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Musical Expertise and Brain Structure: The Causes and Consequences of Training

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Abstract and Keywords

Brain imaging studies have demonstrated that music training can change brain structure, predominantly in the auditor-motor network that underlies music performance. The chapter argues that the observed differences in brain structure between experts and novices, and the changes that occur with training derive from at least four sources: first, pre-existing individual differences that promote certain skills; second, lengthy and consistent training which likely produces structural changes in the brain networks tapped by performance; third, practice during specific periods of development which may result in changes that do not occur at other periods of time; fourth, the rewarding nature of music itself, as well as the reward value of practice which may make music training a particularly effective driver of brain plasticity.

Keywords: brain plasticity, development, auditory-motor integration, music training, expertise, MRI, DTI

Introduction

Over the past twenty years, brain imaging studies have demonstrated that music training can change brain structure, predominantly in the auditory-motor network that underlies music performance. These studies have also shown that brain structural variation is related to performance on a range of musical tasks, and that even short-term training can result in brain plasticity. In this chapter, we will argue that the observed differences in brain structure between experts and novices derive from at least four sources. First, there may be pre-existing individual differences in structural features supporting specific skills that predispose people to undertake music training. Second, lengthy and consistent training likely produces structural change in the brain networks tapped by performance through repeated cycles of prediction, feedback, and error-correction that drive learning. Third, the timing of practice during specific periods of development may result in brain changes that do not occur at other periods of time, and which may promote future learning and plasticity. Fourth, both the rewarding nature of music itself, as well as the reward value of practice and accurate performance may make music training a particularly effective driver of brain plasticity.

Structural Brain Differences in Adult Musicians

There is now a relatively large body of brain imaging data showing differences in gray- (GM) and white-matter (WM) architecture between musicians and non-musicians (see Fig. 1). In adults all of these studies are cross-sectional, and typically compare music students or professionals with controls selected to have very little music training. One of the most common and expected findings is that music training is associated with enhancements in auditory regions, particularly Heschl's gyrus (HG), the region of primary auditory cortex. These studies have found that musicians commonly show greater gyrification of HG (Schneider et al., 2002; Schneider et al., 2005), and greater GM volume or cortical thickness (CT) in this region (Bermudez, Lerch, Evans, & Zatorre, 2009; Foster & Zatorre, 2010; Gaser & Schlaug, 2003; Karpati, Giacosa, Foster, Penhune, & Hyde, 2017; Schneider et al., 2002, 2005). These differences have been shown to be related to indices of music proficiency (Schneider et al., 2002, 2005), hours of music practice (Foster & Zatorre, 2010), variations in EEG and MEG responses to auditory signals (Schneider et al., 2002, 2005), and performance on melody discrimination and rhythm reproduction tasks (Foster & Zatorre, 2010; Karpati et al., 2017).

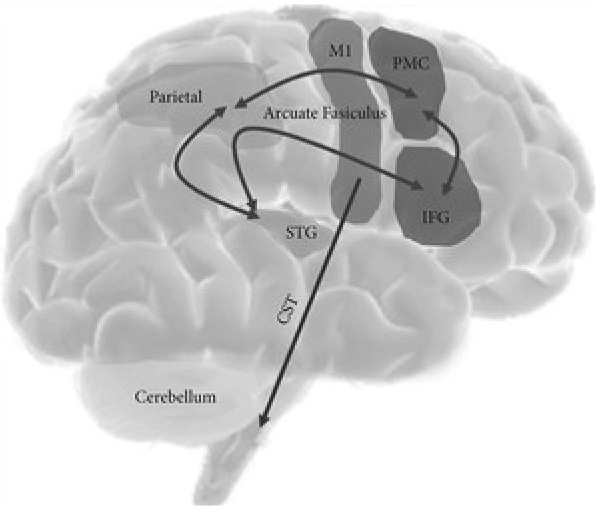

Figure 1. Regions of the dorsal auditory pathway affected by music training. Illustrates brain regions found to show structural changes in musicians compared to non-musicians. These include the auditory (superior temporal gyrus, STG), partietal, premotor cortex (PMC), and inferior frontal gyrus (IFG) regions in the dorsal auditory pathway, as well as the connecting fibers of the arcuate fasciculus. Also pictured are the cerebellum and corticospinal tract (CST). Regions not shown are the corpus callosum and basal ganglia.

