Musical brains:

The influence of musical expertise and gender on brain structure and lateralisation

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Abstract

A growing literature has identified compelling links between musical expertise and structural and functional alterations in the brain. These are thought to reflect *experience-dependent neuroplasticity,* arising from the many years engaged in intensive, multi-modal training on a musical instrument, typically from a young age. Related research has identified enhancements of cognitive processes *beyond* the specific skills trained in music. There is evidence that musicians have enhanced visuospatial abilities, although whether musical training and expertise shapes or influences the neural organisation underlying these general cognitive processes is unknown. The main aims of this thesis were to investigate whether (i) musicians have reduced functional lateralisation of visuospatial processes; (ii) whether altered structural lateralisation, or altered white matter organisation in general, underpins functional and behavioural differences in visuospatial processes in musicians. The effects of gender were also examined, given its known influence on behavioural performance and neural representation of spatial processes.

Thirty-three expert musicians and 30 non-musicians underwent functional magnetic resonance imaging (fMRI) while performing three visuospatial tasks: a Landmark task (a variant of a line bisection), 3D Mental Rotation (3DMR), and a Visual Search task. On the Landmark task, gender modulated the relationship between musical expertise and lateralisation: male controls had more strongly right-lateralised activation than female controls, but both male and female musicians were strongly right-lateralised and did not differ from each other. In *Study Two*, the connectivity of the corpus callosum, superior longitudinal fasciculus (SLF), and corticospinal tract was assessed using diffusion tensor imaging (DTI). Gender once again had a moderating effect in the corpus callosum and the

SLF, with differences in white matter connectivity between male and female controls which were not present in musicians. Additional differences between musicians predominantly engaged in instrumental versus vocal training were observed for structural lateralisation of the SLF. Overall these results suggest the neural organisation underlying visuospatial attention, a non-musical cognitive process, was influenced by musical training and expertise, predominantly with a rightward shift in lateralisation in female musicians. The findings underscore the importance of considering moderating variables such as gender and instrument of training when studying the neural correlates of musical expertise.

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Chapter 1: General Introduction

Since the advent of neuroimaging techniques in the early 1990s, a growing literature has identified compelling links between musical training and structural and functional alterations in the brain. Many researchers in the field argue that these brain changes arise directly from learning to play a musical instrument. In other words, they are argued to reflect *experience-dependent neuroplasticity* (e.g. Merrett, Peretz, & Wilson, 2013; Münte, Altenmüller, & Jäncke, 2002).

Music training is thought to have the potential to induce brain plasticity for a number of reasons. Firstly, expert musicians typically begin taking lessons at a very young age when the brain is undergoing rapid development. Secondly, musicians continue training for many years, spending extraordinary amounts of time practicing their instrument and performing. It has been shown that professional pianists and violinists have spent on average 7,500 hours practicing before the age of 18 (Ericsson et al., 1993). Thirdly, music training requires not just the development of fine motor skills, but also cross-modal integration across multiple sensory systems. To successfully play a piece of music, a musician must execute a series of perfectly timed motor movements by rapidly translating visual musical notation into the corresponding motor sequence. At the same time, they must monitor and adjust their auditory output. Music training also recruits higher-order cognitive functions such as memory and executive functions. Playing in an ensemble places additional demands on the musician to coordinate with other players, which may recruit the executive control system. Professional musicians typically also develop the ability to memorise lengthy musical pieces.

This intensive and multimodal music training undertaken by proficient musicians has resulted in considerable research efforts devoted to identifying likely cognitive and neural markers of neuroplasticity in musicians. Most research has focused upon the neural representation of music abilities, including structural and functional brain differences in proficient musicians, altered cerebral lateralisation of music processing and factors that may moderate the relationship between music training and plasticity.

Related research has focused upon whether extensive musical training and musical expertise is associated with enhancements of cognitive processes beyond the specific skills trained in music, for example language or visuospatial ability. To date, however, there is relatively little research investigating whether musical training and expertise is associated with the neural organisation underlying these more general cognitive processes. For example, no research has investigated directly whether lateralisation of *non-musical* processes also differs in expert musicians. There is also limited research investigating hemispheric differences in white matter tracts which may underlie different patterns of functional lateralisation in musicians.

Thus, the primary aim of this thesis is to further investigate lateralisation in musicians by focussing upon functional lateralisation of a *non-musical* cognitive domain, namely visuospatial cognition, and structural lateralisation of the brain that may underlie these variations in function. In the first study, we used functional magnetic resonance imaging (fMRI) to examine whether lateralisation of visuospatial processing differed between musicians and non-musicians while performing three visuospatial tasks. In the second study we used diffusion tensor imaging (DTI) to assess whether musicians have altered microstructural organisation of white matter structures relative to non-musicians that could be related to modified lateralisation of visual processes.

Brain structure and function in musicians

A wealth of research devoted to identifying music-related differences in brain structure and function, suggests that music can induce experience-dependent plasticity in the brain. The brains of musicians and non-musicians differ in morphology, volume, density, structural connectivity, and functional activity across a range of brain regions (e.g. Amunts et al., 1997; Bangert et al., 2006; Bengtsson et al., 2005; Bermudez, Lerch, Evans, & Zatorre, 2009; Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Gaser & Schlaug, 2003; Han et al., 2009; Hyde et al., 2009; Sluming et al., 2007). In addition to cross-sectional work, longitudinal work provides especially compelling evidence that music training can induce plastic changes in the brain (e.g. Hyde et al., 2009; Lappe, Herholz, Trainor, & Pantev, 2008; Lappe, Trainor, Herholz, & Pantev, 2011; Pascual-Leone et al., 1995).

Most research in this area has sought out differences in brain regions associated with motor and auditory processes that are directly trained by music, with the particular aim of determining whether music training can induce neuroplasticity. Indeed, several studies have identified changes in morphology and function of the primary motor and auditory cortices. As this research strand has been discussed in reviews elsewhere (e.g. Herholz & Zatorre, 2012; Zimmerman & Lahav, 2012), the following review will focus upon the smaller literature identifying neural differences in musicians in regions linked to other aspects of music performance.

Musical notation conveys pitch information spatially, so musicians must learn to translate this spatial information into the associated motor sequence. One region which may mediate this sensorimotor translation is the superior parietal cortex (Dong et al., 2000; Poldrack & Gabrieli, 2001), a region involved in numerous visuospatial processes (Corbetta & Shulman, 2002; Fan, McCandliss, Fossella, Flombaum, & Posner, 2005; Halari et al., 2006). Gaser and Schlaug (2003) found that this region, along with the inferior temporal gyrus, had increased grey matter density in musicians. They hypothesised that this structural difference could reflect the demands placed on the visuospatial system by sight-reading. Gartner and colleagues (2013) also found that professional keyboard players had increased volume of the left superior parietal lobule, compared both to non-musicians and to a less intensively practicing group of musicians. This was again interpreted as reflecting the greater sight-reading demands involved in more intensive music training.

Several studies of music reading have also found activation in the superior parietal lobule in musicians (Schön et al., 2002; Sergent et al., 1992; Zatorre, Halpern, & Bouffard, 2010). Professional musicians also activate the nearby intraparietal sulcus in musical tasks such as mentally transposing a melody from one key to another (Foster & Zatorre, 2010) or melody reversal (Foster, Halpern, & Zatorre, 2013). Similarly, Stewart and colleagues (2003) conducted a training study where adult non-musicians were taught to play the piano and read music over 15 weeks. The participants received fMRI scans before and after training in which they made key presses in response to musical notation. Increased post-training activation was observed bilaterally in the superior parietal lobule.

Using both manual segmentation and voxel-based morphometry (VBM), Sluming and colleagues showed that, relative to age-matched non-musicians, professional orchestral musicians had increased grey matter density in Broca's area (left inferior frontal gyrus), which was associated with the length of musical training (Abdul-Kareem, Stancak, Parkes, & Sluming, 2011; Sluming et al., 2002). This region is typically associated with language production, but has also been shown to be involved in several aspects of music processing including musical score reading and processing of musical syntax (Koelsch et al., 2002; Maess & Koelsch, 2001; Sergent et al., 1992). Sluming et al. (2007) surprisingly found that musicians also activated Broca's area more than non-musicians during a non-musical visuospatial task, mental rotation. Whether or not this activation reflects visuospatial elements of the tasks, or a different cognitive process that might be utilized is unclear at this stage. Interestingly, however, Broca's area is also recruited by musicians when they sight-read music, a process with an important visuospatial component, although again this may reflect other processes involved in the process of sight-reading. An additional study by James et al. (2013) found a correlation between level of musical expertise and grey matter density in regions involved in higher-order cognitive processing, including Broca's area, right mid-orbital gyrus, left intraparietal sulcus, and right fusiform gyrus, while there were negative correlations between expertise and grey matter density in somatomotor and striatal areas. The authors suggested that decreased grey matter density in somatomotor regions could reflect increased automaticity or efficiency of motor performance, while the increased grey matter in frontal and parietal regions could relate to more neural resources being made available for the higher-order cognitive processes involved in music performance.

Finally, several studies found structural differences in individuals with musical expertise in areas linked to language processing. Musicians have increased cortical surface area in the left planum temporale (Elmer, Hänggi, Meyer, & Jäncke, 2013), and musicians possessing absolute pitch (AP) have increased leftward asymmetry of the planum temporale relative to other musicians (Keenan, Thangaraj, Halpern, & Schlaug, 2001; Luders, Gaser, Jäncke, & Schlaug, 2004; Schlaug, Jäncke, Huang, & Steinmetz, 1995). The left planum temporale forms the heart of Wernicke's area, and so is an important region in language and auditory processing. Research also suggests that the planum temporale, along with the rest of the posterior superior temporal gyrus, is involved in pitch processing and auditory-motor interactions in musicians (e.g. Baumann et al., 2007; Ohnishi et al., 2001), and thus it is possible that intensive music training produces plastic changes to this region.

The considerable research discussed so far in this section has demonstrated that musicians have various adaptations in grey matter relative to non-musicians. A much smaller literature also provides evidence that white matter tracts may also differ between musicians and non-musicians. Studies utilising DTI have mostly investigated differences in fractional anisotropy (FA), a measure of the degree of alignment of white matter fibres, or mean diffusivity (MD), which gives an indication of the total amount of diffusion in the tissue. Most of the studies published to date have focused on the corticospinal tract, with mixed results. Some studies found that musicians have higher FA than non-musicians (Bengtsson et al., 2005; Han et al., 2009; Rüber, Lindenberg, & Schlaug, 2013), while others observed *lower* FA in musicians than in non-musicians (Imfeld, Oechslin, Meyer, Loenneker, & Jancke, 2009; Schmithorst & Wilke, 2002).

Several studies have employed volumetric MRI analyses to show that sections of the corpus callosum are enlarged in musicians. The anterior corpus callosum connects the prefrontal and motor cortices (Pandya & Seltzer, 1986), while the posterior corpus callosum connects the posterior parietal, temporal, and occipital areas (Barbas & Pandya, 1984). Some groups found that the anterior corpus callosum was enlarged in musicians (Hyde et al., 2009; D. J. Lee, Chen, & Schlaug, 2003; Schlaug, Jäncke, Huang, Staiger, & Steinmetz, 1995), while other work has found that the posterior corpus callosum is enlarged in musicians (Burunat et al., 2015; Oztürk, Tasçioglu, Aktekin, Kurtoglu, & Erden, 2002). As corpus callosum size has been linked to the number of axons crossing the midline (Aboitiz, Scheibel, Fisher, & Zaidel, 1992), increased corpus callosum size in musicians could reflect increased efficiency of interhemispheric information processing (Jancke & Steinmetz, 1994; Witelson, 1985). In support of this notion, Burunat et al. (2015) calculated the symmetry of activation (as measured by fMRI) during music listening. They found that musicians had increased interhemispheric functional symmetry compared to non-musicians, in addition to increased posterior corpus callosum size in musicians.

Although there is considerable evidence that the volume of the corpus callosum is increased in musicians, only one study to date has utilised DTI to directly address whether microstructural complexity of this structure is also altered. This study found that musicians who began training before the age of seven had greater FA in the posterior corpus callosum than musicians who started their training later (Steele, Bailey, Zatorre, & Penhune, 2013). Greater FA in this region was linked to greater sensorimotor synchronisation performance. One other study found that musicians had significantly higher FA in the anterior section of the corpus callosum (Schmithorst & Wilke, 2002). The sample in this study consisted of just five musicians and six controls, however, hence more research with a larger sample size is needed to replicate this finding.

A small number of studies have examined white matter tracts linked to auditory and language processes, such as the superior longitudinal fasciculus (SLF). These studies have mostly focused on the subgroup of musicians who possess AP, the rare ability to name the pitch of a musical note without reference to a standard note. Recent work shows that AP exists on a continuum; that is, pitch identification performance varies amongst musicians who self-report having this ability (Bermudez & Zatorre, 2009). Relative to musicians who do not possess this ability, research findings suggest that musicians with AP have increased leftward asymmetry of FA within the left SLF (Oechslin, Imfeld, Loenneker, Meyer, & Jäncke, 2010), increased volume of bilateral temporal lobe tracts (Loui, Li, Hohmann, & Schlaug, 2011), and increased FA in the right inferior fronto-occipital fasciculus and uncinate fasciculus (Dohn et al., 2015). Singers and instrumentalists also differ in microstructural properties of the arcuate fasciculus, a component of the SLF linking auditory and motor regions in the frontal and temporal lobes. While AP ability was associated with increased FA in the SLF in the aforementioned studies, singers had *lower* FA, but higher volume of the left arcuate fasciculus than instrumentalists (Halwani, Loui, Rüber, & Schlaug, 2011). Further complicating matters, both singers and instrumentalists had *higher* FA than non-musicians in the left and right arcuate fasciculi.

In summary, the literature examining white matter changes in expert musicians is still in its infancy, with a number of contradictory findings. Further research is needed to clarify the nature of differences in white matter architecture between expert musicians and non-musicians, and whether changes underlie music-specific processes (including whether there are instrument-specific changes), or whether they also underlie changes in the neural organisation of more general cognitive processes.

Moderating variables of plasticity in musicians

Several variables have been identified that influence whether, how, and where neural changes occur in response to music training. These include the age of onset of music training, practice intensity, duration of training, instrument of training, and the possession of AP.

Age of onset of music training

The age when music lessons are begun is a factor which seems to play a key role in determining the extent of music-related plasticity, leading some researchers to hypothesise that there may be a "sensitive period", or a limited period in which music training can contribute long lasting changes in the brain and behaviour (Penhune, 2011). Evidence for this sensitive period as it relates to music training comes from both brain imaging and behavioural studies. A series of behavioural studies in which musicians were matched for duration of music training found that early-trained musicians (who began lessons before the age of seven) outperformed late-trained musicians on melody discrimination and rhythm synchronisation tasks (Bailey & Penhune, 2010, 2012, 2013; Watanabe, Savion-Lemieux, & Penhune, 2007). Bailey, Zatorre, and Penhune (2014) also found group differences between early-trained and late-trained musicians in the morphometry and cortical surface area of right ventral premotor cortex, which correlated with performance on an auditory-motor synchronisation task. Early-trained musicians also had structural differences relative to late-trained musicians in the motor cortex and corpus callosum (Amunts et al., 1997; Schlaug, Jäncke, Huang, Staiger, et al., 1995; Steele et al., 2013). Finally, Bengtsson and colleagues (2005) found that musicians' practice intensity in childhood was correlated the most with FA, relative to their practice intensity later in life.

Absolute pitch (AP)

The development of AP also seems to critically depend on musical training early in life. Research has indicated that most musicians who possess AP began their musical training before the age of nine (Baharloo, Johnston, Service, Gitschier, & Freimer, 1998; Costa-Giomi, Gilmour, Siddell, & Lefebvre, 2001; Miyazaki & Rakowski, 2002). Musicians with AP have more extensive brain differences than musicians without AP. For example, three studies found increased leftward asymmetry of the planum temporale in musicians with AP, relative to other musicians (Keenan et al., 2001; Luders et al., 2004; Schlaug, Jäncke, Huang, & Steinmetz, 1995). Others have also found that musicians with AP have structural alterations in the left primary auditory cortex (Heschl's gyrus) and dorsal frontal cortices (Bermudez et al., 2009; Wengenroth et al., 2014). Using a graph theory approach to analyse cortical thickness covariations (as an indirect indicator of connectivity), Jäncke, Langer, & Hänggi (2012) found that AP musicians had diminished connectivity between distant brain structures, but increased connectivity in peri-sylvian areas including the posterior superior temporal gyrus.

More recently, DTI has been employed to characterise differences in white matter microstructure related to AP ability. Oechslin, Imfeld et al. (2010) found that musicians with AP had a left-greater-than-right lateralisation of FA in the SLF, a white matter tract which connects language regions in the inferior frontal gyrus and posterior superior temporal gyrus. Higher FA in the left SLF was also associated with better performance on a test of AP ability within the AP group. Similarly, Loui, Li, Hohmann, and Schlaug (2011) found that musicians with AP had greater connectivity between the bilateral superior and middle temporal gyri compared to musicians without AP. The volume of this tract in the left hemisphere was also significantly correlated with level of AP ability, such that AP musicians who performed more accurately on a test of AP had higher tract volume. This association suggests that left hemisphere temporal lobe structures are particularly associated with the ability of AP musicians to make absolute pitch categorisations in music. Taken together, these findings indicate that AP is associated with significant grey matter and white matter changes compared to musicians without AP, which suggests that AP may have an additive impact on neuroplastic changes when present.

Instrument

There is evidence that music-related plasticity may relate to the instrument of training. This research helps strengthen the argument that the brain changes in musicians are the direct result of music training, rather than reflecting differences present prior to training. For example, Bangert and Schlaug (2006) showed that a gross anatomical feature (the "omega sign") that is associated with functional hand movement representation was more pronounced in the left motor cortex in keyboard players, while in string players it was larger on the right. This finding likely reflects the specific motor demands of each instrument. That is, finer motor control is required of the left hand in string players, and while keyboard players use both hands more equally, the left hand often has more of an accompaniment function. Using DTI, Rüber et al. (2013) found rightward asymmetry of FA in the descending motor tracts of string players, while there was no hemispheric difference in keyboard players. Buick, Kennedy, and Carson (2016) conducted a focal TMS study to elicit motor evoked potentials (MEPs) in three muscles of the left hand of skilled harpists. Playing the harp involves plucking the string with all fingers of the left hand except for the little finger. Compared to non-musicians, the harpists had larger MEPs in the muscle which moves the index finger, but not in the muscle which moves the little finger. Finally, limited research has suggested that singing may also be associated with neural plasticity in specific regions. A recent fMRI study found that professional opera singers and conservatory-level singers had increased recruitment of primary somatosensory cortices in the area representing the articulators and larynx, compared to non-singers (Kleber, Veit, Birbaumer, Gruzelier, &

Lotze, 2010). Halwani, Loui, Rüber, and Schlaug (2011) also found that singers had structural differences in the left arcuate fasciculus compared to instrumentalists and non-musicians.

In the auditory domain, musicians have increases in neural activation which are specific to the timbre of the instrument played. For example, auditory responses to violin and trumpet tones were enhanced relative to sine tones, with violinists and trumpeters exhibiting selectively increased activation for tones from their own instrument (Pantev, Roberts, Schulz, Engelien, & Ross, 2001). Similarly, an electrophysiological study found that gamma band activity was increased when musicians listened to sounds from their instrument of practice (Shahin et al., 2008). Finally, trumpeters had instrument-specific activation increases in the cerebellum and sensorimotor cortex relative to pianists, during silent playing of the trumpet (Gebel, Braun, Kaza, Altenmüller, & Lotze, 2013).

In summary, a sizeable body of research indicates that expert musicians have structural and functional differences in the brain. There is also mounting evidence that these brain changes are influenced by several factors, such as the age when training is begun, the instrument of training, and AP; this research helps to strengthen the case for music-induced neuroplasticity reflecting music training and expertise.

In a recent review, Robert Zatorre discussed the role that pre-existing differences in behaviour or brain anatomy could play in successful learning and performance of music (Zatorre, 2013). For example, Zatorre, Delhommeau, and Zarate (2012) found that faster learning in a pitch discrimination task was associated with better initial encoding of pitch differences, as indexed by a greater modulation of BOLD activity in the left and right auditory cortex by pitch interval size. Evidence of this sort is consistent with the view that the brain differences associated with musical expertise reflect a combination of both pre-existing neural variability and training-induced neuroplasticity.

Cognition and intellectual ability in musicians

The second main research strand in the expert musician population has examined musicians' cognitive abilities, in an effort to determine whether musical expertise is associated with general cognitive enhancements. There is considerable evidence that musicians do display superior *non-musical* cognitive abilities to non-musicians across a range of domains, including language, visuospatial processing, processing speed, and executive functioning (for a comprehensive review of this literature, the reader is referred to Schellenberg and Weiss, 2013).

There is debate as to whether advantages in the cognitive performance of musicians are general or specific. According to the domain-general account, music training may be associated with heightened general intelligence (e.g. Schellenberg & Peretz, 2008), thereby conferring a generalised advantage across performance on all or most cognitive tasks. In contrast, the domain-specific account holds that musicians have selective enhancements in specific cognitive domains, such as in verbal, spatial, or mathematical ability, reflecting the specific neural systems engaged by music training. To demonstrate a *specific* benefit of music training on a certain cognitive ability, some researchers have argued that it is important to show that people with musical training are not generally superior to non-musicians across all cognitive domains, i.e., that participants are matched for general intelligence (e.g. Schellenberg, 2009). Whilst this appears a straightforward argument (i.e., controlling for the possibility that people who become expert musicians are inherently of high intelligence), it is perhaps more complex than it appears. In general, standard measures of general intelligence (such as the Wechsler intelligence batteries) derive their “Intelligence Quotients” from subtests that assess the cognitive domains of interest in the musician literature, such as verbal ability and visuospatial abilities. Thus controlling for general intelligence may involve controlling for the ability, or variables, of interest.

Different research designs have been used to assess the effects of musical training and expertise on cognition and intellectual ability. In cross-sectional studies, people with and without music training are compared. This type of research is subject to self-selection bias, which makes it difficult to determine whether any differences between the trained and untrained groups are directly caused by music training. The possibility that there are pre-existing differences in cognition or the brain in individuals who choose to pursue music cannot be ruled out. Longitudinal research, on the other hand, assesses people at multiple time points, typically before music lessons are begun and again after a period of time has passed. These types of studies may or may not include random assignment of participants to a lessons or no lessons group. Longitudinal studies, especially when there is random assignment, provide more convincing evidence of the direct influence of music training.

Intelligence quotient (IQ)

Increased IQ in individuals with musical training relative to non-musicians is often reported, but IQ differences are a controversial topic in this literature. Tests of IQ encompass a wide range of cognitive abilities, and IQ is determined by both genetic and environmental factors (e.g. Devlin, Daniels, & Roeder, 1997; Plomin, Pedersen, Lichtenstein, & McClearn, 1994). Thus it is difficult to clarify the exact contribution of music training to IQ, particularly in correlational research. Only a few studies have utilised a longitudinal or experimental design to determine the direction of this relationship. The most convincing study was carried out by Schellenberg (2004), who took a large sample of six-year-old children and randomly assigned them different types of lessons: music lessons, drama lessons, or no lessons. After 36 weeks, the music group demonstrated a modest but significantly greater increase in IQ relative to both the drama and no lessons groups. As Schellenberg points out, it is important to include a control group where students are engaged in an alternative programme outside of school requiring an equivalent time investment. This can control for general factors associated with engaging in extracurricular activities which might otherwise be driving the effect in the music group, such as additional time spent receiving educational instruction from an adult, or increased motivation and concentration (Schellenberg, 2001).

Three other longitudinal studies utilised an experimental or partly experimental design to explore the effect of music training on IQ. A large study by Costa-Giomi (1999), carried out over three years, found at the two year point that children who received piano lessons performed better than the no-lessons group in the total cognitive abilities score on the Developing Cognitive Abilities Test (DCAT). However, after three years of music lessons, this group difference had disappeared. In another three-year longitudinal study of nine-year-old children, the piano group self-reported higher self-esteem after receiving lessons, but no significant group differences in maths or language ability, or in DCAT scores, were observed at any time point (Costa-Giomi, 2004). In contrast, Kaviani, Mirbaha, Pournaseh, and Sagan (2013) showed that preschool children who received music lessons over 12 weeks had significantly greater increases in IQ relative to the control group who received no lessons. However, none of these studies included an alternative training programme, so it remains possible that group differences were related to the other, non-specific effects of engagement in extra-curricular training, as discussed above. An additional issue in studies of children is that they are usually unable to speak to the durability of the effect into adolescence and adulthood. In other words, it is unknown whether the IQ boosts observed in children receiving music lessons represent a long-term effect, or whether they may simply reflect an acceleration of the normal development of IQ, giving musically trained children a temporary “head start”. The finding that differences in cognitive abilities were present after two years, but were no longer apparent after three years (Costa-Giomi, 1999) may support the latter proposition.

Correlational studies provide additional support for the view that music training may influence IQ. Schellenberg (2006) found robust associations between IQ and duration of music lessons in 6- to 11-year old children, even when controlling for family income, parental education and involvement in non-musical activities. In an additional sample of undergraduate university students who had played music in childhood, but had mostly discontinued lessons, he identified a weaker, but still significant relationship between IQ and the number of years that participants had played music regularly. In another study of undergraduates, Schellenberg (2011b) also showed that participants with at least eight years of musical training scored higher on the Kaufman Brief Intelligence Test, even when controlling for a number of potential confounds.

Other studies which have used Raven’s Progressive Matrices as a single measure of IQ did not identify a difference between musicians and non-musicians (Bidelman, Hutka, & Moreno, 2013; Schellenberg & Moreno, 2009). Raven’s Progressive Matrices is often considered to be the best stand-alone measure of general intelligence, or *g* (Carpenter, Just, & Shell, 1990). It is also considered to index fluid intelligence (the capacity to reason and solve novel problems) rather than crystallised intelligence (acquired skills and knowledge; e.g. Gray, Chabris, & Braver, 2003). This raises the possibility that group differences which have been found in other studies using a comprehensive IQ assessment may be driven by crystallised, rather than fluid, intelligence.

Verbal abilities

In addition to research demonstrating enhancements of general intelligence in musicians, there is considerable evidence that children and adults with music training have enhanced performance on a range of linguistic tasks (for a review, see Moreno, 2009). Individuals with music training outperform non-musicians on a wide range of language tasks ranging from detection of low level speech elements to more complex processes like reading and verbal memory (Butzlaff, 2000; Corrigall & Trainor, 2011; Degé & Schwarzer, 2011; Franklin et al., 2008; Gromko, 2005; Jakobson, Lewycky, Kilgour, & Stoesz, 2008; Kilgour, Jakobson, & Cuddy, 2000; Moreno, Bialystok, et al., 2011; Moreno & Besson, 2006; Musacchia, Sams, Skoe, & Kraus, 2007; Parbery-Clark, Tierney, Strait, & Kraus, 2012; Strait, O'Connell, Parbery-Clark, & Kraus, 2013). The mechanism thought to underpin musicians' superior language abilities is the overlapping neural substrates of both music and language (for reviews, see Patel, 2008, 2011). Music has many similarities with language. For example, both consist of sounds which can be segmented into discrete elements (music is composed of notes which are grouped into phrases, while the basic element of speech is the phoneme, which is grouped into words and then sentences). Most research in this area has focused on the parallels between linguistic syntax and musical syntax. The major-minor tonal system used in Western music follows certain regularities in melodic, harmonic, and rhythmic structure. Even non-musician listeners who are familiar with this music style develop expectancies regarding the harmonic closures of musical phrases (Bigand & Poulin-Charronnat, 2006). The arrangement of musical chords into harmonic progressions can thus be regarded as a type of musical syntax.

Electrophysiological investigations in non-musicians have found that harmonically incongruent musical chords evoke an early right anterior negativity (ERAN; Koelsch, 2009; Maess, Koelsch, Gunter, & Friederici, 2001), which mirrors the early left anterior negativity evoked by syntactic violations in language (Herrmann, Maess, Hahne, Schröger, & Friederici, 2011; Lau, Stroud, Plesch, & Phillips, 2006). Even small children display the ERAN response to syntactically irregular harmonies (Jentschke, Friederici, & Koelsch, 2014), suggesting that implicit knowledge of these harmonic-syntactic regularities is acquired early in human development. While these components are right- and left-lateralised respectively, a study using intracranial electroencephalography (EEG) and source localisation (brain surface current density mapping) found that there was a considerable overlap of evoked activation in the superior temporal lobe for syntactic violations in both music and language in non-musicians (Sammler et al., 2013).

However, other researchers debate the extent of the overlap between language and music processing. For example, Isabelle Peretz and others have devoted considerable research to individuals with congenital or acquired amusia. Amusia, also known as “tone-deafness”, is a condition characterised by a lifelong deficit in the perception and production of musical melodies. People with amusia have normal language abilities both in comprehension and production of spoken language (for a review, see Peretz, 2013). There are also cases in the literature of non-musicians who lose their ability to comprehend speech, but retain their musical abilities (e.g. Mendez, 2001). Thus, there is a dissociation between music and language abilities (Peretz & Coltheart, 2003). However, studies of patients with lesions that have caused deficits in music processing also report parallel deficits in the detection of speech prosody (Nicholson, Baum, Cuddy, & Munhall, 2002; Patel, Peretz, & Tramo, 1998), and at least some people with amusia also have lower performance on speech prosody tasks (Patel, Wong, Foxton, Lochy, & Peretz, 2008). These studies suggest that at least some aspects of music and language may share a common neural substrate.

Expert musicians may have a greater degree of overlap between music and language processing than non-musicians. For example, musicians frequently demonstrate increased recruitment of left hemisphere regions that are associated with language processing during music perception or performance (Baumann et al., 2007; Ohnishi et al., 2001; Ono et al., 2011). Additionally, musicians outperform non-musicians in the perception of pitch incongruities in both musical melodies and speech prosody (Magne, Schön, & Besson, 2006; Schön, Magne, & Besson, 2004), and are better at detecting pitch violations in a foreign language that they do not speak (Marques, Moreno, Castro, & Besson, 2007). Finally, Patston and Tippett (2011) showed that the presence of background music, particularly when it contained errors, selectively interfered with performance on a language comprehension task (and not a visuospatial processing task) in musicians, but not in non-musicians. This result suggests that the networks associated with language and music processing overlap to a greater extent in musicians. In line with this notion, several studies have suggested that left hemisphere brain regions are recruited by musicians during music perception. This idea is discussed further in the *cerebral lateralisation in musicians* section of this chapter.

Processing Speed

Musicians also typically outperform non-musicians on tests of processing speed, a general measure of how quickly an individual is able to mentally process information. Proficient musicians might be expected to be faster at processing information due to the demands of music performance, where they must register a multitude of incoming information from different modalities and make use of that information in real time to adjust their performance. Patston (2007) showed that while error rates did not differ between groups, musicians completed significantly more items than non-musicians on the Symbol-Digit Modalities Test, the Symbol Search subtest of the Weschler Adult Intelligence Scale-III (WAIS-III), and the word and colour baseline conditions of the Stroop Colour Naming and Word Reading Test, all of which index processing speed. Importantly, musicians outperformed non-musicians on both the written and verbal forms of these tasks. This indicates that musicians are not solely advantaged on written tasks, where their extensive motor skill training alone could enable faster responding, but also outperform non-musicians on verbal tests of processing speed. Bugos and Mustafa (2011) also report better performance for musicians compared with non-musicians on measures of auditory processing speed (Paced Auditory Serial Addition Test) and visual processing speed (Trail Making Test). In contrast, Rodrigues, Guerra, and Loureiro (2007) did not find a musician advantage on the Digit Symbol subtest of the WAIS-III, which indexes perceptual and psychomotor speed. Finally, Bugos et al. (2007) provide evidence of enhanced processing speed directly due to music training. They randomly assigned musically naïve older adults to either receive piano lessons or not and found that the group receiving lessons outperformed the control group on the Digit Symbol Test.

Executive functions

Executive functions are a set of cognitive control mechanisms including cognitive flexibility, selective attention and inhibition, working memory, updating, planning, problem solving, and monitoring (Blair, Zelazo, & Greenberg, 2005; Lezak, 2004). A small number of studies have demonstrated enhanced executive functioning in individuals with musical training. In a longitudinal study of pre-schoolers, Moreno et al. (2011) found that after training children who received music lessons were more accurate on a go-no go task (measuring the ability to inhibit a prepotent response) than a group who received visual arts lessons. The music group also had a larger P2 ERP component on no-go trials after training than the visual arts group. Supporting this study, cross-sectional studies with adult musicians found superior inhibition on both musical and non-musical tests of inhibition ability (Bialystok & DePape, 2009; Travis, Harung, & Lagrosen, 2011). Both cross-sectional and longitudinal work has shown that children who receive music training score higher than untrained children on tests of working memory (Y. Lee, Lu, & Ko, 2007; Roden, Grube, Bongard, & Kreutz, 2013). Moreover, Zuk, Benjamin, Kenyon, and Gaab (2014) demonstrated that musically trained children outperformed controls on a verbal fluency task, while musically-trained adults outperformed controls on tasks of both verbal fluency and cognitive flexibility. Verbal fluency tasks require executive function to generate novel strategies to search the mental lexicon, and to maintain earlier responses in working memory to avoid repetition (Fisk & Sharp, 2004). Bugos and colleagues (2007) trained music-naïve older adults to play the piano over a six-month period, and report improved performance over time on the Trail Making Test Part B (which assesses mental flexibility) whereas performance did not improve for a no-lessons group. As the control group did not receive an alternative intervention, the specific benefit of music training was not established. Contradicting these findings, Schellenberg (2011a) found that nine to 12-year-old children with and without music training did not significantly differ on five measures of executive function (verbal fluency, attention and working memory, inhibition, problem solving and planning, and set shifting). However, the musically trained children had higher IQ than the untrained children. In general, though, most research agrees that individuals with music training have superior executive functioning on tasks of inhibition, verbal fluency, working memory, and mental flexibility.

Visuospatial Ability

Finally, a number of studies suggest that musicians have enhanced visuospatial skills. A meta-analysis of research in children found that receiving music training increased performance on spatial-temporal tasks which involve the maintenance and transformation of mental images, and also on other types of visuospatial tasks (Hetland, 2000). Degé, Wehrum, Stark, and Schwarzer (2011) also conducted a longitudinal study and found that children who received music instruction had improved visual memory performance relative to a no-lessons control group, with no differences between groups in intelligence. Some studies, however, have not identified a visuospatial advantage in musically trained children (Forgeard, Winner, Norton, & Schlaug, 2008; Hyde et al., 2009; Roden et al., 2013). These studies tend to use constructional tasks such as the Block Design subtest, raising the possibility that musicians may only show enhancements on certain types of visuospatial tasks.

Studies comparing adult musicians and non-musicians also indicate that musicians outperform non-musicians on a range of visuospatial tasks, including judgements of line orientation (Sluming et al., 2002); basic tests of visual perception (Brochard, Dufour, &

Després, 2004); efficiency of saccadic eye movements in tracking (Kopiez & Galley, 2002); constructional ability (Block Design subtest; Stoesz, Jakobson, Kilgour, & Lewycky, 2007); mental rotation (Sluming et al., 2007); line bisection accuracy (Patston, Corballis, Hogg, & Tippett, 2006); visual search (Patston & Tippett, 2011; Stoesz et al., 2007); divided visual attention (Rodrigues et al., 2007); copying of impossible figures, thought to represent enhanced processing of local details (Stoesz et al., 2007); and visual memory (Chan et al., 1998; Ho et al., 2003; Jakobson et al., 2008).

Additionally, a small number of behavioural studies by Patston and colleagues have lent support to the idea that, while non-musicians' visual attention and spatial performances show a left visual field advantage (thought to reflect a right hemisphere advantage in these abilities), visual attentional performance in musicians shows reduced (or absent) advantages for the left visual field, suggesting that these abilities may be less lateralised in musicians. Patston, Hogg, and Tippett (2007) asked participants to decide whether a dot appeared to the left or right of a vertical line. While both groups were more accurate for left-sided dots than for right-sided dots, musicians were significantly more accurate than non-musicians for right-sided dots, suggesting more balanced visual attention to both sides of space, and the possibility that there is more bilateral neural representation of the function. On a line bisection task, non-musicians showed a significant leftward bias in marking the centre of lines, yet musicians had a slight rightward bias and were more accurate overall (Patston, Corballis et al., 2006). These findings may be the result of altered visual attention in musicians, however it is also possible that musicians who read music are generally proficient at making small discriminations in a spatial array (Patston, 2007). As evidence against this, Patston and colleague's finding was also replicated by Rodrigues, Loureiro, and Caramelli (2013) in a sample of orchestral musicians, on three different measures of visual attention:

selective attention, sustained attention, and divided attention. While performance in the selective attention condition could have benefited from enhanced discrimination ability, performance in the other two conditions relied less on spatial discriminations. Performance enhancements in musicians on these measures were significantly associated with the age of commencement of lessons, such that musicians who began lessons earlier had higher performance.

Finally, in an electrophysiological study, Patston and colleagues investigated potential differences in inter-hemispheric transfer time (IHTT) for visual information between musicians and non-musicians (Patston, Kirk, Rolfe, Corballis, & Tippett, 2007). While non-musicians had faster IHTTs when visual information travelled from the right-to-left hemispheres than from left-to-right hemispheres, and a shorter latency of the N1 event-related potential (ERP) component in the left hemisphere, musicians displayed no directional difference in IHTT, and no hemispheric difference in N1 latency.

Together these studies provide convincing evidence of enhanced visuospatial abilities in musicians, and the possibility that the underlying neural organisation of visual attention may be different in expert musicians. Theories about the aspect of music training which leads to an advantage on visuospatial tasks tend to refer to the spatial arrangement of a musical score. Musical notation is arranged such that higher pitch notes are positioned higher on the vertical stave than lower pitch notes. For a number of instruments, such as the piano, musicians must simultaneously read notes at multiple positions on the stave (as in chords), or even multiple lines of musical notation. Other information about how to play a musical piece is also conveyed visually, for example through the use of different symbols for notes of different lengths. Additionally, the visuomotor translation process of converting sheet music into its associated finger movements has to be carried out very rapidly, especially in sight-reading, where musicians play a piece of unpractised music by following the sheet music (Stewart, 2008). Regions associated with visuospatial processing are often shown to be activated by musicians during music reading and sight-reading (e.g. Roux et al., 2007; Schön, Anton, Roth, & Besson, 2002; Sergent, Zuck, Terriah, & MacDonald, 1992). Stewart et al. (2003) also observed increased activation in visuospatial regions in musically naïve adults who learned to play the keyboard and read sheet music. Because music reading and sight-reading processes draw on the visuospatial system, there is reason to expect that musicians may perform better on other, non-musical, visuospatial tasks which depend on the same network.

In summary, music instruction is associated with enhanced functioning across a range of cognitive domains. There is limited causal evidence that domain-general factors, such as IQ, are enhanced by musical training. On the other hand, several experimental studies have identified specific cognitive abilities (language, executive function, visuospatial ability, and processing speed) which seem to be selectively boosted by music training. This suggests that music training can confer benefits that go beyond the specific skills trained in music. Little is known, however, about whether the lateralisation of non-musical processes such as visuospatial ability is also altered in expert musicians. In the next section, evidence for altered lateralisation of music processing in musicians is discussed, as well as our rationale for investigating musicians' neural lateralisation of visuospatial processing.

Cerebral lateralisation in musicians

It is an established fact of human brain organisation that certain cognitive functions rely more heavily on one of the two brain hemispheres. Some 96% of right-handers and 70% of left-handers are left cerebrally dominant for language processing (Badzakova-Trajkov, Häberling, Roberts, & Corballis, 2010; Knecht, 2000; Rasmussen & Milner, 1977), while other functions such as spatial attention, emotion, and music tend to be preferentially associated with the right hemisphere, although lateralisation is not as clear as it is for language (Everts et al., 2009; Lidzba, Staudt, Wilke, Grodd, & Krägeloh-Mann, 2006; Sack et al., 2007; Whitehouse & Bishop, 2009).

Studies of music listening in non-musicians have tended to find right-lateralised activation (Bernal, Altman, & Medina, 2004; Evers, Dannert, Rodding, Rotter, & Ringelstein, 1999; Santosa, Hong, & Hong, 2014; Tervaniemi et al., 2000), although some studies have found bilateral activation (Koelsch et al., 2002; Nakamura et al., 1999), or left-lateralised activation (Levitin & Menon, 2003). In general, however, while there is some evidence that the left hemisphere is dominant for the processing of rhythm (e.g. Vignolo, 2003), most other aspects of music, such as pitch, melody, contour, meter, and emotion are processed primarily in the right hemisphere in non-musicians (Brown, Martinez, & Parsons, 2004; Hyde, Peretz, & Zatorre, 2008; Ohnishi et al., 2001; Ono et al., 2011; Zatorre & Gandour, 2008).

In musicians, music processing may be lateralised differently. Early dichotic listening studies found that musicians show a right ear advantage for melodies, indicating left hemisphere dominance (Bever & Chiarello, 1974; Johnson, 1977; Larmande, Dongmo, Belin, & Limodin, 1985; Messerli, Pegna, & Sordet, 1995). A more recent study failed to replicate this finding, however (Spajdel, Jariabková, & Riecanský, 2007), instead finding a left ear advantage for two tone stimuli in both musicians and non-musicians, indicating right hemisphere dominance. Work utilising fMRI has also revealed a leftward shift in music processing for musicians. For example, Ellis, Bruijn, Norton, Winner, and Schlaug (2013) found a significant leftward asymmetry in functional activation during melodic discrimination and rhythmic discrimination in a cross-sectional analysis of children and adults with music training, which was correlated with subjects' cumulative hours of practice. They also examined lateralisation in a longitudinal sample of children receiving music instruction over 3 to 5 years, and similarly report a correlation between leftward asymmetry and subjects' cumulative hours of practice. Burunat and colleagues (2015) also showed that musicians had more symmetric brain activation than non-musicians during music listening. Other studies have also indicated more left hemisphere recruitment in musicians during music perception (e.g. Baumann et al., 2007; Ohnishi et al., 2001; Ono et al., 2011). In contrast, Herholz, Lappe, Knief, and Pantev (2008) used MEG to investigate the MMN during a musical imagery task with familiar melodies. Only musicians had an evoked MMN to a tone which was an incorrect continuation of the imagined melody. However, this MMN was right-lateralised, though it is possible that this discrepancy is because the melodies were imagined, and not actually perceived. These studies suggest overall that music perception is associated with more bilateral activation, or in other words more recruitment of left-hemisphere regions, in musicians than in non-musicians.

Very little research, however, has examined the laterality of processing of cognitive functions other than music in musicians. Of interest to this thesis, two behavioural studies published by Lucy Patston and colleagues (Patston, Corballis et al., 2006; Patston, Hogg et al., 2007; see also Brochard et al., 2004, Lega, Cattaneo, Merabet, Vecchi, & Cucchi, 2014) suggested that musicians may have a more bilateral neural representation of visuospatial attention. This group also published an EEG study which indicated musicians had more equilateral IHTT for visual information, also suggestive of a bilateral (not lateralised) visual attention system (Patston, Kirk et al., 2007). Evidence that the posterior corpus callosum, which connects the left and right parietal and occipital lobes, is enlarged in musicians also suggests that musicians may have more efficient interhemispheric communication between these regions (Burunat et al., 2015; Steele et al., 2013). Enhanced interhemispheric communication could enable the development of greater functional symmetry of the visual attention system. This thesis aims to follow up on these results by more directly investigating the functional lateralisation of visuospatial attention in musicians, using fMRI.

Moderating influence of gender

There is an extensive literature on gender differences in cognitive processes and brain structure and function in healthy adults, yet the possibility that these differences may interact with effects of musical training, musical expertise, and neuroplasticity is seldom considered.

The cognitive domains in which gender differences in the general population are the largest and most robust are language and spatial ability. Globally, girls typically outperform boys in reading ability, with differences in the range of 0.2 to 0.6 standard deviations (Hedges & Nowell, 1995; Reilly, 2012; Stoet & Geary, 2013). Larger female advantages have been observed in lower-performing students (Stoet & Geary, 2013; Reilly, 2012), and for writing tasks (Hedges & Nowell, 1995). Developmentally, a female advantage for reading has been observed in children entering kindergarten (Robinson & Lubienski, 2011).

In contrast, there are robust gender differences favouring males on certain types of visuospatial tasks, particularly on a common test of mental rotation ability, the Mental Rotation Test (Christova, Lewis, Tagaris, Uğurbil, & Georgopoulos, 2008; Kaufman, 2007; Linn & Petersen, 1985; Voyer, Voyer, & Bryden, 1995). These effects range in size from 0.5

to one standard deviation. Studies of preschool and kindergarten aged children have mixed results, with some studies finding gender differences (Auyeung et al., 2012; Hahn, Jansen, & Heil, 2010; Jansen, Kellner, & Rieder, 2013) and others not (Frick & Möhring, 2013; Gunderson, Ramirez, Levine, & Beilock, 2012; Ramirez, Gunderson, Levine, & Beilock, 2012). Male advantages are larger for mental rotation of 3D, rather than 2D, objects (Voyer et al., 1995), and when time limits are imposed, suggesting that the key difference between males and females may be the *speed* of mental rotation, especially for complex shapes (Voyer, 2011).

