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Review

Biological impact of auditory expertise across the life span: Musicians as a model of auditory learning

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ABSTRACT

Experience-dependent characteristics of auditory function, especially with regard to speech-evoked auditory neurophysiology, have garnered increasing attention in recent years. This interest stems from both pragmatic and theoretical concerns as it bears implications for the prevention and remediation of language-based learning impairment in addition to providing insight into mechanisms engendering experience-dependent changes in human sensory function. Musicians provide an attractive model for studying the experience-dependency of auditory processing in humans due to their distinctive neural enhancements compared to nonmusicians. We have only recently begun to address whether these enhancements are observable early in life, during the initial years of music training when the auditory system is under rapid development, as well as later in life, after the onset of the aging process. Here we review neural enhancements in musically trained individuals across the life span in the context of cellular mechanisms that underlie learning, identified in animal models. Musicians' subcortical physiologic enhancements are interpreted according to a cognitive framework for auditory learning, providing a model in which to study mechanisms of experience-dependent changes in human auditory function.
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1. Introduction

Learning is a fundamental human capacity; not only does it underlie the gradual development of basic skills from infancy (e.g., language) but it also accounts for our attraction to new experiences, the resources we invest in educational opportunities and the effort we put into maintaining a dynamic nervous system in hopes of keeping aging's cognitive detriments at bay. In light of our continuous reliance on learning, it is surprising how much of its neurobiological underpinnings—especially within the auditory system—still eludes us. We have made considerable headway toward defining neuronal correlates of learning in addition to identifying the characteristics that contribute to an organism's readiness to learn. The bulk of this work has been cellular in nature, carried out in animal models; we have only recently begun to apply principles derived from this research to outcomes of learning in humans (e.g., Zatorre et al., 2012). The study of musicians' auditory processing provides a window into auditory learning, not only shedding light on neural mechanisms underlying learning in humans but further contributing to a definition of what makes a good learner.

Investigations into human learning through the study of musicians profit from an almost infinite variety of auditory experts. Musicians' auditory learning approaches vary not only according to instrument, style and level of expertise but also according to their reliance on memory, improvisation, aural learning/mimicry and engagement of the visual modality. Furthermore, music is an inherently rewarding auditory activity, in part due to its activation of the brain's mesolimbic reward network (Koelsch et al., 2006; Menon and Levitin, 2005; Salimpoor et al., 2011; Salimpoor et al., 2013). This may account for why humans view music as one of the top ten most pleasurable things, sometimes even ranking music

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above the notable rewards of money and food (Dube and Lebel, 2003). This property of music confers emotional benefits that promote its practice and performance and, by co-activating meso-limbic neuromodulatory control centers, promotes long-term learning success (for review see Puschmann et al., 2012).

Here we interpret principles derived from cellular studies of learning in the context of how auditory experience in the form of music training shapes the structure and function of the human brain. By considering cellular approaches for studying learning alongside the biological evidence of lifelong, interactive auditory enrichment in musicians, we can infer the processes by which the human brain is shaped by the development of expertise and test their boundaries. The parallel consideration of cellular and far-field approaches may encourage further investigations into the capacity of interactive, acoustically rich and cognitively engaging auditory activities, such as that provided through music training, to shape basic auditory mechanisms. We begin by reviewing progress toward identifying neuronal substrates of learning in animal models and the potential for musicians to provide further conceptual advances as a model of auditory learning in humans.

2. Biological mechanisms of auditory learning

Neurobiological approaches have uncovered a variety of neuronal substrates of learning, the activity of which is modified by development, experience, gene expression and the neuro-modulatory system, among others. We herein discuss major themes in this line of research and their application to musicians, comprising neurogenesis, synaptic plasticity, gene expression and factors guiding metaplasticity (i.e., the potential for plastic changes to take place).

2.1. Neurogenesis

Joseph Altman was one of the first to recommend adult neuro-genesis as a neural substrate of learning (Altman, 1967). Since then, the birth of new neurons has been associated with environmental enrichment and learning (Deng et al., 2009; Gould et al., 1999a; Nilsson et al., 1999; Patel et al., 1997) but it is possible that this relationship reflects covariance with alternate neuronal changes (e.g., synaptic plasticity; see Leuner et al., 2006; for discussion). Neurogenesis has been observed throughout life (Curtis et al., 2007; Eriksson et al., 1998; cf. Sanai et al., 2007), although it is more significant during the prenatal period and decreases with age (Kuhn et al., 1996). Furthermore, neurogenesis in adults is largely constrained to the dentate gyrus of the hippocampus and the lateral ventricles that supply the olfactory cortex (cf. Gould, 2007; Gould et al., 1999b). Without evidence for the experience-related post-natal birth of new neurons in sensory cortices, local neuro-genesis is an unlikely candidate to account for the extent of experience-related changes in neural structure that have been associated with music training (for further discussion see Zatorre et al., 2012). It is possible, however, that experience-related changes in sensory cortices are mediated, at least in part, by structural and functional changes in hippocampus that are known to accompany music training (Groussard et al., 2010; Herdener et al., 2010; Hutchinson et al., 2003) and which may reflect neu-rogenesis. Still, music training, especially during developmental years, may have a more significant impact on the survival and connectivity of existing neurons by increasing the activation of neural circuits involved in auditory processing, stabilizing and sustaining those circuits into adulthood (Alladi et al., 2005; Ben-Ari, 2001; Katz and Shatz, 1996).

2.2. Synaptic plasticity and inhibitory networks

Synaptic plasticity is the experience-dependent change in the connectivity between two neurons, which can comprise syn-aptogenesis or the strengthening of previously-existing connec-tions. It can be evidenced by the growth and redirection of axonal branching (Galimberti et al., 2006; Holahan et al., 2006; Ramirez-Amaya et al., 2001) and morphological changes in dendritic spine heads that, when enlarged, increase synaptic efficacy. While spines have significant structural diversity, their size correlates with synaptic strength (Matsuzaki et al., 2004) and the long-term stability of the synapse (Holtmaat et al., 2005). Their morpho-logical stability appears to underlie long-term learning (T. Xu et al., 2009) and is dependent on changes in gene expression and protein synthesis (e.g., Tanaka, et al., 2008). While it is generally accepted that synaptic plasticity underlies learning, the complexity of interactions among ion channels, enzymes and genes that contribute to synaptic plasticity has prevented its thorough characterization (for review see Caroni et al., 2012; Ho et al., 2011).