The second most common finding is enhancement in motor regions of the brain, including GM in primary motor, premotor, and parietal regions, as well as the cerebellum and basal ganglia. In addition, consistent increases have been observed in white-matter pathways, including the corpus callosum, descending motor tracts, and sensorimotor connections. One of the first studies in this domain found that the length of the central sulcus, and by inference the size of the motor cortex (M1), was larger in trained musicians, and that earlier onset of training was related to greater length (Amunts et al., 1997). This finding has been replicated in subsequent studies using whole-brain analysis techniques (Bermudez et al., 2009; Gaser & Schlaug, 2003). Differences between musicians and non-musicians have also been observed in the corpus callosum (CC), the primary white-matter pathway connecting the two hemispheres. In another early investigation, it was found that the surface area of the anterior half of the CC was larger in musicians, and that this difference was greatest for those who began training before age 7 (Schlaug, Jancke, Huang, Staiger, & Steinmetz, 1995). Musicians have also been found to have greater white-matter integrity in the CC as measured using diffusion tensor imaging (DTI), with these measures being related to hours of practice (Bengtsson et al., 2005), as well as to age of start and performance on a sensory-motor synchronization task (Steele, Bailey, Zatorre, & Penhune, 2013). In the descending motor pathways, changes in DTI measures have been observed to be related to hours of practice in childhood (Bengtsson et al., 2005). Changes in subcortical structures have also been observed, with a recent study reporting that musicians have greater gray-matter volume in the putamen (Vaquero et al., 2016), and others showing enhancements in cerebellar gray- (Gaser & Schlaug, 2003; Hutchinson, Lee, Gaab, & Schlaug, 2003) and white-matter (Abdul-Kareem, Stancak, Parkes, Al-Ameen, et al., 2011). However, a more recent study from our laboratory using cerebellar-specific segmentation techniques found no differences in either gray- or white-matter volumes between musicians and non-musicians, but that musicians who began training before age 7 had reduced volumes in cerebellar regions specifically related to motor timing (Baer et al., 2015).

Other regions found to differ between musicians and non-musicians are in frontal and parietal cortex, including regions important for language (pars opercularis and triangularis; areas 44 and 45) and working memory (dorsolateral: 9/46; and ventrolateral prefrontal cortex: 47/12). Enhanced GM density has been observed in areas 44/45 that is related to years of music experience (Abdul-Kareem, Stancak, Parkes, & Sluming, 2011; James et al., 2014; Sluming et al., 2002), and to performance on a test of absolute pitch (Bermudez et al., 2009). Importantly, musicians have also been found to have greater white-matter integrity as measured with DTI in the arcuate fasciculus, the pathway connecting auditory, parietal, and inferior frontal regions (Halwani, Loui, Ruber, & Schlaug, 2011). Musicians have also been reported to have greater cortical thickness in DLPFC; and interregional variability in cortical thickness is correlated across a broader range of auditory and motor regions in musicians compared to controls (Bermudez et al., 2009). Finally, several studies have reported greater gray-matter volume in parietal regions (Foster & Zatorre, 2010; Gaser & Schlaug, 2003; James et al., 2014), which are engaged in sensorimotor transformations and planning that are relevant for playing a musical instrument (Andersen & Cui, 2009; Gogos et al., 2010; Rauschecker, 2011). In particular, Foster and Zatorre (2010) found that both gray-matter volume and cortical thickness were related to performance on a test of melodic discrimination in a group of people with varying levels of music experience.

Taken together, cross-sectional studies in adult musicians provide evidence that long-term practice produces structural changes in regions of the dorsal auditory-motor network that has been shown in functional imaging studies to be recruited during playing (Brown, Zatorre, & Penhune, 2015; Chen, Penhune, & Zatorre, 2008; Herholz & Zatorre, 2012; Novembre & Keller, 2014).

