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Music and Brain Plasticity

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Abstract and Keywords

Learning and making music are complex multimodal activities which put a high load on our brain functioning. They engage perceptual, cognitive, motor, and sensorimotor processes and the associated neuronal circuitries. Long- and short-term musical training and practice can shape brain structure and functions. In this chapter, evidence supporting the neuroplastic effects of music is reviewed, by examining the differences in musicians' and nonmusicians' brains, in terms of structure and function. In addition, the effects of musical training and early music experience on brain development are examined. Conclusions are drawn on the role played by music-driven neuroplasticity for the purposes of neuroprotection and rehabilitation.

Keywords: music, brain plasticity, learning, perception, action, sensorimotor processes, development, neurorehabilitation

Introduction

Musical training and performance are an ideal human model for examining the brain effects of learning specialized sensorimotor skills. They are both examples of multisensory experiences that put a high load on our sensory, motor, and cognitive systems. Years of dedicated and constant practice are necessary to master the skills displayed by professional musicians. Playing a musical instrument is typically initiated early during development, and proficient performance in adults is grounded in extensive learning and practice of a variety of skills over the course of a musician's lifetime. Acquiring and maintaining musical skills has important and quantifiable effects on brain networking and functioning, which are manifestations of brain plasticity. In cognitive neurosciences, the term "brain plasticity" generally refers to the malleability of the human brain, which in response to experience or training partly modifies its structure and/or functions. These changes are not confined to the developing brain, but, albeit less pervasive, they are also visible in adults (e.g., Wan and Schlaug, 2010). Brain plasticity is most important when the training task is meaningful to the subject (e.g., Jenkins, Merzenich, Ochs, Allard and Guic-Robles, 1990), a fact which is particularly relevant for targeted musical training, and is modulated by the degree of awareness of sensory information or action planning (e.g., Pascual-Leone, Grafman and Hallett, 1994). Moreover, brain plasticity is associated with behavioral effects and is underpinned by processes at the cellular and molecular level (e.g., Buonomano and Merzenich 1998).

In this chapter the effects of musical training and practice on brain structure and functioning are reviewed. Particular attention is paid to the effects of musical training in the adult musician, and to the mechanisms underlying music learning during development.

Where Musicians' and Nonmusicians' Brains Differ

A first approach to identify the effects of musical training on brain plasticity is to compare adult musicians and

nonmusicians. Plastic changes associated with short-term and long-term musical training encompass different levels of brain organization spanning primary perceptual and motor regions to sensorimotor integration and cross-modal association areas (for reviews, see Barrett, Ashley, Strait and Kraus, 2013; Habib and Besson, 2009; Herholz and Zatorre, 2012; Jäncke, 2009; Merrett, Peretz and Wilson, 2013; Münte, Altenmüller and Jäncke, 2002; Rauschecker, 2001; Strait and Kraus, 2014; Wan and Schlaug, 2010; Zatorre and McGill, 2005).

Structural and Functional Differences in the Brains of Musicians and Nonmusicians

Important differences between musicians and nonmusicians are visible at different levels of the auditory pathway, from the brainstem (Kraus and Chandrasekaran, 2010; Strait and Kraus, 2014), through primary and neighbor auditory regions (Bermudez, Lerch, Evans and Zatorre, 2009; Gaser and Schlaug, 2003; Schneider et al., 2002), up to high-level auditory processing (James et al., 2014; Loui, Zamm and Schlaug, 2012). Structural differences emerge at the level of primary auditory cortex and auditory association areas, such as the planum temporale (Bermudez et al., 2009; Gaser and Schlaug 2003; Keenan, Thangaraj, Halpern and Schlaug, 2001; Loui, Li, Hohmann and Schlaug, 2011; Schlaug, Jäncke, Huang and Steinmetz, 1995; Schneider et al., 2002; Zatorre, Perry, Beckett, Westbury and Evans, 1998). A particularly pronounced asymmetry of the right/left planum temporale is observed in musicians who are possessors of absolute pitch. In general, trained musicians exhibit greater volume and cortical thickness in auditory cortex (Heschl's gyrus). These regions are most likely responsible for fine pitch categorization and discrimination, as well as for temporal processing.