Besides mental rotation, men, on average, also consistently outperform women on tests of navigation ability (Astur, Tropp, Sava, Constable, & Markus, 2004; Cánovas, Espínola, Iribarne, & Cimadevilla, 2008; Malinowski & Gillespie, 2001; Moffat, Hampson, & Hatzipantelis, 1998). Gender differences, however, are not observed on other types of spatial tasks, such as geometry problems in mathematics (Else-Quest, Hyde, & Linn, 2010; Lindberg, Hyde, Petersen, & Linn, 2010), and females have an advantage for remembering object locations (Voyer, Postma, Brake, & Imperato-McGinley, 2007). When asked to draw a complex figure from memory, a task requiring visuospatial ability and memory, boys had better recall when the task was described as a test of geometry ability. However, when it was described as a test of drawing ability, girls did better (Huguet & Régner, 2009). Overall, the most robust gender differences in spatial ability are for mental rotation tasks, but these differences can be reduced by varying task conditions such as the type of objects to be rotated or the inclusion of a time limit.

This literature also provides somewhat conflicting results with regards to the neural correlates of this gender difference in mental rotation ability. Most studies have found significant gender differences in brain activity during mental rotation (Butler et al., 2006; Gootjes, Bruggeling, Magnée, & Van Strien, 2008; Gur et al., 2000; Hahn et al., 2010; Hugdahl, Thomsen, & Ersland, 2006; Jordan, Wüstenberg, Heinze, Peters, & Jäncke, 2002; but see Halari et al., 2006). Generally activation in men is right lateralised and predominantly parietal, while in females it is more bilateral and includes more recruitment of frontal regions (Butler et al., 2006; Hugdahl et al., 2006; Jaušovec & Jaušovec, 2012; Vogel, Bowers, & Vogel, 2003, but see Jordan et al., 2002). This may reflect that males and females engage different strategies to perform mental rotation; activation of frontal regions in females could reflect the use of language-based strategies (Hugdahl et al., 2006).

Beyond differences in the neural correlates of visuospatial processing, there is also a broader literature finding gender differences in brain structure. At a global level, males have larger total brain volumes (Allen, Damasio, & Grabowski, 2002; Courchesne et al., 2000; M Peters et al., 1998). When total brain volume is controlled for, women have a higher ratio of grey matter to white matter, while men show the reverse (Allen, Damasio, Grabowski, Bruss, & Zhang, 2003; X. Chen, Sachdev, Wen, & Anstey, 2007; Gur et al., 2000; Luders, Steinmetz, & Jäncke, 2002, but see Good et al., 2001). Some studies have also found that specific brain regions such as the corpus callosum and the cerebellum are enlarged in males (Allen et al., 2002; Carne, Vogrin, Litewka, & Cook, 2006; but see Zarei et al., 2006).

Several DTI studies have also identified gender differences in the connectivity of white matter structures. In the corpus callosum, while many studies have found that males have higher FA, indicating more directional diffusion (Menzler et al., 2011; Oh et al., 2007; Pal et al., 2011; Shin et al., 2005; Westerhausen et al., 2003), some have found the reverse, that is, where females have higher FA (Chou, Cheng, Chen, Lin, & Chu, 2011; Kanaan et al., 2012).

These gender differences of FA in the corpus callosum are in line with other research which has found that men have larger corpus callosum volumes than women (Allen et al., 2002; Carne, Vogrin, Litewka, & Cook, 2006; but see Zarei et al., 2006). Higher FA in men has also been observed in the mid-cingulum bundle (Huster, Westerhausen, Kreuder, Schweiger, & Wittling, 2009), the cerebellum (Kanaan et al., 2015), the SLF (Kanaan et al., 2015), the internal capsule (Chou et al., 2011), and in the deep temporal lobe (Hsu et al., 2008). Higher FA in women has been found in the left frontal lobe (Szeszko et al., 2003), and the inferior fronto-occipital fasciculus (Chou et al., 2011).

Overall, a substantial body of research points to the importance of considering gender as a variable of interest when studying visuospatial ability and brain structure. Few studies in the musician literature, however, have considered gender as a variable of interest. Lee, Chen, and Schlaug (2003) found that the anterior corpus callosum was enlarged in male musicians, relative to non-musicians, but was not enlarged in females. Luders and colleagues (2004) also found an increased leftward asymmetry of the postcentral gyrus in male non-AP musicians compared to female non-AP musicians, and interactive effects of gender and AP on localisation of asymmetry along STG. Yet many musician studies have only included males, perhaps because of concerns that gender could be a moderating variable (Amunts et al., 1997; Gaser & Schlaug, 2003; Sluming et al., 2002, 2007). More research is clearly needed to determine how gender may modulate the effects of musical expertise on brain structure and function.

Overall summary

In summary, the existing literature indicates that musical expertise is associated with widespread neural differences. Often these differences are specific to the instrument played, or can be correlated with aspects of music training such as length or intensity of training, providing evidence for the view that these brain differences are the result of music training, rather than pre-existing differences. Factors such as the age of onset of training and AP have also been shown to influence whether and how neural plasticity may occur. Other factors, particularly gender, have been less well-studied in relation to musical expertise. There is also evidence that musicians have less lateralised processing of music.

Other studies show that musicians have cognitive enhancements in domains such as language and visuospatial processing, which music training does not train directly. Behavioural and electrophysiological studies have indicated that there may also be altered lateralisation of visual processing, however to date no studies have directly addressed this using a method such as fMRI. In general, more research is needed to elucidate differences between musicians and non-musicians in the neural correlates of non-musical cognitive abilities such as visuospatial processing.

Thesis aims

The overall aim of this thesis was to investigate the functional lateralisation of visuospatial processing in expert musicians and related differences in structural connectivity of the corpus callosum. *Study One* aimed to investigate functional lateralization of visuospatial processing by collecting fMRI scans while participants performed three tasks tapping into visuospatial processes. Performance on these tasks was also compared across groups to replicate previous research finding musician advantages on visuospatial tasks. *Study Two* aimed to identify differences in structural asymmetries using DTI, and to use tractography techniques to characterise differences in key white matter tracts between musicians and non-musicians. Singers and instrumentalists were also compared to determine whether these different types of music training are associated with differences in white matter organisation. In both studies, gender was considered a variable of interest, given the limited previous literature exploring gender differences in cognition and brain structure in expert musicians.

Chapter 2: Study One - Lateralisation of visuospatial processing in musicians and non-musicians is modulated by gender

Introduction

The idea that music training can enhance *non-musical* cognitive abilities has gained considerable research interest in recent years (for a review, see Schellenberg & Weiss, 2013). Musicians have been shown to outperform non-musicians in a range of cognitive domains, including language skills (Corrigall & Trainor, 2011; Moreno et al., 2009), mathematics (Bahr & Christensen, 2000; Vaughn, 2000), and memory (Chan, Ho, & Cheung, 1998; Ho, Cheung, & Chan, 2003; Jakobson et al., 2008).

Visuospatial processing may also be enhanced in musicians, as it plays a crucial role in a number of aspects of musical processes. In musical scores, musical notation is arranged spatially, such that the vertical positioning of notes on the stave determines their pitch. Musicians are required to rapidly translate this visuospatial information into its associated motor sequences. Proficient musicians are able to sight-read, where they can perform this visuomotor translation process with musical scores they have not previously seen. Pitch itself is associated with a vertical spatial dimension even in non-musicians (Connell, Cai, & Holler, 2013), so it is possible that extended practice of pitch discrimination, as occurs in musical training, may also benefit more general spatial skills. It is also possible that playing a bimanual instrument, especially a midline instrument such as the keyboard, may enhance musicians' abilities to direct their visual attention equally to both sides of space. Intensive and extended musical training may therefore enable superior performance on visuospatial tasks, perhaps via enhanced visuospatial attention.

A number of studies have found enhanced visuospatial processing in both children and adults with musical training. In children, a meta-analysis of 15 studies showed that overall those who took music lessons outperformed those who did not on both spatial-temporal tasks and on other visuospatial measures (Hetland, 2000). Spatial-temporal tasks involve arranging the elements of an object into a specific spatial configuration to match a mental image (Rauscher & Zupan, 2000), and included tasks such as Object Assembly and Puzzle Solving. The other visuospatial measures tapped into a range of visuospatial abilities including spatial memory, spatial recognition, mental rotation, and spatial visualisation. It is important to note, however, that just five of those 15 studies randomised their subjects to the music or control groups. Additionally, the control group in two thirds of the studies was simply a “no-lessons” group – that is, no alternative activity was provided to the children in the control group. This raises the possibility that music lessons could affect children’s performance through some other factor not specific to music training itself, such as increasing their motivation. In response to this issue, Hetland demonstrated that there was no difference in the effect sizes from studies which did and did not include an alternative activity for their control groups.

While more recent studies in children have observed the same pattern that emerged from the Hetland meta-analysis (e.g. Bilhartz, Bruhn, & Olson, 1999; Zafranas, 2004), enhanced visuospatial attention in musically-trained children is not a universal finding. For example, Forgeard, Winner, Norton, and Schlaug (2008) found no difference between their music and control groups on Object Assembly or Block Design tasks. The children in the music group in this study had an average of 4.6 years of music training, where the studies reviewed by Hetland (2000) were all shorter in duration. This raises the possibility that music training may only accelerate the development of spatial skills rather than conferring a permanent benefit. Findings by Costa-Giomi (1999) also support this interpretation. In a three-year longitudinal study, children receiving piano lessons improved more than a control group when tested after one and two years, however after three years the differences between groups had disappeared. She also found, however, that spatial abilities at the three-year point were significantly predicted by children's engagement with lessons, as measured by average practice time per week and number of lessons missed. This finding suggests that spatial enhancements may only persist long term for students who continue to remain actively engaged in the process of learning music.

Research findings that adult musicians also show enhancements in visuospatial processing may provide evidence of long-term effects of music training on performance in this cognitive domain. A range of studies with adults have found that musicians have enhanced performance on various tests of visuospatial ability, such as the Benton Judgement of Line Orientation Test (Sluming et al., 2002), as well as on measures of visual attention (Patston, Hogg, & Tippett, 2007; Rodrigues, Loureiro, & Caramelli, 2013), visual memory (Jakobson et al., 2008), and visual search tasks (Patston & Tippett, 2011; Stoesz, Jakobson, Kilgour, & Lewycky, 2007). On mental rotation tasks, non-musicians typically show a linear increase in response times as the orientation angle of the stimulus increases away from the upright (Shepard & Metzler, 1971). Flattened reaction time slopes are common following mental rotation training (Kaushall & Pearsons, 1981). An intriguing study by Sluming and colleagues (2007) found that male orchestral musicians displayed a flatter response function than non-musicians during mental rotation. Musicians also activated Broca's area (left inferior frontal gyrus) to a greater extent during mental rotation than non-musicians, with a direct link between the amount of activation in this region and flatter response functions. As Broca's area has been shown to be recruited in visuospatial sight-reading of music (Bengtsson & Ullén, 2006; Sergent et al., 1992), this finding raises the possibility that musicians' enhanced visuospatial abilities could be subserved by training-related neural plasticity in this region.

While both cross-sectional and experimental research in children points to a causal role of music training in enhancing spatial cognition, research in adult musicians usually involves proficient musicians and is cross-sectional in design. As such, a self-selection bias could come into play, whereby musicians who have better spatial abilities at the onset of music training are more likely to excel at music performance, and so are more likely to become expert in adulthood. No studies have assessed visuospatial ability in adults randomly assigned to take music lessons.

Stewart et al. (2003), however, observed increased activation in a region subserving visuospatial processing in a group of music-naïve adults who were taught to play the piano over 15 weeks. Relative to before training, playing music by reading from the musical notation was associated with increased post-training activation in the superior parietal lobule. The superior parietal lobule and the neighbouring intraparietal sulcus are known to play an important role in visuospatial processes including visuospatial attention, mental rotation, visual search and detection (Corbetta & Shulman, 2002; Fan et al., 2005; Halari et al., 2006). Thus although this study does not speak directly to the impact of music training on visuospatial skills, it does provide evidence of music training-related plasticity in a key brain region involved in visuospatial processing.

Recent research has also suggested there may be alterations in the *laterality* of visuospatial processing in musicians. Visuospatial processing is generally associated with right hemisphere dominance in non-musicians (Badzakova-Trajkov, Häberling, & Corballis, 2010; Vogel et al., 2003; Wilkinson, 2002). A hypothesis put forward by Patston and colleagues to account for altered patterns of behavioural performance on visuospatial tasks is that musicians have reduced hemispheric lateralization of visuospatial processing (Patston et al., 2006; Patston, Hogg et al., 2007; Patston, Kirk et al., 2007). For example, on line bisection tasks non-musicians tend to systematically mark to the left of the true centre of the line, a phenomenon that is frequently termed *right pseudoneglect* (Hausmann, 2005; Hausmann, Ergun, Yazgan, & Güntürkün, 2002; Hausmann, Waldie, & Corballis, 2003), suggesting the presence of a mild neglect of right hemispace. Pseudoneglect is typically interpreted as reflecting the dominance of the right hemisphere for visuospatial attention (Heilman & Valenstein, 1978; Heilman & Van Den Abell, 1980; Kinsbourne, 1970; Mesulam, 1981).

In contrast to these findings of pseudoneglect in controls, musicians show a smaller, non-significant bias to the right (Patston et al., 2006). Lega and colleagues (2014) replicated this study with haptic and visual line bisection paradigms, and found a significant rightward bias in both modalities for musicians, although contrary to the findings of Patston and colleagues' (2006) and those of numerous other studies (Hausmann et al., 2002, 2003) a (smaller) rightward bias in non-musicians in the visual condition was also reported. In another study, while non-musicians were more accurate in detecting stimuli presented to the left of a vertical line, whether stimuli were located in the left hemispace or the right hemispace did not influence accuracy for musicians, suggesting more balanced attentional capacity (Patston, Hogg, et al., 2007). Finally, in an EEG study assessing inter-hemispheric transfer times (IHTT) for visual stimuli, non-musicians had faster transfer in the right-to-left direction, yet no directional difference was observed in IHTT for musicians (Patston, Kirk, et al., 2007). Collectively, these studies suggest that musicians do not show the typical bias to the left hemispace when processing visual information. Instead they appear to detect and respond to visual stimuli equally well in both sides of space. One possible explanation of these findings is that, unlike the usual pattern of right hemisphere dominance for visuospatial processing, in musicians the left hemisphere may also be involved in visuospatial processing to a greater extent than is typical.

Gender differences in visuospatial processing

In addition to evidence of superior visuospatial ability in musicians, there is also a significant literature reporting gender differences in performance on visuospatial tasks. Males commonly outperform females, however the magnitude and reliability of these differences varies between tasks. Mental rotation, particularly the paper-and-pencil Mental Rotation Test (MRT), produces the most robust gender differences, which typically range from 0.5 – 1 standard deviation (Christova et al., 2008; Peters, Lehmann, Takahira, Takeuchi, & Jordan, 2006; Voyer et al., 1995). Females also have a larger leftward bias on line bisection tasks than males, and show this bias regardless of whether they use their left or right hand to respond, whereas males typically only have this bias when using their left hand (Hausmann et al., 2002; Hausmann, 2005). However, other tests of spatial ability such as the Block Design task and mental paper folding do not show reliable gender differences (Harris et al., 2013; Voyer et al., 1995). Interestingly, gender differences on spatial tasks seem to be ameliorated by students' areas of study, with smaller gender differences on the MRT in students of engineering (Peters et al., 2006). This observation could reflect an inherent difference in spatial aptitude in students who pursue study in fields such as engineering.

Alternatively, it is possible that the types of activities and experiences to which an individual is exposed may influence their spatial ability. In support of this notion, another study found that females improved more than males on a mental rotation task after four weeks of action video game training, reducing the gender difference that was seen at pre-test (Feng, Spence, & Pratt, 2007). This finding suggests that gender differences in spatial ability are not fixed, and can be reduced by training. Relevant to the current study, Pietsch and Jansen (2012) found that while male sports and education students correctly completed more items on the MRT than their female counterparts, there was no difference in the performance of male and female music students. This raises the possibility that music training may interact with gender to influence visuospatial ability.

One hypothesis to account for gender differences in visuospatial tasks is that there is an underlying difference in hemispheric lateralization for visuospatial processing. There is evidence from fMRI studies that spatial tasks evoke right-lateralised brain activation in men, while women display more bilateral activation (Hugdahl et al., 2006; Semrud-Clikeman, Fine, Bledsoe, & Zhu, 2012; Siegel-Hinson & McKeever, 2002; Vogel et al., 2003). Using EEG, a study of preschool boys and girls found that females had greater left hemisphere involvement on a mental rotation task than males, as indexed by left-lateralised parietal ERPs in girls. In contrast to the fMRI findings, in this study the hemispheric difference in ERP amplitudes in boys was not significant (Hahn et al., 2010).

One explanation for a gender difference in lateralisation is that males and females may use different strategies to process visuospatial information. Corballis (1997) suggests that the right hemisphere is preferentially activated when a holistic strategy is used, whereas the left hemisphere is activated when more piecemeal strategies are implemented. There is some evidence to suggest that women are more inclined than men to use a piecemeal strategy when performing mental rotation, which would be consistent with this account of less lateralisation in females for this function. For example, Heil and Jansen-Osmann (2008) showed that women's reaction times on a mental rotation task were adversely affected by increasing stimulus complexity, while men's were not. This finding was interpreted by the authors as reflecting the use of a piecemeal strategy in women which would differentially slow reaction times for shapes of increasing complexity. However, it is also possible that other factors could potentially explain this difference, such as a reduction in motivation caused by the difficulty of the task.

To summarise, evidence in children and adults with music training suggests that musicians have enhanced visuospatial abilities. While there is some evidence from behavioural and EEG work suggesting that musicians may have reduced lateralisation of visuospatial processing, no studies have assessed this directly using fMRI. Other research has found superior male performance on visuospatial tasks, and that males are more right lateralised for visuospatial processing than their female counterparts. Only one study to date has utilised fMRI to compare activation in musicians and non-musicians during performance on a visuospatial task. This study did not investigate potential group differences in the *lateralisation* of activation, however, and only included males.

The current study

The research undertaken in the following study sought to examine these issues further by looking at the patterns and lateralisation of brain activation of expert musicians (compared to non-musicians) when performing visuospatial tasks, including an investigation of whether gender influenced findings.

In order to assess whether musicians' enhanced visuospatial processing is associated with altered functional lateralisation, we conducted a cross-sectional study in which musicians and non-musicians underwent functional magnetic resonance imaging (fMRI) while performing three different tests of visuospatial functioning: a Landmark task (a variant of a line bisection task), a 3D Mental Rotation (3DMR) task, and a Visual Search task. Laterality indices were calculated to assess and compare the degree of lateralization of activation in each group. We hypothesised that musicians would have less lateralised neural activity during performance of the three visuospatial tasks, in line with the theory advanced by Patston and colleagues (see Patston et al., 2006; Patston, Hogg et al., 2007; Patston, Kirk et al., 2007). As visuospatial tasks are typically associated with right hemisphere dominance (e.g. Vogel et al., 2003), non-musicians were expected to have right-lateralised activation during performance on all three tasks.

Musicians were also predicted to have superior performance on the three tasks, based on previous positive findings in the literature. More specifically, given previous research demonstrating greater accuracy by musicians at line bisection (Lega et al., 2014; Patston et al., 2006), musicians were predicted to maintain a higher level of accuracy on the Landmark task than controls, particularly on the more difficult trials where the line was bisected just 2% from the veridical centre. Given that musicians were more accurate than controls in detecting stimuli in the right visual field (Patston, Hogg et al., 2007), we considered the possibility that musicians might perform more accurately than controls in detecting 2% deviations from centre when they occurred on the right.

On the 3DMR task, based on the findings of Sluming and colleagues (2007), we also predicted that musicians would be faster than non-musicians, and may not display the typical linear increase in reaction times with increasing rotation from upright associated with this task. On the basis of the Sluming et al. study, we also expected that musicians would activate brain regions involved in sight-reading, such as the left inferior frontal gyrus, in addition to regions involved in visuospatial processing, more than non-musicians during mental rotation.

Finally, Patston and Tippett (2011) found that musicians completed significantly more trials on the Visual Search task, thus the musicians in our sample were also expected to complete more trials, or perhaps display faster reaction times on this task. We also predicted again that musicians might be more accurate than controls in the detection of changes in the right visual field on the Visual Search task. In both cases this pattern would indicate more balanced performance between the left and right visual fields.

An additional variable of interest in our analyses was gender. This was for two reasons: firstly, there is an established literature demonstrating gender effects in visuospatial processing; and secondly, the only study to date which has utilised fMRI to compare activation in musicians and non-musicians during a visuospatial task only included males (Sluming et al., 2007). We considered the possibility that musical training might differentially affect males and females, however we had no specific hypotheses about what the nature of this difference might be.

The rest of this chapter contains a description of participant information, the screening tasks used, and the general procedure. After this, for ease of reading the study is divided into three sections, one for each visuospatial task, where the relevant method, results, and discussion are discussed in turn. The chapter concludes with a general discussion in which the findings from the three tasks are considered together.

Method

Participants

Two groups of right-handed adults took part in this study: musicians and non-musicians aged between 18 and 50 years. All participants gave full informed consent as approved by the University of Auckland Human Participants Ethics Committee. General exclusion criteria for this study included left-handedness, an Edinburgh Handedness Inventory (EHI) score of less than 75 (indicating the individual was not strongly right-handed), English as a second language, a history of major neurological conditions such as epilepsy or stroke, and inability to be scanned in an MRI scanner (for example, due to the presence of ferromagnetic metal in the body).

The musician group consisted of 33 participants (16 female) who were currently playing an instrument and/or singing at a national or university level. Musicians were recruited for this study from a number of sources: music students from the music performance programme in the School of Music at the University of Auckland (10 participants); singers from Voices New Zealand, Viva Voce Choir, the New Zealand Youth Choir, and the NZ Opera company (8); musicians from orchestras in the Auckland region including the Auckland Philharmonic Orchestra, Auckland Symphony Orchestra, Bach Musica, and Auckland Chamber Orchestra (8); and proficient and active musicians who heard about the study and volunteered (7).

All musicians had received a minimum of 8 years of professional music lessons (*M* = 13.61 years, *SD* = 4.99), had begun those lessons before the age of 10 (*M* = 6.3 years, *SD* = 1.85 years), and could read music. While musicians were required to have attained at least Grade 5 from the Associated Board of the Royal Schools of Music in an instrument or voice, all but two of the musicians in this study had attained Grade 8. Of the remaining two musicians, one had passed the Grade 6 exam and one the Grade 7 exam, however both had auditioned and been accepted into a university music performance degree.

A summary of the main instrument played by each musician (i.e., the instrument used by the musician in their professional music career or in their university performance degree) is provided in Table 1. Also summarised in this table are the instruments that each musician was actively playing at the time of study participation (on which the musician had passed at least a Grade 5 music exam; see Appendix A for more detail). Sixteen musicians played only one instrument (or sang), 14 musicians were currently playing two instruments, and 3 musicians played three or more. Based on their main instrument, 11 musicians were categorised as singers, 21 musicians were categorised as instrumentalists, and 1 musician was categorised as both, meaning that they both sang and played an instrument at a professional or university level. Note that 7 of the 11 singers were currently only singing (i.e., were not currently playing another instrument); however, all of these 7 singers had at one point been at least moderately proficient on another instrument (i.e., had passed at least the Grade 5 exam).

Table 1. Musical instruments played by musician participants.

	Voice	Piano/Keyboard	String	Brass	Woodwind	Percussion	TOTAL
Main instrument	11	10	4	6	1	1	33
Currently played	15	22	6	7	3	1	55

Note: *“Main instrument” refers to the instrument that the musician used in their professional music career or in their university performance degree. “Currently played” refers to all instrument/s which the musician reported playing at the time of their study participation. Only instruments on which the musician had passed at least the Grade 5 music exam are included.

The non-musician control group comprised 30 participants (15 female) who had not had formal music training and could not read music. Non-musicians were recruited through advertising to students at the University of Auckland (12 participants), through www.researchstudies.co.nz, a free online tool for connecting researchers and volunteers (8), and through "word-of-mouth" (10).

Independent-samples *t*-tests were used to test whether participants in the musician and non-musician groups were matched on key demographic variables (see Appendix B for raw demographic information for this study). These analyses revealed that there were no significant differences between the groups for age, years of education, handedness as established by the EHI or estimated performance IQ (PIQ) derived from the Weschler Abbreviated Scale of Intelligence (WASI; all p values > .32). However, the difference between groups approached significance on the WASI Verbal IQ (VIQ): $t(61) = 1.96$, $p = .055$, and the WASI Full-Scale IQ (FSIQ): $t(61) = 2.0$, $p = .050$, with musicians having higher IQ estimates. These results are displayed in Table 2. The EHI and WASI are described in detail in the Materials section.

To check that there were no differences on these variables between males and females, or any interaction between group and gender, a series of 2 x 2 factorial ANOVAs were performed with group and gender as between-subjects factors. Where normality was violated, the Aligned Rank Transform procedure described by Wobbrock, Findlater, Gergle, and Higgins (2011) was used to covert raw numbers into aligned ranks. This procedure "aligns" the dependent variable by stripping all effects from it except the one of interest. Then factorial ANOVAs can be conducted as normal on the aligned data. For all variables (age, EHI, years of education, and the three estimates of intelligence), there were no significant main effects of gender or interactions of group and gender (all *p* values > .10).

Table 2. Demographic characteristics of musician and non-musician participants for Study One.

	Musicians Mean (SD)	Non-musicians Mean (SD)	*t* (*df*)	*p*
Age in years	29.42 (10.35)	28.83 (9.06)	.24 (61)	.81
Years of education	17.11 (1.90)	17.02 (2.72)	.15 (61)	.88
EHI score	96.39 (7.17)	96.06 (7.26)	.19 (61)	.85
WASI Full-Scale IQ	125.76 (7.32)	122.23 (6.61)	1.96 (61)	.055
WASI Verbal IQ	123.33 (7.97)	119.60 (7.08)	2.0 (61)	.050
WASI Performance IQ	122.12 (10.02)	119.67 (9.40)	1.0 (61)	.32

Note. *EHI = Edinburgh Handedness Inventory; WASI = Weschler Abbreviated Scale of Intelligence*

General Materials

General materials for this study are described below. The three experimental measures (Landmark, 3DMR, and Visual Search) are described in detail with relevant results in the sections following the Method.

Screening Tasks

Edinburgh Handedness Inventory

The EHI (Oldfield, 1971) measures an individual's degree of handedness. This consists of 10 questions assessing handedness preference for a variety of daily tasks (e.g. writing, throwing a ball). A laterality quotient of + 100 represents extreme right-handedness, - 100 represents extreme left-handedness, and 0 represents no preference for either hand, or perfect ambidexterity. All participants were required to have a laterality quotient of at least 75; this ensured they were all at least moderately right-handed.

Weschler Abbreviated Scale of Intelligence

The WASI (The Psychological Corporation, 1999) comprises four subtests (Vocabulary, Block Design, Similarities, and Matrix Reasoning). In the Vocabulary subtest participants must give definitions for 34 words (e.g. “What is a calendar?”). In Block Design, participants are required to arrange a group of red and white-coloured blocks so that they match a target design. In the Similarities subtest, participants are asked to describe how two words are alike (e.g. “How are a plane and a bus alike?”). In Matrix Reasoning, a matrix of coloured shapes is presented, with one section of the matrix missing. Participants are asked to choose from one of five options which was the most logical choice to fill in the missing section.

For each subtest, a standardised *T* score (*M* = 50, *SD* = 10) was calculated based on norms derived from a large sample of adults from the United States. The WASI provides a FSIQ (*M* = 100, *SD* = 15) derived from the *T* scores of all four subtests, and also a VIQ score, derived from the Vocabulary and Similarities subtests, and a PIQ score, derived from the Matrix Reasoning and Block Design subtests. These WASI IQ measures are highly correlated with those derived from the WAIS-III (FSIQ: *r* = .92; VIQ: *r* = .88; PIQ: *r* = .84).

General Procedure

Signed informed consent was obtained from all participants. Participants first completed (via email) the EHI and a screening questionnaire containing questions on demographic variables and musical background. In the first session, participants were administered the WASI individually in a quiet room, which took approximately 45 minutes. For the musician group, a small number of follow-up questions were asked regarding their musical history. These questions were tailored to each participant and were intended to resolve any ambiguities in details given in the screening questionnaire, as well as to build a fuller picture of each participant's musical involvement.

In the second session, participants first practiced the experimental tasks on a laptop outside of the scanner before undergoing a series of MRI scans. For each of the three tasks (see Task sections for descriptions of the tasks) participants first went through a series of instruction screens at their own pace which provided example stimuli and explained the two conditions (experimental and control) in each task, how to perform them, and how to make their responses. Participants then completed six 15 s practice blocks for each task. The experimenter ensured that the participant understood each task thoroughly and was performing accurately. Participants were given the opportunity to repeat the practice if needed.

In the scanner, each run consisted of one task. The same blocked design was used for each of the three scanner tasks, shown in Figure 1. Before each experimental and control block, an instruction screen was presented for 3 s to remind participants which hand to use and which task condition to perform. For each task, a total of 10 task blocks (five experimental, five control, each block 30 s duration) and 20 rest blocks (each 12 s duration) were presented. Rest blocks consisted of a central black fixation cross; all stimuli were presented in black on a white background. Experimental and control blocks alternated, while the hand used to make responses was alternated after every two blocks. The order in which experimental and control blocks were presented, as well as the hand order, was counterbalanced between participants. The order in which participants completed the three tasks was also counterbalanced. Stimuli were presented and behavioural data (in the form of response times, number of trials completed, and accuracy) were collected using Presentation (Neurobehavioral Systems, Inc., 2016). Two MR-compatible two-button response boxes were used to collect participants' responses in the scanner.

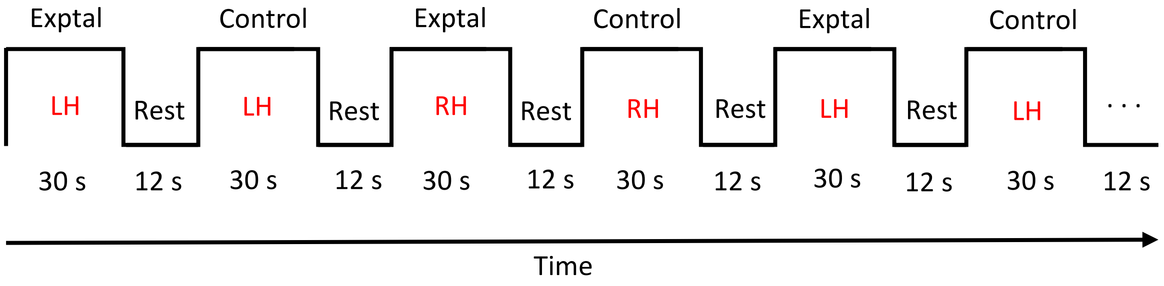

Figure 1. Schematic of scanner task design for Study One. Each task was presented within a separate run and consisted of two conditions (experimental condition, control condition) arranged in a block design. Before each task block an instruction screen was presented for 3 s (not pictured). Task blocks had a duration of 30 s, during which participants used their left or right hand as indicated to make button responses to visuospatial stimuli. Rest blocks (duration of 12 s) followed each task block. Note that due to counterbalancing, participants could be presented with the control condition first, or begin with their right hand rather than left hand. Exptal = experimental; LH = left hand; RH = right hand.

Image acquisition

All MRI scans were performed in a 3 T whole-body scanner (Siemens Skyra, Erlangen, Germany). Firstly, a T1-weighted structural volume was acquired using a 3-D single-shot magnetization prepared rapid acquisition gradient echo (MPRAGE) sequence (TR = 1900ms; TE = 2.07ms; flip angle = 9°; FoV = 256mm; matrix size= 256 x 256; 176 axial slices, whole brain coverage, parallel to AC–PC line; slice thickness = 1 mm; interslice gap = 50%). Acquisition time was 4 min 26 s.

Three echo-planar imaging (EPI) sequences (runs) were acquired while participants performed the three visuospatial tasks described in Materials. Each run yielded a total of 150 T2*-weighted volumes (interleaved acquisition; TR = 3000ms; TE = 27ms; flip angle = 90°; FoV = 192mm; matrix size = 64 x 64; 50 axial slices parallel to AC-PC line providing whole brain coverage; slice thickness = 3.5mm; interslice gap = 20%). Three “dummy” scans were discarded at the beginning of each run to allow for signal saturation. GRAPPA parallel imaging parameters were used (acceleration factor = PE 2). Scan time for each run was 7 min 30 s. A field map measuring magnetic field inhomogeneities was also collected after the first EPI run (scan time 1 min 10 s).

During the functional runs, the task stimuli were projected onto a screen in the scanner room and reflected into a mirror within the head coil. All participant responses were collected using two MR-compatible two-button response boxes. Due to a software malfunction, only 120 of 150 volumes were collected for one participant for the Visual Search run, while for another participant the Landmark run was split into two runs of 75 scans each.

Image pre-processing

SPM8 software (Wellcome Department of Imaging Neuroscience, London, UK; www.fil.ion.ucl.ac.uk) was used for image pre-processing and analysis. Standard pre-processing steps were applied. The fMRI data were first realigned to correct for head motion, using second degree B-spline interpolation. Unwarping was applied to correct for geometric (B0) distortions, with fourth degree B-spline interpolation, and using a voxel displacement map derived from the acquired field map. The T1-weighted structural image was co-registered to the mean of the unwarped functional volumes, and was then segmented into grey matter, white matter and cerebrospinal fluid. The structural and functional images were normalised to the Montreal Neurological Institute (MNI) template (resampled at 2 x 2 x 2 mm), using normalization parameters derived during segmentation. The functional volumes were spatially smoothed using an isotropic Gaussian filter of 8 x 8 x 8 mm at full-width at half maximum (FWHM). Finally, the time-series fMRI data were high-pass filtered to remove low-frequency signal drift, using a cut-off value of 128 seconds. An AR(1)-model was used to account for possible serial correlations.

After preprocessing, motion plots generated during the realignment and unwarping step were visually examined for all participants to identify runs where overall movement exceeded the width of one voxel (3mm), or runs with rapid spikes of movement greater than ~1mm. This procedure identified a total of 16 runs from 12 participants which violated these limits. These runs were repaired using the art_global tool in the ArtRepair toolbox (Mazaika, Whitfield-Gabrieli, & Reiss, 2007). This tool identifies volumes with excessive movement and repairs them by interpolation of the immediately preceding and following volumes.

Statistical analysis

Behavioural data

For each experimental task, mixed-design ANOVAs with two between-group factors (group and gender) and within-subject factors (e.g. condition) were performed in SPSS (Version 22) separately for reaction time (correct trials only) and accuracy. Where significant main effects or interactions were present, Bonferroni-corrected pairwise comparisons were performed. Where the assumption of sphericity was violated, degrees of freedom were corrected using Greenhouse-Geisser estimates. If differences in task performance between musicians and non-musicians were observed, FSIQ was added as a covariate. This was to control for the possibility that the small average difference in FSIQ between musicians and non-musicians could influence group-level task performance or task-related activation.

Functional brain scan data

First-level analysis

Each experimental task run was modelled in a separate within-subject (first-level) analyses block-based general linear model. Blocks of each condition (experimental and control) were modelled using a boxcar waveform convolved with SPM8's canonical hemodynamic response function. Contrast images were created for each subject for experimental condition > control condition (i.e. task effect) and submitted to second-level analyses.

Second-level analysis

The "full factorial" option in SPM8 was used to set up a 2-way analysis of variance (ANOVA) with group and gender as between subjects factors, using the task effect contrast images generated for each subject at the first-level. Using this approach, contrast images that assessed the main effects of condition, group, and gender, as well as the interaction of group and gender, were produced. Activation associated with the main effect of condition (task effect) was assessed in each group separately. A voxelwise threshold of $p < .001$ was combined with a cluster extent threshold (3DMR: 182 voxels; Landmark: 181 voxels; Visual Search: 184 voxels)[1] to provide a threshold of $p < .05$, corrected for multiple comparisons. The required cluster extents for corrected significance on the basis of the whole-brain search volume (range: 178998 - 179491 voxels) were derived from Monte-Carlo simulations, each with 10,000 permutations (calculated using AFNI's 3dClustSim script). Only clusters

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[1] The cluster extent threshold differed between tasks due to slight differences in noise smoothness.

surviving this corrected threshold are reported. Peak voxel coordinates for these clusters are reported in MNI-space. The SPM Anatomy toolbox was used to localise significant activations. Where signal was extracted from a region, the MATLAB REX toolbox was used to extract signal from the peak voxel, then the signal was converted to percent signal change. For display, activations were then overlaid on the ICBM 2009b asymmetric template (Fonov et al., 2011; Fonov, Evans, McKinstry, Almli, & Collins, 2009) in MRIcroGL (Rorden, http://www.cabiatl.com/mricro/mricrogl).

Laterality Index

Laterality indices were calculated from the first-level task effect contrast images for each participant, using the SPM LI-toolbox (Wilke & Lidzba, 2007). This analysis is a robust method of determining lateralization of activation across a range of statistical thresholds. It applies a bootstrapping technique which calculates approximately 10, 000 laterality indices at different thresholds. This generates an overall weighted bootstrapped laterality index. Laterality indices range from -1 to +1, with extreme values representing complete lateralization to the left and right, respectively. Laterality indices were calculated across the whole brain, and also within specific regions of interest (ROIs), described for each task within the relevant Results section. The laterality indices calculated for each participant were then subjected to a factorial (group x gender) ANOVA in SPSS.

Task One: Landmark

Method

Materials and task procedure

The Landmark Task (Harvey, Milner, & Roberts, 1995; Milner, Harvey, Roberts, & Forster, 1993) is a variant of a line-bisection task in which the lines are pre-bisected. The version of the task used was adapted from that used by Badzakova-Trajkov and colleagues (Badzakova-Trajkov et al., 2010; Häberling, Badzakova-Trajkov, & Corballis, 2011). In the experimental condition, participants decided whether or not a horizontal line was bisected exactly in the middle. The stimuli consisted of lines of three different lengths (5, 8 and 10 cm), with a vertical mark 0.5 cm in length placed either in the middle of the line (0% deviation), or at 2%, 5%, 10%, or 15% deviation from the middle. Example stimuli are shown in Figure 2. Lines were bisected in the middle (0% deviation) on 50% of trials. Of the 50% of trials where the line was not bisected in the middle, 10% of trials were bisected at 2% deviation from the middle, 20% at 5% deviation from the middle, 10% at 10% deviation, and 10% at 15% deviation. At each deviation, approximately half of the trials were bisected to the left or right of the middle.

As the task was self-paced, stimuli were presented centrally on a white screen until participants made their response by pressing one of two buttons. Participants used their index finger to respond “yes” to the question “Is the line bisected exactly in the middle?” and the middle finger to respond “no”. There was a 200ms delay between the button press and the appearance of the next stimulus, which was included to remove visual motion artifacts.

In the control condition, participants judged whether a horizontal line was bisected at all. The same stimuli were used as in the experimental condition, with the addition of a line that did not contain a vertical bisection mark. This line was presented in 50% of trials. Of the 50% of trials where the line was bisected, 10% of trials were bisected at each of the five possible deviations from the middle (0%, 2%, 5%, 10%, and 15%). The procedure was the same as for the experimental condition. Participants used their index finger to respond “yes” to the question “Is there a vertical mark?” and the middle finger to respond “no”. Both response time and accuracy were considered to be behavioural variables of interest in this task.

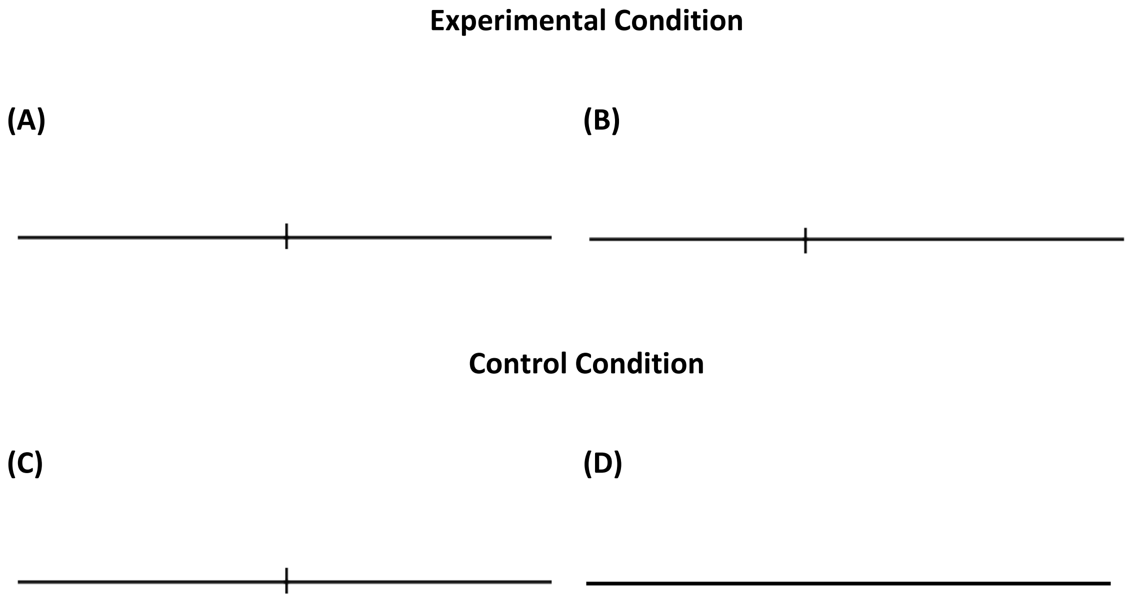


Figure 2. Examples of stimuli for the Landmark task. A, B, Lines for the experimental condition. Participants decided if a line was bisected in the middle (A) or not (B). The example shown in (B) is bisected 10% to the left of the middle. C, D, Lines for the control condition. Participants decided if a vertical mark was present (C) or not (D).

Results

Behavioural data

Due to a software error, behavioural data were not collected for one musician participant, reducing the sample size for these analyses to 32 musicians (15 female) and 30 controls (15 female). For raw data see Appendix D. The mean number (range) of trials attempted was as follows: control condition, musicians 200.94 (133-246), non-musicians 189.43 (80-244); experimental condition, musicians 112.47 (72-171), non-musicians 121.60 (44-165). Attempted trial counts were submitted to a 2 x 2 x 2 (group x gender x condition) mixed-design ANOVA. This revealed a main effect of condition, with significantly more trials attempted in the control condition (*M* = 195.37, *SD* = 29.02) than in the experimental condition (*M* = 116.89, *SD* = 25.58, *F*(1, 58) = 503.64, *p* < .001). A significant interaction of group and condition was also present (*F*(1, 57) = 7.95, *p* = .007, controlling for IQ), yet pairwise comparisons reveal that in neither condition did the group difference in trials attempted reach significance (both *p* values > .12). Finally, there was a significant interaction of gender and condition (*F*(1, 58) = 5.41, *p* = .02). Pairwise comparisons showed that males completed more trials than females in the control condition (*p* = .01), but there was no gender difference in the experimental condition (*p* = .81).

Reaction time

To investigate whether musicians were differentially faster in either condition, a 2 x 2 (group x condition) mixed-design ANOVA was performed with correct trials only. This revealed a significant main effect of condition (*F*(1, 60) = 132.09, *p* < .001), showing that across all subjects reaction times were faster for the control condition than for the experimental condition. Neither the main effect of group nor the interaction of group and condition were significant (both p values > .33).

For the purposes of the remaining reaction time and accuracy analyses, experimental trials were collapsed into four categories: no deviation from centre, 2% deviation, 5% deviation, and both 10% and 15% deviation from centre (i.e. collapsed across left and right trials). Trials with 10% and 15% deviations were collapsed together as mean reaction times and accuracy were very similar between these two deviations. Planned contrasts were also used to test for linear and quadratic trends.

Reaction time data for correct trials was submitted to a 2 x 2 x 4 (group x gender x deviation) mixed-design ANOVA. As two participants had no correct trials at one deviation, this further reduced the sample size to 31 musicians (15 female) and 29 controls (15 female). This analysis revealed, firstly, a significant main effect of deviation ($F(2.2, 123.2) = 43.13$, $p < .001$). This effect was associated with a significant linear trend, indicating that the further away from the veridical centre that lines were bisected, the faster the response times ($F(1, 56) = 60.03$, $p < .001$). The quadratic trend was also significant ($\mathrm{F}(1, 56) = 56.26$, $p < .001$), reflecting a dip in mean reaction times for 2% deviations. There was also a significant interaction between gender and deviation ($F(2.2, 123.15) = 4.08$, $p = .02$). Pairwise comparisons revealed that females were marginally faster than males for 2% deviations only ($p = .075$). This result is shown in Figure 3. No other main effects or interactions were significant (all p values > .37).