Developmental Impacts on Training-Related Plasticity

Studying effects of music training in childhood is important because that is when lessons typically begin, but also because we know that sensorimotor experience during early sensitive periods in development can have differential impacts on long-term brain plasticity. The first longitudinal study in children examined the effects of 15 months of piano training study in 6- to 8-year-olds (Hyde et al., 2009). Longitudinal studies are critical because they allow us to establish more direct causal connections between training and any observed changes in the brain. This study found that children who received training did not differ from untrained children at baseline, but showed gray-matter enhancements in auditory and motor cortex, as well as enlargement of the corpus callosum. Most importantly, the volume of auditory cortex was found to be related to performance on tests of melody and rhythm discrimination, and the volume of motor cortex was found to be related to performance on a test of fine-motor skill. These results are supported by a second longitudinal study which found that 6- to 8-year-old children participating in a music training program were found to have greater WM integrity in the CC after two years (Habibi et al., 2017). There was also some evidence of reduced cortical thinning in right compared to left posterior auditory cortex. Taken together, these longitudinal results indicate that even relatively short-term training in childhood can produce changes in behavior and brain structure. Most importantly, changes occurred in the same regions of the auditory-motor network—auditory cortex, M1, and the CC—that have been shown to differ after long-term training in adults. The parallel between longitudinal changes in childhood and cross-sectional findings in adults supports the inference that the structural differences observed in adults are indeed the result of training.

The only other anatomical study in children found that in a large group of 8- to 10-year-olds, the volume of HG was larger in those who practiced more, and was associated with measures of music aptitude, as well as behavioral and MEG measures of auditory processing (Seither-Preisler, Parncutt, & Schneider, 2014). This is consistent with a longitudinal EEG study in children showing enhancements of auditory evoked responses to musical features (Putkinen, Tervaniemi, Saarikivi, Ojala, & Huotilainen, 2014). Interestingly, however, no changes in HG volume were observed when examining possible longitudinal effects after 13 months of additional training. Further, hierarchical regressions models predicting HG volume found that aptitude accounted for a greater proportion of the variance than practice time. The authors interpreted these last two findings as indicating that anatomical predispositions make a greater contribution to musical outcomes than training. However, it is also possible that training-related plastic changes had already occurred in the period preceding the study. Most children began lessons between 6 and 7 years old, and thus had already been playing for one to two years.

The issue of whether predispositions or training contribute most to observed structural differences between musicians and non-musicians has long been debated, with little data that can directly contribute to settling the argument. As will be discussed further in this chapter, some data from untrained adults show that individual differences in specific anatomical features are related to performance or learning of musical tasks, providing indirect evidence that pre-existing anatomical features may mediate the potential to acquire musical skills (Foster & Zatorre, 2010; Li et al., 2014; Paquette, Fujii, Li, & Schlaug, 2017; Schneider et al., 2005). The finding described earlier of larger HG volume in children who practice more, and which does not change over time can also be considered as evidence for a pre-existing structural feature associated with musical skill (Seither-Preisler et al., 2014). Work with twins has shown that the propensity to practice is heritable, and that genes appear to account for a large portion of the variance in music abilities (Mosing, Madison, Pedersen, Kuja-Halkola, & Ullén, 2014). However, a very recent study from this same group compared brain structure in monozygotic twins discordant for music practice. They found that the twins who played had greater cortical thickness in auditory and motor regions as well as WM enhancements in the corpus callosum compared to those who did not (de Manzano & Ullén, 2018). These findings provide the most definitive support yet for the causal effect of music training on brain structure. In an effort to synthesize these apparently opposing results, the authors have proposed a gene–environment interaction model of the musical skills and its impact on the brain (Ullén, Hambrick, & Mosing, 2016). This model proposes that multiple genetic predispositions subserving specifically musical skills, such as auditory and motor abilities, as well as non-specific cognitive and personality factors contribute to the likelihood that someone will engage in training. They also hypothesize that environmental factors interact with genetic predispositions to either promote or discourage persistence. We would further propose that the timing of music experience interacts with both predispositions and normative brain maturation to influence long-term behavioral and brain plasticity (see Fig. 2).