Axonal sprouting and the expansion, generation and relocation of dendritic spines occur throughout life but are regulated by development and sensory experience. Specifically, synaptic plas-ticity decreases with development (Grutzendler et al., 2002; Pestronk et al., 1980; Trachtenberg et al., 2002) but can be augmented by enriched sensory experiences (Bednarek and Caroni, 2011; Bose et al., 2010; Globus et al., 1973). Developmental and experience-related changes are underscored by shifts in the bal-ance of inhibitory and excitatory networks: while inhibitory net-works generally strengthen from childhood to adulthood, the application of agents that weaken them prevent decreased synaptic plasticity in the adult brain, resetting synaptic plasticity to child-hood levels (Bavelier et al., 2010; Morishita et al., 2010). Exposure to sensory experiences during development mediates this excitatory-inhibitory balance (Takesian et al., 2010); in fact, enriched sensory environments reduce inhibition even when this experience is not initiated until adulthood (Sale et al., 2007). Because of this, the enriched acoustic environment provided by music training may preserve synaptic plasticity within musicians. Music experience early in life is likely to bear even more significant effects on synaptic plasticity than that reported in adults, with the potential to contribute to an increased potential for synaptic remodeling throughout life (see sections on *Gene expression* and *Metaplasticity: musicians as a model of auditory learning*, below).

Although synaptic remodeling occurs both with environmental enrichment and the learning of specific tasks, their effects can be differentiated. Whereas exposure to enriched sensory environ-ments increases dendritic spine count throughout the exercised sensory domain (Bednarek and Caroni, 2011; Bose et al., 2010; Globus et al., 1973), task-learning induces changes in synaptic structure that are specific to the circuitry involved in the task's execution. Synaptic changes with task-learning can be lasting if sufficient task repetition triggers memory consolidation and might be considered a procedural memory trace (Hofer et al., 2009; Xu et al., 2009b; Yang et al., 2009). Although the generalization of task learning-induced synaptic plasticity to other behaviors has not been determined, it may be reasonable to assume minimal-to-no advantages for behaviors, even within the same sensory domain, that do not call on sufficiently overlapping circuitry. The variety of auditory, visual and tactile experiences provided by music training may engender outcomes more similar to environmental enrich-ment than procedural learning by contributing to synaptic remodeling within and across sensory systems that enhances the diversity of synaptic connections and promotes the generalization of expertise.

2.3. Gene expression

Dendritic morphology and, thus, synaptic transmission are largely regulated by gene expression, which is in turn controlled by a host of proteins called transcription factors. Given that we have identified over 2000 transcription factors and that they tend to work in combination to influence gene expression, investigations into their relationships to sensory experience and development have only scratched the surface. Here we touch on two well-known topics related to gene expression that bear consequences for the brain's readiness to learn from the perspective that they, among others, have the capacity to contribute to music training's impact on brain structure and its development: the expression of N-Methyl-aspartate receptor (NMDAR) subunits and tyrosine kinase receptor B (TrkB), which has a high affinity for brain-derived neurotrophic factor (BDNF), a neurotrophic factor implicated in learning and memory.

NMDA glutamate receptors facilitate the experience-dependent synaptic plasticity that undergirds learning by increasing synaptic efficacy (for review see Lau and Zukin, 2007). Enriched auditory experiences during childhood, such as that engendered by music training, have the potential to increase the NMDAR population throughout the auditory system (and, potentially, throughout the nervous system). Within the auditory brainstem, NMDARs mediate the malleability of neuronal responses with new auditory experiences during development (Feldman et al., 1996). Within the auditory cortex, NMDARs have been linked to enriched auditory exposure early in life: young music-exposed rats demonstrate more populous NMDAR subunit protein expression than rats raised in a typical laboratory environment. These outcomes stand in contrast to observations in post-pubescent music-exposed rats that show no measurable change with enrichment (J. Xu et al., 2009). NMDAR subunit population has a clear impact on learning potential, relating to enhanced auditory perceptual acuity (i.e., signal detection and duration discrimination) and more proficient learning performance, even outside the auditory domain (Tang et al., 1999), and augmented neurobiological benefits of environmental enrichment (Tang et al., 2001). If, as in rodents, children who regularly engage in musical activities have more populous NMDAR subunits, they may similarly demonstrate an increased capacity to benefit from learning opportunities and further enriched sensory experiences. These effects are doubtfully exclusive to music, however: auditory enrichment by means of music exposure has not yet been compared to other approaches that can be initiated during early childhood and may yield similar effects (e.g., increased language exposure).

The expression of neurotrophic factor BDNF and its receptor, TrkB, relates to experience-related neuroplasticity akin to NMDARs by promoting synaptic plasticity but with a focus on increasing synapto- and neurogenesis (for review see Cunha et al., 2010) and enhancing the survival of existing cells (Acheson et al., 1995). Like NMDARs, enriched auditory stimulation during early developmental stages regulates BDNF and TrkB expression (Chaudhury and Wadhwa, 2009; Chikahisa et al., 2006), concurrent with enhanced learning performance even outside the auditory domain (Chikahisa et al., 2006). Studies such as these indicate that early exposure to auditory-rich, interactive and engaging environments during initial development, such that facilitated by music training, sets the stage for later auditory learning success by promoting gene expression that enhances immediate synaptic plasticity and cell survival. NMDAR subunit and BDNF/TrkB expression may in part account for musicians' enhanced learning performance, including foreign and novel language learning (Schon and Francois, 2011; Shook et al., 2013), and increased sensitivity to statistical regularities in ongoing sound streams (Herholz et al., 2011).

2.4. Metaplasticity: musicians as a model of auditory learning

The term "metaplasticity" describes experience-dependent neural changes that shape the brain's capacity for subsequent synaptic plasticity—"the plasticity of synaptic plasticity." Initially coined by Abraham and Bear (1996), this term has provided a framework for the study of cellular mechanisms that prime the nervous system for experience-related neuronal and synaptic restructuring. This priming can be contrasted with the effects of intercellular signaling molecules, such as neuromodulators, catecholamines and hormones, which regulate plasticity online; instead, metaplasticity brings about lasting physiological or biochemical neuronal changes that increase an organism's later learning potential. Many metaplastic mechanisms overlap with mechanisms of plasticity themselves, a number of which are introduced above. These include the concentration of NMDARs and TrkB/BDNF but also comprise the activation of other metabotropic glutamate receptors and the priming of plastic changes through potentiation at neighboring synapses, all of which promote lasting changes in synaptic transmission (for review see Abraham, 2008). Although we have identified a number of biological mechanisms that underlie the brain's readiness to learn, their practical implications for everyday performance remain poorly understood. The study of musicians may yield insights into the practical implications of metaplasticity by providing an example of improved learning and memory in humans, above and beyond their advantaged sensory skills (as demonstrated by Boh et al., 2011; Chan et al., 1998; George and Coch, 2011; Herholz et al., 2011; Ho et al., 2003; Jakobson et al., 2008; Parbery-Clark et al., 2009b, 2011b; Ragert et al., 2004; Schon and Francois, 2011; Shook et al., 2013; Strait et al., 2013a, 2012b).

