

Chapter 7

MUSIC AND NEURAL PLASTICITY

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Abstract

This chapter reviews material on the effects of music training on the brain. The review is framed within the broader theoretical context of neuroplasticity and experience, as well as the relationship between behaviour and brain structure and function. It presents a comprehensive account of studies that have investigated differences in the brains and behaviour of musicians compared with non-musicians, with an emphasis on variables that may moderate the relationship between music training and neuroplastic change. Evidence for a causal relationship between music training and changes in the brain is provided in the context of longitudinal studies of training-induced plasticity in novice musicians. Training effects in both healthy children and adults and in patients with neurological disorders are also discussed.

Introduction

Observations of the way the brain perceives and produces music, and the influence that music has on the brain, have formed a long-standing fascination for scientists and popular culture alike. Recent best-selling books, such as *Musicophilia: Tales of Music and the Brain* by Oliver Sacks and *This Is Your Brain on Music: The Science of a Human Obsession* by Daniel Levitin, testify to the widespread appeal of this topic. After all, music is something that almost everyone enjoys and is ubiquitous in our culture. The idea that something so common for us, and yet so special to us, might have a major influence on our minds and our brains is very intriguing. However, this has often led to presumptive conclusions about music-brain interactions that go far beyond the available scientific evidence. The aim of this chapter is to synthesize current scientific knowledge of the influence of music training on brain structure and function and, by extension, on cognition and behaviour. In particular, we will look at the evidence for music-induced neuroplasticity, or in simple terms, the capacity of the brain to change in response to musical experience. The effects of music training on the brains

of healthy children and adults, of novice and experienced musicians, and of patients with neurological disorders will be reviewed.

Although the field of music neuroscience is considered relatively new, links between music and brain structure and function have been postulated for centuries. For example, post mortem examinations of the brains of prominent musicians from the 19th and early 20th centuries revealed purported “abnormalities” that were thought to underlie their extraordinary musical abilities (Auerbach, 1906, 1908, 1911, 1913, cited in Meyer, 1977). More recently, researchers have noted that musicians, who acquire complex skills over many years of practice, provide ideal models of brain plasticity. Yet Ramón Y Cajal (1904), a father of modern neuroscience and one of the first to write about neuroplasticity, voiced this same idea over 100 years ago! This idea has now stood the test of time and with the advent of modern neuroimaging techniques, the study of music and brain plasticity has become an established and popular area of research.

Neuroplasticity

The term ‘neuroplasticity’ refers to changes in the central nervous system as a result of experience or adaptation to environmental demands. It is a general term and can denote structural or functional changes at either a cellular or a systems level. Structural changes in individual brain cells, modification of the gross anatomy of the brain, and reorganisation of the neural networks that subservise complex cognitive processes are all examples of neuroplasticity. For the sake of clarity in this chapter, a distinction will be made between structural and functional neuroplasticity. In particular, structural neuroplasticity will refer to macrostructural changes in the brain – changes in size, shape, density, and connectivity that can be measured in a living brain. Functional neuroplasticity will refer to changes in brain processing, for example, increases or decreases in activation, modification of patterns of cortical activation, or changes in the neural substrates or networks involved in a given task. These large-scale structural and functional neuroplastic changes are likely to reflect microstructural changes in cells and their synapses. These microstructural changes, in turn, are thought to follow from early functional changes, such as long-term potentiation and long-term depression (Barnes & Finnerty, 2010). The relationship between structure and function is complex, and the degree to which extensive structural remodelling of the nervous system relates to functional adaptations, or vice versa, remains unclear (Draganski & May, 2008).

Despite early writings on neuroplasticity, such as the work of Ramon Y Cajal, the majority of neuroscientists have, until recently, believed that the adult brain is largely static and unchangeable. Neuroplasticity was thought to be a special property of the developing brain and to occur only during memory formation in the mature brain. Quite controversially, in the 1970s and 1980s animal models began to demonstrate that the adult brain could change in response to experiences (Buonomano & Merzenich, 1998). For example, deafferentation, amputation, and later, training studies in primates and other animals showed that cortical sensory representations could be significantly altered. These types of studies led researchers to search for neuroplasticity in humans across the lifespan, revealing that the human adult brain is far more malleable than previously thought. The sensory environment and experience have now been shown to remodel the cerebral cortex of both children and adults to an astonishing degree.

Box 7.1. The negative side of neuroplasticity

In most contexts, experience-dependent neuroplasticity is a positive outcome. In fact, given that neuroplasticity underlies our ability to learn, it is not just helpful, but essential. However, there are times when the brain's ability to change can lead to negative consequences. A relevant example is focal dystonia in musicians, (also called musician's cramp), which occurs in about 1% of professional musicians (Jabusch & Altenmüller, 2006). One of the most famous sufferers of this condition was composer and pianist Robert Schumann (Altenmüller, 2006). The primary symptom is deterioration and loss of control of skilled, highly-trained movements. Current evidence suggests that maladaptive plasticity induced by intensive training, combined with genetic and behavioural factors, leads to focal dystonia (see Jabusch & Altenmüller, 2006, for a comprehensive review).

Musicians are just one of many groups, such as taxi drivers, novice jugglers, new language learners, or medical students, in whom experience- or training-dependent neuroplasticity has been demonstrated (Boyke et al., 2008; Draganski et al., 2004; Draganski et al., 2006; Golestani & Zatorre, 2004; Maguire et al., 2000). So why have musicians been hailed as ideal models for investigating this phenomenon? In recent reviews of experience-dependent plasticity, Kleim and Jones (2008) and Green and Bavelier (2008) discussed some of the prerequisites for inducing neuroplasticity, which include repetition, intensity, and complexity of training. Most professional adult musicians have engaged in an enormous amount of practice over many years that is both repetitive and intense to reach a high level of expertise. Producing music is a complex task, requiring finely-tuned motor movements, highly developed sensory abilities (in auditory, visual, tactile, and kinaesthetic modalities), the integration of motor and sensory information to monitor and correct performance, and higher-order executive and attentional functions. Musicians therefore provide a wealth of opportunities to study changes in brain structure and function across multiple information processing systems, using both 'bottom-up' and 'top-down' approaches. Different musical instruments also provide unique sensory stimulation and demand specific motor skills, so comparisons between musicians can be instructive. The large amount of natural variation in the training, practice, and skill acquisition of musicians creates, in the words of Peretz and Zatorre (2005, p. 102), a "formidable laboratory" for the study of experience-dependent neuroplasticity.

The study of musicians and neuroplasticity not only enhances our basic understanding of neuroplasticity, but also our understanding of music and its capacity to influence brain and behaviour. A large body of literature suggests that music interacts with other cognitive functions, including memory, language, attention, and spatial reasoning. It is also inextricably linked to our emotions and to movement. Given these extensive associations, music training may have a unique effect on brain functioning and human behaviour and may help us unravel some of the mysteries of cognitive neuroscience. Yet, these assumptions require empirical investigation, as the conclusions drawn about the consequences of music training across the

lifespan have wide-spread implications, particularly for music education and medicine. The growing interest in using music and music training in a wide variety of therapeutic contexts underscores the necessity of accurately assessing and understanding how music might shape our brains.

Current Methods of Studying Neuroplasticity

There are a number of non-invasive ways to investigate the structure and function of the human brain that have rapidly advanced the study of neuroplasticity and the field of music neuroscience. Common methods currently in use to investigate structural neuroplasticity are voxel-based morphometry (VBM) and diffusion tensor imaging (DTI), both of which are based on magnetic resonance imaging (MRI). Methods for exploring functional neuroplasticity include functional MRI (fMRI), positron emission tomography (PET), electroencephalography (EEG), and magnetoencephalography (MEG). Transcranial magnetic stimulation (TMS) and optical imaging are also used in neuroplasticity research. Each of these techniques provides different information about brain structure and function, and for that reason multiple techniques are often used conjointly.

VBM uses high-resolution structural images to compare differences between groups or changes within a group in brain shape and composition (Ashburner & Friston, 2000). It is 'voxel-based' because comparisons are made across each voxel (a volume element in a three-dimensional image) in the whole brain or in a region of interest. The technique is often used to compare the concentration of grey matter (brain matter that contains neuronal cell bodies) between groups. In contrast, DTI is more commonly used to investigate white matter (brain matter that contains the axonal connections between cells). DTI uses water molecule diffusion to provide information about white matter integrity and structure (Bihan et al., 2001; Mori & Zhang, 2006). In healthy white matter, the cell axons are covered in a fatty sheath called myelin, and many of these axons are arranged into bundles, or tracts, that connect cells in different areas of the brain. Water molecules will diffuse more quickly parallel to a tract than perpendicular to that tract; therefore, water diffusion can provide information about the extent and trajectory of white matter. Fractional anisotropy, a frequently reported measure in diffusion imaging, is an index of the degree to which water diffusion is directionally constrained by the tracts of myelinated axons (Bihan, et al., 2001). Tractography is another relatively new DTI application that is being developed to investigate anatomical connectivity using three-dimensional mapping of fibre trajectories (Assaf & Pasternak, 2008).

fMRI and PET are used to infer the location and intensity of brain activity, although they cannot measure brain activity directly. These imaging techniques measure markers of brain activity such as cerebral blood flow or glucose metabolism, which have been shown to increase when neuronal activity increases (Huettel, Song, & McCarthy, 2008). In this way they are able to show with great spatial accuracy which regions of the brain are activated or deactivated during a given cognitive task. They are especially useful for identifying networks of structures associated with particular functions. fMRI is a safe and non-invasive method that uses powerful magnetic fields and radio frequency pulses to create images. It has become the preferred functional imaging method, since PET requires the injection of radioactive isotopes and the images take much longer to acquire than with fMRI.

