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Balanced Brains:
An investigation of visuospatial ability and
lateralization in musicians

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A thesis submitted in partial fulfillment of the requirements
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Abstract

Musicians comprise a unique population whereby persistent musical practice involving complex cognitive and motor tasks dates back to childhood when the potential for neural plasticity is at its highest. Accordingly, it has been speculated that musical training results in neural structural and functional differences between musicians and non-musicians. In particular, there is evidence to indicate parietal regions are more equally lateralized in musicians, but research investigating visuospatial abilities and lateralization in musicians is scarce. Studies 1 and 2 aimed to assess the visuospatial ability and cognitive processing speed of adult musicians versus demographically and educationally matched non-musicians. Musicians performed more quickly and more accurately than non-musicians in two tasks of visuospatial ability, and completed more items than non-musicians in three tasks of processing speed, suggesting musicians had better visuospatial ability and a faster speed of processing. Studies 3 and 4 aimed to investigate visuospatial attention in these groups using a line-bisection task and a visual discrimination task. On both tasks musicians demonstrated more balanced visuospatial attention with a slight bias to the right hemispace, which was in contrast to the non-musicians' bias to the left hemispace, a natural phenomenon known as 'right pseudoneglect'. In Study 5, the laterality of visual processing in musicians and non-musicians was further investigated by comparing electrophysiological interhemispheric transfer time (IHTT) of lateralized visual stimuli across the corpus callosum. Non-musicians had faster right-to-left than left-to-right IHTT consistent with previous research, whilst musicians had more balanced IHTT in both directions and faster left-to-right transfer than non-musicians. Absolute latency patterns revealed similar results and consistently demonstrated more balanced visual processing in musicians. The behavioural data, analysed in Study 6, revealed a tendency (n.s.) for the musician group to respond more quickly to stimuli presented in the right visual field than to stimuli presented in the left visual field, whilst non-musicians did not show this pattern. Overall, the results indicate that musicians have enhanced visuospatial ability and are less lateralized for visuospatial attention and perception than non-musicians. The results are discussed in relation to plastic developmental changes that may be caused by extended musical training from childhood. Specifically, it is proposed that musical training in early life may elicit a process of myelination that is more bilaterally distributed than myelination in non-musicians.

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Table of Contents

Abstract	ii
Acknowledgements	iii
Table of Contents.....	iv
List of Tables	vii
List of Figures	viii
List of Appendices	x
 Chapter 1: Introduction	 1
Cognitive ability in musicians	2
The Mozart effect	2
Music training and cognitive abilities	5
Plasticity in musicians	10
Structural and functional differences between musicians and non-musicians	11
Nature versus nurture	18
Lateralization in musicians	22
The language-left music-right dichotomy	23
A general network for music and language	24
Leftward lateralization for music processing in musicians	25
Thesis aims	29
 Chapter 2: Visuospatial abilities and cognitive processing speed in musicians	 31
Introduction	31
Study 1: Visuospatial processing	32
Method	33
Participants	33
Materials	35

Visual discrimination task	35
Visuospatial search task	36
Procedure	37
Results	38
Visual discrimination task	38
Visuospatial search task	40
Discussion	41
Study 2: Processing speed	44
Method	44
Participants	44
Materials	45
Symbol-Digit Modalities Test	45
Symbol Search subtest	46
Colour Naming and Word Reading Test	46
Procedure	47
Results	47
Discussion	49
Conclusions	51
 Chapter 3: Visuospatial attention in musicians	 52
Introduction	52
Study 3: Line-bisection task	53
Method	55
Participants	55
Stimuli and Procedure	56
Results	56
Discussion	59
Study 4: Visual discrimination task (vertical condition)	60
Method	60
Participants	60
Stimuli and Procedure	61
Results	61
Discussion	64
General Discussion	65

Chapter 4: Electrophysiological interhemispheric transfer time in musicians	69
Introduction	69
Method	74
Participants	74
Stimuli and Apparatus	75
Analysis	75
Procedure	76
Results	77
Interhemispheric transfer time	77
Absolute latency of the N1	79
Discussion	80
 Chapter 5: Behavioural interhemispheric transfer time in musicians: The Poffenberger paradigm	85
Introduction	85
Method	91
Participants	91
Stimuli and Procedure	91
Analysis	92
Results	92
Reaction time	92
Accuracy	94
Discussion	95
 Chapter 6: General discussion	97
Enhanced cognitive abilities in musicians	97
Plasticity and musical training	99
Visuospatial attention and lateralization	101
Myelination in musicians	104
The CUD and simple reaction time	106
Conclusions	107
 References	109
Appendices	133

List of Tables

Table 1: Demographic characteristics of musician and non-musician group participants for Study 1.....	34
Table 2: Mean reaction times (ms) on the easy and hard discriminations of the visual discrimination task for the vertical and horizontal line conditions, for both groups of participants.	38
Table 3: Mean percent correct (SD) on the easy and hard discriminations of the visual discrimination task for the vertical and horizontal line conditions, for both groups of participants.	39
Table 4: Demographic characteristics of musician and non-musician group participants for Study 2.	45
Table 5: Mean scores (SD) for number correct and error data for the SDMT (written and verbal) and Symbol Search task for musicians and non-musicians.	48
Table 6: Averaged means (SE) for the written and verbal response modalities shown for musicians and non-musicians.	49
Table 7: Demographic characteristics of musician and non-musician group participants for Study 3.	56
Table 8: Demographic characteristics of musician and non-musician group participants for Study 4.	61
Table 9: Reaction times for easy and hard discriminations on the vertical line condition for both groups (SEM).	63
Table 10: Percent correct for easy and hard discriminations of the vertical line condition when dots were to the left and right side (SEM).	64
Table 11: Demographic characteristics of musician and non-musician group participants for Study 5.	75
Table 12: Demographic characteristics of musician and non-musician group participants for Study 6.	91
Table 13: Mean RTs (SE) for each hand to stimuli presented in the LVF and RVF for each group.....	93

List of Figures

Figure 1: Procedure for horizontal line condition of visual discrimination task.	36
Figure 2: Example design from the visuospatial search task. Correct answer = 1.	37
Figure 3: Mean reaction times for vertical and horizontal line conditions across easy and hard discriminations of the visual discrimination task for musicians and non-musicians. Error bars indicate standard error of the mean.	39
Figure 4: Mean number correct for the first and second trials of the visuospatial search task for musicians and non-musicians. Error bars indicate standard error of the mean. .	40
Figure 5: Example of the SDMT stimuli (Smith, 1991) (top = key, bottom = first response line).	46
Figure 6: Example of the Symbol Search task (first line = yes, second line = yes, third line = no).	46
Figure 7: Diagram depicting the theoretical underpinnings of right pseudoneglect.	54
Figure 8: Mean percentage deviation from the true centre in the line-bisection task according to position on the page (right, centre and left) and hand used. Negative numbers denote leftward bias, and positive numbers denote rightward bias. Error bars indicate standard error of the mean. *This bar is significantly different from all other bars.	57
Figure 9: Mean percentage deviation from the true centre in the line-bisection task according to group (musicians vs. non-musicians) and hand used. Negative numbers denote leftward bias, and positive numbers denote rightward bias. Error bars indicate standard error of the mean.	58
Figure 10: Mean reaction times for left- and right-sided dots for musicians and non-musicians. Error bars indicate standard error of the mean.	62
Figure 11: Mean percent correct for left- and right-sided dots for musicians and non-musicians. Error bars indicate standard error of the mean.	64
Figure 12: Stimulus presentations to the left and right visual fields and theoretical callosal crossover. Diagram also shows example ERP recordings for each condition and each hemisphere demonstrating typical fast and slow interhemispheric transfer. ...	72
Figure 13: Diagram of electrode positions for Electrical Geodesic 128-electrode net. Circles indicate electrode clusters used for the right and left hemispheres.	76

Figure 14: Grand mean waveforms averaged across hands in right and left hemisphere occipital electrode clusters for musicians and non-musicians recorded during stimulus presentation in the RVF and LVF.	78
Figure 15: Mean IHTT for each direction averaged across hands for musicians and non-musicians. Error bars indicate standard error of the mean.	78
Figure 16: Mean IHTT for each direction averaged across hands for males and females. Error bars indicate standard error of the mean.	79
Figure 17: Mean absolute latency for direct pathways averaged across hands for each hemisphere for musicians and non-musicians. Error bars indicate standard error of the mean.	80
Figure 18: Diagram depicting Poffenberger's theory of interhemispheric transfer time as measured by the crossed-uncrossed difference. Left panel represents uncrossed conditions. Right panel represents crossed conditions.	86
Figure 19: Mean reaction times (ms) for each visual field for the left and right hands. Left panel represents data for the musician group. Right panel represents data for the non-musician group.....	94

List of Appendices

Appendix A: Visuospatial Search Task Examples	134
Appendix B: Raw Data for Study 1: Visual Discrimination Task	135
Appendix C: Raw Data for Study 1: Visuospatial Search Task.....	136
Appendix D: Raw Data for Study 2	137
Appendix E: Raw Data for Study 3.....	138
Appendix F: Raw Data for Study 4.....	139
Appendix G: Raw Data for Study 5	140
Appendix H: Raw Data for Study 6	141
Appendix I: Musician Instruments Studies 1 and 4	142
Appendix J: Musician Instruments Study 2	143
Appendix K: Musician Instruments Study 3.....	144
Appendix L: Musician Instruments Studies 5 and 6	145

Chapter 1: Introduction

“Performing music at a professional level is arguably among the most complex of human accomplishments.” (Münste, Altenmüller, & Jäncke, 2002, p. 473).

In the last two decades there has been a surge of interest in the musical brain, especially as research has begun to focus on the cognitive benefits associated with musical training. Musicians undergo intense training from a young age involving hours of practice per week perfecting swift combinations of individual movements in precisely timed sequences. In many cases children as young as two are introduced to their instruments and are often still training well into adulthood. Adult musicians, therefore, represent a unique cohort of people who have been exposed to years of rigorous training, both in motoric bimanual coordination but also in auditory and other, general cognitive skills. These may include the acquisition of the musical notation system, which can arguably be considered a language, the ability to translate musical notation into timed motoric movements, which may engage visuospatial cognition, the ability to memorize lengthy musical phrases, and the ability to coordinate oneself into a myriad of different contexts in ensemble situations, which may rely on executive function. Consequently, there is a growing body of research investigating musicians and the musician brain. This research can be divided into three main constituents. First, there is evidence for enhanced cognitive performance in musicians, especially in children. Second, there is growing research documenting the anatomical and functional differences in musicians' brains compared with those of non-musicians'. Third, there is the suggestion that musicians may have differing laterality to non-musicians, particularly with regard to the hemispheric dominance of music processing.

Cognitive abilities in musicians

Recent research findings indicate that there is a relationship between musical training and superior performance in non-musical cognitive abilities, such as visuospatial abilities. This phenomenon has generally been termed the 'Mozart effect', but the proposed relationship between musical training and non-musical cognitive abilities actually refers to two reasonably separate effects (Schellenberg, 2001). The first involves short-term improvement in non-musical cognitive abilities subsequent to exposure to music of the composer Mozart (Rauscher, Shaw, & Ky, 1993, 1995). The second effect relates to longer-term enhancement of cognitive abilities due to formal musical training.

The Mozart effect

The first phenomenon, commonly referred to as the Mozart effect, deals specifically with the suggestion that temporary cognitive benefits can be acquired by short-term exposure to classical music. Rauscher et al. (1993, 1995) asked undergraduate students with unspecified musical backgrounds to listen to 10 minutes of Mozart's sonata K488 and then to complete spatial reasoning tasks from the Stanford-Binet Intelligence Scale. In both studies exposure to Mozart resulted in improved performance in spatial reasoning for the 10-15 minute period during which participants were engaged in the tasks. Conversely, performance was not significantly enhanced by listening to repetitive music, taped short stories, a relaxation tape or silence. Rauscher et al. (1995) argued that exposure to music primed spatial abilities as a result of the activation of similar cortical firing patterns in the right cerebral hemisphere, and proposed the trion model (Leng, Shaw, & Wright, 1990) as a possible mechanism for the phenomenon. The trion model asserts that exposure to music enhances visuospatial ability due to synchronous cortical firing between the two hemispheric regions involved. Support for the trion model has come from EEG coherence studies

(in individuals with unspecified musical backgrounds), where an increase in coherence between right frontal and temporoparietal (visuospatial) areas has been found during listening to Mozart (Jaušovec & Habe, 2003, 2004, 2005; Sarnthein et al., 1997).

In a study investigating the Mozart effect in musicians and non-musicians, Twomey and Esgate (2002) hypothesized that, in accordance with the trion model, right hemispheric activation in non-musicians whilst listening to Mozart would cause an increase in performance in right hemispheric tasks, such as spatiotemporal reasoning. Musicians, on the other hand, who are thought to activate left hemispheric regions in response to music (refer to section 'Lateralization in musicians'), would activate bilateral hemispheric regions and be advantaged at the right hemispheric task as well as left hemispheric tasks, such as synonym and rhyming generation. Results supported the trion hypothesis for the non-musician group only, which showed an impressive increase of spatiotemporal reasoning in those who listened to Mozart before performing the task. In contrast, for musicians there was no advantage for the Mozart group compared to the silence group, and, contrary to predictions, there was no increase in verbal task performance (Twomey & Esgate, 2002). One explanation for the failure of musicians to produce data supporting the trion model is that long-term musical training may have enhanced spatiotemporal ability so that any further advantage produced by coherence in the relevant cortical regions was not detectable (Twomey & Esgate, 2002). Consistent with this claim, musicians performed significantly better than non-musicians in the spatiotemporal and rhyming tasks.

Although there have been numerous replications of the Mozart effect (Gilletta, Vrbancic, & Elias, 2003; Jaušovec, Jaušovec, & Gerlič, 2006; Jaušovec & Habe, 2005; Rideout, Dougherty, & Wemert, 1998; Rideout & Laubach, 1996; Rideout & Taylor, 1997; Twomey & Esgate, 2002; Wilson & Brown, 1997), there are also many examples of failures to replicate the effect (Črnčec, Wilson, & Prior, 2006; Lints & Gadbois, 2003;

McCutcheon, 2000; McKelvie & Low, 2002; Newman et al., 1995; Schellenberg & Hallam, 2005; Steele, Ball, & Runk, 1997; Steele, Bass, & Crook, 1999; see also review by Fudin & Lembessis, 2004). Moreover, Schellenberg and colleagues have produced several studies that have replicated the Mozart effect but have also identified that it may be due to enhancement of other cognitive states, such as arousal and mood, and not to Mozart's music per se.

Nantais and Schellenberg (1999) administered a spatial task to 28 college students after they listened to Mozart and a narrated Stephen King story. Participants' performance on the task improved in relation to which condition the participants preferred. If subjects reported that they liked the narrated story more than Mozart's music, they performed better on the spatial task after hearing the story, whereas participants who preferred listening to Mozart performed better after hearing Mozart. There was no overall benefit for the Mozart condition. Nantais and Schellenberg thus concluded that there was no evidence for improved performance following Mozart compared to any other equally pleasing auditory stimulus.

A second study (Thompson, Schellenberg and Husain, 2001) directly tested the impact of arousal and mood on a spatial test (Paper Folding and Cutting subtest from the Stanford-Binet intelligence test) with a group of University students. Students in the 'Mozart' group (Mozart sonata) performed significantly better on the test than those in the 'Silence' group, thus replicating the Mozart effect. Those given a different piece of classical music by Albinoni (Adagio in G minor), however, did not show improved performance in comparison with the 'Silence' group. In contrast to the invigorating, happy tone of the Mozart sonata, the Albinoni piece is slow and would be considered sad by most people. In conjunction with the paper folding test, four measures of arousal, mood and enjoyment were also completed by each participant. Those in the Mozart group scored more positively than baseline after the Mozart music excerpt,

while those in the Albinoni group scored more negatively than baseline after the Albinoni music excerpt. The authors concluded the musical pieces induced different levels of arousal and mood, which in turn affected performance on the cognitive task.

In another study Husain, Thompson and Schellenberg (2002) manipulated the K488 sonata into fast, slow, major and minor versions and then tested participants on spatial ability, arousal and mood. The study revealed enhanced spatial performance when the sonata was played quickly and also in a major key. Arousal was also heightened, however, when the sonata was played quickly, and mood was positively affected when the sonata was played in the major key. Husain et al. concluded that the apparent Mozart effect could not be disentangled from the confounding variables of arousal and mood. They further suggested that the effect found by Rauscher et al. (1993, 1995) was due, at least partly, to the tempo (quite fast) and key (major) of the piece used in the experimental session, which would have in turn affected arousal and mood.

Music training and cognitive abilities

A second phenomenon appearing in the literature links musical training and longer-term superior non-musical cognitive abilities. Most studies investigating the advantages of music training on cognitive abilities have concentrated on children and often compare participants who receive music lessons to those who do not. Unfortunately this methodology usually does not rule out the alternative explanation that superior performance by those receiving lessons may be due to the positive effects of extra instruction or attention by an adult, or that music lessons induce generally heightened mood and motivation that in turn may affect cognition and cognitive development. Furthermore, the general difficulty of publishing null results may result in a bias toward literature reporting effects between musical training and cognitive enhancement. However, the magnitude of this is impossible to test or even estimate.

Despite this, Schellenberg (2001, 2005) argues that research in this area has produced consistent results showing positive associations between musical training and non-musical abilities using linguistic, numerical and spatial tasks and measures of overall intelligence. Standley and Hughes (1997) investigated prekindergarten-aged children on pre-reading and writing skills after 15 music lessons, which included reading, writing and playing music. After a period of two months they found that children receiving lessons had enhanced literacy. More recently Gromko (2005) found similar results in primary school-aged children. The phonemic awareness of participants in four classes receiving music lessons, which involved reading and playing music, showed greater improvement than participants in four classes in a different school who were not receiving lessons.

Mathematical improvement, but not enhanced literacy, was found in 5-7 year-olds who participated in a Kodály music program (Gardiner, Fox, Knowles, & Jeffrey, 1996). The Kodály program has a strong emphasis on music appreciation, incorporating singing, hand signals, and clapping, but teaches traditional musical notation at only a simple level. After 7 months children in the program, especially those who were particularly behind at kindergarten, had caught up to, and surpassed, the standard of their non-program peers in mathematics. In addition, Cheek and Smith (1999) found students who had more than two years of private music lessons (especially keyboard lessons where participants were required to listen to music as well as learn to play and read music) showed superior mathematical abilities than those who had not had lessons. Finally, a meta-analysis investigating the association between music and maths found “a modest positive association” (Vaughn, 2000, p. 154) in 20 correlational studies in which participants voluntarily studied music. Additionally, a “small causal relationship” (Vaughn, 2000, p. 163) was found in 6 experimental studies where participants were involuntarily exposed to music in school. Notably, there are three main issues to consider when contemplating these results. First, most of the studies used in the meta-

analysis (22 of 26) were unpublished data for doctoral dissertations and College Board statistics. Second, correlational studies cannot imply causation, and third, the sample size for the experimental studies was very small. The meta-analysis did show, however, that although effect sizes were small, all but two of the 26 studies showed an effect in the positive direction.

Evidence for spatial-temporal enhancement in children receiving music lessons has been more convincing than those of mathematical ability. Bilhartz, Bruhn and Olson (2000) studied the effect of a 30-week, 75-minute weekly, music program involving singing, playing instruments and music theory, on the spatial-temporal abilities of children aged 4-6. Participants receiving music instruction showed significant improvements on the Young Child Music Skills Assessment (MSA) and the Bead Memory subtest of the Stanford-Binet Intelligence Scale compared to those in the control group who received no musical or other extra instruction. Graziano, Peterson and Shaw (1999) showed mathematical and spatial-temporal reasoning could be enhanced in 6-8 year-olds after 6 months of traditional piano lessons. Rauscher, Shaw and Levine (1997) found that short piano lessons (10 minutes) once or twice a week produced superior spatial skills in 4 year-olds after 6-8 months, and Rauscher and Zupan (2000) replicated this finding with slightly older children (5-6 year-olds) and longer piano lessons (20 minutes). In this study, spatial-temporal reasoning was significantly increased in children receiving piano lessons after only 4 months, and was increased again after another 4 months, at which point the difference between groups was even greater.

Extended musical training has also been associated with enhanced general intelligence. Nering (2002) experimentally investigated 10 sets of monozygotic twins, where only one of each set was randomly selected to receive two private piano lessons per week for seven months. The twins did not differ prior to musical training, but after

training the 'lessons' group had significantly higher scores than the 'no lessons' group on verbal, mathematical, spatial, language comprehension, and general IQ. In contrast, however, Costa-Giomi (1999) tested nine-year old children before, during, and after three years of piano instruction. She found that although weekly piano lessons did improve the children's general, and in particular, spatial cognitive development in comparison to their matched control peers, the magnitude of the effect was small and had disappeared after three years.

Given the difficulty of drawing firm conclusions from studies with 'music' versus 'no music' groups as mentioned above, a study by Schellenberg (2004) has provided the most convincing evidence to date for the effect of music training on IQ. This study controlled for at least some of the alternative explanations of positive effects in the experimental music groups by including a control group who received drama lessons. Thus, control participants received the same beneficial side-effects of music lessons (e.g., attentional input from an adult, enhanced motivation), but without the music. Thus, the subsequent relative increase in general full-scale IQ (measured by the WISC-III) of both music groups (keyboard and voice lessons) compared to the drama group could not simply be ascribed to more positive experiences in these children.

Norton et al. (2005) are currently running a longitudinal study on the effects of musical training on cognitive and brain development. The study aims to address questions regarding whether there are pre-existing cognitive and/or anatomical differences in children who practice music and those who do not, in an attempt to discern nature from nurture. The study also aims to follow the cognitive/neural development of all the children (who were not randomly assigned), regardless of whether they drop-out of lessons or go on to become musically talented. In this way, a retrospective approach can be taken when the musical outcome of the children is known. In the first investigation, Norton et al. (2005) found no cognitive (visual-spatial, verbal, motoric,

music perception) or structural differences between those intending to start music lessons and those not intending to, suggesting that at the outset of lessons the development of the two groups could not be differentiated.

Despite the evidence supporting the positive benefits of musical training for other cognitive abilities in children, only a few studies have been conducted that investigate this phenomenon in adult populations. Overall, these studies also find beneficial effects of musical training, although, again, most attempt to draw conclusions from self-selected groups that may differ in more ways than musical experience. For example, a recent assessment of elderly musicians revealed superior cognitive abilities (global cognition, psychomotor function, memory recall, and executive function) compared to the normative data for their age group (Moser as cited in Lammers, 2005, p. 89). However, because the musician participants were compared to a normative sample the results may be confounded by the author's inability to match the groups for other aspects affecting cognitive ability, such as participation in an intellectual hobby and years of education.

Brochard, Dufour and Despres (2004) directly investigated the long-term effects of musical training on visuospatial abilities by comparing the performance of 10 adult musicians and 10 adult non-musicians on a task of visuospatial discrimination. The musicians were Musicology students with at least 8 years of formal musical training, could sight-read, and practiced at least one instrument for more than 4 hours per day. The non-musicians were Psychology students who had no formal musical training and could not sight-read, but it was not apparent whether the groups had been matched for demographic variables, such as age, gender, handedness, years of education, or cognitive abilities. Participants had to determine on which side of a horizontal, or vertical, reference line a target dot appeared. Although performance accuracy did not differ between the groups, musicians had faster reaction times than non-musicians in

both the vertical and horizontal line conditions with differential benefit when the line was horizontal. Brochard et al. suggested that skills involved in music score reading, in which notes are placed not only in a horizontal line but also vertically (representing differing pitch), enhanced the musicians' performance on this task.

In a third study investigating adults, Chan, Ho and Cheung (1998) tested 30 female adult musicians, with at least 6 years of formal music training, and 30 female adult non-musicians matched for age, grade point average and years of education, on two sets of verbal and visual memory tasks. The authors found that the musician group consistently and significantly outperformed the non-musician group across three trials of an orally presented 16-item word list, but that the groups did not differ on the Benton visual-retention test or the Rey-Osterreith figure immediate recall task.

To summarize, there is a growing body of literature suggesting listening to music benefits short-term cognitive performance (although there is doubt as to whether music per se is the mechanism responsible) and that musical training benefits long-term cognitive ability in many different domains. Although most of this research is centred on children beginning music lessons, there are a few examples of enhanced cognition apparent in adulthood, although only one of these matched groups sufficiently to control for possible confounding variables. These examples are consistent with numerous imaging studies demonstrating neural differences between adult musicians and non-musicians, which have been suggested to have occurred due to neural plasticity from extended musical training from childhood.

Plasticity in musicians

There is currently considerable interest in the musical brain as a window into neurodevelopmental plasticity. Although changes in the brain can be maladaptive, as in the case of focal hand dystonia where the cortical representations of individual digits

become less distinct resulting in involuntary contractions of the fingers or hand (V. Lim, personal communication, February 22, 2007; Pantev, Engelien, Candia, & Elbert, 2001), the anatomical and functional changes in the musician brain are usually advantageous. Recent structural and functional neuroimaging research has revealed an array of cortical regions that differ between musicians and non-musicians, including motor, parietal, frontal and temporal regions, the cerebellum, and the corpus callosum.

Structural and functional differences between musicians and non-musicians

Increased gray matter volume and activation in musicians compared with matched controls has been reported in the superior parietal cortex and inferior frontal cortex (Gaser and Schlaug, 2003a, 2003b; Schmithorst & Holland, 2003). The superior parietal region is known to be involved in visuospatial attention, orientation to the spatial location of visual signals, visual search and detection (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Corbetta & Shulman, 2002; Fan, McCandliss, Fossella, Flombaum, & Posner, 2005) and may be associated with music reading ability in musicians. Several studies investigating music reading have reported activation in parietal regions suggesting that reading musical notation requires spatial processing. In one study, 12 musically naïve participants were scanned using fMRI before and after they were taught to play the piano and read music for 15 weeks (Stewart et al., 2003a, 2003b). During scanning, participants were required to execute a series of keypresses in response to stimuli comprising musical notation, that, prior to training only, were superimposed with correct finger numbers. The post-training scans revealed increased activation of the right superior parietal cortex and left supramarginal gyrus (Stewart et al., 2003a, 2003b). This was consistent with imaging studies by Schön, Anton, Roth and Besson (2002) and Sergent, Zuck, Terriah and MacDonald (1992) that also showed bilateral parietal lobe activation in music sight-reading tasks.