3. Auditory learning in musicians: what can music teach us?

Despite our progress toward identifying neuronal mechanisms that underscore experience-related plasticity and subsequent learning potential, the complexity of interactions among these mechanisms and their different relationships to development and environmental factors make it difficult to determine how they work in concert to shape system-wide behavior. Furthermore, the bulk of this work has taken place in animal models, challenging its generalization to everyday learning in humans. Here we discuss our research in musicians from ages three to sixty-five as an example of the physiological outcomes that are possible with auditory learning, *in situ*.

3.1. Overview of auditory enhancements in musicians

Music training has been associated with significant physiological enhancements throughout the auditory system that underscore general (i.e., not music-specific) auditory processing. For example, adult musicians have heightened auditory perception (Kishon-Rabin et al., 2001; Micheyl et al., 2006; Parbery-Clark et al., 2009b, 2011a; Rammsayer and Altenmuller, 2006; Strait et al., 2010; Zendel and Alain, 2009) and more differentiated cortical evoked potentials to slight acoustic distinctions compared to nonmusicians (Chobert et al., 2011; Marie et al., 2010; Marques et al., 2007; Schon et al., 2004; Tervaniemi et al., 1997; van Zuijen et al., 2005). Functional cortical distinctions between musicians and nonmusicians are accompanied by structural differences: musicians have more gray matter within auditory and sensorimotor cortices (Bermudez et al., 2009; Gaser and Schlaug, 2003a; Schneider et al., 2002) in addition to more voluminous white matter tracts that underscore cortical connectivity (Bengtsson et al., 2005; Halwani et al., 2011; Lee et al., 2003; Schlaug, 2001; Schlaug

et al., 2009a, 1995; Schmithorst and Wilke, 2002). Cortical distinctions that stem from training rather than innate predispositions are sometimes greater in musicians who received auditory enrichment in the form of music training during early childhood, a sensitive developmental period (e.g., Steele, et al., 2013). This could account for correlations that are often observed between structural and functional musician-distinctions and years of music training or age of training onset (e.g., Gaser and Schlaug, 2003a; Hutchinson et al., 2003; Pantev et al., 1998).

Work from our lab and others has extended what we know about musicians' neural responses to the neural encoding of specific sound characteristics by means of the auditory brainstem response to complex sounds (cABR; see Kraus and Chandrasekaran, 2010). Because it can be elicited in humans from infancy to adulthood and is measurable in both humans and animal models, the cABR provides a promising avenue for unifying cellular and far-field approaches across both developmental stages and model organisms. Furthermore, the cABR can provide a meaningful marker of an individual's auditory processing characteristics, with signatures that indicate good and poor speech-in-noise perception, auditory working memory, or reading ability and that segregate musicians from nonmusicians, language-impaired from typically-developing,
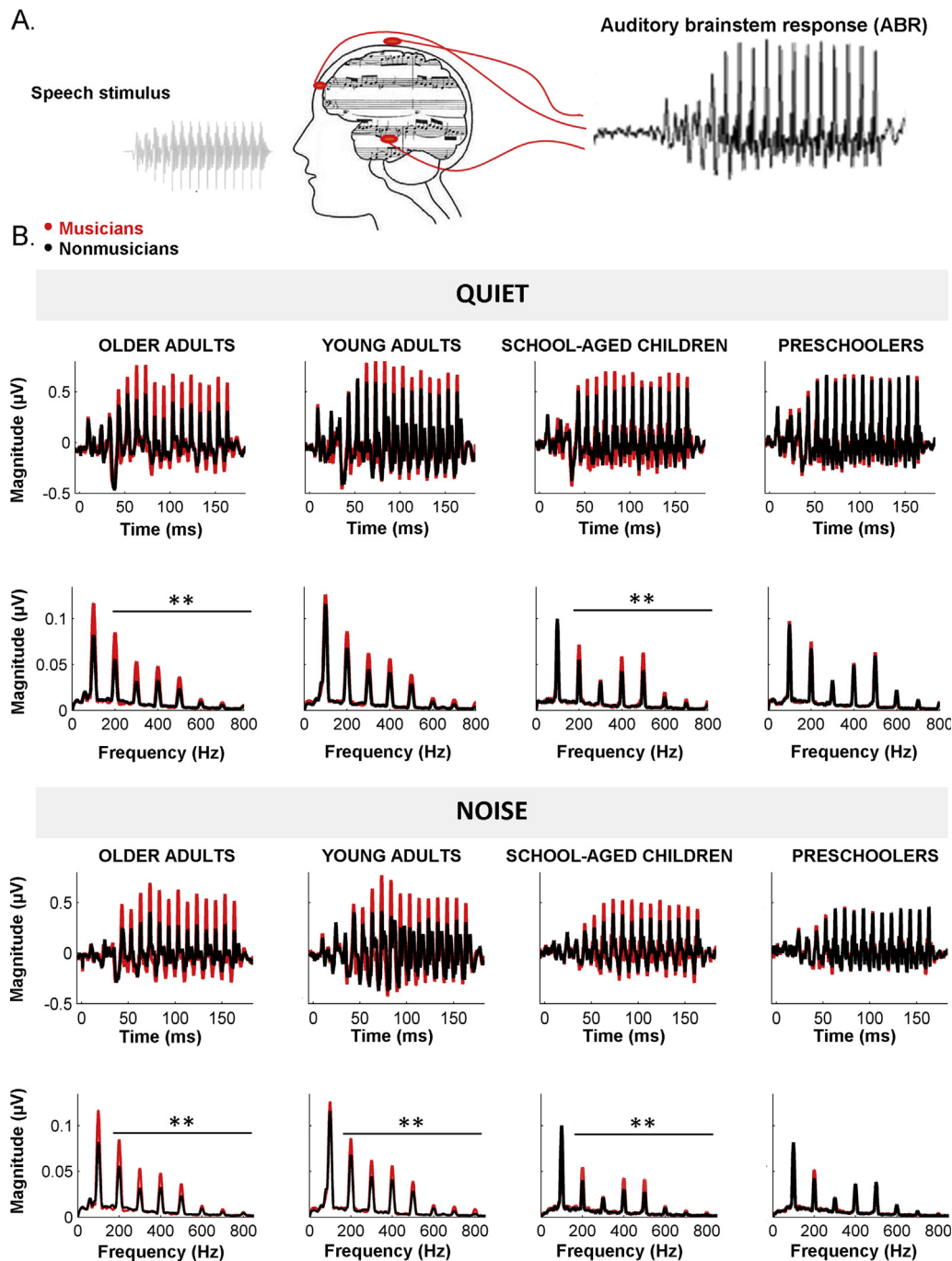