Differences are also found at a functional level, as revealed by functional neuroimaging and neurophysiological techniques (e.g., auditory evoked potentials). Yet, the regions involved are not always consistent with the results of structural brain imaging studies. While structural studies point toward differences in primary auditory areas (Gaser and Schlaug 2003; Schneider et al., 2002), functional studies reveal stronger responses in higher-level auditory regions when comparing musicians with nonmusicians. Moreover, nonmusicians appear as needing more neuronal resources for processing auditory information, as shown by stronger activation of primary auditory regions relative to musicians (Besson, Faïta and Requin, 1994; Bosnyak, Eaton and Roberts, 2004; Gaab and Schlaug 2003; Shahin, Bosnyak, Trainor and Roberts, 2003; Shahin, Roberts and Trainor, 2004; Trainor, Desjardins and Rockel, 1999). Thus, it is not always obvious whether training is associated with increased or decreased activation in the underlying brain regions.

Structural differences due to musical training extend to motor and sensorimotor cortices, to premotor and supplementary motor regions, and involve subcortical structures such as the basal ganglia and the cerebellum (Amunts, Schlaug and Jäncke, 1997; Bangert and Schlaug, 2006; Bermudez et al., 2009; Elbert, Pantev, Wienbruch, Rockstroh and Taub, 1995; Gaser and Schlaug 2003; Hutchinson, Lee, Gaab and Schlaug, 2003). This neuronal circuitry is engaged in motor control and fine motor planning (e.g., finger motions) during music performance as well as in motor learning (Schmidt and Lee 2011). Differences are also observed in terms of brain connectivity (i.e., white matter). For example, musicians exhibit greater midsagittal size of the corpus callosum (Lee, Chen and Schlaug, 2003; Oztürk, Tasçioğlu, Aktekin, Kurtoglu and Erden, 2002; Schlaug, Jäncke, Huang, Staiger and Steinmetz, 1995). This structure, supporting the interaction between the two hemispheres, may be the substrate of coordinated movement of right and left hand (e.g., for the performance of complex bimanual motor sequences; for instance, see Wiesendanger and Serrien 2004). Finally, the amount of musical practice is associated with greater integrity of the corticospinal pathway (Bengtsson et al., 2005).

More recently, there are indications that training is not systematically associated with increased brain volume. For example, a decrease in striatal volume is observed in ballet dancers (Hänggi, Koeneke, Bezzola and Jäncke, 2010) and skilled pianists (Granert et al., 2011) as a function of efficiency in motor performance (see also James et al., 2014). Similar mixed effects of musical training are found in functional neuroimaging studies, and are not always coherent with the observed anatomical differences. Musicians exhibit either lower or more localized activation in the primary motor cortex than nonmusicians and more variable levels of activation in motor association regions such as the premotor and supplementary motor areas (Haslinger et al., 2004; Hund-Georgiadis and von Cramon, 1999; Jäncke, Shah and Peters, 2000; Krings et al., 2000; Meister et al., 2005). These inconsistencies in functional changes may reflect differential recruitment of resources and mechanisms in skilled musicians. Musical training and performance require greater involvement of higher-order cognitive processes (e.g., tonal processing, working memory, syntax), thus they may favor increased density in the associated brain regions. Yet, other processes,

likely to be automatized and requiring less resources to be executed (e.g., sensorimotor functions and basic motor control), might recruit less brain volume (James et al., 2014). A similar explanation may shed light on inconsistencies between visible structural changes and variable functional correlates (i.e., increased or decreased activation in musicians) in primary auditory and motor regions. This problem is inherent in the complex relation between structural differences and functional changes associated with musical training (see Zatorre, Fields and Johansen-Berg, 2012). A system (perceptual or motor) extending its representation in the brain as a result of musical training may process information more efficiently using fewer neuronal resources than a less-specialized system. Enhanced efficiency might manifest in lower blood flow demands in skilled musicians as compared to nonmusicians when performing a complex motor sequence (Hund-Georgiadis and von Cramon, 1999; Jäncke et al., 2000; Koeneke, Lutz, Wüstenberg and Jäncke, 2004; Krings et al., 2000; Meister et al., 2005).