Musical notation essentially consists of components assembled in a spatial context so it would be expected that regions crucial to spatial perception are activated during tasks involving reading music. Interestingly however, there are at least three studies where parietal activation has been reported when musicians were performing music tasks that did not involve reading music. Gaab and Schlaug (2003) reported greater bilateral parietal activation in musicians compared to non-musicians in a simple tone discrimination task, where non-musicians were matched to the performance of the musicians, and Beisteiner et al. (1999) reported increased temporoparietal activation in musically trained participants when they listened to harmonic chord progressions. Similarly, Lotze, Scheler, Tan, Braun and Birbaumer (2003) reported bilateral activation in the superior parietal lobes when musicians were asked to play a section of a violin concerto from memory. The authors suggested the parietal activation may be a reflection of the participants visualising the music notation, a function which may become automatic in musicians.

Another non-music related area that has been reported to have increased gray matter volume in musicians compared with non-musicians is the inferior frontal region, which includes Broca's area in the left hemisphere (Bangert et al., 2006; Gaser & Schlaug, 2003a, 2003b; Schmithorst, 2005; Sluming et al., 2002; Zatorre, Perry, Beckett, Westbury, & Evans, 1998). In addition to language processing, this area has also been shown to be involved in projecting signals to the prefrontal cortex when participants learn actions elicited by visual prompts (Passingham & Toni, 2001). This is suggested to be an analogous process to reading music, whereby visual markings cue particular fingering combinations or other musical entities, such as crescendos (increased force), decrescendos (decreased force), slurs (joined fingering) and staccato (separated fingering), etc. Studies reporting increased gray matter in regions other than those directly related to the performance of music suggest that plasticity induced by training may be distributed widely throughout the brain. This is consistent with suggestions that

musical training transfers to other cognitive domains, such as visuospatial and verbal ability (Schellenberg, 2001, 2004, 2005, 2006).

Another region implicated in the processing of both language and music is the planum temporale (PT), which is located in the posterior superior temporal gyrus and is known as Wernicke's area in the left hemisphere. The PT has been assumed to be a structural marker for the dominance of language since it is usually larger in the left hemisphere of right-handers (Geschwind & Levitsky, 1968), and left-handers have been found to have either rightward asymmetry or symmetrical PT (Foundas, Leonard, & Hanna-Pladdy, 2002; Steinmetz, Volkman, Jäncke, & Freund, 1991). As well as a structure implicated in language processing, however, the right homologue of the PT has been shown to be involved in higher auditory processing (Zatorre, 1998) and has been a focal point of investigation in musicians, both in anatomical and functional spheres.

Due to a widely-held belief that music is processed largely in the right temporal lobe (see section 'Lateralization in musicians') it seems paradoxical that the anatomical PT asymmetry in musicians has consistently been found to be greater in the leftward direction rather than in the rightward direction. This leftward asymmetry has been associated with the growing consensus that there is a difference in the lateralization of music processing between musicians and non-musicians (for further discussion see section 'Lateralization in musicians'). Briefly, musicians are thought to process music in the left hemisphere (Bhattacharya & Petsche, 2001; Marinoni, Grassi, Latorraca, Caruso, & Sorbi, 2000; Schmithorst & Holland, 2003; Vuust et al., 2005), while non-musicians are thought to process music predominantly in the right hemisphere (Evers, Dammert, Rödding, Rötter, & Ringelstein, 1999; Tervaniemi et al., 2000).

Keenan, Thangaraj, Halpern and Schlaug (2001) reported that the leftward PT asymmetry in musicians is due to a smaller right PT in comparison to non-musicians', rather than a larger left PT per se, although the left PT is marginally bigger in

musicians. These authors suggest there is early pruning of the right PT during the development of musical expertise. Interestingly, this asymmetry is usually only seen in musicians with absolute pitch (AP) (Keenan et al., 2001; Luders, Gaser, Jancke, & Schlaug, 2004; Schlaug, Jäncke, Huang, & Steinmetz, 1995; Zatorre, 1998), although at least two studies have shown leftward lateralization in both musicians with AP and musicians without AP (Bermudez & Zatorre, 2005; Pantev et al., 1998). A possible explanation for the differentiation between groups of musicians is that those with AP tend to have started their musical training at a younger age (before age 7) than musicians who have not developed this trait (Baharloo, Johnston, Service, Gitschier, & Freimer, 1998; Sergeant, 1969). Further to this, correlations between the leftward PT asymmetry and age of training onset are reliably found in these studies, indicating the effect may be related to early training-induced plasticity rather than absolute pitch ability per se.

Musicians have also been found to differ functionally in the auditory modality. For example, Schneider et al. (2002) found musicians to have a gray matter volume in Heschl's gyrus that is 130% larger than non-musicians, but also to elicit MEG activity 102% larger than non-musicians. Using EEG, the mismatch negativity (MMN) paradigm is a popular way of exploring early, pre-attentive electrophysiological processes and is particularly pertinent in the area of auditory musical processing. The paradigm involves exposing participants to a train of similar stimuli (e.g., 1000Hz tones) with randomly added deviants (e.g., a 1140Hz tone). Shortly after the onset of the deviant tone the participant emits a negative deflection in response to the auditory change, the so-called MMN. These responses are usually generated from the auditory cortices and surrounding regions, and have been suggested to reflect the neural accuracy of memory traces for sound (Alho et al., 1996). The MMN shows latencies and amplitudes that are sensitive to individual differences, such as musical expertise, and musicians have been found to display a series of qualitative differences compared to non-

musicians using this paradigm. First, musicians are better able to detect missing stimuli at longer timeframes than non-musicians, and are more precise than non-musicians in detecting minuscule aberrations in timing (Rüsseler, Altenmüller, Nager, Kohlmetz, & Münte, 2001). Second, musicians show greater recognition of impure notes embedded in chord structures than non-musicians (Koelsch, Schröger, & Tervaniemi, 1999) and elicit greater MMNs to changes in contour and melodies (Tervaniemi, Rytkönen, Schröger, Ilmoniemi, & Näätänen, 2001). Finally, musicians show stronger processing to sound source localization and, in particular, conductors are additionally able to identify the source of the aberration (Nager, Kohlmetz, Altenmüller, Rodriguez-Fornells, & Münte, 2003). In general, musicians are usually found to elicit greater MMN components to smaller musical aberrations than non-musicians, and have larger MMN amplitudes than non-musicians.

Another region showing leftward asymmetry in normal right-handed individuals is the primary motor cortex, where greater cortical volume in the left hemisphere reflects superior dexterity of the fingers of the right hand (Pascual-Leone et al., 1993). Amunts et al. (1997) measured the intrasulcal length of the precentral gyrus (ILPC) as an anatomical marker for the size of the primary motor cortex. They found the right ILPC to be significantly longer in keyboard and string instrument musicians than in non-musician controls, reflecting increased cortical volume for the non-dominant left hand in musicians. In addition, string players have been shown to have greater representations for the fingers of the left hand in the motor cortex compared with non-musicians, suggesting the extended use of these fingers has served to enlarge the cortical area devoted to their use (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Pantev et al., 2001). These results suggest non-dominant finger use elicits greater cortical growth in the primary motor cortex, consistent with reports of greater symmetry for finger tapping in musicians than in non-musicians (Kopiez, Galley, & Lee, 2006; Schlaug, Jäncke, Huang, Staiger, & Steinmetz, 1995). In addition, the effects found in these

studies have also been negatively correlated to the age at which training had begun. Together these results suggest that early onset of training with both hands causes an increased cortical representation in the motor areas of the non-dominant hemisphere in musicians.

The cerebellum is also involved in motor output and has been implicated in the functioning of movement coordination, planning and execution involving bimanual finger movements (Gaser & Schlaug, 2003a, 2003b), and timing of sequential movements (Penhune, Zatorre, & Evans, 1998). Like the motor cortex, the cerebellum has also been shown to be larger in musicians than in non-musicians in studies investigating morphometric gray matter volume (Gaser & Schlaug, 2003a, 2003b; Hutchinson, Lee, Gaab, & Schlaug, 2003) and to have greater fractional anisotropy in musicians compared with non-musicians in a study investigating white matter (Schmithorst & Wilke, 2002). Fractional anisotropy (FA) is a measure of the ease at which water diffuses along the myelinated cell axons in the brain. Diffusion is less constrained along well myelinated axons that run in parallel, so higher FA values are obtained when there is an increase of myelination and when the white matter tracts are organized in parallel. Magnetic resonance diffusion tensor imaging (DTI) is a technique used to determine FA and has been used in a further two studies to specifically investigate differences in white matter organization between musicians and non-musicians.

Schmithorst and Wilke (2002) reported increased FA values for musicians in the cerebellum, basal ganglia (caudate and putamen) and anterior corpus callosum. Similarly, Bengtsson et al. (2005) reported greater FA in musicians compared with non-musicians, suggesting musicians may have greater and better organized myelination in the main communication tracts, particularly in the internal capsule and corpus callosum. Other studies investigating the anatomical size of the corpus callosum have

reported the anterior region of the corpus callosum to be larger in musicians than in non-musicians (Lee, Chen, & Schlaug, 2003; Schlaug, Jäncke, Huang, Staiger et al., 1995). This region of the corpus callosum contains mainly fibres connecting the prefrontal and motor cortices (Pandya & Seltzer as cited in Schlaug, Jäncke, Huang, Staiger et al., 1995, p. 1050), and the enlargement of this part of the callosal tract in musicians has been suggested to reflect adaptation during the development of bimanual mechanical skills that need superior interhemispheric communication (Schlaug, Jäncke, Huang, Staiger et al., 1995). The corpus callosum is the main interhemispheric tract in the brain and plays a key role in interhemispheric transferal, integration and communication. The relative size of the corpus callosum has been associated with the number of fibres passing through it (Aboitiz, Scheibel, Fisher, & Zaidel, 1992) indicating increased anatomical size may be correlated with superior connectivity between the hemispheres. The corpus callosum is the last fiber tract to mature in humans and has been shown to develop and myelinate slowly, even into the third decade of life (Pujol, Vendrell, Junqué, Martí-Vilalta, & Capdevila, 1993). For this reason, callosal development may be particularly affected by intensive and prolonged bimanual training in childhood and adolescence.

In summary, there have been several reports of anatomical and functional differences between musicians and non-musicians, many of which correlate the age of training commencement with the magnitude of the effect under investigation. Anatomically, gray matter increases in the brains of musicians compared to non-musicians have been found in the superior parietal regions, Broca's area, primary motor cortex and cerebellum, and the planum temporale has been found to be more left lateralized in musicians, suggesting musical auditory processing may occur in the opposite hemisphere to non-musicians. White matter increases in musicians have been found in the cerebellum, internal capsule and anterior region of the corpus callosum, possibly reflecting greater interhemispheric communication. Functionally, in comparison to non-

musicians, musicians show increased activation in the right motor cortex, implying increased cortical representations for the left hand, greater activation for musical stimuli in auditory regions, increased and more bilateral activation of parietal cortices to visual and auditory stimuli, and greater pre-attentive activation to subtle musical entities. Overall, differences between musicians' and non-musicians' brain structure and function is almost undeniable. The question of whether these differences predated the musical training, or occurred as a result of that training, however, has not yet been answered.

Nature versus nurture

A major consideration in research involving musicians is the issue of investigating a group that is self-selected. Broadly, there are two opposing explanations for why musicians may show different anatomical and functional neural organization compared with non-musicians. First, it is possible that musicians are genetically predisposed to characteristics favouring the development of musical ability. An early study investigating the familial propensity of musicality in the families of professional musicians reported that when both parents were musical 70% of the siblings (of the professionals) had musical talent. However, of those professional musicians where neither parent had any musical talent only 15% of the siblings were musical (Scheinfeld as cited in Rowley, 1988, p. 196). Thus, it may be concluded that musical parents pass on their genetic predispositions favouring the neural, muscular and personality attributes needed to pursue musical performance. However, the extent musical parents influence the development of their children by exposing them early in life to musical environments and instrument learning opportunities is unknown, and this necessitates an explanation that encompasses environmental as well as genetic factors.

Studies investigating the heritability and correlation of musical aptitude in families, particularly twins, have returned mixed results. Heritability is the degree of the

contribution of genes and environment to observable behaviour, and is calculated as a proportion within the range of 0 (total contribution by environment) to 1.0 (total contribution by genes). Shuter (1969) reported estimates ranging between .26 and .63 in mothers and fathers, respectively, with their children, and .42 in twin pairs. Vanderberg (1962) assessed 33 monozygotic and 43 dizygotic twin pairs on the Wing Test of Musical Ability and Appreciation (Wing, 1968) and Seashore Measures of Musical Talent (Seashore, Lewis, & Saetweit, 1960) and found low heritability for the pitch recognition subtests, but quite high heritability scores (.42 to .52) for the Loudness, Rhythm and Music Memory subtests. Coon and Carey (1989) analysed musical attainment using measures such as performance in and out of school, holding an honours degree in music, and interest in a profession in music. They found wide correlational variation in twins (.44 to .90 for monozygotic pairs and .34 to .83 for dizygotic pairs), and reported that the effects of a common environment were larger than evidence of heritable variation. One criticism of twin studies is that developmental environment effects from being raised together cannot be disentangled from gene effects. In one study, where five sets of twins reared apart were tested on the Wing test, scores within two twin sets were remarkably similar (only 2 points difference each out of a possible 160) even though their musical training differed vastly within the pairs (Shuter, 1969). The other three twin pairs' scores, however, differed by 12, 15 and 20 points, suggesting the extent to which genes determined the musical ability in these pairs was of a smaller degree.

More recently the genetic influence on musical abilities has been investigated in relation to absolute pitch (AP), which is the ability to name notes in the absence of a reference. A sample pool of 74 individuals with AP reported that 23% of their siblings ($n = 113$) had AP ability. When 13 of these siblings were tested, 12 tested positive for AP (Baharloo et al., 1998). A subsequent study revealed that only 2.9% of a pool of 625 music camp students had AP (Baharloo, Service, Risch, Gitschier, & Freimer, 2000),

suggesting that AP is more prevalent in families than in the musically trained population. Although a genetic substrate does appear to be an important factor for developing AP, careful investigation of the 11 pedigrees reported in Baharloo et al. (1998) shows that in all but one family, children with AP had at least one parent who played a musical instrument, raising the possibility that early exposure to music was provided and this may be important in the facilitation of this ability. Additionally, all formally tested AP individuals in the preceding studies had begun music training before the age of seven. Schlaug (2001) suggests there are two main contributing factors to the development of AP. The first is exposure to music before the age of seven. In Schlaug's sample of 50 AP musicians only 1 began after this age, indicating there may be a critical period for the development of this trait. The second factor is increased left-sided planum temporale asymmetry, which is not known to be environmentally or genetically induced. Thus, it is possible that external factors, such as early exposure to music, interest by a parent, and early initiation of instrumental training play an important role in the development of AP, and that the genetic contribution is only partly determinative.

The second, opposing explanation for the anatomical and functional differences between musicians and non-musicians is that numerous hours of music practice in childhood leads to training-induced changes at the neural level. Several lines of evidence support this suggestion. Animal studies have shown that environmental stimulation can affect the development of neural organisation. Microstructural changes in motor regions and the cerebellum have been reported in rats after prolonged motor activity (Black, Isaacs, Anderson, Alcantara, & Greenough, 1990; Isaacs, Anderson, Alcantara, Black, & Greenough, 1992), and rats trained on an obstacle course that increased in difficulty over time led to greater motor cortical thickness than in rats given a wheel only (Anderson, Eckburg, & Relucio, 2002). Additionally, rats reared in socially and cognitively complex environments showed increased myelination of the corpus

callosum due to changes in axon number and size (Juraska & Kopcik, 1988) and increased number of hippocampal cells (Kempermann, Kuhn, & Gage, 1998) compared with rats reared in isolation.

In addition to animal research, studies with humans also provide convincing evidence that music training may cause differences in brain structure and function. In particular, studies investigating musical acquisition in novices have reported convincing findings. Using transcranial magnetic stimulation targeting the flexor and extensor muscles of the middle right finger, Pascual-Leone et al. (1995) showed an increased size of finger cortical representation (in comparison with baseline) when a simple five-finger keyboard exercise was taught to musically naïve adults and practiced over a 5 day period. This effect, however, was only seen within a short (30 minute) timeframe directly after practice, suggesting the movement caused a transitory effect at the neural level. Subsequently, however, participants were divided randomly into two groups, one where participants ceased practice, and one where participants continued to practice for a further 4 weeks. For the 'continued practice' group transcranial magnetic stimulation cortical output maps obtained following weekend rest periods continued to increase in size, indicating a more persistent neural change was occurring, whereas those who discontinued practice returned to baseline (Pascual-Leone, 2001).

In a similar study employing fMRI, Karni et al. (1995) have also shown neural changes following daily practice of a four-finger opposition task. Again, daily training of finger-to-thumb sequences over a 4-week period resulted in a larger area of activation of the primary motor cortex which persisted for months, this time in comparison to unpracticed sequences. The authors concluded that this result is suggestive of an "experience-dependent reorganization" (Karni et al., 1995, p. 155). Additionally, Kim et al. (2004) found increased motor cortical activation for the left little finger in adults after 6 months of violin training. These results strongly suggest that specific neural changes

occur as a result of prolonged activity targeting particular muscle groups, and provide weight to the argument that extended musical instrument training during childhood could produce changes at the neural level.

In conclusion, although it is likely that genetic predisposition is important in the development of a musician, there is convincing evidence that training may be ultimately responsible for the organisation of brain regions permitting the performance of music. Many of the reports demonstrating anatomical and functional differences between musicians and non-musicians suggest a causative link between extensive musical training and neural changes in both white and gray matter. If neural changes do occur as a result of training, then it may be that the nature of these changes is related to the nature of the training. Many musical instruments require the coordination of both hands and attention to both sides of space (for example, the piano which extends equally to both sides of the player). Therefore, it is possible that the development of the musician brain may be more equally lateralized due to the necessity of more equal hemispheric proficiency, both manually and cognitively. To date, there is accumulating evidence that musicians are lateralized differently to non-musicians for music processing, but as yet there are no studies investigating the lateralization of non-music domains (such as visuospatial processing) in musicians versus non-musicians.

Lateralization in musicians

Musicians have also been shown to differ from non-musicians in cerebral lateralization for music processing, a concept that dates back to the mid 1970s when the dichotic listening paradigm was used extensively to determine cerebral dominance for auditory cognitive abilities. The technique involves presenting the participant with two different auditory stimuli simultaneously to each ear via headphones. The participant is usually required to provide subsequent recognition of one or both of the stimuli heard. The assumption underlying the method is that contralateral pathways to the auditory cortex

are strong and block those of the ipsilateral pathways, so a stimulus presented to the right ear is processed by the left hemisphere and vice versa. If the participant's results suggest that more correct answers were given after stimuli presented to the right ear, then a left hemispheric dominance for the task is implied (Basso, 1999). Kimura (1961) established a right ear (left hemisphere) advantage for language processing in neurologically normal right-handers, and later, a left ear (right hemisphere) advantage for melody perception in non-specified non-musicians (Kimura, 1964). This dissociation has since been replicated by the use of imaging techniques (Mazziotta, Phelps, Carson, & Kuhl, 1982).

The language-left music-right dichotomy

More recent imaging studies have provided further evidence for the language-left, music-right dissociation in normal adults. In a PET study involving non-musician participants that compared phonemes and chords, phonetic processing was lateralized to the left hemisphere whilst musical processing was lateralized to the right hemisphere (Tervaniemi et al., 2000). Similarly, a transcranial Doppler sonography study demonstrated that language perception was lateralized to the left hemisphere whilst music perception was lateralized to the right hemisphere (Evers et al., 1999). Additionally, singing in musically unspecified participants has been shown to elicit the activation of the right motor cortex, anterior insula and cerebellum, whereas speaking elicited the left hemisphere homologues of these regions (Riecker, Ackerman, Wildgruber, Dogil, & Grodd, 2000).

Imaging studies focusing purely on the lateralization of music have revealed right hemispheric dominance in normal adults (Bernal, Altman, & Medina, 2004; Griffiths, Johnsrude, Dean, & Green, 1999; Zatorre, Evans, & Meyer, 1994). Others, however, have found bilateral activation (Koelsch et al., 2002; Nakamura et al., 1999), or left hemispheric dominance (Levitin & Menon, 2003). Furthermore, some groups have

demonstrated differing lateralization depending on the domain of music investigated. For example, using PET Platel and colleagues have shown preferential left hemispheric activation for familiarity, pitch and rhythm, but right hemispheric activation for timbre (Platel et al., 1997). Moreover, a later study revealed bilateral activation that was more prominent on the right for episodic musical memory (recognition) but mostly left hemispheric activation for semantic musical memory (familiarity) (Platel, Baron, Desgranges, Bernard, & Eustache, 2003). Accordingly, the precise cerebral music processing network is still under scrutiny, but it seems likely that the prevailing evidence will focus on right hemispheric dominance.

A general network for music and language

Other researchers oppose the distinct left-right dissociation between language and music, and maintain the two processes are served by a more general cerebral network (Koelsch, 2005; Koelsch & Friederici, 2003; Koelsch, Maess, Grossmann, & Friederici, 2003; Patel, 2003). Language and music are two cognitive domains that are increasingly being investigated conjointly due to mounting evidence that the neural mechanisms involved in processing each are more similar than once thought. It is suggested that music and language are both universal entities that are acquired innately for the purpose of communication and exist in acoustic and written forms (McMullen & Saffran, 2004). Both evolve serially over time via the use of sound patterns containing discrete entities that are segmented for the purposes of easier perception and greater understanding. For example, language is formed by words grouped into sentences and music is formed by notes grouped into phrases.

Much of the research investigating the neural similarities between music and language networks has focussed on the arena of syntax. It has been argued that the syntactical processing involved in musical harmony and harmonic expectancy parallel that of language syntax, since non-musician listeners are able to detect incongruities in an

original sequence of music not heard before (Krumhansl, 1990). This implies there is an implicit underlying musical grammar that the general population has some knowledge of, which is used to generate expectancies. When these expectancies are violated the P600, an evoked potential thought to reflect syntactic processing, is generated. Syntactic incongruities in music (i.e., concluding a chord progression with an unexpected Neapolitan 6th chord, which is out of the key context; Koelsch, 2005) and language (i.e., “some of the senators endorsed the promoted an old idea of justice”, which is ungrammatical; Patel, Gibson, Ratner, Besson, & Holcomb, 1998) have been shown to elicit indistinguishable P600s. Similarly, an earlier component, the early right anterior negativity (ERAN), which is also elicited by musical incongruities, has been localised by MEG to Broca’s area and its right-hemisphere homologue in non-musicians, providing further evidence for a general syntactic processing network as opposed to separate music and language systems (Maess, Koelsch, Gunter, & Friederici, 2001). Further to this, fMRI data demonstrating activation of Broca’s area, Wernicke’s area and other temporal lobe structures during syntactically violated musical chord sequences concurs with the MEG finding (Koelsch et al., 2002).

Leftward lateralization for music processing in musicians

There is evidence to suggest musical training results in an increased involvement of the left hemisphere for music processing in musicians, and it is speculated that the leftward activation seen in musicians represents their tendency to process music like a language in language areas of the brain. Bever and Chiarello (1974) were the first to demonstrate that the musical experience of the participant could affect the hemispheric dominance of musical processing. They studied a group of musically experienced participants and a group of non-musicians. The authors employed a monaural technique, where participants were presented stimuli in one ear or the other. Participants were asked to identify whether a two-note sequence had occurred in a longer target melody and also whether the entire melody had been presented earlier.

Results showed that non-musicians performed better with their left ear than with their right ear and that the musicians performed better with their right ear than with their left ear. Bever and Chiarello suggested that musically naïve participants may listen to melodies in a holistic manner reflected as a right hemisphere advantage, and that musicians may perceive melodies analytically in terms of their individual units, requiring the use of the left hemisphere.

More recent behavioural studies have also provided evidence for a language-music overlap in musicians. Musical training has been shown to facilitate pitch processing in music as well as in language (Schön, Magne, & Besson, 2004) and to improve linguistic skills in dyslexic children (Overy, Nicholson, Fawcett, & Clarke, 2003). Previously we found an interference effect in musicians carrying out a language comprehension task in the presence of background music that was not present in non-musicians undertaking the same experimental condition. The result indicated musicians had difficulty processing music and comprehending language at the same time, suggesting there may be neural coalescence of music and language in the musician brain as a result of musical training from childhood (Patston, Corballis, & Tippett, 2005).

Imaging studies also lend credence to the notion that musicians may utilize their left hemisphere to a greater extent than non-musicians during music processing. Structural morphometry applied to MR images has demonstrated stronger leftward PT asymmetry in musicians compared with non-musicians (Schlaug, Jäncke, Huang, & Steinmetz, 1995) and increased gray matter in Broca's area (left hemisphere) in musicians than in non-musicians (Sluming et al., 2002). A study investigating the anatomical marker for hand and finger representation, called Omega Sign, has shown more pronounced expression of the marker in musicians than in non-musicians, and interestingly within the musician group, a left-hemispheric predominance in keyboard players contrasting

with a right-hemispheric predominance in string players (Bangert & Schlaug, 2006). The authors suggested this finding reflected the training-induced plasticity incurred by learning an instrument that involves the primary use of the left hand (string players) or the right hand (keyboard players).

Recently, functional imaging has been extensively employed to investigate the laterality of music processing in musicians versus non-musicians. During monaural listening, musicians showed greater left than right temporal activation, whereas non-musicians showed greater right than left asymmetry (Mazziotta et al., 1982). Passive binaural music listening has also produced the same result whether using transcranial Doppler sonography (Evers et al., 1999), PET (Marinoni et al., 2000), or fMRI (Ohnishi et al., 2001) techniques. Beisteiner, Altenmüller, Lang and Lindinger (1994) monitored the brain activity of 18 music students using EEG as they performed musical analytic, memory and creative tasks. Results showed bilateral activation with a left hemispheric tendency for the analytic task where a 4-note sequence had to be reversed, right hemispheric activation for the memory task in which a well known tune had to be continued, and left hemispheric activation for the creative task whereby participants composed a conclusion to a 4-note sequence. In addition, Hasegawa et al. (2004) reported left PT activation in musicians observing finger movements on a keyboard, but no activation of the left PT in non-musicians. Furthermore, jazz musicians were found to process rhythmic incongruities in the left hemisphere in comparison to non-musicians, whose processing was right-lateralized (Vuust et al., 2005). Recently, after finding a left hemispheric preference in musicians compared to non-musicians for melodic processing, Bangert et al. (2006) stated, “Maybe the simplified notion popular in the 70s and 80s that music processing is generally lateralized to the right in non-musicians, but ‘switches’ to the left in the course of becoming a professional musician... still has some truth to it.” (Bangert et al., 2006, p. 923). Collectively, these studies support the view that musicians process music more preferentially in the left

hemisphere than do non-musicians, however, as Bangert et al's statement implies, not all studies investigating music processing in musicians concur with the proposed hypothesis.