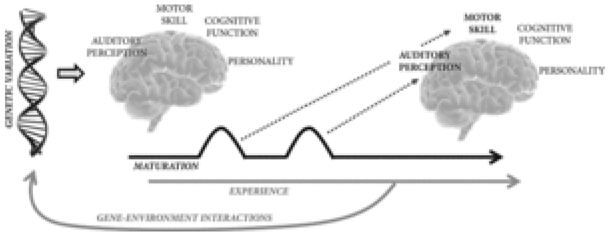

Figure 2. Gene–maturation–environment interactions. Illustrates the interaction between genes, brain maturation, and specific training. *Genetic variation* leads to individual differences in brain structures for musical aptitudes such as auditory perception and motor dexterity. Genetic variation also regulates other non-specific aptitudes, such as cognitive skills and personality factors, including openness and the propensity to practice. *Maturation* produces normative changes that peak at different times depending on the brain region. *Experience*, such as music training, then interacts with both pre-existing individual differences, and normative maturation to change brain structure and plasticity. Experience also feeds back on genes through *gene–environment interactions* that can further enhance or limit plasticity.

The Interaction between Development and Training

A very important question in understanding the effect of music training on brain structure is the interaction between brain development and music training. Anecdotal evidence from the lives of famous musicians suggests that an early start of training can promote the development of extraordinary skill in adulthood (Jorgensen, 2011). Evidence from animal and human studies also shows that early experience, such as specific auditory exposure (Chang & Merzenich, 2003; de Villers-Sidani, Chang, Bao, & Merzenich, 2007), or enriched sensorimotor environments (Kolb et al., 2012), can have long-term effects on behavior and the brain.

Two important early studies provided suggestive evidence that the impact of music training on brain structure was related to the age of start, with those who begin earlier showing greater enhancements in the size of M1 (Amunts et al., 1997) or the surface area of the corpus callosum (Schlaug et al., 1995). However, without specific controls, the age of start of training is typically confounded with the total years of training, making it impossible to attribute the observed differences to the age at which training began. In addition, these studies did not link the observed neuroanatomical differences to relevant behavior.

To address these issues, a series of studies have compared behavior and brain structure in early- (ET < age 7) and late-trained (LT > age 7) musicians (see Fig. 3; see also Baer et al., 2015; Bailey & Penhune, 2010, 2012, 2013; Bailey, Zatorre, & Penhune, 2014; Steele et al., 2013; Vaquero et al., 2016). In these studies we matched ET and LT groups on important potential confounding variables including: years of music experience, years of formal training, and hours of current practice. In addition, we assessed cognitive measures such as non-verbal IQ and auditory working memory which might be thought to be related to the capacity for early training. Most importantly, we assessed performance on relevant musical skills, such as rhythm reproduction and melody discrimination. The age 7 cut-off for ET and LT groups was initially drawn from the study by Schlaug et al. (1995) and was essentially arbitrary. However, using a large sample of behavioral data, we have been able to show that the likely age range where early training has its strongest effect is between 7 and 9 (Bailey & Penhune, 2013). Behaviorally our studies have shown that adult musicians who begin training before age 7 outperform those who begin later on rhythm reproduction and melody discrimination tasks (Bailey & Penhune, 2010, 2012). Drawing on this work, we collected a large sample of ET and LT musicians with behavioral, T1 and DTI data. Analysis using deformation-based morphometry on the T1 data found that ET musicians show enlargement in the region of the ventral premotor cortex (vPMC), and that the volume of this region is related to performance on the rhythm synchronization task (Bailey et al., 2014). These findings are consistent with fMRI studies showing that vPMC is active when both musicians and non-musicians are performing the same rhythm task (Chen et al., 2008). In the same sample, DTI measures showed that ET musicians also had enhanced WM integrity in the posterior mid-body of the corpus callosum, the location of fibers connecting M1 and PMC in the two hemispheres (Steele et al., 2013). We interpreted these findings based on data about normative maturation in these regions, and the relative contribution of genes and environment to their variability. A large, cross-sectional developmental sample showed that GM volume in anterior motor regions, including MI and PMC, have their peak period of growth between 6 and 8 years old (Giedd et al., 1999). Similarly, the size of the anterior region of the CC shows its peak increase at the same time (Westerhausen et al., 2011), and variability of this region is more strongly influenced by environmental than genetic factors (Chiang et al., 2009). Based on these data, we can hypothesize that early training at the time of peak maturational change in motor regions and the CC may enhance brain plasticity. In addition, the relatively stronger contribution of environment to the size of anterior CC in adults suggests that it might be more susceptible to the impact of music training. We interpreted these findings as demonstrating a scaffold, or metaplastic, effect where early training promotes brain plasticity which is sustained or augmented by later practice (Steele et al., 2013).