Structural differences in the brain of musicians and nonmusicians are not confined to the auditory pathway or to motor circuitries. They extend to parietal regions (e.g., to the superior parietal lobe, including the intraparietal sulcus and the inferior lateral temporal lobe) and to the inferior frontal gyrus. Although the functional role of these differences is still unclear, it is likely that they are involved in multisensory encoding and integration. Since musical training and performance are rich and intense multimodal experiences it is expected that these activities will have brain effects on the interaction between modalities (i.e., on cross-modal integration) (Zatorre, Chen and Penhune, 2007). Notably, structural differences in frontal lobe have been consistently reported in the inferior frontal gyrus (Bermudez and Zatorre 2005; Bermudez et al., 2009; Gaser and Schlaug 2003; Han et al., 2009; Sluming et al., 2002). In general, frontal structures are associated with a variety of processes spanning from integration of individual auditory events into larger units, mapping actions to sounds, to musical tonal syntax (Bangert and Altenmüller 2003; Bangert et al., 2006; Koelsch et al., 2002; Lahav, Saltzman and Schlaug, 2007; Levitin and Menon 2003; Lotze, Scheler, Tan, Braun and Birbaumer, 2003; Tillmann et al., 2006; Zatorre, Chen and Penhune, 2007). In particular the left inferior frontal gyrus seems to play a relevant role in the auditory-motor network. This region has been referred to in the past as Broca's area due to its function supporting audio-motor interaction in speech production.

Functional neuroimaging in musicians and nonmusicians reveal major differences in brain activations linked to musical training, including parietal and frontal regions. It is intriguing that these differences emerge also when people merely listen to music. For example, prior instrumental practice is associated with increased activity in the auditory and visual sensorimotor networks when performing a perceptual task (Bangert and Altenmüller 2003; Bangert et al., 2006). There exist strong functional connections linking auditory perception and motor processing during both music perception and performance. Mere exposure to sounds of well-learned actions triggers a neural network extending well beyond auditory regions (Bangert and Altenmüller 2003; Bangert et al., 2006; D'Ausilio, Altenmüller, Olivetti Belardinelli and Lotze, 2006; Hasegawa et al., 2004; Haslinger et al., 2005; Haueisen and Knösche 2001; Keysers et al., 2003; Kohler et al., 2002; Lahav et al., 2007; Zatorre et al., 2007). A region which has attracted particular attention within this neuronal circuitry is Broca's area, corresponding to the posterior inferior frontal gyrus. The inferior frontal gyrus is part of a network referred to as "mirror neuron system" (Rizzolatti and Craighero 2004; Rizzolatti, Fadiga Gallese and Fogassi, 1996). Mirror neurons were initially discovered in region F5 in monkey brain, which is treated as the homolog of human Broca's area (Rizzolatti and Arbib, 1998). The inferior frontal gyrus is involved when actions are performed but also when we see meaningful and goal-directed movements, or when we are presented with sounds linked to well-known actions (e.g., hearing action words, grasping food or playing a musical instrument; Aziz-Zadeh et al., 2006; Buccino, Binkofski and Riggio, 2004; Buccino, Vogt, et al., 2004; Lahav et al., 2007; Pulvermüller, Shtyrov and Ilmoniemi, 2005; Rizzolatti et al., 1996). There are some indications that musicians exhibit increased gray matter volume in the inferior frontal gyrus when compared to nonmusicians (Sluming et al., 2002; Gaser and Schlaug 2003; for a confirmation of functional involvement of Broca's area, see Sluming, Brooks, Howard, Downes and Roberts, 2007), in association with parietal and dorsal premotor activation. Thus musical expertise may be associated with greater involvement of a multimodal sensorimotor-integration system, when musicians listen to, read the score of, or watch performances of well-known music.