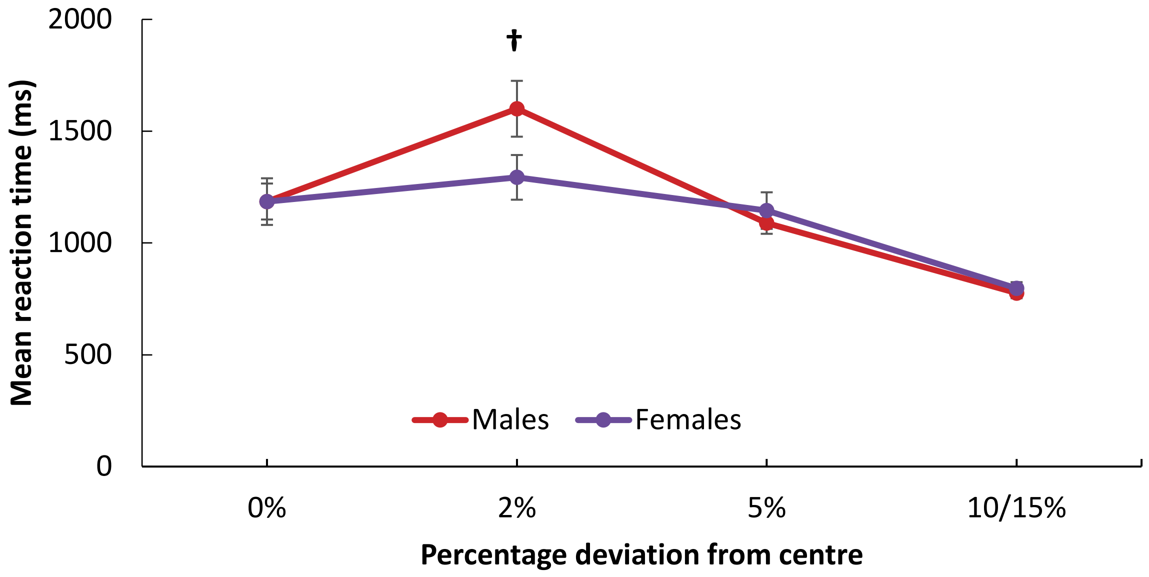


Figure 3. Mean reaction times on the Landmark task for males and females, plotted as a function of percentage of deviation of the vertical mark from the centre of the line. Error bars indicate standard error of the mean. Note that "10/15" refers to the fact that the 10% trials and 15% trials were collapsed together. † *p* < .10

Accuracy

Accuracy (percent correct) was also submitted to a 2 x 2 x 4 (group x gender x deviation) mixed-design ANOVA. Once again there was a significant main effect of deviation (*F*(1.5, 89.42) = 292.55, *p* < .001; see Figure 4), with an associated significant linear trend, indicating that trials which were bisected further away from the true centre were associated with greater accuracy (*F*(1, 58) = 478.47, *p* < .001). The quadratic trend was also significant (F(1, 58) = 214.34, *p* < .001), reflecting a dip in accuracy for 2% deviations. No other main effects or interactions were significant (all *p* values > .32).

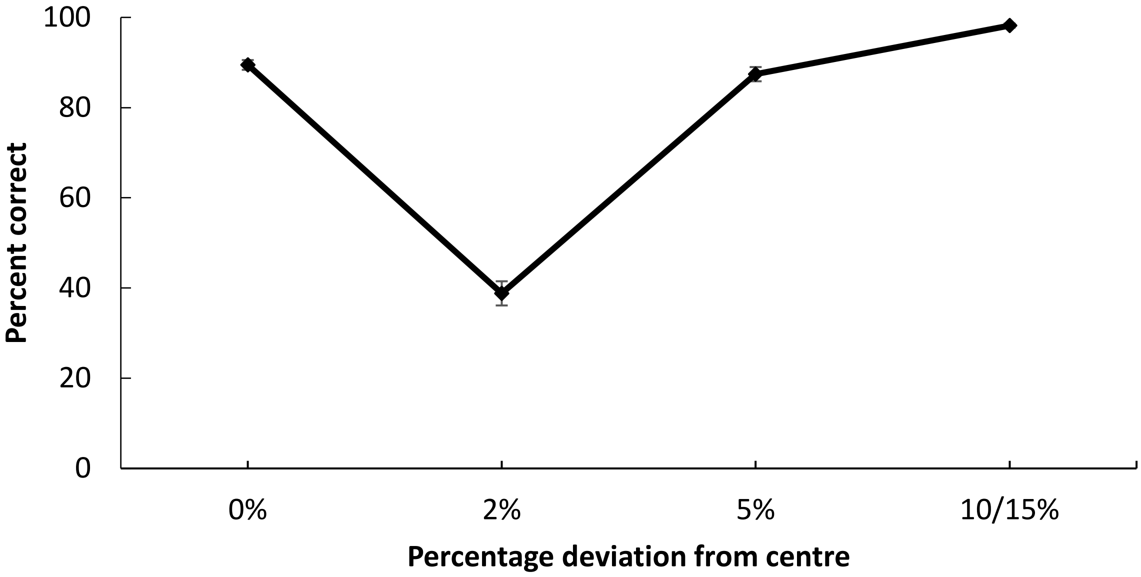


Figure 4. Percent correct on the Landmark task across all subjects, plotted as a function of percentage of deviation of the vertical mark from the centre of the line. Error bars indicate standard error of the mean. Note that "10/15" refers to the fact that the 10% trials and 15% trials were collapsed together.

To test whether musicians were more accurate than non-musicians on the difficult trials (where the line was bisected 2% from centre), and more specifically whether musicians were more accurate detecting stimuli bisected 2% to the right of the centre, we conducted an ANOVA specifically on accuracy for those trials where the line was bisected 2% to the left of centre, and those where it was bisected 2% to the right of centre ("direction").

A 2 x 2 x 2 (group x gender x direction) mixed-design ANOVA revealed a significant main effect of direction, where both groups were more sensitive to left-sided deviations (M = 44.49%, SD = 30.15%) than to right-sided deviations (M =32.71%, SD = 28.27%; $F(1, 58)$ = 5.10, p = .03). This result is shown in Figure 5. As per our prediction, musicians (M = 38.20%, SD =27.88%) appeared to have higher sensitivity for lines bisected 2% to the right of centre than non-musicians (M = 26.85%, SD = 27.94%), however, the interaction of group and direction was not significant (*F*(1, 58) = .46, *p* = .50). No other main effects or interactions were significant.

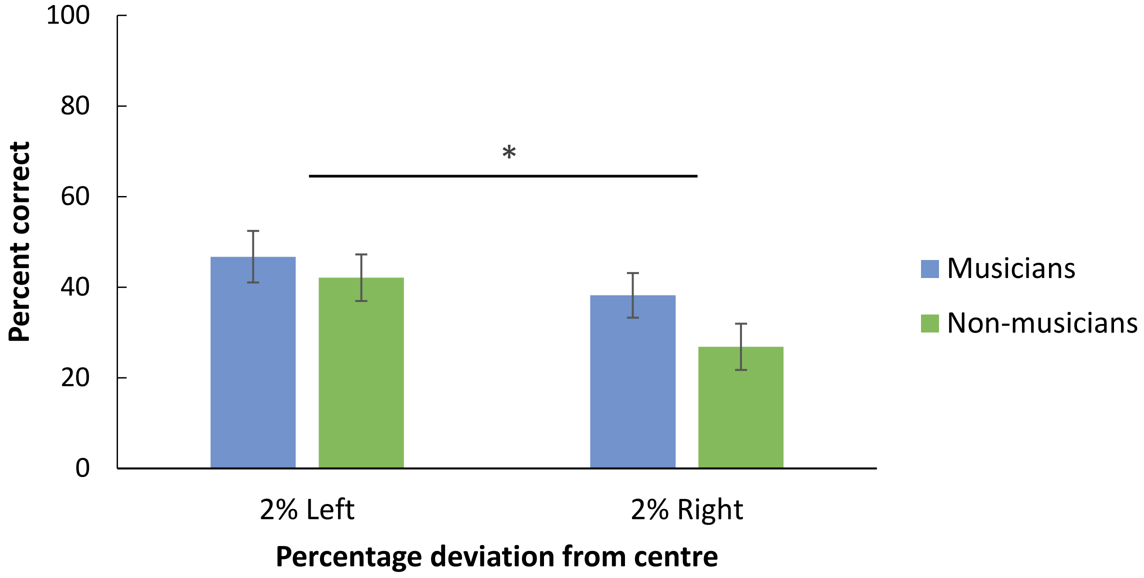


Figure 5. Percent correct plotted for musicians and non-musicians, for trials bisected 2% to the left and to the right of centre in the Landmark task. Error bars indicate standard error of the mean. * *p* < .05

fMRI data

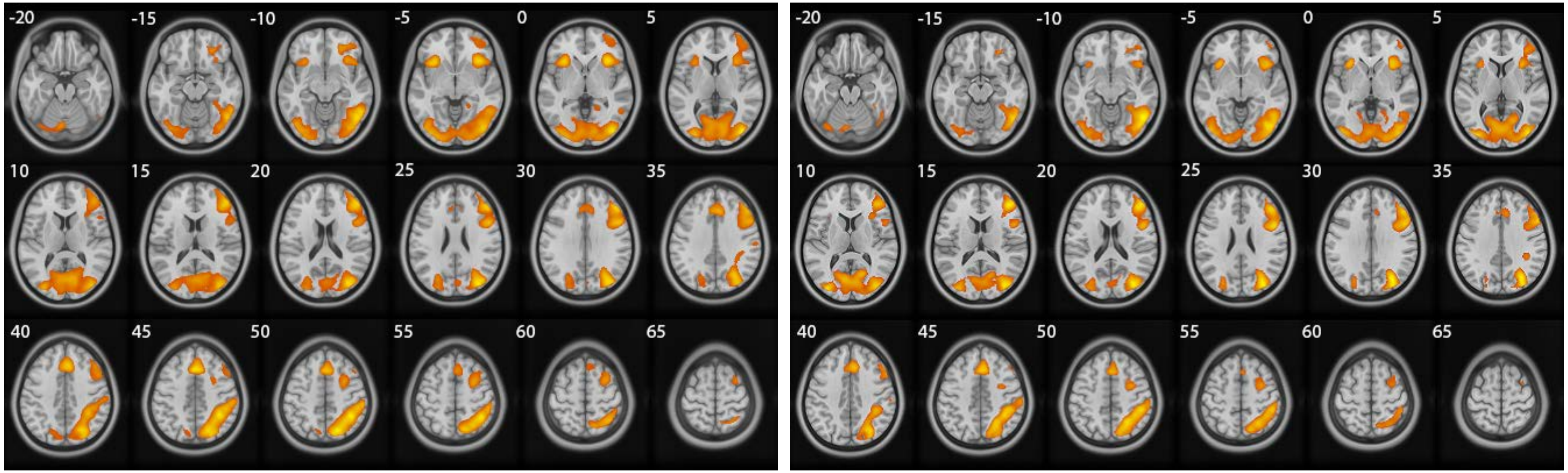
Group effects

As the raw functional images for one male musician were corrupted, the final analysis comprised 32 musicians (16 female) and 30 non-musicians (15 female). In general, the Landmark task, relative to the control task, was associated with activation in similar regions in each group: middle occipital gyrus, superior parietal lobule, inferior temporal gyrus, middle frontal gyrus, superior medial gyrus, insula, and the cerebellum (shown in Table 3 and Figure 6).

Table 3. Regions activated by musicians and non-musicians during the experimental condition relative to the control condition in the Landmark task.

Cluster size[1]	Brain Region	MNI coordinates			z-score
		x	*y*	*z*	
Musicians					
19626	R middle occipital gyrus[2]	40	-84	2	8.36
8363	Superior medial frontal gyrus	0	22	44	7.95
860	L insula lobe	-32	22	-2	7.60
243	L cerebellum (Crus IX)	-12	-54	-48	5.52
Non-Musicians					
16849	R inferior temporal gyrus[2]	48	-62	-12	7.79
4726	R middle frontal gyrus	44	40	16	7.60
1019	R superior medial gyrus	4	22	44	6.92
614	R middle frontal gyrus	30	-2	52	5.72
486	L insula lobe	-32	22	-4	6.44

Note: All clusters are significant at $p < .05$, corrected for multiple comparisons. Where z-scores were reported as infinite in SPM, *t*-scores were converted to non-infinite z-scores using a method developed by Jenkinson and Woolrich (2002). [1]Cluster size (*k*) indicates the number of voxels comprising the cluster; only clusters with a minimum extent of 181 voxels are reported. MNI = Montreal Neurological Institute, L = left, R = right. [2]Cluster extends into right superior parietal lobule.



Musicians

Non-Musicians

Figure 6. Regions engaged by Landmark task in musicians and non-musicians. The contrast of the experimental condition relative to the control condition is displayed on axial slices. Activations are shown at a voxelwise threshold of *p* < .001 uncorrected and an extent threshold of 181 voxels, providing correction for multiple comparisons at *p* < .05.

Contrary to predictions, no regions exhibited an increased or decreased task effect in musicians compared to non-musicians. However, males activated the right inferior parietal lobule significantly more than females during the Landmark task (shown in Table 4 and Figure 7). No regions demonstrated a significant group by gender interaction (that is, a greater gender effect in one group than in the other).

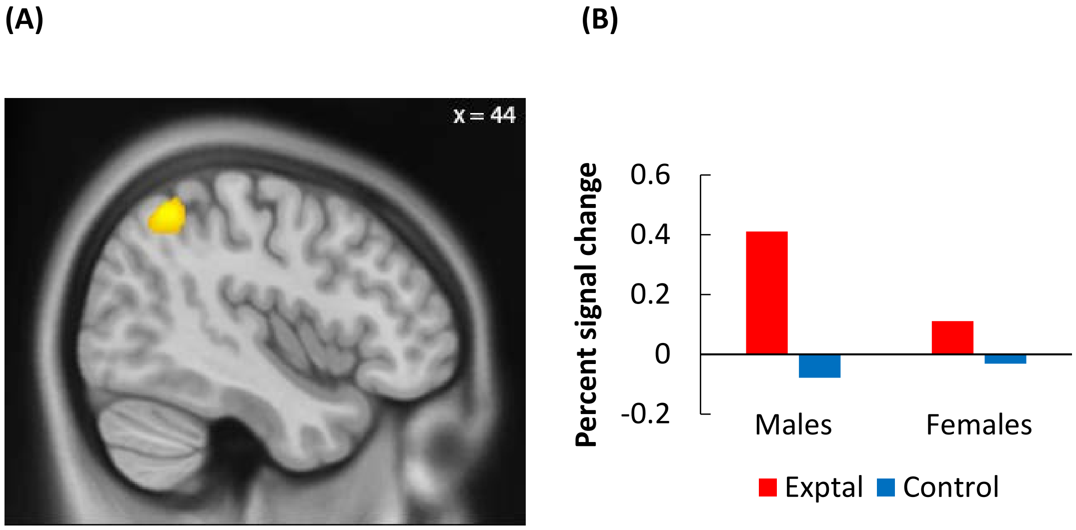


Figure 7. Gender effect in right inferior parietal lobule in the Landmark task. (A) An analysis of gender differences in activation revealed a cluster in the right inferior parietal lobule which displayed a greater task effect (experimental condition > control condition) in males than females. Activations are shown at a voxelwise threshold of *p* < .001 uncorrected and an extent threshold of 181 voxels, providing correction for multiple comparisons at *p* < .05. (B) Percent signal change data were extracted from a 5mm sphere centred on the peak voxel (*xyz* = 44 -54 52), shown here as a function of each gender and condition.

Table 4. Regions exhibiting a larger task effect in males than in females in the Landmark task.

Cluster size*	Brain Region	MNI coordinates			z-score
		x	*y*	*z*	
418	R inferior parietal lobule**	44	-54	52	4.46

Note: Cluster is significant at $p < .05$, corrected for multiple comparisons.[2] *Cluster size (k) indicates the number of voxels comprising the cluster; only clusters with a minimum extent of 181 voxels are reported. MNI = Montreal Neurological Institute, L = left, R = right. **Cluster extends into right supramarginal gyrus

Laterality effects

The laterality of activation was assessed firstly within the whole brain, and secondly within an *a priori* set of regions previously reported to be associated with line bisection. A mask of these regions was downloaded from the Neurosynth database (http://www.neurosynth.org) of reported fMRI activations. Specifically, the meta-analytic "Topics" tool was used, which uses a latent variables analysis partitioning keywords into 100 topics. Topic number 9 was selected, associated with keywords such as "attention", "visual", "spatial", "target", and "orienting". This mask, which included bilateral activations of the primary motor cortex, superior parietal lobule and precuneus, middle occipital gyrus, superior frontal gyrus, and middle frontal gyrus, was then multiplied by a custom MNI-space grey matter mask to exclude non-grey matter voxels. The resulting mask was not symmetrical, however the LI-toolbox is able to accommodate this by incorporating a "mask weighting factor" (MWF), which is a ratio of left hemisphere voxels to right hemisphere voxels within the mask.

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[2] Note that this cluster is still significant at a corrected level when IQ is covaried (cluster size = 317 voxels).

This MWF is included in the calculation of laterality to correct for the difference in mask size between the left and right hemispheres:

$$\frac{(L/MWF - R)}{(L/MWF + R)}$$

Laterality indices were entered into factorial (group x gender) ANOVAs. For raw data, see Appendix G. Across the whole brain, there was a significant interaction of group and gender (*F*(1, 58) = 6.59, *p* = .01).[3] Pairwise comparisons revealed that female controls (*M* = -.43, *SD* = .53) were less strongly right-lateralised than male controls (*M* = -.75, *SD* = .11; *p* = .005), while the difference between male musicians (*M* = -.63, *SD* = .25) and female musicians (*M* = -.71, *SD* = .16) was not significant (*p* = .49). Female controls were also less strongly right-lateralised than female musicians (*p* = .02). This result is shown in Figure 8.

There was also a significant interaction of group and gender in the fronto-parietal ROI (*F*(1, 58) = 6.03, *p* = .02; see Figure 8)[4]. Pairwise comparisons showed that female controls (*M* = -.37, *SD* = .46) were significantly less right-lateralised than female musicians (*M* = -.61, *SD* = .19, *p* = .02), though not than male controls (*M* = -.54, *SD* = .13, *p* = .07).

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[3] Note that this interaction is still significant when IQ is included as a covariate (*F*(1, 57) = 6.56, *p* = .01).

[4] This interaction also remains significant when IQ is included as a covariate (*F*(1, 57) = 5.91, *p* = .02).

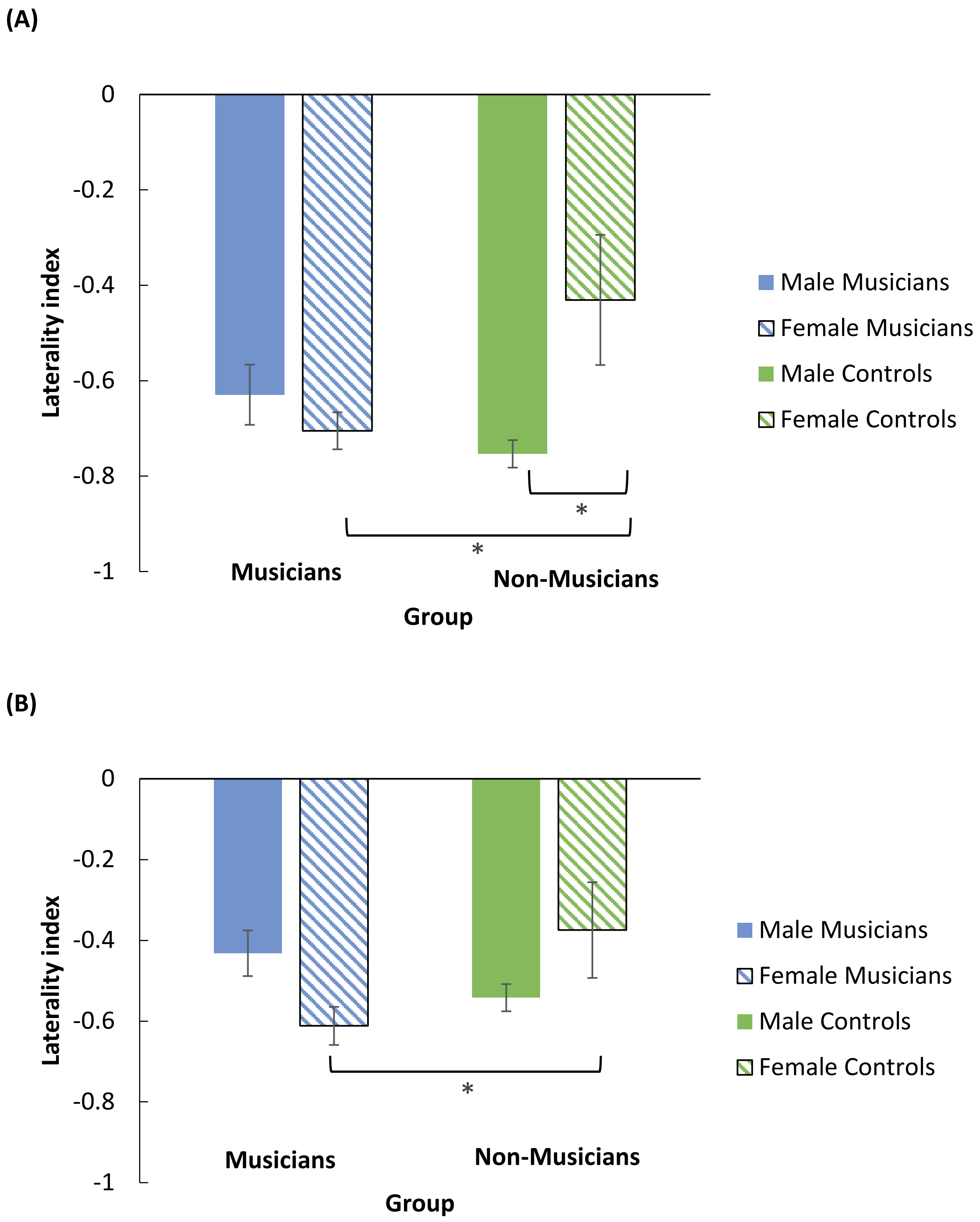


Figure 8. Laterality indices for the Landmark task across *(A)* the whole brain, or *(B)* the fronto-parietal regions of interest, shown for each grouping by musician status and gender. Negative values denote right-lateralisation, while positive values denote left-lateralisation. Error bars indicate standard error of the mean. * *p* < .05

Discussion

The key finding in the Landmark task was that the lateralisation of activation during task performance differed between males and females in the non-musician group, but did not differ between male and female musicians. Female musicians appear to have increased rightward lateralisation during visuospatial processing, reflected both in the fact that female musicians are more right-lateralised than female non-musicians, and in the lack of a gender difference within the musician group. We also found that males had stronger activation of the right inferior parietal lobule than females during the experimental condition. Contrary to our predictions, musicians were not more accurate than non-musicians on the Landmark task, even when considering just the trials where the line was bisected 2% from the veridical centre.

We predicted that musicians would have more bilateral neural activity than non-musicians during the Landmark task. The reasoning behind our prediction was based on previous behavioural findings in which musicians have shown more accurate performance on visuospatial tasks, and an apparent reduction in bias towards the left side of space. For example, musicians had a reduced leftward bias and more accurate line bisection performance, and faster and more accurate visual detection of stimuli appearing fleetingly in the right side of space than matched control participants (Patston et al., 2006; Patston, Hogg et al., 2007). We reasoned that this more “spatially balanced” performance suggested that the left hemisphere may be more equally involved in visual attentional processes in musicians, allowing the more effective orienting of attention to the right side of space in musicians than non-musicians. However, this hypothesis was not borne out; in fact, we found the opposite pattern. Female controls were significantly less lateralised than male controls, but both male and female musicians were strongly right-lateralised. These data suggest that musicians' generally more accurate performance on visual attention tasks (Patston et al., 2006; Patston, Hogg et al., 2007) may instead reflect enhanced or more finely-tuned attentional processes, as a result of heightened functioning in the right-hemispheric regions known to be involved in these processes.

Contrary to our predictions, there were no significant performance differences between musicians and non-musicians in the Landmark task. It is likely, however, that this task is not sensitive enough to detect the changes in performance which were previously observed on manual line bisection tasks (Lega et al., 2014; Patston et al., 2006). With the exception of the trials bisected 2% from centre, the other deviations were very easy to detect as evidenced by the high accuracy of both groups. It is certainly true that this task is not commonly used to assess fine-grained differences in visuospatial abilities between groups, being more typically used as a functional localiser to determine hemispheric dominance for spatial ability (Çiçek, Deouell, & Knight, 2009; Fink et al., 2000). It is also possible that administering this task in a scanner environment minimised group differences by removing the manual element of the task. Perhaps it is this aspect of the task, the manual drawing of a transection mark, on which musicians are more proficient. The novel inclusion of the 2% trials in our study was intended to reveal differences in visuospatial ability between musicians and non-musicians, evident when more subtle discriminations were required, particularly when lines were bisected to the right of centre. Despite trends in the expected direction, there were no accuracy differences on these trials between groups. What was most striking was the very poor performance of both groups on the 2% deviations, indicating they were very difficult to discriminate from trials that were bisected in the centre. The difficulty was undoubtedly enhanced because only 10% of trials (*M* = 11.42, *SD* =

3.17) were bisected 2% from centre (and only half of those were bisected to the right), whereas 50% of trials (*M* = 58.40, *SD* = 12.98) were bisected in the centre, which likely biased participants' responses. While a measure of sensitivity such as *d'* would have enabled the calculation of participants' ability to detect 2% deviations while removing response bias, such an analysis was not suited to this task because of the unequal numbers of 2% and centre trials. Future research should match the number of "centre" and 2% trials to enable the use of sensitivity measures.

There was also an overall gender difference in activation in the right inferior parietal lobule, during performance on the Landmark task, such that males recruited this region more than females. This is consistent with previous work showing that males engage right parietal regions more than females during visuospatial tasks (Hugdahl et al., 2006, Jordan et al., 2002; Weiss et al., 2003). Given that a group by gender interaction was present in the laterality indices, both at a whole brain level and within a set of fronto-parietal regions of interest, it is a little surprising that no such interaction was found in the activation analysis. However, this discrepancy may highlight the enhanced sensitivity of our method to detect differences in lateralisation. Laterality indices assess the relative levels of activity across hemispheres, rather than the level of activity in each independent voxel. Additionally, they take into account activations at a series of statistical thresholds, whereas traditional fMRI analyses only consider activation that survives one corrected threshold.

One explanation for the increased rightward lateralisation in female musicians is that long-term, intensive music training has induced experience-dependent plastic changes in regions related to visuospatial processing. Currently, however, there is no empirical evidence to support this explanation. While there is experimental evidence that music training can increase visuospatial ability in children (Hetland, 2000), no research to date has assessed whether this increase in visuospatial ability in musically trained children is accompanied by an increased rightward lateralisation of visuospatial processing. As our study is quasi-experimental in design, inferences of causation cannot be made directly from these data. The musicians in our sample were a self-selected population, who began training relatively early in life, who persisted with this training, and who have become very proficient. In other words they may have differed from the general population before beginning their musical training, having characteristics that would make them more likely to take up music lessons. Nonetheless, while we cannot rule out this possibility, our groups were matched on several potential confounds, including age, years of education, nonverbal IQ (PIQ), and handedness, and there is no evidence that the marginal differences in verbal (VIQ) and FSIQ influenced our results.

In summary, this study revealed for the first time that the lateralisation of activation during the Landmark task is modulated by gender and musical expertise. Two other visuospatial tasks were also analysed to determine whether this pattern could be observed for other types of visuospatial processing.

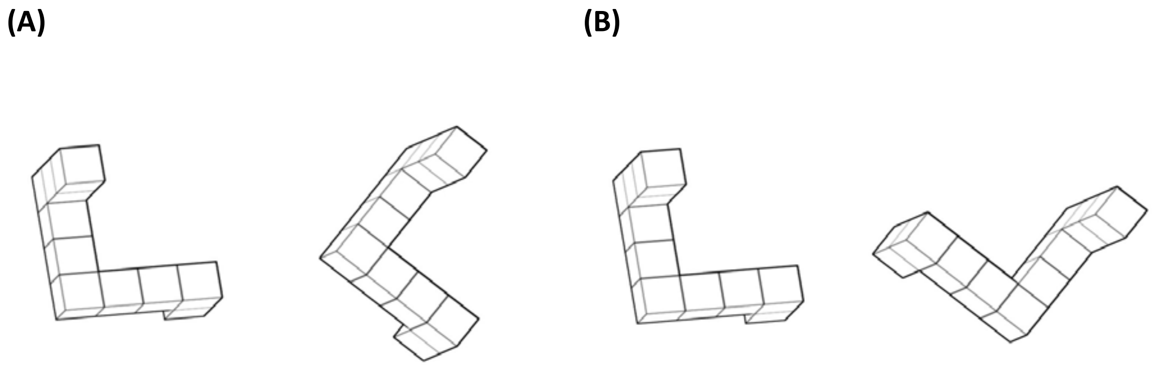
Task Two: 3D Mental Rotation Task (3DMR)

Materials and task procedure

The 3DMR task was based on Shepard and Metzler's (1971) experimental design. Pairs of three-dimensional perspective drawings were displayed simultaneously on the screen; each drawing was composed of 10 cubes arranged in a pattern (see Figure 9). For the current study, two different cube patterns were taken from the stimuli created by Peters and Battista (2008) and manipulated to create 64 pairs of 3D cubes. In each pair, the left-hand form was presented with the major axis vertically oriented, while the right-hand form was rotated in the picture plane to be presented at one of eight possible angles from vertical (0°, 45° to 180° in 45° increments, both clockwise and anti-clockwise). For 12.5% of the trials, the right hand form was presented at each possible angle from vertical, including 0°. In 50% of trials, the paired cube patterns were identical, while in 50% of trials they were mirror images of each other.

Participants were asked to decide whether the two cube patterns were the same, or different (i.e., whether the cube patterns were mirror images of each other), and were given the instruction to mentally rotate the right-hand form of the pair until they could decide whether it did or did not match the left-hand form. Participants used their index finger to respond "same", and their middle finger to respond "different".

Experimental Condition



Control Condition

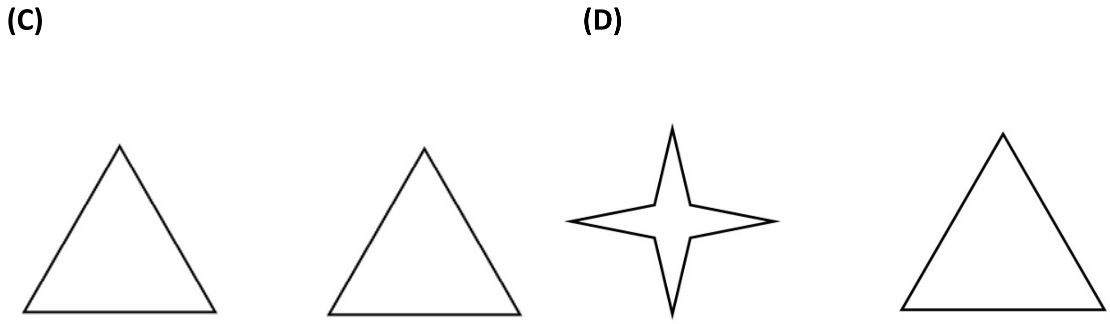


Figure 9. Examples of stimuli for the 3D Mental Rotation task. Experimental condition: “Same” pairs (A) and “different” pairs (B) of 3D perspective drawings of 10 cubes arranged in a chiral pattern with the first of each pair (left-hand pattern) presented with the major axis vertically oriented, and the second (right-hand pattern) presented at one of eight angles from vertical (see Materials; right-hand patterns in (A) and (B) are both at 45°). Subjects decided whether the right-hand figure was identical, but rotated, relative to the left-hand figure, or if the patterns were mirror images of each other (“different”). Control condition: “Same” pairs (C) and “different” pairs (D) of 2D shapes in which subjects decided whether the shapes were identical or not.

The control condition required participants to decide whether a pair of 2D shapes was the same or different (see Figure 9). Ninety-six pairs of 2D shapes were created for this study. On 50% of trials, the pairs of shapes presented were the same, and in 50% of trials they were different. The procedure for this condition was virtually identical to the experimental condition, with the omission of the instruction to mentally rotate either shape. Thus participants were instructed simply to decide whether the two shapes were the same (index finger), or different (middle finger).

The key behavioural variable of interest in both conditions was reaction time (in milliseconds); accuracy (percent correct) was also considered. As the task was self-paced, stimuli were presented centrally until participants made their response by pressing one of two buttons.

Results

Behavioural data

Figure 10 shows that the musician and non-musician groups both demonstrated a pattern of response times generally consistent with what is typically observed in mental rotation tasks (Shepard & Metzler, 1971; Hamm, Johnson, & Corballis, 2004). That is, response times increased in a curvilinear manner as the angle of orientation increased from 0° to 180°, and decreased in the same way from 180° to 315°.

For raw data see Appendix E. The mean number (range) of trials attempted was as follows: control condition, musicians 205.30 (146-266), non-musicians 204.23 (121-267); experimental condition, musicians 37.58 (13-54), non-musicians 45.53 (17-110). Attempted trial counts were submitted to a 2 x 2 x 2 (group x gender x condition) mixed-design ANOVA. This revealed a main effect of condition, with significantly more trials attempted in the control condition (*M* = 204.79, *SD* = 28.92) than in the experimental condition (*M* = 41.37, *SD* = 15.39, *F*(1, 59) = 2388.63, *p* < .001). No other main effects or interactions were significant (all *p* values > .17).

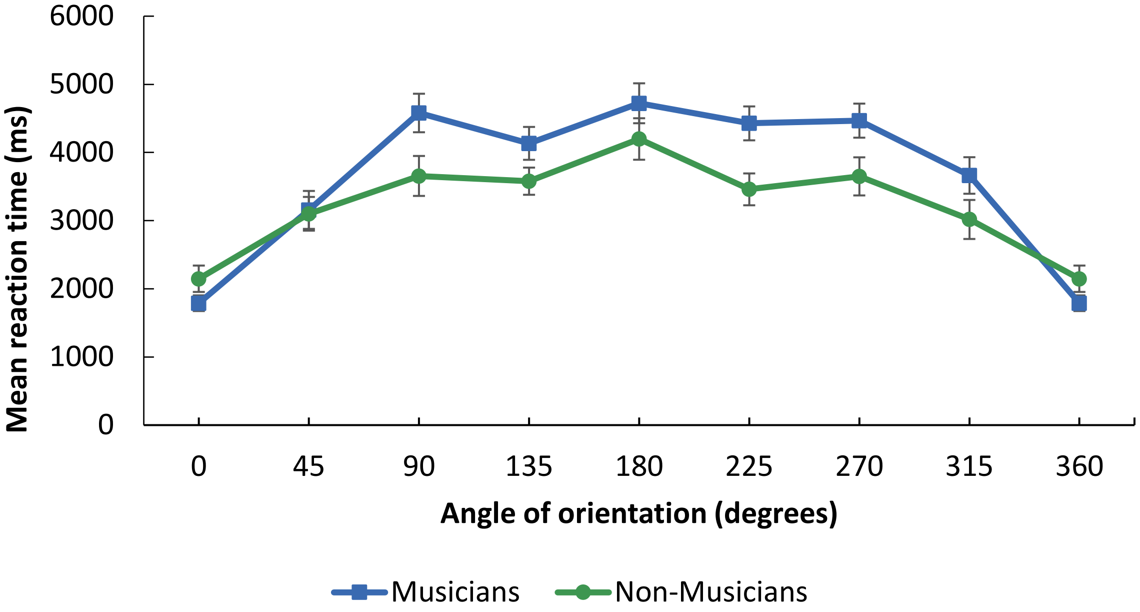


Figure 10. Mean response times for the 3D Mental Rotation task for the musician and non-musician groups. Error bars indicate standard error of the mean. Note that the data points in the figures for 0° and 360° are identical, and are only included to aid visual assessment of symmetry of the orientation effects.

Reaction time

To investigate whether musicians were differentially faster in either condition, a 2 x 2 (group x condition) mixed-design ANOVA was performed with correct trials only. This analysis revealed a significant main effect of condition (*F*(1, 61) = 442.53, *p* < .001), showing that across all subjects reaction times were faster for the control condition than for the experimental condition. Neither the main effect of group (*F*(1, 61) = 2.32, *p* = .13) nor the interaction of group and condition (*F*(1, 61) = 2.85, *p* = .10) were significant.

For the purposes of the remaining reaction time and accuracy analyses, trials on either side of 180° that required the same amount of rotation were collapsed, giving five rotation angles: 0°, 45°, 90°, 135°, and 180°. This procedure is in line with other studies in the mental rotation literature (e.g. Shepard & Metzler, 1971; Lineweaver, Salmon, Bondi, & Corey-Bloom, 2005). After collapsing about the 180°, planned contrasts were used to test for linear, quadratic, and cubic trends. The linear trend component was of primary interest, in light of the Sluming et al. (2007) finding.

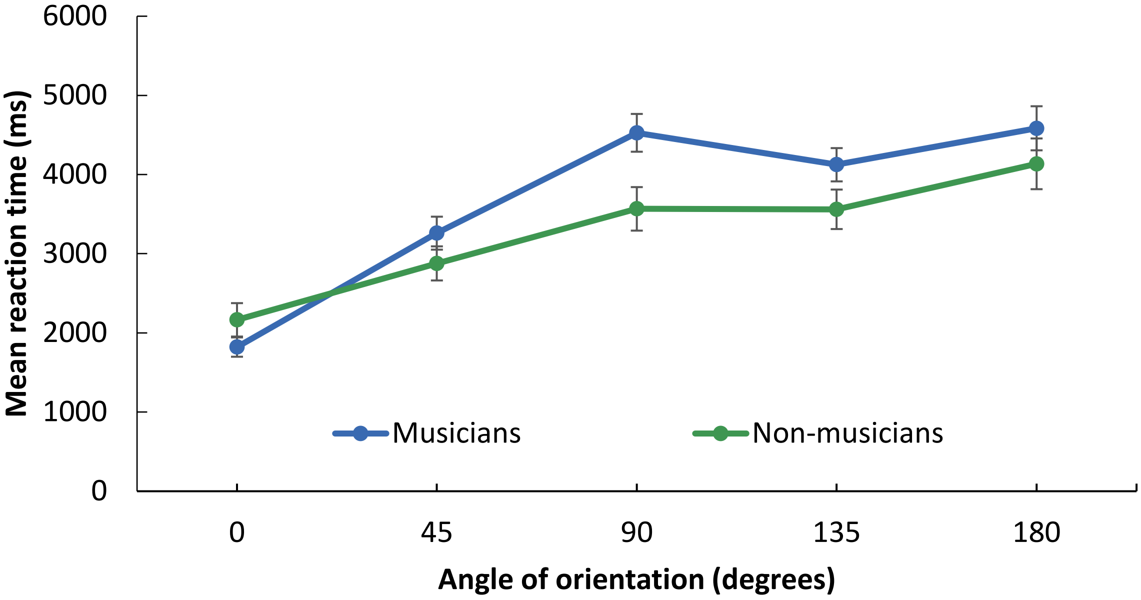


Figure 11. Mean reaction times for the 3DMR Mental Rotation task for musician and non-musicians, plotted as a function of angle of orientation of the right cube pattern. Error bars indicate standard error of the mean.

Reaction time data for correct trials was submitted to a 2 x 2 x 5 (group x gender x orientation) mixed-design ANOVA. As six participants had no correct trials at one or more orientations, this reduced the sample size to 30 (13 female) musicians and 27 controls (13 female). The ANOVA revealed a significant main effect of orientation (*F*(3.4, 181.1) = 76.9, *p* < .001). This effect was associated with a significant linear trend, indicating that reaction times were slower as the cube shapes were rotated further from upright (0°) towards 180° (*F*(1, 53) = 187.87, *p* < .001). There was also a significant linear interaction between group and orientation (*F*(1, 53) = 5.48, *p* = .02), indicating that the slopes of the reaction time functions differed between groups. From examination of Figure 11, it appears that this slope was steeper for non-musicians than for musicians, indicating that non-musicians rotated faster than musicians. However, when planned contrasts were performed separately for musicians and non-musicians, a significant linear trend was evident for both groups (musicians: *F*(1, 28) = 102.13, *p* < .001; non-musicians: *F*(1, 25) = 96.27, *p* < .001). No other main effects or interactions were significant (all *p* values > .15).

Accuracy

Accuracy (percent correct) was also submitted to a 2 x 2 x 5 (group x gender x orientation) mixed-design ANOVA. A significant main effect of orientation was found (*F*(3.40, 179.93) = 35.09, *p* < .001). This effect was associated with a significant linear trend, indicating that accuracy decreased as the cube patterns were rotated further from upright (0°) towards 180° (*F*(1, 53) = 102.09, *p* < .001), as seen in Figure 12, which displays accuracy for males and females at each orientation. There was alsoa significant main effect of gender, with males (*M* = 84.26%, *SD* = 10.01%) being more accurate than females (*M* = 74.48%, *SD* = 12.65%)

overall ($F(1, 53) = 11.89$, $p = .001$). No other significant main effects or interactions were present (all p values > .14).

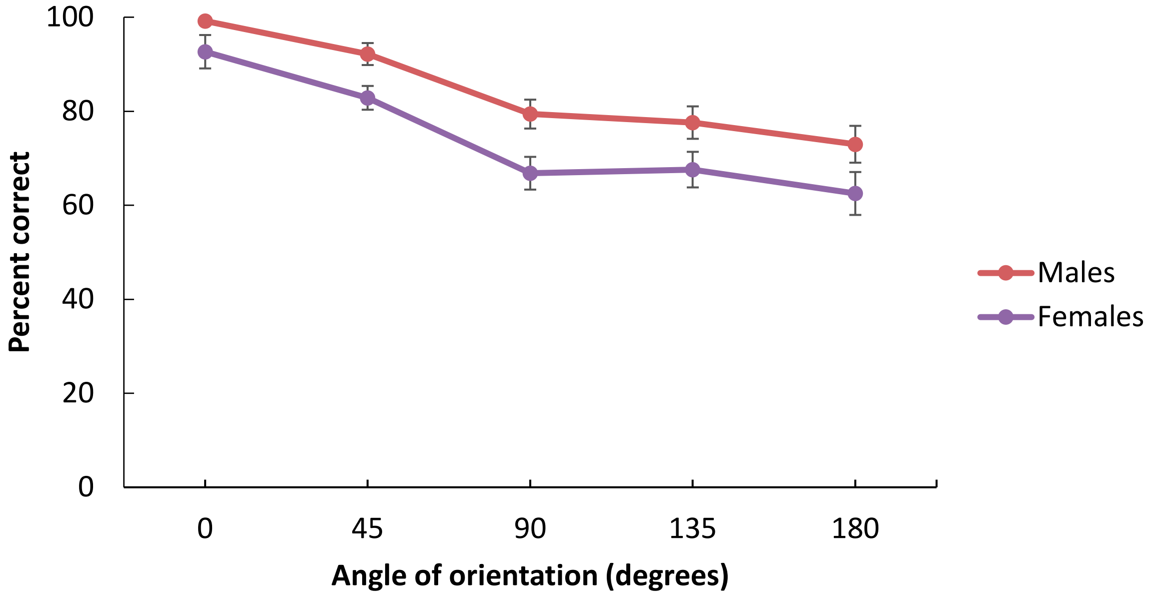


Figure 12. Percent correct on the 3D Mental Rotation task for males and females, for each angle of orientation of the right cube pattern. Error bars indicate standard error of the mean. Males were more accurate than females ($p < .05$).

fMRI data

Group effects

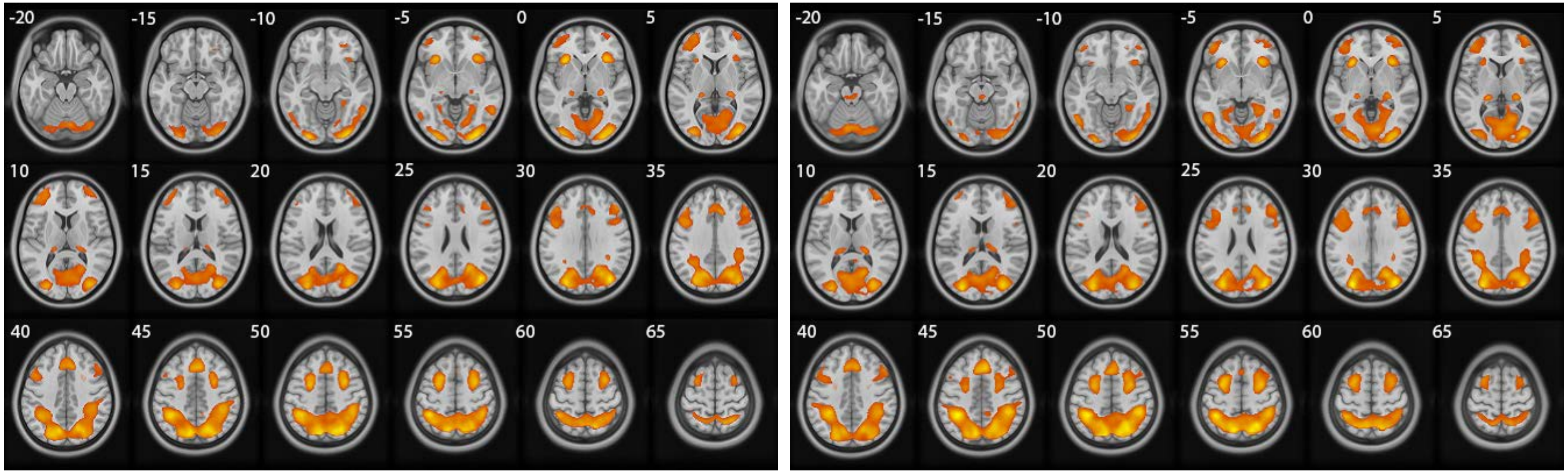
Participants with lower than 60% accuracy for rotated trials in the experimental condition were excluded from the fMRI analyses: 25 musicians (12 female) and 26 non-musicians (12 female) survived this cut-off. In this sample, musicians had significantly higher FSIQ than non-musicians ($p = .01$), with an average IQ increase of 5 points. Despite there being no behavioural differences between the groups on 3DMR, given the size of the between-group difference in FSIQ we took a conservative approach and conducted the group effects and laterality index analyses both with and without FSIQ as a covariate. The groups remained matched on the other characteristics listed in the Method section.