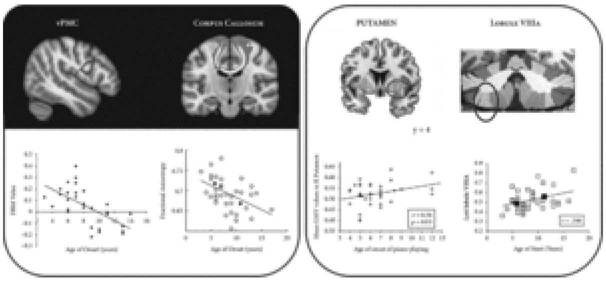

Figure 3. Regions showing increases or decreases related to music training. Findings from studies examining structural differences between early-trained (ET; before age 7) and late-trained (LT; after age 7) musicians. The top, far left panel is taken from Bailey et al. (2014) and shows gray matter (GM) enhancement in the ventral premotor cortex (vPMC) in ET musicians. The second panel is taken from Steele et al. (2013) and shows enhanced fractional anisotropy (FA) in the posterior midbody of the corpus callosum. The third panel is taken from Vaquero et al. (2016) and shows reduced GM in the putamen in early trained ET musicians. The fourth panel (top, far right) is taken from Baer et al. (2015) and shows reduced volume of left cerebellar lobule VIIIa. The graphs at the bottom of each panel show the relationship of volume changes with the age of onset of training.

Our findings in the PMC and CC appear to tell a straightforward story in which early training produces enlargement or enhancement of brain structure. However, more recent findings make it clear that reality is not so simple. Using the same sample described earlier, we examined GM and WM volumes in the cerebellum using a novel multi-atlas segmentation technique that labels all thirteen lobules in both hemispheres (Baer et al., 2015). In addition, we tested these musicians and controls on a classic auditory-motor tapping and continuation task (Repp, 2005). The cerebellum has been linked to a range of sensory and motor timing functions that are likely to be relevant for music training and performance (Koziol et al., 2014; Sokolov, Miall, & Ivry, 2017). And, as described earlier, previous work had found greater cerebellar GM volume in trained musicians (Gaser & Schlaug, 2003; Hutchinson et al., 2003). However, the results of our study showed that ET musicians had smaller volumes of cerebellar lobules IV, V, and VI compared to LT musicians. Strikingly, earlier age of start, greater music experience, and better timing performance were all correlated with smaller cerebellar volumes. Better timing performance was specifically associated with smaller volumes of right lobule VI which has been functionally linked to perceptual and motor timing (E, Chen, Ho, & Desmond, 2014; Ivry, Spencer, Zelaznik, & Diedrichsen, 2002). This is consistent with another recent study which found that early-trained pianists had smaller GM volume in the right putamen, and lower timing variability when playing scales (Vaquero et al., 2016).

So, why does training affect the cerebellum differently than the cortex, and how do these findings challenge our understanding of the effects of early experience? There are several features of cerebellar anatomy that may explain this result. First, developmental studies show that peak growth in the cerebellum occurs much later than in most of the cortex, between the ages of 12 and 18 (Tiemeier et al., 2010). Thus early experience may have a different effect on cerebellar plasticity, such that experience leads to greater efficiency and reduced expansion. Second, the cerebellum is unique in being structurally homogeneous, with the identical cytoarchitecture and input–output circuitry throughout (Schmahmann, 1997). In the motor system, the cerebellar circuits are known to play a role in error-correction and optimization. Because these circuits are uniform across the structure, it is hypothesized that they perform the same role in optimizing a wide variety of functions in the regions to which it is connected (Balsters, Whelan, Robertson, & Ramnani, 2013; Koziol et al., 2014; Sokolov et al., 2017). The cerebellar regions that are smaller in ET musicians in our study are connected to frontal motor and association regions, including M1, PMC, and prefrontal cortex (Diedrichsen, Balsters, Flavell, Cussans, & Ramnani, 2009; Kelly & Strick, 2003). Based on this information, it is possible that training-related skills and cortical expansion might be supported by greater optimization and reduced expansion in the cerebellum. If this is true, then cortical and cerebellar changes with training should be inversely related.