In contrast to findings indicating the left lateralization in musicians, several studies have shown that both hemispheres are utilized in music processing and that there is no hemispheric lateralization in musicians (although laterality was not the subject of investigation). Using fMRI, Lotze et al. (2003) compared amateur and professional violinists while they performed or imagined the fingering patterns of the first 16 bars of a Mozart violin concerto. Scans revealed a predominance of bilateral frontoparietal activation, especially in the professionals, but no obvious lateralization except for primary motor activation contralateral to the fingering hand. In a similar fMRI study investigating performance versus imagery in 12 music academy pianists, Meister et al. (2004) also reported bilateral frontoparietal activation when participants played the right hand of a Bartok piece. Gaab and Schlaug (2003) even reported the opposite state, with more rightward activations in musicians and leftward temporal activation in non-musicians performing a pitch memory task. Other researchers using fMRI (Koelsch, Fritz, Schulze, Alsop, & Schlaug, 2005; Nakada, Fujii, Suzuki, & Kwee, 1998) and PET (Halpern & Zatorre, 1999; Satoh, Takeda, Nagata, Hatazawa, & Kuzuhara, 2001) methodologies have reported varied bilaterally activated regions in musicians but no lateralization to the left or right. Taken together, there is mixed evidence for the existence of different lateralization in musicians for music processing and some support for the notion that the leftward shift is due to analytical musical processing in areas once thought to be specifically wired for language.

In summary, there are three main directions in the literature surrounding musicians. First, there is mounting evidence, especially in children, that music training operates to enhance general cognitive abilities. Second, anatomical and functional differences

have been documented in the brains of musicians, and often these differences can be correlated with the degree of music training supporting the “nurture” standpoint that training may elicit neural plasticity. Third, musicians have also been shown to differ in terms of neural laterality, showing more leftward activation for music processing compared with non-musicians. Although there is evidence to support the idea that musicians are lateralized differently to non-musicians for music processing, there are no studies that test the prediction that musicians may be lateralized differently to non-musicians for other, non-music domains. A consistent finding in the imaging literature has been differences in superior parietal lobe function between the two groups (Gaser & Schlaug, 2003a, 2003b; Schmithorst & Holland, 2003), which are suggested to be due to music reading ability in musicians (Schön et al., 2002; Sergent et al., 1992; Stewart et al., 2003a, 2003b). There is also evidence that there is less laterality in the function of this region in musicians (Gaab & Schlaug, 2003; Lotze et al., 2003). Since the superior parietal region is known to be involved in visuospatial processing (Corbetta et al., 2000; Corbetta & Schulman, 2002; Fan et al., 2005), this domain was selected to be investigated further.

Thesis aims

The overall aim of this thesis was to investigate the visuospatial ability and the lateralization of visuospatial attention and perception in adult musicians with long-term musical training, which involved six studies. The purpose of these investigations was to determine whether musicians perform differently than matched non-musicians, and if so, what the nature of any differences might be. Studies 1 and 2 focused on visuospatial abilities and cognitive processing speed in musicians versus non-musicians. Studies 3 and 4 investigated the lateralization of visuospatial processing in musicians versus non-musicians. Study 5 extended this research using an electrophysiological measure of interhemispheric transfer, the N1. This component is known to show asymmetrical lateralization due to the right hemispheric dominance for

visual information transfer across the corpus callosum in normal adults. Study 6 reports the behavioural findings of Study 5.

Chapter 2: Visuospatial abilities and cognitive processing speed in musicians

Introduction

Recent research findings suggest musical expertise may be associated with enhanced cognitive abilities that extend beyond the cognitive domains directly related to music, such as mathematical (Cheek & Smith, 1999), language (Standley & Hughes, 1997), and visuospatial abilities (Bilhartz, Bruhn, & Olson, 2000). Concurrently, a plethora of literature produced in the last decade suggests there are anatomical and functional differences between the brains of expert musicians and non-musicians (Amunts, et al., 1997; Bengtsson et al., 2005; Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Gaser & Schlaug, 2003a, 2003b; Hutchinson, Lee, Gaab, & Schlaug, 2003; Schlaug, Jäncke, Huang, & Steinmetz, 1995; Schmithorst & Wilke, 2002), but very few cognitive-behavioural studies exist to relate these neural differences with behavioural correlates. Furthermore, most cognitive-behavioural studies addressing music recruit children involved in musical instruction, whereas most imaging studies investigate the morphological and functional differences between adult musicians and non-musicians.

Recently, Brochard, Dufour and Despres (2004) investigated the relationship between musical expertise and visuospatial ability in adult musicians and non-musicians and found that musicians had faster reaction times compared with non-musicians on a visual discrimination task but not on a task of simple reaction time. The authors suggested musicians have better visuospatial ability than non-musicians. Study 1 of this chapter aimed to replicate this research and extend the investigation by introducing an additional task requiring visuospatial processing that did not require manual responses, which may advantage musicians. Subsequently, another study (Study 2) investigating the processing speed of musicians versus non-musicians was conducted

in order to establish whether the findings of Study 1 may have been confounded by faster cognitive speed in musicians, since both visuospatial tasks included a speeded component.

Study 1: Visuospatial processing

Brochard et al. (2004) administered two tasks of visuospatial perception and imagery to expert musicians and matched non-musicians. In both tasks a line was first presented in either of two orientations, vertical or horizontal, followed by a dot to either side and participants were asked to judge on which side of the line the dot had appeared (left or right for the vertical condition, above or below for the horizontal condition). In the perception condition the line remained on the screen during the presentation of the dot, whereas in the imagery condition the line was removed before the dot appeared. The main finding revealed musicians were faster to respond to all stimuli irrespective of condition and line orientation and that the accuracy of the two groups did not differ.

Musicians were also found to do particularly well in comparison to non-musicians when the line was horizontal and this led the authors to conclude that musicians were advantaged by their ability to read musical notation, in which the location of dots above or below horizontal lines is important and meaningful. The authors also noted that the prolonged motor skill training inherent in becoming a musician may have led to faster reaction times and conducted a second experiment investigating simple reaction time versus colour discrimination. The simple reaction time task required participants to press the space bar upon detection of a stimulus located in four possible positions on the screen. The colour discrimination task required participants to press the left arrow for green stimuli and the right arrow for red stimuli. Results showed musicians were faster at the discrimination task but were not faster at the simple reaction time task. The authors, thus, concluded the faster reaction times by musicians in the forced-

choice discrimination paradigm were a result of enhanced visuospatial ability, especially as the speeded translation of visual information to motor output was required. Unfortunately the authors did not disclose whether or not groups in this study were matched for demographic variables such as age, sex, IQ, years of education or handedness.

In the present study the hypothesis that there is a relationship between formal musical training and visuospatial abilities was investigated by comparing the performance of adult musicians and closely-matched non-musicians on two tests of visuospatial ability. The two tasks were chosen on account of their differing visuospatial compositions and response types. The first task was a computer-generated visual discrimination task that required manual responses using the preferred hand, and the second task was a paper visuospatial search task that required verbal responses.

Method

Participants

Two groups of adult musicians and adult non-musicians participated in the experiment. The musician group was composed of 16 participants (10 female) who had received a minimum of eight years of music lessons ($M = 12.25$, $SD = 2.24$ years) and could read music (see Appendix I). Of the 16 musicians, 14 played the piano (and in 13 cases this was the first instrument learned in childhood), 11 were choral singers and 5 played the violin. Fifteen of the 16 played more than one instrument and 12 played more than two. Other instruments represented in the sample included flute ($n = 3$), percussion ($n = 3$), cello ($n = 2$), clarinet ($n = 2$), recorder ($n = 2$), trumpet ($n = 2$), guitar ($n = 2$), French horn ($n = 1$) and saxophone ($n = 1$). The non-musician group consisted of 16 participants (10 female) who had little (a maximum of two years) or no formal musical training ($M = 0.41$, $SD = 0.71$ years) and could not read music.

The Edinburgh Handedness Inventory (Oldfield, 1971) was used to assess participant's degree of handedness. 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 had a laterality quotient of greater than +50, thus ensuring they were at least moderately right-handed. General exclusion criteria included epilepsy, colour blindness, a handedness laterality quotient of less than +50, and formal music training for more than 2 years but less than 8 years.

Participants in the musician and non-musician groups did not differ on sex, $\chi^2 = 0$, $p > .99$, age, $t(30) = 0.93$, $p = .36$, years of education, $t(30) = 0.26$, $p = .80$, handedness, $t(30) = 0.31$, $p = .76$, or visuospatial reasoning ability as assessed by the Matrix Reasoning subtest of the WAIS-III (Wechsler, 1997), $t(30) = 1.00$, $p = .33$ (see Table 1). The Matrix Reasoning task was selected as it is considered a measure of fluid intelligence requiring problem-solving skills and mental manipulation ability (Tulsky, Sakolske, & Zhu, 2003), and can be administered within a 10-20 minute timeframe. It has been likened to the Raven's Standard Progressive Matrices task (Raven, Raven, & Court, 1998), which is celebrated as a culturally and linguistically fair assessment of intelligence. The University of Auckland Human Participants Ethics Committee approved this study and informed consent was obtained from all participants prior to testing.

Table 1: Demographic characteristics of musician and non-musician group participants for Study 1.

	Age (years)	Years of Education	Laterality Quotient	Matrix Reasoning (scaled score)
	Mean (SD)	Mean (SD)	Mean (SD)	Mean (SD)
Musicians	21.13 (2.80)	15.69 (2.32)	88.83 (14.92)	16.13 (1.36)
Non-musicians	22.06 (2.93)	15.50 (1.79)	87.27 (13.74)	15.50 (2.10)

Materials

Visual discrimination task

The visual discrimination task was modelled on the “imagery” condition of the visual discrimination task of Brochard et al. (2004). A fixation cross, displayed on a computer screen, was presented for 200ms before each trial. A reference line (6° long and 0.05° thick) was flashed on the screen for 500ms, followed by a target dot (0.2° in diameter) for 200ms. The reference line appeared in either horizontal, or vertical, orientation in different blocks. To control for expectancy effects the position of the reference line varied among five possible locations on the screen for each line orientation. For the horizontal condition the line appeared either in the centre or to the left or right of centre by 1.5° or 3° . For the vertical condition the line appeared either in the centre or above or below the centre by 1.5° or 3° . The position of the target dot relative to the reference line also varied among four positions for each line orientation. For the horizontal condition dots appeared 0.2° or 0.6° above or below the line. For the vertical condition dots appeared 0.2° or 0.6° to the right or left of the line. Discriminations in which the dot was close to the line (0.2°) were classified as hard, and those in which the dot was further from the line (0.6°) were classified as easy. To control for temporal expectancy the inter-trial interval varied randomly between 500ms, 700ms, 900ms, and 1100ms.

Participants were required to decide on which side of the line the dot had appeared. When the line was horizontal they pressed the “1” key on the number pad of a keyboard with their right index finger to respond “above”, and the “0” key with their right middle finger to respond “below”. When the line was vertical participants pressed the “1” key to respond “left” and the “2” key to respond “right”. Each participant sat 57cms from the computer screen and completed four 40-trial blocks containing two vertical and two horizontal line conditions in a counterbalanced order. The first 40-trial block in each orientation condition was preceded by 10 practice trials and the second by five

practice trials. These were not included in the final analysis. The participants were not given feedback in the practice trials as the purpose of these was only to familiarize the participants with the program and their response choices. Percent correct and reaction times were measured from the onset of the target dot (see Figure 1 for horizontal line condition procedure).

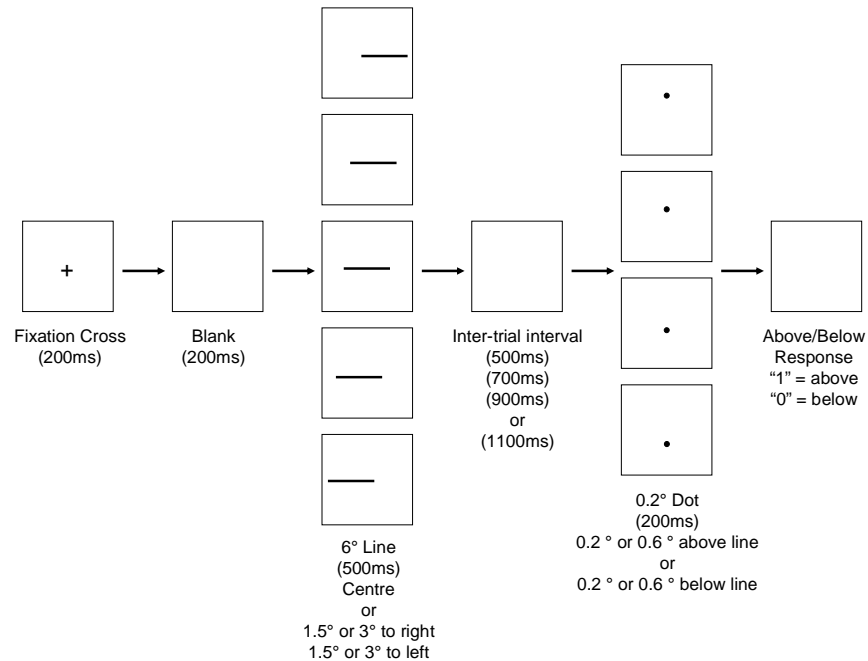


Figure 1: Procedure for horizontal line condition of visual discrimination task.

Visuospatial search task

Participants were required to locate a difference between two nearly identical visual designs and verbally report the quadrant number in which this difference appeared. The designs consisted of 12 geometric shapes and six, seven, or eight coloured dots (red, blue, green, and yellow) arranged evenly within an 8cm x 8cm box (see Figure 2 and Appendix A). Participants were told that in the right hand design one coloured dot could move, or change colour in one of the four quadrants, which were distinguished by dashed lines. Participants were given a template to refer to with the numbers 1, 2, 3

and 4 typed into the corresponding quadrants. Participants were given eight minutes and performed the task twice with two different stimuli sets, each containing 120 items. They were asked to work as quickly as possible without making mistakes and to return to the beginning and keep going should they complete the 120 items within the 8-minute timeframe. The dependent variables were number correct and number of errors.

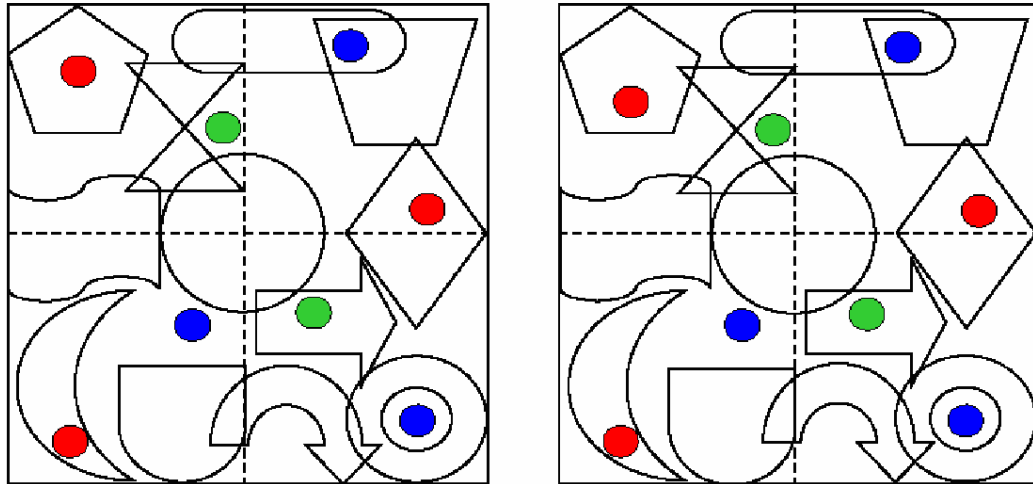


Figure 2: Example design from the visuospatial search task. Correct answer = 1.

Procedure

Participants were tested individually in a quiet room and participation took 50 to 75 minutes. The participants completed the four matching tasks and then the experimental tasks in a counterbalanced order across participants. The matching tasks were the Matrix Reasoning subtest of the WAIS-III (raw scores were converted to age-appropriate scaled scores), Ishihara's test for colour blindness, the Edinburgh Handedness Inventory, and a questionnaire containing items concerning demographic variables and musical background.

Results

Visual discrimination task

Reaction times and percent correct were analysed separately using three-way split-plot ANOVAs, with group (musicians and non-musicians) a between-subjects factor, and condition (horizontal line and vertical line) and difficulty (easy and hard discrimination) as within-subject factors. For raw data see Appendix B.

The analysis of reaction times revealed significant main effects for group, $F(1,30) = 9.14$, $p = .005$, condition, $F(1,30) = 18.56$, $p < .001$, and difficulty, $F(1,30) = 43.28$, $p < .001$. The key finding was that musicians had faster reaction times than non-musicians (see Figure 3). Responses were faster when the line was vertical, and the easy discrimination resulted in faster reaction times than the hard discrimination (see Table 2). There was also a significant interaction between condition and difficulty, $F(1,30) = 8.15$, $p = .008$, with reaction times differentially slowed when the line was horizontal and the discrimination was difficult (see Table 2). The three-way interaction was not significant ($F(1,30) = 1.38$, $p = .25$).

Table 2: Mean reaction times (ms) on the easy and hard discriminations of the visual discrimination task for the vertical and horizontal line conditions, for both groups of participants.

	Vertical Line		Horizontal Line	
	Easy Discrimination	Hard Discrimination	Easy Discrimination	Hard Discrimination
Musicians	280 (94)	335 (106)	312 (98)	397 (126)
Non-musicians	426 (184)	455 (164)	446 (143)	547 (165)

NB: Standard deviation in brackets

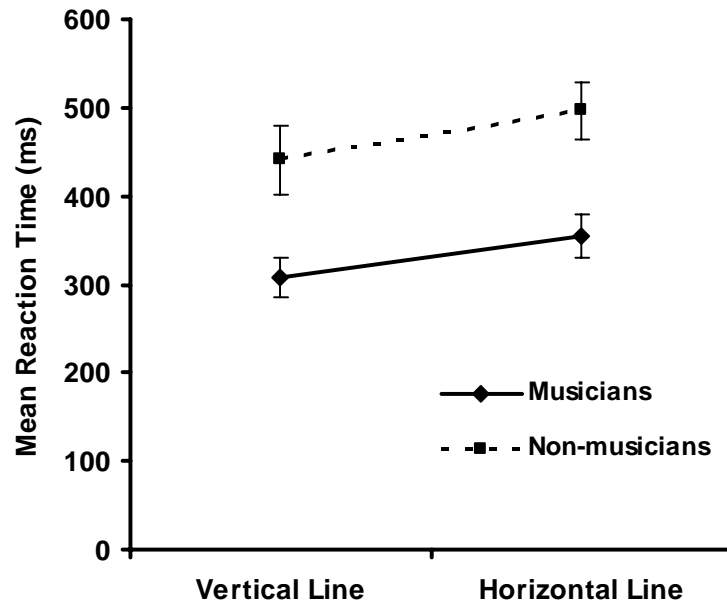


Figure 3: Mean reaction times for vertical and horizontal line conditions across easy and hard discriminations of the visual discrimination task for musicians and non-musicians. Error bars indicate standard error of the mean.

Analysis of percent correct on the visual discrimination task revealed a significant main effect of group, $F(1,30) = 5.83$, $p = .022$, with musicians making fewer errors than non-musicians (see Table 3). There was also a significant main effect of difficulty, $F(1,30) = 356.37$, $p < .001$, with participants in both groups performing more accurately on the easy discrimination condition (see Table 3).

Table 3: Mean percent correct (SD) on the easy and hard discriminations of the visual discrimination task for the vertical and horizontal line conditions, for both groups of participants.

	Vertical Line		Horizontal Line	
	Easy Discrimination	Hard Discrimination	Easy Discrimination	Hard Discrimination
Musicians	96.56 (3.40)	73.28 (13.28)	96.72 (4.05)	73.59 (9.66)
Non-musicians	89.38 (9.77)	70.31 (9.03)	90.63 (9.24)	68.44 (8.84)

Visuospatial search task

Two dependent variables, number of items completed correctly and number of errors, were analysed separately using split-plot ANOVAs, with group (musicians and non-musicians) a between-subjects factor and trial (first and second) a within-subjects factor. For raw data see Appendix C.

Musicians completed significantly more items correctly than non-musicians as shown by a significant main effect of group, $F(1,30) = 29.87$, $p < .001$, (see Figure 4). A main effect of trial revealed that significantly more items were completed correctly on the second trial ($M = 83.19$, $SE = 2.30$) than the first trial ($M = 72.13$, $SE = 2.22$), $F(1,30) = 78.75$, $p < .001$, but there was no significant interaction between these two variables, $F(1,30) = 1.97$, $p = .17$.

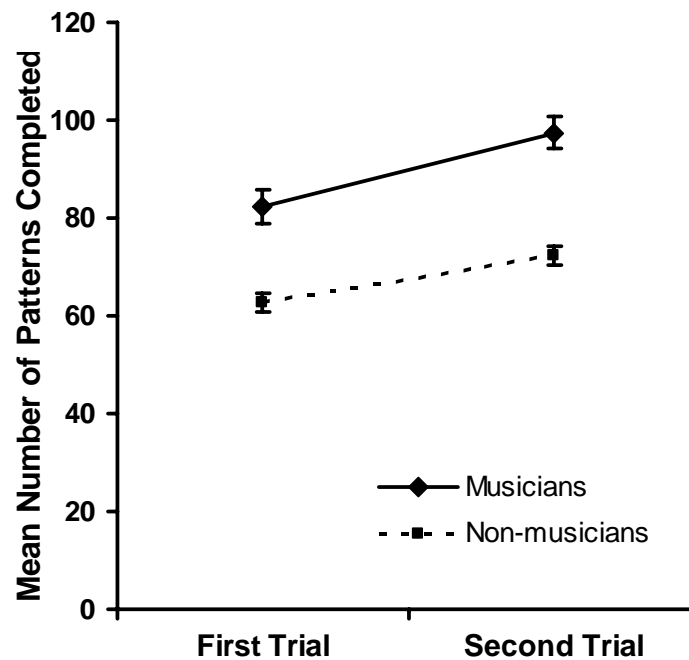


Figure 4: Mean number correct for the first and second trials of the visuospatial search task for musicians and non-musicians. Error bars indicate standard error of the mean.

The musician group ($M = 0.22$, $SE = 0.23$) made fewer errors than the non-musician group ($M = 0.94$, $SE = 0.23$) as shown by a significant main effect of group, $F(1,30) = 4.98$, $p = .033$. The main effect of trial approached significance, $F(1,30) = 3.47$, $p = .072$, with a greater number of errors made during the first trial ($M = 0.75$, $SE = 0.22$) than in the second trial ($M = 0.41$, $SE = 0.15$). The interaction between group and trial was not significant, $F(1,30) = 2.32$, $p = .14$.

Discussion

A visual discrimination task and a visuospatial search task were administered to musicians and matched non-musician control participants to assess visuospatial ability. Musicians performed more quickly and more accurately on both the visual discrimination task and the visuospatial search task.

Musicians were faster than non-musicians on both the horizontal and vertical line conditions of the visual discrimination task. This finding is consistent with that of Brochard et al. (2004), although in this study the mean reaction times of both groups were approximately 100ms faster. Although the most literal interpretation of the musician advantage on this task is that they are simply faster at associating a visual stimulus with a motor response due to years of practice of a musical instrument, Brochard et al. provided evidence that enhanced sensorimotor ability could not wholly account for the differences in processing speed between the two groups. They showed that musicians were only faster when making a choice between two visual attributes, but were not faster on a simple reaction time task. This, in combination with this study's finding of greater speed and greater accuracy, suggests that the musicians have higher levels of visuospatial abilities, a theory finding some support in the cognitive-behavioural literature in children (Bilhartz et al., 2000; Costa-Giomi, 1999; Rauscher, Shaw, & Levine, 1997; Rauscher & Zupan, 2000; Schellenberg, 2004).

Difficulty of the discrimination (dots closer to and further from the line), as expected, affected performance as hard discriminations produced slower reaction times and more errors than easy discriminations, but this pattern did not vary by group. Consistent with Brochard et al., responses were slower for horizontal than vertical lines, and, in this study, response speed to horizontal lines was differentially slowed when the discrimination was difficult. Thus, combining the two more difficult conditions resulted in differential slowing relative to either difficult condition alone for both groups.

The main difference revealed by this replication of the Brochard et al. study is that of accuracy. Brochard et al. report no difference between groups, whereas here, non-musicians were less accurate overall than musicians. Two main explanations emerge. First, Brochard et al.'s samples consisted of only 10 individuals per group. In the current study there were 16 participants per group, and this may have decreased between-subjects variation in order to show the effect of accuracy. Second, this study used slightly different distances between the lines and dots and increasing the difficulty of the task may have led to increased sensitivity of the effect.

Brochard et al. (2004) reported their musicians were differentially faster than non-musicians on the horizontal line condition and suggested this could be explained by their ability to read music. In this study, however, there was no evidence of differential benefit for musicians in the horizontal line condition. Musicians in the two studies may have differed in their expertise at reading scores, but unfortunately information on score-reading ability was not collected in either study. Nevertheless, score-reading may be related to enhanced visuospatial ability and is one explanation for why musicians may show this benefit.

On the visuospatial search task, musicians completed on average 24 more patterns than non-musicians on both the first and second times they attempted the task. The

musician group also made fewer mistakes than the non-musician group, suggesting the musicians were more efficient in searching the patterns and more accurate in judging where true differences lay. As in the visual discrimination task, the accuracy data for this task suggests better visuospatial ability in the musician group. Greater speed and efficiency could reflect either a specific advantage for visuospatial processing, or, a more rapid speed of processing generally amongst musicians. Yet another possible account of the better performance by musicians relates to the eye movements involved in performing this task. Detecting the subtle differences present in each item involves rapidly glancing back and forth between two designs. Kopiez and Galley (2002) compared eye movements of musicians and non-musicians when performing simple tracking tasks, and found that professional musicians produce faster and more efficient saccades, with more anticipatory movements, than psychology students. Superior saccadic movements could account for the greater number of patterns completed by musicians than non-musicians, although there are no direct measures of eye movements during task performance to confirm this.