In general, the 3DMR task, relative to the control task, was associated with activation in similar regions in each group: superior parietal lobule, superior frontal gyrus, medial cingulate cortex, inferior frontal gyrus, bilateral insula, middle occipital gyrus, the cerebellum, and the thalamus (shown in Table 5 and Figure 13).

Table 5. Regions activated by musicians and non-musicians during the experimental condition relative to the control condition in the 3DMR task.

Cluster size[1]	Brain Region	MNI coordinates			z-score
		x	*y*	*z*	
Musicians					
26359	R middle occipital gyrus[2]	38	-74	28	8.24
3385	L middle frontal gyrus	-24	0	52	6.94
1856	R inferior frontal gyrus (pars triangularis)	50	32	28	5.90
1289	R superior medial gyrus	4	24	46	6.71
1270	R superior frontal gyrus	28	2	52	7.25
640	L cerebellum (VII)	-34	-68	-50	6.17
535	R insula lobe	32	24	-2	7.27
416	L insula lobe	-30	22	-2	7.56
303	R thalamus	24	-30	6	5.59
199	L thalamus	-20	-30	4	5.48
Non-Musicians					
29453	L middle occipital gyrus[2]	-30	-80	30	8.53
5826	R superior medial gyrus	6	26	44	7.53
2928	L middle frontal gyrus	-30	2	54	7.60
1077	L middle frontal gyrus	-44	50	10	6.02
566	R cerebellum (IX)	18	-48	-46	6.55
538	R insula lobe	32	24	-2	7.57
532	L cerebellum (IX)	-14	-48	-50	7.54
441	L insula lobe	-28	24	-2	7.77
284	L thalamus	-20	-30	4	6.43

Note: All clusters are significant at $p < .05$, corrected for multiple comparisons. Where z-scores were reported as infinite in SPM, *t*-scores were converted to non-infinite z-scores using a method developed by Jenkinson and Woolrich (2002). [1]Cluster size (*k*) indicates the number of voxels comprising the cluster; only clusters with a minimum extent of 182 voxels are reported. MNI = Montreal Neurological Institute, L = left, R = right. [2]Cluster extends into bilateral superior parietal lobule.



Musicians **Non-Musicians**

Figure 13. Regions engaged by 3D Mental Rotation task in musicians and non-musicians. The contrast of the experimental condition relative to the control condition is displayed on axial slices. Activations are shown at a voxelwise threshold of *p* < .001 uncorrected and an extent threshold of 182 voxels, providing correction for multiple comparisons at *p* < .05.

Contrary to predictions, no regions exhibited an increased or decreased task effect in musicians compared to non-musicians. However, relative to females, males activated a cluster in the right superior parietal lobule, extending to the right precuneus, during the 3DMR task (shown in Table 6 and Figure 14). Finally, no regions demonstrated a significant group by gender interaction (that is, a greater gender effect in one group than in the other).

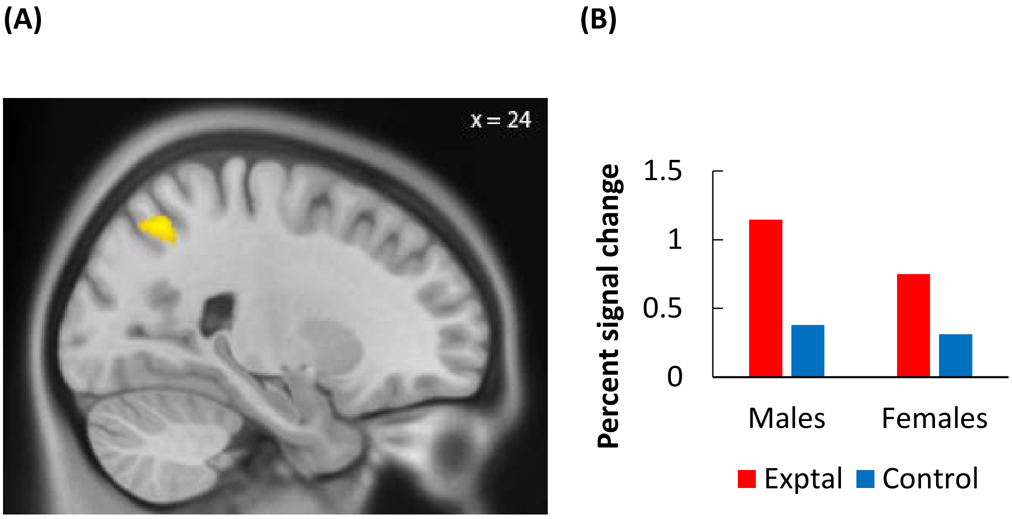


Figure 14. Gender effect in right superior parietal lobule during the 3D Mental Rotation task. (A) An analysis of gender differences in activation during the 3DMR task revealed a cluster in the right superior parietal lobule, extending into the right precuneus which displayed a greater task effect (experimental condition > control condition) in males than females. Activations are shown at a voxelwise threshold of *p* < .001 uncorrected and an extent threshold of 182 voxels, providing correction for multiple comparisons at *p* < .05. (B) Percent signal change data were extracted from a 5mm sphere centred on the peak voxel (*xyz* = 24 -62 50), shown here as a function of each gender and condition.

Table 6. Regions exhibiting a larger task effect in males than in females in the 3DMR task.

Cluster size[1]	Brain Region	MNI coordinates			z-score
		x	*y*	*z*	
256	R superior parietal lobule[2]	24	-62	50	4.17

Note: Cluster is significant at $p < .05$, corrected for multiple comparisons. [1]Cluster size (*k*) indicates the number of voxels comprising the cluster; only clusters with a minimum extent of 182 voxels are reported. MNI = Montreal Neurological Institute, R = right. [2]Cluster extends into right precuneus.[5]

Laterality effects

The laterality of activation was assessed firstly within the whole brain, and secondly within two ROIs (the parietal lobes and the occipital lobes), by entering laterality indices into factorial (group x gender) ANOVAs. These ROIs, inbuilt into the LI-toolbox, were selected on the basis of *a priori* evidence that mental rotation activates parietal and occipital regions (Hattemer et al., 2011; Milivojevic, Hamm, & Corballis, 2009). For raw data, see Appendix G. Across the whole brain, there was a main effect of gender, such that males (*M* = -.22, *SD* = .27) were more right-lateralised overall than females (*M* = -.05, *SD* = .32; *F*(1, 47) = 4.51, *p* = .04).[6] This result is shown in Figure 15. Neither the main effect of group nor the interaction of group and gender were significant (all *p* values > .53).

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[5] Note that when FSIQ is covaried, the activations are still evident but the cluster size does not reach the extent threshold required for corrected significance (cluster size = 142 voxels, threshold = 182 voxels). Including a covariate takes away one degree of freedom; thus it is likely that the cluster is no longer significant due to a slight decrease in power.

[6] Note that this result remains significant when FSIQ is covaried (*F*(1, 46) = 5.82, *p* = .02).

Turning to the ROI analyses, there was a main effect of gender on laterality indices within the occipital lobes. Again, males (*M* = -.29, *SD* = .24) were more right-lateralised than females (*M* = -.1, *SD* = .39; *F*(1, 47) = 4.21, *p* = .046; see Figure 15).[7] Neither the main effect of group nor the interaction of group and gender were significant (all *p* values > .93). Within the parietal lobes, there was no effect of group or gender on laterality indices (all *p* values > .17).

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[7] As for the whole brain, this result remains significant when FSIQ is covaried (*F*(1, 46) = 5.31, *p* = .03).

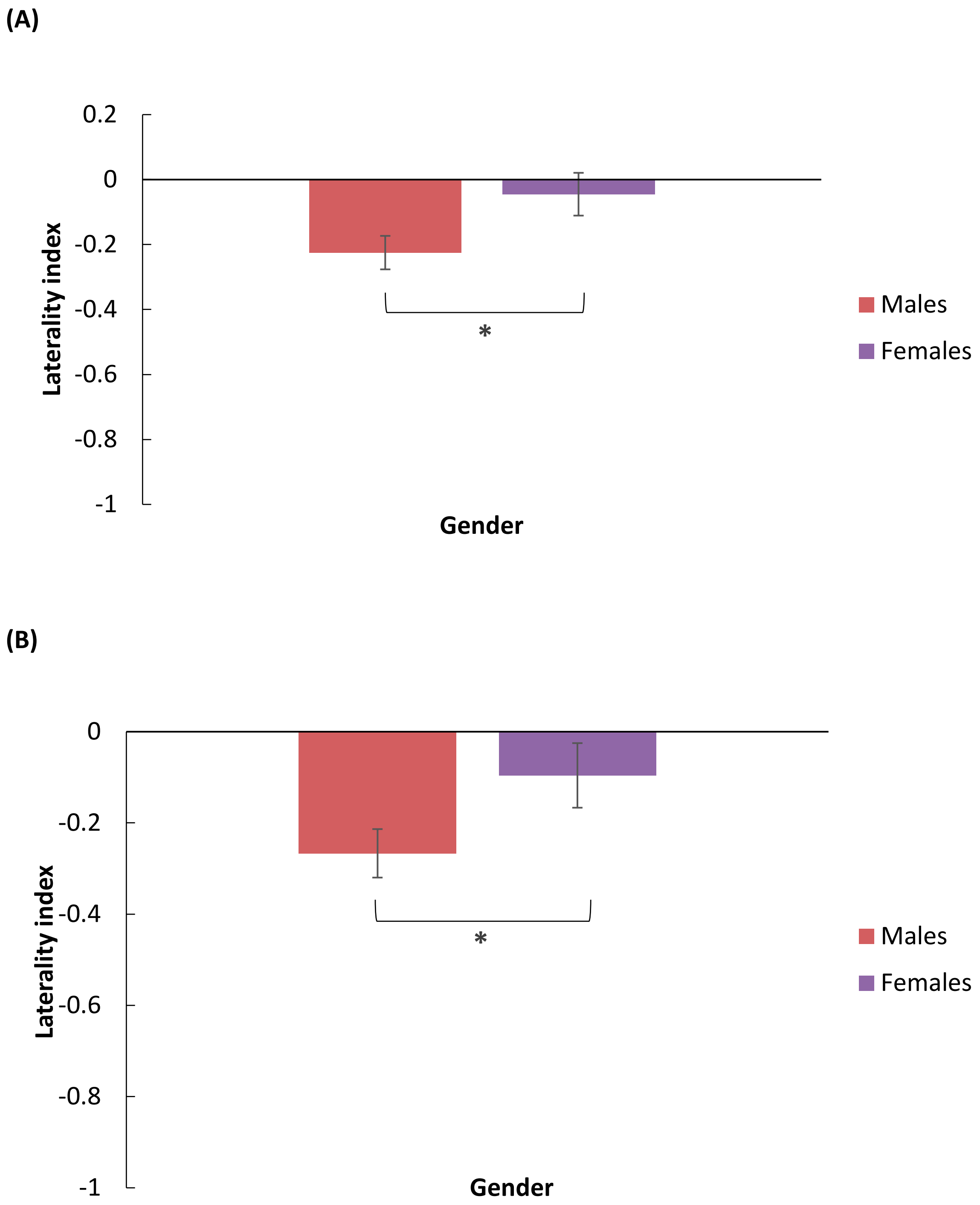


Figure 15. Laterality indices for the 3D Mental Rotation task across *(A)* the whole brain, or *(B)* the occipital lobes, for males and females. Negative values denote right-lateralisation, while positive values denote left-lateralisation. Error bars indicate standard error of the mean. * $p < .05$

Discussion

The main finding in the 3DMR task were that males were both more accurate than females, and had more right lateralised activation within the parietal and occipital lobes during task performance. Males also recruited the right superior parietal lobule to a greater extent than females. The superior parietal lobule borders the intraparietal sulcus, a region previously shown to be involved in mental rotation (Harris, Egan, Sonkkila, Tochon-Danguy, Paxinos, & Watson, 2000; Milivojevic et al., 2009). Together, these results strongly indicate a male advantage in both musicians and non-musicians on this chronometric mental rotation task. On the other hand, contrary to predictions, musicians were not faster than non-musicians on the task, nor did they activate any regions to a greater extent than non-musicians during mental rotation.

The gender difference in accuracy is consistent with previous findings that have demonstrated that gender differences in visuospatial ability are most prevalent on the Mental Rotation Test and on chronometric mental rotation tasks which utilise complex polygons (Heil & Jansen-Osmann, 2008; Jansen & Kaltner, 2014; Peters et al., 2006; Voyer et al., 1995). Although most previous work has identified gender differences in speed of mental rotation, which we did not observe, Jansen and Kaltner (2014) did find that male older adults were more accurate than females on a mental rotation task (the mirror-normal letter task). Using the same cube stimuli as we did, Neubauer, Bergner, and Schatz (2010) also found that males performed more accurately than females.

In comparison to females, males activated the superior parietal lobule more strongly and were also more strongly right-lateralised during mental rotation. Some previous literature has shown that males activate right-hemispheric parietal regions more than females during visuospatial processing (Hugdahl et al., 2006, Jordan et al., 2002; Weiss et al., 2003). Here we also demonstrate an increase in the rightward *lateralisation* of processing in males, showing that activation associated with mental rotation is more heavily concentrated in the right-hemisphere in males than in females.

Contrary to predictions, we could not identify any differences between expert musicians and non-musicians in performance or activation elicited by the 3DMR task. This is surprising given the work of Sluming and colleagues (2007), who found that male orchestral musicians were faster than non-musicians and did not exhibit the typical linear increase in reaction time with increasing rotation from upright. Sluming et al. also found three small areas which musicians activated more strongly than non-musicians during mental rotation performance, the left inferior frontal gyrus (Broca's area), right angular gyrus, and left anterior cingulate gyrus. In contrast, in the current study musicians were not faster than non-musicians, both musicians and non-musicians displayed a clear linear increase in response times with increasing rotation of the stimuli, and we found no regions which musicians activated to a greater extent than non-musicians during execution of mental rotation.

Sluming and colleagues (2007) recruited expert musicians with similar characteristics to our group (although their sample included only male musicians while we included both genders), and used a nearly identical mental rotation task. Given these similarities, the complete failure to replicate their findings is surprising. One way the studies differ is in the nature of the stimuli used. While the 3DMR stimuli used by Sluming et al. were similar in shape to ours, our stimuli pictured a series of cubes joined together into a pattern, whereas theirs were smooth grey-scale shapes. This may have resulted in the use of a different, slower, strategy in which participants may have tried to count the number of cubes in each pattern, or the number of cubes in a particular “arm” of the pattern. This difference alone does not account for our failure to find differences in performance between musicians and non-musicians; however one speculative suggestion is that musicians may be more likely to engage in this strategy due to their exposure to musical notation in which notes are arranged into connected groups, as in chords.

The musician and non-musician groups in Sluming et al.’s (2007) study differed in behavioural performance as well as in brain activation during mental rotation. In addition to the aforementioned group differences in response times, the error rate was significantly higher in controls than in musicians. As the error rates were not equated between groups, the differences in activation between groups could be confounded by the performance differences. That is, musicians likely used mental rotation processes on a greater proportion of trials, as they were more accurate. This suggests that the group differences in activation may relate to a difference in strategy use which supported musicians’ superior performance.

It was striking that both the musician and non-musician groups in our study had much slower response times, on average, than those reported by Sluming and colleagues, who also used a self-paced task design. While our response times are quite slow compared to some previous mental rotation findings (e.g. Kung & Hamm, 2010; Searle & Hamm, 2012), these studies typically recruited young undergraduate students, had many more trials, and were not performed in an MRI scanner. Of note, Olsen, Laeng, Kristiansen, and Hartvigsen (2013) included participants with a wider age range of participants that closely approximates ours, and reported mean response times which were much closer to our means, suggesting that these slower response times are not necessarily atypical of those found in studies involving participants with a broad range of ages. This does not, of course, explain Sluming et al.’s findings, as the mean age of their participants was in fact older than ours.

To conclude, this study found robust gender differences between males and females, both in their performance on a mental rotation task, and in the lateralisation of activation during this task. Unlike the Landmark task, there were no differential patterns across musicians and non-musicians. In the next section, the Visual Search task was employed to determine whether the lateralisation of activation evoked by visual search is also influenced by gender and musical training.

Task Three: Visual Search

Materials and task procedure

The Visual Search Task was a modified version of the task used by Patston and Tippett (2011). The adapted task comprised 20 novel designs, each made up of 12 geometric shapes and 6 grey-coloured dots arranged evenly within an 8cm x 8cm box.

In the experimental condition, a trial comprised two copies of a design presented side-by-side. The two designs were either identical or different in that one dot in the right-hand design had shifted location slightly, relative to its position in the left-hand design. A total of 40 stimuli were designed for this condition using the 20 designs (20 same, 20 different). In 50% of trials the stimuli pairs were the same, and in 50% of trials the stimulus pairs were different. In the different pairs, the dot change had the same chance of occurring in each of the four quadrants of the right-hand design. Example stimuli for the experimental condition are shown in Figure 16.

Participants were asked to determine whether the images were the same or different. As the task was self-paced, stimuli were presented on either side of centre until participants made their response by pressing one of two buttons (index finger “same”, middle finger “different”).

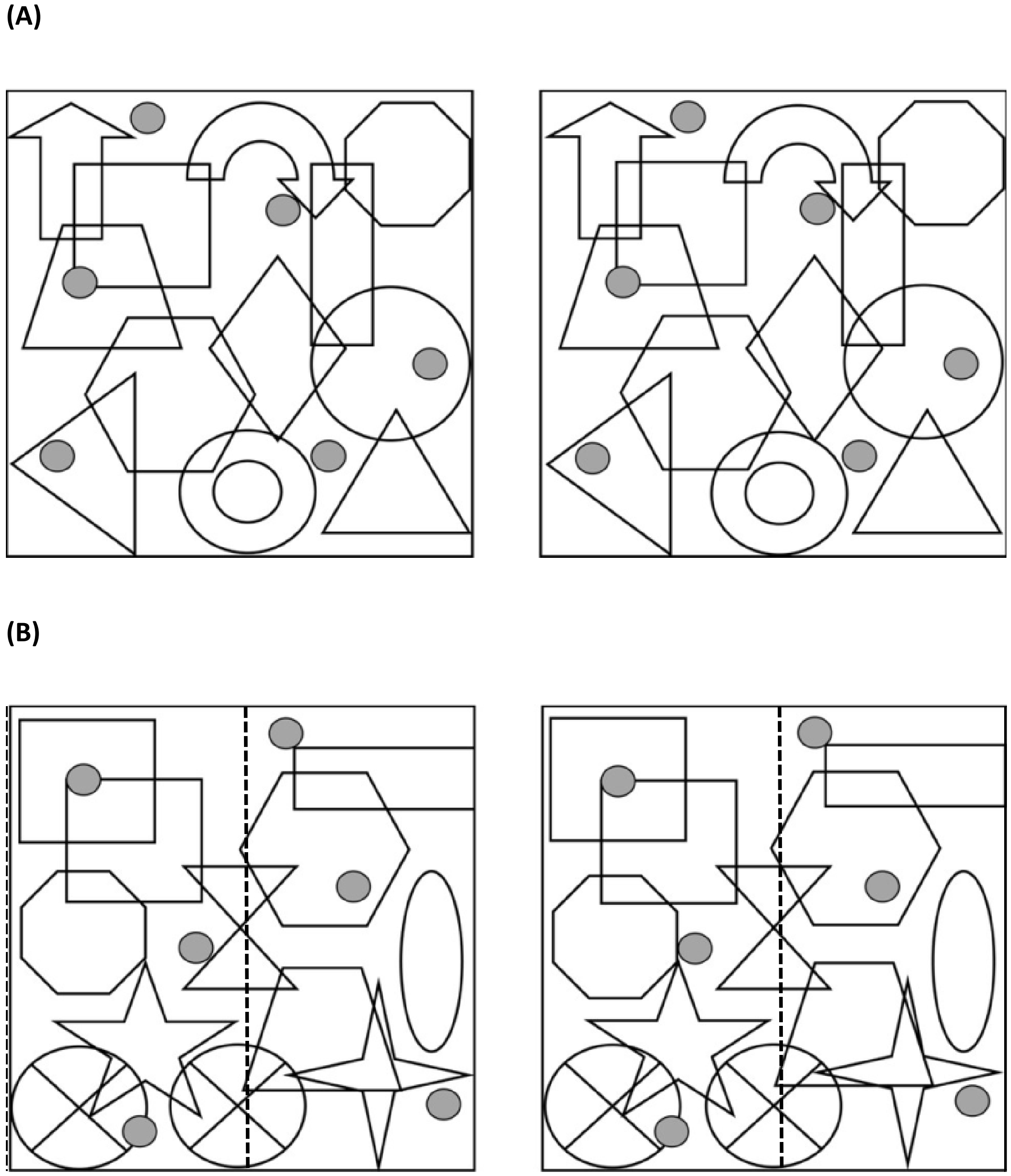
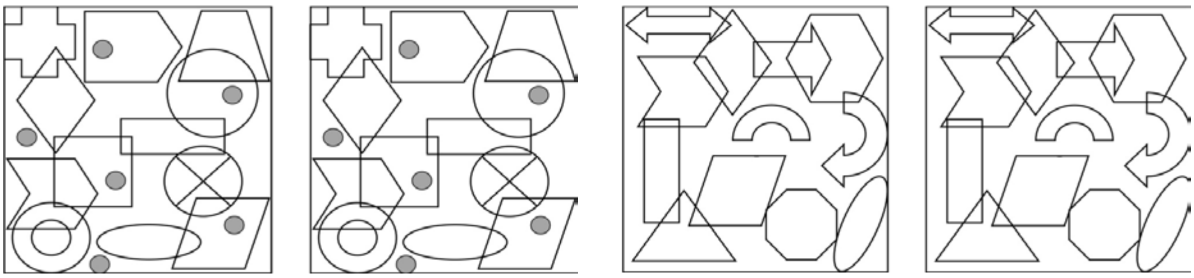


Figure 16. Examples of stimuli for the experimental condition of the Visual Search task. Participants determined if pairs of complex visual designs were the same or different. “Same” pairs contained two identical copies of a design (*A*). For “different” pairs, one of the dots in the right-hand image was moved slightly relative to its position in the left-hand image (*B*, central dot).

In the control condition, participants were presented with pairs of designs which had the same layout of geometric shapes in each design. The two designs were again either identical or different, however in this condition participants only had to decide if there were dots present in both images, or not. The “same” designs from the experimental condition were used for the control condition, but with three extra versions created from each pair, giving a total of 80 stimuli. The images could either have the same configuration of dots in both images (the original images), or no dots in either image, or the stimuli differed in that there were dots in one image but not in the other image. Example stimuli for the control condition are shown in Figure 17.

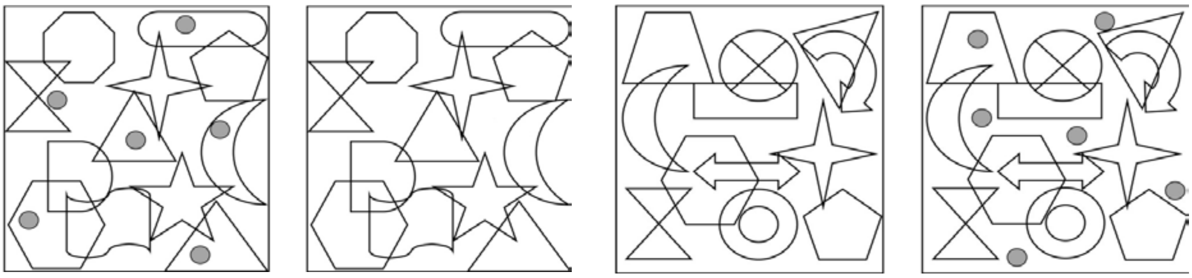
Participants were asked to decide whether the paired designs were the same or different. To make this decision they were instructed to focus only on gross visual differences between the paired designs (that is, whether there were dots present in both images, or not). The procedure for this condition was identical to that of the experimental condition. The key behavioural variable of interest in this task was the reaction time (in milliseconds); accuracy was also considered.

“Same” pairs



(A) **(B)**

“Different” pairs



(C) **(D)**

Figure 17. Examples of stimuli for the control condition of the Visual Search task. As in the experimental condition, participants determined if pairs of complex visual designs were the same or different. “Same” pairs either contained the same configuration of dots and shapes in both images (*A*) or the same configuration of shapes but no dots in both images (*B*). “Different” pairs had dots in one image only, either in the left design (*C*) or the right design (*D*).

Results

Behavioural data

For raw data see Appendix F. The mean number (range) of trials attempted was as follows: control condition, musicians, 178.33 (102-235), non-musicians, 177.27 (117-253); experimental condition, musicians, 28.70 (11-39), non-musicians, 29.93 (11-48). Attempted trial counts were submitted to a 2 x 2 (group x gender x condition) mixed-design ANOVA. This revealed a main effect of condition, with significantly more trials attempted in the control condition (*M* = 177.83, *SD* = 35.0) than in the experimental condition (*M* = 29.29, *SD* = 7.13, *F*(1, 59) = 1301.9, *p* < .001). No other main effects or interactions were significant (all *p* values > .10).

Reaction time

To investigate whether musicians were differentially faster than non-musicians in either condition, a 2 x 2 (group x condition) mixed-design ANOVA was performed with correct trials only. This revealed a significant main effect of condition (*F*(1, 61) = 1196.8, *p* < .001), showing that across all subjects reaction times were faster for the control condition than for the experimental condition. Neither the main effect of group nor the interaction of group and condition were significant (both *p* values > .80).

For the purposes of the remaining reaction time and accuracy analyses, the experimental trials were collapsed into three categories: no dot change, dot change occurring to the left of centre in the design, or dot change occurring to the right of centre in the design (dotted lines in Figure 16 denote the centre of each design; in the example in Figure 16 (B), the dot change occurs to the left of centre). This independent variable was named “dot side”.

Reaction time for correct trials only was submitted to a 2 x 2 x 3 (group x gender x dot movement) mixed-design ANOVA. This analysis found a main effect of dot movement (*F*(1.79, 105.50) = 44.72, *p* < .001). Pairwise comparisons revealed that reaction times were slower on trials where there was no dot movement, compared to trials where there was a left- (*p* < .001) or right-sided (*p* < .001) dot change. The difference in response times to left-sided dot movements and right-sided dot movements, however, was not significant (*p* = 1.00; see Figure 18). No other main effects or interactions were significant (all *p* values > .17). Mean reaction times for each grouping by musician status and gender are shown in Table 7.

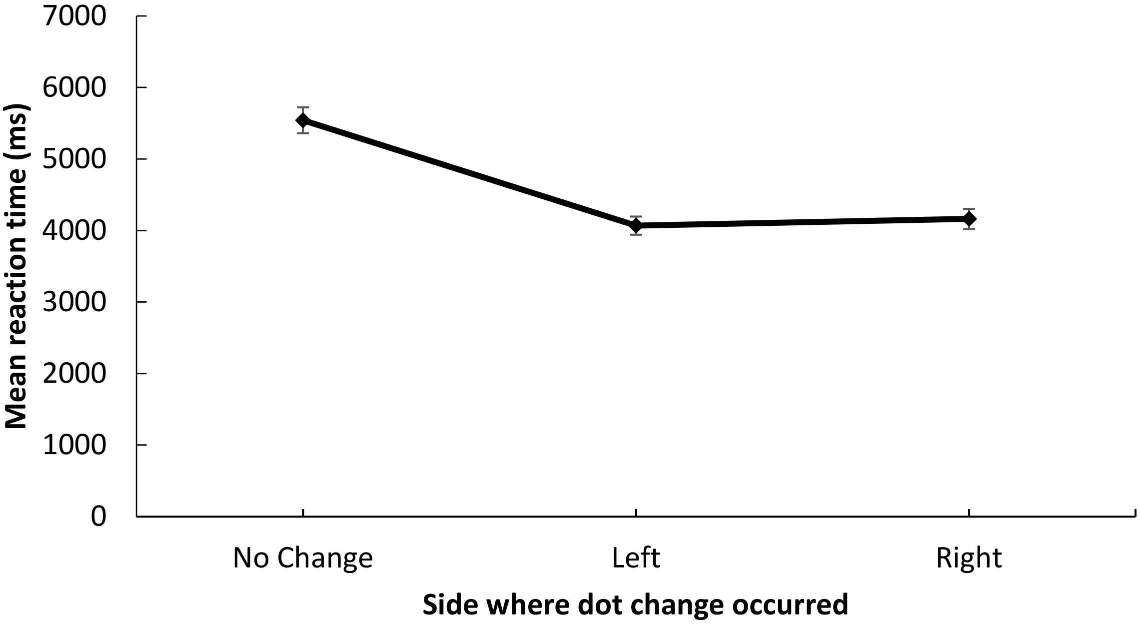


Figure 18. Mean reaction times for the Visual Search task, plotted as a function of side where dot movement occurred. Error bars indicate standard error of the mean.

Table 7. Mean reaction times for the Visual Search experimental trials in male and female musicians and non-musicians.

	Mean RT No Change (SD)	Mean RT Left (SD)	Mean RT Right (SD)
Male Musicians	5579.62 (1652.76)	3742.91 (876.49)	3879.40 (826.35)
Female Musicians	5790.21 (1027.90)	4135.24 (845.59)	4197.35 (942.76)
Male Non-Musicians	5401.83 (1119.21)	4229.02 (1246.71)	3989.26 (954.79)
Female Non-Musicians	5375.16 (1881.09)	4205.90 (1058.26)	4618.20 (1605.80)

Note: RT = reaction time

Accuracy

Accuracy (percent correct) was also submitted to a 2 x 2 x 3 (group x gender x dot movement) mixed-design ANOVA. This analysis also revealed a significant main effect of dot movement ($F(2, 118) = 40.30$, $p < .001$). Bonferroni-corrected pairwise comparisons showed participants were more accurate for trials where there was no dot movement compared to trials where there was a dot movement, whether to the left, or right of centre (both *p* values < .001). There was no difference in accuracy between left-sided and right-sided dot movements ($p = .69$). This result is shown in Figure 19. While it appeared that female controls were less accurate for detecting right-sided dot movements than all other groups, neither the main effect of gender nor the interaction of group and gender were significant (both *p* values > .30). No other main effects or interactions were significant (all *p* values > .11). Percent correct for each grouping by musician status and gender are shown in Table 8.

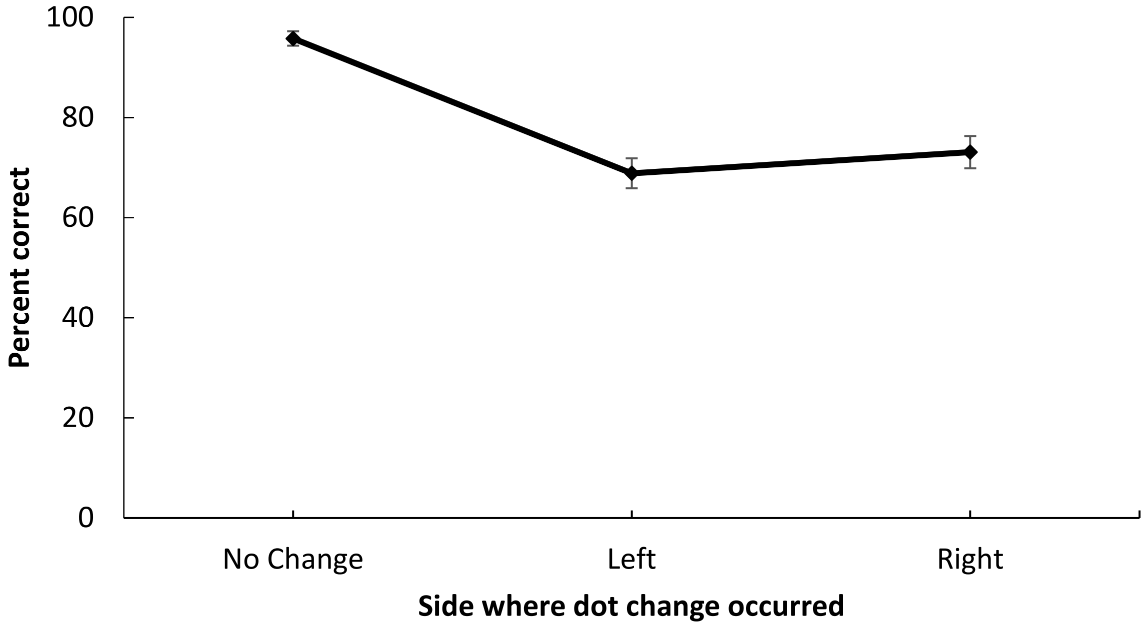


Figure 19. Percent correct for the Visual Search task, plotted as a function of side where dot movement occurred. Error bars indicate standard error of the mean.

Table 8. Percent correct for the Visual Search experimental trials in male and female musicians and non-musicians.

	Acc No Change (SD)	Acc Left (SD)	Acc Right (SD)
Male Musicians	0.94 (0.18)	0.68 (0.27)	0.77 (0.24)
Female Musicians	0.96 (0.10)	0.72 (0.23)	0.78 (0.24)
Male Non-Musicians	0.98 (0.04)	0.72 (0.18)	0.78 (0.24)
Female Non-Musicians	0.96 (0.08)	0.63 (0.27)	0.59 (0.28)

Note: Acc = accuracy (percent correct).

fMRI data

Group effects

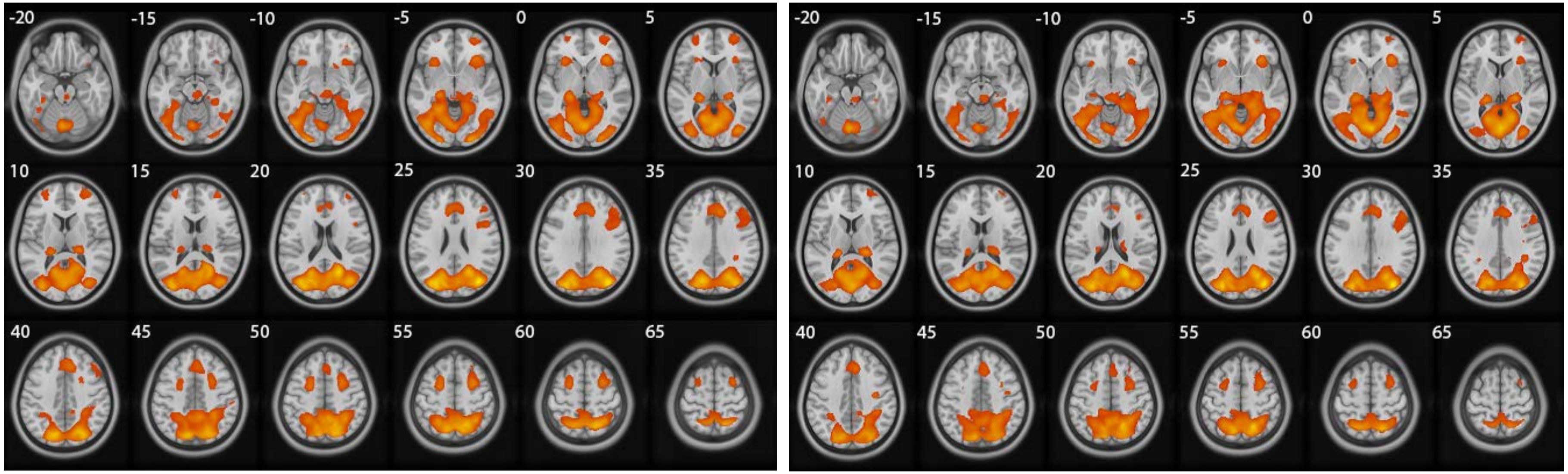
Participants with at least 65% accuracy in the experimental condition were considered to have satisfactory behavioural performance for inclusion in the fMRI analyses. 30 musicians (14 female) and 27 non-musicians (13 female) survived this cut-off. With this sample size, musicians had significantly higher FSIQ than non-musicians (p = .03), with an average IQ increase of 4 points. Although there were no behavioural differences between the groups on the Visual Search task, we conducted the group effects and laterality index analyses both with and without FSIQ as a covariate. The groups remained matched on the other characteristics listed in the Method section.

In general, the Visual Search task, relative to the control task, was associated with activation in similar regions in each group: middle occipital gyrus, cuneus, middle cingulate gyrus, superior, middle and inferior frontal gyri, insula, and the cerebellum (shown in Table 9 and Figure 20).

Table 9. Regions activated in musicians and non-musicians during the experimental condition relative to the control condition in the Visual Search task.

Cluster size[1]	Brain Region	MNI coordinates			z-score
		x	*y*	*z*	
Musicians					
32876	R middle occipital gyrus[2]	36	-78	28	9.89
3147	R superior frontal gyrus	28	2	56	6.76
1683	R insula lobe	34	28	-2	7.19
1241	R inferior frontal gyrus (pars opercularis)	48	10	26	4.86
792	L superior frontal gyrus	-22	-2	52	6.46
544	L insula lobe	-28	26	0	5.97
426	L middle frontal gyrus	-32	60	14	4.90
236	L cerebellum (VII)	-38	-66	-50	4.77
Non-Musicians					
36836	R middle occipital gyrus[2]	36	-78	28	9.58
1481	R middle cingulate gyrus	6	28	38	5.68
966	R middle frontal gyrus	30	2	54	5.86
857	R inferior frontal gyrus (pars triangularis)	48	26	28	5.03
648	R inferior frontal gyrus (pars opercularis)	30	28	-4	6.66
431	L middle frontal gyrus	-26	0	56	4.82
410	R superior frontal gyrus	28	64	12	4.36
240	L insula lobe	-28	24	-6	4.41

Note: All clusters are significant at $p < .05$, corrected for multiple comparisons. Where z-scores were reported as infinite in SPM, *t*-scores were converted to non-infinite z-scores using a method developed by Jenkinson and Woolrich (2002). [1]Cluster size (*k*) indicates the number of voxels comprising the cluster; only clusters with a minimum extent of 184 voxels are reported. MNI = Montreal Neurological Institute, L = left, R = right. [2]Cluster extends into right superior parietal lobule.



Musicians

Non-Musicians

Figure 20. Regions engaged by Visual Search task in musicians and non-musicians. The contrast of the experimental condition relative to the control condition is displayed on axial slices. Activations are shown at a voxelwise threshold of $p < .001$ uncorrected and an extent threshold of 184 voxels, providing correction for multiple comparisons at $p < .05$.

Contrary to predictions, no regions exhibited an increased or decreased task effect in musicians compared to non-musicians. However, males activated the right superior parietal lobule more than females during the Visual Search (shown in Table 10 and Figure 21). Finally, no regions demonstrated a significant group by gender interaction (that is, a greater gender effect in one group than in the other).

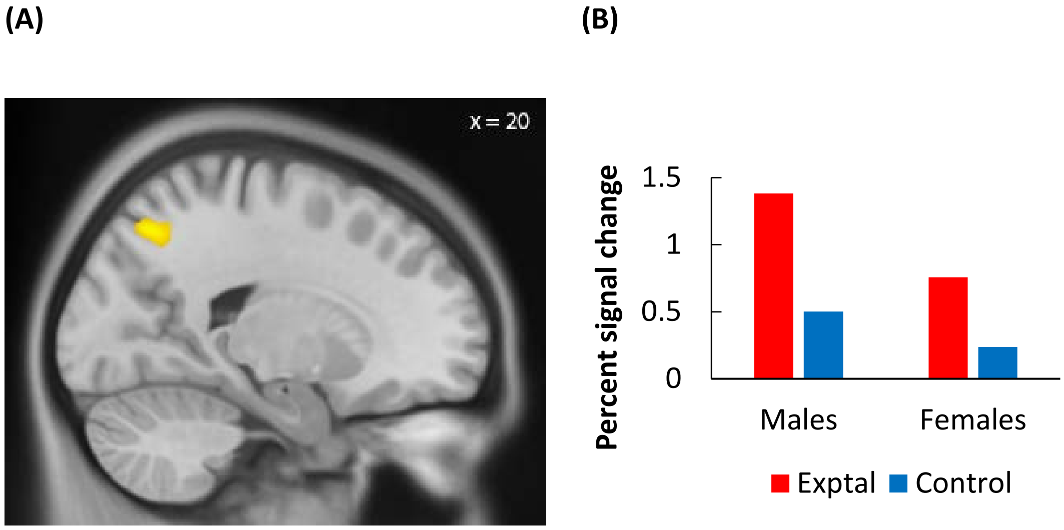


Figure 21. Gender effect in right superior parietal lobule during the Visual Search task. (A) An analysis of gender differences in activation revealed a cluster in the right superior parietal lobule which displayed a greater task effect (experimental condition > control condition) in males than females. Activations are shown at a voxelwise threshold of p < .001 uncorrected and an extent threshold of 184 voxels, providing correction for multiple comparisons at p < .05. (B) Percent signal change data were extracted from a 4mm sphere centred on the peak voxel (*xyz* = 20 -68 50), shown here as a function of gender and condition.

Table 10. Regions exhibiting a larger task effect in males than in females during the Visual Search task.

Cluster size*	Brain Region	MNI coordinates			z-score
		x	*y*	*z*	
312	R superior parietal lobule**	20	-68	50	4.25

Note: Cluster is significant at $p < .05$, corrected for multiple comparisons.[8] *Cluster size (*k*) indicates the number of voxels comprising the cluster; only clusters with a minimum extent of 184 voxels are reported. MNI = Montreal Neurological Institute, R = right. **Cluster extends into right angular gyrus.

Laterality effects

The laterality of activation was assessed firstly within the whole brain, and secondly within two ROIs (the parietal lobes and the frontal lobes), by entering laterality indices into factorial (group x gender) ANOVAs. These ROIs, inbuilt into the LI-toolbox, were selected on the basis of *a* priori evidence that visual search studies engages parietal and frontal regions, especially during serial search conditions with multiple distractors (Anderson et al., 2007; Ogawa & Macaluso, 2015). For raw data, see Appendix G.

There were no significant main effects or interactions of laterality indices across the whole brain, or within either ROI (all p values > .10). In general, it appeared that this task was not associated with lateralised activation. To test this observation statistically, laterality indices for the whole brain were subjected to a one-sample t-test. This analysis found that laterality indices did not differ significantly from zero ($t(56) = 1.52$, $p = .14$), indicating a lack of significant lateralisation. To illustrate this result, laterality indices across the whole brain are plotted by group and gender in Figure 22.

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[8] Note that this cluster is still significant at a corrected level when IQ is covaried (cluster size = 211 voxels).