Fig. 1. Musicians' neural enhancements to speech build up over the life span. Average auditory brainstem responses to the speech sound /da/ in musicians and nonmusicians in each of four age groups. Responses were recorded using three scalp-electrodes (A) in quiet and noise and are presented in both temporal and spectral domains (B). **$p < 0.01$ Adapted from Parbery-Clark et al. (2012, 2009b) and Strait et al. (2012a, 2013b).

and older from younger adults (Kraus and Nicol, 2014). By means of the cABR we have been able to determine the driving characteristics distinguishing musicians' auditory brainstem function, which bears a distinct signature compared to nonmusicians. This is because cABRs permit the selective assessment of the neural encoding of specific acoustic features (e.g., the neural encoding of fundamental frequency versus harmonics) and over distinct acoustic regions within a single stimulus, even very short speech stimuli (e.g., the onset, formant transition and vowel portions of a 170-ms speech syllable; Fig. 1). The fine temporal precision and high-frequency phase-locking capacity of the auditory brainstem and midbrain nuclei that generate cABRs result in neural responses that can be reliably measured on the order of fractions of a millisecond and that acoustically resemble evoking stimuli (for review see the cABR tutorial provided by Skoe and Kraus, 2010). Rather than demonstrating overall enhanced cABRs, musicians have selectively enhanced neural encoding of specific acoustic features (e.g., speech sound harmonics but not fundamental frequency; Fig. 1). Musicians also have faster cABRs and more precise response timing compared to nonmusicians but only in response to the most spectrotemporally dynamic and informationally salient regions of speech stimuli. Whereas musicians and nonmusicians have equivalent response timing in response to the sustained vowel region of speech syllables, musicians have faster and more precise timing in response to the onset and formant transition regions of these same

syllables that reflect the encoding of consonants (Figs. 2 and 3). While general cABR signature enhancements have been identified in musicians, it is important to note that musicians' enhancements change as a function of stimulus context: although musicians typically do not demonstrate enhanced encoding of an invariant fundamental frequency, for example, their responses become enhanced when sounds are presented with differing statistical probability (Parbery-Clark et al., 2011) or acoustic complexity (Strait et al., 2009; Wong et al., 2007).

Musicians' cABR enhancements are especially apparent to spectrotemporally rich signals (i.e., speech or music but not click stimuli; Musacchia et al., 2007; Strait et al., 2009; Wong et al., 2007). They are most consistently observed in challenging listening environments, such as in the presence of background noise (Parbery-Clark et al., 2009) or reverberation (Bidelman and Krishnan, 2010), and between responses to sounds that are difficult to differentiate, such as the similar speech sounds "ba" and "ga" (Parbery-Clark et al., 2012; Strait et al., 2013a). Whereas musician and nonmusician young adults have equivalent response timing and neural encoding of speech harmonics in quiet, for example, young adult musicians have faster responses and more robust encoding of speech harmonics in the presence of background noise or acoustic complexity (Figs. 1 and 2). These neural enhancements appear to undergird musicians' better performance on auditory tasks, such as hearing speech in noise (Parbery-Clark et al., 2009;
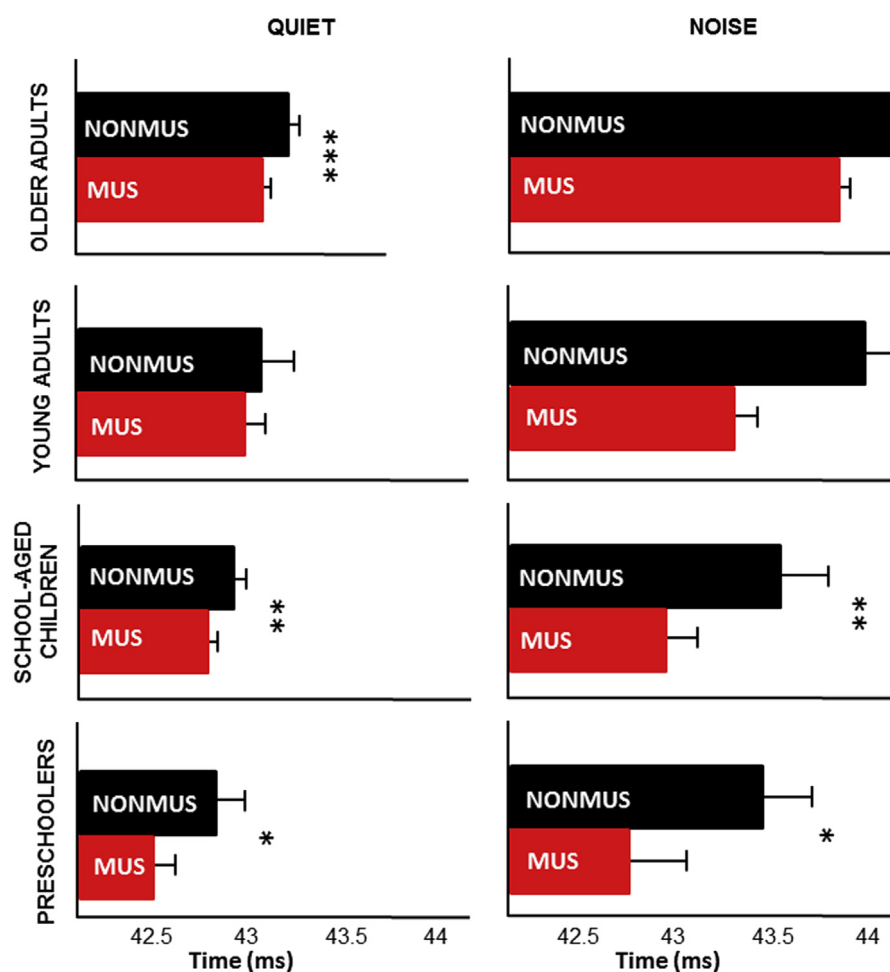