Aptitude and Short-Term Training

Differences in brain structure between musicians and non-musicians have generally been attributed to long and intensive training. However, it is more likely that they result from an interaction between training-induced plasticity and pre-existing individual differences in the brain that predispose certain people to engage in music (see Fig. 2). While there is little direct evidence for specific brain features that predispose an individual to become a musician, evidence from studies of individual differences in music ability and response to training can provide some clues. Individual differences in auditory and motor regions of untrained individuals have been linked to performance on specific musical tasks, and to the ability to learn to play an instrument. GM concentrations in auditory regions and the amygdala were found to be correlated with interval discrimination in a large sample unselected for music training (Li et al., 2014). Similarly, in a sample selected to have a range of musical experience, GM concentration and cortical thickness in auditory and parietal regions were found to be related to the ability to discriminate melodies that had been transposed (Foster & Zatorre, 2010). Finally, a recent study found that cerebellar volumes were related to beat perception in musicians (Paquette et al., 2017). Individual differences in WM tracts connecting auditory and motor regions, and in motor output pathways have been found to be related to faster learning of short melodies (Engel et al., 2014). Further, WM integrity in the left arcuate fasciculus and the temporal segment of the CC have been found to predict individual differences in auditory-motor synchronization (Blecher, Tal, & Ben-Shachar, 2016). Findings showing that brain structural features can predict musical skills are consistent with results in related domains, where the volume of auditory cortex was found to be associated with the ability to learn linguistic pitch discrimination (Wong et al., 2008), and the volume of both auditory cortex (Golestani, Molko, Dehaene, LeBihan, & Pallier, 2007; Golestani, Paus, & Zatorre, 2002) and the arcuate fasciculus have been found to be related to foreign language sound learning (Vaquero, Rodriguez-Fornells, & Reiterer, 2017).

Very importantly, however, aptitude for music training likely relies on more than pure auditory or motor skill. Heritability studies show that the propensity to practice appears to be genetically transmitted (Mosing et al., 2014), and that personality variables such as "openness to experience" are also associated with lifetime practice (Butkovic, Ullén, & Mosing, 2015). Thus, an individual with exceptional pre-existing skills must also have the right personality characteristics to undertake long-term training, and the openness to engage with new people, places, and ideas. A talented individual who does not like to practice, or hates stress, travel, and challenge is unlikely to become a professional musician.

Bringing It All Together

Taken together, the current data on brain structure in musicians suggests that there may be pre-existing structural features—likely in the auditory-motor network supporting musical skill—that predispose individuals to pursue music training. Once training begins, the long-term effects on behavior and brain structure depend on the age of start, and thus on the interaction between training and the maturational trajectories of these regions and their connections. Early training may produce a type of scaffold or metaplasticity effect. Metaplasticity is a term that originates from studies of hippocampal learning mechanisms, and denotes the idea that experience can change the potential for plasticity of a synapse (for review see Altenmüller & Furuya, 2016; Herholz & Zatorre, 2012). When applied to the context of music, it is the idea that training during specific phases of brain development can have long-term effects on how those regions change in response to future experience. Evidence for metaplastic effects resulting from music training comes from studies showing that musicians have enhanced learning of sensory and motor skills (Herholz, Boh, & Pantev, 2011; Ragert, Schmidt, Altenmüller, & Dinse, 2004; Rosenkranz, Williamon, & Rothwell, 2007), and greater increases in M1 activity during learning (Hund-Georgiadis & von Cramon, 1999). Thus we can think of early training as a scaffold on which later training can build (Bailey et al., 2014; Steele et al., 2013). Along with these training-specific metaplastic effects, evidence from heritability studies indicates that skills and abilities not specific to music may also contribute to promoting or limiting plasticity; these include the propensity to practice (Mosing et al., 2014), as well personality and cognitive variables that can support training (Butkovic et al., 2015).