Instrument-Specific, Training-Induced Plasticity

The evidence reviewed above from cross-sectional studies shows that brain plasticity can differentiate musicians from nonmusicians. Notably, additional differences are found when comparing musicians who have received

different types of instrumental practice. Changes in the cortical representations within the motor cortex depend on the played instrument (i.e., instrument-specific plasticity). For example, cortical representation of the hand is dependent on the side which is most involved in fine motor control during music training and performance. Greater cortical representations of fingers in violinists' left hand, as compared with right hand, have been found with magnetoencephalography (MEG) (Elbert et al., 1995). Use-specific functional reorganization of the motor cortex is observed when comparing the shape of the regions containing hand representations in pianists and violinists, showing gross anatomical differences in the precentral gyrus (Bangert and Schlaug 2006). String players require highly developed fine motor skills in particular in their left hand. In contrast, in keyboard players, both hands are associated with highly trained fine motor skills with a preference for the right hand as it typically supports melody and more articulated technical passages whereas the left hand realizes the accompaniment. Moreover, most keyboard performers exhibit a particular configuration referred to as "Omega sign" on the left more than on the right hemisphere, whilst most string players show this sign only on the right. The prominence of this sign is correlated with the age at which musicians started musical practice and to the cumulative amount of practice time. The observation of this configuration in relation to the type of performer argues in favor of a structural plasticity mechanism driven by specific instrumental practice.

Instrument-specific neuroplasticity interestingly extends to perception. Musicians show greater evoked potentials in the presence of auditory stimuli as compared to nonmusicians (Pantev et al., 1998). This effect is modulated by the specific musical training, as indicated by timbre-specific neuronal responses observable in different groups of instrumentalists. For example, string and trumpet players reveal stronger evoked cortical responses when presented to the sound of their respective instrument (Pantev, Roberts, Schulz, Engelen and Ross, 2001), an effect particularly visible in the right auditory cortex (Shahin et al., 2003). In addition, musicians display increased gamma-band activity induced by the sound of their own instrument as compared to others (Shahin, Roberts, Chau, Trainor and Miller, 2008). These findings are supported by functional imaging evidence in violinists and flutists (Margulis, Milsna, Uppunda, Parrish and Wong, 2009) indicating that instrument-specific plasticity is not restricted to the primary auditory cortex but rather spans across a network including association and auditory-motor integration areas. Recent studies provide additional evidence that experience-specific plasticity may be visible at the level of the brainstem (Strait, Chan, Ashley and Kraus, 2012; for a review, Barrett et al., 2013). In sum, there is compelling evidence of important and measurable differences in brain structure and function associated with musical training and listening experience in a heterogeneous group of musicians. Even though these studies are cross-sectional, thus making it difficult to conclude about a causal role of training on brain differences, instrument- or timbre-specific plasticity still supports the notion of dedicated brain adaptations.