Fig. 2. Musicians across the life span have faster neural responses than nonmusicians to the formant transition of the speech syllable /da/. Bar graphs depict average latencies for the first consistent peak in the response to the formant transition of /da/ in quiet and noise conditions (occurring at ∼43 ms post-stimulus onset). Error bars depict one standard error. Adapted from Parbery-Clark et al. (2012, 2009b) and Strait et al. (2012a, 2013b). *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.
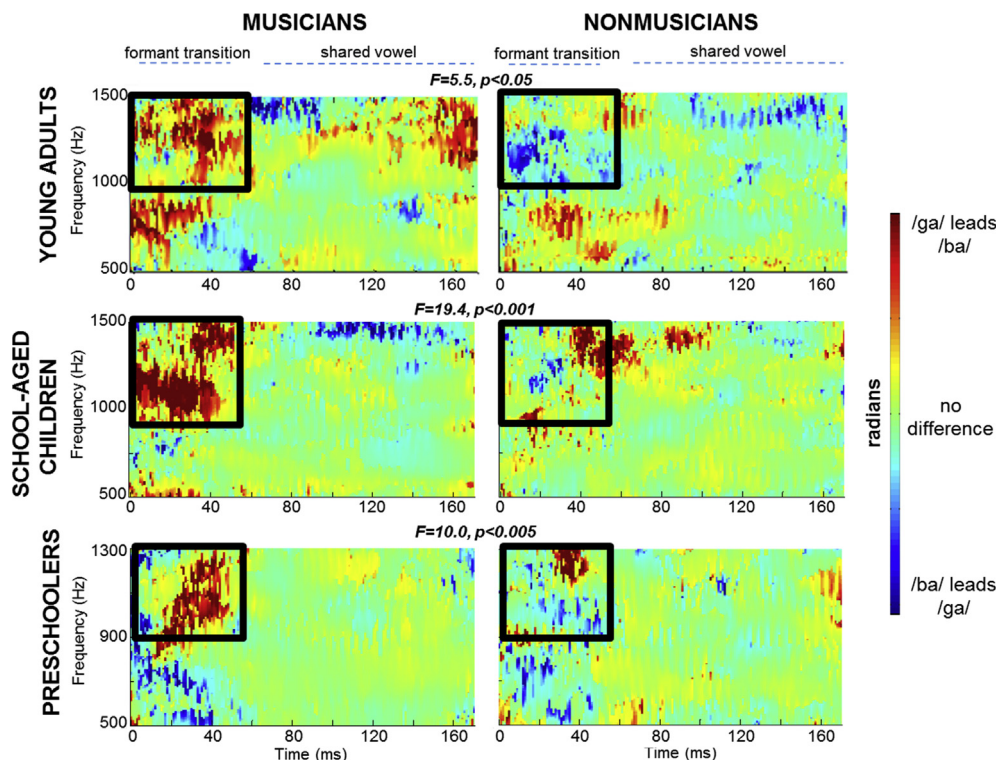
Fig. 3. Musicians have more distinct neural responses to contrasting speech sounds than nonmusicians across the life span. Cross-phaseograms indicate phase differences between responses to /ga/ and /ba/ as a function of frequency over time. Phase shift in radians is indicated by color, with warm colors indicating phase-lead and cool colors indicating phase-lag. Musicians have greater phase shifts than nonmusicians in response to the formant transition, indicated by a greater phase-lead in the response to /ga/. The acoustics of the sustained vowel are identical between stimuli and responses show an appropriate lack of phase shift. Adapted from Strait et al. (2013a).

Parbery-Clark et al., 2011; Zendel and Alain, 2011), and correspond to better auditory but not visual cognitive performance in musicians (Strait et al., 2013a). While music training may impact visual cognitive performance to some degree (e.g., Jakobson, et al., 2008), relationships between cABR properties and cognitive behavior have been most strongly observed in the auditory domain.

3.2. Musicians' enhanced cABRs across the life span

We have since compared speech-evoked cABRs in musicians and nonmusicians over different developmental stages, from early childhood to late adulthood. This work has revealed that enhanced speech-evoked auditory brainstem function in musicians can be observed in school-aged children and preschoolers as young as age three and with as little as one year of music training (Skoe and Kraus, 2013; Strait et al., 2013a, 2012a, 2013b). Investigations in older adult musicians and nonmusicians further reveal that young adults' cABR advantages persist into older adulthood (Parbery-Clark et al., 2012a, 2012b; Skoe and Kraus, 2013; White-Schwoch et al., 2013) and, despite some degree of modification, through the onset of hearing loss (Parbery-Clark et al., 2013). Together, this work reveals that some aspects of musicians' auditory brainstem function emerge (and fade) with development prior to others. That is, musicians' signature cABR characteristics reflect development and aging and are not identical across the life span.

Even with their differences, musicians across the life span do share a number of cABR characteristics: for example, young adults, school-aged children and preschoolers all have more precise cABR timing to the contrasting syllables /ba/ and /ga/, resulting in more differentiated responses to these commonly confused speech sounds (Fig. 3; this has not yet been explored in older adults). Similarly, young adults, preschoolers, school-aged children and

older adults involved in music training all have faster cABR timing than nonmusicians in response to the spectrotemporally dynamic formant transition of speech in the context of background noise but not in response to the sustained vowel. In contrast to young adults, however, older adult and child musicians have faster responses to the formant transition of speech not only in noise but also in quiet (Fig. 2). This observation in children may indicate that music training steepens the neurodevelopmental trajectory of subcortical timing mechanisms irrespective of the listening environment. Although the musician advantage in quiet fades with increasing development, musicians' faster neural timing in the presence of noise persists through young adulthood and into the middle-aged years. Distinctions between older and younger adult musicians' cABR enhancements have been interpreted in the context of music training's interactions with the aging process: older adult musicians experience less detrimental effects of aging on auditory processing than nonmusicians (Parbery-Clark et al., 2013; Parbery-Clark et al., 2012a; Parbery-Clark et al., 2011a; Zendel and Alain, 2011). This may account for why the musician advantage for processing speech in quiet re-emerges with aging, reflecting less age-related delays in musicians' cABRs compared to nonmusicians'.

The developmental interpretation of cABR distinctions between musician and nonmusician children and young adults may be further supported by their encoding of speech harmonics: as with timing, adult musicians only demonstrate more robust encoding of harmonics in the context of background noise but school-aged musician children have more robust harmonics encoding in both noise and quiet, relative to nonmusicians (Fig. 1). In contrast to our formant transition timing results, however, musicians' enhanced cABRs to speech harmonics are not always observed in musically trained preschoolers (Strait et al., 2013b; cf. Skoe and Kraus, 2013); this may indicate the emergence of this musician-enhancement

with more years of music training and development. The neural encoding of speech harmonics is not only the last to emerge with music training during childhood but also the first to fade in the aging process as hearing thresholds become compromised (Parbery-Clark et al., 2013). The later emergence of musicians' enhanced encoding of speech harmonics may reflect better-honed subcortical timing mechanisms with more years of music training. Its disappearance in older adult musicians with compromised hearing, in contrast, may reflect cochlear damage and/or the delayed timing and decreased neural response variability known to accompany the aging process (Anderson et al., 2012; Schmiedt et al., 1996; Turner et al., 2005).