Why Is Music Such an Effective Driver of Brain Plasticity?

Why does music training produce such robust changes in brain structure? One very obvious answer is practice—lots of practice. For the studies reviewed here, the average length of training for musicians was 15–20 years. This is the equivalent of thousands of hours of practice across a large portion of the person's life. While the idea that simply practicing long enough will result in expertise has been largely debunked (for review, see Mosing et al., 2014), long-term, consistent practice is strongly associated with expertise in a range of domains (Macnamara, Hambrick, & Oswald, 2014). Further, in the studies reviewed here, the length of training is typically strongly related to both structural brain differences and task performance. The impact of practice on brain organization is supported by studies in animals showing that practice on new motor tasks is associated with expanded representations in motor areas (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Nudo, Milliken, Jenkins, & Merzenich, 1996), changes in MR measures of gray- and white-matter (Scholz, Allemang-Grand, Dazai, & Lerch, 2015; Scholz, Niibori, Frankland, & Lerch, 2015), and increased numbers of synapses and dendritic spines (Kleim, Barnaby, et al., 2002; Kleim, Freeman, et al., 2002; Kleim et al., 2004). Neuronal changes in gray matter that are related to learning include neurogenesis, synaptogenesis, and changes in neuronal morphology. In white matter, changes related to learning including increases in the number of axons, axon diameter, packing density of fibers, and myelination can be found (Zatorre, Fields, & Johansen-Berg, 2012).

A second reason that music training may be particularly effective in driving brain plasticity is the highly specific nature of practice. The majority of musicians are experts on a single instrument; thus they perform millions of repetitions of the same movements, and listen attentively to an even larger number of associated sounds. When practicing, a musician imagines and plans a precise sequence of sounds and the movements required to produce them. Once the plan is set in motion, they use auditory and somatosensory information to detect subtle deviations in sound and movement, implementing adjustments to enhance performance. Practice is therefore a repeated prediction, feedback, and error-correction cycle. Auditory-motor prediction is thought to be a central function of the dorsal stream, particularly of the premotor cortex. Brain imaging studies have shown increased activity in the PMC when people listen to melodies that they have learned to play (Chen, Rae, & Watkins, 2012; Lahav, Saltzman, & Schlaug, 2007), and recent work from our laboratory has shown that transcranical magnetic stimulation (TMS) over dorsal PMC disrupts learning of auditory-motor associations (Lega, Stephan, Zatorre, & Penhune, 2016). Feedback and error-correction are key components of motor learning (Diedrichsen, Shadmehr, & Ivry, 2010; Sokolov et al., 2017; Wolpert, Diedrichsen, & Flanagan, 2011), and studies of both motor and sensory learning show that functional and structural changes in the brain are driven by decreases in error and improved precision. For example, learning to juggle (Scholz, Klein, Behrens, & Johansen-

Berg, 2009), balance on a tilting board (Taubert et al., 2010), or to perform a complex visuomotor task (Lakhani et al., 2016; Landi, Baguear, & Della-Maggiore, 2011) have all been shown to produce changes in gray- or white-matter architecture that were related to decreases in error with learning. Thus error-driven learning, particularly during periods of high developmental plasticity may be an important contributor to structural brain changes measured in adult musicians.

Another reason that music training may be so successful in producing brain plasticity is that it is inherently multisensory. To produce music, performers must learn to link sounds to actions, but they must also link visual, somatosensory, and proprioceptive feedback to these sounds and actions. As described earlier, training is a prediction to feedback to error-correction cycle in which musicians use all their sensory resources to produce the perfect sound. Sounds are linked to actions relatively rapidly, as has been shown by changes in the strength of motor activity during passive listening to learned melodies after short-term training (Bangert et al., 2006; D’Ausilio, Altenmüller, Olivetti Belardinelli, & Lotze, 2006; Lega et al., 2016; Stephan, Brown, Lega, & Penhune, 2016). In particular, it was shown that learning to play a melody resulted in greater changes in the activity of auditory cortex than learning to remember the melody by listening alone (Lappe, Herholz, Trainor, & Pantev, 2008). This may partly be based on strong intrinsic connections between the auditory and motor systems (Chen et al., 2012; Poeppel, 2014; Zatorre, Chen, & Penhune, 2007). But it can also be hypothesized that co-activation of circuits deriving from multiple senses may drive plasticity even more strongly than input from a single sense (Lee & Noppeney, 2011, 2014).