EEG and MEG also measure neural activity by using sensors on or near the scalp to record the combined electrical activity of large numbers of neurons (in the case of EEG) or the magnetic fields generated by the electrical activity (in the case of MEG) (Huettel, et al., 2008). When the brain perceives and processes stimuli, small changes in electrical potentials and magnetic fields can be detected over several hundred milliseconds. These changes, which are time-locked to the stimulus, create measureable waveforms called event-related potentials (ERPs) or event-related fields (ERFs). ERP and ERF waveforms often have characteristic components (positive and negative deflections) and latencies. For example, the N1 or N100 is a negative component that arises in the cortex approximately 100 ms after stimulus onset. (Note: ‘m’ is added to the name of a component to indicate that it is magnetic, as in N100m). Other components that have commonly been investigated include the P2, P3, and the mismatch negativity (MMN). These different components appear to reflect specific aspects of brain processing, such as encoding of stimulus features (early components), change detection (MMN), and expectancy (P3), and they are modifiable by experience (Martin, Tremblay, & Stapells, 2007; Starr & Golob, 2007).

TMS uses a high-intensity magnetic field to excite or inhibit a particular region of the cortex through the skull (Hallett, 2007). TMS has the capacity to temporarily disrupt brain function in the stimulated region, and consequently the behaviour subserved by that region. TMS is especially useful for identifying brain regions necessary for a particular function. It has also been used to map motor function by stimulating the motor cortex and recording the motor evoked potentials in muscles. Finally, in optical imaging, images are created by transmitting light through the brain (or other parts of the body) and measuring the resulting absorption and scatter of the light (Gibson & Dehghani, 2009). Optical imaging has some advantages over fMRI including cost, portability, and insensitivity to movement. While it has yet to be used extensively in human plasticity studies, it is likely to see increased use as the technology advances.

The Neuroanatomy of Music

While questions of where and how the brain processes music have now been addressed to a considerable degree, there is still a great deal to be discovered. What is certain is that the perception and production of music require extensive neural networks, allowing the integration of information from sensory domains (auditory, tactile, kinaesthetic, visual) with motor output, memory, emotion, attention, and other higher-order cognitive processes. Although a detailed discussion of the neuroanatomy of music is beyond the scope of this chapter, a brief overview of general brain organisation and some of the major structures and networks known to be involved in music processing will provide the necessary framework from which to interpret the findings of music neuroplasticity research.

Apart from its major division into right and left hemispheres, the brain is also divided into lobes (See Figure 7.1). Some of the lobes have anatomically distinct boundaries, particularly between the frontal and parietal lobes, which are divided by a deep fissure known as the central sulcus, and between the frontal and temporal lobes, which are divided by the lateral, or Sylvian, fissure. The surface of the brain is convoluted, and these convolutions are called gyri (bumps) and sulci (valleys). A variety of anatomical terms are used to indicate orientation or direction within the brain, including dorsal and superior to refer to the top,

ventral or inferior to refer to the bottom, anterior or rostral to refer to the front, and posterior or caudal to refer to the back. The medial surface of the brain is “in the middle,” where the two hemispheres meet, while the lateral surface refers to the sides of the brain. The gyri and sulci, in combination with these orienting terms, are often used to name different parts of the brain. For example, the superior temporal gyrus is the most superior (uppermost) gyrus in the temporal lobe.

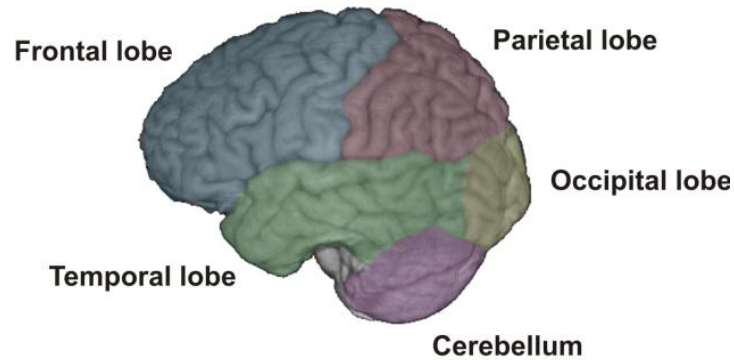


Figure 7.1. Major divisions of the human brain.

Each sensory modality is processed in specialized primary and secondary areas of the cortex. The motor system also has primary and secondary regions. Additional areas called association cortex play a role in integrating information from different senses and between the senses and the motor system. These cortical regions are connected via a number of white matter tracts, including the superior and inferior longitudinal fasciculi (anterior-posterior connections), the corpus callosum (cross-hemispheric connections), and the corticospinal tract (which carries information from the motor region to the spinal cord). Although these connections between regions are not specific to music, they are used extensively to connect the networks for music perception and production. The corpus callosum is of particular importance as it allows communication between the two hemispheres. This is crucial given the brain’s contralateral organisation, such that the left hemisphere controls motor output for the right side of the body and vice versa. The somatosensory and visual systems, and to a certain extent the auditory system, are also contralaterally organized, with sensory inputs processed on the opposite side of the brain.

The processing of sound is fundamental to music processing and occurs first within the ear and the brainstem, and then within the auditory cortex, which is located in the temporal lobes. The primary auditory cortex (A1) lies within the transverse gyri of Heschl (Heschl’s gyri) and is tonotopically organized. This means that frequency information, which gives rise to pitch perception, is carried from the periphery to the cortex in an ordered array from low to high. Heschl’s gyri lie mostly within the deep sulcus known as the lateral, or Sylvian, fissure. Secondary areas around the primary auditory cortex, including the planum temporale in the posterior superior temporal gyri, are also important for pitch and music perception, among other things. These regions appear to underlie the ability to represent relationships between pitches that form the basis of melodies, as mediated by auditory short term memory (McLachlan, Greco, Toner, & Wilson, in press; Peretz & Zatorre, 2005). Although music processing occurs bilaterally in the brain, a degree of hemispheric

specialisation has been demonstrated, with the right auditory cortex particularly involved in spectral processing for timbre and fine-grained pitch discrimination, as well as the perception of melodic contour (Hyde, Peretz, & Zatorre, 2008; Stewart, von Kriegstein, Warren, & Griffiths, 2006). The left auditory cortex has been implicated in the perception of melodic intervals and appears specialized for rapid temporal processing (Zatorre & Belin, 2001). The temporal aspects of music also display some degree of hemispheric specialisation, with the perception of beat and meter more dependent on the right hemisphere and the perception of temporal groupings or rhythm more dependent on the left hemisphere (reviewed in Peretz & Zatorre, 2005).

Sensorimotor functions are essential to music processing and production. The primary sensory cortex is located on the post-central gyrus, a convolution just posterior to the central sulcus that divides the frontal and parietal lobes. Primary and secondary sensory areas are involved in music as they provide necessary tactile and kinaesthetic feedback during music production, such as singing or playing an instrument. The primary motor cortex is located on the pre-central gyrus, just anterior to the central sulcus. It sends signals through the corticospinal tract to control movement. Other brain regions are involved in the planning and control of motor functions. These include the premotor and supplementary motor areas, located anterior to the primary motor cortex, as well as the basal ganglia and the cerebellum. Not only do these motor regions play a role in the physical production of music, they are also critically involved, along with the auditory cortex, in rhythmic aspects of music processing (Grahn & Brett, 2007). The integration of information from sensory domains with motor output is another crucial function for music production, and this is thought to occur in a widespread network, including posterior association cortex and the premotor cortex as key regions (Zatorre, Chen, & Penhune, 2007).

The frontal lobes make a diverse contribution to music perception and production. In general, they are involved in both motor functions and higher-order cognitive processes, such as working memory, planning, and monitoring. The inferior frontal gyrus, and in particular the region known as Broca's area, appears to play a significant role in music processing. Broca's area is best known as a language region, but is involved in many music-relevant tasks as well. These include, but are not limited to, the sequential ordering of sound stimuli and the processing of music syntax and expectancy (Maess, Koelsch, Gunter, & Friederici, 2001; Tillmann et al., 2006). The inferior frontal gyrus is also involved, along with the superior parietal cortex, in the mental manipulation of melodies (Zatorre, Halpern, & Bouffard, 2010). Other regions of the frontal lobes, such as the dorsolateral prefrontal cortex, are involved in music processing because of their role in executive functioning skills like working memory (D'Esposito, Detre, Alsop, & Shin, 1995), on which music performance can place high demands. Even from this basic summary, it is evident that music processing is widely distributed throughout the brain. For this reason, the search for music-induced neuroplasticity has evolved from an investigation of structure and function in specific areas, such as primary auditory or motor cortices, to a search that encompasses the entire brain.

Box 7.2. What makes a musician?

Much of the literature in the field of music neuroscience has focused on differences in the structure and function of the brains of musicians compared with nonmusicians. This first requires an understanding of the features that differentiate a ‘musician’ from a ‘nonmusician’, which is more difficult than one might think. Musicians can be classified based on the amount or type of training they have received, the age at which they started training, the level of skill attained, or the amount of time that they engage with music, either currently (such as practice hours per week) or in the past (lifetime accumulated practice). One of the most common strategies is to differentiate between professional musicians, amateur musicians, and nonmusicians. Professional musicians are typically defined as those who make the majority of their living from music, while amateurs may have received some formal training but do not make a living from music (Stebbins, 1992). Professional musicians are often found to have more training from an earlier age, higher levels of expertise, greater accumulated hours of practice, and greater current engagement in music than amateur musicians (Ericsson, Krampe, & Tesch-Romer, 1993), but this is not always the case. Nonmusicians, often called novices, typically have limited or no exposure to music training and practice. This category can also be difficult to consistently define, as most people living in modern Western societies have an extremely high level of exposure to music (passive listening) and at least some degree of experience with active music making through school or community music programs. Many of the studies discussed in this chapter have carefully selected nonmusician groups who have never played an instrument and have no formal music training. Other studies use more liberal criteria to define nonmusicians, such as a maximum of two years of training or scoring below a ‘cut-off’ on particular skills. In general, definitions of musicianship are poorly standardised, leading to variability in group comparisons across studies and difficulty generalising study findings.