Although up to now we have interpreted these outcomes to reflect training rather than innate differences predistinguishing musicians from nonmusicians, it is not only possible but *likely* that innate differences contribute in part to the effects observed. While we discuss this point in depth below, more work, especially longitudinal work, is necessary to isolate training-related contributions of musicians' neural enhancements. Still, in light of cellular evidence for long-term effects of experience-related plasticity setting the stage for later learning success, we propose that neural enhancements in musically-trained children during early developmental years may optimize child development by strengthening learning facility.

3.3. Processes underlying musicians' auditory enhancements: cognitive-sensory reciprocity

Although we cannot directly access the cellular mechanisms that drive musicians' auditory advantages, we can make inferences by interpreting outcomes from research focusing on different brain regions in the context of what we know about cellular mechanisms of learning. Recently we proposed that musicians' speech-evoked ABR enhancements reflect strengthened top-down control over sensory processing (Kraus and Chandrasekaran, 2010; Strait and Kraus, 2011b; Strait et al., 2013a; see also Patel, 2011 and 2013 for discussion) by means of descending cortico-thalamic, -collicular and -cochlear nuclear projections (Bauerle et al., 2011; Luo et al., 2008; Yan et al., 2005). These descending connections are crucial for engendering behavioral learning and its cellular correlates (e.g., descending innervations to the inferior colliculus and medial geniculate body: Bajo et al., 2010; Bauerle et al., 2011). Here we evaluate data in musician and nonmusician children and adults that may corroborate this claim, reflecting strengthened corticofugal systems with auditory expertise.

Increasing evidence indicates that adult musicians more heavily recruit extra-sensory and association cortices that underlie cognitive involvement associated with attention and memory for auditory task performance than nonmusicians (Baumann et al., 2008; Gaab and Schlaug, 2003; Haslinger et al., 2005; Pallesen et al., 2010; Stewart et al., 2003). Musicians' frequent exercising of higher-order brain regions during sensory processing may induce long-range synaptic plasticity that facilitates strengthened top-down control over basic auditory response properties (e.g., sharpened frequency tuning, faster response timing, heightened neuronal recruitment). Strengthened cognitive-sensory connectivity would bear implications for both passive and active sound processing: much like an athlete's muscle, once the circuitry has been strengthened it retains its capacity even during the most basic auditory activities. This strengthened circuitry may account for musicians' increased neural sensitivity to acoustic regularities (Francois and Schon, 2011; Schon and Francois, 2011; reviewed in Francois and Schon, 2013) and more robust cortical indices of memory and attention performance (George and Coch, 2011; Strait and Kraus, 2011a), evident even in passive recording paradigms

(Boh et al., 2011; Herholz et al., 2011; Parbery-Clark et al., 2012; Seppanen et al., 2012a, 2012b; van Zuijen et al., 2005). Musicians' auditory cognitive advantages persist into older adulthood, potentially offsetting aging- or hearing loss-related cognitive declines (Parbery-Clark et al., 2011a; Parbery-Clark et al., 2013; see also Alain et al., 2013).

Scalp-recorded speech-evoked ABRs provide insight into musicians' cognitive-sensory circuitry; even when recorded passively, while participants watch unrelated movies, cABRs reflect auditory cognitive performance (i.e., performance on auditory working memory and attention tasks). Correlations between cABR properties and auditory attention and working memory have recently been reported across development, in school-aged children (Kraus et al., 2012; Strait et al., 2011; Strait et al., 2013a; 2012a), adolescents (Krizman et al., 2012), young adults (Strait et al., 2013a) and older adults (Anderson et al., 2013). Accordingly, musicians' enhanced auditory cognitive performance correlates with the degrees of enhancement observed in their cABRs compared to age- and IQ-matched peers. As such, we argue that the cABR provides a window into a fundamental characteristic of auditory learning in musicians: namely, the strengthening of the cognitive-sensory circuitry that underscores better auditory performance.

3.4. Musicians' auditory enhancements reflect experience-related neuroplasticity

A thorough treatment of musician-nonmusician distinctions must consider both innate and training-related factors that may underlie the development of auditory expertise. It is well-established that cognitive and neural functions, including cABRs, reflect a confluence of genetic (Blokland et al., 2008; Blokland et al., 2011; Hornickel et al., 2013; O'Connor et al., 1994; Rust, 1975) and experience-related contributions (e.g., Anderson et al., 2013; Carcagno and Plack, 2011; Engineer, et al., 2004; Fujioka et al., 2006; Hayes et al., 2003; Hornickel et al., 2012; Mailloux et al., 1974; Russo et al., 2005; Skoe and Kraus, 2012; Song et al., 2012; Song et al., 2008). Shared genetic influences may account for why music and language abilities appear to be inherently connected, even among a nonmusician population (Anvari et al., 2002; Milovanov et al., 2009; Milovanov et al., 2008; Milovanov et al., 2010; Overy et al., 2003; Slevc and Miyake, 2006; Strait et al., 2011; see also Patel, 2008). Although innate characteristics may contribute to covariance between language and music skills (for example see Corrigall et al., 2013), cellular and systems studies have established an added impact of sensory experience on neural structure and function that extends beyond innate predispositions (see *Biological mechanisms of auditory learning*, above). Regular engagement with musical sound—both in its production, manipulation and perception—further shapes biological and cognitive foundations of human sound processing.

Evidence from our lab has substantiated relationships between extent of music practice and speech-evoked neural responses, with increased training yielding a greater degree of neural enhancement in both children (Strait et al., 2013a; Strait et al., 2012a) and young adults (Musacchia et al., 2007; Musacchia et al., 2008; Parbery-Clark et al., 2011; Strait et al., 2009; Wong et al., 2007) (Fig. 4). These relationships are not exclusive to musicians who are actively pursuing musical activities at the time of testing but extend to all individuals with any degree of music training. While observed in both children and young adults, relationships between neural metrics and extent of training are most prevalent in children, inconsistently observed in young adults but have not yet been observed in middle-aged adults. It is possible that these age-related distinctions reflect a plateau in the strengthening of neural function with music training, with more years of training beyond a certain

point yielding no additional neural benefit. It is also possible that the lack of relationships between extent of training and neural responses in older adults reflects effects of aging, which may obviate the impact of additional experience.