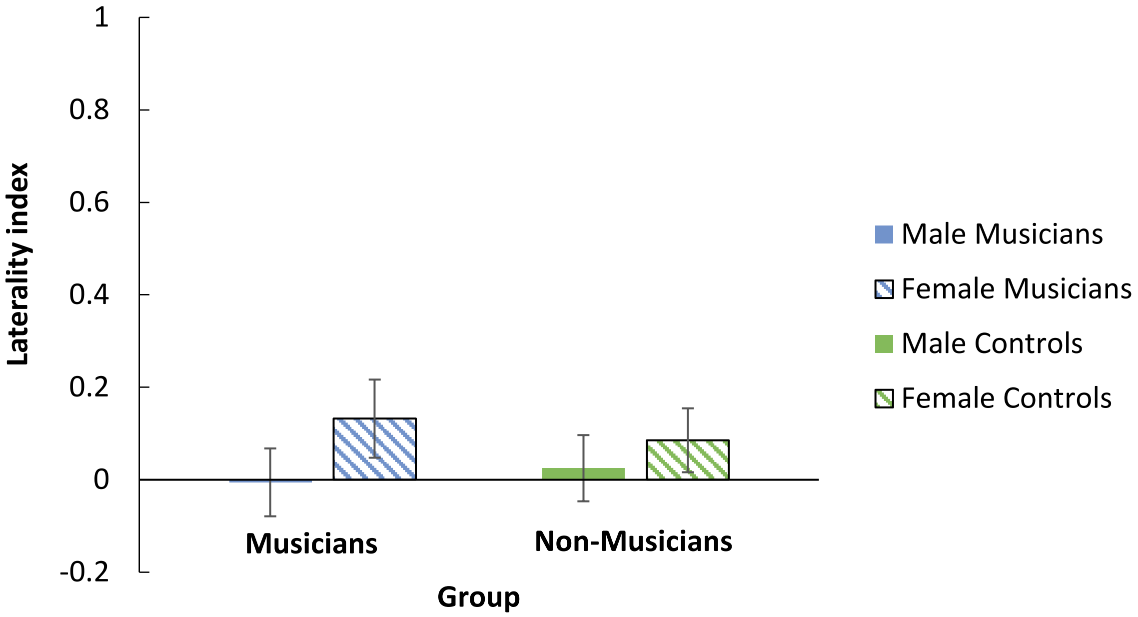


Figure 22. Laterality indices for the Visual Search task across the whole brain, shown for each grouping by musician status and gender. Negative values denote right-lateralisation, while positive values denote left-lateralisation. Error bars indicate standard error of the mean.

Discussion

The only finding of note on the Visual Search task is that males activated the right superior parietal lobule more than females during task performance. This region overlaps substantially with the cluster which males activated more than females on the Landmark task, and neighbours the cluster showing the same effect on the mental rotation task. This finding once again suggests that males are recruiting right hemisphere regions linked with visuospatial processing more than females, although in this task there was no difference between males and females in the laterality of visuospatial processing. Contrary to our hypothesis, there was no difference between musicians and non-musicians in their performance on this task or in the patterns of activation elicited by this task, which looked very similar between the two groups. We also did not observe a reduction in laterality of processing during this task in musicians; indeed, in general, activation was not significantly lateralised for this task.

Across musicians and non-musicians of both genders, reaction times were slower but accuracy was higher when there was no dot movement (i.e. the two images were identical). The faster reaction times when a dot movement is present indicates self-terminating visual search, where as soon as a dot movement is detected a “different” judgement can be made (e.g. Hoffman, 1979). The slower reaction times where no dot movement was present reflect the fact that all dot positions must be compared between the left and right images before the decision can be made that the images are the same. There was no difference between the performance of males and females; while it appears that female controls were selectively less accurate for dot movements in the right image, this observation did not reach significance.

There was also no difference between musicians and non-musicians in terms of the number of trials completed, reaction time, or accuracy. Patston and Tippett (2011) found in their behavioural study that musicians completed significantly more items than non-musicians on this task, so we expected musicians in this study to have the same advantage. However, where Patston and Tippett used a paper-and-pencil test, our task was computerised and administered in the MRI scanner, an environment shown to influence performance on cognitive tasks (Koten, Langner, Wood, & Willmes, 2013; van Maanen, Forstmann, Keuken, Wagenmakers, & Heathcote, 2015). The direction of this influence is unclear, however, with one study finding slower response times and a higher error rate on a perceptual decision task in the scanner (van Maanen et al., 2015), while another observed *faster* response times in the scanner (Koten et al., 2013). There were additionally differences in the stimuli between studies: Patston and Tippett used coloured dots, where ours were greyscale. This change may have made the dot movements harder to detect in our study.

In general, this task elicited a bilateral network of regions, including visual cortices, cuneus, cingulate cortices, and several frontal regions including the frontal eye fields, which may reflect the need for rapid saccades between the left and right image pairs (e.g. Petit, Clark, Ingeholm, & Haxby, 1997). The set of regions activated is similar to those reported in previous visual search tasks with complex displays (Anderson et al., 2007; Kim, Eliassen, Lee, & Kang, 2012; Ogawa & Macaluso, 2015). The involvement of lateral frontal regions likely reflects the working memory requirements of this task, or a mechanism guiding the serial allocation of visuospatial attention (Anderson et al., 2007). The lack of hemispheric asymmetry of task-related activation associated with this task was confirmed by the laterality indices for the whole brain, which did not differ significantly from zero.

To conclude, consistent with the results of the Landmark Task and the 3DMR task, this study found a robust effect of gender on the neural correlates of visuospatial processing during the Visual Search task. There was however no difference between musicians and non-musicians in terms of neural function or behaviour. This pattern of results is discussed in more depth in the General Discussion.

General Discussion

Overall, the three tasks presented in this study produced two key findings. Firstly, there were robust gender differences in brain activations during performance of visuospatial tasks. Secondly, musical training selectively altered the lateralisation of activation in females during the Landmark task. These results are discussed in the following sections.

Gender differences in visuospatial processing

In all three studies, activation in regions within the right posterior parietal cortex was modulated by gender, with males recruiting these regions to a greater extent than females. The posterior parietal cortex, particularly the superior parietal lobule, is known to play an important role in visuospatial attention, and is a key node within the dorsal attention network (Corbetta & Shulman, 2002; Fan et al., 2005). Some previous studies have similarly found greater visuospatial-related activation in males in posterior parietal cortex (Gur et al., 2000; Hugdahl et al., 2006, Jordan et al., 2002; Weiss et al., 2003; but see Halari et al., 2006). Our study adds to this literature by demonstrating a consistent increase in activation in males across three visuospatial task which tap into different visuospatial processes (visuospatial attention, mental rotation, and visual search).

Males also outperformed females on the 3DMR task, congruent with other research finding male advantages on mental rotation (Heil & Jansen-Osmann, 2008; Jansen & Kaltner, 2014; Peters et al., 2006; Voyer et al., 1995). Males and females were matched on years of education, verbal and nonverbal IQ, ruling out these potential confounds. Our data do not speak to the underlying causes of these gender differences. In previous work, however, gender differences in spatial ability have been variously attributed to levels of prenatal androgen exposure, brain lateralisation, and differences in exposure to sex-typed activities and experiences that enhance spatial skill (Feng et al., 2007; Hahn et al., 2010; Puts, McDaniel, Jordan, & Breedlove, 2008). Importantly for our study, experimental research indicates that musical training may be one such experience that increases spatial abilities (Hetland, 2000).

Gender differences influenced by musical expertise

Performance on the Landmark task, which predominantly indexes visuospatial attention, revealed a difference in the laterality of visuospatial processing between musicians and non-musicians that was modulated by gender. That is, while male and female musicians were both strongly right-lateralised, female controls were significantly less strongly right-lateralised than male controls. This is, to our knowledge, the first time such an interaction between musical training and gender and lateralisation has been demonstrated with fMRI data.

In the general population, males frequently outperform females on visuospatial tasks (Christova et al., 2008; Hausmann et al., 2002; Hausmann, 2005). Previous studies have also found that while males have right-lateralised patterns of brain activity during visuospatial tasks, females have more bilateral activation (Hugdahl et al., 2006; Semrud-Clikeman et al., 2012; Siegel-Hinson & McKeever, 2002; Vogel et al., 2003). We found that this gender difference in lateralisation was reduced in musicians, which suggests that musicial training may shift the lateralisation of visuospatial attention rightward for females, whereas males may already have a strong, perhaps “optimal” rightward pattern of lateralisation. Theories of cerebral lateralisation posit that functional specialisation of the hemispheres for specific cognitive functions is computationally beneficial (Plaut & Behrmann, 2011), and some research shows that the degree of lateralisation is associated with level of ability on verbal, nonverbal, and mathematical tasks (Crow, Crow, Done, & Leask, 1998). Musical training could facilitate a neuroplastic change in this direction in females by training musicians to make rapid spatial discriminations between notes on the stave, and translate those into their associated motor movements. Of course, as this research was cross-sectional, it is also possible that the female musicians in our samples had differences in cerebral lateralisation which were not due to their music training, but that may have even predated their training. Longitudinal research would be required to prove that music training induces this shift in laterality. Previous work in children, however, has demonstrated at least short-term enhanced visuospatial processing after music training which was not present before training (Costa-Giomi, 1999; Hetland, 2000).

These findings were contrary to our prediction that musicians would have reduced lateralisation of visuospatial processing. Our hypothesis was based on our interpretation of previous behavioural and electrophysiological studies in which musicians appeared to have enhanced visuospatial attention in the right side of space and had more equal rates of visual information transfer between the two hemispheres (Patston et al., 2006; Patston, Hogg et al., 2007; Patston, Kirk et al., 2007). Clearly this hypothesis was not correct. On reflection, the patterns of performance in those studies are not incompatible with the opposite position, that of enhanced visuospatial functioning of the right hemisphere. More accurate line bisection performance and the ability to detect dots equally well regardless of whether they are presented to the left or right side of space could reflect superior visuospatial processing overall, rather than greater recruitment of the left hemisphere in these processes.

No regions in any of the tasks were associated with significant increases or decreases in activation in musicians relative to non-musicians. Two previous studies using fMRI have found differences between musicians and controls in activations related to visuospatial processing. In a longitudinal training study Stewart and colleagues (2003) found that adults taught to play piano melodies activated the right superior parietal lobule during a music reading task to a greater extent after training. However, the cluster they identified is quite small and is reported at an uncorrected threshold, increasing the chance that this result is a false positive. Only one other study assessed the functional neural correlates of visuospatial ability using a *non-musical* task in musicians and non-musicians. Using a mental rotation task Sluming and colleagues (2007) found three very small clusters (at a corrected threshold) in the left inferior frontal gyrus (6 voxels), right angular gyrus (6 voxels), and left anterior cingulate gyrus (14 voxels) that were differentially activated by musicians during mental rotation. Sluming's musician group was strikingly more homogeneous than ours, composed entirely of male orchestral musicians who in fact all belonged to the same orchestra. We included male and female musicians from a diversity of musical settings (a university performance music programme, orchestras, and choirs), who, while still possessing a high level of proficiency, likely varied more in their level of expertise than Sluming's group. As indicated above, the clusters reported by Sluming and colleagues are so small that it is conceivable that they would be harder to detect in our more heterogeneous sample.

What is more surprising was the lack of a behavioural advantage for musicians on our three tasks. Previous findings led us to expect group differences, at least on the 3DMR and Visual Search tasks (Patston & Tippett, 2011; Sluming et al., 2007). One previously unmentioned factor that could have played a role in the absence of behavioural differences between the groups is that musicians may have been more affected than non-musicians by the scanner noise. MRI noise, especially during EPI functional runs, often falls into rhythmic patterns. There is evidence that in older adults, who are more sensitive to distraction, scanner noise can affect performance on memory tasks (Stevens, Hasher, Chiew, & Grady, 2008). Musicians have highly tuned auditory systems, and, compared to non-musicians, have better beat perception and increased audio-motor coupling when listening to musical rhythms (Grahn & Rowe, 2009). Therefore, it is possible that musicians might be particularly sensitive to the increased and rhythmic noise in the scanning environment. There is currently no empirical evidence demonstrating a link between musical expertise and scanner performance, so this suggestion remains speculative for the time being.

In summary, despite the lack of behavioural differences on these tasks, the lateralisation of visuospatial attention, as indexed by the Landmark task, is modulated by musical expertise and gender. This finding is novel and could be expanded on in the future by considering whether training on certain types of instruments is more conducive to producing these kinds of changes in lateralisation, or identifying which specific aspects of musical training might lead to this change. Longitudinal research is also needed to confirm the causal link between music training and lateralisation differences. Gender differences in visuospatial processing were observed on all three tasks, with the most robust effects evident on the 3DMR task. These findings expand on the existing literature and provide a new variable, gender, which should be considered in research with expert musicians.

Chapter 3: Study Two - Structural connectivity and laterality in musicians

Introduction

Study One examined *functional* lateralisation in musicians and non-musicians during visuospatial task performance in an fMRI paradigm. The original plan for *Study Two* was to use regions in which there were task-based activation differences between musicians and non-musicians as seeds for the study of underlying *structural* connectivity of associated white matter tracts. The aim was to investigate whether altered structural lateralisation, or altered white matter organisation in general, underpinned functional and behavioural differences in visuospatial processes. The more general rationale for this study was based on the premise that in expert musicians, myelination of white matter tracts could be a key mechanism of neuroplasticity (Fields, 2005), and underlie variations in proficiency and lateralisation of visual processes. Given that normal development of myelination continues through adolescence and at least until early adult life (Giedd, 2004; Tamnes et al., 2010), prolonged training during childhood and adolescence, when neuroplasticity may be enhanced by developmental processes, may have shaped the white matter architecture underlying not only musical processes, but also cognitive processes *beyond* specific trained skills.

As there were no activation differences between the musician and non-musician groups in the fMRI tasks, the aims of this study were broadened, to include between-group comparisons of white matter tracts identified as important in musical processes.

DTI as an imaging method

The main method used to non-invasively examine the organisation of white matter *in vivo* in humans is diffusion tensor imaging (DTI). DTI is a type of diffusion-weighted MRI scan which measures water diffusion through the displacement of water molecules within each voxel. According to the principle of Brownian motion, particles suspended in a fluid move randomly. However, this motion is not completely random in biological tissues, with different tissues constraining water diffusion to varying extents. In isotropic diffusion, such as in the cerebrospinal fluid, water can diffuse freely in all directions. In anisotropic diffusion, water diffuses preferentially in one direction. In normal white matter, cell axons are highly aligned and myelinated. This constrains diffusion such that water preferentially diffuses along the length of the axon rather than across it. In DTI, water diffusion is modelled by fitting a tensor (ellipsoid) at each voxel. This tensor is associated with three eigenvectors modelling the three main directions in 3D space. From these three eigenvectors, key measurements can be derived.

The most commonly reported parameter is fractional anisotropy (FA), which gives information about the degree of directionality of water diffusion (anisotropy) in each voxel. FA has been associated with different structural properties of white matter including axonal size and density, alignment of fibres, level of myelination, and fibre complexity (Beaulieu, 2002). FA values range between 0 and 1, where 0 is completely isotropic diffusion, and 1 is completely anisotropic diffusion (occurring only along one axis). Mean diffusivity (MD) provides a measurement of the mean amount of diffusion in all directions, again ranging from 0 to 1. MD is typically higher in damaged tissues as a result of increased free diffusion, and higher FA values are typically associated with lower MD values (e.g. Pfefferbaum & Sullivan, 2003).

Other parameters such as axial diffusivity (AD) and radial diffusivity (RD) can also be derived. AD, also known as parallel diffusion, represents the amount of diffusion along the main direction of diffusion, or the principal diffusion direction. RD, also known as perpendicular diffusion, represents the mean amount of diffusion along the other two diffusion directions which are modelled by the diffusion tensor model. Higher FA values typically reflect high AD and low RD. However, as Beaulieu (2002) points out, it is possible for two regions with the same anisotropy values to have very different underlying diffusion profiles, and thus, AD and RD can be used to characterise the white matter microstructure more completely than FA alone. A schematic of the diffusion tensor model, demonstrating how the three eigenvectors are used to calculate these parameters, is shown in Figure 23.

Tractography is used to track white matter fibres and visualise white matter tracts by following the principal diffusion directions of each voxel. The two major approaches are deterministic tractography and probabilistic tractography. In deterministic tractography, tracking continues until the anisotropy value of a voxel falls below a predetermined cut-off value, or if the angle between the principal diffusion directions for two voxels exceeds 35-40 degrees. On the other hand, probabilistic tractography estimates the *uncertainty* in the direction of tracking at each voxel. It estimates a principal fibre orientation at each voxel, as well as a probability distribution. Unlike deterministic tractography, the algorithm does not use stopping criteria such as an anisotropy value cut-off, allowing for tracking into areas with lower anisotropy.

Isotropic

Anisotropic

Fractional anisotropy (FA):

$$\sqrt{\frac{3}{2}}\sqrt{\frac{(\lambda_1-\overline{D})^2+(\lambda_2-\overline{D})^2+(\lambda_3-\overline{D})^2}{\sqrt{\lambda_1^2+\lambda_2^2+\lambda_3^2}}}$$

Where $\overline{D}$ is the trace of the diffusion tensor defined as:

$$\overline{D} = \lambda_1+\lambda_2+\lambda_3$$

Mean diffusivity (MD): $$\frac{(\lambda_1+\lambda_2+\lambda_3)}{3}$$

Axial diffusivity (AD): $$\lambda_1$$

Radial diffusivity (RD): $$\frac{(\lambda_2+\lambda_3)}{2}$$

Figure 23. Schematic of the diffusion tensor model and mathematical equations for the key DTI parameters. * λ_1 = first eigenvector; λ_2 = second eigenvector; λ_3 = third eigenvector

DTI studies in musician populations

Several studies have utilised the principles of DTI to investigate differences between musicians and non-musicians in white matter microstructure. Musical expertise has been commonly associated with increased FA in several white matter tracts. For example, early work with a sample of eight pianists found that one cluster of voxels within the right posterior limb of the internal capsule had higher FA in musicians than in non-musicians (Bengtsson et al., 2005). A later study with a larger sample of pianists found increased FA in musicians in a more extensive set of regions including the right posterior limb of the internal capsule, midbrain, and the left inferior frontal gyrus (Han et al., 2009). Other research has also found increased FA in musicians in the corticospinal tract (Rüber et al., 2013). As the corticospinal tract carries descending motor fibres from primary motor cortex through the internal capsule to the motor neurons in the spinal cord, increased FA in these areas has generally been interpreted as reflecting increased connectivity due to music-induced neuroplasticity.

Higher FA in expert musicians is not a universal finding, however. Abdul-Kareem, Stancak, Parkes, Al-Ameen, et al. (2011) found that musicians had higher tract volume in the right cerebellum, but did not find a group difference in FA of the superior and middle cerebellar peduncles. While FA in the corticospinal tract was increased in musicians in the studies described above (Bengtsson et al., 2005; Han et al., 2009; Rüber et al., 2013), two other studies found that musicians had *decreased* FA within this tract, relative to non-musicians (Imfeld et al., 2009; Schmithorst & Wilke, 2002). Additionally, as Hänggi, Koeneke, Bezzola, and Jäncke (2010) point out, although increasing practice intensity in the pianist group was associated with higher FA values in the posterior limb of the internal capsule, mean FA values were *lower* (although not significantly so) in expert pianists than in controls. Merrett et al. (2013) suggest that one explanation for the discrepancy between studies in the direction of group differences in FA may be the types of instruments played by the musicians in these studies. Both studies that found decreased FA in the corticospinal tract had mixed samples of musicians, while two of the three studies finding increases in FA included pianists only. The third study, that of Rüber and colleagues (2013), included a keyboard and string group, both of whom exhibited increased FA in the right corticospinal tract relative to non-musicians. It is not clear, however, why training on some instruments could produce decreased FA, relative to the general population, while training on keyboard and string instruments produces increased FA.

One variable that seems to influence white matter connectivity in musicians is the possession of AP. AP is a rare ability in which the pitch of a tone can be verbally labelled without using a reference note. Most musicians have relative pitch (RP), or the ability to determine pitch using a reference note and identifying the interval between the two notes. The main anatomical correlate of AP is increased size of the left planum temporale, part of Wernicke's area (Keenan et al., 2001; Luders et al., 2004). In terms of white matter connectivity, Loui and colleagues (2011) found that musicians with AP had greater volume of the tracts connecting the posterior superior temporal and gyrus and posterior middle temporal gyrus in both hemispheres. Oechslin, Imfeld, and colleagues (2010) observed differences between musicians with AP, musicians with RP, and non-musicians in the asymmetry of FA in the superior longitudinal fasciculus (SLF). The SLF is a large bundle of association fibres in each hemisphere connecting parietal, temporal, and occipital lobes with the ipsilateral frontal lobe (Schmahmann, Smith, Eichler, & Filley, 2008). Of relevance to music processing, the "direct pathway" of the SLF connects temporal areas involved in auditory processing with frontal areas involved in executive control processes, while the "indirect pathway" links frontal, temporal, and parietal cortices (Catani, Jones, & Ffytche, 2005; Catani & Mesulam, 2008). Musicians with AP had leftward asymmetry, non-musicians had rightward asymmetry, and musicians with RP had no hemispheric difference of FA. Finally, a very recent study used a whole-brain, voxelwise approach (tract based spatial statistics [TBSS]) to compare white matter in musicians with and without AP (Dohn et al., 2015). Musicians with AP had higher FA than musicians without AP in a single cluster encompassing the right inferior fronto-occipital fasciculus, uncinate fasciculus, and inferior longitudinal fasciculus. These results suggest AP is characterised by increased connectivity of left and right temporal lobe regions involved in the perception and categorisation of pitch.

In support of a causal role of music training in producing white matter changes, there is some evidence to suggest that training on different musical instruments is associated with different neural adaptations of white matter tracts. In the aforementioned study by Rüber et al. (2013), while both keyboard and string musicians exhibited increased FA in the right corticospinal tract relative to non-musicians, only keyboard players had increased FA in the left corticospinal tract. This likely reflects the more equal demands placed on the left and right hands by keyboard playing. Halwani and colleagues (2011) compared tract volume and FA of the arcuate fasciculus between singers, instrumentalists, and non-musicians. The arcuate fasciculus is a white matter tract which connects Broca's area in the inferior frontal gyrus and Wernicke's area in posterior temporal gyrus, and so is commonly associated with language processing (for a review, see Catani & Mesulam, 2008). While musicians in general had higher FA in the arcuate fasciculus than non-musicians, singers had higher volume and lower FA than instrumentalists. The authors contended that this difference between singers and instrumentalists may reflect the additional demands placed on the vocal motor system by training in singing, relative to instrumental training. Specifically, they suggest that the need for singers to monitor their breathing and proprioceptive feedback from the vocal tract may necessitate stronger connectivity with motor, premotor and somatosensory cortices. Thus, the reduced FA in singers could reflect more fibre crossings or more branching of the tract into motor and somatosensory cortices.

There is also evidence to suggest that there may be a sensitive period in which music training has the greatest impact on the development of white matter pathways (see Penhune, 2011 for a review of this topic). In the study by Bengtsson and colleagues (2005), greater amounts of music practice across different lifetime periods were associated with higher FA in the corpus callosum, internal capsule, and the arcuate fasciculus, with the most extensive associations observed for childhood practice intensity. Steele and colleagues (2013) showed that musicians who started their training before the age of seven had higher FA in the posterior midbody and isthmus of the corpus callosum, relative to musicians who began training later. Finally, Imfeld et al. (2009) also found that the age of onset of training influenced microstructure of the corticospinal tract; however their findings indicated that musicians who began training before age seven had greater MD, rather than greater FA, compared to musicians who began training later.

Pre-existing structural variability may also influence the outcome of music training. Engel et al. (2013) taught music-naïve adults to play short melodies on the piano in three training sessions across consecutive days. The day after the conclusion of the training sessions, participants underwent a DTI scan. Higher FA values in the bilateral corticospinal tract and right SLF were associated with faster learning of the melodies on the first day of training. Associations between FA and initial speed of motor learning were interpreted by the authors as reflecting pre-existing variability in structural organisation which then influence performance. If this interpretation is correct, this suggests that success in developing musical skills is at least partially driven by the state of the brain before training is begun, which has important implications for cross-sectional musician studies such as those described in this section.

DTI studies in other expert populations

A broader question is whether expertise might be expected to be associated with increased, or decreased, FA. While increased FA has been taken in the past to represent increased "white matter integrity", an influential paper by Jones, Knösche, and Turner (2013) strongly cautions against interpreting FA in this way in the context of healthy populations. As FA is a complex and indirect measure that can be influenced by many factors (including axon size and density, axon diameter, axon permeability, and degree of myelination), it is impossible to infer that FA changes are related to changes to a specific microstructural property. While FA increases across development (e.g. B. D. Peters et al., 2012; Qiu, Tan, Zhou, & Khong, 2008; Schmithorst & Yuan, 2010) and increased FA is often thought to index increased myelination or greater integrity of the axonal membrane (Alexander, Lee, Lazar, & Field, 2007), it has also been found to increase in certain disorders, such as attention deficit hyperactive disorder (Peterson et al., 2011) and Williams syndrome (Hoeft et al., 2007). On the other hand, reduced FA has been observed in phantom fibre bundles with a larger diameter (Fieremans et al., 2008; Fieremans, Deene, Baete, & Lemahieu, 2009), and can also occur due to crossing, bending, or twisting fibres, particularly when only one fibre is modelled for each voxel (Hänggi, Koeneke et al., 2010).

An examination of the literature on FA in varied expert groups yields mixed results in terms of the directionality of FA differences. A number of studies in different populations have found lower FA in their expert groups. For example, Huang, Lu, Song, and Wang (2013) found that professional gymnasts had decreased FA in the SLF, inferior longitudinal fasciculus, and inferior fronto-occipital fasciculus. This decrease in FA was interpreted by the authors as an increase in fibre diameter. In ballet dancers, Hänggi, Koeneke et al. (2010) found decreased FA in the white matter underlying bilateral premotor cortices. Jäncke, Koeneke, Hoppe, Rominger, and Hänggi (2009) also found that more skilled golfers had decreased FA in the internal capsule, posterior corpus callosum, and other white matter tracts, relative to less skilled golfers and non-golfers. The authors suggested that reduced FA could reflect the increased automaticity of motor programmes in professional golfers. Elmer, Hänggi, Meyer, and Jäncke (2011) found that simultaneous interpreters (interpreters providing translation in real-time) had lower FA in the corpus callosum and other white matter regions, including the left corticospinal tract, right inferior parietal lobule, and right caudate nucleus.

On the other hand, other studies have found increased FA in association with expertise. For example, a study of practitioners of meditation revealed significantly increased FA in the corpus callosum, relative to controls (Luders et al., 2012). Wang and colleagues (2013) also found that elite gymnasts had increased FA bilaterally in the corticospinal tract relative to controls. The gymnasts also had decreased RD relative to controls, but there was no group difference in AD, suggesting that the increased FA in gymnasts reflects less diffusion across the axon. In general, increased FA could reflect more numerous or more densely-packed white matter fibres, increased myelination, or more coherent orientation of fibres (Beaulieu, 2002).

To summarise, while some studies of musicians found increased FA in association with musical expertise in motor tracts (Bengtsson et al., 2005; Han et al., 2009; Rüber et al., 2013) and the corpus callosum (Steele et al., 2013), while others found decreased FA (Imfeld et al., 2009; Schmithorst & Wilke, 2002). Other studies have variously found that specific subsets of musicians, such as those possessing AP, have increased FA relative to other musicians in left hemispheric tracts connecting peri-sylvian regions linked to language processes (Loui et al., 2011; Oechslin, Imfeld et al., 2010), while other work found that singers had *lower* FA in the arcuate fasciculus (Halwani et al., 2011). It is difficult at present to reconcile these discrepant findings with each other. Perhaps it is the case that different white matter structures have different profiles of microstructural change related to the development of expertise, or that specific types of behavioural training differentially affect white matter architecture.

Gender differences in white matter connectivity

Gender differences in whole brain volume and in certain brain structures are well-known. Total brain volume and the volumes of most brain regions are larger in males than in females, however regional differences are reduced when corrected for total brain volume (Allen et al., 2002; Courchesne et al., 2000; M Peters et al., 1998). When controlling for total brain volume, women have a higher percentage of grey matter (Allen, Damasio, Grabowski, Bruss, & Zhang, 2003; X. Chen, Sachdev, Wen, & Anstey, 2007; Gur et al., 2000; Luders, Steinmetz, & Jäncke, 2002, but see Good et al., 2001), while men have a higher percentage of white matter (Chen et al., 2007; Filipek, Richelme, Kennedy, & Caviness, 1994; Goldstein et al., 2001; Gur et al., 2000). Some studies have found that men have larger corpus callosum and cerebellar volumes than women (Allen et al., 2002; Carne, Vogrin, Litewka, &

Cook, 2006; but see Zarei et al., 2006). A recent meta-analysis of 16 VBM studies also found that, on average, males had larger grey matter volumes than females in a range of limbic regions including the amygdalae, hippocampi, posterior cingulate gyri, precuneus, and temporal poles. Females had larger grey matter volumes in a set of mostly right-hemispheric regions including the frontal pole, inferior and middle frontal gyri, primary auditory cortex and planum temporale (Ruigrok et al., 2014). This meta-analysis was not limited to studies that controlled for total brain volume, however.

Gender differences in a number of white matter structures have also been implicated using DTI; however, as in the expertise literature, the direction of the differences in FA between males and females has been mixed. For example, in the corpus callosum, while some studies found higher FA in males than females (Menzler et al., 2011; Pal et al., 2011; Shin et al., 2005; Westerhausen et al., 2003), other studies have found the reverse: higher FA in females than males (Chou et al., 2011; Kanaan et al., 2012). Still others have found no gender difference in this structure (Abe et al., 2002; C. E. C. Lee, Danielian, Thomasson, & Baker, 2009; Sullivan et al., 2001; Wu, Field, Whalen, & Alexander, 2011). Kanaan and colleagues (2012) found that men had higher FA than women in the left SLF; in contrast, King, Yurgelun-Todd, Stoeckel, DiMuzio, and Lopez-Larson (2015) reported higher FA in men in the right SLF. Gender differences in the same direction have also been reported in the internal capsule and in the deep temporal lobes (Herting, Maxwell, Irvine, & Nagel, 2012; Hsu et al., 2008). Meanwhile, Ugwu, Amico, Carbadello, Fagan, and Frodl (2015) found no gender differences in diffusivity measures from the cingulum, uncinate fasciculus, fornix, SLF, and fronto-occipital fasciculus. However, gender did interact with other study variables such as presence of depression or of adverse events in childhood.

Overall, there is some evidence that gender differences are present in white matter structures, and that gender can interact with other factors to produce complex patterns of white matter architecture. For this reason, gender appears to be an important factor to consider in any investigation of white matter. Despite this, no studies exploring white matter differences in musicians and non-musicians have taken gender into account.

The current study

In *Study Two*, we aimed to explore underlying white matter changes that might contribute to musicians' enhancements in visuospatial ability, or that might influence the functional lateralisation of visuospatial processing in musicians. As we did not found any areas of enhanced visuospatial-task activation in musicians in *Study One*, we were unable to use such regions in a seed-based approach as originally planned. Instead, we selected the corpus callosum as a tract of interest. The corpus callosum is the major interhemispheric tract in the brain and so may have a significant influence on lateralisation of the function, with the posterior segment specifically connecting parietal and occipital regions of cortex of particular interest for lateralisation of visuospatial functions. Previous studies have found that musicians have increased FA in the corpus callosum (Schmithorst & Wilke, 2002; Steele et al., 2013), which has been linked to greater intensity of music practice (Bengtsson et al., 2005). A previous EEG study also found that musicians had more equal rates of transfer of visual information between hemispheres, suggesting a more equilateral speed of information transfer across the corpus callosum (Patston, Kirk et al., 2007). We predicted that musicians would have increased FA in the corpus callosum, particularly in the posterior segment which connects parietal and occipital regions involved in visual and sensory processing (Barbas & Pandya, 1984).

Our secondary aim was to further investigate neural plasticity of the white matter in response to music training, and to add to the small existing literature examining differences between musicians and non-musicians in white matter architecture. It was predicted on the basis of previous research that musicians, relative to non-musicians, would have differences in FA or MD in the corticospinal tract and the SLF. These tracts were selected firstly because of their known involvement in music-related processes, and secondly because previous literature using MRI and DTI techniques demonstrated structural adaptations in musicians in these tracts or in the brain regions they connect. Given the mixed findings in the literature to date, no specific directional predictions were made.

We also explored differences between singers and instrumentalists in microstructural properties of the corticospinal tract and SLF. Differences between musicians undergoing vocal and instrumental music training have received little attention to date in the musician literature; yet the demands placed on the motor system differ significantly between these different types of music training. Instrumentalists typically develop fine motor control of the hands and bimanual coordination, while singers uniquely utilise the vocal motor system. On the basis of this difference in motor requirements, we expected that microstructural properties of the corticospinal tract would differ between singers and instrumentalists. As Halwani et al. (2011) showed that tract volume and FA of the arcuate fasciculus differed between singers and instrumentalists, we aimed to replicate and extend on this work by comparing volume and FA between singers and instrumentalists in the SLF, a more extensive tract that encompasses the arcuate fasciculus. Finally, we explored whether there was an interaction between gender and musical training with respect to the white matter tracts of interest. Gender has not been considered previously in the musician literature which has used DTI. Given the known gender differences in white matter connectivity, and our findings in *Study One,* we predicted that non-musicians would show gender differences in FA of the corticospinal tract, SLF, and corpus callosum, while there would be no gender differences in the musician group.

Method

Participants

The participants from *Study One* also underwent a DTI scan in the same MRI session. A minor white matter abnormality was noted in the MRI scan of one male musician, and a scanner malfunction prematurely discontinued the DTI sequence acquisition for one male non-musician. Therefore, the musician group in this study consisted of 32 participants (16 female), whose musical training characteristics are described in *Study One*, and the non-musician group comprised 29 participants (15 female) who had no formal music training, and could not read music. As per *Study One*, the groups were matched for age, gender, years of education, handedness, and WASI PIQ (see Appendix 3 for raw demographic information for this study). Musicians had marginally higher estimated WASI VIQ ($t(59) = 2.02$, $p = .05$) and estimated WASI FSIQ ($t(59) = 2.02$, $p = .05$) than non-musicians (see Table 11 for means and standard deviations). The reader is referred back to *Study One* for full details on this participant sample.

Table 11. WASI IQ measures of musician and non-musician participants for Study Two.

	Musicians (SD)	Non-Musicians (SD)
WASI VIQ*	123.66 (7.87)	119.76 (7.16)
WASI PIQ	122.16 (10.17)	119.66 (9.56)
WASI FSIQ*	125.97 (7.34)	122.31 (6.71)

* Difference between groups is significant at $p < .05$

For additional analysis of differences between singers and instrumentalists, the musicians were classified into one of two groups: Voice (11 musicians), and Instrument (20 musicians). The instruments played by the Instrument group are shown in Table 12. As in *Study One*, this classification was based on their main instrument, i.e. the instrument used by the musician in their university performance degree or in their professional music career. One musician was excluded from these analyses, as they both played an instrument and sang at a professional level, so could not be readily classified into either group. The voice and instrumentalist groups were matched for age, years of education, EHI, and the three WASI IQ estimates (all p values > .08; see Table 13). Key musical characteristics of the voice and instrumentalist groups are summarised in Table 14.

Table 12. Number of musicians playing each instrument in the Instrument group.

Piano	String	Percussion	Brass
10	4	1	5

Self-reports regarding whether musicians had AP or RP were obtained via email from 25 of the 33 musicians (75.8%). Two musicians (both instrumentalists) self-reported possessing AP; the remaining 23 musicians self-reported having RP.

Table 13. Demographic characteristics of Voice and Instrument groups for Study Two.

	Voice (SD)	Instrument (SD)
N males, N females	3, 8	13, 7
Age in years	33.45 (11.58)	26.8 (9.46)
Years of education	17.41 (1.87)	17.05 (2.01)
EHI score	94.47 (8.42)	97.09 (6.72)
WASI VIQ	124.09 (9.51)	123.2 (7.22)
WASI PIQ	121.81 (13.02)	121.75 (8.48)
WASI FSIQ	126.27 (9.19)	125.35 (6.22)

Table 14. Musical characteristics of Voice and Instrument groups for Study Two.

	Voice (SD)	Instrument (SD)
Age started	6.64 (1.29)	6.40 (2.06)
Years of playing	27.00 (12.51)	20.40 (9.33)
Practice intensity[1]	7.44 (8.06)[2]	20.58 (13.57)

[1]Estimated number of hours played per week in the last six months. [2] Nine of the 11 singers and all of the instrumentalists provided an estimate of practice intensity.

DTI image acquisition

Diffusion tensor images (DTI) were acquired with a 3 Tesla whole-body MRI imaging system (Siemens Skyra, Magnetom, Germany). This included the collection of 64 images with noncollinear diffusion gradients (b=1,400 s/mm2) and one nondiffusion-weighted image (b=0 s/mm2; B0), employing a single shot echo planar imaging sequence (67 slices, TR=8900ms, TE=95ms, FoV=240x240mm, acquisition matrix=122x122mm, slice thickness=2mm, voxel size = 2x2x2mm, 1 average). Scan acquisition time was 10 mins, 7 secs. A field map measuring magnetic field inhomogeneities was also collected after the DTI sequence (scan time 2 min 43 s). The T1-weighted structural image described in *Study One* was also utilised in the diffusion-weighted image pre-processing.

DTI image analysis

DTI image pre-processing was carried out using the dti_preprocess script created by Takuya Hayashi, which is freely available at http://www.bic.mni.mcgill.ca/~thayashi/dti.html. This script uses routines implemented in FSL's FDT toolbox: (http://fsl.fmrib.ox.ac.uk/fsl/fslwiki//FDT). The preprocessing steps involved were: 1) eddy current correction and affine registration (12 degrees of freedom) to correct for head motion; 2) correction for inhomogeneities in the nondiffusion-weighted (B0) image, using the B0 field map collected as part of the DTI scan; 3) correction of the b-vector by using rotations derived from motion estimates; 4) brain extraction of the B0 and anatomical brain images (*BET*); and 5) fitting of diffusion tensors to the data, which produces MD, FA, and eigenvalue/eigenvector images (*dtifit*).

Two additional steps were performed to prepare the data for probabilistic tractography. First, probabilistic distributions of fibre directions at each voxel were calculated, modelling two fibres per voxel (Behrens, Berg, Jbabdi, Rushworth, & Woolrich, 2007; *BEDPOSTX*). Second, using the FMRIB Linear Image Registration Tool (*FLIRT*), diffusion-weighted images were registered to the skull-stripped T1 anatomical image and to a standard brain image based on MRI scans of 152 people (the MNI152 standard brain image).

Voxelwise analysis

Voxelwise analysis of the FA maps generated by *dtifit* was performed using TBSS. First, the FA maps for each participant were non-linearly registered onto the FMRIB58_FA standard template, and averaged and thinned using a threshold of 0.2 (Smith et al., 2006) to create a mean FA skeleton at a 1 x 1 x 1mm^3 resolution. The goal of this procedure was to remove any remaining cross-subject spatial variability after normalisation by generating a skeleton that represents the centre of the tracts common to all participants. Voxelwise inferential statistics for performing group analyses were carried out with permutation-based nonparametric testing (using 5000 permutations), implemented in the FSL tool *randomise* (Winkler, Ridgway, Webster, Smith, & Nichols, 2014). Using this tool, an independent two sample t-test was run with a significance level of $p < .05$, corrected for multiple comparisons using the threshold-free cluster enhancement option.

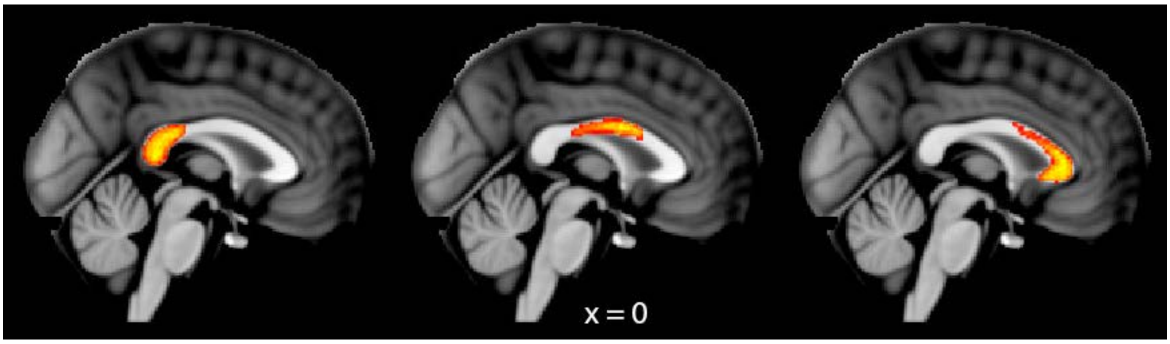
Region of interest (ROI) analyses

Corpus callosum

The second analysis involved extraction of key DTI parameters (mean FA, mean MD, and volume) from the corpus callosum. The corpus callosum was manually outlined for each participant on the mid-sagittal slice of their T1 anatomical image. To do this, firstly the anatomical images were registered to the MNI152 1mm standard brain using a rigid body transformation with six degrees of freedom (three rotations, three translations), using the FLIRT tool. This registration preserves individual differences in brain size, as it moves but does not scale the brain to fit the standard template. The images were then segmented into grey and white matter using FSL’s automated segmentation tool (FAST; Zhang, Brady, & Smith, 2001). Following this, the white matter segmentation image was overlaid onto the anatomical image to facilitate manual outlining. The manual tracing was carried out by the author, who was blinded to the identity and group membership of each image. To assess reliability, a second blinded researcher also manually outlined the corpus callosum for 20 randomly chosen participants (10 musicians, 10 controls), and a comparison of the areas of these masks was undertaken, resulting in a Kronbach's alpha intraclass correlation of .99, indicating very high reliability. Total brain volume for each participant was calculated with SIENAX, an algorithm for automated brain extraction in FSL (Smith, 2002), and included as a covariate in the statistical analyses of tract volume.

In order to segment the corpus callosum into three subdivisions, specific cortical target masks were created on the MNI152 1mm standard brain using the MNI structural atlas in FSL. These masks comprised: 1) the prefrontal cortex (the frontal lobe sparing the motor cortex); 2) the motor cortex (derived from the Jülich histological atlas in FSL including M1 and premotor cortex); 3) the parietal, temporal, and occipital lobes. For each participant, probabilistic tractography was run from every voxel in the corpus callosum mask to each of the three target masks (separately for the left and right hemispheres) by drawing 5000 samples with a step length of 0.5mm and a curvature threshold of 0.2mm. The resulting value in each voxel represents the number of samples reaching the relevant target mask, and therefore the probability of the connection. Each output mask was thresholded at 10% of the maximum connectivity value to the relevant target mask, using a similar threshold as in previous research (Häberling et al., 2011; Häberling, Badzakova-Trajkov, & Corballis, 2012; Zarei et al., 2006). For each target, tracts connecting to the left and right hemispheres were then combined such that only overlapping areas were included (as in Westerhausen, Grüner, Specht, & Hugdahl, 2009). Finally, to prevent overlap between the three resulting segments, or in other words to ensure that each voxel within the corpus callosum was counted as connecting to just one of the three cortical targets, a hard segmentation was performed using the *find_the_biggest* tool in FSL. This assigned each callosal voxel to a particular target region by determining for that voxel which output mask had the highest connectivity value. The resulting masks were then binarised and used to extract mean FA, MD and volume for each callosal segment.

To visualise the results of the connectivity-based segmentation, the callosal segments for each participant were added together. This generated a population-based probability mask in which the values for each voxel represent the number of participants with a connection to the relevant target mask. A threshold of 70% was applied to ensure that only those voxels that were shared by at least 70% of the participants are displayed (as per Häberling et al., 2011). This is a somewhat arbitrary threshold and was only used to visualise the segments. These results are shown in Figure 24.



Parietal-Occipital-Temporal **Motor** **Prefrontal**

Figure 24. Group probability maps showing the location of the cortical connections within the corpus callosum shared by at least 70% of the participants. Areas connecting to parietal, occipital, and temporal lobes, motor cortices, and prefrontal cortices are shown.

Corticospinal tract

The remaining ROI analyses involved the derivation of white matter tracts of interest and their connections using probabilistic tractography. Firstly, the corticospinal tract, which conveys projection fibres from the primary motor cortex down to the spinal cord, was estimated in each hemisphere using seeds placed in the left and right pons. These seeds were manually traced on a single axial slice (z= -30) of the MNI152 standard brain image, using Oishi, Faria, van Zijl, and Mori's (2010) white matter atlas as a guide. In this atlas, the corticospinal tract (among several other white matter tracts) was reconstructed using probabilistic tractography. The delineated corticospinal tract was displayed on 2D slices of a DTI-based colour-coded orientation map, spaced apart by 2.5mm. This was used to facilitate the manual tracing.