Beyond a Cross-Sectional Approach: Short-Term Effects of Training in Adults

Cross-sectional studies are supportive of structural and functional discrepancies between the brains of musicians and nonmusicians. In addition, factors such as age of commencement, intensity, or duration of musical training/practice can account for the amount of brain differences (e.g., Amunts et al., 1997; Bangert and Schlaug, 2006; Elbert et al., 1995; Gaser and Schlaug, 2003; Schneider et al., 2002; Sluming et al., 2002). These findings and relations point toward a causal relation between musical training/practice and their structural and functional brain correlates. Yet, the main problem of this cross-sectional approach is that preexisting factors such as predispositions or genetic causes may be responsible for some of the observed differences between musicians and nonmusicians. Longitudinal studies on short-term or long-term effects of training are a viable alternative which can allow drawing causal inferences. In adults, effects of short-term training at the brainstem level are found in linguistic and musical pitch discrimination (Carcagno and Plack 2011; Song, Skoe, Wong and Kraus, 2008). Electroencephalography (EEG) and MEG studies reveal cortical changes (e.g., increased evoked potentials and increased synchronization in secondary auditory cortex) due to pitch discrimination training, associated with enhanced detection of pitch discrepancies (Bosnyak et al., 2004; Menning, Roberts and Pantev, 2000; Schulte, Knief, Seither-Preisler and Pantev, 2002), or in response to improbable sounds following rapid learning of a novel musical system (Loui, Wu, Wessel and Knight, 2009). Transcranial magnetic stimulation (TMS) also reveals changes in hand cortical representation resulting from short-term training of novel fine motor skills (e.g., learning five-finger exercises on the piano) (Pascual-Leone et al., 1995). However, functional neuroimaging yields results which are less consistent and more difficult to interpret. Pitch-related learning tasks are associated with either decreased (Jäncke, Gaab, Wüstenberg, Scheich and Heinze, 2001; Zatorre, Delhommeau and Zarate, 2012) or increased activation (Gaab, Gaser, and Schlaug, 2006) of the auditory regions. Similar discrepancies are observed

following short-term sensorimotor training (e.g., piano-like instrumental learning). In this case, listening to melodies before and after the training is associated with either increased activation of regions associated with action observation (e.g., the premotor region, Broca's area, and the inferior parietal region) (Lahav et al., 2007), or with decreased activation of the dorsal auditory action pathway (Chen, Rae and Watkins, 2012). These findings are reminiscent of the situation encountered in cross-sectional studies, where musical training manifested itself in increased or decreased activation. Similarly, it is possible that under certain circumstances, learning improves efficiency in encoding or processing information (for an example in vision, see Yotsumoto et al., 2008), thus requiring less neuronal resources.

Training in an experimental setting can bring about short-term brain changes (e.g., Chen et al., 2012; Lahav et al., 2007). Recent studies show that the nature of the training plays a relevant role in fostering plastic changes. Comparing auditory exposure per se to auditory-motor training is particularly insightful. Lappe and collaborators (Lappe, Herholz, Trainor and Pantev, 2008; Lappe, Trainor, Herholz and Pantev, 2011) submitted nonmusicians to 2 weeks of musical training. In one group, the sensorimotor training consisted of learning to play a musical sequence on the piano. In the other group, nonmusicians detected errors in performances after listening to the stimuli played by other participants. Following the sensorimotor training, participants showed enhanced detection of incorrect pitch or timing, as compared to mere listening. This difference was accompanied by larger brain response (i.e., increased auditory mismatch negativity) to pitch and duration deviations, indicating greater enhancement of musical representation in the auditory cortex fostered by sensorimotor training. Similar results showing greater benefits of auditory-visual multimodal training as compared to unimodal training are reported (Paraskevopoulos, Kuchenbuch, Herholz and Pantev, 2012). To summarize, short-term changes in behavior and brain activity can be observed in adults as a result of a brief period of musically-related training. Sensorimotor and multimodal training, typical of learning a musical instrument, is more efficient in driving neuroplastic changes than unimodal training. This effect is likely to be underpinned by brain changes occurring between auditory, motor, and sensorimotor integrations regions, and involving both feedforward mechanisms capable of predicting the outcome of motor activity as well as feedback mechanisms for monitoring the performance (Herholz and Zatorre 2012; for examples in speech, see Hickok and Poeppel 2007; Rauschecker and Scott 2009).