A frequent question facing this research reflects a common trend in current-day music education, which often persists throughout childhood but is discontinued in adolescence or early adulthood: what happens to musicians' neural enhancements after music training has ceased? Skoe and Kraus recently demonstrated a lasting impact of music training during childhood on neural function by recording cABRs to musical tones in adult nonmusicians with zero to eleven years of music training during childhood (on average participants had five years of training; Skoe and Kraus, 2012). In addition to systematic increases in the subcortical encoding concurrent with less background noise in the neural responses (i.e., smaller responses in the absence of stimulation), these data indicate that neural enhancements associated with even small amounts of music training are preserved into adulthood. Similar results reported by White-Schwoch and colleagues indicate that benefits related to small amounts of prior music training may even persist into early aging: older adults ages 55-70 demonstrate faster cABRs to the formant transitions of consonant-vowel syllables as a function of the extent of music training received during childhood and adolescence, long-since discontinued (White-Schwoch et al., 2013). Still, both of these studies relied on correlational designs: longitudinal studies addressing questions of music training's lasting impact would be enormous undertakings given the time-scales of decades, in the case of Skoe and Kraus (2012), and generations, in the case of White-Schwoch et al. Taken together, however, these outcomes bear practical implications by indicating a lasting impact of childhood music education on neural function, even when continued training is not feasible or desired. Although we can only speculate as to the cellular origins of these results, they may in part reflect cellular changes stemming from synaptic plasticity or the expression of glutamate/BDNF receptors with increased interactive auditory exposure early in life (see section 2: *Biological mechanisms of learning*, above). Such effects could account for more efficient auditory processing later in life, years after music training has ceased.

Although correlational analyses conducted after music training has initiated reveal covariance between the extent of music training and neural outcomes of auditory learning, longitudinal studies that measure within-subject neural changes from pre- to post-music training onset are necessary to directly test how auditory learning with music shapes the nervous system. Few studies have attempted longitudinal approaches, attesting to their enormous practical and financial challenges. The research that has examined longitudinal data, however, has established that music training in school-aged children engenders more robust cortical responses to changes in pitch (Besson et al., 2007; Moreno et al., 2009) and voice-onset time (Chobert et al., 2012), neural resilience in noise (Tierney et al., 2013) as well as increased growth of primary auditory and motor cortices (Hyde et al., 2009). We recently demonstrated the first longitudinal evidence of music training's impact on auditory brainstem function in preschoolers already engaged in music training, with preschoolers involved in music classes developing less of an impact of background noise on cABR timing over the course of one year compared to age- and IQ-matched nonmusician peers (Strait et al., 2013b). These data further reveal that cABRs recorded in preschoolers undergoing music training are not differentiated from nonmusicians' to the extent observed in older children and adults. Whereas school-aged, young adult and older adult musicians demonstrate both faster cABR timing and more robust cABRs (i.e., larger spectral harmonic magnitudes) compared to nonmusicians, music-trained preschoolers are only distinguished by faster cABR timing to the formant transitions of consonant-vowel syllables (cf. Figs. 1 and 2). Although some aspects of auditory brainstem function emerge with as little as one year of training during preschool years (and/or may be more constrained by innate contributors) (Strait et al., 2013a, 2013b), continued music training over development appears to be necessary to further distinguish musicians from nonmusicians.

3.5. Music as an optimal vehicle for studying auditory learning in humans

In addition to yielding insights into cognitive contributors to sensory malleability and innate versus training-related features of experience-associated neural characteristics, the study of musicians may further our understanding of auditory learning by providing a diverse auditory-trained human population. Music's acoustic, stylistic and educational diversity offers an ideal framework for testing the outcomes of different types of sound exposure or educational strategies on learning and its generalization. While
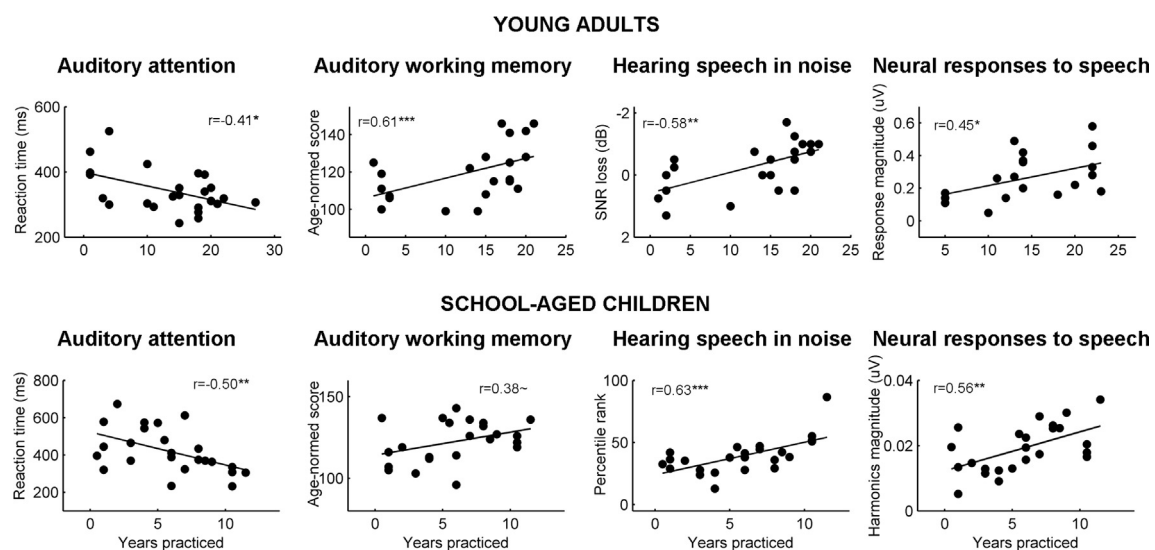

Fig. 4. Auditory abilities and neural responses to speech relate to extent of music training in young adults and children. $\sim p < 0.1$, $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

cellular definitions of neural mechanisms that take place with learning give us an exceptional starting point for understanding human learning, the study of musicians may move us toward determining how to optimize training approaches for long-term learning success.