Brain Structure in Musicians and Nonmusicians

Based on current knowledge of the principles governing neuroplasticity, it is reasonable to hypothesize that the specialized, intense, and long-term training of musicians leads to measurable changes in brain structure. This hypothesis appears to be supported in the literature, and in many cases musician status (described in Box 7.2) has been correlated with significant differences in regional brain morphology (shape), size, and connectivity. As demonstrated in Figure 7.2, musician—nonmusician differences have been found in many regions of the brain, and particularly in frontal, motor, and auditory regions. However, a number of these findings have not been replicated in subsequent experiments, have differed in lateralisation, or have led to contradictory findings in some studies. These contradictions and the lack of replication have not yet been adequately explained, but they may be due in part to between-study differences in variables such as the age of onset of music training or sex. These and other variables have often been considered extraneous and thus are unaccounted

for, but they appear to moderate the relationship between music training and brain structure. We draw attention to these variables and to the often-ignored disparities in the findings, since they indicate the need for more carefully controlled studies to arrive at a full and accurate understanding of the effects of music training on brain structure. Nevertheless, the available evidence reviewed below suggests that musicians and nonmusicians do have different brains.

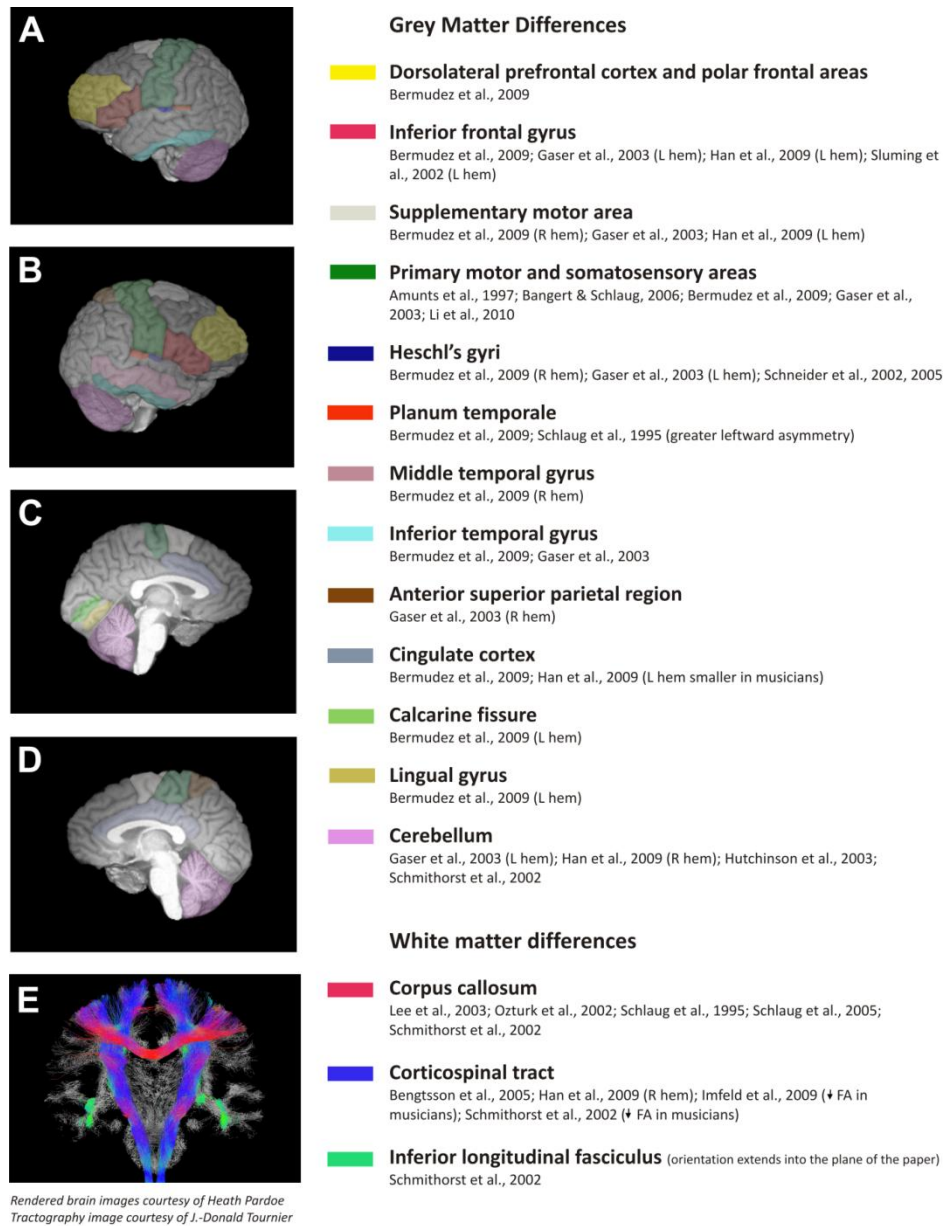


Figure 7.2. Approximate locations of structural brain differences found in studies of musicians compared to nonmusicians. All findings are bilateral and greater in musicians unless otherwise noted. Structural brain differences are reported for (A) the left lateral brain surface, (B) the right lateral brain surface, (C) the left medial brain surface, (D) the right medial brain surface, and (E) the white matter tracts of the brain. L hem = left hemisphere, R hem = right hemisphere.

In two seminal structural neuroimaging papers published in 1995, Gottfried Schlaug and colleagues reported that musicians had a larger anterior half of the corpus callosum and greater leftward asymmetry of the planum temporale compared to nonmusicians (Schlaug, Jancke, Huang, Staiger, & Steinmetz, 1995; Schlaug, Jancke, Huang, & Steinmetz, 1995). These were the first demonstrations of structural brain differences between musicians and nonmusicians *in vivo*. Following on from these findings, musician—nonmusician differences were investigated in many other brain regions that were thought likely to demonstrate such disparities, given the specialized skills and training of musicians. These included the auditory cortex (Schneider et al., 2002; Schneider et al., 2005), the sensorimotor cortex (Amunts et al., 1997; Bangert & Schlaug, 2006; Li et al., 2010), the inferior frontal gyrus (Sluming et al., 2002), the cerebellum (Hutchinson, Lee, Gaab, & Schlaug, 2003), and white matter tracts (Bengtsson et al., 2005; Imfeld, Oechslin, Meyer, Loenneker, & Jäncke, 2009; Oechslin, Imfeld, Loenneker, Meyer, & Jäncke, 2010; Schmithorst & Wilke, 2002). A picture of widespread structural modification of the musician's brain has begun to emerge from the literature, but it is also evident that the picture is more complex than first thought. Rather than a straightforward relationship between musician status and differences in brain structure, a more intricate relationship exists in which numerous variables interact with musician status. The most salient of these variables are age at commencement of music training, sex, the presence of absolute pitch, and the instrument of study (see also chapter by Chin & Rickard in this volume for a hypothesized role for music engagement).

Onset of Music Training

Although neuroplasticity has been demonstrated throughout the lifespan, there is evidence to suggest that the capacity for neuroplasticity peaks during certain developmental periods (Knudsen, 2004). Thus, experiences that occur during early, sensitive periods of development are expected to have a greater impact on brain structure and function. In their 1995 study of the corpus callosum, Schlaug and colleagues found that their results only held for the group of musicians who began their music training prior to age seven, while those who began their training after age seven did not have a significantly larger corpus callosum than nonmusicians (Schlaug, Jancke, Huang, Staiger, et al., 1995). In other investigations of the size and fractional anisotropy of the corpus callosum, several studies that used early-trained musicians found a significant difference from nonmusicians (Lee, Chen, & Schlaug, 2003; Öztürk, Taşçıoğlu, Aktekin, Kurtoglu, & Erden, 2002; Schmithorst & Wilke, 2002, but see Imfeld et al., 2009) while a study using later-trained musicians did not (Han et al., 2009). Although they did not find a significant musician—nonmusician difference, Bengtsson et al. (2005) found a strong correlation between amount of practice time in childhood and adolescence and fractional anisotropy of the corpus callosum, but no significant relationship between practice time in adulthood and corpus callosum anisotropy. Taken together, these findings support the hypothesis that structural changes in the corpus callosum may only occur when music training is present during early periods of greater plasticity. The extent to which early training influences plasticity in other brain regions is uncertain. Studies of the pre-central sulcus, central sulcus, and corticospinal tract have found negative correlations between the degree of structural change and age at commencement of music training (Amunts, et al., 1997; Imfeld, et al., 2009; Li, et al., 2010), but studies of the cerebellum and

planum temporale have not shown a significant correlation (Hutchinson, et al., 2003; Keenan, Thangaraj, Halpern, & Schlaug, 2001). A number of additional studies do not report the age at which musicians began training. Given the current findings, age at commencement of training appears to be an important moderating variable of music-induced neuroplasticity.

Sexual Dimorphism and Music Training

Sex is another variable that may moderate structural differences in musicians. In a follow-up to the 1995 study of the corpus callosum, Lee, Chen, and Schlaug (2003) reported that only male musicians demonstrated an increase in corpus callosum size compared to nonmusicians, while female musicians did not. A sex-based disparity has also been reported in the cerebellum, with only males showing a significant musician—nonmusician difference (Hutchinson, et al., 2003). A number of explanations have been suggested for these findings, including hormonal differences or pre-existing sexual dimorphisms that might mask the effects of musicianship in females. For example, females have greater cerebellar volumes relative to the rest of the brain (Hutchinson, et al., 2003), and male and female brains are known to have gender-specific asymmetries (Good et al., 2001; Luders, Gaser, Jäncke, & Schlaug, 2004), with female brains more symmetrical overall. These types of dimorphisms could interact with neuroplastic processes that alter brain volumes or normal symmetries/asymmetries. Given that a number of studies have used musician groups with a large proportion of females and have shown structural brain differences, specific effects of sex on structural plasticity in musicians require replication. In this respect, the research has been complicated by the fact that many previous studies have not obtained large enough or appropriately balanced samples in which sex could be included as a variable. Additionally, a number of musician—nonmusician studies have only used male participants due to the findings mentioned above (for example, Amunts, et al., 1997; Gaser & Schlaug, 2003). Of note, studies from outside the music research field have found potential sex differences in functional neuroplasticity using TMS to modulate cortical excitability (Chaieb, Antal, & Paulus, 2008; Kuo, Paulus, & Nitsche, 2006), providing further support for the idea of sex as a moderating variable in neuroplastic processes.