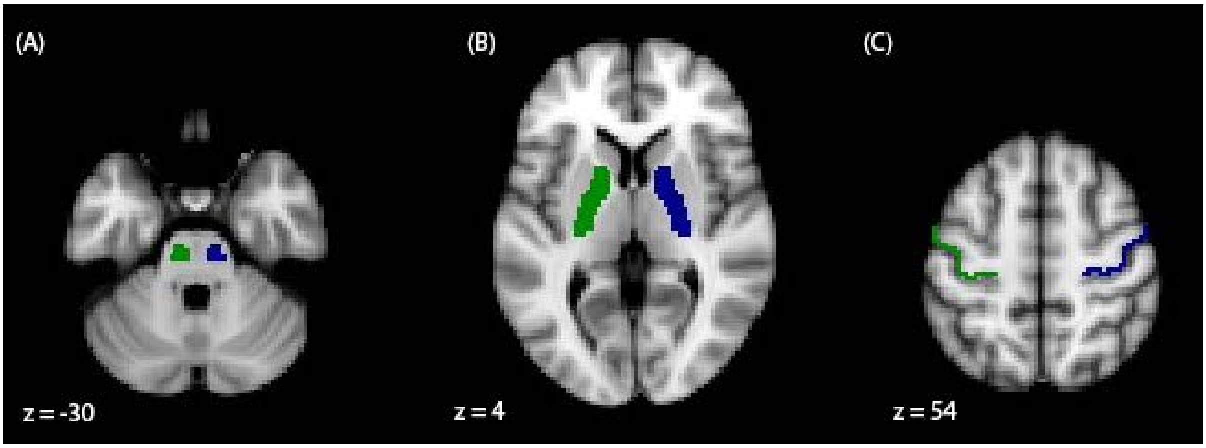
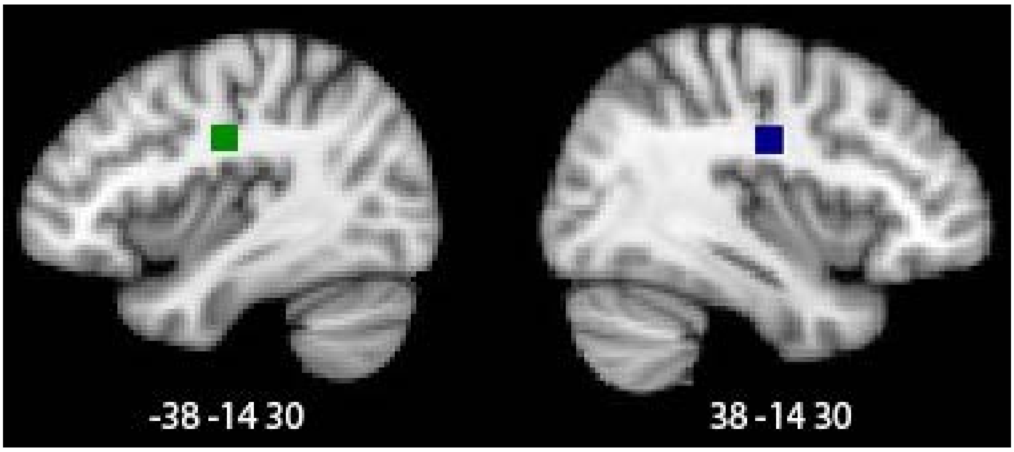


Figure 25. Seeds and waypoints for tractography of corticospinal tract. (A) Seeds in left and right pons. (B) Waypoints in left and right internal capsule. (C) Waypoints in left and right primary motor cortex (green = left hemisphere, blue = right hemisphere).

Left- and right-hemispheric waypoint ROIs were additionally drawn in the posterior limb of the internal capsule (z= 4) and in the dorsal primary motor cortex (z= 54). As the cytoarchitectonic boundaries between primary and dorsal premotor cortices are not clear (Geyer, Matelli, Luppino, & Zilles, 2000), the primary motor ROIs were drawn at the posterior bank of the precentral gyrus in each hemisphere, following the technique used by Rüber et al. (2013). Seeds and waypoint ROIs are shown in Figure 25. Additionally, a midline exclusion mask was used to prevent the algorithm from tracking into the contralateral hemisphere.

Superior longitudinal fasciculus (SLF)

The second tract of interest, estimated using tractography, was the SLF, which connects frontal regions to the ipsilateral parietal, temporal, and occipital lobes. The SLF was estimated in each hemisphere using 5x5x5-voxel seeds placed in the anterior part of the SLF. The seed locations were determined using the probabilistic JHU White Matter Tractography atlas built into the FSL package. The most anterior point in the probabilistic atlas with a greater than 60% probability of being part of the SLF was located (see Figure 26 for exact seed placement). A midline exclusion mask was again used to prevent tracking into the opposite hemisphere.



Left Hemisphere **Right Hemisphere**

Figure 26. Seed placement for tractography of the SLF (green = left hemisphere seed, blue = right hemisphere seed). Coordinates indicate the centre of the 5x5x5 voxel seed.

In both analyses, fibre tracking was conducted using 5000 samples, a step length of 0.5mm, and a curvature threshold of 0.2. This technique calculates the primary orientation of the tract at each voxel, and the probability of the tract passing through that voxel. A conservative threshold was used to ensure that only those voxels where at least 25% of the samples passed through them were included (e.g. Iwabuchi et al., 2011). Finally, these thresholded and binarised tracts were used to extract mean FA, mean MD, and volume from the FA and MD images for each participant.

Statistical analysis

SPSS (Version 22) was used for all statistical analyses, with the exception of the voxelwise analysis, which was performed using the randomise tool in FSL (see Voxelwise analysis section). For the ROI analyses, three main approaches were employed:

1) Investigation of differences in mean FA, mean MD, and volume related to musical training or gender. To test this, separate mixed-design ANOVAs were performed with between-subject factors group (musician, non-musician), and gender (male, female), and hemisphere (left, right)[9] a within-subjects factor. Whole brain volume was included as a covariate for the tract volume analysis.

2) Investigation of differences in mean FA and mean MD between singers and instrumentalists. To test this, mixed-design ANOVAs were performed with between-subject factors training type (voice, instrument), and gender (male, female), and within-subjects factor hemisphere (left, right)[1].

When significant main effects or interactions were present, Bonferroni-corrected pairwise comparisons were performed. Where the assumption of sphericity was violated, degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity.

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[9] Note that for the corpus callosum analysis, this factor was segment and had three levels, representing the three callosal segments resulting from the connectivity-based segmentation (prefrontal, motor, and parietal-temporal-occipital).

3) If significant differences in mean FA or MD were found between musicians and non-musicians, Pearson's correlations were performed in the musician group between mean FA or mean MD and music training variables (age of onset of music training, years of training, and practice intensity [estimated hours played per week in the last six months]). As two musicians did not provide an estimate of their practice intensity, the sample size for this correlation was 30 musicians. The set of correlations performed for each tract was corrected for multiple comparisons using the false discovery rate (FDR) correction.

Results

Voxelwise analysis

First, we tested whether there were significant differences in FA or MD values at a whole-brain level between musicians and non-musicians, using TBSS. No significant differences could be found at a significance level of $p < .05$, nor at a more liberal significance level of $p < .10$, corrected for multiple comparisons.

ROI analyses

Corpus callosum

Mean corpus callosum size (over all participants) was 707.67mm^2 (± 75.18mm^2). For raw data see Appendix I. The following analyses were performed using parameters extracted from each of the three segments defined by connectivity-based segmentation (voxels in the corpus callosum connecting to prefrontal, motor, and parietal-temporal-occipital cortices), as described in the Method. This factor was termed "segment".

Fractional anisotropy (FA)

The mixed-design ANOVA to test for differences in mean FA in the corpus callosum relating to musical training or gender revealed firstly a main effect of segment (*F*(2, 114) = 140.52, *p* < .001). Bonferroni-corrected pairwise comparisons revealed that all segments differed significantly from each other (all *p* values < .001). The parietal-temporal-occipital segment had the highest mean FA, followed by the prefrontal segment, then the motor segment. While there was no significant main effect of either group (*F*(1, 57) = 1.56, *p* = .22) or gender (*F*(1, 57) = 1.0, *p* = .32), there was a significant group by gender interaction (*F*(1, 57) = 7.40, *p* = .009; see Figure 27). Pairwise comparisons showed that male controls had higher FA than female controls (*p* = .01), where there was no gender difference within the musician group (*p* = .22). Male controls also had higher FA than male musicians (*p* = .007), where the FA of female musicians and non-musicians did not differ significantly (*p* = .30). No other main effects or interactions were significant.

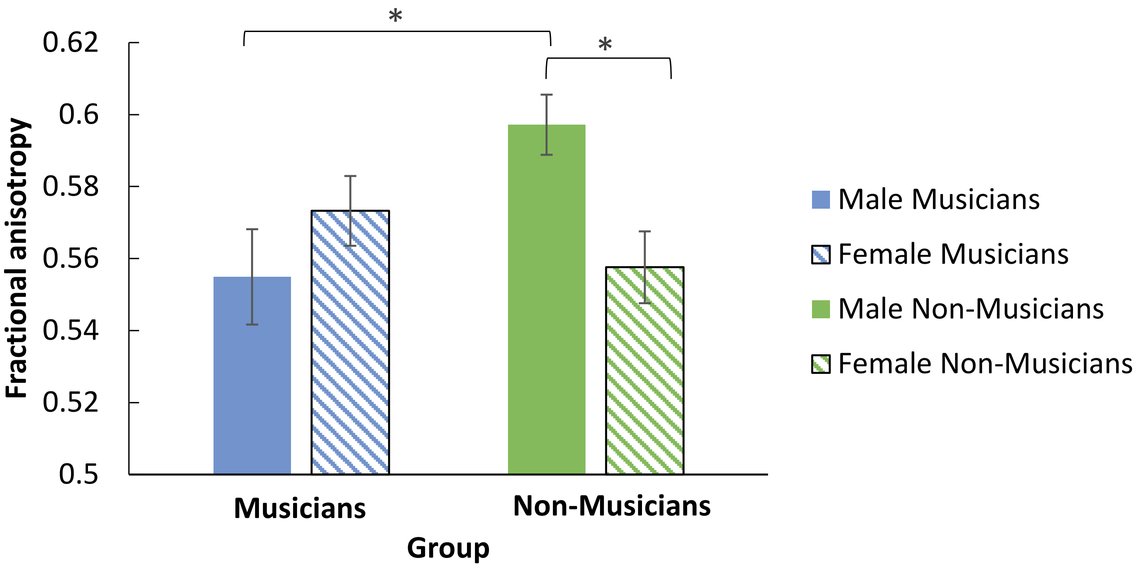


Figure 27. Mean FA collapsed across the three corpus callosum segments, broken down by group and gender. Errors bars are mean standard errors. * *p* < .05

Mean diffusivity (MD) and tract volume

The same analyses as described above were also performed for mean MD and tract volume. For MD, there was a main effect of segment (*F*(2, 114) = 26.31, *p* < .001). Pairwise comparisons showed that, in addition to having higher mean FA than the motor and prefrontal segments, the parietal-temporal-occipital segment also had higher mean MD (both *p* values < .001). MD did not differ significantly between the prefrontal and motor segments (*p* = .13). While there were no significant main effects or interactions with group, the interaction between gender and segment was significant (*F*(2, 114) = 3.34, *p* = .04). Pairwise comparisons found, however, that MD did not differ significantly between males and females in any of the three segments (all *p* values > .1). Within females only, MD was significantly higher in the motor segment relative to the prefrontal segment (*p* = .009), where there was no significant difference in MD between the motor and prefrontal segments in males (*p* = 1.0). In both males and females, MD was significantly higher in the posterior segment compared to the motor segment (both *p* values < .001), and compared to the prefrontal segment (both *p* values < .005).

Finally, the same mixed-design ANOVA was performed for tract volume, with whole brain volume included as a covariate. The only significant effect in this analysis was a main effect of segment (*F*(2, 112) = 10.86, *p* < .001), which is unsurprising considering the different sizes of the segments (review

Figure 24).

Associations with training variables

To determine whether years of training, age of onset of training, or practice intensity influenced microstructural properties of the corpus callosum, Pearson's correlations were performed for the motor, prefrontal, and parietal-temporal-occipital callosal segments between FA and these musical training variables. This revealed significant (FDR-corrected) negative correlations between mean FA and years of training in all three segments (motor segment: *r* = -.48, *p* = .005; prefrontal segment: *r* = -.42, *p* = .02; parietal-temporal-occipital segment: *r* =-.46, *p* = .008; see Figure 28), indicating that more years of musical training were associated with lower FA. There were no significant correlations between FA and age of onset or practice intensity (all *p* values> .05).

Age is, of course, very highly correlated with the number of years of training (*r* = .99, *p* < .001), and could plausibly confound the correlations with FA. To examine whether age was generally correlated with FA and MD, we conducted correlations between age and FA in each segment of the corpus callosum in non-musicians, applying the FDR correction to correct for multiple comparisons. The correlation with age was not significant in the prefrontal segment (*r* = -.20, *p* = .31), or the motor segment (*r* = -.36, *p* = .056), while the correlation in the parietal-temporal-occipital segment was significant at an uncorrected level only (*r* = -.41, *p* = .03; does not survive FDR correction).

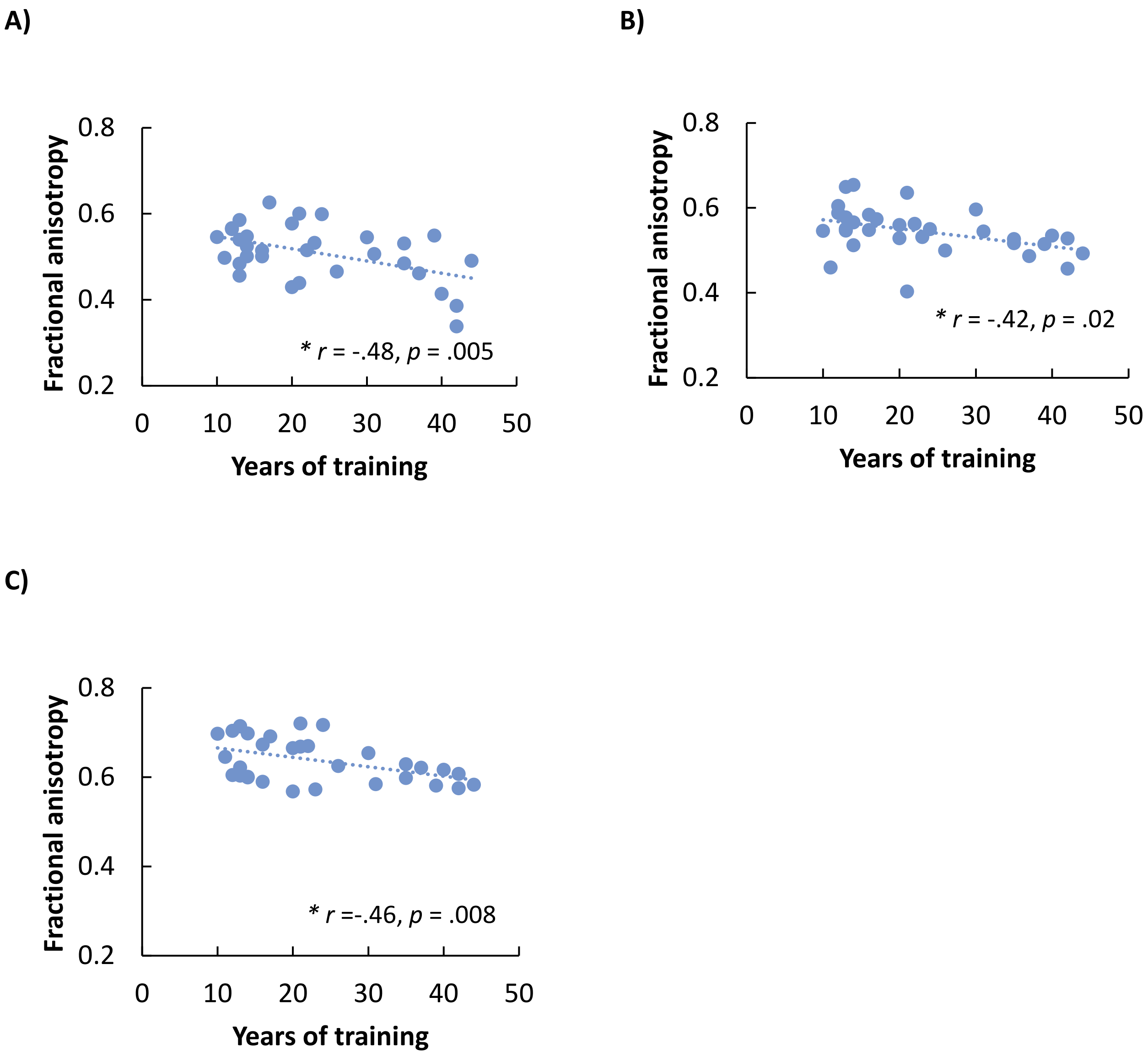


Figure 28. Correlation between FA in each corpus callosum segment and years of training (musicians only). A) motor segment; B) prefrontal segment; C) parietal-temporal-occipital segment. * *p* < .05 (FDR corrected)

Comparison of singers and instrumentalists

The mixed-design ANOVA comparing FA values in singers and instrumentalists revealed a significant main effect of segment (*F*(2, 54) = 77.16, *p* < .001), as seen in the main analysis of FA. There was also a main effect of gender (*F*(1, 27) = 5.89, *p* = .02), with females in both the voice and instrument groups having higher FA than males. Finally, there was a significant main effect of training type (*F*(1, 27) = 8.89, *p* = .006; see Figure 29), with instrumentalists having higher FA than singers. For MD, the only significant effect was a main effect of segment (*F*(2, 54) = 8.86, *p* < .001). Pairwise comparisons showed that the parietal-temporal-occipital segment had significantly higher MD than the prefrontal segment only (*p* = .002).

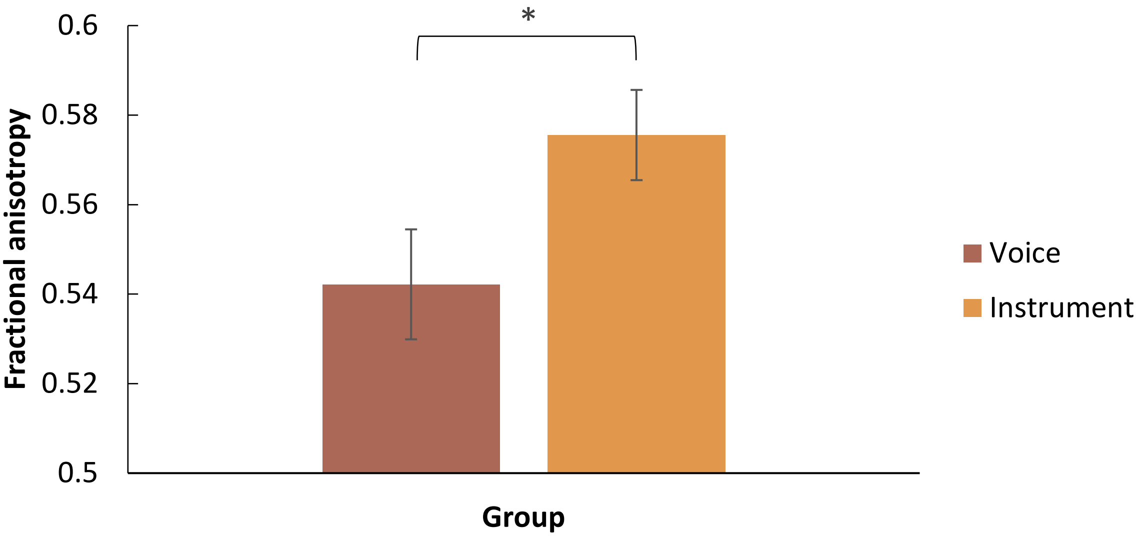


Figure 29. Mean FA for the corpus callosum in singers and instrumentalists. Error bars indicate mean standard errors. * *p* < .05

Corticospinal tract

The estimated left and right corticospinal tracts from tractography are shown in Figure 30. For raw data see Appendix H. After thresholding the tracts generated for each participant, an average tract across all subjects was created. Mean tract volume across all subjects was 1334.56mm^2 (± 350.14mm^2) for the left corticospinal tract, and 1207.74mm^2 (± 344.18mm^2) for the right corticospinal tract.

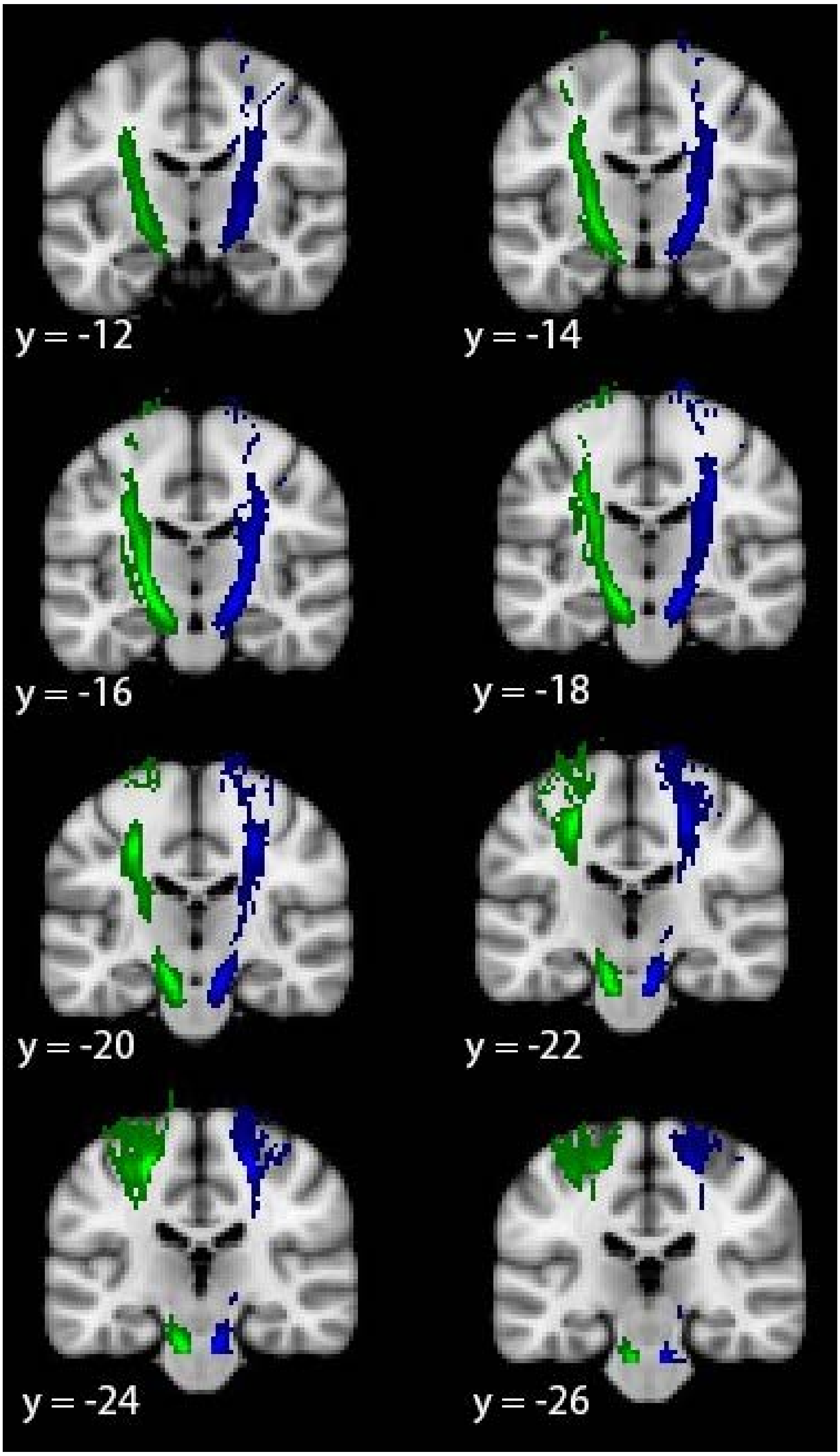


Figure 30. Corticospinal tract tractography result shown on 8 coronal slices at y levels indicated (green = left corticospinal tract, blue = right corticospinal tract). Tract depicted is the average tract derived from all participants.

Fractional anisotropy (FA)

The mixed-design ANOVA to test for differences in mean FA in the corticospinal tract relating to musical training or gender revealed a significant main effect of group (*F*(1, 57) = 4.44, *p* = .04), whereby musicians had lower mean FA than non-musicians within the corticospinal tract (see Figure 31). There was no significant main effect of hemisphere, nor was there a significant interaction between group and hemisphere. There was additionally no significant main effect or interactions with gender.

To address the possibility that our findings were influenced by the “mixed” instrumental backgrounds of our instrumental group, and to enable comparisons with other research which included only pianists, we compared the 10 pianists in our musician group to 20 age- and gender-matched controls. A mixed-design ANOVA was performed with between subjects factors group (pianist, non-musician) and gender, and hemisphere as a within subjects factor. As in the full sample, there was a significant main effect of group (*F*(1, 26) = 4.46, *p* = .04), such that pianists (*M* = .51, *SD* = .04) had lower FA than non-musicians (*M* = .54, *SD* = .04).

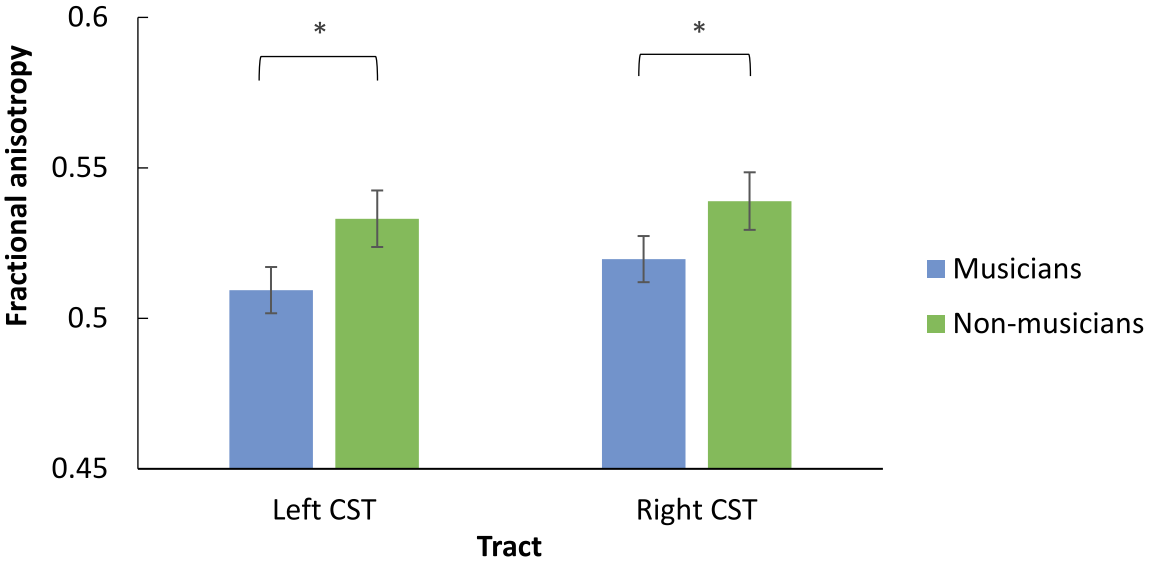


Figure 31. Mean FA of musicians and non-musicians in the left and right corticospinal tract. Error bars are mean standard errors. * *p* < .05

Mean diffusivity (MD)

The same analysis was also performed for MD. Once again, there was a significant main effect of group ($F(1, 57) = 16.0$, $p < .001$), reflecting higher mean MD in musicians than non-musicians within the corticospinal tract (see Figure 32). Consistent with the FA analysis, the main effect of hemisphere and interaction between group and hemisphere were not significant, indicating that mean MD did not differ between the left and right corticospinal tract and that this pattern was the same for musicians and non-musicians. There was also no significant main effect or interaction with gender.

As with the FA analysis, an additional mixed-design ANOVA was performed to compare MD in pianists and non-musicians. Once again there was a significant main effect of group ($F(1, 26) = 5.07$, $p = .03$), such that pianists ($M = 9.22\text{x}10^{-4}$, $SD = 1.18\text{x}10^{-4}$) had higher MD than non-musicians ($M = 8.41\text{x}10^{-4}$, $SD = 6.92\text{x}10^{-5}$).

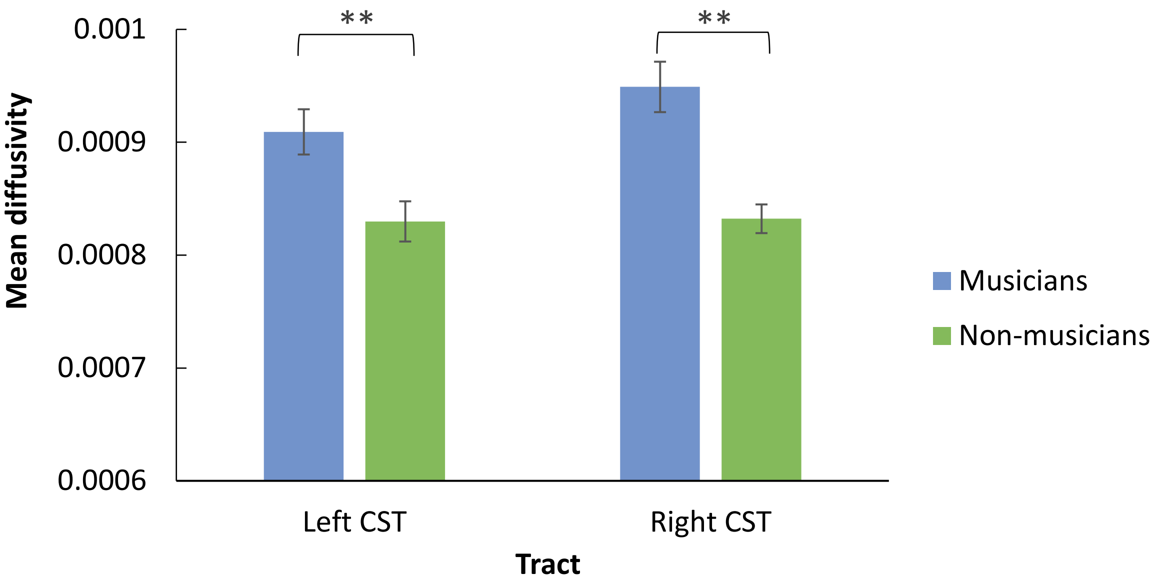


Figure 32. MD of musicians and non-musicians in the left and right corticospinal tract. Error bars are mean standard errors. ** *p* < .001

Tract volume

Finally, the same analysis was performed for corticospinal tract volume, with whole brain volume included as a covariate. While there was no significant main effect of group, or interaction between group and hemisphere, there was a main effect of gender ($F(1, 56) = 6.22$, $p = .02$), such that females had higher tract volume than males in the corticospinal tract (see Figure 33). There was a trend towards significance of the interaction of gender and hemisphere ($F(1, 56) = 3.76$, $p = .06$); pairwise comparisons showed that females had significantly higher volumes than males in the left hemisphere ($p = .002$), whereas the gender difference was not significant in the right hemisphere ($p = .6$).

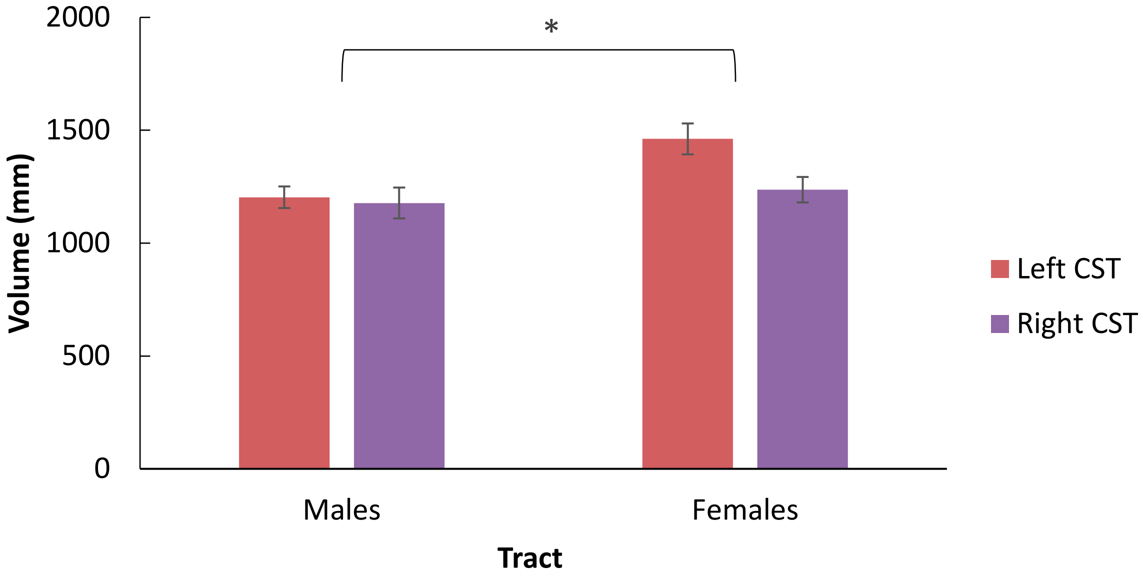
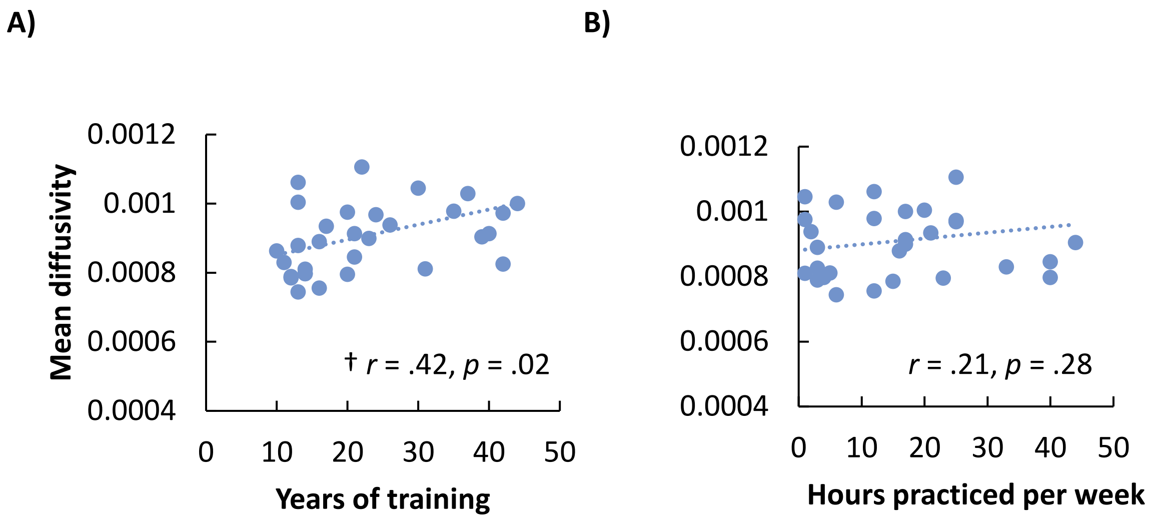


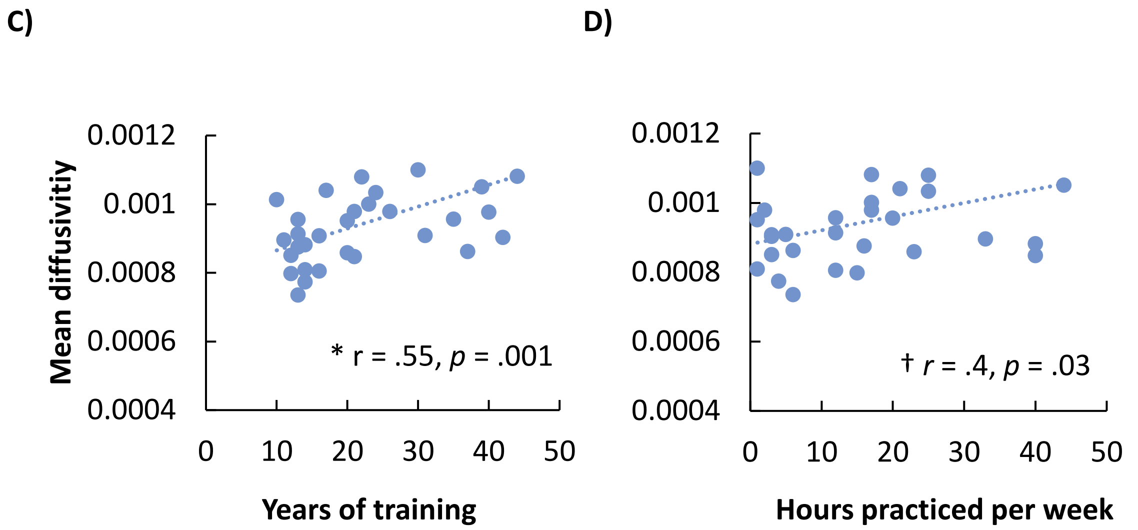
Figure 33. Volume of males and females in the left and right corticospinal tract. Error bars are mean standard errors. * *p* < .05

Associations with training variables

To determine whether years of training, age of onset of training, or practice intensity influenced microstructural properties of the corticospinal tract, Pearson's correlations were performed for the left and right corticospinal tract between FA, MD, and these musical training variables. No significant correlations were found for FA (all *p* values > .05), and there were no significant correlations between MD and age of onset of music training. However, MD in the right corticospinal tract was correlated significantly with both years of training (*r* = .55, *p* = .001, FDR-corrected; see Figure 34). Two other correlations were significant at an uncorrected level only: the correlation between MD in the left corticospinal tract and years of training (*r* = .42, *p* = .02), and the correlation between MD in the right corticospinal tract and hours practiced per week (practice intensity; *r* = .4, *p* = .03).



Left corticospinal tract



Right corticospinal tract

Figure 34. Correlations of MD in corticospinal tract and musical practice parameters (musicians only). A) Correlation between MD in left corticospinal tract and years of training. B) Correlation between MD in left corticospinal tract and hours practiced per week. C) Correlation between MD in right corticospinal tract and years of training. D) Correlation between MD in right corticospinal tract and hours practiced per week. * *p* < .05 (FDR corrected); † *p* < .05 (uncorrected).

To examine whether age was correlated with FA, we conducted correlations between age and FA and MD in the corticospinal tract of non-musicians, applying the FDR correction to correct for multiple comparisons. All *p*-values were above .2, indicating that age was not generally correlated with these microstructural parameters in this group.

Comparison of singers and instrumentalists

The mixed-design ANOVA comparing FA values in singers and instrumentalists found that there were no significant main effects or interactions. For MD, there was a significant main effect of hemisphere ($F(1, 29) = 9.54$, $p = .004$), indicating that MD was higher in the right than left corticospinal tract. No other main effects or interactions were significant.

Superior longitudinal fasciculus (SLF)

The estimated SLF tracts, and the placement of the seeds used in tractography, are shown in Figure 35. For raw data see Appendix H. These are the average tracts across all subjects. Mean tract volume across all subjects was 3470.69mm^2 (± 876.76mm^2) for the left SLF and 3330.75mm^2 (± 732.41mm^2) for the right SLF.

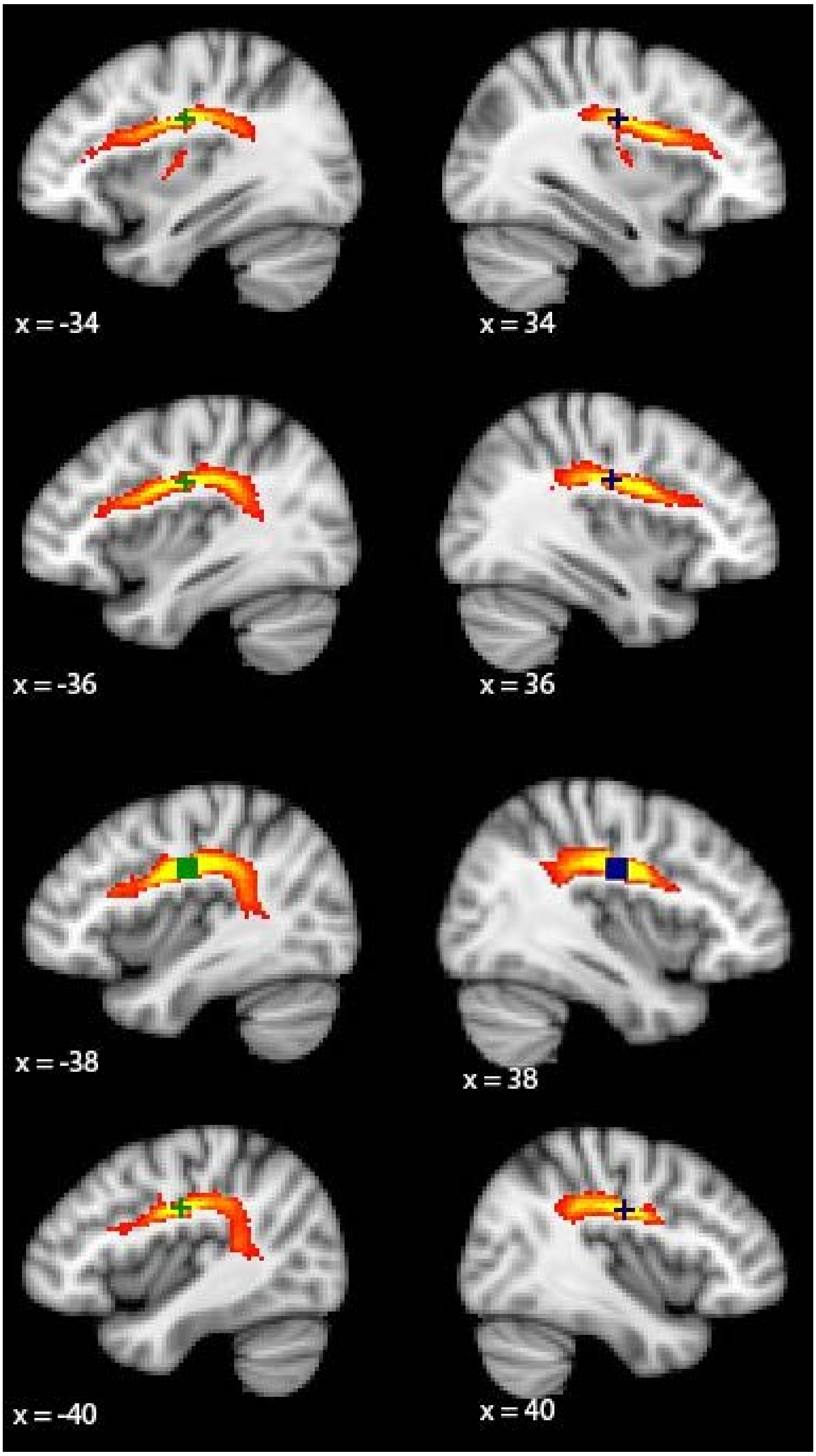


Figure 35. Seeds and resulting tracts for the SLF shown on 8 sagittal slices at x levels indicated (green = left hemisphere seed, blue = right hemisphere seed).

Fractional anisotropy (FA)

The mixed-design ANOVA to test for differences in mean FA in the SLF relating to musical training or gender found that while there was no significant main effect of hemisphere (*F*(1, 57) = 1.55, *p* = .22) or group (*F*(1, 57) = .00, *p* = .98), there was a significant main effect of gender (*F*(1, 57) = 10.73, *p* = .002), such that males had higher FA than females. Importantly, there was also a significant interaction between group and gender (*F*(1, 57) = 13.2, *p* = .001). Bonferroni-corrected pairwise comparisons revealed that male controls had higher FA than female controls (*p* < .001), while there was no such gender difference within the musicians (*p* = .8). Male controls also had higher FA than male musicians (*p* = .01), while female musicians had higher FA than female controls (*p* = .01). This result is shown in Figure 36.

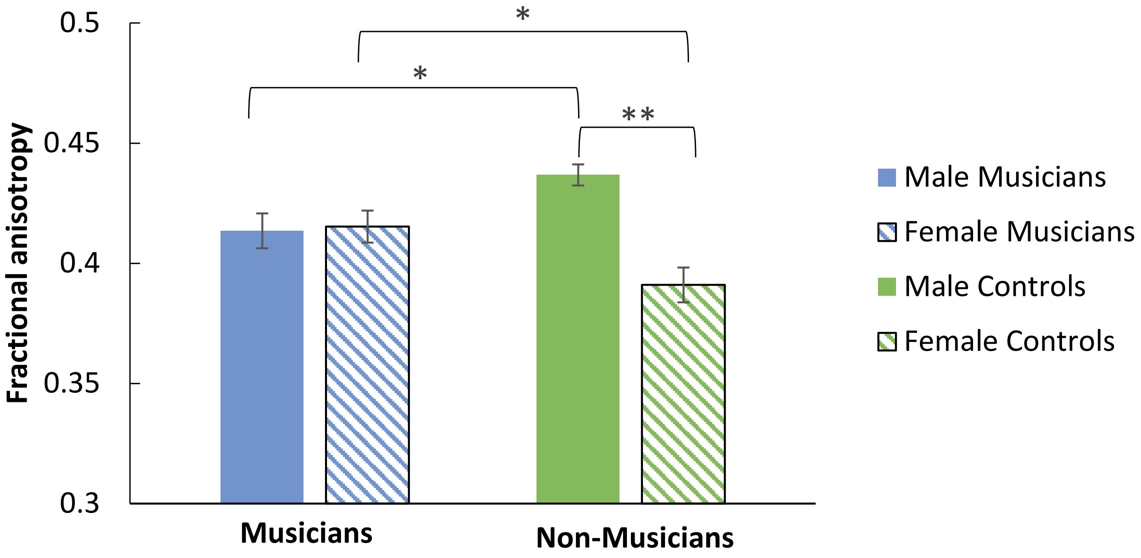


Figure 36. Mean FA across left and right SLF, broken down by group and gender. Error bars indicate mean standard errors. * *p* < .05; ** *p* < .001

Mean diffusivity (MD) and tract volume

The same analyses as described above were also performed for MD and volume of the SLF. For MD, there was a significant main effect of hemisphere (*F*(1, 57) = 27.5, *p* < .001), showing that MD was higher in the left hemisphere than in the right. No other main effects or interactions were significant. For tract volume, there were no significant main effects or interactions, indicating that there are no group or gender differences in volume of the SLF.