We have only touched the surface of the variety available within musicians but this approach has already advanced the study of human learning. For example, research has determined that musicians' auditory (Margulis, 2009; Pantev et al., 2001; Strait et al., 2012a) and sensorimotor enhancements (Bangert and Schlaug, 2006; Elbert et al., 1995) reflect their instruments of practice; further research should determine the impact of different instruments on nonmusical abilities. For example, we might determine whether musical practice involving certain musical timbres (or a combination of timbres) more easily generalizes to speech processing or if instruments requiring manual opposition (e.g., the piano over the trumpet) more significantly increase inhibitory control, which is one aspect of executive function. Musicians' training strategies, such as a focus on solo versus ensemble playing or the reliance on written music versus playing "by ear," are also bound to lead to different impacts on neural structure and function. An effect of the latter comparison has been established by cortical evoked potentials to music recorded in musicians who varied in their reliance on aural training strategies (Seppanen et al., 2007). This work indicates that aurally-focused music practice, which emphasizes "playing by ear," leads to faster neural responses to musical interval and contour changes, concurrent with heightened performance on an auditory discrimination task comprising musical patterns. Future work might define implications of these outcomes for general auditory processing, behavior and learning outside the musical domain.

In addition to providing a diverse population of auditory experts, the application of music as an auditory learning medium has the added benefit of engaging the brain's mesolimbic reward network (Koelsch et al., 2006; Menon and Levitin, 2005; Salimpoor et al., 2011; Salimpoor et al., 2013; for review see Zatorre and Salimpoor, 2013), which promotes long-term learning success (e.g., see Puschmann et al., 2012). Activation of this network promotes the release of neuromodulators that contribute to synaptic plasticity and gene expression, including acetylcholine, serotonin and the catecholamines dopamine and noradrenaline. Although the cell bodies of neuromodulatory neurons reside within different brainstem, midbrain and forebrain sites, their projections extend throughout the brain and widely impact sensory processing and its experience-dependency (for examples in the auditory domain see Bao et al., 2001; Cardin and Schmidt, 2004; Hurley and Hall, 2011; Kilgard and Merzenich, 1998a, 1998b; Velho et al., 2012). Music's activation of the reward network also confers a practical advantage for the study of auditory learning, providing an emotionally rewarding and satisfying medium for auditory training.

4. Moving forward: what do musicians still have to teach us about auditory learning?

The insights provided by basic science give us a strong starting point from which to consider restructuring auditory training approaches and learning strategies, especially with regard to sensitive developmental periods during which they can be most effective (e.g., see Sanes and Woolley, 2011). But how do principles taken from cellular approaches translate into recommendations for human habits that raise one's learning potential? Considering musicians as a model of auditory learning may yield advances toward defining the limits of human learning, how they can be stretched by distinct learning strategies over different developmental time points and how they shape later brain and behavioral functions

even after training has ceased. Auditory training during developmental years, for example, may impact later auditory performance, as has been observed in rats (Sarro and Sanes, 2011), in addition to enhanced neural response properties, as evidenced by cABRs in adult nonmusicians with some degree of childhood music training (Skoe and Kraus, 2012; White-Schwoch et al., 2013). Furthermore, auditory training early in life may shape later learning facility by strengthening metaplastic mechanisms that underlie learning potential. Moving forward, we might better define the impact of music on learning performance, such as through the comparison of online learning and short-term training outcomes in musically trained and untrained populations.

Principles of music training may be further applied toward optimizing existing auditory training regimens to increase their efficacy. Music training itself, in fact, may be a profitable strategy for improving auditory processing in clinical populations, such as for training the brains of new cochlear implant users to optimally use available acoustic input (Abdi et al., 2001; Chen et al., 2010) or for stroke patients struggling to regain language function (Norton et al., 2009; Schlaug et al., 2009b). Although we have determined that music training throughout life prevents or reduces the impact of a number of age-related cognitive, perceptual and neural declines (Hanna-Pladdy and Gajewski, 2012; Parbery-Clark et al., 2012a, 2012b, 2011a; Zendel and Alain, 2011), even in the presence of hearing loss (Parbery-Clark et al., 2013), no studies have yet addressed the extent of training required, how recent it must be nor whether training during advanced adulthood confers immediate benefits.

Furthermore, principles of auditory learning observed in musicians have the potential to shed light on mechanisms of learning and to reinforce their applications in non-auditory domains. Few studies have assessed the impact of music training on neural processes underlying sensory and motor behavior outside the auditory system, although visual and tactile neural and cognitive musician advantages have been observed to some extent (Jakobson et al., 2008; Musacchia et al., 2007; Musacchia et al., 2008; Ragert et al., 2004). Motor synchronization is also improved in musicians compared to nonmusicians, observed to pairings with auditory or visual cues in the form of beat synchronization (Krause et al., 2010; Repp, 2010; Repp and Doggett, 2007; Slater et al., 2013; Steele et al., 2013; Watanabe et al., 2007). The malleability of auditory-motor synchronization with music training may yield insights for mechanisms by which music training affects everyday, non-musical functions given that this ability has been tied to language and cognitive skills. In fact, beat synchronization (and, not surprisingly, rhythm perception) relates to auditory attention and reading abilities (Tierney and Kraus, 2013), is deficient with language-based learning impairment (Huss et al., 2010; Strait et al., 2011; Thomson and Goswami, 2008; see also Leong and Goswami, 2013) and appears to be remediated with music-based training (Slater et al., 2013; see also Strait and Kraus, 2011b, and Tierney and Kraus, 2013a for discussion). The interaction between beat synchronization and language skills may drive the generalization of musicians' perceptual, cognitive and neural enhancements to the language domain, engendered through music's consistent emphasis on auditory-motor synchronization according to a governing beat (Tierney and Kraus, 2013b). Future work should determine musicians' learning potential across sensory domains and define its limits in addition to assessing its generalization to other skills (e.g., reading and executive function).

5. Conclusions

Here we have interpreted principles derived from cellular studies alongside evidence for the impact of auditory expertise on human

brain structure and function. While the most effective approach would comprise a thorough integration of knowledge gained from cellular work with outcomes from far-field metrics in humans, present knowledge cannot bridge these approaches. Many reports have revealed effects of learning on subcortical physiology using cellular measurements in animal models but to our knowledge no work has yet defined how cellular metrics relate to scalp-recorded cABRs. These effects may reflect mechanisms of learning that involve synaptic plasticity, gene expression or others, especially those involved in metaplasticity, but this knowledge gap could be bridged by concurrent cellular and far-field approaches in animal models such as that reported by Warrier et al. (2011), either following auditory training or over the course of the learning process. Together, these approaches may not only lead to a better definition of the musician as a model organism but have the capacity to further our understanding of the potential of human experience to fundamentally shape the biology underlying everyday learning.

Acknowledgments

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