Absolute Pitch Ability and Brain Structure

Absolute pitch (AP), the ability to identify or produce specific pitches without a reference, has been correlated with certain structural and functional findings in the brain. The 1995 study by Schlaug and colleagues reported a larger leftward asymmetry of the planum temporale in musicians than in nonmusicians; however, it was found that this difference in asymmetry only existed in musicians who had AP, while musicians without AP did not differ from nonmusicians. The leftward asymmetry in AP musicians has been replicated across a number of other studies, although it has been variously attributed to a larger left planum temporale (Zatorre, Perry, Beckett, Westbury, & Evans, 1998) or a smaller right planum temporale (Keenan, et al., 2001; Wilson, Lusher, Wan, Dudgeon, & Reutens, 2009) in AP musicians. Other anatomical differences that have been reported in musicians with AP compared to musicians without AP and nonmusicians include reduced thickness of the dorsal

frontal cortices (Bermudez, Lerch, Evans, & Zatorre, 2009) and leftward asymmetry of fractional anisotropy in the superior longitudinal fasciculus (Oechslin, et al., 2010). Functional differences in the pitch processing of AP possessors are consistent with the anatomical findings (Klein, Coles, & Donchin, 1984; Ohnishi et al., 2001; Zatorre, et al., 1998) and suggest that cognitive processing of pitch is less reliant on working memory in those with AP (Wilson, et al., 2009).

Although there may be a genetic component to AP, its emergence is typically dependent on early music training (Levitin & Rogers, 2005; Zatorre, 2003) and its expression appears related to ongoing music engagement (Wilson, Lusher, Martin, Rayner, & McLachlan, submitted). The brain-based effects of AP should be considered distinct from music training; however, as not all early trained musicians develop AP and the effects of AP on brain structure are distinct from those of music training alone. For example, compared to musicians without AP, AP musicians have smaller right planum temporale volumes, reduced cortical thickness of posterior dorsal frontal regions, and reduced activation of frontotemporal areas involved in pitch discrimination and working memory (Bermudez, et al., 2009; Wilson, et al., 2009). Unfortunately, AP has not been taken into account in all musician—nonmusicians studies, and given the widespread influence that it appears to have on brain structure and function, this variable may confound training-related effects. The differences in brain structure that arise due to AP may be pre-existing genetic differences rather than training-induced, although longitudinal studies are needed to assess this hypothesis. Thus, further research is required to disentangle the influence of music training, AP, and the interaction between them on brain structure and function. The possibility of interactions between AP and other variables such as sex must also be considered. For example, Luders et al. (2004) reported that only male AP musicians demonstrated increased leftward asymmetry of the planum temporale, while female AP musicians showed asymmetries within Heschl's gyri.

Type of Music Training and Neuroplastic Specificity

The musical instrument of training may also play a large role in the type and location of neuroplastic changes. Specialisation may lead to instrument-specific modification since motor and sensory demands vary between instruments. In a study that was elegant in its simplicity, Bangert and Schlaug (2006) showed that the shape of the central sulcus could differentiate not only musicians and nonmusicians, but it could also differentiate between keyboard and string players within the musician group. The prominence of the omega sign (an anatomical landmark in the hand area of the primary motor cortex) was visually inspected by raters blind to group and hemisphere, and a more prominent omega sign was found in the left hemisphere of keyboard players and in the right hemisphere of string players. This is currently the only direct investigation of the effect of specific types of instrumental training on brain structure, but evidence from the functional neuroplasticity literature (reviewed below) reinforces its salience. It is possible that this variable could explain some of the contradictory findings within the literature, because the composition of musician samples varies from study to study. For example, a number of DTI studies measuring white matter integrity have reported inconsistent results. Two studies found an increase in fractional anisotropy in the cerebrosplinal tract of musicians (Bengtsson, et al., 2005; Han, et al., 2009), while two other studies found a decrease (Imfeld, et al., 2009; Schmithorst & Wilke, 2002). In both of the studies with increased

fractional anisotropy, the musicians were pianists, while the studies that found a decrease used mixed samples of musicians. Whether differences in instrumental training might account for these disparities remains to be tested, as the results of DTI studies are heavily influenced by the methodology employed (Jones, 2010). Nevertheless, the influence of highly specific instrumental training on structural plasticity should not be discounted.

Structural Analyses across the Entire Brain

The studies described above compared specific brain regions of musicians and nonmusicians that were thought likely to show music-related differences. As the use of VBM and DTI techniques has become more widespread, a number of researchers have analysed grey or white matter across the entire brain, without any *a priori* hypotheses about which regions might be different in musicians. Although an important step in the evolution of this line of research, these studies have not clarified the overall picture of music-induced structural neuroplasticity. All of the VBM studies to date have reported multiple areas of increased or decreased grey matter density in musicians compared to nonmusicians, but these areas have not been consistent across studies (Bermudez, et al., 2009; Bermudez & Zatorre, 2005; Gaser & Schlaug, 2003; Han, et al., 2009; Sluming, et al., 2002). The inconsistency is perhaps unsurprising given that the musician samples were different in each of these studies with respect to known moderating variables described above. Despite differences in the samples, one region that has been implicated in all of these studies is the inferior frontal gyrus, particularly on the left, although the exact localisation within the anterior-posterior dimension of this gyrus has varied. The volume of the left inferior frontal gyrus has been positively correlated with musician status (Gaser & Schlaug, 2003), and other techniques have shown increased gray matter density (Sluming, et al., 2002), increased cortical thickness (Bermudez, et al., 2009), and increased fractional anisotropy of the white matter underlying this region (Han, et al., 2009). Two of the studies also reported differences in the supplementary motor area (Brodmann's area 6) and in the inferior temporal gyrus (Bermudez, et al., 2009; Gaser & Schlaug, 2003). All other musician differences in these VBM studies have varied in lateralisation or in localisation.

In summary, although more work is needed to arrive at a complete understanding of structural modifications, there is a substantial evidence base for brain differences between musicians and nonmusicians. Musicians demonstrate differences in the size, shape, and connectivity of motor and auditory regions, as well as alterations of normal symmetry or asymmetry. A number of musician variables, such as age at commencement of training, sex, AP, and instrument of training, may affect the relationship between music training and brain structure.

Brain Function in Musicians and Nonmusicians

In addition to differences in brain structure, musician status has also been linked to differences in the way the brain functions. Functional neuroimaging methods, such as EEG, MEG, PET, and fMRI, have demonstrated enhanced processing of information, more efficient or altered brain activation, and superior integration across different modalities in musicians.

These functional differences between musicians and nonmusicians have been demonstrated in both musical and non-musical contexts. It must be noted that, as with the structural neuroplasticity findings, the differences between musicians and nonmusicians are far from straightforward. A careful review of this literature reveals a number of findings that have not been consistently replicated, but in which the balance of evidence may lean toward enhancements of brain function in musicians. Thus, until such results are clarified, general conclusions should be drawn cautiously, although a large degree of overlap between structural and functional findings provides converging evidence for widespread neuroplastic changes associated with music training.

Differences in Auditory Function

Of all of the brain systems that might be influenced by music training, the auditory domain has been studied most extensively in terms of functional differences between musicians and nonmusicians. Most commonly, this has been investigated by measuring brain electrophysiology with EEG and MEG. Auditory stimuli evoke time-locked electrical or magnetic responses called auditory evoked potentials (AEPs) or auditory evoked fields (AEFs), respectively. These evoked responses have allowed investigators to assess how the brain responds to basic features of sound, such as frequency, intensity, and timbre, and to more complex sound features that form the basis of music, such as melody, harmony, and rhythm. AEPs and AEFs can be measured from the brainstem and from the cerebral cortex. They are often classified into ‘sensory-evoked’ components from the brainstem and cortex, which occur early and are determined primarily by the characteristics of the stimulus, and later ‘processing-contingent’ cortical components, which involve higher-level cognitive processing (Martin, et al., 2007). Both the sensory-evoked and processing-contingent components generated by a wide variety of stimuli have been shown to have shorter latencies and/or larger amplitudes in musicians. Faster and larger evoked responses are often correlated with improved behavioural performance in tasks of detection and discrimination and, therefore, appear to reflect superior processing. This suggests that music training is related to enhancements in function across multiple levels of the auditory system.

Subcortical Auditory Processing

Musicians demonstrate psychoacoustic and physiological enhancements at the early stages of auditory processing in the brainstem and the cochlear efferent pathway. These enhancements are evident across a variety of auditory stimuli, including clicks, tones, music, and speech. For example, musicians show reduced transiently-evoked otoacoustic emissions to clicks with contralateral auditory stimulation. This suggests stronger feedback to the cochlea from the brainstem, as well as reduced loudness adaptation to continuous tones, than is evident with nonmusicians (Micheyl, Carbonnel, & Collet, 1995; Micheyl, Khalfa, Perrot, & Collet, 1997; Perrot, Micheyl, Khalfa, & Lionel, 1999). Musicians also show shorter latency in brainstem responses to auditory and audio-visual speech stimuli (Musacchia, Sams, Skoe, & Kraus, 2007). Additionally, the fundamental frequency (F0) of speech sounds from both tonal and non-tonal languages is better represented by musicians in the ‘frequency

following response'. This forms part of the auditory brainstem response, and includes stronger F0 response amplitude and better phase locking (Musacchia, et al., 2007; Musacchia, Strait, & Kraus, 2008; Wong, Skoe, Russo, Dees, & Kraus, 2007). When listening to music intervals, musicians show an increased brainstem response to the harmonic components of the upper note of the interval and more accurate phase-locking to the temporal envelope (Lee, Skoe, Kraus, & Ashley, 2009). These differences are behaviourally relevant given their relationship to music tasks such as processing the harmonic characteristics of an interval and following the melody line (which is typically in the upper voice). Consistent with this, significant correlations have been found between brainstem responses and sound discrimination abilities, as well as brainstem responses and music training and exposure. This evidence, although indirect, suggests that music training leads to better encoding of sound features, such as pitch, timing, and timbre, in subcortical auditory processing.