Musicians had faster reaction times and greater accuracy on both the visual discrimination task and the visuospatial search task, and thus, were shown to be more efficient at processing visuospatial stimuli, via motor and verbal responses, under time constraints. Given the better performance of the musicians on these timed tasks, it is possible that at least part of the explanation for this pattern of findings is that the musicians' performances reflect superior processing speed rather than simply better visuospatial ability per se. To address this question a study was conducted to ascertain whether cognitive processing speed differed between musicians and non-musicians.

Study 2: Processing speed

In this study musicians and matched non-musicians were compared on three tasks of cognitive processing speed. It could be argued that because musicians have had specific and extended manual training, they may incur an advantage on written tasks due to greater visuomotor ability. In an attempt to reduce any possible advantage, the tasks administered were in both written and verbal modalities. The three tasks were the Symbol-Digit Modalities Test (written and verbal), the Symbol Search subtest of the Wechsler Adult Intelligence Scale-III (written), and the two baseline conditions of the Stroop Colour and Word Test (verbal). The aim was to assess whether there were differences between the groups for speed of processing expressed in both written and verbal modalities.

Method

Participants

Two groups of adult musicians and non-musicians participated in the experiment. The musician group was composed of 20 participants (10 female) who had received a minimum of eight years of music lessons and could read music (see Appendix J). In the musician sample, 17 participants played the piano (15 of these played the piano as their first childhood instrument), and of the 20 musicians, 16 played more than one instrument. The other instruments represented in the sample in order of frequency were voice ($n = 8$), cello ($n = 5$), flute ($n = 3$), recorder ($n = 2$), guitar ($n = 2$), percussion ($n = 2$), violin ($n = 1$), clarinet ($n = 1$), trombone ($n = 1$), saxophone ($n = 1$) and oboe ($n = 1$). The non-musician group consisted of 20 participants (10 female) who had little (a maximum of two years) or no formal musical training and could not read music.

The Edinburgh Handedness Inventory (Oldfield, 1971) was used to assess participant's degree of handedness. All participants were right-handed and had a laterality quotient of greater than +60. General exclusion criteria included a handedness laterality quotient of less than +60 and formal music training for more than 2 years but less than 8 years. There were no significant differences between the musician and non-musician groups for sex, $\chi^2 = 0$, $p > .99$, age, $t(38) = 0.72$, $p = .47$, years of education, $t(38) = 0.56$, $p = .58$, or handedness, $t(38) = 0.96$, $p = .34$ (see Table 4).

Table 4: Demographic characteristics of musician and non-musician group participants for Study 2.

	Age (years) Mean (SD)	Years of Education Mean (SD)	Laterality Quotient Mean (SD)
Musicians	23.20 (5.61)	16.10 (2.47)	87.89 (14.19)
Non-musicians	24.30 (3.84)	16.55 (2.65)	91.67 (10.38)

Materials

Symbol-Digit Modalities Test (SDMT; Smith, 1991)

This was administered in written and verbal forms and assesses visual scanning and tracking (Spreen & Strauss, 1998). Participants were given a key coding nine geometric symbols for the digits one through to nine (see Figure 5). The task was to substitute digits along rows of symbols in sequence as quickly as possible for 90 seconds. There were two trials. The first involved written responses and the second required verbal responses.

(÷	┌	┐	└	>	+)	÷
1	2	3	4	5	6	7	8	9

(└	÷	(┌	>	÷	┐	(>	÷	(>	(÷

Figure 5: Example of the SDMT stimuli (Smith, 1991) (top = key, bottom = first response line).

Symbol Search subtest (WAIS-III; Wechsler, 1997)

Participants were required to indicate whether either of two target symbols appeared in a reference line of 5 symbols by ticking 'yes' or 'no' boxes (see Figure 6). Participants were asked to respond to as many items as possible within a 120 second timeframe. This task assesses speed of visual scanning and there is no memory component.

┐	└	<	+	└	┐	±	YES	NO
÷	>	⊖	┌	→	⊕	>	YES	NO
→	┐	(±	<•	┐	⊖	YES	NO

Figure 6: Example of the Symbol Search task (first line = yes, second line = yes, third line = no).

Colour Naming and Word Reading Test (Stroop, 1935)

Participants were asked to respond verbally to two sets of stimuli as quickly as possible in 45 seconds. The first list consisted of colour words (i.e., blue, red, green) printed in

black and participants were required to read the words aloud (word condition). The second list consisted of 'xxxx' printed in the ink colours blue, red and green and participants were required to name the ink colour (colour condition). The interference trial of this task (Stroop Test) was not considered in this research.

Procedure

Participants were tested individually in a quiet room and participation took approximately 15 minutes. Participants completed the Edinburgh Handedness Inventory, a short questionnaire containing items concerning demographic variables and musical background, and the three experimental tasks in the order presented. The study was approved by the University of Auckland Human Participants Ethics Committee and written informed consent was obtained from all participants.

Results

For raw data see Appendix D. Table 5 provides the raw mean scores and error data for the SDMT (written and verbal trials) and Symbol Search task for both groups. In the 90 second timeframe musicians completed significantly more items on the SDMT for the written, $t(38) = 3.15$, $p = .003$, and verbal, $t(38) = 2.54$, $p = .016$, trials in comparison to non-musicians. Non-musicians made twice as many errors as musicians on the written trial, but this was not significant, $t(38) = 1.44$, $p = .16$, nor was number of errors for the verbal trial, $t(38) = 0.29$, $p = .77$.

For the Symbol Search task musicians completed significantly more items than non-musicians, $t(38) = 2.04$, $p = .048$. There was no difference in number of errors for this task, $t(38) = 0.15$, $p = .88$ (see Table 5).

Table 5: Mean scores (SD) for number correct and error data for the SDMT (written and verbal) and Symbol Search task for musicians and non-musicians.

	Number correct			Number of errors		
	SDMT written	SDMT verbal	Symbol Search	SDMT written	SDMT verbal	Symbol Search
Musicians	68.25 (10.95)	82.30 (14.35)	47.20 (6.26)	0.55 (0.69)	0.45 (0.61)	0.75 (1.02)
Non-musicians	58.15 (9.23)	72.10 (10.77)	43.20 (5.96)	1.05 (1.40)	0.55 (1.40)	0.70 (1.03)

For the Colour Naming and Word Reading Test, number of words was analysed using a repeated measures ANOVA with condition (word and colour) as the within-subjects factor and group (musicians and non-musicians) as the between-subjects factor. The analysis revealed a main effect of group, $F(1,38) = 11.83$, $p = .001$, with musicians ($M = 99.95$, $SE = 2.47$) completing more items than non-musicians ($M = 87.93$, $SE = 2.47$). There was also a main effect of condition, $F(1,38) = 173.67$, $p < .001$, with a greater number of items completed in the word condition ($M = 108.15$, $SE = 2.14$) than in the colour condition ($M = 79.73$, $SE = 1.97$). There was no interaction between condition and group.

To test for an effect between groups for the two modalities of response, written and verbal, a repeated-measures ANOVA was run using the averages for each modality (written = average of SDMT(written) and Symbol Search; verbal = average of SDMT(verbal) and both conditions of the Colour Naming and Word Reading Test) as the within-subjects factors and group as the between-subjects factor. Again, there was a significant main effect of group, $F(1,38) = 14.98$, $p < .001$, with musicians ($M = 74.41$, $SE = 1.66$) scoring higher than non-musicians ($M = 65.34$, $SE = 1.66$), but there was no group by modality interaction, $F(1,38) = 2.85$, $p = .10$, indicating musicians did not score differentially higher or lower than non-musicians in either written or verbal

responses (see Table 6). The main effect of modality, $F(1,38) = 670.74$, $p < .001$, was redundant as the tests within the two modalities were not equated for scoring.

Table 6: Averaged means (SE) for the written and verbal response modalities shown for musicians and non-musicians.

	Written Response	Verbal Response
Musicians	57.70 (1.72)	91.13 (2.00)
Non-musicians	50.68 (1.72)	80.01 (2.00)

Discussion

Participants in this study completed three timed tasks that assessed written and verbal processing speed. On all tasks (and trials within tasks) the musician group completed significantly more items than the non-musician group. There were no differences between groups in number of errors indicating there was no speed/accuracy trade-off by the musicians. As it could be argued that musicians may be advantaged by extensive dexterity and motor skill training, this study attempted to reduce any possible advantage of the musician group by varying the response modality between written and verbal responses. No difference in modality of response was found between groups, indicating musicians were not advantaged by the written modality. The results strongly suggest musicians have a faster speed of cognitive processing than non-musicians matched for sex, age, handedness and education.

Recently, Bengtsson et al. (2005) provided evidence that musicians, in particular pianists, have more heavily myelinated white matter tracts than non-musicians. This was consistent with an earlier study that also reported a greater degree of white matter organization in musicians (Schmithorst & Wilke, 2002). The advent of diffusion tensor magnetic resonance imaging (DTI) has enabled researchers to indirectly assess

myelination in white matter tracts through a method known as fractional anisotropy (FA). In this method the speed, or ease, of water diffusion along the white fibre tracts gives a functional approximation of the degree of myelination and is a technique that can be used in conjunction with the older method of gross anatomical morphometry, which measures the size of structures such as the corpus callosum. Using morphometry, the corpus callosum has been found to be larger in musicians than in non-musicians (Lee, Chen, & Schlaug, 2003; Schlaug, Jäncke, Huang, Staiger, & Steinmetz, 1995), which is indirectly suggestive of greater myelination.

The amount of myelination in the brain may be associated with cognitive processing speed because myelin is known to increase the rate of conduction of signals along axons (Trapp, 2004). Myelin effectively increases the diameter of axons and confines the electro-chemical exchange of the action potential to the Nodes of Ranvier, enabling conduction to ensue in a saltatory (hopping) manner along wider vessels. Studies examining the relationship between cognitive abilities and white matter structure have focused on patient populations and normal development in children and indicate an association between poorer cognitive skills and degeneration of myelin. Verbal fluency and recall (Rovaris et al., 2002) and general cognitive performance (Edwards, Liu, & Blumhardt, 2001) were impaired in patients with multiple sclerosis, and individuals with congenital amusia showed a reduction in white matter in the right inferior frontal gyrus, an area implicated in pitch encoding and memory (Hyde, Zatorre, Griffiths, Lerch, & Peretz, 2006). White matter diffusion dysfunction has also been associated with Alzheimer's disease (Rose et al., 2000) and normal aging cognitive decline in executive function (O'Sullivan et al., 2001). In a normal pediatric population, white matter development and IQ scores have been positively correlated indicating white fibre organization is associated with heightened cognitive functioning. Evidence suggesting musicians have greater myelin production may, therefore, be associated with their

more efficient speed of cognitive processing although this has not been directly tested. It is proposed that extended musical training from childhood, when the brain is most plastic and myelin is being laid, may result in greater production of myelin leading to faster axonal conduction and cognitive processing benefiting the musician into adulthood.

Conclusions

Study 2 was conducted in order to investigate whether the enhanced performance of musicians on some visuospatial tasks reflects a more general ability, namely a faster speed of cognitive processing. Musicians scored consistently higher in all tasks, whether in the written or verbal modality indicating that musicians do have a faster speed of cognitive processing than non-musicians. This result, therefore, suggests that the superior performance of musicians on the tasks in Study 1 was likely to reflect two factors. The first is superior visuospatial abilities (indicated by the superior accuracy on both tasks) but the second is superior processing speed (reflected in the consistently more rapid performance). An experiment would need to be devised whereby these variables could be considered separately in order to distinguish between the relative contributions of these two factors. Certainly these studies highlight the need to disentangle tests of visuospatial ability from their processing speed demands in order to elucidate the particular aspects of cognition that are enhanced by musical training.

Chapter 3: Visuospatial attention in musicians

Introduction

When asked to mark the centre of a horizontal line, people with right-sided brain damage typically err markedly to the right of true centre, a phenomenon known as left hemineglect (Binder, Marshall, Lazar, Benjamin, & Mohr, 1992). The systematic error associated with hemineglect is a consequence of failure to attend to the hemispace contralateral to brain damage (Luh, 1995). Hemineglect is usually a result of inferior parietal or temporoparietal lobe damage and occurs more frequently when the right hemisphere is affected (Jewell & McCourt, 2000). It has been suggested that both hemispheres allocate attentional capacity to the contralateral hemispace, but that the right hemisphere is capable of directing attention ipsilaterally as well (Heilman, Watson, & Valenstein, 1993). Another theory postulates that the right hemisphere has a stronger bias to contralateral space than does the left hemisphere (Heilman, Jeong, & Finney, 2004). Thus, damage to the right hemisphere results in reliance on the left hemisphere for visual attention, whereby only the right side of hemispace is wholly attended to, and consequently the midpoint of a line is erroneously located toward the right end. Recent imaging studies have also indicated the right hemisphere is dominant for attention to visual stimuli and report greater activation of the right parietal regions when participants perform tasks similar to line bisection (e.g., Landmark task, Fink et al., 2000).

Due to right-hemispheric dominance, attention for visual stimuli in normal adults tends toward the left side of space. Evidence for this tendency has come predominantly from studies of line bisection in which adults bisect lines reliably to the left of veridical centre (Barnett, 2006; Brodie & Pettigrew, 1996; Hausmann, Ergun, Yazgan, & Güntürkün, 2002; Hausmann, Waldie, Allison, & Corballis, 2003; Hausmann, Waldie, & Corballis, 2003; Luh, 1995; and see review by Jewell & McCourt, 2000). Participants also judge

lines that are pre-bisected to the left of centre to be bisected accurately (McCourt & Jewell, 1999). Attention favouring the left hemispace has also been established in greyscale luminance-gradient tasks (Mattingley, Bradshaw, Nettleton, & Bradshaw, 1994). In this paradigm participants are asked to choose which of two mirror-image luminance gradients is darker. They choose the gradient with the darker side to the left more often than they choose the one darker to the right, suggesting more attention has been given to the left hemispace (Nicholls, Mattingley, Berberovic, Smith, & Bradshaw, 2004; Nicholls, Mattingley, & Bradshaw, 2005).

In this chapter two studies are presented that investigate visuospatial attention in musicians. In Study 3 participants completed the manual line-bisection task with their left and right hands. In Study 4 the vertical line condition of the visual discrimination task from Chapter 2 was re-analysed as a task of spatial attention. This task consisted of dots presented to the left and right of a vertical line and may, thus, provide information about the processing laterality of stimuli flashed to the left and right visual fields.

Study 3: Line-bisection task

Evidence to support the superiority of the right hemisphere for visuospatial attention has come from neurologically intact right-handers who show a slight yet reliable tendency to bisect about 2% to the left of true centre (Bradshaw, Nettleton, Wilson, & Bradshaw, 1987; Brodie & Pettigrew, 1996; Hausmann et al., 2002; Hausmann, Waldie, Allison et al., 2003; Hausmann, Waldie, & Corballis, 2003). This has been termed “right pseudoneglect” (Bowers & Heilman, 1980) implying a mild, natural neglect of part of the right hemispace (see Figure 7). Recently imaging studies have revealed greater activation of the right parietal regions (Fink et al., 2000; Flöel, Buyx, Breitenstein, Lohmann, & Knecht, 2005; Wilkinson & Halligan, 2003) when participants are asked to judge whether pre-bisected lines have been bisected correctly or not

(Landmark task), further supporting dominance of the right hemisphere for spatial attention.

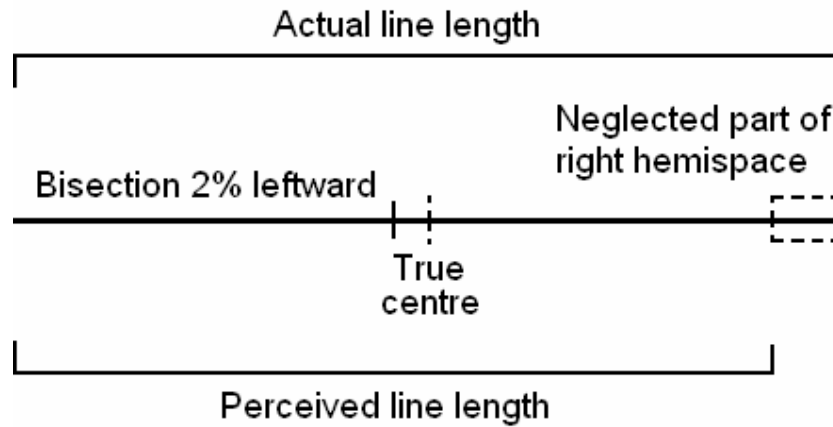


Figure 7: Diagram depicting the theoretical underpinnings of right pseudoneglect.

Line bisection can be influenced by variables, such as the hand used and the direction of scanning (Brodie & Pettigrew, 1996). There is general consensus that lines placed further to the right produce bisections further to the right (Hausmann et al., 2002; Luh, 1995; Milner, Brechmann, & Pagliarini, 1992), and that leftward bias is more pronounced when individuals use their left hand (Brodie & Pettigrew, 1996; and see Jewell & McCourt, 2000). There are also individual differences. Handedness affects the manual line-bisection task, with sinistrals erring more to the left than dextrals (Luh, 1995; Scarisbrick, Tweedy, & Kuslansky, 1987). Most studies either do not report, or do not find, sex effects (e.g., see the review by Jewell & McCourt, 2000), however, two studies that did report sex effects produced contrary results: Wolfe (1923) found that females erred more to the left than males did, whereas Roig and Cicero (1994) found the reverse. Corpus callosum size has also been found to affect judgment on the line-bisection task (Yasgun, Wexler, Kinsbourne, Peterson, & Leckman, 1995). Participants with a larger callosal area bisected lines further to the right, which was suggested to be due to a greater speed of activation from the right hemisphere resulting in reduced

dominance and more balance. This research finding is particularly pertinent to the current study given musicians are known to have larger corpus callosa than non-musicians (Schlaug, Jäncke, Huang, Staiger, & Steinmetz, 1995).

This study investigated visuospatial attention in musicians and non-musicians. Using the manual line-bisection task, the aim was to compare both accuracy and the extent of possible pseudoneglect. It was predicted that musicians would be more accurate, and therefore bisect lines closer to the true centre. It might also be expected that musicians would bisect lines further to the right than non-musicians as a reflection of larger callosa.

Method

Participants

Two groups of right-handed adults, musicians and non-musicians, participated in the experiment. The musician group was composed of 20 participants (11 females) who had received a minimum of eight years of music lessons and music-reading ability (see Appendix K). Of the 20 musicians, 18 played more than one instrument and 12 played more than two. The most commonly played instrument was the piano ($n = 19$), while 15 members of the sample were choral singers and 5 played the recorder. Other instruments played by the musician sample in order of frequency were flute ($n = 3$), guitar ($n = 3$), clarinet ($n = 2$), percussion ($n = 2$), violin ($n = 2$), cello ($n = 1$), trumpet ($n = 1$), and saxophone ($n = 1$). The non-musician group consisted of 20 participants (10 females) who had little (a maximum of two years) or no formal musical training and no music-reading ability.

All participants completed the Edinburgh Handedness Inventory (Oldfield, 1971) and those with a laterality quotient of less than +60 were excluded (+100 represents extreme right-handedness, -100 represents extreme left-handedness, zero represents

perfect ambidexterity). General exclusion criteria included left handedness and formal music training for more than two years but less than eight years. The groups did not differ significantly on sex, $\chi^2 = 0.10$, $p = .75$, age, $t(38) = 1.21$, $p = .24$, or handedness, $t(38) = 0.70$, $p = .49$ (see Table 7).

Table 7: Demographic characteristics of musician and non-musician group participants for Study 3.

	Age (years) Mean (SD)	Laterality Quotient Mean (SD)
Musicians	25.75 (7.32)	91.12 (12.59)
Non-musicians	23.60 (3.15)	88.51 (11.00)

Stimuli and Procedure

The materials for the line-bisection task (Hausmann et al., 2002) consisted of one page with 17 horizontal lines (displayed randomly in the centre, and to the right and left of the page). The line lengths varied from 10 to 26 cm in 2-cm intervals. Participants were instructed to bisect each line into two equal parts, starting from the top of the page and working down, covering the previously bisected lines as they proceeded. Half the participants from each group performed the task with their left hand first, and half with their right hand first. Deviation (measured to the nearest millimeter) from the true centre was converted to a percentage of line length. Leftward deviation was scored as negative and rightward deviation was scored as positive.

Results

For raw data see Appendix E. Repeated measures analysis of variance for percentage of deviation from the true centre was performed with group and sex as between-subject factors and hand (left and right) and line position (left, centre, and right) as within-subjects factors. Main effects for each of the four variables were found. Deviation to the

left was also more pronounced for the left hand ($M = -1.18$, $SE = 0.40$) than for the right hand ($M = -0.30$, $SE = 0.30$), $F(1,33) = 4.10$, $p = .050$, and for females ($M = -1.56$, $SE = 0.39$) than for males ($M = 0.08$, $SE = 0.39$), $F(1,36) = 8.61$, $p = .006$. A main effect of line position, $F(2,72) = 13.26$, $p < .001$, and an interaction between line position and hand, $F(2,72) = 6.77$, $p = .002$, reflected the fact that bisection was further to the right for lines on the right side of space than for lines on the left side of space, especially when the right rather than the left hand was used (see Figure 8). There were no significant interactions with group.

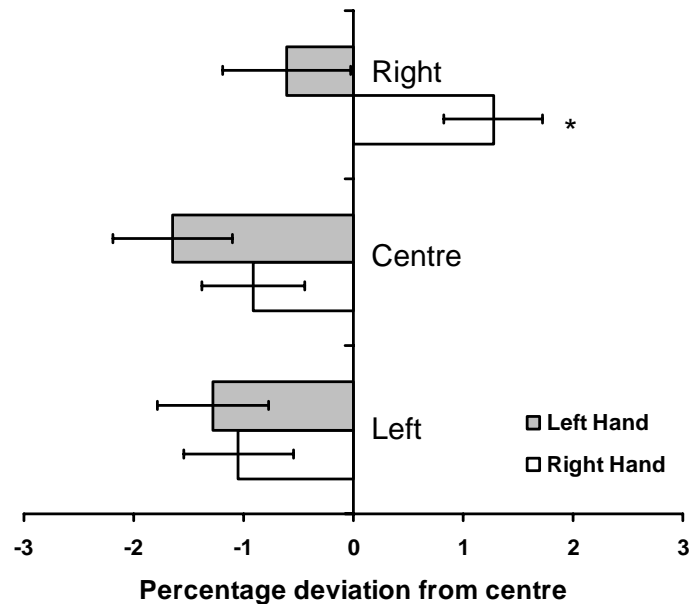


Figure 8: Mean percentage deviation from the true centre in the line-bisection task according to position on the page (right, centre and left) and hand used. Negative numbers denote leftward bias, and positive numbers denote rightward bias. Error bars indicate standard error of the mean. * This bar is significantly different from all other bars.

Non-musicians showed greater deviation to the left than musicians who showed deviation to the right of centre, $F(1,36) = 34.96$, $p < .001$. One-sample t -tests were used to test whether the biases were significantly different from zero. The leftward bias among non-musicians was significant for both hands: left hand, $t(19) = 4.67$, $p < .001$;

right hand, $t(19) = 3.20$, $p = .005$. In contrast, the rightward bias among musicians was significant only for the right hand, $t(19) = 2.47$, $p = .023$.

To compare accuracy between groups, the scores were converted to absolute deviation from zero, and the analysis repeated with hand and group as variables. The musicians were more accurate than the non-musicians, showing significantly lower deviations from true centre, $F(1,38) = 6.43$, $p = .015$. The interaction with hand was also significant, $F(1,38) = 4.25$, $p = .046$, reflecting more accurate bisection with the right hand than the left hand among the non-musicians, $p = .038$, but not among the musicians, $p = .446$. This result suggests greater symmetry between the hands among the musicians, which is evident in Figure 9, although the values plotted there are original values, not absolute values.

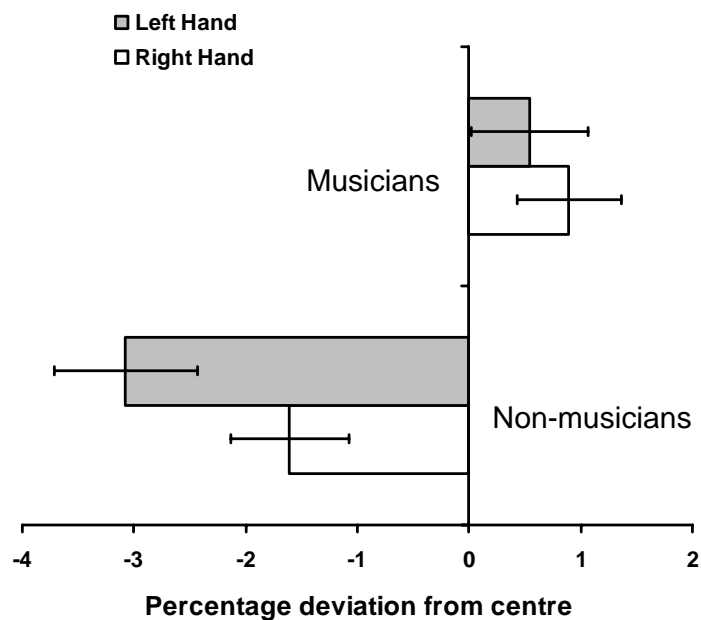


Figure 9: Mean percentage deviation from the true centre in the line-bisection task according to group (musicians vs. non-musicians) and hand used. Negative numbers denote leftward bias, and positive numbers denote rightward bias. Error bars indicate standard error of the mean.

Discussion

These results confirm the left bias, or right pseudoneglect, in normal dextrals (Bowers & Heilman, 1980; Hausmann et al., 2002; Hausmann, Waldie, Allison et al., 2003; Hausmann, Waldie, & Corballis, 2003) and support Wolfe's (1923) claim that females err more to the left than males. The effects of hand and line position agree with those of most studies: The leftward bias was greater for lines placed to the left rather than the right of the page and also was greater when participants used the left rather than the right hand. (Brodie & Pettigrew, 1996; Hausmann et al., 2002; Milner et al., 1992).