Music Shaping Child Brain Development

There is a significant body of evidence showing structural and functional differences in the adult brains of musicians and nonmusicians. However, whether these differences are the result of nature or of nurture is still subject to debate. They may be the outcome of factors which existed prior to training (i.e., brain predispositions or aptitude) or result from brain adaptations due to musical training or experience (e.g., mere exposure fostering implicit learning) during sensitive periods of brain development. There are indications from cross-sectional studies in adults in favor of experience-dependent factors driving brain adaptation. Early onset of musical training (before 7 years of age), within a sensitive period, is particularly efficient in stimulating brain changes (for reviews, see Barrett et al., 2013; Penhune 2011; Zatorre 2013; for other domains, such as speech, see Kuhl 2010). A sensitive period indicates a time frame when early experience (e.g., musical training) has the greatest effect on brain and behavior related to training later in life (Knudsen 2004). Structural differences in the corpus callosum between musicians and nonmusicians and the extent of hand representations in motor cortex are greater for musicians who began training before 7 years (Amunts et al., 1997; Elbert et al., 1995; Schlaug, Jäncke, Huang, Staiger and Steinmetz, 1995). Moreover, early training is associated with greater auditory cortex and brainstem responses to tones (Pantev et al., 1998; Wong, Skoe, Russo, Dees and Kraus, 2007). The dependence of structural changes on the age of commencement is confirmed when controlling for the amount of training (Bailey and Penhune, 2010; Watanabe, Savion-Lemieux and Penhune, 2007). For example, early-trained musicians (< 7 years) display better sensorimotor synchronization skills as compared to late-training musicians (> 7 years). This difference is underpinned by brain connectivity (in terms of white matter) and structural discrepancies (in terms of gray matter) (Bailey and Penhune, 2012; Bailey, Zatorre and Penhune, 2014; Steele, Bailey, Zatorre and Penhune, 2013). Finally, in a recent cross-sectional functional magnetic resonance imaging (fMRI) study, a linear regression approach is used to tease apart age-related maturation effects, linked mostly to frontal (e.g., premotor) and parietal regions, and training-related effects, involving mostly the superior temporal gyrus (Ellis et al., 2012).

In sum, previous cross-sectional studies point toward experience-dependent factors in shaping musicians' brains. However, to determine the relative contribution of nature and nurture in the development of musical skills,

longitudinal studies are needed. Longitudinal studies show beneficial effects of musical lessons on musical abilities as well as behavioral effects on a number of extramusical areas. This phenomenon is referred to as “transfer” (Bangerter and Heath, 2004; for a review, see Kraus and Chandrasekaran, 2010). Near transfer is observed when the training domain and the transfer domain are highly similar (e.g., when learning a musical instrument affords fine motor skills which subserve other activities beyond music, such as typing). Far transfer occurs when there is relatively little resemblance between the trained ability and the transfer domain (e.g., when musical training is associated with enhanced mathematical thinking). Far transfer of musical training, typically more difficult to achieve than near transfer, is found in verbal, spatial, mathematical thinking and on intelligence quotient (IQ) (e.g., Chan, Ho, and Cheung, 1998; Ho, Cheung and Chan, 2003; Rauscher, Shaw and Ky, 1993; Schellenberg 2004; Tierney and Kraus 2013; Vaughn 2000; for reviews, Schellenberg 2001, 2011; Schellenberg and Weiss 2013). Some of these findings, in particular those related to short-term effects of limited musical exposure (e.g., the so-called Mozart effect), are controversial and difficult to replicate (Chabris 1999; Steele et al., 1999). For example, Schellenberg (2004) tested 6-year-old children who underwent keyboard or voice lessons for 36 weeks. Control groups of children received drama lessons or no lessons. After the training, children who received music lessons showed a small, albeit consistent, increase in full-scale IQ and higher performance in standardized educational achievement tests, as compared to the control groups. Considering that simple attendance to school raises IQ (Ceci and Williams 1997), musical lessons may provide an additional boost in IQ by providing a rich educational option which is highly motivating and involves a wide range of multimodal and sensorimotor activities. At a neural level, far transfer of musical training might be fostered by sustained involvement of the multimodal sensorimotor integration network during repeated musical lessons, driving brain plasticity changes. Cross-modal plasticity induced by musical training is likely to affect regions which are relevant for other tasks such as mathematics (parietal; Chochon, Cohen, van de Moortele and Dehaene, 1999), working memory (parietal; Gaab and Schlaug, 2003; Gaab et al., 2006), sequential mental operations (frontal; Sluming et al., 2007), speech/language, auditory-motor mapping, auditory integration or prediction (frontal; Koelsch et al., 2002; Koelsch, Fritz, Schulze, Alsop and Schlaug, 2005; Lahav et al., 2007; Patel, 2003; Tettamanti and Weniger, 2006).

