounds – an event-related potential study comparing musicians and nonmusicians. J. Cogn. Neurosci. 16, 331–338.

Weinberger, N.M., 2011. Reconceptualizing the primary auditory cortex: learning, memory and specific plasticity. In: Winer, J.A., Schreiner, C.E. (Eds.), The Auditory Cortex. Springer, pp. 465–491.

Weinberger, N.M., Javid, R., Lepan, B., 1993. Long-term retention of learning-induced receptive-field plasticity in the auditory cortex. Proc. Natl. Acad. Sci. U. S. A. 90, 2394–2398.

Wong, P.C., Skoe, E., Russo, N.M., Dees, T., Kraus, N., 2007. Musical experience shapes human brainstem encoding of linguistic pitch patterns. Nat. Neurosci. 10, 420–422.

Wright, B.A., Zhang, Y., 2009. A review of the generalization of auditory learning. Philos. Trans. R. Soc. Lond. B Biol. Sci. 364, 301–311.

Zatorre, R., McGill, J., 2005. Music, the food of neuroscience? Nature 434, 312–315.

Zatorre, R., Fields, R.D., Johansen-Berg, H., 2012. Plasticity in gray and white: neuroimaging changes in brain structure during learning. Nat. Neurosci. 15, 528–536.

Zatorre, R.J., Perry, D.W., Beckett, C.A., Westbury, C.F., Evans, A.C., 1998. Functional anatomy of musical processing in listeners with absolute pitch and relative pitch. Proc. Natl. Acad. Sci. U. S. A. 95, 3172–3177.

Zendel, B.R., Alain, C., 2009. Concurrent sound segregation is enhanced in musicians. J. Cogn. Neurosci. 21, 1488–1498.

Zendel, B.R., Alain, C., 2013. The influence of lifelong musicianship on neurophysiological measures of concurrent sound segregation. J. Cogn. Neurosci. 25, 503–516.