The novel findings of this study are, first, that the musicians showed a slight rightward bias, suggesting *left* pseudoneglect, and second, that the musicians bisected the lines more accurately than the non-musicians. The greater accuracy and the smaller intermanual difference in the musicians suggest that spatial attention may be more balanced in musicians than in non-musicians. This may be due to either reduced dominance of the right hemisphere or an increased role in spatial attention for the left hemisphere. The latter explanation fits well with recent research that suggests musicians, unlike non-musicians, process music more effectively in the left hemisphere (Marinoni, Grassi, Latorraca, Caruso, & Sorbi, 2000; Schmithorst & Holland, 2003), indicating that musicians may have developed greater use of the left hemisphere in cognitive functions that are usually right hemisphere dominant.

An alternative explanation may be that the right-sided tendency found in musicians is merely a reflection of a larger corpus callosum size, as demonstrated by Yazgun et al. (1995). The association between the three variables – musical expertise, larger callosal size, and more balanced spatial attention is interesting, and will be considered further in Chapter 4.

Study 4: Visual discrimination task (vertical condition)

The rightward deviation of musicians on the line-bisection task was unexpected and prompted a re-analysis of the vertical line condition of the visual discrimination task used in Chapter 2. Analyses were performed to investigate whether musicians and non-musicians differed in reaction times and/or accuracy when the dots were on the left or right of the line, and whether there were any attentional disparities between the groups on this task. With regard to the line bisection results it was hypothesised that non-musicians would show an effect of leftward attentional bias whereas musicians would show a more balanced allocation of attention, with either no bias to either side of space, or a slight bias to the right.

Method

Participants

The participants and method used in this analysis were identical to those in Chapter 2. Briefly, participants included 16 musicians (10 female) and 16 matched non-musicians (10 female), each with a laterality quotient above +50. Members of the musician group had received a minimum of eight years of music lessons ($M = 12.25$, $SD = 2.24$ years) and could read music (see Appendix I). Of the 16 musicians, 15 played more than one instrument (exception: one violin only) and 12 played more than two. The most commonly played instrument was the piano ($n = 14$), while 12 members of the sample were choral singers and 5 played the violin. Members of the non-musician group had little (a maximum of two years) or no formal musical training ($M = 0.41$, $SD = 0.71$ years) and could not read music.

Participants in the musician and non-musician groups did not differ significantly on sex, $\chi^2 = 0$, $p > .99$, age, $t(30) = 0.93$, $p = .36$, years of education, $t(30) = 0.26$, $p = .80$, handedness as established by the Edinburgh Handedness Inventory, $t(30) = 0.31$, $p =$

.76, or visuospatial reasoning ability as assessed by the Matrix Reasoning subtest of the WAIS-III (Wechsler, 1997), $t(30) = 1.00$, $p = .33$ (see Table 8). General exclusion criteria included a handedness laterality quotient of less than +50, and formal music training for more than 2 years but less than 8 years.

Table 8: Demographic characteristics of musician and non-musician group participants for Study 4.

	Age (years) Mean (SD)	Years of Education Mean (SD)	Laterality Quotient Mean (SD)	Matrix Reasoning (scaled score) Mean (SD)
Musicians	21.13 (2.80)	15.69 (2.32)	88.83 (14.92)	16.13 (1.36)
Non-musicians	22.06 (2.93)	15.50 (1.79)	87.27 (13.74)	15.50 (2.10)

Stimuli and Procedure

Vertical lines were flashed on a computer screen for 500ms followed by a dot to either the left or right of the line. Participants were required to decide on which side of the vertical line the dot had appeared by pressing the “1” key on the number pad of a keyboard with their right index finger to respond “left”, and the “2” key with their right middle finger to respond “right”. Discriminations in which the dot was close to the line (0.2°) were classified as hard, and those in which the dot was further from the line (0.6°) were classified as easy. Each participant completed two 40-trial blocks, the first of which was preceded by 10 practice trials that were not included in the final analysis. Percent correct and reaction times were measured from the onset of the target dot.

Results

For raw data see Appendix F. Three-way split-plot ANOVAs were run with group as the between-subjects factor, and side (left and right) and difficulty (easy and hard) as within-subjects factors. The analysis of reaction times revealed a significant main effect of group, $F(1,30) = 6.77$, $p = .014$, with musicians responding more quickly than non-

musicians, and difficulty, $F(1,30) = 20.44$, $p < .001$, with slower reaction times by both groups for dots closer to the line (hard discrimination). Interestingly, dot side interacted with group, $F(1,30) = 4.28$, $p = .047$, with musicians showing faster responses to right-sided dots than left-sided dots, and non-musicians showing faster responses to left-sided dots than right-sided dots (see Figure 10). Neither of the within-group comparisons were significant, although the non-musician difference approached significance (musicians: $p = .310$; non-musicians: $p = .068$). Musicians, however, were significantly faster at responding to stimuli on the right side of the line in comparison to non-musicians ($p = .004$) but only marginally faster to the left-sided stimuli ($p = .062$), indicating musicians have a particular bias toward stimuli presented in the right side of space.

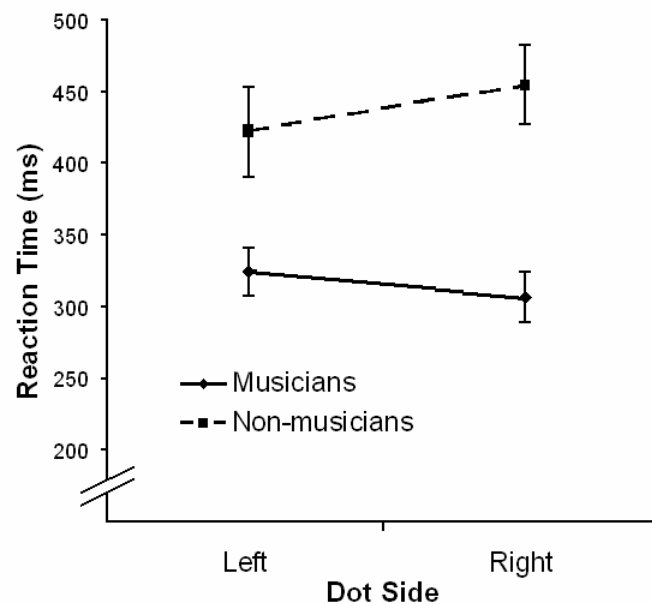


Figure 10: Mean reaction times for left- and right-sided dots for musicians and non-musicians. Error bars indicate standard error of the mean.

The interaction between group and difficulty approached significance, $F(1,30) = 3.44$, $p = .074$ (see Table 9) in which musicians showed a greater difference in response time

between easy and hard discriminations than non-musicians. There was no main effect of side, $F(1,30) = 0.37$, $p = .55$, which was due to the interaction between groups.

Table 9: Reaction times for easy and hard discriminations on the vertical line condition for both groups (SEM).

	Easy Discrimination	Hard Discrimination
Musicians	280.16 (36.45)	347.43 (33.97)
Non-musicians	426.48 (36.45)	454.61 (33.97)

Analysis of percent correct, however, did reveal a significant main effect of side, $F(1,30) = 27.20$, $p < .001$, indicating that participants were more accurate when dots appeared to the left of the line (see Figure 11), and difficulty, $F(1,30) = 182.11$, $p < .001$, indicating that participants were more accurate in the easy discriminations ($M = 92.73$, $SE = 1.28$) than the hard discriminations ($M = 71.48$, $SE = 2.01$). The main effect of group approached significance, $F(1,30) = 3.57$, $p = .068$, with musicians performing more accurately overall (see Figure 11), but more importantly, dot side interacted significantly with group, $F(1,30) = 5.19$, $p = .03$. Bonferroni pairwise comparisons revealed that, although performance was significantly poorer on the right-sided dots for each group (musicians: $p = .046$; non-musicians: $p < .001$), this was more pronounced in the non-musicians implying more right-sided dots were judged to be on the left of the line in this group (see Figure 11). Post hoc tests also revealed that accuracy for right-sided dots was significantly poorer in non-musicians than in musicians ($p = .019$), but there was no difference in accuracy to left-sided dots.

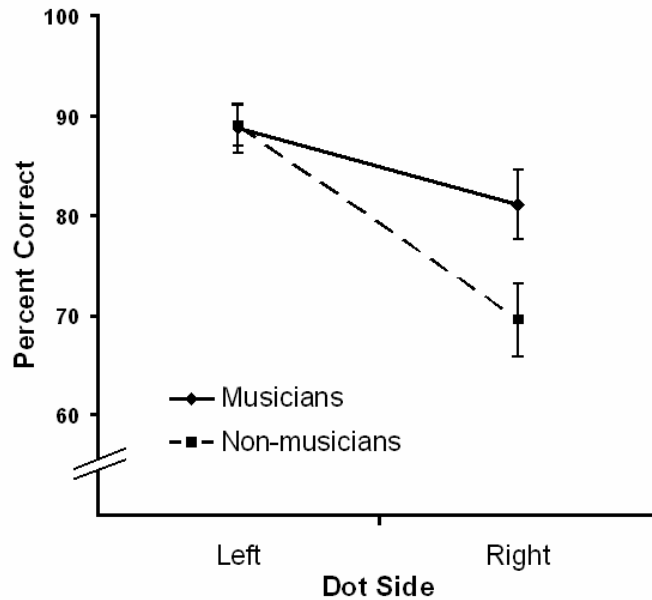


Figure 11: Mean percent correct for left- and right-sided dots for musicians and non-musicians. Error bars indicate standard error of the mean.

Dot side also interacted significantly with difficulty, $F(1,30) = 16.97$, $p < .001$, with participants decreasing their accuracy more so on right-sided dots in the hard discrimination (see Table 10). In both difficulty discriminations accuracy for left-sided dots was significantly greater than accuracy for right-sided dots.

Table 10: Percent correct for easy and hard discriminations of the vertical line condition when dots were to the left and right side (SEM).

	Left-sided dots	Right-sided dots
Easy Discriminations	96.09 (0.89)	89.38 (2.23)
Hard Discriminations	81.72 (2.50)	61.25 (2.98)

Discussion

The analyses revealed that both groups performed more accurately when the dots were to the left of the line, suggesting participants had better visual attention for stimuli presented to the left side of space. This is in keeping with evidence that suggests

neurologically normal dextrals have better attentional capacities for the left side of space (Jewell & McCourt, 2000; Nicholls et al., 2004; Nicholls et al., 2005). Additionally, however, when the dots were to the right of the line musicians made fewer errors than non-musicians, suggesting musicians have better visual attentional capacity than non-musicians for stimuli presented to the right side of space. Consistent with this, the RT analysis revealed that musicians responded faster to the right-sided dots than left-sided dots, and non-musicians responded faster to the left-sided dots than right-sided dots. Furthermore, musicians were faster than non-musicians to respond to right-sided dots.

General Discussion

The results of Study 4 were consistent with those of Study 3, which showed that musicians were more accurate at bisecting lines than non-musicians, and that they were biased slightly to the right rather than to the left. Together the results infer that visuospatial attention is more balanced in musicians than in non-musicians.

Studies of structural brain changes in musicians provide a possible correlate of the findings of a balanced visuospatial attentional capacity. Gaser and Schlaug (2003a, 2003b) found increased gray matter volume in professional keyboard players in regions known to be involved in musical performance (i.e., sensorimotor cortex, Heschl's gyrus and cerebellum), but also in regions known to be involved in visuospatial attention (superior parietal cortex). Superior parietal cortex is known to contribute to orienting to the spatial location of visual signals and attentional processes in visual search and detection (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Corbetta & Shulman, 2002; Fan, McCandliss, Fossella, Flombaum, & Posner, 2005). Gaser and Schlaug found the extent of the increased parietal volume in the musicians was greater in the left hemisphere, suggesting pianists have differentially more development in this

region than non-musicians, which may be directly related to the findings of less lateralized visuospatial attention in musicians.

The balanced attentional capacity seen in this sample of musicians could be associated with the cognitive demands of playing a bimanual instrument from childhood. It is possible that playing an instrument from a young age may facilitate the plasticity that enables the development of a more balanced representation of space. The piano, for example, extends equally to both sides of the player and swift attentional changes to each hand are required continuously to manage the perfection of performance (Peters, 1986). Also, the necessity for specific, engaged attention to the filigree right hand whilst playing may relocate the natural visuospatial attentional tendency further toward the right side of space. Although 85% of the musicians in this sample had played the piano from childhood, unfortunately these data do not provide a direct test of this account as 90% of the musicians played at least two instruments and only a small number of the musicians did not play piano.

Kopiez, Galley and Lee (2006) have provided further evidence that ambilaterality is an important attribute in pianists. They found increased sight-reading ability as the extent of right-handedness decreased, suggesting that less lateralization is advantageous for the rapid transmission of visuospatial information to motor output. Furthermore, Amunts et al. (1997) measured the intrasulcal length of the precentral gyrus and showed that the primary hand motor area was larger and more symmetrical in musicians (mostly keyboard players) than in non-musicians, due to a more pronounced increase in the non-dominant hand region. This finding was in conjunction with a more symmetrical finger tapping rate in musicians, suggesting that the bimanual coordination required for most instruments, like the piano, may lead to enhanced development of the cortical regions associated with the non-dominant hand. Similarly, it is possible that piano playing from a young age may facilitate the plasticity that enables the development of a

more balanced representation of space. It remains possible, of course, that children with a biologically more balanced attentional capacity may have more success in their progression of piano playing abilities, and may, therefore, be more likely to become musicians. Animal studies provide some indirect support, however, that environmental experiences can affect the development of neural organisation. Anderson, Eckburg and Relucio (2002) showed that rats trained on an obstacle course that increased in difficulty over time led to greater cortical thickness, and Juraska and Kopcik (1988) found that rats reared in socially and cognitively complex environments had increased myelination of the corpus callosum due to changes in axon number and size.

In Study 4, the musicians were also generally quicker in their responses. It is possible that musicians are advantaged on tasks, such as those used here, due to their familiarity with these components from reading music. Notes in music are discriminated by their location on and within the lines of a stave, which are horizontally positioned. In Study 4, however, the line was vertical with dots occurring to either side, removing the direct comparability of the stimuli to musical notation. However, it is also possible that musicians who read music are generally proficient at making small discriminations in a spatial array, which may lead to faster reaction time when a choice is needed under pressure and better judgment for the exact centre of a line. Studies that compare the performance of musicians who read music with those who do not, could help determine whether or not skills related to the reading of music underlie the better performance of musicians in these studies.

In summary, musicians in these studies showed more balanced attention and faster choice reaction times than non-musicians. More balanced attention may be associated with the bimanual requirements of playing an instrument, and studies have shown that musicians show relative equivalence in the motor dexterity of the two hands, as well as more structural symmetry of parietal and motor regions in the brain. Enhanced

visuospatial ability of musicians may also, in part, be due to the spatial processing involved in reading musical notation, contributing to more developed visuospatial networks in the brain. To date, however, this evidence is based largely on correlational studies, and longitudinal studies are needed to help clarify the causative relation between the neural and cognitive attributes of musicians.

Chapter 4: Electrophysiological interhemispheric transfer time in musicians

Introduction

Results from the two studies reported in Chapter 3 brought into question the lateralization of visuospatial attention in musicians. In line bisection, for example, people typically err by locating the midpoint about 2% to the left of true centre (Brodie & Pettigrew, 1996; Hausmann, Ergun, Yazgun, & Güntürkün, 2002), consistent with dominance of the right hemisphere for visuospatial attention (Fink et al., 2000; Heilman, Jeong, & Finney, 2004; Mattingley, Bradshaw, Nettleton, & Bradshaw, 1994). In contrast, the research in Chapter 3 showed that musicians bisected lines to the right of centre, and were also more accurate overall at bisection than non-musicians. In addition, when discriminating on which side of a vertical line a dot had been presented, musicians showed more accurate and faster performance to right-sided stimuli in comparison to non-musicians, whose performance was significantly poorer for dots appearing on the right side of the line. These findings suggest that spatial attention is represented more bilaterally in musicians than in non-musicians.

More balanced attention among musicians may be the result of extended musical training and practice from an early age, which is well documented to induce changes at the neural level, in both white and gray matter. Plasticity resulting from musical training is further supported by correlations between the amount of change and the age at which training commenced. String players have been found to have larger cortical representations for the digits of their left than of their right hand, suggesting the increased use of the left hand for fingering in string instruments induces cortical reorganization in these musicians (Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995). The effect was especially pronounced in string players who had begun training at an early age. Additionally, by measuring the intrasulcal length of the precentral

gyrus, Amunts et al. (1997) showed that the primary hand motor area is larger, but also less asymmetrical, in musicians than in non-musicians. This indicates an enhanced development of the cortical regions associated with the non-dominant hand, probably due to the bimanual coordination required for most instruments. This effect was also negatively correlated with the age at which training commenced.

Using fractional anisotropy as an indirect measure of white matter structure, Bengtsson et al. (2005) compared myelination in professional pianists and matched non-musicians. They found more heavily myelinated white matter tracts in musicians, particularly in the internal capsule, corpus callosum and arcuate fasciculus, and this was also positively correlated with the number of hours spent practicing in childhood, adolescence, and adulthood. Interestingly, although the actual number of hours practicing in childhood was less than in adolescence and adulthood, the number of brain regions showing increased fractional anisotropy was greater, suggesting the degree of myelination is most malleable in childhood and decreases with age. This work has sparked the suggestion that the process of myelination may be a mechanism of neural plasticity, and not simply a fixed developmental process (Fields, 2005).

Bengtsson et al.'s finding is consistent with other research demonstrating white matter differences associated with musical training. Schlaug, Jäncke, Huang, Staiger and Steinmetz (1995) investigated the macroscopic size of the midsagittal area of the corpus callosum in musicians and non-musicians using *in-vivo* magnetic resonance morphometry. They found the anterior region of the corpus callosum to be larger in musicians than in non-musicians, and larger in musicians who commenced training before age 7 than those whose training began after age 7. The size of the corpus callosum has been attributed to the number of axons crossing the midline (Aboitiz, Scheibel, Fisher, & Zaidel, 1992), leading to two predictions. First, musicians may have enhanced interhemispheric communication (Münste, Altenmüller, & Jäncke, 2002;

Schlaug et al., 1995), and second, extended musical training from childhood may decrease the number of connections lost during natural aging. Animal studies provide some indirect support. Neonatal mice have been shown to have more callosal axons than young adults, suggesting the maturation of the corpus callosum involves the elimination of axons (Clarke, Kraftsik, van der Loos, & Innocenti, 1989), and enriched, stimulating environments have been shown to delay loss of cerebral volume in transgenic Huntington's Disease mice (van Dellen, Blakemore, Deacon, York, & Hannan, 2000).

Larger callosal size has also been correlated with increased ambidexterity (Habib et al., 1991). Schlaug et al. (1995) found musicians to be more ambidextrous than non-musicians in index-finger tapping rate and a hand dominance test containing three paper-and-pencil dexterity tasks, despite the fact that all described themselves as right-handed. They suggested that better performance with the non-dominant hand in musicians could be the result of increased training of motor skills in both hands, and not necessarily a reflection of the dominant hemisphere. Regardless, their morphometric result suggests the anatomical structure of the corpus callosum in musicians is similar to that of individuals who tend to be ambilateral.

One way to assess callosal function is to measure interhemispheric transfer time (IHTT) using event-related potentials (ERPs) (see Figure 12). In this paradigm, stimuli are presented to each visual field individually and the latencies of occipital event-related potentials ERPs (N1) in the hemisphere contralateral (direct pathway) to the stimuli are subtracted from that in the hemisphere ipsilateral (callosal pathway). This methodology allows for firstly, the comparison of IHTT in the two directions, left-to-right and right-to-left, and secondly, for the assessment of the absolute latency of the N1 in each hemisphere.

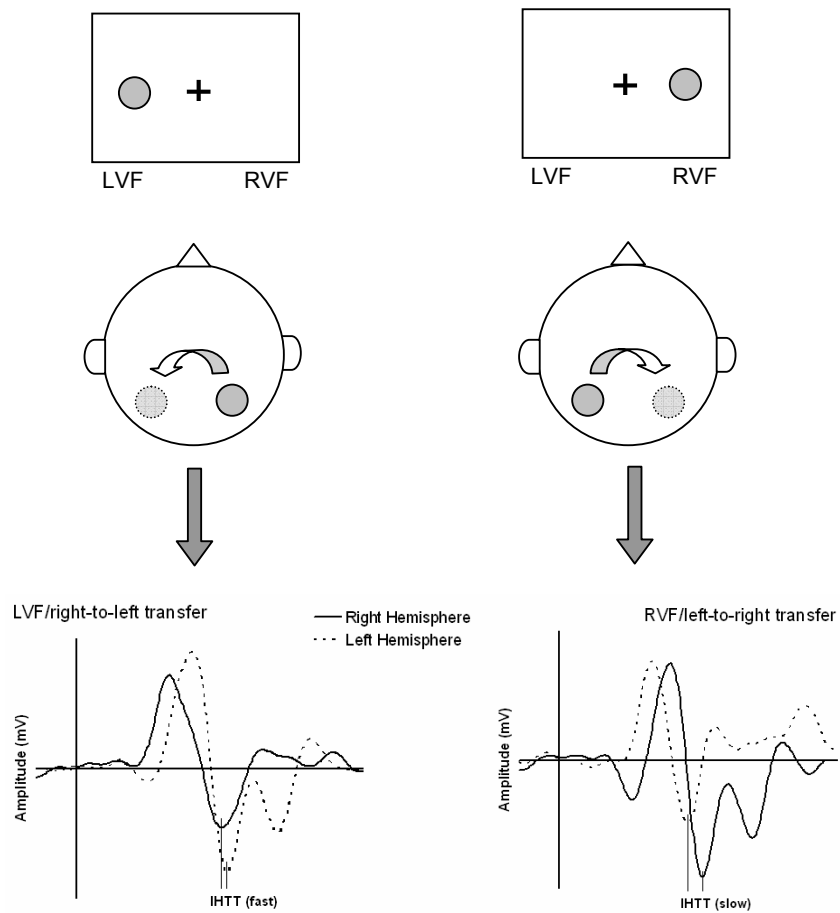


Figure 12: Stimulus presentations to the left and right visual fields and theoretical callosal crossover. Diagram also shows example ERP recordings for each condition and each hemisphere demonstrating typical fast and slow interhemispheric transfer.

The absolute latency of the N1 has been suggested to reflect a discriminative process for attended stimuli (Luck, 1995), in which latency lengthens as the attentional load increases (Callaway & Halliday, 1982; Schwent, Synder, & Hillyard, 1976). For example, Peeke, Callaway, Jones, Stone and Doyle (1980) reported shorter N1 latencies and more errors for participants who were sleep deprived and intoxicated with alcohol in comparison to alert, rested participants.

Studies of IHTT using reaction-time and ERP measures have consistently indicated faster transfer from the right to the left hemisphere than from left to right in

neurologically healthy adults (Barnett & Corballis, 2005; Barnett, Corballis, & Kirk, 2005; Barnett & Kirk, 2005; Brown & Jeeves, 1993; Brown, Larson, & Jeeves, 1994; Larson & Brown, 1997; Marzi, Bisiacchi, & Nicoletti, 1991). This asymmetry is generally found for both verbal and non-verbal tasks (Brown & Jeeves, 1993; Brown et al., 1994; but also see Nowicka, Grabowska, & Fersten, 1996), suggesting that it is unrelated to which hemisphere is dominant for any given task. Miller (1996) has proposed that the right hemisphere is specialized for fast, efficient neural transmission resulting in superiority over the left hemisphere for instantaneous processing of spatial patterns. This, it is argued, is due to a higher proportion of fast-conducting, myelinated axons in the right hemisphere, as indicated by the higher ratio of white to gray matter. Alternatively, Marzi et al. (1991) proposed that faster right-to-left transfer may be attributable to more numerous axons projecting from the right hemisphere than vice versa. Furthermore, Barnett and Corballis (2005) found greater evoked potential amplitude in the right hemisphere, as well as right-to-left asymmetry, suggestive of greater post-synaptic summation in the right hemisphere. The authors argued this was consistent with a greater number of more rapidly conducting axons in the right hemisphere.

In the present study (Study 5), IHTT and absolute latency of the N1 were electrophysiologically assessed in musicians and non-musicians¹. Faster right-to-left than left-to-right transfer was expected in non-musicians, consistent with previous research (Barnett & Corballis, 2005; Barnett, Corballis et al., 2005; Larson & Brown, 1997). Furthermore, given previous behavioural evidence demonstrating more balanced function between the two hemispheres in musicians than in non-musicians (see Chapter 3), it was anticipated that the asymmetry between left-to-right and right-to-left transfer would be less evident in musicians, and perhaps absent altogether. In

¹ NB: Reaction time and accuracy data are presented in Chapter 5.

addition, possible N1 absolute latency differences arising between the hemispheres and/or groups were explored.

Method

Participants

Two groups of adult musicians ($n = 16$, 8 female) and adult non-musicians ($n = 16$, 8 female) participated in this experiment, which was approved by the University of Auckland Human Participants Ethics Committee. All participants had normal or corrected-to-normal vision and provided written informed consent prior to testing. All members of the musician group had received at least eight years of music lessons ($M = 13.44$ years, $SD = 4.07$) and could read music (see Appendix L). Of the 16 musicians, 13 played more than one instrument and nine played more than two. Fourteen played the piano, eight were vocalists and five played the recorder. The other instruments represented in order of frequency were the violin ($n = 3$), cello ($n = 3$), flute ($n = 3$), saxophone ($n = 2$), guitar ($n = 1$), percussion ($n = 1$), French horn ($n = 1$), clarinet ($n = 1$), double bass ($n = 1$) and oboe ($n = 1$).

All members of the non-musician group had very little (less than 2 years) or no formal music training and could not read music. All participants had an Edinburgh laterality quotient of greater than +60, thus ensuring they were all at least moderately right-handed. The groups did not differ significantly on sex, $\chi^2 = 0$, $p > .99$, age, $t(30) = 1.01$, $p = .32$, years of education, $t(30) = 0.79$, $p = .44$, or handedness, $t(30) = 0.98$, $p = .34$ (see Table 11). General exclusion criteria included epilepsy, a handedness laterality quotient of less than +60, and formal music training for more than 2 years but less than 8 years.

Table 11: Demographic characteristics of musician and non-musician group participants for Study 5.