The Auditory Mismatch Negativity (MMN)

The auditory MMN(m) is a cortical component of the AEP or AEF that has been comprehensively compared between musicians and nonmusicians. The MMN is a negative deflection, with sources in the supratemporal plane and the frontal regions, that peaks approximately 150-250 ms after a stimulus that deviates from a standard in a presented set (May & Tiitinen, 2010; Näätänen, Paavilainen, Rinne, & Alho, 2007). MMN responses are thought to reflect automatic change detection and are usually recorded while participants are watching a silent video or reading, with instructions to ignore the auditory stimuli. However, it is acknowledged that the MMN can be modulated by attentional or top-down processes (Tervaniemi et al., 2009). The auditory MMN can be elicited with many types of deviants, including deviations in frequency (pitch), intensity, timbre, rhythm, and also more abstract features of the stimulus. The amplitude, latency, and source locations of the MMN are the most common parameters compared between musicians and nonmusicians, with the assumption that increased amplitude and decreased latency reflect superior automatic encoding or pre-attentive processing of change in the stimulus.

It is interesting, then, to note that the MMN to pitch deviations is not different between musicians and nonmusicians, despite the observation that musicians are better behaviourally at discriminating pitch changes (Brattico, Näätänen, & Tervaniemi, 2001; Fujioka, Trainor, Ross, Kakigi, & Pantev, 2004; Koelsch, Schroger, & Tervaniemi, 1999; Tervaniemi, Castaneda, Knoll, & Uther, 2006; Tervaniemi, Ilvonen, Karma, Alho, & Näätänen, 1997; Tervaniemi, Just, Koelsch, Widmann, & Schroger, 2005; Tervaniemi, et al., 2009). An exception to this finding is when participants are instructed to pay attention to the stimuli; in this case, the MMN of musicians to pitch deviants appears to be larger than that of nonmusicians (Lopez et al., 2003; Tervaniemi, et al., 2009). Another exception is when the pitch deviation is presented within the context of a chord, a melody, or polyphonic music (Brattico, et al., 2001; Brattico et al., 2009; Fujioka, Trainor, Ross, Kakigi, & Pantev, 2005; Koelsch, et al., 1999), which may be more familiar for musicians. Koelsch (1999) also suggested that multidimensional stimuli provide more auditory information that expert listeners might use for processing. Contradictory results have been obtained for more abstract pitch deviants, such as deviations in the contour or intervals of melodies. Fujioka et al (2004) found that deviations in contour and interval led to a larger MMN in musicians than in

nonmusicians, while Tervaniemi et al (2006) found no difference. An earlier study by Tervaniemi and colleagues (2001) suggested that attentional modulation and type of music training could play a role, since differences in the MMN to contour deviants emerged during the attend condition and only in a group of musicians who played primarily by ear.

The influence of other types of deviants on the MMN response in musicians and nonmusicians has been investigated. Group differences were observed with deviations in intensity, in location of the presented sound source (Tervaniemi, et al., 2006; Tervaniemi, et al., 2009), and in noise bandwidth (Nager, Kohlmetz, Altenmüller, Rodriguez-Fornells, & Münte, 2003). A variety of rhythmic deviants have also shown MMN differences, including changes in interstimulus interval (Münte, Nager, Beiss, Schroeder, & Altenmüller, 2003; Rüsseler, Altenmüller, Nager, Kohlmetz, & Münte, 2001), stimulus duration (Tervaniemi, et al., 2006), stimulus omissions (Rüsseler, et al., 2001), syncopation (Vuust, Ostergaard, Pallesen, Bailey, & Roepstorff, 2009), and grouping of auditory patterns (Herholz, Lappe, & Pantev, 2009; van Zuijen, Sussman, Winkler, Näätänen, & Tervaniemi, 2004, 2005). In contrast, no group differences were found in the MMN for timbral deviants while performing a timbre discrimination task (Poulin-Charronnat, Bigand, & Koelsch, 2006) or for small gaps (silences) inserted into presented tones (Tervaniemi, et al., 2006). It appears that larger or earlier MMNs in musicians may reflect enhanced processing of change for some sound features, but as noted above for pitch, musicians can show superior behavioural performance in detecting change without showing enhanced functional responses.

Table 7.1. Findings of studies investigating differences between musicians and nonmusicians on components of the auditory evoked potential or auditory evoked field in response to the presentation of individual sine tones, spectrally complex tones, or instrumental tones

	Differences	No differences
N19(m)-P30(m) complex	<i>Schneider et al., 2002</i>	
P50(m)	<i>Schneider et al., 2005</i>	<i>Lütkenhöner et al., 2006</i>
N1(m)	<i>Pantev et al., 2001</i>	<i>Pantev et al., 1998</i>
	<i>Schultz et al., 2003</i>	<i>Schneider et al., 2002</i>
	<i>Kuriki et al., 2006</i>	<i>Shahin et al., 2003</i>
	<i>Baumann et al., 2008</i>	<i>Shahin et al., 2005</i>
		<i>Lütkenhöner et al., 2006</i>
N1c	<i>Shahin et al., 2003</i>	
P2(m)	<i>Shahin et al., 2003</i>	
	<i>Shahin et al., 2005</i>	<i>Baumann et al., 2008</i>
	<i>Kuriki et al., 2006</i>	
P3		<i>Wayman et al., 1992</i>

N = negative waveform deflection; P = positive waveform deflection; numbers represent the approximate number of ms after stimulus onset that the deflection occurs (with 1, 2, and 3 depicting 100, 200, and 300 ms, respectively); m = magnetic counterpart of the auditory evoked potential; c = denotes a component that has similar latency to N1 but with a different source.

Table 7.2. Findings of studies investigating differences between musicians and nonmusicians on components of the auditory evoked potential or auditory evoked field in response to the presentation of complex sound stimuli, including intervals, melodies, chords, noise, rhythms, and speech

	Differences	No differences
P1(m)		<i>Kuriki et al., 2006 (chords)</i>
N1(m)	<i>Regnault et al., 2001 (consonant chords)</i> <i>Kuriki et al., 2006 (chords)</i>	<i>Schön et al., 2005 (consonant vs dissonant intervals)</i>
N1-P2 complex	<i>Schön et al., 2005 (consonant vs dissonant intervals)</i>	
P2(m)	<i>Müller et al., 2009 (harmonic incongruity)</i> <i>Regnault et al., 2001 (dissonant chords)</i> <i>Kuriki et al., 2006 (chords)</i>	
N2	<i>Schön et al., 2005 (consonant intervals - larger in nonmusicians)</i>	
P300	<i>Nager et al., 2003 (attended noise)</i> <i>Hantz et al., 1992 (pitch interval or contour deviants)</i> <i>Crummer et al., 1994 (timbre)</i>	<i>Poulin-Charronnat et al., 2006 (timbre)</i> <i>Jongsma et al., 2004 (rhythmic expectancy)</i> <i>Koelsch et al., 2002 (harmonic incongruity)</i>
P3a	<i>Trainor et al., 1999 (pitch interval)</i>	<i>Trainor et al., 1999 (pitch contour)</i>
P3b	<i>Trainor et al., 1999 (pitch interval)</i>	<i>Trainor et al., 1999 (pitch contour)</i>
ERAN	<i>James et al., 2008 (harmonic incongruity)</i> <i>Müller et al., 2009 (harmonic incongruity)</i> <i>Koelsch et al., 2002 (harmonic incongruity)</i> <i>Koelsch et al., 2007 (harmonic incongruity)</i>	
ND	<i>Müntz et al., 2001 (spatial attention to noise)</i> <i>Müntz et al., 2003 (attended pitch stream)</i>	
N5	<i>Poulin-Charronnat et al., 2006 (harmonic incongruity)</i>	<i>Koelsch et al., 2002 (harmonic incongruity)</i>
LPC	<i>Besson et al., 1995 (melodic and harmonic incongruity)</i> <i>Schön et al., 2004 (pitch incongruities in music and language)</i>	<i>Besson et al., 1995 (rhythmic incongruity)</i>

P = positive waveform deflection; N = negative waveform deflection; numbers represent the approximate number of ms after stimulus onset that the deflection occurs (with 1, 2, 3, and 5 depicting 100, 200, 300, and 500 ms, respectively); m = magnetic counterpart of the auditory evoked potential; letters (such as *a* and *b*) denote waveforms with similar latencies but different sources; ERAN = early right anterior negativity; ND = negative deflection; LPC = late positive component.

Cortical Auditory Evoked Responses

Both middle- and late-latency cortical AEPs and AEFs have shown musician—nonmusician differences in amplitude, latency, and/or source location to a wide variety of auditory stimuli, but inconsistencies in the findings preclude firm conclusions from being drawn. For example, an early study by Pantev et al. (1998) found that musicians showed increased representation of piano tones in the N1m evoked response of the auditory cortex compared to their representation of pure tones, with no such difference in nonmusicians. Later research, however, has suggested that spectrally complex tones have larger representations than pure tones in nonmusicians as well (for example, Lütkenhöner, Seither-Preisler, & Seither, 2006). As illustrated in Table 7.1, some of the more well-studied components evoked by either spectrally complex or pure tones, such as the P50, N1, and P2, have shown differences between musicians and nonmusicians in some studies but not others. Similarly, Table 7.2 lists studies that have found differences or no differences in evoked auditory responses to complex sound stimuli, such as intervals, melodies, chords, noise, rhythms, and speech. Although disparities are again evident, several more consistent findings emerge. For example, the early right anterior negative (ERAN) component shows differences between musicians and nonmusicians when processing harmonic incongruities, pointing to superior music syntactic processing in musicians.