Associations with training variables

To determine whether years of training, age of onset of training, or practice intensity influenced microstructural properties of the SLF, Pearson's correlations were performed for the left and right SLF between FA and these musical training variables. While there were no significant correlations for the left SLF (all *p* values > .05), there was a negative correlation between FA in the right SLF and years of training that was significant at an uncorrected level only (*r* = -.38, *p* = .03). In other words, the more years of training completed, the lower the FA. FA in the right SLF did not significantly correlate with age of onset or practice intensity (both *p* values > .05). Once again we checked whether age itself was correlated with FA in the right SLF of non-musicians; this correlation was not significant (*r* = -.10, *p* = .62).

Comparison of singers and instrumentalists

The mixed-design ANOVA comparing FA values in singers and instrumentalists revealed that while the main effect of training type was not significant (*F*(1, 27) = 2.41, *p* = .13), there was a significant interaction between hemisphere and training type for FA (*F*(1, 27) = 6.13, *p* = .02; see Figure 37). Bonferroni-corrected pairwise comparisons showed that in instrumentalists, mean FA was significantly higher in the right than left SLF (*p* = .01), where there was no difference in singers between FA of the left and right SLF (*p* = .28).

Additionally, instrumentalists had higher FA than singers in the right SLF (*p* = .01). For MD, there was a significant main effect of hemisphere (*F*(1, 27) = 13.54, *p* = .001). No other main effects or interactions were significant, indicating no significant differences between singers and instrumentalists.

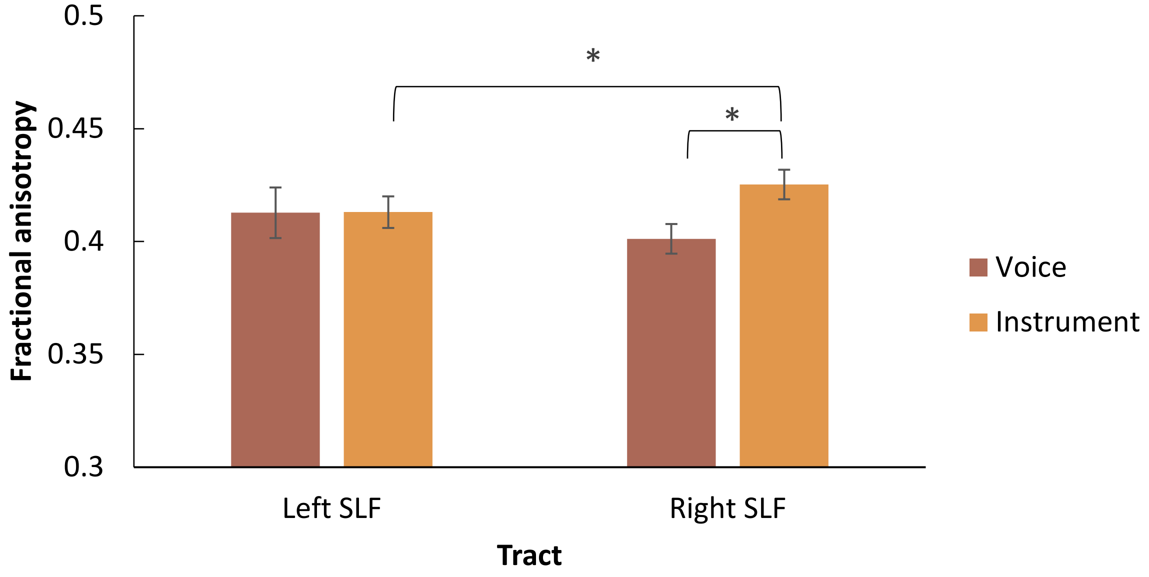


Figure 37. Mean FA for the left and right SLF, in singers and instrumentalists. Error bars indicate mean standard errors. * *p* < .05

Discussion

This study revealed several novel findings regarding differences in white matter microstructure modulated by musical expertise and gender. While there was no difference between musicians and non-musicians at a whole-brain level, closer examination of the corpus callosum, corticospinal tract, and SLF using probabilistic tractography and manual tracing techniques yielded nuanced results. First, consistent with the results of *Study One*, gender once again emerged as a moderating variable in the relationship between musical expertise and structural outcomes, with male non-musicians having higher FA than female non-musicians, and no gender difference in musicians, in the corpus callosum and in the SLF.

Overall, lower FA was associated with musical expertise and more musical training, across the three white matter tracts under investigation. In the corticospinal tract, musicians also had greater diffusivity (MD) than non-musicians, and MD in the right tract was associated with more musical training. Additionally, in the SLF, singers and instrumentalists differed in their lateralisation of FA, pointing to altered structural asymmetry relating to different types of music training. Instrumentalists also had higher FA in the corpus callosum than singers. Contrary to predictions, playing an instrument as opposed to singing did not differentially influence microstructural properties of the corticospinal tract.

Differences between musicians and non-musicians modulated by gender

We found that gender modulated FA differences between musicians and non-musicians in the corpus callosum. While male controls had higher FA than female controls across the whole corpus callosum, there were no significant differences in FA between male and female musicians. This pattern of results is generally consistent with the results of *Study One*, in which functional lateralisation of visuospatial processing also did not differ between male and female musicians, while male non-musicians had more right-lateralised processing than their female counterparts. The corpus callosum is the main tract allowing communication between the hemispheres in the brain, and so these alterations to its microstructural organisation could underlie the functional lateralisation of visuospatial processes which were the focus of *Study One*, or the lateralisation of processing in other sensory or cognitive domains.

FA in the SLF also did not differ between male and female musicians, whilst male non-musicians had higher FA than female non-musicians. These findings in non-musicians are in keeping with the limited previous research on gender differences in these tracts. In the SLF, two studies reported that males had higher FA than females in the left and right hemispheres, respectively (Kanaan et al., 2002; King et al., 2015), although gender differences were not found by Ugwu and colleagues (2015). In the corpus callosum, while some studies found that females had higher FA than males, participants in those studies tended to be children or adolescents (Lebel & Beaulieu, 2011; Schmithorst et al., 2008). When the previous literature is restricted to findings in adult populations, the majority of studies observed that males have higher FA than females in the corpus callosum (Menzler et al., 2011; Pal et al., 2011; Shin et al., 2005; Westerhausen et al., 2003, 2004; but see Chou et al., 2011; Kanaan et al., 2012).

Previous studies in musicians have found that they have higher FA in the genu and posterior midbody of the corpus callosum (Schmithorst & Wilke, 2002; Steele et al., 2013), or that higher FA in the isthmus of the corpus callosum was associated with greater musical practice intensity (Bengtsson et al., 2005). These reports of increased FA in musicians could be interpreted as evidence that musicians have increased, or more efficient, interhemispheric communication than non-musicians. However, it is not clear that this should be the case. To illustrate this point, an example from the gender differences literature is discussed. As we pointed out above, most DTI investigations published to date have shown that adult females have lower FA than males in the corpus callosum (Menzler et al., 2011; Pal et al., 2011; Shin et al., 2005; Westerhausen et al., 2003, 2004). However, there is a great deal of evidence that females have *greater* interhemispheric connectivity than males. Females have more bilateral activations than males during language and visual tasks (Badzakova-Trajkov et al., 2010; Vogel et al., 2003). In addition, recent large-scale investigations of the structural connectome have used graph theory to show that females have more interhemispheric connectivity than males, as well as more connectivity between the frontal, temporal, and parietal lobes, which is argued to reflect females' superior performance in language and memory domains (Ingalhalikar et al., 2014; Tunç et al., 2016).

Both male and female musicians appear to have lower FA, compared to male non-musicians. As the modulation of FA by expertise and gender is not specific to any subregion of the CC, but is an effect observed across the three segments, it is certainly plausible that lower FA in more experienced musicians could reflect more interhemispheric communication or more cross-modal connectivity in general. This could subserve their superior performance on language and memory tasks, as well as on tasks requiring bimanual coordination or audiomotor integration (e.g. Franklin et al., 2008; H. Lee & Noppeney, 2011; Moreno, Friesen, et al., 2011; Moreno et al., 2009; Watanabe et al., 2007). As the posterior segment connects parietal and occipital regions, which are known to be involved in visuospatial processing, it is possible that the lack of gender differences in musicians in this segment could be related to the similarity of functional lateralisation of visuospatial attention between male and female musicians that we reported in *Study One*.

In general, our findings give some preliminary indications that music training may sculpt these tracts in such a way that promotes more similarity between males and females, but are not able to speak directly to what the underlying mechanisms might be. Of course, as this study is not longitudinal, musicians in our sample may have also had individual variations in white matter prior to beginning their training that enabled faster mastery of musical skills and so increased their likelihood of continuing their musical training into adulthood (Zatorre, 2013). Nevertheless, as all of our musicians began training at a time when white matter maturation was still ongoing (≤ 10 years of age; Giedd, 2004; Tamnes et al., 2010), it is certainly plausible that music training could have altered the course of white matter development.

Gender did not influence the relationship between musical expertise and FA or MD in the corticospinal tract. As there was also no gender effect (on FA or MD) even in controls, this suggests that in our sample microstructural properties of the corticospinal tract are not influenced by gender. On the other hand, we did find a gender effect on tract volume, with females having larger volume than males in both the left and right tracts, something that has not been previously reported (*c.f.* Kamson, Juhász, Chugani, & Jeong, 2015; Kumar et al., 2009). Other studies have examined gender differences in FA for this tract, and have yielded contradictory results. While two studies (Bede et al., 2014; King et al., 2015) found increased FA in males relative to females, Bava and colleagues (2011) found that early adolescent females had higher FA than males. On the other hand, we did not find gender differences in FA in the corticospinal tract. Future research is needed to replicate our finding, and to determine why females may have greater corticospinal tract volumes than males.

Reduced FA is associated with greater amounts of musical training

Contrary to our predictions that musicians would have higher FA in the corpus callosum, *lower* FA in all three segments of the corpus callosum (segments connecting to motor, prefrontal, and posterior cortices) was associated with greater durations of music training. This finding contrasts with the small existing literature, which indicates that musicians have higher FA than non-musicians (Bengtsson et al., 2005; Schmithorst & Wilke, 2002; Steele et al., 2013). It is not clear why our results differ; as in those studies, our musicians were also highly proficient and began their training before age 10. Our sample size is considerably larger than in those studies, however, suggesting that our divergent result does not simply reflect a reflection of reduced power. As age is, not surprisingly, very highly correlated with the number of years of training, we considered the possibility that the significant correlations between microstructural parameters and this training variable in fact reflect the underlying variable of age. In non-musicians, when the FDR correction was applied, there were no significant correlations between age and FA or MD in the corpus callosum, the corticospinal tract or the SLF. This suggests that the significant correlations between these microstructural parameters and years of training in those tracts are unlikely to be explained by age.

Musicians also had lower FA and higher MD than non-musicians in the bilateral corticospinal tract. Furthermore, higher MD was associated with longer durations of music training in the right tract, with a trending association with years of training in the left tract. The corticospinal tract carries fibres from the primary motor cortex, as well as premotor and supplementary motor areas, down to the brainstem and spinal cord, where the axons synapse onto motor neurons to convey motor impulses to the muscles. Our finding suggests that the intensive sensorimotor training undertaken by musicians could induce plastic changes in the micro-architecture of the corticospinal tract. The strongest training correlation with MD was in the right corticospinal tract, which conveys motor signals relating to the left side of the body. All of our participants were right-handed, and the main instrument for a considerable number of the musicians in this analysis (17 of 32 musicians) required fine motor control of the fingers of the left hand. Therefore, this association between years of training and diffusivity in the right tract may reflect the role of bimanual music training in sculpting the motor tract connected with the non-dominant left hand.

As some of the musicians included in this analysis were singers rather than instrumentalists, this suggests that vocal training may also engender plasticity of motor tracts. While singers do not develop fine motor control of the hands or fingers, singing places considerable demands on the vocal motor system. It takes many years of training for singers to develop the sound characteristics (such as timbre, pitch, loudness, and range) and high levels of vocal control that are needed for classical singing (Sundberg, 1988). During overt singing in the MRI scanner, Kleber et al. (2010) found that professional opera singers have increased recruitment of motor and sensory regions than non-musicians, including right primary somatosensory cortex, the basal ganglia, and the cerebellum. This finding certainly suggests that classical voice training strongly engages the motor network and so may be sufficient to have an impact on structural properties of the motor tracts. However, an important caveat is that all musicians, including singers, in the current study had achieved at least moderate levels of proficiency on a musical instrument, as all musicians had achieved at least Grade 5 on an instrument. The majority of singers (seven of 11) were currently playing an instrument regularly in addition to singing. This makes it difficult to determine whether the decreased FA in the singers in our sample reflects their vocal or instrumental training.

Previous investigations of the corticospinal tract in musicians have yielded mixed results. Imfeld et al. (2009) and Schmithorst and Wilke (2002) both found that musicians had lower FA than non-musicians in the corticospinal tract. Imfeld and colleagues also found that musicians who began their training earlier had higher MD than those who began later. In contrast, both Han et al. (2009) and Rüber et al. (2013) found that musicians had higher FA than non-musicians in the corticospinal tract. Bengtsson and colleagues (2005) additionally found that higher FA in the internal capsule was correlated with greater childhood practice intensity. Merrett et al. (2013) argued that experiments which recruited mixed groups of musicians (as we did) found reduced FA (Imfeld et al., 2009; Schmithorst & Wilke, 2002), while studies using only pianists have found increased FA (Bengtsson et al., 2005; Han et al., 2009). However, when the pianists in our sample were compared to a sample of age- and gender-matched controls, the pianists displayed the same pattern of FA and MD differences as our full sample of musicians (that is, significantly lower FA and higher MD than non-musicians). Thus our findings do not support Merrett et al.'s claim.

While there were no significant group level differences between musicians and non-musicians in the SLF for either FA or MD, there was a trend for an association between lower FA in the right SLF with greater duration of music training. While this finding should not be over-interpreted, the coordinated interplay between frontal and temporal regions is argued to be important for both language and music processes (Bermudez et al., 2009; Glasser & Rilling, 2008; Oechslin et al., 2010; Rilling et al., 2008), with several studies finding co-activation of frontal and temporal regions during musical tasks (e.g. Burunat et al., 2015; Halpern & Zatorre, 1999). The association we found with years of training might therefore reflect adaptation of this tract in response to long-term music training.

Altogether, our findings suggest that lower FA is associated with more musical training. While this pattern of results contradicts some of the musician literature, studies of professional gymnasts, ballet dancers, and simultaneous interpreters have all found decreased FA in these expert groups relative to controls (Elmer et al., 2010; Hänggi, Koeneke et al., 2010; Huang et al., 2013). Researchers in those studies have variously suggested that reduced FA may reflect larger axon diameter, reduced AD and increased RD, or an increased number of crossing, bending, or twisting fibres. Alternate methods of modelling diffusion in the brain, such as diffusion spectrum imaging, could help to shed light on this possible explanation by modelling more fibre directions within a single voxel (Tuch, 2004). Although more research is needed to elucidate exactly which aspects of the white matter microstructure are altered in expert musicians, and to demonstrate a causal link, our findings add to the literature by demonstrating that, within musicians who began their training early in life, greater amounts of music training are linked to greater adaptations within multiple white matter tracts.

Altered lateralisation in the SLF related to instrument of training

We hypothesised that singers and instrumentalists would show differences in the SLF, on the basis of previous work by Halwani and colleagues (2011). While singers had no asymmetry of FA in the SLF, instrumentalists had a significant rightward asymmetry of FA. Instrumentalists also had higher FA than singers in the right SLF. This raises the possibility of use-dependent adaptation of this structure reflecting the instrumental rather than vocal music training. While this finding is preliminary, one possible explanation is that the sheet music used by instrumental musicians is rather more complex (often with multiple lines of notation which must be read simultaneously) than that used by singers. Arguably, playing an instrument requires more demanding visuomotor translations between musical notation and the associated motor sequences. This may place more demands on the right-lateralised visuospatial system, which may be reflected structurally in microstructural alterations of the “indirect pathway” of the right SLF that passes through the inferior parietal lobule (as described by Catani et al., 2005; Catani & Mesulam, 2008). Future research could test this explanation by assessing SLF microstructure in musicians who can read music and those who cannot (such as guitar players that can only read non-spatial tab notation).

A study by Oechslin, Imfeld and colleagues (2010) compared FA in the SLF between musicians with AP, musicians with RP, and non-musicians (all musicians in this study played a musical instrument; none were singers). They found that non-musicians had rightward asymmetry of FA, musicians with AP had leftward asymmetry, and musicians with RP had no asymmetry in this tract. In contrast, our instrumentalist group (who mostly did not possess AP, and so are best compared to the RP group in the Oechslin study) had rightward FA asymmetry in the SLF. Among other possible explanations, differences in the tractography algorithms could account for this: Oechslin and colleagues employed deterministic tractography, where we used a probabilistic method. As probabilistic tractography allows for the tracking of tracts with lower anisotropy values (Behrens et al., 2007), our technique may have been more effective at tracking the SLF in the nondominant right hemisphere. Previous work has suggested that the use of deterministic tractography likely factored into the inability to identify arcuate fasciculus pathways in the right hemisphere of some participants (Glasser & Rilling, 2008).

Our findings also stand in opposition with those of Halwani et al. (2011), who found that instrumentalists had higher FA than singers in the left dorsal arcuate fasciculus, but unlike our result there was no difference between musician groups in the right tract. The arcuate fasciculus is considered to be part of the SLF (Bernal & Altman, 2010; Martino et al., 2013), and was included in the tracts estimated in the current study. Additionally, while our singers had more recent involvement in instrumental music practice than in their study, the average number of years of vocal training was actually greater for our sample of singers (24 years) than in Halwani and colleague's study (15 years). It is possible, however, that our singers, due to their greater involvement in instrumental music practice, did not have the same *vocal* practice intensity as in their sample. Unfortunately there is no empirical evidence to prove or disprove this possibility: Halwani et al. do not report an estimate of practice intensity in their musicians, and we did not ask musicians to separately estimate their amounts of vocal and instrumental practice.

Finally, instrumentalists had higher FA than singers in the corpus callosum, a finding which has not been reported before. This again suggests that vocal and instrumental music training may differentially influence the microstructure of the corpus callosum. On the other hand, we observed no differences in microstructural properties of the corticospinal tract between singers and instrumentalists. It is possible that our ability to detect a difference between singers and instrumentalists was reduced as all of the singers in our sample were also proficient on at least one instrument, and most currently also played an instrument regularly. Thus, the singers could have motor adaptations closely resembling those seen in instrumentalists. In the Halwani et al. (2011) study, which did observe differences between singers and instrumentalists, while the singers had all previously played an instrument, none had played within the last year. This suggests that recent practice of an instrument may be more relevant in determining whether singers will have the same white matter structure as instrumentalists.

IQ scores and FA

There is limited evidence that FA in structures including the corpus callosum, internal capsule, and uncinate fasciculus is associated with IQ (e.g. Navas-Sánchez et al., 2014; Schmithorst, Wilkes, Dardzinski, & Holland, 2005; Yu et al., 2008). As the difference in FSIQ between musicians and non-musicians in *Study Two* was marginally significant, this raises the question as to whether FSIQ could have a confounding influence on the group differences we report. However, the previous research findings of associations between FA and IQ involve samples with a wider range and distribution of IQ scores, whereas the IQs of both groups of participants in our study were largely in the upper regions of the normal bell curve. For example, the IQ of participants in the study by Navas-Sánchez and colleagues had a range of 88 – 140, while the range reported by Yu and colleagues was 71 - 145. By comparison, the ranges of FSIQ in the current study were considerably truncated, and almost completely overlapped between musicians and non-musicians (musicians: 109 – 137; non-musicians: 109 – 139, in other words almost all participants were in the high average range or higher). Moreover, the actual average difference between our two groups was 3.66 points, which falls just outside of the standard error of measurement for the FSIQ (2.38 points, according to the WASI manual). Finally, to ensure FA and IQ were not correlated within our sample, we performed additional correlational analyses for all three tracts (corpus callosum, corticospinal tract, and SLF). No correlations were significant, or close to significant (all p values > .2). Overall, then, it seems highly unlikely that IQ is a significant confound in the current study.

Limitations of the DTI technique

The DTI method has acknowledged limitations. For example, partial volume effects at the borders between white matter and grey matter can lead to a biasing of FA estimates (Smith et al., 2006). The size of partial volume effects can vary, though, as for instance in thicker fibre bundles the contribution of voxels with partial voluming to the mean FA of the estimated tract will be smaller (Vos, Jones, Viergever, & Leemans, 2011). The three tracts we singled out for ROI analyses are all major white matter pathways, thus we could expect that the contaminating influence of partial volume effects would be diminished. Even more importantly, we did not detect significant differences in tract volume between musicians and non-musicians for any of the three tracts, which minimises the likelihood that partial voluming would have differential effects in each group.

Another possible limitation is that the alignment between study data and the standard template image is rarely perfect, which could lead to incorrect conclusions about location (Johansen-Berg & Behrens, 2013). We decided to select standard-space seeds and waypoints for tractography in order to enable replication, and to ensure a degree of consistency between subjects. Moreover, the individual tracts were manually checked and deemed to be satisfactory (in terms of fidelity to the anatomy) at the 25% threshold. This enables a certain degree of confidence that the tracts we have derived are what we say they are. The algorithm we employed to perform probabilistic tractography also represents an improvement even on other recent publications as it models two fibres per voxel. This increases the sensitivity and accuracy of tracking, particularly in non-dominant pathways (Behrens et al., 2007).

Finally, while TBSS represents an improvement on the ROI approach insofar as it fixes misalignment issues by “skeletonising” the tracts, it is also a more conservative approach as it requires correction for multiple comparisons across the whole brain. We did not find any significant differences between musicians and non-musicians using TBSS; however, our selection of *a priori* ROIs was informed by the previous DTI literature in musicians.

In conclusion, the results presented in the current study indicate that lower FA within key white matter structures is associated with the length of music training, providing further evidence that more training is associated with greater changes in white matter microstructure. Laterality in the SLF also differs between singers and instrumentalists, suggesting that use-dependent adaptation of this structure can vary depending on the type of music training. Similarly, FA in the corpus callosum was higher in instrumentalists than in singers, also implying an effect of music training type on white matter connectivity. Finally, gender was once again an important moderating factor in the relationship between musical expertise and white matter adaptations in both the SLF and the corpus callosum.

Chapter 4: General Discussion

The current state of the literature investigating neural differences between musicians and non-musicians strongly suggests that music training can induce plasticity of brain structure and function, particularly within the sensorimotor cortices (Amunts et al., 1997; Bangert & Schlaug, 2006; Bermudez et al., 2009; Gebel et al., 2013; Hyde et al., 2009; James et al., 2013). Longitudinal studies in which non-musicians are taught to play music provide the strongest evidence that music training causes these changes (e.g. Hyde et al., 2009; Lappe et al., 2008, 2011; Pascual-Leone et al., 1995). A more limited body of research has utilised DTI to identify differences linked to music training in white matter microstructure in tracts including the corpus callosum, corticospinal tract, the cerebellum, and the SLF (Abdul-Kareem, Stancak, Parkes, Al-Ameen, et al., 2011; Bengtsson et al., 2005; Han et al., 2009; Imfeld et al., 2009; Rüber et al., 2013).

What is less clear is whether music training can shape the proficiency and neural organisation of cognitive processes beyond trained skills. While cross-sectional and longitudinal research has linked music training to enhanced cognitive abilities in domains including language, visuospatial processing, and executive functioning (e.g. Bialystok & DePape, 2009; Hetland, 2000; Standley, 2008), there is little research investigating whether there are corresponding differences in musicians in the neural representation of abilities such as visuospatial processing. The primary aim of this thesis was therefore to investigate whether visuospatial processing is associated with altered functional lateralisation in expert musicians. In addition, we investigated whether there were also differences in musicians in the microstructural organisation of white matter tracts, particularly the corpus callosum, which could underlie variations in the lateralisation of visual processes. Our secondary aim was to further investigate specific white matter tracts that are likely to have undergone neuroplastic changes as a result of music training and expertise by exploring the role of gender and different types of music training (vocal and instrumental) in influencing the nature of these changes.

In line with our first aim, *Study One* demonstrated that while visuospatial processing was significantly less right-lateralised in female controls relative to male controls, female musicians and male musicians were equally strongly right-lateralised. Results from investigation of the white matter microstructure of the corpus callosum in *Study Two* are consistent with the functional lateralisation results from *Study One*: while male non-musicians had higher FA than female non-musicians in the corpus callosum, there was no difference between male and female musicians. The same pattern of results was also observed in the SLF. *Study Two* also fulfilled our secondary aim by providing evidence that the instrument of training influenced white matter microstructure. Instrumentalists had higher FA than singers in the corpus callosum, and showed a rightward asymmetry of FA in the SLF where there was no hemispheric asymmetry in singers. These findings provide preliminary evidence that singing as a form of music training is associated with different structural adaptations to those seen in musicians who play a musical instrument.

Visuospatial processing in musicians and the role of gender

In *Study One*, we found that the lateralisation of visuospatial attention was modulated by both musical expertise and gender. While previous work found altered lateralisation of music processing in musicians (e.g. Burunat et al., 2015; Ellis et al., 2013), this is the first study to our knowledge that used fMRI to find a difference in lateralisation of processing during a *non-musical* task. This finding suggests that musical expertise can influence the neural correlates of skills beyond those which are directly practiced in music training, such as auditory and motor skills. The proposed mechanism by which music training could promote altered lateralisation of the visuospatial attention network is through music reading, and particularly sight-reading. Playing music while reading musical notation is associated with activation of right parietal regions (Roux et al., 2007; Schön et al., 2004; Sergent et al., 1992) which are also known to be engaged by visuospatial processing more generally (Corbetta & Shulman, 2002; Fan et al., 2005). Thus, it seems plausible that music training could influence the function of these right hemisphere regions not just in a musical context but for other spatial tasks that draw on the same regions. While we did not find corresponding differences in behavioural proficiency of visuospatial processing in the scanner task, it is likely that this reflects the limited sensitivity of the task that was used.

We also found a similar modulation of FA in the corpus callosum by musical expertise and gender; while male controls had higher FA than female controls, male and female musicians did not differ. The similar pattern of results between *Study One* and *Study Two* does imply a possible relationship; female controls have both lower FA and more bilateral visuospatial processing than their male counterparts. Conversely, male and female musicians do not differ in their lateralisation of visuospatial processing, and also do not differ in FA of the corpus callosum, including the posterior segment, which connects parietal and occipital regions involved in visuospatial processing. This result provides some support for the notion that the patterns of functional asymmetry we observed in *Study One* are associated with corresponding differences in structural organisation of white matter.

No previous studies comparing musicians and non-musicians on measures of task-based activation or white matter connectivity have considered the moderating impact of gender.

Our studies address this hole in the literature by assessing the joint impact of musical expertise and gender on brain function and structural connectivity. Our study design only allowed us to determine whether gender differences exist, and thus cannot shed light on the explanations for those gender differences. Nonetheless, previous literature allows us to make some speculations.

In terms of visuospatial processing, there is some evidence that exposure to androgens, particularly in the prenatal period, may contribute to gender differences in spatial ability. For example, female fraternal twins and females with congenital adrenal hyperplasia, who are exposed to high levels of androgens *in utero*, perform better on spatial tasks than control females (Heil, Kavšek, Rolke, Beste, & Jansen, 2011; Puts et al., 2008). One explanation for this is that androgen exposure could influence the types of activities that males and females seek out. There is some evidence that females exposed to higher levels of prenatal androgens may participate more in “male-typical” activities which boost spatial cognition (Berenbaum, Bryk, & Beltz, 2012). There is also evidence that engagement in male-typical activities such as action video games can improve spatial skills in women, effectively reducing the gender gap (Feng et al., 2007). Twelve hours of spatial training was also found to reduce gender differences in spatial skills in the short term (Miller & Halpern, 2013). This suggests that gender differences in spatial ability are able to be reduced through experience.

Perhaps music training is another experience which can ameliorate gender differences in visuospatial processing. There is evidence that in general music training is associated with enhanced ability in this domain (Hetland, 2000). We extend this by suggesting that females who receive music training may receive a greater benefit than males, as they tend to have lower baseline levels of performance than men. This contention is supported by a recent study by Pietsch and Jansen (2012), which found that female musicians performed at the same level as males on a mental rotation task, whereas males in the two control groups (sports and education students) significantly outperformed females. Importantly, this study did not find that male musicians had superior performance to the males in the control groups, supporting our claim that females who undergo music training receive a particular benefit in the visuospatial domain. While we have no evidence of increased visuospatial proficiency of female musicians, as discussed previously this is likely because the Landmark task is not sensitive enough to detect this. Alternatively, the scanner environment could have minimised differences between musicians and non-musicians, as discussed in *Study One.* In the general population, females have both poorer visuospatial performance than males (Voyer et al., 1995) and less lateralised activation on spatial tasks (Hugdahl et al., 2006, Vogel et al., 2003). It has been suggested that the increased left-hemisphere involvement in female controls reflects the additional use of non-optimal (e.g., piecemeal) or non-spatial (verbal) strategies (Hugdahl et al., 2006). It therefore seems reasonable to conclude that female musicians' more right-lateralised activations during visuospatial task performance may reflect that they are using (or using to a greater extent) the more "spatial" strategies that males use to perform the task. By this account, with a more sensitive task, our female musicians would also be expected to have superior performance than female non-musicians.

In terms of the gender differences in brain structure, again it is possible that the experience of music training has more impact on females than males, for similar reasons. Once again, there are known gender differences in FA of white matter tracts, generally with males having higher FA than females (including the corpus callosum, SLF, and the corticospinal tract; Kanaan et al., 2012; King et al., 2015; Menzler et al., 2011). The reduction of these differences in musicians could reflect plastic changes in females who undertake prolonged music training throughout late childhood and adolescence. The findings of both studies presented in this thesis suggest that gender should be taken into account in future studies examining pre-existing and neuroplastic changes in the brains of musicians. Unfortunately, our results do not speak to whether the differential effects of gender in musicians are linked to the specific instrument of training, as we simply did not have a large enough sample to examine this question, but this also is a question of interest.

Vocal and instrumental music training

Several studies have revealed that musicians who play different instruments have structural and functional changes in the motor and auditory cortices which are specific to the instrument they play (Bangert & Schlaug, 2006; Gebel et al., 2013; Pantev et al., 1998; Rüber et al., 2013; Shahin et al., 2008). Only one previous study, on the other hand, has directly compared singers and instrumentalists to assess whether vocal music training is associated with differences in brain structure relative to instrumental training, finding that singers had lower FA than instrumentalists in the arcuate fasciculus (Halwani et al., 2011).

Our DTI results extend on this study by indicating that voice and instrumental music training differentially affect a related but more extensive white matter tract, the SLF. While musicians who were predominantly singers had no directional asymmetry of the SLF, musicians classified as instrumentalists had higher FA in the right SLF than in the left. However, it is difficult to draw conclusions about what is driving this different pattern and how it relates to Halwani et al.’s findings, given that unlike their findings, the main difference between singers and instrumentalists in our study is that singers had lower FA than instrumentalists in the *right* SLF, with no difference in the left SLF. So although our study suggests that vocal training impacts on neural microstructure of the SLF, the likely mechanisms remain unclear.

The finding that instrumentalists have higher FA than singers in the right SLF may also have implications for our findings relating to the lateralisation of visuospatial processing. We speculate that greater adaptation of this tract in instrumentalists reflects the more complex sheet music that musicians who play instruments read from. This is especially the case for pianists, who must read two lines of music simultaneously to play with their left and right hands. Perhaps, then, we could also expect that instrumentalists may have greater enhancements of visuospatial processing than singers. This possibility could be followed up in future work by directly comparing the performance of singers and instrumentalists on more sensitive visuospatial tasks such as the line bisection paradigm. In addition, the neural correlates of visuospatial processing should be compared between the two musician groups.

We also found that instrumentalists have higher FA than singers in the corpus callosum, which again indicates that these different types of music training may lead to different structural adaptations. Of course musicians in this study were selected only by level of expertise, not on the basis of having exclusive vocal or instrumental training. As a result the training experiences of these two groups are more overlapping than distinct. Clearly further studies are needed that are either more selective in their musician group membership, or that utilise a training study design where individuals without any formal singing or instrument practice receive one of these types of training.

Plasticity in musicians

Ultimately, however, as with the majority of research published in this area, this thesis had a cross-sectional design in which we recruited individuals who already had extensive music training and musical expertise. This self-selection bias limits the strength of the conclusions we can draw regarding whether the differences we observed between musicians and non-musicians are the direct result of music training, or whether there are pre-existing differences in the brain predisposing some individuals to attain greater success in music. As there is evidence that pre-existing variability in brain structure and function influence speed of learning in musical contexts (for a review, see Zatorre, 2013) as well as evidence of music training-induced neuroplasticity (e.g. Hyde et al., 2009), it is likely that our findings reflect a combination of predisposition and plasticity.

Aspects of our experimental design and results arguably provide some support for the plasticity account. Firstly, our groups were matched for confounding variables such as handedness, years of education, and performance (nonverbal) IQ. Although musicians had a slight advantage on verbal and full-scale IQ, there is no evidence that this influenced our findings in either study. It is still possible, of course, that there were differences between groups in some other factor which was unaccounted for. Secondly, all of our musicians began training before the age of 10, increasing the likelihood that they began training within the proposed "sensitive period" in which experience-dependent plasticity is more likely to occur (Penhune, 2011). Finally, the associations that we observed between estimates of white matter microstructure and musicians' years of training are also suggestive of a causal relationship.

This thesis was primarily motivated to assess differences related to music training *in general*. For this reason, we did not initially set out to control for AP in our musician group. In recent years, published research has increasingly shown that musicians with AP have structural adaptations above and beyond those associated with music training in general (Dohn et al., 2015; Jäncke et al., 2012; Loui et al., 2011; Oechslin et al., 2010). In light of these findings, we decided at the mid-point of data collection to attempt to obtain self-reported AP status from our sample of musicians. Of the 25 musicians (75.8%) who responded to an email request, only two (both instrumentalists) reported possessing AP. This suggests that the influence of AP on our results is likely to be minimal, although of course it cannot be ruled out as a possible confound. Future research should control for AP, perhaps even by administering an objective test of AP ability, in light of recent work showing that AP exists on a continuum, rather than being a binary trait that musicians either do or do not possess (Bermudez & Zatorre, 2009).

Future directions

The findings in this thesis extend the literature by demonstrating that musical expertise may be associated with modified functional lateralisation of visuospatial processing, a non-musical cognitive ability. By highlighting the moderating influence of gender on neural differences between musicians and non-musicians, our results also increase scientific understanding of the neural correlates of musical expertise. Our results also indicate that musicians who sing rather than play an instrument may have differential brain adaptations. The reduction of gender differences in brain structure and function of musicians which we observed may also be relevant to developmental or educational practice. For example, our research provides some preliminary evidence that music training begun in early childhood could differentially alter the lateralisation of visuospatial processing in girls. Although more research is needed, this finding suggests that perhaps early music training could also enable enhanced performance on spatial tasks in girls.

Future research should attempt to replicate, and to investigate further, our findings in the visuospatial domain. Further use of fMRI to assess functional lateralisation, perhaps using a better designed version of the Landmark task, is warranted. This task consistently evokes right-lateralised activity in most right-handed people, and, as we have shown, is easy enough (at least, when the difficult 2% deviation trials are not included) to prevent significant group differences in behaviour that complicate the interpretation of activation differences. Then, outside of the scanner, performance of male and female musicians and non-musicians could be compared on a standard line bisection task, which seems to be more sensitive to fine-grained differences in visuospatial ability. This would enable a direct assessment of whether the increased lateralisation that we observed in female musicians is associated with greater visuospatial proficiency. As there are some preliminary indications that musicians with expertise on a musical instrument (rather than voice) have altered microstructural organisation of the right SLF, a tract connecting frontal and parietal regions that are involved in visuospatial processing, another question that could be followed up in future work is whether the relationship between musical expertise and altered lateralisation of visuospatial processing is stronger in instrumentalists than in singers.

It would also be of interest to more directly relate expertise-related differences in brain structure and function to each other. One technique could be to use the activated brain regions from fMRI as seed points for tractography, or to use these to assess structural connectivity using graph theory. The differences we observed between singers and instrumentalists should also be followed up with more targeted research recruiting musicians with more uniform music histories.

In general, as stressed throughout this thesis, a longitudinal study design (ideally with random assignment of participants) is needed to provide causal evidence that music training causes the changes in brain structure and function that we observed. This kind of research is fraught with difficulty, however. For example, it is very challenging to effectively randomise children to music training programmes or alternative control activities, with issues of differential attrition, and difficulty in keeping children in both groups engaged and motivated, and in the cooperation of parents. Particularly, to make a claim that music training can have long-lasting impacts on the brain, this research would need to be extended over several years. Clearly this would be a very costly and logistically difficult endeavour.

Future cross-sectional research can be improved by including a group of musicians with “intermediate” skill levels, such as amateur musicians, as in some previous studies (e.g. Gartner et al., 2013; Schneider et al., 2002; Travis et al., 2011), or by recruiting a group of musicians with a range of ability in order to perform associations between level of skill and neural outcomes. In particular, it would be of interest to further explore the lateralisation of visuospatial processing in musicians with varying levels of musical proficiency to determine the nature of the relationship. Musicians’ lateralisation of other non-musical cognitive abilities such as language could also be assessed further using this design. Further, targeted recruitment of musicians with varying ages of onset of music training (from early childhood through to late adolescence or adulthood), but who were matched for skill level, would also enable comparisons between musicians who began training during the “sensitive period” and those who did not.

Overall summary

The main findings of this thesis are that gender differences in functional lateralisation of visuospatial processing are reduced in musicians, as are gender differences in the directionality of FA in the SLF and corpus callosum. Gender also influenced performance and activation of the right posterior parietal cortex on visuospatial tasks. This suggests that future research needs to consider the role of gender as a possible moderating variable between music training and structural and functional changes in the brain. Finally, we also found altered lateralisation in the SLF related to the instrument of training, suggesting that vocal training and instrumental training are not necessarily associated with equivalent structural changes. Future research should thus consider singers and instrumentalists separately. Overall, this thesis sheds new light on how and why long-term musical expertise can impact on the brain’s structure and function, both for directly trained skills and beyond.