	Age (years) Mean (SD)	Years of Education Mean (SD)	Laterality Quotient Mean (SD)
Musicians	25.31 (5.92)	17.63 (2.68)	92.19 (12.42)
Non-musicians	23.31 (5.25)	16.81 (3.15)	87.87 (12.64)

Stimuli and Apparatus

Stimuli were circular white/black checkerboards with a diameter of 3° of visual angle that appeared for 100ms against a gray background. The stimuli had 17 checkerboard squares at the widest diameter of the circle. Stimuli were presented to the left visual field (LVF) and right visual field (RVF), with their centre 6° from a central fixation cross.

EEG was recorded continuously at a 1 kHz sampling rate (0.1–100 Hz bandpass) with a high-density 128-channel Ag/AgCl electrode net (Electrical Geodesics Inc., Eugene, OR, USA). Electrode impedances ranged from 30 to 50 k Ω . Data were acquired using a common reference electrode (Cz), positioned anatomically, and later re-referenced to the average.

Analysis

EEG was segmented into epochs 140ms pre-stimulus onset to 360ms post-stimulus onset, and those contaminated by eye movement (blink threshold set at 70 μ V detected by electrodes 128 (left) and 125 (right)) were discarded. The percentage of epochs remaining for musicians was 78.84 ($SD = 24.73$) for the LVF and 79.70 ($SD = 24.02$) for the RVF, and for non-musicians was 75.71 ($SD = 23.69$) for the LVF and 75.17($SD = 24.23$) for the RVF. Independent samples t -tests revealed no difference between the groups for either the LVF, $t(30) = 0.92$, $p = .72$, or the RVF $t(30) = 0.85$, $p = .60$. Data were re-filtered to 30 Hz lowpass offline and average evoked potentials were constructed for LVF and RVF conditions.

The N1 component of the evoked potential was defined as the greatest amplitude peak of the first negative wave occurring at least 140ms after stimulus presentation. N1 latencies were recorded for each participant from a cluster of six lateral occipital electrodes including 'O1' and 'O2' (standard 10-20 system), and averaged. The exact electrodes used for each hemisphere cluster are shown in Figure 13. Estimates of IHTT were calculated for individual participants by subtracting the latency of the contralateral N1 from the latency of the ipsilateral N1 for both LVF and RVF conditions.

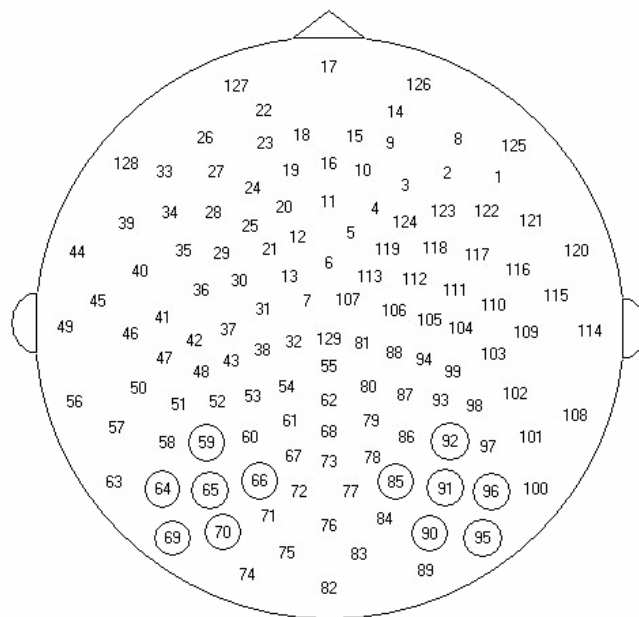


Figure 13: Diagram of electrode positions for Electrical Geodesic 128-electrode net. Circles indicate electrode clusters used for the right and left hemispheres.

Procedure

Participants were tested in a quiet, electrically shielded Faraday chamber and were seated 57cm from a 15-inch SVGA computer monitor (640 x 480 pixel resolution) on which stimuli were presented. A fixation cross persisted throughout the experiment and participants were instructed to maintain their gaze on the cross at all times during the stimulus blocks. A brief block of 17 practice trials preceded four experimental blocks in which either the left (LH) or right hand (RH) was used in a counterbalanced order,

either RH-LH-RH-LH, or LH-RH-LH-RH. Participants were instructed to respond to any visible stimulus by pressing the space bar. Stimuli were preceded by variable interstimulus intervals of 1550, 1750, or 1950 ms. Each block contained 130 trials which were randomised between 60 presentations to the LVF, 60 to the RVF, and 10 catch trials (no stimulus). Catch trials were inserted to ensure participants maintained their attention on the task. Participants were able to rest, if needed, at the beginning of each block where instruction screens showed which hand to use next.

Results

Interhemispheric transfer time

Effects for IHTT were analysed using a repeated-measures ANOVA with direction (right-to-left and left-to-right) as the within-subjects factor, and group (musicians and non-musicians) and sex (males and females) as between-subjects factors. Data were averaged across hands. For raw data see Appendix G.

The grand mean waveforms for N1 elicited to LVF and RVF stimuli are shown in Figure 14 for musicians and non-musicians. The ANOVA for IHTT did not reveal a significant main effect of group, $F(1,28) = 2.23$, $p = .15$, but a main effect of direction showed right-to-left transfer to be significantly faster than left-to-right transfer, $F(1,28) = 27.07$, $p < .001$. More importantly, there was an interaction between group and direction, $F(1,28) = 20.26$, $p < .001$. Post hoc pairwise comparisons showed faster right-to-left than left-to-right transfer for the non-musicians ($p < .001$) but this difference was not seen for the musicians ($p = .62$; see Figure 15). In addition, musicians showed significantly faster transfer in the left-to-right direction in comparison to non-musicians ($p = .001$), but not significantly slower transfer in the right-to-left direction in comparison to non-musicians ($p = .12$).

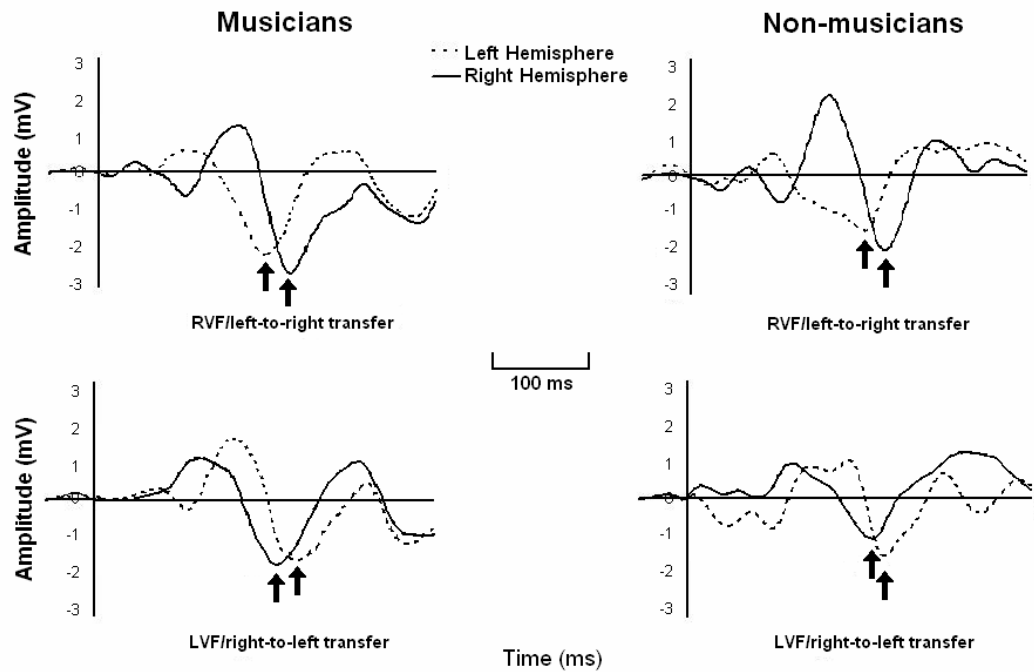


Figure 14: Grand mean waveforms averaged across hands in right and left hemisphere occipital electrode clusters for musicians and non-musicians recorded during stimulus presentation in the RVF and LVF.

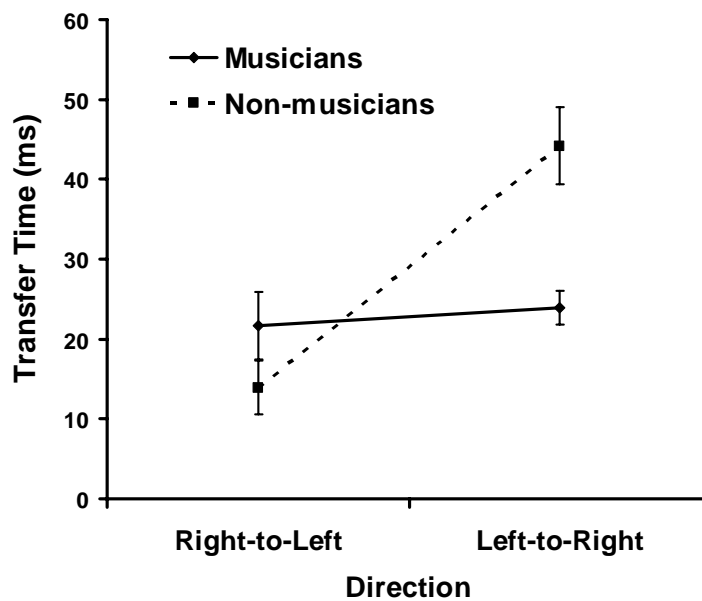


Figure 15: Mean IHTT for each direction averaged across hands for musicians and non-musicians. Error bars indicate standard error of the mean.

There was also a significant interaction between sex and direction, $F(1,28) = 5.46$, $p = .03$, indicating females had significantly faster left-to-right transfer compared to males ($p = .046$), but were not faster in the right-to-left direction ($p = .56$). Furthermore, while females did show significantly faster right-to-left than left-to-right transfer ($p = .052$), this effect was far more pronounced in males ($p < .001$). Figure 16 shows mean IHTT for both directions for males and females. There were no other main effects or interactions.

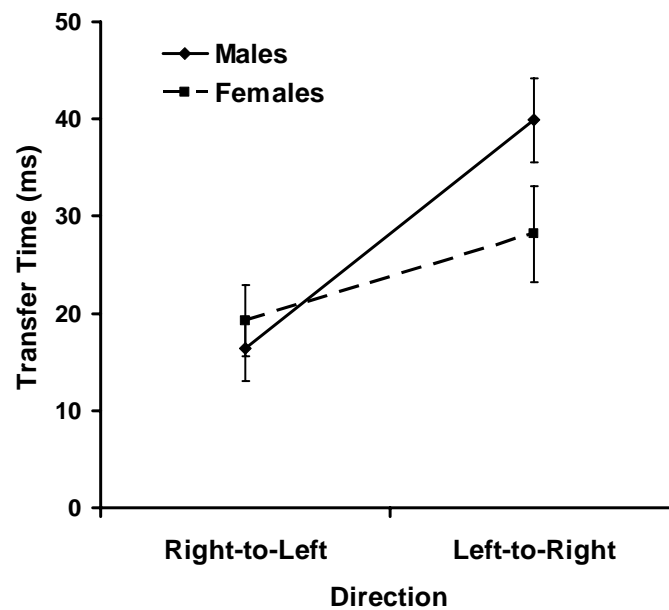


Figure 16: Mean IHTT for each direction averaged across hands for males and females. Error bars indicate standard error of the mean.

Absolute latency of the N1

N1 latency for the direct pathways only (i.e., contralateral visual fields and hemispheres) were evaluated by a repeated-measures ANOVA with hemisphere (left and right) as the within-subjects factor, and group and sex as between-subjects factors. Again, data were averaged across hands. For raw data see Appendix G.

The main effect of hemisphere was significant, $F(1,28) = 10.96$, $p = .003$, reflecting longer latency in the right hemisphere ($M = 187.53$, $SE = 3.80$) than in the left hemisphere ($M = 176.22$, $SE = 3.12$). While the main effect for group was not significant, $F(1,28) = 0.48$, $p = .49$, there was a hemisphere by group interaction, $F(1,28) = 20.26$, $p < .001$. Bonferroni pairwise comparisons revealed the latency to be significantly longer in the right than the left hemisphere in non-musicians ($p < .001$), but this difference was not significant in the musicians ($p = .60$; see Figure 17). Also, latency in the left hemisphere was significantly slower in musicians than in non-musicians ($p = .047$), but there was no difference between groups in the right hemisphere ($p = .553$). There were no other main effects of interactions.

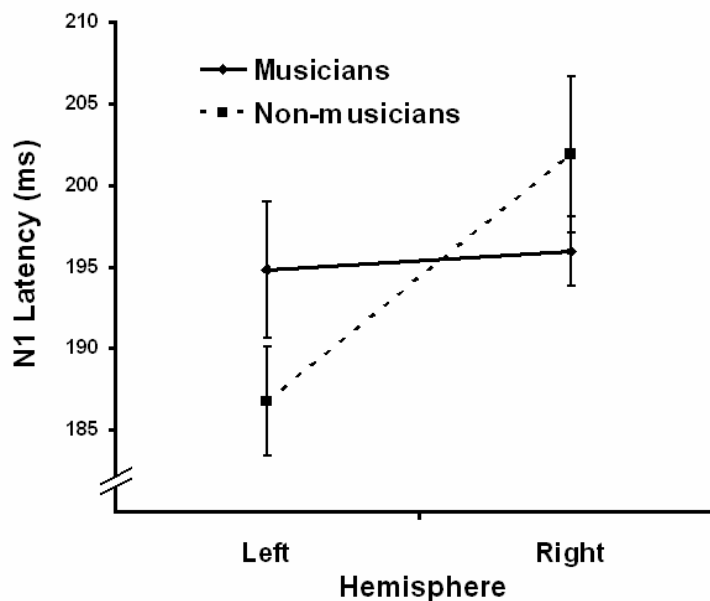


Figure 17: Mean absolute latency for direct pathways averaged across hands for each hemisphere for musicians and non-musicians. Error bars indicate standard error of the mean.

Discussion

Using the latencies of N1 responses to measure IHTT, it was found that musicians did not exhibit the usual directional asymmetry. As expected from previous studies (Barnett

& Corballis, 2005; Barnett, Corballis et al., 2005; Barnett & Kirk, 2005; Brown & Jeeves, 1993; Brown et al., 1994; Larson & Brown, 1997) the non-musicians showed faster IHTT from the right to the left hemisphere than from left-to-right. In contrast, the musicians showed no directional advantage, indicating the speed of transfer for visual information across the corpus callosum was more equilateral in this group. In addition, musicians were found to be faster than non-musicians for left-to-right transfer, but not for right-to-left transfer, suggesting musicians may have better developed neural architecture in the left hemisphere or better interhemispheric connectivity from the left hemisphere than non-musicians. As Figure 15 shows, the enhanced function of the left hemisphere in musicians may be at the expense of function in the right hemisphere, although the musician group was not significantly slower than the non-musician group in this direction.

The absolute latencies showed a similar trend. Visual information was received earlier by the left hemisphere relative to the right hemisphere in non-musicians, while in the musician group the latency between hemispheres did not differ. Additionally, in the left hemisphere absolute latency was faster in non-musicians than in musicians. Together, the data support the assertion that musicians have a greater degree of bilateral neural connectivity than non-musicians.

The data reported here show that non-musicians receive visual information most efficiently to the left hemisphere, but this information is then sluggishly transferred across the corpus callosum. In contrast, information is received later by the right hemisphere in non-musicians, but is then transferred quickly. The latency of the N1 component has been suggested to reflect visual processing for attended stimuli (Luck, 1995), and previous research has shown the N1 latency to lengthen when attentional demands are increased (Callaway & Halliday, 1982; Schwent et al., 1976). The longer latency in the right hemisphere of non-musicians may thus be explained by the right

hemisphere's dominant role in visuospatial attention (Fink et al., 2000; Heilman et al., 2004; Mattingley et al., 1994). In other words, a longer N1 latency in the right hemisphere of non-musicians may reflect an increased attentional capacity for LVF stimuli. Consistent with the current results, a shorter N1 latency in the left hemisphere than in the right hemisphere of healthy adults has been reported elsewhere (Brown et al., 1994), but N1 latency analysis for direct pathways is often overlooked in ERP studies of visual attention.

In musicians, visual information is received by both hemispheres with more equal proficiency than in non-musicians and also transferred in a more equal manner. This is consistent with behavioural evidence suggesting that visuospatial attention is represented more bilaterally in musicians than non-musicians (see Chapter 3). Here, it is proposed that the white matter changes seen in morphometric (Schlaug et al., 1995) and diffusion tensor imaging studies (Bengtsson et al., 2005) are associated with the more balanced capacity for attentional perception of visual stimuli and interhemispheric transfer in musicians. As most of the musicians in this sample (13/16) played more than one instrument it was not possible to classify them as particular instrumentalists, although nearly all (15/16) played a midline, bimanual (played in the centre of the body using both hands) instrument, such as the piano, recorder, clarinet, etc. It is possible that factors such as the cognitive demands of playing a bimanual instrument, and the need to transfer visual inputs from musical scores to bilateral motor outputs, produce equilateral neural connectivity and myelination in both hemispheres, and that this is advantageous for both speed and accuracy in musical performance. Thus, there now seems to be an association between early musical training, anatomical plasticity and functional adaptation in musicians. It would be interesting to investigate the IHTT in individuals such as video gamers, who have had intensive practice of other bimanual tasks during childhood, in order to determine whether this hypothesis can be extended to situations outside musical training.

It is intriguing to note that other studies investigating IHTT using EEG have also found a lack of IHTT asymmetry in schizophrenia, which has been attributed to callosal dysfunction (Endrass, Mohr, & Rockstroh, 2002) or lateralized hemispheric dysfunction (Barnett, Corballis et al., 2005). In comparison to control participants, who showed faster right-to-left IHTT, individuals with schizophrenia have shown more balanced transfer. The schizophrenia patients differ, however, from the musicians in showing longer N1 latencies (Barnett & Kirk, 2005; Barnett, Corballis et al., 2005), and slower RT, and more errors (Endrass et al., 2002). Interestingly, the relation between symmetry and myelination seems to be opposite in the two groups, with schizophrenia patients showing a lack of myelination (Hulshoff Pol et al., 2004; Kubicki et al., 2005) and musicians enhanced myelination (Bengtsson et al., 2005). Thus, there appears to be a connection between atypical myelin production and subsequent hemispheric equilaterality, regardless of whether myelination is decreased or increased relative to normal.

In addition to the finding that musicians were less lateralized than non-musicians for IHTT, this effect was also found for females in comparison to males, though to a lesser extent. In a comparable ERP study measuring N1 latency, less interhemispheric lateralization in females has been previously reported by Nowicka and Fersten (2001). They presented lateralized word stimuli to males and females and found strikingly similar results to this study in regard to sex. First, Nowicka and Fersten reported faster right-to-left than left-to-right transfer in males, but not in females. In the current study, while both sexes showed faster right-to-left transfer, the magnitude of difference was far less in females than in males. Second, females in the Nowicka and Fersten study had shorter transfer time in the left-to-right direction in comparison to males as they did in this study. Third, Nowicka and Fersten found no sex effects in their absolute latency analysis suggesting that the IHTT findings were not related to latency differences. This was also the case in the current study.

It is interesting to note that the pattern of findings for males and females was similar to the pattern of findings for musicians and non-musicians whereby the less lateralized group had faster left-to-right transfer in both cases. In contrast, the lateralization effect was similar in both IHTT and absolute latency for musicians versus non-musicians, whereby this was not the case for females versus males. This suggests there may be a more fundamental difference in hemispheric neural organization and callosal transfer between musicians and non-musicians than between males and females, and this would account for the more convincing statistical significance revealed for the group interaction compared with the sex interaction.

In conclusion, there was a lack of the normal asymmetry for interhemispheric transfer and latency of the N1 component for lateralized visual stimuli in musicians. It is suggested that this reflects a more bilateral neural constitution in the musician brain that may be the result of extended musical training in childhood when the reorganisation of neural connections is still abundant. It is proposed that bimanual training, inherent in learning an instrument, facilitates an unusual process of extra myelination that results in more balanced connections between hemispheres than that normally found in those without musical training. More equal efficiency of transfer across the corpus callosum would be advantageous to musicians because of the requirement for speeded bilateral motor outputs in response to musical score reading. More generally, the findings suggest that the brains of musicians differ from those of non-musicians in ways other than those related to music itself.

Chapter 5: Behavioural interhemispheric transfer time in musicians: The Poffenberger paradigm

Introduction

The transfer of information from one hemisphere to the other has traditionally been measured by a simple reaction time (RT) task in which stimuli are presented to the left (LVF) and right visual fields (RVF) and responses to the presence of these stimuli are made by the right (RH) and left hands (LH) (Poffenberger, 1912). In this way four combinations of stimulus-response types transpire. RH-LVF and LH-RVF are termed crossed conditions because the hemisphere receiving the stimulus is opposite the hemisphere initiating the motor response and this information must first be transferred across the corpus callosum before the motor output can be initialized. RH-RVF and LH-LVF are termed uncrossed conditions because the hemisphere receiving the stimulus is the same hemisphere responsible for initiating the motor response and does not require interhemispheric transmission (Poffenberger, 1912). The crossed-uncrossed difference (CUD) is, therefore, a measure of interhemispheric transfer time (IHTT) and is calculated by subtracting the mean RT for uncrossed conditions from the mean RT for crossed conditions (see Figure 18).

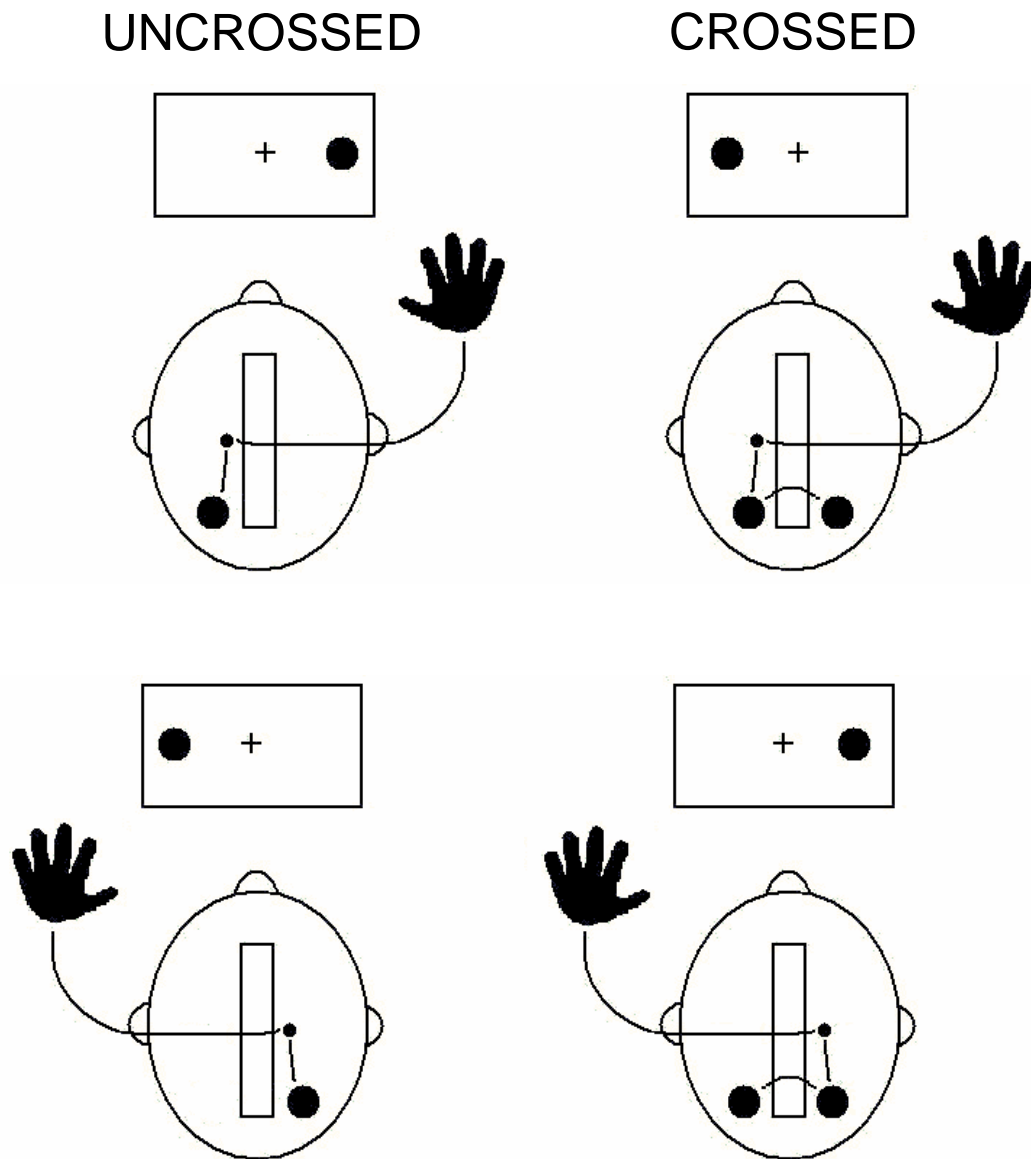


Figure 18: Diagram depicting Poffenberger's theory of interhemispheric transfer time as measured by the crossed-uncrossed difference. Left panel represents uncrossed conditions. Right panel represents crossed conditions.

Empirical evidence from three different groups of participants supports the IHTT theory of the CUD. First, neurologically normal participants generally take between 2 and 6 ms longer to respond to the crossed, compared to the uncrossed, conditions (Marzi, Bisiacchi, & Nicoletti, 1991). Second, individuals diagnosed with callosal agenesis have elongated CUDs of between 12 and 50 ms (Aglioti, Berlucchi, Pallini, Rossi, &

Tassinari, 1993; Clarke & Zaidel, 1989; Corballis, 1998; Corballis, Hamm, Barnett, & Corballis, 2002; Milner, Jeeves, Silver, Lines, & Wilson, 1985, Roser & Corballis, 2002; although see Barr, Hamm, Kirk, & Corballis, 2005 for shorter CUDs in acallosal individuals). Third, the CUD is increased to approximately 30–90 ms for callosotomized patients (Aglioti et al., 1993; Clarke & Zaidel, 1989; Corballis, 1998; Corballis et al., 2002; Marzi et al., 1999; Roser & Corballis, 2002; Tassinari, Aglioti, Pallini, Berlucchi, & Rossi, 1994). It may be problematic to generalise findings from patients to the normal population, however, due to the probability that considerable neural changes may have already taken place (Martuzzi et al., 2006). There is functional evidence to suggest callosal patients may differ neurally to healthy controls (Marzi, et al., 1999).