It should be noted that the actual number of studies reporting no differences in Tables 7.1 and 7.2 for particular evoked components is likely underestimated, as negative findings often go unreported. With this in mind, a more systematic investigation of the basis of the discrepancies is required. One possibility is that studies have underestimated the effects that even slight changes in stimuli or their presentation could have on the intensity and timing of evoked components. This is particularly true for the early components that have been assumed to directly encode basic sound features. Conceivably, recognition mechanisms initiated early in processing may alter subsequent encoding of stimulus features, leading to variation in the AEP and AEF components (McLachlan & Wilson, 2010). Related to this, the extent and specific type of an individual's music training is likely to play a role, with varying familiarity with stimulus features impacting recognition and the efficiency of encoding. This idea is supported by the well-known study by Pantev and colleagues (2001). They demonstrated that the N1m response to different timbres was instrument specific, with violinists showing stronger N1m responses to violin tones and trumpeters showing stronger N1m responses to trumpet tones. Finally, as in the structural studies discussed above, a number of variables moderating the relationship between musicianship and auditory processing may be relevant. Some components of auditory evoked potentials, such as the N1 and MMN, have been shown to exhibit age- and sex- related differences (Koelsch, Maess, Grossmann, & Friederici, 2003; Martin, et al., 2007), while other studies have reported differences between musicians with and without AP (Crummer, et al., 1994; Hantz, et al., 1992; Wayman, et al., 1992).

Other Studies of Cortical Auditory Processing

Although the cortical auditory evoked response studies described above lack consistency, other studies of cortical auditory processing provide support for the idea of functional differences in musicians. Using EEG, Shahin and colleagues (2008) found musician—

nonmusicians differences and timbre specificity in induced oscillatory gamma band activity. This is consistent with the findings of Pantev et al. (2001) and provides further support for improved timbral processing in musicians. Likewise, in a fMRI study using the same harmonic incongruity detection task as in AEP studies described above, both adult and child musicians showed greater activation of the inferior frontolateral cortex (pars opercularis) and the right anterior superior temporal gyrus compared to nonmusicians (Koelsch, Fritz, Schulze, Alsop, & Schlaug, 2005). Auditory temporal processing also appears to be enhanced in musicians, with improved behavioural performance (Rammsayer & Altenmüller, 2006) and differences in fMRI activation in the anterior hippocampus during temporal deviance detection (Herdener et al., 2010). Gaab et al. (2005) found that musicians used a more efficient functional network than nonmusicians for rapid spectrotemporal processing, and this was accompanied by superior performance on a spectrotemporal sequencing task. Given the above studies, the balance of evidence suggests that musicians have functional enhancements of auditory processing.

Differences in Music Processing

Prior to the modern era of neuroimaging, a number of intriguing behavioural studies suggested that musicians processed music differently than nonmusicians. Among these, a classic paper by Bever and Chiarello (1974) showed that musicians had a right-ear superiority and nonmusicians a left-ear superiority for melody recognition in a monaural listening task. This was interpreted as evidence that music expertise leads to left hemisphere dominance for music processing and was attributed to a more analytic processing style in musicians. This finding has not been consistently replicated in dichotic listening tasks (Zatorre, 1979) or dual-task paradigms (Lim, Lambert, & Hamm, 2001). Nevertheless, the idea that musicians tend to use the left hemisphere more than nonmusicians for some aspects of music processing remains a dominant hypothesis. Neuroimaging studies have suggested that music processing is a bilateral task for both musicians and nonmusicians, but there may be increased left lateralisation in musicians for tasks such as listening to tone sequences (Mazziotta, Phelps, Carson, & Kuhl, 1982), passive music listening (Ohnishi, et al., 2001), rhythm perception (Limb, Kemeny, Ortigoza, Rouhani, & Braun, 2006; Vuust et al., 2005), and imagined singing (Wilson, Abbott, Lusher, Gentle, & Jackson, in press). Lateralisation in music processing may also be influenced by sex differences. For example, syntactic irregularities in chord progressions elicited an early negative ERP component that was right lateralized in males, but bilateral in females (Koelsch, et al., 2003).

Musicians also show differences in the extent of neural activation and in the regions involved for musical tasks such as singing, playing instruments, and improvisation. For example, recent papers suggest that singing experience may lead to the use of partially different functional networks when singing that are more specialized for task performance (Kleber, Veit, Birbaumer, Gruzelier, & Lotze, 2010; Wilson, et al., in press; Zarate & Zatorre, 2008). In order to compare neural activation associated with instrumental playing in musicians and nonmusicians, Meister and colleagues (2005) taught participants to play simple and complex sequences on a keyboard. Although musicians and nonmusicians did not vary in behavioural performance, musicians had significantly less activation of the dorsal premotor and supplementary motor areas than did nonmusicians. In another study, violinists with

different amounts of training and practice were evaluated with electromyography and fMRI while fingering a Mozart concerto with the left hand (Lotze, Scheler, Tan, Braun, & Birbaumer, 2003). The amateurs had more diffuse bilateral activation compared to the professional violinists, who showed less overall activation, but larger motor responses and more prominent primary auditory, contralateral primary motor, and ipsilateral cerebellar activation. Increases in regional activation in musicians are assumed to reflect greater recruitment for salient processing, while decreases in activation (which typically occur in secondary regions) are thought to reflect more efficient processing. In the case of improvisation, musicians appear to inhibit part of the brain, with a recent study showing that they deactivated the right temporoparietal junction. In contrast, nonmusicians showed no change in this region, despite behaviourally equivalent performance (Berkowitz & Ansari, 2010). This deactivation was interpreted to reflect differences in top-down versus bottom-up driven attentional processing.

Differences in Sensorimotor Function

In addition to the motor differences described above that have been detected during active music tasks, a number of other musician—nonmusician differences in sensorimotor representations and abilities have been described in the literature. An early study by Elbert and colleagues (1995) found that somatosensory stimulation of the thumb and little finger showed stronger responses and enlarged cortical representations of the left hand fingers in violinists than in nonmusicians. More recently, an EEG and TMS study demonstrated enlarged left hand representations in both the motor and sensory cortices of violinists (Schwenkreis et al., 2007). Despite these functional differences, however, there were no significant differences in motor skills between musicians and nonmusicians. In contrast, other studies have reported a difference for complex tapping performance, which was superior in musicians (Jäncke, Schlaug, & Steinmetz, 1997), and associated primary and secondary motor activation, which was more focal (Jäncke, Shah, & Peters, 2000; Krings et al., 2000). While nonmusicians showed increasing activation in secondary motor areas with increased task complexity, activation in musicians remained constant in both simple and complex tasks (Meister, et al., 2005). Reduced activation has also been reported in the cerebellum of musicians during complex bimanual movements (Koeneke, Lutz, Wüstenberg, & Jäncke, 2004). These studies suggest that musicians have more efficient representations and use fewer neural resources to support their often superior performance of motor tasks.

In line with the structural differences discussed previously, motor information transfer along white matter tracts also appears to be more efficient in musicians. Under normal circumstances, stimulation applied to the motor cortex of one hemisphere is known to facilitate or inhibit, through the corpus callosum, the motor potential evoked when stimulation is applied to the other hemisphere. Using TMS, Ridding, Brouwer, and Nordstrom (2000) showed that musicians have reduced transcallosal inhibition. These authors hypothesized that reduced inhibition may be related to increased corpus callosum area in musicians and to musicians' enhanced bimanual motor coordination. Another TMS study found that speech modulation of corticospinal excitability is less lateralized in musicians and indicates that music training may lead to differences in the lateralisation of language and motor functions (Lin, Kobayashi, & Pascual-Leone, 2002). Also in line with the literature on structural

differences, age at commencement of music training plays a role in the sensorimotor function of musicians. Although not consistently reported, a number of studies have found significant correlations between age at start of training and sensorimotor abilities or neural representations (Elbert, et al., 1995; Jäncke, et al., 1997). When years of music training, amount of music experience, and current practice hours are controlled, early-trained musicians still outperform late-trained musicians on a variety of motor tasks (Watanabe, Savion-Lemieux, & Penhune, 2007). These differences are particularly evident in motor tasks that require synchronisation, and therefore integration across motor and multiple sensory modalities (cross-modal integration), which we turn to next.

Differences in Cross-modal Integration

Given the degree to which the motor and sensory systems are involved in coordinated activity in music production, it is perhaps unsurprising that musicians demonstrate superior cross-modal integration. Musicians' sensory and motor systems appear to be more strongly linked for a range of sensorimotor functions than those of nonmusicians. For example, musicians experience involuntary motor activity when listening to rehearsed music. In a MEG study investigating pianists and singers, Haueisen and Knösche (2001) showed that pianists activated areas of the primary motor cortex while listening to well-learned music, and these activations showed a spatial dissociation within the motor area for notes that would be played with thumb versus little finger. When listening to music and asked to imagine the finger movements, musicians showed increased activity of the dorsal premotor area and the supplementary motor area (Baumann et al., 2007), although it should be noted that the task demands might have been slightly different between the two groups, with an implicit practiced motor sequence in musicians but an explicit random choice of bimanual keypresses in nonmusicians. Under the opposite condition of observing silent piano playing, musicians had stronger activation within a fronto-temporo-parietal network, particularly involving auditory cortices, than nonmusicians (Haslinger et al., 2005). Such links between motor and auditory areas in musicians have been observed even in pre-attentive reflexes evoked through a classical conditioning paradigm (Bangert, Jürgens, Häusler, & Altenmüller, 2006). In another silent observation study using a "key-touch reading" task which required transformation from the visual to auditory modality, musicians had greater activation across motor and association regions, as well as activation of the left planum temporale which was not seen in nonmusicians (Hasegawa et al., 2004). The planum temporale may process learned audio-visual associations, which would explain why it was only activated in trained musicians. Musicians also demonstrated a more distributed activation pattern during an auditory only task (listening to short piano sequences) and a motor only task (making key presses), with a specific network activated during both tasks only in musicians (Bangert et al., 2006). This network for audio-motor integration included dorsolateral and inferior frontal cortex, supplementary motor and premotor areas, and the superior temporal and supramarginal gyri.