A growing body of studies focuses on the structural and functional changes occurring in children’s brains as a result of musical training. In some studies, the effect of children taking specific instrumental lessons with the Suzuki method is examined. This method, based on training to listen by ear and learning by imitation, is standardized, and thus particularly appropriate for systematic studies. In a study, 4–6-year-old children trained with the Suzuki method (training group) revealed changes in auditory evoked responses to a violin and a noise stimulus. In particular, the training group showed faster responses to violin sounds than the control group (Fujioka, Ross, Kakigi, Pantev and Trainor, 2006; see also Shahin et al., 2008). Notably, these changes were accompanied by enhanced performance in a behavioral musical task and improved working memory in a nonmusical task. Effects of musical training on electrophysiological brain responses are not confined to children learning with Suzuki method. Standard musical training is linked to greater mismatch negativity (MMN) responses to melodic and rhythmic modulations in children between 11 and 13 years of age (Putkinen, Tervaniemi, Saarikivi, de Vent and Huotilainen, 2014), and larger induced gamma-band responses in 5-year-old children (Trainor, Shahin and Roberts, 2009). Notably, enhanced brain response to musical sounds does not require extensive training. Four-month-old infants exposed to melodies in either guitar or marimba timbre for about 2.5 hours over the course of a week exhibited MMN selectively to the timbre at which they were exposed (Trainor, Lee and Bosnyak, 2011). Furthermore, the effects of musical training during development are not limited to cortical functionality but extend to brainstem responses when processing speech in noise (Strait, Parbery-Clark, O’Connell and Kraus, 2013). Electrophysiological changes are accompanied by functional changes, as revealed by fMRI, suggesting leftward asymmetry in task-related activity during music processing (same/different discrimination), with peaks in the auditory cortex and supramarginal gyrus (Ellis, Buijn, Norton, Winner and Schlaug, 2013).

Finally, musical training can bring about changes in brain anatomy. After about 2.5 years of musical training, 5–7-year-old, high-practicing children showed increased size of the anterior part of the corpus callosum, a group of fibers connecting motor related-areas of the two hemispheres (Schlaug et al., 2009). The number of weeks of musical exposure was associated with changes in this region, as well as with the performance in a motor-sequencing task. Structural brain changes are also found at the level of temporo-occipital and insular cortex, regions related to musical reading (Bergman Nutley, Darki and Klingberg, 2014). Notably, brain deformation changes in motor and auditory areas critical for instrumental music training are visible as soon as after 15 months of training in 6-year-old children (Hyde et al., 2009). Some of these changes are associated with the performance

in behavioral testing. For example, the deformation changes in right auditory area underlie improved melodic/rhythmic discrimination. To summarize, musical training and practicing a musical instrument are associated with cognitive benefits which manifest in terms of near or far transfer effects. There is increasing evidence pointing to the functional mechanisms and structural changes underpinning these transfer effects during development based on longitudinal approaches. These findings begin to uncover the processes which allow musical training to shape functional and structural brain development. The effect would be most evident when the training is delivered within a given sensitive period, whose boundaries have still to be clearly identified.