In addition to the normal and patient population findings, three studies have found activation in the corpus callosum associated with crossed conditions (Tettamanti et al., 2002; Omura et al., 2004; Weber et al., 2005), and multiple studies have found greater RTs for crossed than uncrossed stimuli (Badzakova-Trajkov, Hamm, & Waldie, 2005; Corballis, 2002; Fendrich, Hutsler, & Gazzaniga, 2004; Iacoboni & Zaidel, 1995, 2000; Marzi et al., 1991; Roser & Corballis, 2002; Schulte, Sullivan, Muller-Oehring, Adalsteinsson, & Pfefferbaum, 2005; Thut et al., 1999). Furthermore, when participants perform the Poffenberger task with their hands crossed the CUD is preserved in its correct anatomical form (i.e., the anatomically uncrossed stimulus-response pathway is faster) (Anzola, Bertoloni, Buchtel, & Rizzolatti, 1977).

Another aspect supporting the IHTT theory of the mechanism underlying the CUD is that in the normal population the CUD for the right hand is smaller (although not necessarily significantly so) than the CUD for the left hand (Badzakova-Trajkov et al., 2005; Fendrich et al., 2004; Iacoboni & Zaidel, 1995; Martuzzi et al., 2006; Marzi et al., 1991). It has been suggested that this is because IHTT from the right to the left hemisphere is faster than IHTT from left-to-right (see Figure 18). There is debate as to

whether the CUD represents true callosal transfer due to the inherent difficulty in interpreting the CUD, which is always confounded by response hand and hemispheric differences in processing time (Corballis et al., 2002). Participants, who are right-handed, could be more skilled at using their right hand for responses, or, more importantly, the hemispheres could differ in their speed of registry. For example, if the right hemisphere is faster to register incoming stimuli than the left hemisphere, then right-handed responses will be faster for this reason, not because of faster interhemispheric transfer speed (M. Corballis, personal communication, January 15, 2007).

Empirical lines of evidence also question the credibility of the callosal relay hypothesis. It is not uncommon for CUDs to fall within impossible timeframes for the conduction of myelinated axons, i.e., less than 3 ms (Aboitiz, Scheibel, Fisher, & Zaidel, 1992; Anzola et al., 1977; Badzakova-Trajkov et al., 2005; Barnett, Kirk, & Corballis, 2005; Clarke & Zaidel, 1989; Corballis, 2002; Iacoboni & Zaidel, 2000; Lines, Rugg, & Milner as cited in Marzi et al., 1991, p. 1165), or for crossed RTs to be faster than uncrossed RTs, resulting in theoretically impossible negative CUDs (Barnett, Corballis, & Kirk, 2005; Barnett, Kirk et al., 2005; Fendrich et al., 2004). Iacoboni and Zaidel (2000) investigated the stability of the CUD in three individuals across 15 sessions and reported between three and six negative CUDs in each participant, implying the CUD is naturally variable and does not decrease with practice.

There is also wide debate surrounding the mechanism responsible for the transfer of information across the corpus callosum and whether this is motoric or visual in nature. Conflicting results in this area have suggested the transfer occurs at the motor level (Basso et al., 2006; Iacoboni & Zaidel, 2003; Tettmanti et al., 2002; Thut et al., 1999), at the visual level (Brown, Larson, & Jeeves, 1994; Murray, Foxe, Higgins, Javitt, & Schroeder, 2001), and via a combination of both (Saron, Foxe, Schroeder, & Vaughan,

2003; Saron, Foxe, Simpson, & Vaughan, 2003). One predominant model asserts fast RTs are produced by motor transfer and slow RTs are produced by visual transfer (Saron, Foxe, Schroeder et al., 2003; Saron, Foxe, Simpson et al., 2003). Support for this view was provided in a case study where the CUD was slowed after callosal motor fibres were removed by callosotomy, suggesting the CUD may occur at both posterior (visual) and anterior (motoric) regions of the corpus callosum, but that posterior visuo-visuo transfer is slower than motoric transfer (Iacoboni, Fried, & Zaidel, 1994). A recent imaging study has suggested transfer occurs at the visual level because bilateral activity occurred in the visual cortices during crossed conditions, whereas only unilateral activation occurred in the motor cortex of the contralateral hand (Martuzzi et al., 2006).

As well as a measure of the CUD, and possibly IHTT, the Poffenberger paradigm is also a task of simple RT to visual stimuli and may be used to investigate other aspects of cognition. For example, because perceptuomotor ability is tested it might be expected that musicians would have an advantage because of their extensive motor, and visuomotor, training. Brochard, Dufour and Despres (2004) investigated this possibility by contrasting the responses of musicians and non-musicians on a simple RT task and a choice RT task. The simple RT task involved responding when small white circles were presented on a screen, whereas on the choice RT task participants responded by pressing the right arrow when red circles were presented and the left arrow when green stimuli were presented. They found that musicians were faster in the red/green choice RT task, but not different to non-musicians in the simple RT task. Thus, it was concluded that musicians are only advantaged when there is a requirement for visual to motor decision-making, and not when the task is purely sensorimotor in nature.

The Poffenberger paradigm, however, also involves the presentation of lateralized stimuli, so it can also be applied as a task of lateralized attention, similar to the vertical condition of the visual discrimination task presented in Study 4 of Chapter 3. Recall that the musician group had faster response times and made fewer errors to stimuli presented to the right of the line in comparison to the non-musician group. Musicians were also shown to favour the right side of space in Study 3 of Chapter 3, in which they bisected lines to the right of centre as opposed to the left, as did non-musicians. Both studies demonstrated a more balanced attentional capacity in musicians, with a right-sided bias, and the Poffenberger task provides another method in which to explore this. It could, therefore, be predicted that musicians may have faster RTs and/or greater accuracy to RVF stimuli even if no overall advantage in comparison to non-musicians is evident due to the simplicity of the task. Non-musicians might be predicted to show a bias toward LVF stimuli due to the natural bias toward the left side of space, called right pseudoneglect. This effect in non-musicians was also shown in the studies presented in Chapter 3.

The purpose of this study was to investigate interhemispheric transfer time, reaction time, and lateralized attention in musicians compared with non-musicians, using the Poffenberger paradigm. Three predictions were made. First, it was expected that responses to uncrossed conditions would be faster than responses to crossed conditions overall, in accordance with the IHTT theory of the CUD. Second, non-musicians were expected to show faster RTs and greater accuracy to LVF stimuli because of normal right pseudoneglect. Musicians, in contrast, were expected to show a more bilateral pattern for RT and accuracy than non-musicians, and possibly favour the RVF stimuli as they did in the studies conducted in Chapter 3, even if overall RTs did not differ between groups.

Method

Participants

The participants in this analysis were identical to those in Chapter 4. Briefly, two groups of adult musicians ($n = 16$, 8 female) and adult non-musicians ($n = 16$, 8 female) participated in this experiment. Members of the musician group had received at least eight years of music lessons ($M = 13.44$ years, $SD = 4.07$) and could read music (see Appendix L). Member of the non-musician group had less than 2 years of formal music training and could not read music. The groups did not differ significantly on sex, $\chi^2 = 0$, $p > .99$, age, $t(30) = 1.01$, $p = .32$, years of education, $t(30) = 0.79$, $p = .44$, or handedness, $t(30) = 0.98$, $p = .34$ (see Table 12). General exclusion criteria included epilepsy, a laterality quotient less than +60, and formal music training for more than 2 years but less than 8 years.

Table 12: Demographic characteristics of musician and non-musician group participants for Study 6.

	Age (years) Mean (SD)	Years of Education Mean (SD)	Laterality Quotient Mean (SD)
Musicians	25.31 (5.92)	17.63 (2.68)	92.19 (12.42)
Non-musicians	23.31 (5.25)	16.81 (3.15)	87.87 (12.64)

Stimuli and Procedure

The stimuli and procedure were identical to that in Chapter 4. Briefly, stimuli were circular white/black checkerboards that appeared for 100ms against a gray background and were presented to the left visual field (LVF) and right visual field (RVF). Participants were tested in a quiet room and were seated 57 cm from a computer monitor. A fixation cross persisted throughout the experiment and participants were instructed to maintain their gaze on the cross at all times and respond to any visible stimulus by pressing the space bar. A brief block of 17 practice trials preceded four experimental blocks containing 130 trials (60 LVF, 60 RVF and 10 catch trials, all

randomised). The left (LH) and right (RH) hands were used in a counterbalanced order across blocks.

Analysis

Reaction time (RT) data were collected at a resolution of 1 ms. Correct responses were keypresses occurring after the presentation of a stimulus. Accuracy was determined by the number of correct responses divided by the total number of stimuli, expressed as a percentage. It is important to note that accuracy in this task is akin to a measure of vigilance as opposed to a discriminatory response that may be correct or not. Means for correct responses were obtained for each hand and in each visual field. The crossed-uncrossed difference (CUD) was calculated by subtracting the means of the two crossed conditions (LH-RVF, RH-LVF) from the means for the two uncrossed conditions (LH-LVF, RH-RVF). Statistical effects for accuracy and RTs were evaluated by separate split-plot ANOVAs with hand (LH and RH) and visual field (LVF and RVF) as within-subjects factors, and group (musicians and non-musicians) as the between-subjects factor.

Results

Reaction time

For raw data see Appendix H. It was expected that the IHTT theory of the CUD would be upheld in this experiment, and specifically, that responses to uncrossed conditions would be faster than responses to crossed conditions overall. This was the case. The ANOVA for the RT data (see Table 13) revealed RTs to stimuli presented at the ipsilateral (uncrossed condition) visual field ($M = 321.26$, $SD = 8.71$) were faster than RTs to stimuli presented at the contralateral (crossed condition) visual field ($M = 324.39$, $SD = 9.12$), as indicated by the significant interaction between hand and visual field, $F(1,30) = 16.04$, $p < .001$. There were no differences, however, between the two

visual field conditions, $F(1,30) = 1.38$, $p = .25$, or response hands, $F(1,30) = 1.13$, $p = .30$, and there were no significant interactions between these variables and group.

Table 13: Mean RTs (SE) for each hand to stimuli presented in the LVF and RVF for each group.

	Left Hand		Right Hand	
	LVF (uncrossed)	RVF (crossed)	LVF (crossed)	RVF (uncrossed)
Musicians	323.44 (37.98)	321.26 (39.08)	325.36 (45.22)	320.33 (41.60)
Non-musicians	320.79 (60.47)	326.41 (66.63)	319.91 (56.81)	313.95 (58.80)

There was, however, a significant three-way interaction involving hand, visual field and group, $F(1,30) = 5.86$, $p = .02$, indicating the groups behaved differently with respect to the hand by visual field interaction, or CUD (see Figure 19). The overall CUD for musicians was 1.43 and for non-musicians was 5.79. The groups were analysed separately and results revealed that the non-musician CUD was highly significant ($F(1,15) = 27.63$, $p < .001$), but the musician CUD was not ($F(1,15) = 1.00$, $p = .33$). The musician group ANOVA also revealed a significant main effect of visual field ($F(1,15) = 4.58$, $p < .05$), indicating faster responses for stimuli in the right visual field.

Non-musicians, on the other hand, showed a RT pattern consistent with the expected hand by visual field interaction, or CUD, whereby responses with the right hand were faster to RVF stimuli (uncrossed condition) than to LVF stimuli (crossed condition: $p = .019$), and responses with the left hand were faster, although marginally, to LVF stimuli (uncrossed condition) than to RVF stimuli (crossed condition: $p = .053$). This was not found for the musician data. Finally, the non-musician group responded faster with the right hand to RVF stimuli than with the left hand to RVF stimuli ($p = .006$; see Figure 19).

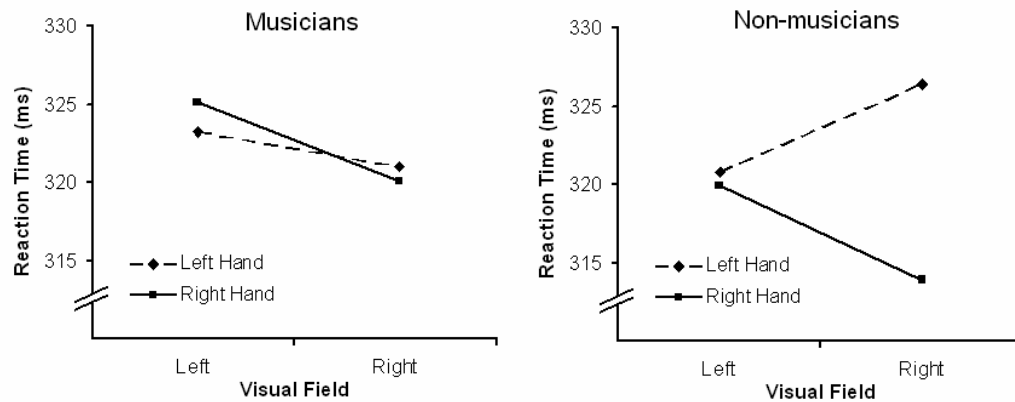


Figure 19: Mean reaction time (ms) for each visual field for the left and right hands. Left panel represents data for the musician group. Right panel represents data for the non-musician group.

Accuracy

For raw data see Appendix H. As expected, accuracy (responding to stimuli when presented) was high with participants performing on average at greater than 98% for all conditions (LH-LVF, LH-RVF, RH-LVF, RH-RVF). The overall mean accuracy for non-musicians ($M = 99.0$, $SE = 0.004$) was less than for musicians ($M = 99.7$, $SE = 0.004$), but this was not significant, $F(1,30) = 1.50$, $p = .23$. Accuracy was not significantly different between hands, $F(1,30) = 0.01$, $p = .92$, or visual fields, $F(1,30) = 1.29$, $p = .26$, and there were no significant two- or three-way interactions.

The number of catch trials responded to by each participant over all conditions was also analysed by an independent-samples t -test. Non-musicians ($M = 1.13$, $SD = 1.23$) responded to significantly more catch trials than musicians ($M = 0.38$, $SD = 0.50$), $t(30) = 2.22$, $p = .034$, suggesting they were either less able to inhibit responses to anticipated stimulus presentations, or that they were more susceptible to lapses in concentration.

Discussion

In this experiment participants were required to respond via keypress to the presentation of stimuli flashed on a computer screen. Checkerboard circles were presented to the left and right visual fields, and the results can be summarised into three main findings.

First, in keeping with the CUD literature initiated by Poffenberger (1912) uncrossed responses were faster than crossed responses, however, this was not significant for the musician group. This illustrates the visual field confound when attempting to use the CUD as a measure of IHTT as in this group, regardless of hand or condition, responses were faster to stimuli presented in the RVF. The CUD is thought to represent the IHTT across the corpus callosum when stimuli are received in the hemisphere contralateral to the hemisphere initiating the required motor response. Thus, it follows that crossed responses should always be retarded compared to uncrossed responses, which do not traverse the callosum. This was not the case.

The second main finding was that the musician group did not show faster overall RTs compared to the non-musician group. This is consistent with the result of the second experiment by Brochard et al. (2004) in which musicians were found not to differ from non-musicians on a task of simple RT. There was, however, a three-way interaction between group, hand and visual field which revealed that musicians responded faster to RVF stimuli than to LVF stimuli with both hands, regardless of condition, whilst non-musicians responded faster in uncrossed conditions with both hands, regardless of visual field. The tendency for musicians to favour the right side of space is consistent with the studies presented in Chapter 3.

Finally, non-musicians responded to catch trials more often than musicians, suggesting they were either less vigilant or less able to inhibit responses to anticipated stimulus

appearances. Non-musicians also missed more target stimuli than musicians, although differences in accuracy failed to reach significance. Taken together these findings suggest musicians may be more vigilant than non-musicians. This could be due to a greater propensity in the musician group for prolonged and intense concentration, which is mandatory for the practice and performance of music. Brochard et al. (2004) commented that their result could be explained by a greater attentional capacity in their musicians, and that musicians may have larger visuospatial attentional fields than non-musicians. Both these propositions are supported by the results in this study, but there is currently no literature investigating specifically the vigilance, concentration, or attention span of musicians in comparison to non-musicians.

In summary, on a simple lateralized stimulus-response task, non-musicians performed in a pattern consistent with the IHTT theory of the CUD but the musician data was biased by their tendency respond faster to RVF stimuli. Consistent with previous work by Brochard et al. (2004) the groups did not differ in overall RT to the stimuli, supporting the hypothesis that musicians are only advantaged on tasks involving discrimination in the visuospatial domain. Musicians displayed a slight bias toward the right hemifield for reaction time, which was not apparent in the non-musician group. The musician group were also less likely than non-musicians to respond to catch stimuli, which, when taken together with fewer missed stimuli, may suggest they were more vigilant than the non-musician group. Further research would be required to substantiate this claim.

Chapter 6: General discussion

Enhanced cognitive abilities in musicians

A strong assertion in the current literature is that musical training positively affects cognitive abilities beyond the music domain. The effect of short-term music training/exposure was popularized by Rauscher, Shaw and Ky (1993) with the publication of their subsequently controversial 'Mozart effect' paper. The Mozart effect refers to enhanced performance of visuospatial tasks after listening to Mozart's music for a short period of time (Rauscher et al., 1993). The substantial body of literature that now exists on the Mozart effect, however, points to the conclusion that the effect is due to states of arousal rather than an effect of music per se (Husain, Thompson, & Schellenberg, 2002; Nantais & Schellenberg, 1999). The longer-term effect of music instruction from an early age on non-musical abilities has not been as easily discounted as many studies indicate enhanced performance on a variety of cognitive skills, including IQ in general, by children receiving music lessons in comparison to those who are not (Bilhartz, Bruhn, & Olson, 2000; Cheek & Smith, 1999; Gardiner, Fox, Knowles, & Jeffrey, 1996; Graziano, Peterson, & Shaw, 1999; Gromko, 2005; Nering, 2002; Schellenberg, 2001, 2004, 2006). Many of these studies should be viewed with caution, however, as alternative explanations for the heightened performance in children receiving music lessons were often not able to be ruled out, such as the effects of attention by an adult or elevation of mood by music. In contrast, very few cognitive-behavioural studies investigating abilities in adult musicians have been conducted. One such study by Brochard, Dufour and Despres (2004) concluded musicians have better visuospatial ability than non-musicians, and Study 1 reported in this thesis aimed to replicate and extend that research.

In Chapter 2 two studies were presented that focussed on the cognitive abilities of musicians. In both studies verbal as well as manual responses were required for

different tasks in an attempt to eliminate any motor advantage the musicians may have had over the non-musicians. In the first study the aim was to test the hypothesis that there is a relationship between formal music training and visuospatial abilities. A computer-generated visual discrimination task that required manual responses and a visuospatial search task that required verbal responses were administered to 16 musicians and 16 matched non-musicians. Musicians performed more quickly and more accurately than non-musicians in both tasks. This suggested that musicians may have enhanced visuospatial processing ability, as previously asserted in the literature (Bilhartz et al., 2000; Brochard et al., 2004; Schellenberg, 2001, 2004, 2006). As both tasks required speeded responses, however, one possible explanation was that the advantage may lie in faster overall processing speed in musicians, not restricted to visuospatial tasks. This was addressed in Study 2.

The aim of the second study reported in Chapter 2 was to address this possibility by investigating processing speed in musicians. Three tasks of cognitive processing speed (Symbol-Digit Modalities Test, Symbol Search task, and Colour Naming and Word Reading Test) that varied in verbal and manual responses were administered to a sample of 20 musicians and 20 matched non-musicians. On each of the three tasks musicians completed more items than non-musicians, but there were no differences in accuracy. It was concluded that musicians do indeed have a faster speed of cognitive processing than matched non-musicians, although further research would be needed to determine whether they have better visuospatial abilities when their faster processing speed was taken into consideration. Although two of the three processing speed tasks used in this study were visual in nature (Symbol-Digit Modalities Test and Symbol Search task), and thus, did not eliminate the visuospatial component, the finding was still apparent in the third task, which although visual, did not tax visuospatial processes (Colour Naming and Word Reading Test). The studies do, however, raise a contentious issue and provide an opening for further research to be conducted.

Generally, faster processing speed in musicians may have implications for those cognitive-behavioural investigations that draw conclusions about cognitive abilities in musicians (or children receiving music lessons) where speed is a confounding factor in the testing process. It is possible that musicians are advantaged in many tests of various cognitive abilities simply because they are more efficient at processing elements of the task at hand. It follows that untimed tasks, where only accuracy is measured, would be a more accurate way to test specific abilities between musicians and non-musicians, although one potential problem is finding tasks that are difficult or sensitive enough to avoid ceiling effects.

Plasticity and musical training

Regardless of the nature of cognitive enhancement in musicians, it is nonetheless undeniable that cognitive enhancement exists. A major issue in research involving musicians and non-musicians is that musicians are self-selected, giving rise to two alternative hypotheses as to why they differ on neural and cognitive attributes. First, children with natural predispositions to cognitive function and structure suitable to the successful progression in musical activity may be likely to become musicians as adults. For example, in one study, where five sets of monozygotic twins reared apart were tested on the Wing Test of Musical Ability and Appreciation, scores within twin sets were remarkably similar even when musical training differed vastly within the pairs (Shuter, 1969).

Second, it is also possible that musical training early in childhood could induce neural changes that lead to the cognitive function and anatomical structure seen in adult musicians. At least one study that aims to distinguish between these two possibilities is currently underway (Norton et al., 2005). To date no cognitive or structural differences have been found between children intending to take music lessons and those not intending to, lending weight to the latter hypothesis that differences between musicians

and non-musicians are training-induced. This is also supported by more general evidence that environmental stimulation can affect the development of neural organisation. Rats reared in socially and cognitively complex environments showed increased myelination of the corpus callosum due to changes in axon number and size (Juraska & Kopcik, 1988) and increased number of hippocampal cells (Kempermann, Kuhn, & Gage, 1998) compared with rats reared in isolation. Additionally, Pascual-Leone et al. (1995) have shown increased finger cortical representation when finger exercises were maintained, and Karni and colleagues (Karni et al., 1995, Karni et al., 1998) have shown enhanced activation of the primary motor cortex following daily practice of a finger opposition task. These results strongly suggest that specific neural changes occur as a result of prolonged activity targeting particular muscle groups, and lend weight to the argument that extended musical instrument training during childhood could produce changes at the neural level.

There have also been several reports of anatomical differences between musicians and non-musicians suggesting a causative link between extensive musical training and neural changes. Elbert, Pantev, Wienbruch, Rockstroh and Taub (1995) found greater representations for the fingers of the left hand in the motor cortex of string players, suggesting the extended use of these fingers had served to enlarge the cortical area devoted to their use. The strength of the effect was also negatively correlated with the age at which training had begun demonstrating those who had begun training the earliest showed the greatest enlargement. Using magnetic resonance imaging Schlaug, Jäncke, Huang, Staiger and Steinmetz (1995) found the anterior region of the corpus callosum to be larger in musicians than in non-musicians, and larger in those musicians who began training before age 7 than in those who began after this age. Furthermore, Bengtsson et al. (2005) found more heavily myelinated white matter tracts (as measured by fractional anisotropy) in professional pianists than in non-musicians, and this was positively correlated with the number of hours spent practicing

in childhood, adolescence, and adulthood. Interestingly, although the actual number of hours spent practicing in childhood was less than in adolescence or adulthood, the greatest number of brain regions showing increased fractional anisotropy was correlated with childhood practising. This suggests the degree of myelination is most malleable in childhood and decreases with age. These studies indicate an association between the amount of training and the amount of structural change in the brain, and demonstrate that training in early childhood is developmentally disproportionate than training in later years. However, although these studies imply that neural plasticity occurs as a result of musical training, only true experimental designs (those in which participants are randomly assigned to groups) can provide greater certainty concerning the direction of causation.

Visuospatial attention and lateralization

Chapter 3 focussed on visuospatial attention in musicians. It has previously been demonstrated that visuospatial processing is a right-hemisphere-dominant task (Fink et al., 2000; Heilman, Jeong, & Finney, 2004), causing normal control participants to err slightly to the left when bisecting lines (Bradshaw, Nettleton, Wilson, & Bradshaw, 1987; Brodie & Pettigrew, 1996; Hausmann, Ergun, Yazgan, & Güntürkün, 2002; Hausmann, Waldie, Allison, & Corballis, 2003; Hausmann, Waldie, & Corballis, 2003). In Study 3 the line-bisection task was administered to 20 musicians and 20 matched non-musicians who performed the task with their right and left hands. Non-musicians bisected lines to the left of centre with both hands, consistent with previous evidence. In contrast, musicians bisected lines to right of centre with both hands. They also bisected lines closer to the true centre than the non-musicians did, and had a smaller intermanual difference than non-musicians. Together, the results suggested that musicians have more balanced visuospatial attention than non-musicians.

The unexpected lateralization for visuospatial attention in musicians found in Study 3 prompted a re-analysis, reported in Study 4, of the vertical-line condition of the visual discrimination task administered in Study 1. In this condition dots were presented to the right or left of a flashed vertical line and participants were required to decide on which side the dots had appeared. Non-musicians responded more quickly to left-sided dots than to right-sided dots, whereas musicians responded more quickly to right-sided dots than to left-sided dots. Musicians also responded more quickly to right-sided dots in comparison to non-musicians, and were more accurate compared with non-musicians to dots presented to the right of the line.

The results of Studies 3 and 4 both showed different patterns of behaviour in musicians and non-musicians, with non-musicians showing a bias to the left side of space and musicians showing bilateral performance that was slightly right-biased. Overall, the pattern of findings for the non-musician group indicated right pseudoneglect, implying right hemispheric dominance for visuospatial attention and perception. First, they bisected lines significantly to the left of true centre with both hands. Second, they were faster to respond to dots appearing to the left of the line in the vertical discrimination task. Finally, they made more errors of judgment when stimuli appeared to the right of the line, judging these to have appeared to the left of the line. The musician group results revealed a right-biased tendency that was weaker than the non-musicians' left-biased tendency. For example, musicians bisected lines to the right of true centre with both hands, yet this was only different from zero with the right hand and the magnitude was far less than that seen in the non-musician group (see Figure 9, Chapter 3). Similarly, in the vertical discrimination task musicians tended to respond faster to right-sided dots than to left-sided dots, but not significantly so. Accuracy data from this task revealed musicians were biased in the same leftward direction as non-musicians, but had a more bilateral distribution between the left and right sides than the non-musicians. These results in concert suggest musicians have more balanced, or

bilateral, visuospatial attention in comparison to non-musicians, and do not necessarily show an opposite laterality *per se*.