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Appendices

Appendix A: Musician instruments for Study One and Two

Participant number	Grouping	Age of training onset	Number of instruments	Piano	Organ	Voice	Violin	Viola	Cello	Guitar	Double bass	Clarinet	Oboe	Recorder	Percussion	Saxophone	Trumpet	Trombone
1	V	8	1			16												
2	n/a	3	2			33							31					
3	V	4	1			32												
4	V	8	2			13	10											
5	V	7	2	12		14												
6	V	6	2	41		42												
7	V	7	2	33		19												
8	V	5	1			36												
9	I	6	1	14														
10	V	7	3	36	27	35												
11	V	7	1			14												
12	I	7	2	11												2		
13	I	7	1	13														
14	I	5	1	44														
15	I	4	2	20											16			
16	V	6	2			28				37								
17	I	7	2	24							17							
18	I	4	4	16		21						16		22				
19	V	8	2	23		17												
20	I	7	1															37

Participant number	Grouping	Age of training onset	Number of instruments	Piano	Organ	Voice	Violin	Viola	Cello	Guitar	Double bass	Clarinet	Oboe	Recorder	Percussion	Saxophone	Trumpet	Trombone
21	I	10	1														32	
22	I	4	2	17		15												
23	I	10	1					10										
24	I	6	2	26					24									
25	I	6	1	13														
26	I	4	2			7												8
27	I	9	1															21
28	I	8	1	13														
29	I	3	2	13			20											
30	I	8	1	12														
31	I	5	1	21														
32†	I	6	3	22												20	21	
33	I	8	1	14														
Frequency:				21	1	15	2	1	1	1	1	1	1	1	1	2	2	3

† Participant not included in Chapter Three

I = instrument, V = voice, n/a = both, so not assigned a grouping

Numbers in instrument columns represent number of years instrument was played

Frequency of sample playing:	one instrument = 16
	two instruments = 14
	three or more = 3

Appendix B: Demographic information for Study One

Participant Number	Sex	Age (years)	EHI	Years of Education	FSIQ	VIQ	PIQ
M1	M	22	88.2	17.5	134	130	129
M2	F	38	100	16	135	128	134
M3†	F	34	92	20	130	120	133
M4	F	18	79	14	132	136	119
M5	F	19	100	14	132	133	123
M6	F	46	100	18	119	112	123
M7	F	38	100	18	119	107	129
M8	M	47	100	18.5	136	136	128
M9	F	20	78	16	125	119	126
M10	F	42	80	17	124	119	124
M11	F	23	100	17.5	117	123	98
M12	M	18	100	14	120	131	106
M13	M	20	100	19	132	129	128
M14	M	49	100	20	129	131	121
M15	M	24	100	17	124	117	126
M16	M	48	100	18	137	128	137
M17	F	31	100	19	123	111	129
M18	F	26	100	14	110	108	109
M19	F	31	100	19	109	121	97
M20	M	46	80	21	119	127	107
M21	M	45	100	16	127	121	127
M22	M	21	100	16	119	119	116
M23	M	23	100	17	133	133	125
M24	F	32	100	19	130	123	129
M25	M	19	94.4	15	119	121	111
M26	M	20	100	15	123	115	126
M27	M	30	100	16	126	123	123
M28	F	21	100	17	124	119	123
M29	F	23	100	19	127	134	115
M30	F	20	100	16	134	128	133
M31	M	26	89.4	19	136	128	135
M32	M	29	100	16	119	113	121
M33	M	22	100	16	127	127	120

Participant Number	Sex	Age (years)	EHI	Years of Education	FSIQ	VIQ	PIQ
C1	M	25	100	19	128	125	126
C2	M	28	100	20	126	118	127
C3	M	40	100	18	131	119	136
C4	M	49	100	16	128	129	120
C5	F	23	100	18	126	122	124
C6	F	31	100	22	125	121	123
C7	F	38	100	17.5	109	117	101
C8	F	44	76.4	16.5	120	106	132
C9	M	24	100	16	129	125	127
C10	M	19	80	17	116	109	119
C11	M	35	89.4	20	126	115	131
C12	F	41	100	21.5	118	120	111
C13	M	40	100	21	120	115	120
C14	M	20	100	14.5	123	118	121
C15	F	43	100	20	124	118	125
C16	F	22	100	16	118	114	118
C17	F	21	100	17	120	130	107
C18	F	25	100	16	111	109	109
C19	F	30	100	20	139	137	132
C20	F	26	91.6	13	109	113	104
C21	M	40	78.6	13	120	118	119
C22	M	27	71.4	17	127	119	129
C23	F	20	100	16	117	121	108
C24	F	19	100	14	123	126	105
C25	F	28	100	19	130	131	123
C26	M	18	88.2	13	127	120	128
C27	F	21	87.5	15	119	120	114
C28	M	23	100	18.5	120	113	124
C29	M	18	90	13	120	128	108
C30	M	27	100	13	118	112	119

† Participant not included in Landmark task

Appendix C: Demographic information for Study Two

Participant Number	Sex	Age (years)	EHI	Years of Education	FSIQ	VIQ	PIQ
M1	M	22	88.2	17.5	134	130	129
M2	F	38	100	16	135	128	134
M3	F	34	92	20	130	120	133
M4	F	18	79	14	132	136	119
M5	F	19	100	14	132	133	123
M6	F	46	100	18	119	112	123
M7	F	38	100	18	119	107	129
M8	M	47	100	18.5	136	136	128
M9	F	20	78	16	125	119	126
M10	F	42	80	17	124	119	124
M11	F	23	100	17.5	117	123	98
M12	M	18	100	14	120	131	106
M13	M	20	100	19	132	129	128
M14	M	49	100	20	129	131	121
M15	M	24	100	17	124	117	126
M16	M	48	100	18	137	128	137
M17	F	31	100	19	123	111	129
M18	F	26	100	14	110	108	109
M19	F	31	100	19	109	121	97
M20	M	46	80	21	119	127	107
M21	M	45	100	16	127	121	127
M22	M	21	100	16	119	119	116
M23	M	23	100	17	133	133	125
M24	F	32	100	19	130	123	129
M25	M	19	94.4	15	119	121	111
M26	M	20	100	15	123	115	126
M27	M	30	100	16	126	123	123
M28	F	21	100	17	124	119	123
M29	F	23	100	19	127	134	115
M30	F	20	100	16	134	128	133
M31	M	26	89.4	19	136	128	135
M32	M	22	100	16	127	127	120

Participant Number	Sex	Age (years)	EHI	Years of Education	FSIQ	VIQ	PIQ
C1	M	25	100	19	128	125	126
C2	M	28	100	20	126	118	127
C3	M	40	100	18	131	119	136
C4	M	49	100	16	128	129	120
C5	F	23	100	18	126	122	124
C6	F	31	100	22	125	121	123
C7	F	38	100	17.5	109	117	101
C8	F	44	76.4	16.5	120	106	132
C9	M	24	100	16	129	125	127
C10	M	19	80	17	116	109	119
C11	M	35	89.4	20	126	115	131
C12	F	41	100	21.5	118	120	111
C13	M	20	100	14.5	123	118	121
C14	F	43	100	20	124	118	125
C15	F	22	100	16	118	114	118
C16	F	21	100	17	120	130	107
C17	F	25	100	16	111	109	109
C18	F	30	100	20	139	137	132
C19	F	26	91.6	13	109	113	104
C20	M	40	78.6	13	120	118	119
C21	M	27	71.4	17	127	119	129
C22	F	20	100	16	117	121	108
C23	F	19	100	14	123	126	105
C24	F	28	100	19	130	131	123
C25	M	18	88.2	13	127	120	128
C26	F	21	87.5	15	119	120	114
C27	M	23	100	18.5	120	113	124
C28	M	18	90	13	120	128	108
C29	M	27	100	13	118	112	119

Appendix D: Raw data for Landmark task (Study One)

Participant Number	Control TrialCount	Exptal TrialCount	Control RT	Exptal RT	RT Centre	RT 2%	RT 5%	RT 10/15%	Acc Centre	Acc 2%	Acc 5%	Acc 10/15%	D' 2% Left	D' 2% Right
M1	227	87	440.5	1457	1693	1794	1697	847.2	0.92	0.5	0.87	1	0.67	1.84
M2	209	135	494.5	882.6	987.6	1273	763.9	646.9	1	0.67	1	1	2.91	2.64
M3	148	72	790.8	1645	2056	1117	1462	995.9	0.87	0.5	1	1	1.04	1.04
M4	133	87	888.9	1461	1702	1309	1331	1157	0.95	0.5	1	1	2.15	1.01
M5	217	141	465.8	769	796.1	931.7	845.5	628.1	0.78	0.46	0.7	0.97	0.07	1.04
M6	168	111	671.6	1053	1073	1320	1182	870.4	0.83	0.56	0.91	1	1.44	0.71
M7	189	113	543.9	1023	1136	1628	933.4	655.3	0.94	0.5	0.9	1	1.7	1.33
M8	232	171	421.4	650.8	664.4	581.8	669.8	624.6	0.74	0.27	0.63	0.95	0.36	-0.24
M9	217	115	467.1	1005	1170	1066	985.5	705.5	0.66	0.5	0.96	0.95	1.19	-0.39
M10	208	120	498.1	984	1022	1264	1105	778.1	0.91	0.29	0.95	1	0.9	0.61
M11	171	110	643.9	1101	1143	1813	1093	818.4	0.92	0.33	0.89	1	0.67	1.19
M12	189	81	568.8	1532	1725	3810	1354	788	1	0.38	1	1	2.58	0.77
M13	206	115	505	1032	1160	1244	1107	705.3	0.9	0.5	0.86	1	0.64	2.51
M14	220	87	456.3	1411	1432	1935	1593	1136	0.88	0.25	0.94	1	0.82	0.45
M15	246	141	386	826.7	848.2	1378	835.6	586.4	0.97	0.27	0.94	1	1.47	0.87
M16	219	120	462.9	999.4	1020	1762	953.2	693.8	0.87	0.69	0.91	0.96	1.89	1.26
M17	141	82	790.4	1554	1623	2499	2281	872	0.95	0.2	0.89	1	0.35	1.48
M18	204	120	515.1	1013	1043	1569	951	790.1	0.75	0.62	0.86	1	2.05	0.36
M19	199	129	535.3	909.4	798.3	2030	1384	838.1	0.97	0.13	0.64	0.96	1.17	0.28
M20	219	109	464	1077	1084	1412	1185	878.4	0.78	0.38	0.9	1	-0.22	1.04

Participant Number	Control TrialCount	Exptal TrialCount	Control RT	Exptal RT	RT Centre	RT 2%	RT 5%	RT 10/15%	Acc Centre	Acc 2%	Acc 5%	Acc 10/15%	D' 2% Left	D' 2% Right
M21	224	141	449.4	807.9	765	1242	980	747.8	0.97	0.11	0.61	0.82	1.08	0.47
M22	198	139	533.6	842.3	857.4	1218	848.6	712.9	0.88	0.38	0.9	0.88	1.51	0.25
M23	191	84	563	1450	1790	1074	1183	867.5	0.89	0.3	1	1	0.6	0.77
M24	184	89	592.2	1407	1587	1084	1547	785.5	0.86	0.79	1	1	1.84	1.65
M25	231	87	427.8	1490	1929	1847	1191	735.1	0.95	0.67	1	0.94	2.08	1.56
M26	213	107	487	1178	1132	1823	1598	759.9	0.91	0.25	0.77	1	0.92	0.51
M27	198	115	523.6	1070	1074	1234	1269	801.6	0.98	0.3	0.96	1	0.48	2.41
M28	189	118	568.6	1053	905	1304	1513	983.4	0.98	0.08	0.81	1	0.6	0.93
M29	218	118	464.2	1040	1123	1221	1008	724	0.92	0.63	0.83	1	1.34	2.34
M30	226	132	445.7	866.5	970.1	994.1	801.6	615.4	0.84	0.59	0.96	0.96	2.51	0.49
M31	214	90	478.7	1382	1687	2040	892.9	694.6	0.78	0.73	1	1	2.29	0.22
M32	182	133	596.9	874.8	807.8		1254	764	0.97	0	0.71	1	0.47	0.35
C1	205	144	507.2	800.8	826.7	812.2	821.7	716.5	0.96	0.08	0.69	0.93	0.77	0.3
C2	215	119	473.4	985.2	1133	1121	1008	674.3	0.86	0.23	0.95	1	0.45	0.36
C3	206	145	499.2	807.1	810	829	850.4	760.3	0.99	0.31	0.97	1	1.88	1
C4	141	109	831.3	1124	1114	3143	1362	821.5	1	0.2	0.81	1	2.12	0.99
C5	188	113	568.3	1083	1159	1954	1018	789.2	0.95	0.5	1	0.96	1.81	1.33
C6	205	144	499.3	800.2	754.9	1132	1061	651.2	0.99	0.08	0.97	1	1.18	0.71
C7	149	115	781.2	1070	1157	1189	1156	811.7	0.93	0.58	0.82	0.96	1.84	1.14
C8	190	128	565.2	910.1	982.1	941.6	858.6	765.5	0.79	0.54	1	1	0.41	1.27
C9	209	123	495.6	947.7	941.1	1605	1071	782.7	0.96	0.15	0.9	1	1.12	0.61

Participant Number	Control TrialCount	Exptal TrialCount	Control RT	Exptal RT	RT Centre	RT 2%	RT 5%	RT 10/15%	Acc Centre	Acc 2%	Acc 5%	Acc 10/15%	D' 2% Left	D' 2% Right
C10	204	117	512.8	1022	1027	2205	1013	887.8	0.93	0.27	0.86	1	1.41	0.53
C11	244	146	395.6	781.3	772.2	1068	885.2	639.6	0.99	0.7	1	1	2.88	0.93
C12	148	136	777.7	832.7	762.6	952.1	1077	846.6	0.95	0.14	0.52	0.93	0.68	0.68
C13	197	128	539.8	909.8	948.6	1021	941.5	818.5	0.79	0.36	0.95	1	1	0
C14	164	61	692	2011	2586	2557	1308	1063	0.7	0.5	0.89	1	-0.18	0.83
C15	206	165	507	688.5	707.2	760.1	757.4	594.5	0.87	0.45	0.82	0.97	1.47	0.41
C16	174	99	632.5	1240	1307	1679	1385	777	0.96	0.83	1	1	1.98	2.82
C17	192	102	561.9	1150	1361	1353	1122	748.5	0.7	0.5	0.95	1	0.72	0.19
C18	211	140	484.5	817.7	879.9	881.5	815.1	667.6	0.91	0.26	0.81	1	-0.27	1.18
C19	80	85	531.7	829.1	908.8	985.6	783	679.4	0.9	0.56	1	1	1.98	0.05
C20	172	125	623.8	971	1057	773.6	958.9	819.2	0.75	0.2	0.61	0.89	0.21	-0.45
C21	182	129	597.2	925.9	938.3		1162	767.5	0.97	0	0.71	1	0.47	0.11
C22	219	161	463.4	701.3	690.7	947.7	822.8	626.4	0.95	0.15	0.7	0.97	0.78	0.68
C23	179	132	609.8	882.3	893.1	1346	937.7	758.1	0.87	0.3	0.88	0.96	0.88	0.41
C24	194	44	564.7	3143	3669	3360	2862	1285	0.89	0.33	0.75	1	1.8	0.17
C25	199	115	531	1001	1021	911.7	1186	817.9	0.91	0.07	0.68	1	-0.42	0.46
C26	208	125	491	941.5	1028	1041	937.8	745.6	0.9	0.25	0.8	1	0.64	0.64
C27	203	136	511.3	862.2	882.9	1060	870.1	766	0.96	0.47	0.96	0.97	1.56	1.4
C28	189	74	530.6	1739	2056	2366	1043	1063	0.76	0.85	0.93	1	1.17	2.15
C29	217	144	469.9	796.5	884	893.1	746	654.7	0.88	0.5	1	0.94	1.35	0.98
C30	193	144	552.9	798.1	799.8	1108	825	725	0.99	0.38	0.97	1	1.73	1.52

Exptal = experimental

Appendix E: Raw data for 3D Mental Rotation task (Study One)

Participant Number	Control TrialCount	Exptal TrialCount	Control RT	Exptal RT	RT 0°	RT 45°	RT 90°	RT 135°	RT 180°	Acc 0°	Acc 45°	Acc 90°	Acc 135°	Acc 180°
M1	252	44	576.4	3076	1413	2374	4081	3659	3430	1	1	0.93	0.5	0.67
M2	204	28	713.3	4239	2106	4142	5253	5494	7765	1	0.78	0.8	0.5	0.33
M3	200	41	733.8	3260	1813	4037	3891	2869	4475	1	0.78	0.78	1	0.57
M4	167	18	867.5	6927		6060	7272	6809	8847		0.5	0.6	0.6	0.5
M5	173	27	847.3	4553	1295	4464	8487	4213	6164	1	0.86	0.75	1	1
M6	234	42	622.3	3055	1084	2399	4834	3597	4529	1	0.85	0.27	0.67	0.25
M7	146	13	978.9	6012	1388		6144	8127		1		0.5	0.4	0
M8	206	33	697	4146	3311	4209	4785	4384	3987	1	1	0.88	1	1
M9	266	45	548.7	2784	1035	2595	3875	3395	3152	1	0.8	0.6	0.77	0.6
M10	220	49	661.3	3004	1302	2599	3049	3458	3764	1	1	0.88	0.92	0.67
M11	198	41	726.8	3895	3389	3079	3550	5154	4838	0.4	0.7	0.55	0.5	0.57
M12	234	33	616	4380	2887	5560	4632	3904	4554	0.75	0.43	0.73	0.5	0.4
M13	165	42	882.1	3267	2099	2940	4101	3435	3006	1	1	1	1	1
M14	180	39	813.7	3606	2079	4861	4097	3101	3526	1	0.8	0.82	0.86	0.57
M15	194	41	744.7	3709	2035	3239	4128	4430	3793	1	1	0.79	0.78	0.57
M16	247	51	582.5	2682	1195	3106	3373	2690	3523	1	1	0.58	0.73	0.6
M17	226	44	642.2	3035	1951	2266	3498	3548	6608	1	0.78	0.7	0.8	0.33
M18	155	21	933.9	6329	1143	6642	6683	7780	7633	1	1	0.75	0.5	1
M19	176	42	833.9	3244	1772	3061	3726	3634	3812	1	0.92	0.73	0.55	0.75
M20	209	29	693	4346	1974	3332	6767	6541	6526	1	1	0.67	0.57	1

Participant Number	Control TrialCount	Exptal TrialCount	Control RT	Exptal RT	RT 0°	RT 45°	RT 90°	RT 135°	RT 180°	Acc 0°	Acc 45°	Acc 90°	Acc 135°	Acc 180°
M21	201	36	723.1	3860	2289	1923	4309	5652	6398	1	1	0.8	0.75	1
M22	252	44	573.4	3226	1297	1905	4416	3613	3792	1	0.78	0.43	0.73	0.75
M23	211	52	684.6	2714	1296	2797	3404	2526	2780	1	1	0.8	0.6	0.43
M24	186	32	781.1	4269	2622	3724	5492	5050	4512	1	0.92	0.86	0.71	0.5
M25	174	18	838.4	5411	2895	4405	6928	4798	8124	1	0.67	0.75	0.33	0.75
M26	225	40	638.3	3051	1393	2896	5300	3972	3842	1	0.9	0.18	0.57	0.67
M27	196	48	744.1	2926	1494	2584	3752	3442	3113	1	1	0.88	0.8	0.25
M28	206	53	704.3	2621	1491	2534	2969	3069	2892	1	0.8	0.79	0.75	0.8
M29	218	28	666.7	3797	1221	4070	3671	5651		1	1	1	0.63	0
M30	226	54	636.5	2644	1126	1934	2602	4268	3596	1	1	0.79	0.79	1
M31	202	46	721	3031	1138	1672	4333	3594	3846	1	1	0.93	1	0.75
M32	231	36	630.1	3817	2169	3671	4331	4702	4418	1	1	0.77	0.86	0.5
M33	195	30	748	3771	1538	2838	5160	3745	5137	1	1	0.88	1	0.75
C1	208	36	707.8	3688	2143	3556	4767	2965		0.25	0.71	0.33	0.5	0
C2	217	70	663.3	1983	1353	1793	1991	2292	2977	1	0.91	0.79	0.56	0.6
C3	215	62	673.9	2329	1171	2046	2717	2751	2957	1	1	0.67	0.78	1
C4	121	36	1196	3818	1525	3654	5092	3678	6649	1	1	0.75	0.91	0.6
C5	193	30	755.7	3942	1676	4174	5243	4143		1	0.82	0.6	0.44	0
C6	212	63	683.5	2166	1546	2247	2226	2473	2504	1	0.89	0.62	0.85	0.63
C7	171	41	855.4	3067	2166	3532	3147	3453	3210	0.88	0.7	0.56	0.63	0.83
C8	186	38	748.5	3393	2395	3828	4251	4034	2653	1	0.67	0.42	0.31	0.33
C9	225	56	640.2	2513	1468	2103	2486	3089	3574	1	0.77	0.67	1	0.8
C10	206	61	705	2393	1216	2283	2622	2684	2434	1	1	1	1	1
C11	267	55	540.3	2353	1276	1894	2742	2673	3179	1	1	0.75	0.86	1
C12	163	50	889.4	2591	1576	2686	2708	2448	4634	0.3	0.62	0.58	0.4	0.2

Participant Number	Control TrialCount	Exptal TrialCount	Control RT	Exptal RT	RT 0°	RT 45°	RT 90°	RT 135°	RT 180°	Acc 0°	Acc 45°	Acc 90°	Acc 135°	Acc 180°
C13	171	28	758.5	4397	4473	3664	4563	4773	5212	1	0.83	1	0.43	0.33
C14	175	43	836.8	3222	2934	2740	3863	3003	4082	1	1	1	1	0.8
C15	222	110	650.5	1320	1191	1586	1024	1406	1124	0.93	0.64	0.35	0.61	0.69
C16	184	31	781.1	4588	4246	3782	4246	4558	7405	1	1	0.78	0.6	0.6
C17	217	22	668.2	5917	2996	5797	7930	8120	4955	1	0.75	0.5	0.67	0.5
C18	208	24	698.1	5804		6749	6181	4886	5885		1	1	0.89	1
C19	213	39	697.1	3760	2203	2643	4691	4286	4883	0.83	0.56	0.8	0.64	0.67
C20	173	30	837.5	4453	3319	3790	4886	5270	4643	1	0.8	0.78	0.43	0.5
C21	212	42	685.7	3161	1605	2757	3921	2869	3640	1	0.91	0.86	0.83	0.67
C22	230	53	631.2	2653	1378	2259	2480	3971	3420	1	0.85	0.88	0.9	0.71
C23	190	47	760.1	2933	2511	2484	3316	3693	3466	1	0.93	0.73	0.44	0.83
C24	185	17	815.2	5067	3552	5947	4739	4328	7024	0.75	1	0.33	0.67	0.5
C25	222	62	647.3	2204	1152	1640	2529	2797	2828	1	0.93	0.94	0.86	0.6
C26	201	48	721.2	2729	1306	1949	2864	3407	4916	1	1	0.89	0.71	1
C27	233	47	612.8	2886	1460	2739	2977	2992	4048	1	0.86	0.73	1	1
C28	220	20	662.4	5105	4896	3527	6074	5083	8104	1	0.8	0.8	1	1
C29	244	56	588.9	2367	1680	2086	2836	2723	2507	1	0.92	0.81	0.78	0.78
C30	243	49	593.5	2979	1859	2242	3374	3291	4632	1	1	0.92	0.71	0.67

Exptal = experimental

Appendix F: Raw data for Visual Search task (Study One)

Participant Number	Control TrialCount	Exptal TrialCount	Control RT	Exptal RT	RT No Change	RT Left	RT Right	Acc No Change	Acc Left	Acc Right
M1	195	32	749.8	4466	5408	3091	3299	1	1	1
M2	184	30	786.5	4546	5527	3706	3684	1	1	0.78
M3	122	30	1191	4813	5583	4636	3901	1	0.83	0.91
M4	134	27	1091	5221	6464	4048	3701	1	0.75	1
M5	199	34	739.7	3984	5384	3663	3565	1	1	0.94
M6	215	34	676.7	4278	4482	4573	3547	0.94	0.88	0.7
M7	123	17	1191	6421	7415	5799	3568	1	0.71	0.25
M8	181	26	791.3	5266	6266	3257	4271	1	0.8	0.86
M9	233	36	632.1	3898	3945	3685	4040	0.75	0.55	0.56
M10	201	34	727.1	4215	4906	2929	3626	1	0.86	0.89
M11	179	23	815.7	6207	6751	4244	6161	1	0.33	0.67
M12	204	27	711.8	4879	5330	3516	5950	0.92	0.86	0.38
M13	185	27	789.9	4850	5623	3472	4896	1	1	1
M14	172	26	847.7	4918	5271	4764	4375	1	0.57	0.75
M15	163	35	889.3	3903	4219	4315	2907	1	1	1
M16	235	35	620	4062	4580	4106	2847	1	1	1
M17	222	30	648.7	4446	5586	2990	3459	1	0.88	1
M18	102	23	1454	5785	6303	4627	4698	0.93	0.5	1
M19	150	26	980.9	5778	6443	4615	5361	0.67	0.29	0.4
M20	162	32	908.7	4796	4912	4694	3347	1	0.5	0.2
M21	177	29	827.8	4837	5417	2868	3982	1	1	0.86
M22	226	31	644.5	4288	4324	5322	3774	1	0.22	0.63
M23	161	32	912.8	4253	5127	4184	2977	0.8	0.57	0.8
M24	109	26	1341	5241	6160	3755	3193	1	0.6	1
M25	145	11	1049	5085	11587	2727	4192	0.25	0.67	0.5
M26	225	34	646.9	3954	4581	2494	3596	1	0.44	1
M27	194	29	755.1	4472	5129	4552	3713	1	0.29	0.62
M28	200	39	722.4	3879	4224	2846	3942	1	0.7	0.56
M29	188	22	770.3	5995	7259	4661	4520	1	1	0.8
M30	189	24	773.3	6091	6212	5387	6193	1	0.6	1
M31	177	31	824.9	4407	5125	2410	3638	1	0.75	1
M32	184	28	794.7	4841	5724	3403	3260	1	0.4	0.67
M33	149	27	987.4	5730	6231	4456	4925	1	0.5	0.75

Participant Number	Control TrialCount	Exptal TrialCount	Control RT	Exptal RT	RT No Change	RT Left	RT Right	Acc No Change	Acc Left	Acc Right
C1	117	21	1218	6294	6925	6692	5401	0.89	0.6	1
C2	220	34	662.2	4198	4871	3953	3443	1	0.73	0.9
C3	193	41	748.6	3487	3892	3000	2883	1	0.91	0.67
C4	145	34	1008	4623	5040	3469	4167	1	0.5	0.25
C5	145	24	1014	5621	7074	4699	4295	1	0.78	0.83
C6	187	28	766.8	4982	5183	4043	5158	1	0.67	0.5
C7	139	13	1037	7206	8277	3114	7790	1	1	0.6
C8	168	34	875.9	3831	3865	3717	3857	0.83	0.45	0.4
C9	222	32	651.8	4489	5372	3923	3682	1	0.75	0.91
C10	153	25	947.9	5832	6452	5797	3824	1	0.45	0.75
C11	252	35	578.4	3808	4691	3263	2663	0.94	0.88	0.9
C12	133	41	1087	3556	3627	3533	3021	1	0.11	0.33
C13	188	25	768.6	5945	6200	5959	5343	1	0.75	0.86
C14	167	23	866.5	6008	6697	4950	5804	1	1	1
C15	224	41	652.3	3519	3497	3782	3459	0.94	0.3	0.54
C16	132	21	1095	6194	6294	7533	5391	1	0.5	0.86
C17	153	11	752.5	7609	8968	4016	7289	1	1	1
C18	208	19	697.7	6451	7613	3843	5670	1	0.8	1
C19	180	28	827.4	5229	5753	4488	4967	0.92	0.55	1
C20	123	32	1156	4190	4261	4060	4073	1	0.4	0.5
C21	155	39	895.2	3778	3990	2786	4229	1	0.42	0.3
C22	187	26	783.3	5262	5738	4747	4248	0.94	0.8	1
C23	178	30	813.8	4478	4860	3966	2471	1	0.89	0.2
C24	163	30	905.5	4533	4008	5177	5912	0.74	1	0.5
C25	195	33	749.5	4022	4471	3265	2709	1	0.6	0.29
C26	198	33	729.9	4306	4998	3177	3395	1	0.78	0.83
C27	202	48	713.6	3183	2878	3855	3210	1	0.47	0.31
C28	177	23	825.7	5959	7405	5150	4494	1	1	1
C29	161	38	828.1	3808	4044	3756	3142	0.9	0.63	0.6
C30	253	36	571.2	3897	4711	2814	3121	1	0.64	0.78

Exptal = experimental

Appendix G: Raw data for laterality indices (all tasks; Study One)

Participant Number	LM Wholebrain LI	LM ROI LI	MR Wholebrain LI	MR ROI LI	VS Wholebrain LI	VS Parietal ROI LI	VS Occipital ROI
M1	-0.63	-0.48	0.42	-0.38	0.46	0.23	0.37
M2	-0.78	-0.43	-0.42	-0.42	0.31	0.26	0.37
M3	-0.75	-0.54	-0.38	-0.46	-0.07	-0.18	-0.062
M4	-0.72	-0.71			0.36	0.24	0.44
M5	-0.72	-0.47	-0.03	0.18	-0.31	-0.49	0.084
M6	-0.87	-0.56			0.27	0.25	-0.13
M7	-0.91	-0.83			0.28	0.075	0.32
M8	-0.49	0.08	-0.07	-0.16	-0.47	-0.48	-0.38
M9	-0.6	-0.47	0.47	0.52			
M10	-0.43	-0.33	-0.06	-0.24	0.66	0.41	0.62
M11	-0.79	-0.57			0.03	0.15	0.015
M12	-0.78	-0.3			0.17	0.33	0.13
M13	-0.77	-0.4	-0.01	-0.24	0.05	0.13	-0.096
M14	0.12	-0.58	-0.26	-0.53	0.19	-0.5	0.21
M15	-0.61	-0.38	0.05	0.24	0.04	-0.01	0.26
M16	-0.87	-0.74	0	-0.39	0.16	-0.13	0.37
M17	-0.37	-0.32	-0.27	-0.24	-0.28	-0.26	-0.21
M18	-0.61	-0.7	0.22	0.28	0.05	-0.12	0.1
M19	-0.55	-0.93	-0.09	-0.66			
M20	-0.8	-0.45	-0.27	-0.27	-0.18	-0.57	-0.11
M21	-0.79	-0.58	-0.53	-0.46	-0.04	-0.07	-0.19
M22	-0.54	-0.28			-0.35	-0.36	-0.099
M23			-0.41	-0.44	0.36	-0.01	0.39
M24	-0.71	-0.56	0.48	0.58	0.61	0.57	0.68
M25	-0.47	-0.24					
M26	-0.39	-0.38			0.04	-0.1	0.36
M27	-0.87	-0.78	-0.63	-0.62	-0.45	-0.55	0.002
M28	-0.79	-0.71	-0.11	-0.02	-0.15	-0.5	-0.059
M29	-0.87	-0.91	-0.5	-0.37	0.32	0.29	0.41
M30	-0.81	-0.75	-0.14	-0.41	-0.23	-0.4	0.085
M31	-0.83	-0.74	-0.37	-0.35	-0.29	-0.35	0.015
M32	-0.56	-0.18	-0.04	-0.18	0.4	0.025	0.47
M33	-0.79	-0.48	-0.42	0	-0.18	-0.35	0.33

Participant Number	LM Wholebrain LI	LM ROI LI	MR Wholebrain LI	MR ROI LI	VS Wholebrain LI	VS Parietal ROI LI	VS Occipital ROI
C1	-0.83	-0.46			-0.02	-0.19	0.19
C2	-0.52	-0.27	-0.02	0.16	0.31	0.24	0.22
C3	-0.54	-0.53	-0.21	-0.22	0.36	0.25	0.48
C4	-0.77	-0.71	-0.52	-0.35	-0.15	-0.46	-0.039
C5	0.06	-0.39	-0.04	0.15	0.55	0.4	0.57
C6	-0.67	-0.6	-0.26	-0.48	-0.07	0.021	-0.11
C7	-0.53	-0.23	-0.16	-0.31	-0.15	-0.56	0.11
C8	0.9	0.96					
C9	-0.69	-0.5	-0.27	-0.51	0.08	0.038	-0.11
C10	-0.91	-0.8	-0.5	-0.49	0.03	0.29	-0.13
C11	-0.76	-0.49	-0.44	-0.66	0.16	0.14	-0.013
C12	0.08	-0.15			-0.27	-0.27	-0.33
C13	-0.73	-0.61	0.39	0.03	0.17	0.11	0.023
C14	-0.74	-0.57	-0.26	-0.47	-0.27	-0.54	-0.12
C15	-0.87	-0.86			0.23	0.38	0.008
C16	-0.74	-0.31	0.19	-0.25	-0.2	-0.26	-0.18
C17	-0.82	-0.79	-0.24	-0.33	0.19	-0.01	0.29
C18	-0.93	-0.91	-0.27	0.06	0.04	0.028	0.08
C19	0.16	-0.23	0.52	0.29	0.07	-0.3	0.25
C20	-0.1	-0.26	-0.37	-0.71	-0.07	-0.34	0.47
C21	-0.8	-0.36	-0.38	-0.25			
C22	-0.83	-0.45	-0.46	0.04	0.3	0.039	0.46
C23	-0.76	-0.27	-0.5	-0.51	0.03	0.23	-0.19
C24	-0.67	-0.2	0.4	0.32	0.44	0.56	0.27
C25	-0.74	-0.88	0.41	0.46	0.32	0.16	0.4
C26	-0.83	-0.59	-0.08	-0.35	0.23	0.22	0.2
C27	-0.83	-0.5	0.07	0.15			
C28	-0.67	-0.61	0.03	-0.11	0.02	-0.22	0.098
C29	-0.88	-0.59	-0.43	-0.66	-0.57	-0.58	-0.61
C30	-0.8	-0.59	-0.38	-0.14	-0.3	-0.68	-0.051

LM = Landmark; MR = 3DMR; VS = Visual Search

Appendix H: Raw data for CST and SLF (Study Two)

Participant Number	WholeBrain_Volume	Years Training	Practice Per Week	FA CST L	FA CST R	MD CST L	MD CST R	Vol CST L	Vol CST R	FA SLF L	FA SLF R	MD SLF L	MD SLF R	Vol SLF L	Vol SLF R
M1	895830.32	14	4	0.52	0.5	0.000797	0.000774	1448	1152	0.39	0.4	0.000775	0.000762	1872	3728
M2	1310732.49	35	12	0.47	0.45	0.000978	0.000957	968	1904	0.39	0.41	0.000768	0.000752	2616	3264
M3	1382577.16	30	1	0.56	0.56	0.001045	0.0011	1168	1304	0.4	0.4	0.000727	0.000706	2936	3456
M4	876606.55	10		0.47	0.45	0.000863	0.001014	1528	1312	0.48	0.44	0.00071	0.0007	5936	3336
M5	978598.41	12	3	0.5	0.52	0.000789	0.000851	1616	992	0.42	0.39	0.000754	0.000751	3824	3872
M6	809973.3	40		0.55	0.58	0.000913	0.000977	1512	864	0.46	0.43	0.000707	0.000698	6480	3168
M7	934796.35	31	5	0.5	0.51	0.000811	0.000909	1592	1784	0.37	0.39	0.000756	0.000713	3632	3208
M8	862852.3	42	3	0.52	0.53	0.000825	0.000904	1504	1648	0.41	0.36	0.00073	0.000755	2880	3088
M9	1197655.22	14	1	0.54	0.53	0.00081	0.000809	976	1168	0.39	0.39	0.000764	0.000737	3640	3960
M10	869767.99	37	6	0.43	0.57	0.001029	0.000863	1800	784	0.4	0.4	0.000771	0.000757	3368	4112
M11	1360309.88	16	3	0.54	0.51	0.00089	0.000908	1448	1912	0.4	0.39	0.00076	0.000715	3624	1448
M12	940433	11	33	0.57	0.55	0.000829	0.000896	1224	1056	0.39	0.38	0.000784	0.000815	3352	3752
M13	900593.63	13	12	0.52	0.51	0.001061	0.000914	1088	920	0.42	0.41	0.000696	0.000685	3664	3248
M14	875096.31	44	17	0.43	0.46	0.001	0.001082	1736	1680	0.41	0.39	0.000758	0.000762	5264	4512
M15	950568.39	20	23	0.53	0.51	0.000795	0.000859	1320	1608	0.38	0.42	0.000755	0.000763	4376	3072
M16	934682.81	42	25	0.51	0.53	0.000972	0.001208	1536	856	0.36	0.39	0.000795	0.000733	3816	2632
M17	1491672.28	24	25	0.48	0.49	0.000968	0.001034	1488	1032	0.41	0.43	0.00075	0.000744	2856	3432
M18	864389.54	22	25	0.51	0.47	0.001106	0.00108	1496	1192	0.45	0.46	0.000658	0.000653	3632	3560
M19	1425346.15	23	17	0.47	0.53	0.000899	0.001001	2480	960	0.45	0.43	0.00072	0.000716	2520	3296
M20	925082.54	39	44	0.55	0.56	0.000904	0.001051	1112	1064	0.36	0.39	0.000772	0.000759	3448	2984

Participant Number	WholeBrain_Volume	Years Training	Practice Per Week	FA CST L	FA CST R	MD CST L	MD CST R	Vol CST L	Vol CST R	FA SLF L	FA SLF R	MD SLF L	MD SLF R	Vol SLF L	Vol SLF R
M21	951358.35	35	42	0.54	0.57	0.001241	0.001325	1024	736	0.41	0.4	0.000736	0.000708	3144	2616
M22	945743.93	17	21	0.46	0.5	0.000934	0.001041	1024	864	0.46	0.45	0.000707	0.000675	3528	3208
M23	1409991.42	13	16	0.46	0.46	0.000879	0.000876	1096	1368	0.4	0.39	0.000729	0.000676	2776	2104
M24	831732.5	26	2	0.55	0.5	0.000938	0.000979	2160	1600	0.42	0.41	0.000738	0.000665	3664	2424
M25	867025.8	13	20	0.46	0.5	0.001004	0.000956	1832	1056	0.4	0.44	0.000723	0.000669	3824	3096
M26	920544.92	16	12	0.58	0.59	0.000755	0.000806	1008	800	0.43	0.47	0.00073	0.000707	4112	4104
M27	829262.89	21	40	0.54	0.6	0.000845	0.000848	1112	568	0.46	0.43	0.000656	0.000657	2632	1904
M28	875325.35	13	6	0.6	0.56	0.000744	0.000736	848	1216	0.44	0.47	0.000698	0.000658	4160	3968
M29	926579.71	20	1	0.47	0.45	0.000975	0.000952	1152	928	0.36	0.41	0.000727	0.000723	1608	3112
M30	908688.11	12	15	0.52	0.47	0.000785	0.000798	1384	1592	0.38	0.43	0.000757	0.000707	2280	3416
M31	871019.9	21	17	0.48	0.56	0.000913	0.000979	1016	904	0.46	0.47	0.000728	0.0007	4560	4008
M32	914363.47	14	40	0.47	0.55	0.000797	0.000882	1344	872	0.43	0.46	0.000684	0.000703	3840	3320
C1	862752.34			0.58	0.52	0.000739	0.000762	1480	1816	0.42	0.43	0.00072	0.000742	3624	3736
C2	907703.79			0.42	0.52	0.001109	0.000789	1200	1232	0.44	0.43	0.000749	0.000674	3064	2352
C3	856865.3			0.41	0.52	0.000828	0.000861	1512	1352	0.42	0.41	0.000767	0.000729	2992	2960
C4	872444.4			0.49	0.53	0.000886	0.000846	656	1312	0.46	0.44	0.000741	0.000741	4824	3632
C5	863254.94			0.59	0.45	0.000875	0.000998	1288	1024	0.38	0.36	0.000762	0.000741	2992	3048
C6	895683.57			0.58	0.52	0.000918	0.000833	1120	1680	0.41	0.41	0.000767	0.00076	3184	2888
C7	906708.79			0.46	0.46	0.000911	0.000853	1632	1296	0.41	0.43	0.00076	0.000748	3992	4152
C8	1475008.23			0.62	0.62	0.000929	0.000841	1344	1288	0.36	0.34	0.000753	0.000733	2776	536
C9	886439.98			0.52	0.48	0.00095	0.000856	1184	1424	0.46	0.45	0.000724	0.000716	3936	2880
C10	874823.72			0.5	0.48	0.000762	0.000815	1328	2184	0.39	0.42	0.000735	0.000724	3152	4144
C11	1422164.94			0.56	0.56	0.000774	0.000751	1096	1064	0.43	0.43	0.000718	0.000748	4136	4688
C12	868960.64			0.47	0.53	0.0007	0.00077	1376	1040	0.4	0.41	0.000717	0.000701	3496	3768

Participant Number	WholeBrain_Volume	Years Training	Practice Per Week	FA CST L	FA CST R	MD CST L	MD CST R	Vol CST L	Vol CST R	FA SLF L	FA SLF R	MD SLF L	MD SLF R	Vol SLF L	Vol SLF R
C13	925616.3			0.53	0.51	0.000781	0.000857	1056	1384	0.43	0.43	0.000712	0.000684	3496	3032
C14	1172129.3			0.51	0.54	0.000781	0.000941	1680	856	0.4	0.39	0.000725	0.000743	2664	3672
C15	1446969.68			0.54	0.55	0.000744	0.00079	1560	856	0.41	0.38	0.000734	0.000713	3624	3376
C16	1462082.78			0.54	0.63	0.000749	0.000783	968	1320	0.35	0.35	0.00074	0.00075	2584	2600
C17	852098.54			0.52	0.53	0.000866	0.000819	1136	1280	0.39	0.4	0.000736	0.000724	3392	3720
C18	898017.82			0.51	0.55	0.000738	0.000759	2144	1360	0.41	0.39	0.000723	0.000691	3232	3352
C19	856235.63			0.56	0.5	0.000896	0.000915	1208	1552	0.34	0.39	0.000761	0.000739	3480	3952
C20	879232.77			0.59	0.58	0.000787	0.000736	808	632	0.44	0.43	0.000761	0.000717	3344	3440
C21	904866.31			0.53	0.54	0.000824	0.00088	1176	1360	0.46	0.46	0.000722	0.000734	2584	3920
C22	844698.99			0.59	0.59	0.000784	0.000803	1984	1008	0.37	0.37	0.00077	0.000731	2696	3816
C23	934339.86			0.59	0.47	0.000825	0.000868	1776	960	0.44	0.47	0.000731	0.00068	3216	3072
C24	926009.53			0.55	0.61	0.000786	0.000783	1200	1248	0.41	0.42	0.000743	0.000708	4072	3288
C25	924419.55			0.55	0.63	0.000946	0.00092	944	880	0.42	0.45	0.00072	0.000716	3096	3568
C26	860789.08			0.52	0.53	0.000757	0.000806	1280	1024	0.38	0.37	0.000878	0.000745	3448	2752
C27	890217.27			0.54	0.48	0.000872	0.000976	1200	1160	0.43	0.45	0.000706	0.000715	2104	3888
C28	958964.14			0.51	0.61	0.000825	0.000761	896	880	0.43	0.45	0.000731	0.000721	5296	4928
C29	899811.82			0.58	0.59	0.000724	0.000762	1136	1504	0.45	0.47	0.000707	0.00068	3352	3608

CST = corticospinal tract; SLF = superior longitudinal fasciculus

Appendix I: Raw data for corpus callosum (Study Two)

Participant Number	FA CC Motor	FA CC Prefrontal	FA CC Parietal-Temporal	FA CC Occipital	MD CC Motor	MD CC Prefrontal	MD CC Parietal-Temporal	MD CC Occipital	Vol CC Motor	Vol CC Prefrontal	Vol CC Parietal-Temporal	Vol CC Occipital
M1	0.5	0.51	0.56	0.69	0.001088	0.001118	0.001129	0.001199	176	234	211	90
M2	0.53	0.52	0.57	0.72	0.001191	0.000956	0.001189	0.001443	155	180	142	35
M3	0.55	0.6	0.63	0.74	0.000989	0.000811	0.001047	0.001099	181	278	144	41
M4	0.55	0.55	0.67	0.8	0.000868	0.000936	0.001042	0.000959	176	284	158	49
M5	0.57	0.59	0.59	0.65	0.001311	0.000928	0.001069	0.001305	129	199	201	51
M6	0.41	0.54	0.59	0.77	0.000862	0.000832	0.000946	0.001	174	310	192	33
M7	0.51	0.54	0.56	0.65	0.000995	0.001003	0.001062	0.000893	166	246	204	63
M8	0.34	0.46	0.59	0.81	0.00098	0.000993	0.000954	0.001138	129	218	163	16
M9	0.52	0.57	0.58	0.68	0.000978	0.000937	0.001037	0.001317	227	259	227	51
M10	0.46	0.49	0.57	0.85	0.001029	0.000953	0.001067	0.000807	163	239	228	50
M11	0.5	0.55	0.57	0.68	0.001013	0.000864	0.001098	0.001405	221	295	195	48
M12	0.5	0.46	0.63	0.73	0.000903	0.00099	0.001171	0.00108	158	253	184	45
M13	0.46	0.55	0.6	0.64	0.000976	0.000895	0.000951	0.001344	197	298	217	52
M14	0.49	0.49	0.59	0.53	0.000943	0.00104	0.000974	0.001522	169	213	228	17
M15	0.43	0.56	0.55	0.64	0.000946	0.000897	0.001035	0.001331	201	276	179	51
M16	0.39	0.53	0.53	0.84	0.001086	0.000903	0.001055	0.000932	176	185	206	35
M17	0.6	0.55	0.68	0.89	0.000876	0.000915	0.001073	0.000918	168	299	191	41
M18	0.52	0.56	0.65	0.75	0.000884	0.000913	0.000881	0.001331	167	264	193	57

Participant Number	FA CC Motor	FA CC Prefrontal	FA CC Parietal-Temporal	FA CC Occipital	MD CC Motor	MD CC Prefrontal	MD CC Parietal-Temporal	MD CC Occipital	Vol CC Motor	Vol CC Prefrontal	Vol CC Parietal-Temporal	Vol CC Occipital
M19	0.53	0.53	0.53	0.71	0.000923	0.000903	0.001139	0.000989	202	266	169	48
M20	0.55	0.51	0.54	0.68	0.000915	0.000972	0.000982	0.000933	184	311	215	89
M21	0.48	0.53	0.62	0.75	0.00109	0.001004	0.000879	0.001209	146	316	169	37
M22	0.63	0.57	0.68	0.81	0.000787	0.000839	0.001051	0.001216	189	309	199	27
M23	0.48	0.58	0.59	0.76	0.000969	0.000947	0.00095	0.001063	168	264	233	47
M24	0.47	0.5	0.59	0.78	0.001035	0.000971	0.001032	0.000901	138	270	163	42
M25	0.54	0.55	0.68	0.84	0.00107	0.001097	0.001101	0.000827	171	230	173	52
M26	0.51	0.58	0.63	0.83	0.000924	0.000903	0.000876	0.00109	166	298	192	48
M27	0.44	0.4	0.67	0.72	0.0011	0.001187	0.000887	0.001062	106	218	174	18
M28	0.59	0.65	0.68	0.88	0.000947	0.000824	0.001014	0.000834	182	226	140	35
M29	0.58	0.53	0.64	0.75	0.000855	0.000978	0.000904	0.001059	210	316	213	56
M30	0.56	0.6	0.66	0.81	0.000912	0.000833	0.000935	0.001349	202	290	134	59
M31	0.6	0.64	0.67	0.92	0.000819	0.000807	0.000975	0.00077	204	383	204	57
M32	0.55	0.65	0.65	0.8	0.000892	0.000836	0.0009	0.001332	159	254	127	62
C1	0.58	0.59	0.63	0.72	0.000892	0.000884	0.000982	0.000931	99	243	186	54
C2	0.49	0.53	0.59	0.8	0.00099	0.000905	0.001203	0.001087	197	268	173	52
C3	0.58	0.57	0.6	0.71	0.000917	0.000902	0.000985	0.001171	164	255	236	50
C4	0.48	0.57	0.59	0.63	0.000999	0.000911	0.00106	0.001265	135	246	127	18
C5	0.51	0.49	0.63	0.78	0.001082	0.001064	0.000998	0.001162	151	312	203	77
C6	0.5	0.54	0.51	0.56	0.000984	0.000929	0.001234	0.001422	171	236	188	66
C7	0.54	0.49	0.6	0.63	0.001042	0.001071	0.001131	0.00173	189	302	155	44
C8	0.42	0.5	0.48	0.69	0.000977	0.000985	0.00103	0.001249	126	199	140	60

Participant Number	FA CC Motor	FA CC Prefrontal	FA CC Parietal-Temporal	FA CC Occipital	MD CC Motor	MD CC Prefrontal	MD CC Parietal-Temporal	MD CC Occipital	Vol CC Motor	Vol CC Prefrontal	Vol CC Parietal-Temporal	Vol CC Occipital
C9	0.56	0.52	0.62	0.8	0.000886	0.000869	0.000999	0.00106	159	305	182	65
C10	0.53	0.54	0.62	0.72	0.000875	0.000978	0.000964	0.001123	161	262	246	36
C11	0.52	0.62	0.62	0.83	0.000908	0.00094	0.001043	0.001345	182	278	195	57
C12	0.53	0.57	0.68	0.78	0.000843	0.000886	0.00091	0.000946	99	253	204	55
C13	0.56	0.56	0.57	0.77	0.000893	0.000945	0.000869	0.000948	174	316	245	64
C14	0.45	0.45	0.53	0.81	0.000887	0.001113	0.001194	0.001172	141	241	157	41
C15	0.52	0.6	0.62	0.81	0.000976	0.000893	0.001045	0.001148	145	243	182	31
C16	0.53	0.52	0.53	0.74	0.000957	0.000953	0.000893	0.001129	211	311	119	65
C17	0.56	0.56	0.63	0.84	0.00092	0.000848	0.00092	0.001024	176	254	253	64
C18	0.54	0.51	0.63	0.79	0.000941	0.000967	0.000956	0.001115	176	231	217	51
C19	0.51	0.5	0.63	0.92	0.000933	0.000921	0.00091	0.001083	124	201	131	38
C20	0.56	0.55	0.59	0.77	0.000871	0.000877	0.000953	0.000833	185	318	231	49
C21	0.54	0.58	0.78	0.71	0.001011	0.001164	0.001055	0.001062	143	202	150	42
C22	0.46	0.6	0.58	0.81	0.001031	0.000867	0.001078	0.001188	145	238	204	36
C23	0.59	0.6	0.67	0.82	0.000897	0.000792	0.000918	0.000816	229	269	162	45
C24	0.53	0.64	0.51	0.68	0.001358	0.000838	0.001252	0.001201	62	157	87	11
C25	0.62	0.59	0.68	0.76	0.000979	0.001034	0.000949	0.000915	106	212	111	45
C26	0.45	0.46	0.63	0.85	0.001114	0.000945	0.000993	0.000826	75	176	175	49
C27	0.64	0.59	0.69	0.79	0.000893	0.000911	0.001023	0.001111	182	278	212	54
C28	0.54	0.57	0.69	0.85	0.000907	0.000894	0.000914	0.001122	162	202	163	32
C29	0.58	0.62	0.67	0.79	0.000898	0.000859	0.000957	0.001114	207	262	176	80

CC = corpus callosum