With different sensorimotor requirements, musicians who play different instruments could experience quite specific types of cross-modal integration. For example, trumpet players showed enhanced auditory responses to trumpet tones and enhanced early multimodal responses to both trumpet tones and somatosensory stimulation of the lower lip compared to nonmusicians (Schulz, et al., 2003). Drummers, whose training places emphasis on precise

timing, showed both behavioural and functional differences from nonmusicians. This included more precise audio-motor synchronisation and stronger interactions at alpha and beta frequencies between premotor cortex and thalamus and between posterior parietal cortex and thalamus (Krause, Schnitzler, & Pollok, 2010). A final example comes from a study of conductors, who showed greater benefit from multimodal stimuli than nonmusicians for accuracy of temporal order judgments and target localisation (Hodges, Hairston, & Burdette, 2005). This was related to greater activation of the occipitotemporal cortex (Brodmann's area 37) in two conductors who underwent fMRI scanning, which is an area known to be involved in audio-visual integration.

Other Functional Differences

Many of the anatomical and functional differences shown in musicians are in regions that are used in music processing, but are not specific to music. For this reason, "transfer effects" to abilities outside the music domain could be expected. Corroborating this idea, differences in brain function have often been correlated with superior abilities in musicians for non-musical tasks. For example, musicians showed increased activation in Broca's area (left posterior inferior frontal gyrus) associated with superior mental manipulation of three-dimensional objects (Sluming, Brooks, Howard, Downes, & Roberts, 2007). Musicians also demonstrated superior visual attention, with more accurate performance for stimuli in the right side of space and faster reaction times overall (Patston, Hogg, & Tippett, 2007). Their visual attention was more bilateral, with equal interhemispheric transfer times, while nonmusicians had a clear asymmetry in transfer time, with slower attention to the right side of space (Patston, Kirk, Rolfe, Corballis, & Tippett, 2007). Musicians outperformed nonmusicians on tests of verbal memory (Brandler & Rammsayer, 2003; Chan, Ho, & Cheung, 1998; Ho, Cheung, & Chan, 2003) and tonal working memory (Schulze, Zysset, Mueller, Friederici, & Koelsch, 2010), and also used slightly different functional networks for verbal and tonal working memory tasks (Schulze, et al., 2010). When solving simple mathematics problems, musicians showed greater activation of the prefrontal cortex and fusiform gyrus than nonmusicians, but reduced activation of visual association areas and the inferior parietal lobule (Schmithorst & Holland, 2004). These authors speculated that musicians have better working memory and a greater ability to abstract numbers. Other abilities that appear to be enhanced in musicians include two point discrimination of the index finger (Ragert, Schmidt, Altenmüller, & Dinse, 2004), spatial abilities (Hetland, 2000), gesture imitation (Spilka, Steele, & Penhune, 2010), and aspects of executive functioning (Bialystok & DePape, 2009).

These studies and others reviewed in this chapter provide evidence that the differences found in the brains of musicians have cognitive and behavioural correlates across a range of domains. Having a musician's brain is likely to be an advantage for many aspects of mental processing (see also chapters by Toukhsati & Rickard, and Chin & Rickard, in this volume for other discussions of music effects on cognition). Although it is not possible to cover the entire literature on musician—nonmusician differences, particularly behavioural differences, in this review we can begin to appreciate just how widespread the musicianship effects are that have been discovered to date. Despite some unresolved controversies, there is reasonable consistency between established structural, functional, and behavioural differences found in

musicians. In addition to the specific differences that have been presented here, researchers have discovered that musicians have increased capacity for learning and neuroplasticity compared to nonmusicians (Ragert, et al., 2004; Rosenkranz, Williamon, & Rothwell, 2007; Tervaniemi, et al., 2001). It appears that musicianship is associated not only with structural and functional changes, but also with priming the brain for future change.

Effects of Music Training in Novices

The studies reviewed above that demonstrate differences in brain structure and function in musicians present a compelling case for the capacity of music to induce neuroplasticity. Although these studies are correlational and cannot establish music training as the cause of the differences, in many cases the degree of structural and functional changes is related to the age at which the musicians began their training, providing reasonable evidence that music training may be responsible for the changes. Another convincing argument is that some of the differences that have been found are specific to the instrument of training. However, these cross-sectional and correlational designs cannot rule out other possible causative explanations. It has been argued that the differences could be pre-existing and genetic and that these innate differences would lead certain people, and not others, to becoming musicians. Ideally, longitudinal studies that examine brain structure and function, as well as behaviour, both before and after music training would provide the necessary evidence that music training causes changes in the brain. While longitudinal designs are not as time- and cost-efficient as the more frequently used cross-sectional designs, these studies offer greater experimental control and the ability to test hypotheses about causality. The few longitudinal music training studies that have been conducted to date and which are reviewed below have proven very informative. Based on this work, it is now thought that music training causally affects brain structure and function across the lifespan. Thus, longitudinal paradigms are likely to gain increasing use in future research in the field.

Music training studies have benefited from the opportunity to build on the findings of related, but not strictly musical, training studies in motor, sensory, and auditory domains. Using animal models, training in each of these domains has been shown to change neural response properties or representations within relevant brain regions (Buonomano & Merzenich, 1998). Studies in human participants have demonstrated similar findings using non-invasive imaging techniques. The training paradigms are usually quite simple and commonly include tasks such as repetitive finger tapping or learning to distinguish between sounds with slight variations in pitch or timbre. While these tasks are components of music perception and production, they do not replicate the complexity of music training, which simultaneously engages many different functional domains. Researchers are now investigating how training in a complex, multimodal task like music performance impacts on brain function. To begin with, a few early studies on simple training will be highlighted, followed by a review of studies using more naturalistic and complete music training paradigms.

Motor and Auditory Training

Repeated brain imaging before, during, and after training in various motor tasks has demonstrated training-related changes in activation in motor regions, including the primary motor cortex, premotor cortex, supplementary motor area, and the cerebellum (for example, Friston, Frith, Passingham, Liddle, & Frackowiak, 1992; Grafton et al., 1992; Hund-Georgiadis & von Cramon, 1999; Karni et al., 1995, 1998; Schlaug, Knorr, & Seitz, 1994). One study of note used a musically relevant paradigm, namely a five-finger exercise on the keyboard. With TMS mapping, the researchers showed that the cortical representation of the fingers changed in response to five daily practice sessions of two hours each (Pascual-Leone et al., 1995). In particular, the cortical motor areas of the flexor and extensor muscles of the fingers enlarged and their activation thresholds decreased. Interestingly, even mental practice alone led to plastic changes in motor representations. In a follow-up study, half of the participants from the first experiment stopped practicing and the others continued to practice for four more weeks. The participants who stopped practicing had motor maps that returned to baseline, while those that continued practicing showed ongoing reorganisation of maps and improved behavioural performance on the task (Pascual-Leone, 2001). These studies indicate that the ongoing motor learning and practice that is part of all active music training can lead to neuroplastic changes in the motor system.

Training in auditory discrimination tasks has also been investigated longitudinally. Over one week of training, participants who showed improvements in discrimination performance also showed decreased fMRI activation in the auditory cortex during an auditory oddball task (Jäncke, Gaab, Wüstenberg, Scheich, & Heinze, 2001). In addition, discrimination training appears to alter various components of the auditory evoked response, including N1, P2, and the MMN, but as in the studies comparing evoked responses in musicians and nonmusicians, some results are contradictory. For example, Cansino and Williamson (1997) reported a decrease in the N1m response with extensive training of one individual, whereas following shorter training of a group, Menning, Roberts, and Pantev (2000) found an increase in N1m and MMNm responses. In both studies, training was associated with improved discrimination performance suggesting that the difference in the evoked response may be attributed to the length of training. However, this does not fully account for the musician—nonmusician differences described above, where extensive training is typically associated with increased response amplitudes. Other studies have failed to find any difference in N1 with short-term discrimination training, although they did find amplitude increases in other components of the AEP (Atienza, Cantero, & Dominguez-Marin, 2002; Bosnyak, Eaton, & Roberts, 2004). Short-term training has been shown to lead to behavioural improvements in pitch discrimination that approximate expert performance (Micheyl, Delhommeau, Perrot, & Oxenham, 2006), with such changes linked to short-term neural plasticity (Atienza, et al., 2002). Longer-term neural changes associated with auditory discrimination training have received less attention in humans and thus require further investigation.

Other forms of auditory training have also been shown to alter brain function. For example, participants were exposed to melodies in which the fundamental frequencies of the tones were removed and the harmonics manipulated so that the resulting melody had the inverse contour of the original melody (Schulte, Knief, Seither-Preisler, & Pantev, 2002). After repeated exposure, the perceived melody switched to that of the missing fundamentals, and was accompanied by decreased latency of the N1m response, increased strength and more

medial source location of the cortical gamma-band response, and greater synchronisation in the gamma-band frequency range. Another listening study used ‘notched’ music, in which a frequency band centred around 1000 kHz was filtered out, to investigate short-term changes in cortical frequency representation (Pantev, Wollbrink, Roberts, Engelien, & Lütkenhöner, 1999). On three consecutive days, listeners were tested before and after three hours of exposure to notched music. The cortical representation for the filtered frequencies diminished after music listening, but then returned to baseline by the following day. As a final example, one week of training in a pitch working memory task led to fMRI activation changes, particularly in left Heschl’s gyrus (Gaab, Gaser, & Schlaug, 2006). In individuals who improved their pitch working memory ability, the left supramarginal gyrus also showed significantly greater activation than individuals who did not improve despite training. It is evident, then, that even very short-term training or short-term manipulations to the auditory environment can lead to rapid functional reorganisation of the auditory system.