Conclusions

The human brain has the remarkable ability to change as a function of training and environmental demands. Musical training and practice are rich sensorimotor and multimodal experiences which can shape both the structure and the functions of human brain and which are associated with cognitive benefits. Learning and repeated practice of an instrument by professional musicians implies the association between fine motor movements with meaningful sound patterns, while receiving real-time multisensory feedback. Brain changes are manifest when comparing musicians to nonmusicians (e.g., training- and instrument-specific brain plasticity), and can be measured in children after a few months of musically related training in longitudinal studies. Behavioral effects and benefits of musical training are undergirded by plastic changes in primary and secondary auditory and motor cortices, as well as in sensorimotor and multimodal integration areas.

Even though brain changes are generally driven by dedicated musical training as shown in group studies, there are important individual differences in people's learning of musical skills. At one end of the continuum there are individuals suffering from lifelong disorders of musical learning (i.e., congenital amusia or tone-deafness; for reviews, see Dalla Bella, Berkowska and Sowiński, 2011; Peretz and Hyde 2003; Williamson and Stewart, 2013). At the other end we find musical prodigies showing precocious musical abilities (e.g., a fine sense of rhythm or exceptional motor control in playing an instrument), which allow them to achieve levels of musical expertise unattainable for the average musician (e.g., Kirnarskaya, 2009). Indeed, the presence of experience-related plasticity does not rule out the contribution of predispositional factors. Practice and experience typically operate on natural abilities with a genetic substrate. Thus, individual anatomical and functional properties of the neural architecture (i.e., genetic predispositions for learning) might be more or less conducive to learning musical skills (Zatorre, 2013). Accordingly, individual differences are an important factor in explaining discrepant results in neuroplasticity due to musical training (Merrett et al., 2013). In particular, genetic differences which may pave the ground to musical learning are devoted increasing attention (Park et al., 2012; Ukkola-Vuoti et al., 2013). There is recent evidence that experience-related neuroplasticity cannot account for all observed variability in expert brains (Foster and Zatorre, 2010; Golestani, Price and Scott, 2011), thus opening the door to genetic/maturational factors.

Finally, alteration of brain functions and structure as a function of training or experience is not confined to the developmental brain, during a particular sensitive period. A certain degree of brain plasticity is also possible in adulthood and in the elderly (e.g., following a juggling training; Boyke, Driemeyer, Gaser, Büchel and May, 2008; Draganski et al., 2004; Draganski et al., 2006). There are indications that neuroplasticity is possible in the adult brain following relatively short-term musical training (e.g., Herdener et al., 2010; Lappe et al., 2008, 2011). This fact has major consequences which motivate the use of music as a tool to limit or delay cognitive decline in the elderly or to act as a neuroprotector (for a review, see Wan and Schlaug 2010). For example, training programs requiring intensive multisensory, cognitive, and motor activities (e.g., half an hour of piano lessons per week, for 6 months) are successful in improving working memory, perceptual, and motor skills (Bugos, Perlstein, McCrae, Brophy and Bedenbaugh, 2007), and in delaying age-related decline in speech perception (Parbery-Clark, Anderson, Hittner and Kraus, 2012; Parbery-Clark, Strait, Anderson, Hittner and Kraus, 2011), nonverbal memory, and executive processes (Hanna-Pladdy and MacKay, 2011). In addition, beneficial effects of music-related activities are found in stroke patients (e.g., Särkämö et al., 2008), and in patients with neurodegenerative disorders, such as Parkinson's disease and dementia (e.g., Lim et al., 2005; Spaulding et al., 2013; Van Wegen, Hirsch, Huiskamp and Kwakkel, 2014; Verghese et al., 2003). Understanding the mechanisms of training-related plasticity underlying these beneficial effects of music is a critical step for developing successful theory-driven rehabilitation strategies and prevention programs.

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