A final feature of music training that is likely crucial in promoting plasticity is the rewarding nature of performance. There are three aspects of reward that may stimulate plasticity: first, the rewarding nature of music itself that is experienced through playing; second, the intrinsic reward of performing, both for the player and through the acclaim it may bring; and finally, the potentially rewarding nature of practice and the pleasure of accurate performance. The intrinsic pleasure derived from music appears to be common to most people (Mas-Herrero, Marco-Pallares, Lorenzo-Seva, Zatorre, & Rodriguez-Fornells, 2011), and is hypothesized to be based on the same dopamine-modulated, predictive systems that regulate reward in other domains with direct biological consequences, including drugs, food, sex, and money (Salimpoor, Zald, Zatorre, Dagher, & McIntosh, 2015). Thus learning to produce a rewarding stimulus, such as music, is likely to be rewarding to the player.

We also know that learning and brain plasticity are strongly affected by the reward value of what is learned. Animal studies show that brain plasticity associated with auditory learning is greater when the information to be learned is rewarded, or behaviorally relevant. For example, the responses of neurons in the auditory cortex of ferrets were modulated by the reward value of stimuli (David, Fritz, & Shamma, 2012). Further, pairing a tone with stimulation of dopamine circuits in the brainstem increased the selectivity of responding in auditory neurons tuned to the same tone (Bao, Chan, & Merzenich, 2001). Importantly, dopamine has been shown to modulate motor learning in both humans and animals (Floel et al., 2005; Tremblay et al., 2009, 2010); possibly through the reinforcement and habit-formation circuitry of the striatum (Graybiel & Grafton, 2015; Haith & Krakauer, 2013). Thus, if the output of practice, a beautiful piece of music, is rewarding and stimulates dopamine release, then playing such a piece should promote learning. It is also likely that the social benefits of playing music add to this type of reward.

Finally, humans seem to have a strong internal motivation to practice and perfect many skills, even if those skills do not have immediate physiological, psychological, or social outcomes. In addition to music, people spend hours perfecting their golf swing, playing video games, or baking elaborate cakes. All of these skills require practice, and the outcome of practice is often not immediate. Thus we hypothesize that practice itself may be rewarding, and that the prediction–feedback–error-correction cycle that is important for learning, may be motivating across a range of domains. When musicians are learning a new and challenging piece, or perfecting an old one, they know exactly what they want it to sound like. This representation is translated into a motor plan, and both the imagined outcome and the plan become predictions against which they will measure their performance. When musicians attempt to play the piece, they will likely make errors, which lead to corrections and learning; but when they play the piece as imagined, they experience the reward of accurate performance. Because error feedback and reward are so important for learning, these mechanisms seem like strong candidates for promoting brain plasticity, but have been little explored.

Where Do We Go From Here?

Bringing together the data from this review, we suggest three directions for future research.

(1) Currently, most studies examine GM and WM differences separately, or do not directly link them through analysis. Analyses typically target differences in individual regions, when it is very likely that plasticity changes occur at the network level. Additionally, groups are defined a priori rather than using data-driven approaches using participant characteristics such as training duration or age-of-start. Implementing these kinds of analyses requires large samples with multiple imaging measures. This implies a multi-center, data-sharing approach where standard behavioral and imaging protocols are implemented to allow aggregation of results.

(2) A related goal for music neuroscientists in the next ten years should be the establishment of standardized test batteries with age-based norms that can be administered across locations. A number of groups have been working on the development of tests aimed at children and adults (Dalla Bella et al., 2017; Ireland, Parker, Foster, & Penhune, in press; Mullensiefen, Gingras, Musil, & Stewart, 2014;

Peretz et al., 2013). Important features of such norms are: availability, standard of administration, and up-to-date norms.

(3) Studies targeting gene–maturation–environment interactions that will allow us to understand the complex interactions between pre-existing individual differences in ability, and the type and timing of music training. Music-specific databases and standard instruments would contribute to the feasibility of such work.

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