Music Training

Even more compelling than these motor and auditory training paradigms are those studies in which nonmusicians have been trained to play music and have demonstrated changes in brain function. One of the first studies of this type was conducted by Bangert and Altenmüller (2003), who trained nonmusicians to play melodies presented aurally with the right hand. They showed that audio-motor integration occurred after just 20 minutes of adaptive training and led to increases in DC-EEG activity in left central and right anterior regions for both motor and auditory probe tasks. Lahav, Saltzman, and Schlaug (2007) showed that when music novices learned to play a new piano piece by ear over five days, they demonstrated changes in fMRI activation patterns when listening to that piece compared to listening to other untrained pieces. Listening to the trained piece was associated with activation of a bilateral fronto-parietal network involved in motor tasks, again revealing rapid training-induced cross-modal integration. This was also demonstrated indirectly in a study investigating MMNm responses to deviants in tone sequences. Lappe and colleagues (2008) had a group of nonmusicians practice a broken chord sequence on the piano for 25 minutes per day for eight days over two weeks, while another group of nonmusicians listened to the broken chord sequence played by the other group and made judgements about its accuracy. Participants who practiced the chord sequence (combined motor and auditory training) showed greater enhancement of the MMN response to deviants in the sequence than those who had only listened (auditory training). These music training studies are in agreement with the musician—nonmusician literature, in which superior integration of sensory and motor function has been established in musicians.

The final studies to be reviewed in this chapter are those in which structural or functional measurements have been taken before and after standard music training, in the form of regular lessons. A number of experiments in both children and adults have utilized this design. Shahin, Roberts, and Trainor (2004) measured AEPs in young children prior to and after one year of Suzuki music lessons. They did not find a significant difference between the two time points; however, the musically-trained children showed different AEP responses from the untrained children even prior to beginning music lessons. This may be related to a difference in the early auditory environment of the children in music lessons, whose parents

were often musicians or had exposed their children to the instrument on which they were going to take lessons. Other studies from this lab have demonstrated training-related changes in the auditory response, including a decrease in amplitude of the N250m component for violin tones in children who received one year of violin Suzuki training (Fujioka, Ross, Kakigi, Pantev, & Trainor, 2006), and increased power of induced gamma band activity for piano tones after one year of piano training (Shahin, et al., 2008). Moreno and colleagues have reported two training experiments in children, the first with a time course of eight weeks and the second over six months. In both studies, they investigated the influence of music training on pitch processing in language compared to controls (a group that received painting lessons). Even over the shorter time period, the trained children showed a decrease in amplitude of the late positive component of the auditory response to large pitch incongruities in language (Moreno & Besson, 2006). In the six month study, trained children showed changes in the AEPs for small pitch incongruities in musical and linguistic phrases. They also improved behaviourally in the detection of pitch shifts and in reading words with inconsistent grapheme to phoneme correspondence (Moreno et al., 2009). In these studies, there is growing support for the idea that music training improves brain functions related to both auditory and language development in children and that it may have significant implications for brain development (Hannon & Trainor, 2007).

A longitudinal study in children has provided the first direct evidence that music training causes changes in brain structure. Schlaug and colleagues have investigated brain structure and behavioural abilities in young children before and after some of the children started taking music lessons. First, they determined that there were no neural or behavioural differences evident between the group of children who were planning to take piano or string lessons (hereafter referred to as musicians) and those who were not (controls; Norton et al., 2005). After approximately one year of music training, they found significantly greater changes on tests of fine motor skills and auditory discrimination in musicians than in controls (Schlaug, Norton, Overy, & Winner, 2005). Using deformation-based morphometry, they also found significant changes in the brain across time, with increases in relative voxel size in the musicians compared to controls in the right primary motor cortex, the right primary auditory cortex, the corpus callosum, bilateral frontal regions, and the left pericingulate region (Hyde et al., 2009). After more than two years of music training, further testing revealed a significant difference in the size of the anterior corpus callosum in musician children, with the extent of change relating to the amount of weekly practice undertaken (Schlaug et al., 2009). These findings converge with previous studies showing differences between musicians and nonmusicians, and they convincingly demonstrate that music training leads to behavioural improvements in motor and auditory tasks, as well as structural changes in the developing brain.

Only a few studies have investigated music training in healthy adult nonmusicians (see Box 7.3 for a brief discussion of music training in adults with neurological disease). These have demonstrated that adult brains can also change as a result of music training. Stewart et al. (2003) compared fMRI activation before and after 15 weeks of piano lessons, which included training in both keyboard skills and music theory. Learning to read and play music led to increased activation in bilateral superior parietal cortex when performing a sight-reading task. Given the role of this brain region in visuospatial processing, this result was interpreted as evidence that plastic changes in the superior parietal cortex underlie the newly acquired ability to translate written music into motor actions.

Box 7.3. Music-induced plasticity and the treatment of neurological disorders

The use of music in neurological rehabilitation is a growing trend. Since music training leads to changes in brain structure and function and since music is known to interact with cognitive and motor functions in healthy individuals, it may be able to induce neuroplasticity that promotes recovery of cognitive or motor function after brain injury or disease. A number of intriguing studies suggest that this is the case. Both active and passive music engagement have been demonstrated to affect rehabilitation and to lead to neuroplastic changes.

Listening to music enhances cognitive recovery and mood after stroke (Särkämö et al., 2008), and has also been shown to enhance early sensory processing after stroke (Särkämö et al., 2010). The amplitude of the MMNm to changes in sound frequency was greater in patients who listened to music for one hour per day for two months after stroke than in patients who did not listen to music. Although this passive music listening is beneficial, active music making is likely even more effective as a rehabilitation tool, especially in the motor domain. Schneider and colleagues had stroke patients with movement deficits use MIDI-tuned drums and keyboards to practice gross and fine movements of the upper limbs (Schneider, Schonle, Altenmüller, & Munte, 2007). This training led to improvement in movement scores, as well as to changes in event-related oscillatory neural activity compared to controls (Altenmüller, Marco-Pallares, Munte, & Schneider, 2009). A number of mechanisms have been suggested to explain these effects, including music providing auditory feedback about the success of motor movements and music promoting audio-motor coupling.

Singing is a form of active music making that has received the most attention in the rehabilitation literature. It has often been used to treat language impairments that occur as a result of neurological disorders such as Parkinson's disease, autism, and stroke (Wan, Ruber, Hohmann, & Schlaug, 2010). One of the earliest singing-based rehabilitation therapies was Melodic Intonation Therapy (MIT). MIT was introduced by Albert, Sparks, and Helm in 1973 for the treatment of stroke-induced non-fluent aphasia, a language impairment in which expression is severely affected. Currently, MIT is thought to stimulate language recovery through the induction of functional neural reorganisation. However, the mechanisms through which this occurs remain uncertain. Some studies have suggested that it leads to greater use of the undamaged hemisphere (Schlaug, Marchina, & Norton, 2008), while other studies suggest reorganisation around the damaged language areas (Belin et al., 1996; Breier, Randle, Maher, & Papanicolaou, 2010). In addition to functional changes, structural plasticity has been identified in individuals treated with MIT. After intense MIT, patients showed an increased number of fibres in the arcuate fasciculus, a white matter tract connecting auditory and motor regions (Schlaug, Marchina, & Norton, 2009).

The findings discussed above are exciting additions to the body of knowledge about music-induced plasticity. Listening to or playing music is usually an enjoyable and engaging experience for neurological patients. With these experiential factors coupled to music's capacity to induce neuroplasticity, music is becoming an important treatment option for neurological disorders that warrants further exploration.

Another study by Kim and colleagues (2004) used fMRI and TMS to look at activation during motor and sensory tasks and at motor maps for the little fingers before and after six months of violin practice. They observed training-related changes in auditory, sensorimotor, and multimodal association regions. One additional study in adults used music students who were just starting university-level music training, and as part of their program, undertook intensive aural training over two semesters (Herdener, et al., 2010). After training, enhanced activation was found in the anterior hippocampus when the students were listening to auditory stimuli that included temporal deviants, likely reflecting the role of the hippocampus in novelty detection. While the number and type of music training studies in adults is still somewhat limited, these studies provide initial evidence that music training and neuroplasticity are causally related and that music training at any age can change the brain.

Conclusions

The field of music neuroscience continues to expand, and more studies investigating the neural correlates of music expertise and the neural implications of music training are published every year. Some general conclusions that can be drawn from research findings to date are summarized in Box 7.4. These indicate that while a strong research foundation has been laid, the field is still in its infancy and promises many future insights, not only into the nature of human music behaviour, but also broader principles of neuroplasticity underpinning the development of cognition across the lifespan.

Box 7.4. Summary of literature review on music training and neuroplasticity

- Structural and functional differences have been found in the brains of musicians and nonmusicians, although variability in the findings requires further exploration.
- There is evidence that the structural and functional differences in the brains of musicians are reflected in improvements in both musical and non-musical abilities.
- A number of longitudinal studies have now confirmed the causal relationship between music training and structural and functional neuroplasticity in novice musicians.
- Neuroplasticity in response to music training has been demonstrated in children, adults, and patients with neurological disorders.

The critical review of current literature undertaken in this chapter has highlighted a number of pertinent issues that warrant further investigation. Notable among these is the need to replicate the findings of structural and functional studies while taking moderating variables into account, such as the age of onset of music training, sex, absolute pitch ability, and the instrument and type of music training. It will also be important to understand the training parameters required to induce neuroplastic changes. Currently it is unclear what intensity or duration of training is necessary to induce and maintain long-term changes in neural structure

and function. The answers to such questions would have obvious implications for music education and therapy. As new neuroimaging techniques emerge and their use becomes more widespread, the goal of understanding the underlying mechanisms by which neuroplastic changes occur and the relationship between structural and functional neuroplasticity becomes more achievable. To further our understanding of these mechanisms and their interrelationships, future studies should endeavour to investigate brain structure, brain function, and behaviour simultaneously whenever possible. A final suggestion for future research is to consider the impact of individual differences. A number of studies reviewed in this chapter have shown that group-level analysis may obscure important differences in learning and plasticity (Atienza, et al., 2002; Gaab, et al., 2006; Jäncke, et al., 2001; Schlaug, et al., 1994). Although this review demonstrates that music-induced neuroplasticity is likely to occur across any age or population, we cannot discount personal experience and the unique constellation of moderating variables that individuals bring to their music experience. For this reason, the effects of music on brain structure, function, and behaviour will always be, to some degree, unique for each person.

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