The data reported in Chapter 3 indicates bilateral awareness and attention for visuospatial stimuli in musicians. This could be associated with the cognitive demands of playing a bimanual midline instrument since attention is required to both sides of the body. The four participant samples used in the studies in this project consisted of musicians with diverse instrument backgrounds. Somewhat surprisingly, it was rare for a musician participant to play only one instrument. In each of the musician samples between 80 and 94 per cent played more than one instrument and between 56 and 75 per cent played more than two instruments (see Appendices I-L). For this reason analyses were not run for different types of instrumentalists, such as pianists or violinists, because so few participants played solely these instruments. The samples are, however, reasonably homogeneous because nearly all musicians played at least one bimanual midline instrument (between 88 and 95 per cent).

Following from the findings presented in Chapter 3, Study 5 (presented in Chapter 4) aimed to further investigate the visuospatial laterality of musicians versus non-musicians by testing the interhemispheric transfer of visual information across the corpus callosum using the electrophysiological measure, the N1. Interhemispheric transfer time (IHTT) was calculated by subtracting the N1 latencies of contralateral (direct pathway) stimuli from the N1 latencies of ipsilateral (callosal pathway) stimuli. Sixteen musicians (8 females) and 16 matched non-musicians (8 female) responded to stimuli presented to the left and right visual fields while 128-channel EEG was recorded. Non-musicians showed faster IHTT in the right-to-left direction than in the left-to-right direction consistent with earlier research (Barnett & Corballis, 2005; Barnett, Corballis, & Kirk, 2005; Barnett & Kirk, 2005; Brown & Jeeves, 1993; Brown, Larson, & Jeeves, 1994; Larson & Brown, 1997), and indicating right-hemispheric

dominance for visual transfer. In contrast, the musician group showed no directional difference between hemispheres in IHTT. This more symmetrical pattern was also reflected in the absolute N1 latencies in each hemisphere. Musicians showed no difference in latency between the two hemispheres, whereby non-musicians had a shorter latency in the left hemisphere compared to the right, indicating a greater attentional load in the right hemisphere. These results suggested that musicians have more bilateral neural connectivity and a more balanced attentional load than non-musicians, reflected in an unusual lack of asymmetry.

Myelination in musicians

The results of Study 5 were consistent with those of the behavioural line bisection and vertical discrimination tasks. As predicted, the musicians showed no asymmetry for transfer speed across the callosum, suggesting the presence of more balanced white matter architecture, with equally efficient processing from the right hemisphere as from the left hemisphere. The absolute latency data also concurred with this hypothesis revealing musicians to have equal rates of information conductance to both hemispheres. It is proposed here that musical training elicits a process of superfluous myelination that is bilaterally distributed. This process may be initiated by the complex use of bimanual motor cortical regions involved in playing an instrument, as well as the high demand on general cognitive ability required for complex and sustained visual (notation reading), auditory and sensori-motor integration. Playing and reading music has been found to incorporate numerous regions of the brain including the primary sensory and motor regions, the planum temporale, Broca's area, parts of the cerebellum and basal ganglia, frontal regions and bilateral parietal lobes. Efficient interhemispheric communication is thus paramount for the successful execution of musical performance. This, in conjunction with intense, daily practice involving such a diffuse area of the brain, is hypothesized to lead to more equilateral myelin development.

Several lines of evidence support the speculation that musicians may have increased myelin development. First, Bengtsson et al. (2005) and Schmithorst and Wilke (2002) reported increased fractional anisotropy (FA) of the main white fibre tracts in musicians compared with non-musicians. Increased FA is indicative of greater myelin mass and increased parallel organisation of white matter tracts. Bengtsson et al.'s and Schmithorst and Wilke's findings are compatible with that of Schlaug et al. (1995), who reported larger callosa in musicians. Hence, there is morphometric and diffusion tensor imaging evidence to suggest greater white matter mass in musicians, and in particular, across the corpus callosum, which is integral in the interhemispheric transfer process assessed in Study 5. Second, the musician group in Study 5 showed faster left-to-right IHTT compared with non-musicians, but not slower right-to-left IHTT compared with non-musicians. This suggests that the left hemisphere in musicians may have been beneficially developed but not at the expense of right hemispheric development. Third, increased myelination in musicians may account for their increased speed of cognitive processing (Study 2) and generally enhanced reaction time (RT) and accuracy performance in visuospatial tasks in comparison to non-musicians (Study 1). This is supported by research in patients with schizophrenia who show decreased RT and accuracy which is associated with decreased development of myelin (Barnett, Corballis et al., 2005; Barnett & Kirk, 2005; Endrass, Mohr, & Rockstroh, 2002). Furthermore, there is a relationship between decreased cognitive ability and decreased myelin (O'Sullivan et al., 2001). Fourth, the production of myelin is greatest in the first decade of life (Giedd, 1996; Pujol, Vendrell, Junqué, Martí-Vilalta, & Capdevila, 1993) when children are generally beginning their music training. Plasticity during this period is at its greatest and music practice at this stage has the most influence on white-matter architecture (Bengtsson et al., 2005). Furthermore, many studies investigating white and gray matter differences between musicians and non-musicians have correlated the measure used to the age at which music training commenced (Amunts et al., 1997;

Hutchinson, Lee, Gaab, & Schlaug, 2003; Pantev, Engelien, Candia, & Elbert, 2001; Schlaug et al., 1995; Sluming et al., 2002).

The four lines of evidence discussed above do not rule out the possibility that children advancing in music are genetically predisposed to greater myelin development and possess the functional and structural characteristics necessary for musical performance. The evidence discussed here also lacks direct scientific proof for the myelination hypothesis raised. An investigation into the progression of randomly assigned children to musical and non-musical activities and their myelin development over many years, correlated to their visuospatial laterality, would be needed in order to provide critical data as to the direction of causality. Another possible investigation addressing this issue would involve other groups where prolonged practice of a skill, other than instrument playing, has been implemented in childhood, such as video gamers, who also recruit meticulous combinations of bimanual motor movements in accordance with visual cues. Such an analogous group to musicians would also be expected to show bilateral visuospatial ability and equilateral IHTT.

The CUD and simple reaction time

The behavioural results collected during Study 5 were presented in Chapter 5 (Study 6). Traditionally IHTT has been measured using the difference in RT between stimuli presented contralateral to the hand of response, the crossed condition, and stimuli ipsilateral to the hand of response, the uncrossed condition (Poffenberger, 1912). The crossed-uncrossed difference (CUD) has been criticised as a measure of IHTT (Barnett & Corballis, 2005; Corballis, 2002) since crossed-uncrossed differences in RT computed separately for each hand are confounded by hemispheric differences. The results of Study 6 were rather inconclusive in relation to the theoretical underpinnings of the IHTT theory of the CUD, and in addition the results varied between groups.

In concurrence with the theory, non-musicians exhibited the predicted interaction between hand and visual field, indicating faster responses to uncrossed conditions than to crossed conditions, which could be interpreted as evidence for callosal delay during transfer. Musicians, on the other hand, responded more quickly to RVF stimuli than to LVF stimuli, regardless of condition (resulting in a theoretically impossible faster RT for the crossed condition in the left hand), highlighting the point made about confounding and the danger of interpreting the CUD as a measure of IHTT.

In terms of the laterality hypotheses, the data from Study 6 did not produce a clear demonstration of the effect of opposite visual field biases expected between the groups or right pseudoneglect in non-musicians. While the musician group did favour RVF stimuli over LVF stimuli, the non-musician group did not favour LVF stimuli over RVF stimuli as predicted. It is possible that this simple RT task was not sensitive enough to produce reliable results with the number of participants available. Further research could explore whether increasing the participant pool would yield the predicted results. Additionally, there was no support for this hypothesis in the accuracy data, which again may have been due to a ceiling effect. Unexpectedly, however, the non-musician group responded to a greater number of catch trials (missing stimuli) than the musician group did, which suggested there may have been a lower level of vigilance in the non-musician group. A generally lower accuracy level in this group supported this idea also. Vigilance and concentration are cognitive states not currently investigated by researchers in musicians and non-musicians.

Conclusions

The main finding from the results presented in this thesis is that musicians show more balanced visuospatial attention and perception and more equilateral information transfer efficiency between the hemispheres than non-musicians. These results are interpreted to indicate that musicians are less lateralized in the visuospatial domain

than non-musicians, who show right hemisphere dominance for visuospatial stimuli. It is suggested that musicians may develop neurally in a more equilateral manner than non-musicians due to persistent practice from an early age (when plasticity is high) in instrument playing, which requires complex bimanual movements as well as bilateral awareness of space. Given recent white-matter imaging evidence, it is proposed that musical training in early life elicits superfluous development of myelination that is more bilaterally distributed than myelination in non-musicians. It is also proposed that enhanced myelination across both hemispheres may benefit cognitive skills, particularly general speed of processing, and that this may instigate advantages in other cognitive domains including visuospatial ability. The research presented here builds upon other literature demonstrating differences between musicians and non-musicians in neural function and structure, and provides behavioural and electrophysiological evidence for a specific laterality difference in musicians compared with non-musicians in the visuospatial domain.

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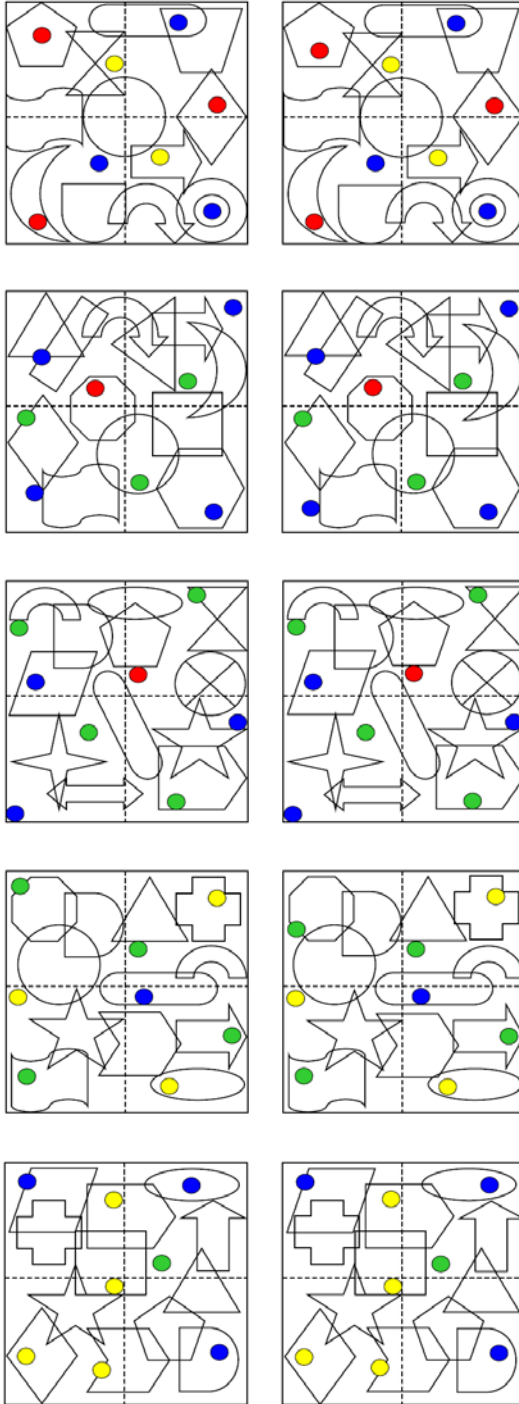
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List of Appendices

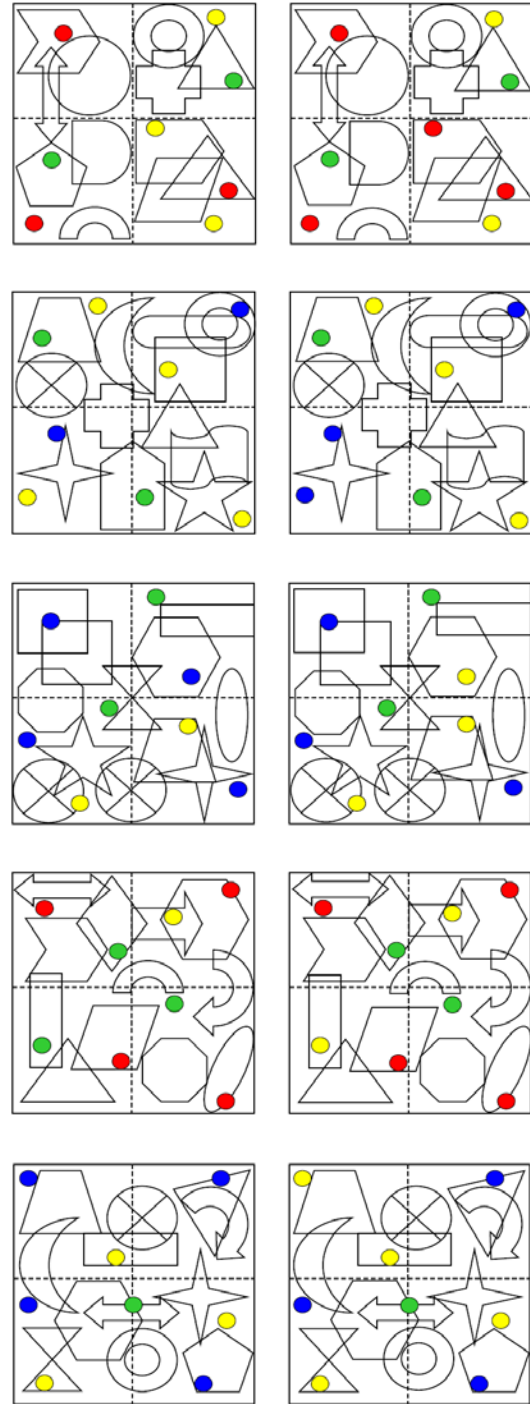
Appendix A: Visuospatial Search Task Examples	134
Appendix B: Raw Data for Study 1: Visual Discrimination Task	135
Appendix C: Raw Data for Study 1: Visuospatial Search Task.....	136
Appendix D: Raw Data for Study 2	137
Appendix E: Raw Data for Study 3.....	138
Appendix F: Raw Data for Study 4.....	139
Appendix G: Raw Data for Study 5	140
Appendix H: Raw Data for Study 6	141
Appendix I: Musician Instruments Studies 1 and 4	142
Appendix J: Musician Instruments Study 2	143
Appendix K: Musician Instruments Study 3.....	144
Appendix L: Musician Instruments Studies 5 and 6	145

Appendix A: Visuospatial Search Task Examples

Position Changes



Colour Changes



Appendix B: Raw Data for Study 1: Visual Discrimination Task

Participant number	Sex	Age (years)	Laterality Quotient	Years of Education	Matrix Reasoning*	Easy Horizontal RT	Hard Horizontal RT	Easy Vertical RT	Hard Vertical RT	Easy Horizontal Acc	Hard Horizontal Acc	Easy Vertical Acc	Hard Vertical Acc
N1	M	20	100	15	17	387	691	449	381	97.5	82.5	92.5	65.0
N2	M	25	100	17	14	480	831	465	543	100	72.5	97.5	80.0
N3	F	18	100	12	11	270	314	221	250	92.5	80.0	97.5	75.0
N4	F	24	81.8	19	15	368	483	391	457	100	60.0	95.0	75.0
N5	M	20	90.9	16	17	389	435	308	337	92.5	75.0	100	77.5
N6	M	20	52.4	16	15	305	575	252	310	100	82.5	92.5	75.0
N7	M	21	72.7	16	17	292	394	253	384	97.5	70.0	97.5	77.5
N8	F	27	77.8	16	17	564	678	796	741	100	67.5	92.5	65.0
N9	F	18	90.5	15	11	610	733	520	595	92.5	60.0	77.5	57.5
N10	F	26	100	13	14	298	308	226	217	92.5	67.5	67.5	62.5
N11	M	26	81.8	18	17	334	395	219	349	75.0	67.5	100	90.0
N12	F	23	100	16	17	616	617	633	680	92.5	65.0	85.0	60.0
N13	F	24	100	13	17	645	693	697	625	82.5	52.5	77.5	65.0
N14	F	20	87.0	15	17	573	563	535	562	82.5	57.5	82.5	65.0
N15	F	21	90.0	16	17	345	357	307	268	72.5	62.5	95.0	75.0
N16	F	20	71.4	15	15	662	687	551	576	80.0	72.5	80.0	60.0
M1	F	21	100	16	14	379	484	378	378	95.0	67.5	92.5	65.0
M2	F	28	100	23	18	225	229	183	280	100	82.5	95.0	55.0
M3	F	25	64.7	17	17	321	483	289	336	100	72.5	100	90.0
M4	F	20	81.8	15	16	442	536	491	599	97.5	67.5	100	72.5
M5	F	23	100	17	17	235	319	213	247	97.5	77.5	95.0	80.0
M6	F	18	57.1	14	14	187	182	194	190	97.5	65.0	90.0	65.0
M7	F	19	100	14	14	413	505	353	325	97.5	67.5	100	90.0
M8	F	19	71.4	14.5	17	226	204	159	182	82.5	70.0	92.5	52.5
M9	F	22	90.5	16.5	16	214	280	197	246	100	80.0	97.5	80.0
M10	F	18	100	14	15	331	510	313	443	100	90.0	100	100
M11	M	20	100	15	17	545	562	392	457	97.5	72.5	95.0	70.0
M12	M	18	100	13	16	243	330	245	363	100	92.5	97.5	77.5
M13	M	20	81.8	15	17	335	475	270	323	95.0	67.5	100	75.0
M14	M	22	100	17	18	355	346	281	317	85.0	55.0	97.5	70.0
M15	M	21	73.9	16	15	271	470	346	389	92.5	70.0	92.5	55.0
M16	M	24	100	14	17	271	437	178	279	100	80.0	100	75.0

* Scaled score

Appendix C: Raw Data for Study 1: Visuospatial Search Task

Participant number	Sex	Age (years)	Laterality Quotient	Years of Education	Matrix Reasoning task	First Trial Number Correct	Second Trial Number Correct	First Trial Number Errors	Second Trial Number Errors
N1	M	20	100	15	17	59	69	0	0
N2	M	25	100	17	14	64	73	1	0
N3	F	18	100	12	11	50	67	2	0
N4	F	24	81.8	19	15	56	74	1	1
N5	M	20	90.9	16	17	68	75	0	0
N6	M	20	52.4	16	15	63	75	6	3
N7	M	21	72.7	16	17	70	81	1	0
N8	F	27	77.8	16	17	64	71	0	0
N9	F	18	90.5	15	11	45	47	2	3
N10	F	26	100	13	14	53	55	4	0
N11	M	26	81.8	18	17	69	75	0	1
N12	F	23	100	16	17	64	68	0	1
N13	F	24	100	13	17	59	67	0	0
N14	F	20	87.0	15	17	69	76	0	0
N15	F	21	90.0	16	17	57	78	2	1
N16	F	20	71.4	15	15	68	76	1	0
M1	F	21	100	16	14	52	65	1	0
M2	F	28	100	23	18	101	115	0	0
M3	F	25	64.7	17	17	81	93	1	1
M4	F	20	81.8	15	16	69	72	0	0
M5	F	23	100	17	17	95	112	0	0
M6	F	18	57.1	14	14	70	81	1	2
M7	F	19	100	14	14	71	77	0	0
M8	F	19	71.4	14.5	17	72	93	1	0
M9	F	22	90.5	16.5	16	116	111	0	0
M10	F	18	100	14	15	86	107	0	0
M11	M	20	100	15	17	101	103	0	0
M12	M	18	100	13	16	90	117	0	0
M13	M	20	81.8	15	17	75	93	0	0
M14	M	22	100	17	18	83	92	0	0
M15	M	21	73.9	16	15	72	88	0	0
M16	M	24	100	14	17	96	113	0	0

Appendix D: Raw Data for Study 2

Participant number	Sex	Age (years)	Laterality Quotient	Years of Education	NC* SDMT written	NC SDMT verbal	NC Symbol Search	NC Stroop words	NC Stroop colors	NE** SDMT written	NE SDMT verbal	NE Symbol Search
N1	M	21	100	16	54	77	42	94	71	0	0	0
N2	F	24	100	19	56	69	39	100	60	0	6	0
N3	M	34	100	19	55	67	38	86	60	0	2	0
N4	M	27	100	20	54	56	40	113	58	0	0	1
N5	M	24	71.4	13	48	62	42	89	72	3	0	1
N6	M	27	100	22	85	105	60	123	89	2	0	0
N7	M	29	100	20	48	65	33	130	107	1	1	2
N8	M	21	72.7	17	56	77	49	93	78	2	1	0
N9	F	28	77.8	16	64	77	44	96	78	2	0	0
N10	M	22	88.9	17	68	83	52	100	83	0	0	0
N11	F	28	100	16	52	65	44	91	70	1	0	0
N12	F	26	100	14	44	60	35	96	81	0	0	1
N13	M	23	82	18	58	66	44	126	73	1	0	2
N14	M	26	81.8	18	63	73	39	95	72	0	0	1
N15	F	23	100	16	67	81	46	96	70	0	0	0
N16	F	24	100	13	51	64	44	100	76	0	0	0
N17	F	19	81.8	14	65	71	40	94	70	3	0	4
N18	F	21	90	16	54	70	43	111	69	0	0	1
N19	F	20	87	15	65	82	47	92	79	1	1	1
N20	F	19	100	12	56	72	43	100	76	5	0	0
M1	F	21	100	17	78	90	55	102	87	0	0	0
M2	M	27	100	16	62	66	47	126	81	2	1	1
M3	F	27	100	19	65	70	46	126	88	0	0	1
M4	F	25	64.7	17	76	89	47	103	86	0	1	0
M5	F	18	100	13	80	92	55	89	80	1	1	0
M6	M	41	100	18	60	76	39	130	83	1	0	0
M7	F	25	71.4	19	69	78	45	102	59	0	0	0
M8	F	28	100	22	83	94	55	96	90	0	0	1
M9	M	17	82	13	57	69	44	135	90	0	0	0
M10	F	22	100	17	72	83	50	110	77	0	0	1
M11	M	25	100	16	57	63	38	103	80	1	1	2
M12	F	18	100	13	73	105	40	105	80	1	0	0
M13	F	18	80	13	77	90	49	101	84	0	1	1
M14	F	20	90.4	15	95	109	60	134	114	0	1	1
M15	M	29	63.6	19	55	61	41	122	85	0	0	2
M16	M	20	72.7	16	60	73	41	134	112	1	0	4
M17	M	20	81.8	16	56	92	40	116	91	0	1	0
M18	M	19	63.6	14	57	76	48	115	79	2	2	0
M19	M	20	87.5	15	62	68	51	121	54	1	0	1
M20	M	24	100	14	71	102	52	131	97	1	0	0

* Number Correct

** Number of Errors

Appendix E: Raw Data for Study 3

Participant number	Sex	Age (years)	Laterality Quotient	Left* - Right Hand	Left - Left Hand	Centre - Right Hand	Centre - Left Hand	Right - Right Hand	Right - Left Hand
N1	M	20	100	-2.22	-1.61	-1.26	0.40	1.35	1.10
N2	M	25	100	5.16	-3.57	-1.04	-7.01	-0.08	-6.84
N3	M	26	78.9	0.69	0.51	3.08	-0.61	4.12	0.30
N4	F	18	100	-6.22	-4.37	-3.88	-4.33	-1.16	-5.86
N5	M	23	71.4	-1.64	-2.78	-2.65	-2.29	1.61	1.59
N6	F	24	81.8	-5.71	-7.33	-5.02	-7.22	0.05	-3.42
N7	M	20	90.9	2.45	-0.51	-0.06	-2.20	0.23	-0.66
N8	M	25	82	-1.61	-1.96	-1.88	-1.03	2.78	-1.55
N9	M	21	72.7	-4.75	-5.76	-6.93	-7.80	-2.83	-7.44
N10	F	27	77.8	-6.29	-2.05	-5.78	-3.15	-2.44	0.59
N11	F	25	90	-5.96	-5.91	-3.39	-9.61	-2.18	-1.55
N12	F	18	90.5	-4.38	0.10	-8.15	-1.42	-2.47	-1.78
N13	F	26	100	-4.05	-9.79	2.47	-8.24	-1.09	-14.47
N14	M	23	81.8	-0.87	-3.17	1.93	-7.68	1.05	-1.10
N15	F	28	100	-3.78	-0.63	-6.04	-4.29	-2.14	-0.26
N16	M	26	100	-0.05	1.47	-1.92	-0.01	-3.49	-3.18
N17	M	28	81	-0.65	-1.19	-1.14	-2.47	1.95	-0.99
N18	F	23	100	-3.58	-7.93	-0.13	-1.67	0.90	1.39
N19	M	26	100	-1.17	-0.88	-1.21	1.57	-0.15	-0.20
N20	F	20	71.4	-3.00	-2.99	-3.33	-2.04	3.35	-1.26
M1	F	21	100	4.76	2.77	3.54	1.53	5.19	4.13
M2	M	26	100	0.24	1.05	-1.49	0.10	0.12	-1.02
M3	F	26	100	2.44	2.35	-1.09	2.68	-5.09	0.74
M4	F	25	64.7	2.54	0.52	0.98	1.48	3.45	4.17
M5	M	29	100	-0.44	2.81	1.25	2.21	1.44	1.37
M6	F	27	100	-1.87	-1.75	0.04	1.22	2.45	2.00
M7	M	21	73.9	3.11	1.94	-2.75	-0.95	-0.23	-1.01
M8	F	29	100	-3.04	-4.72	-4.36	-4.49	0.52	-4.58
M9	F	19	100	-1.49	-4.27	1.94	-4.22	2.02	-5.22
M10	F	19	71.4	1.42	1.93	3.36	-0.90	3.52	1.95
M11	F	22	90.5	-0.18	0.05	1.76	-0.79	2.64	0.71
M12	M	41	100	-1.76	-1.31	-0.60	0.47	1.40	1.39
M13	F	18	100	1.88	1.85	3.98	0.58	6.10	0.76
M14	M	20	100	6.12	3.91	2.16	2.48	4.97	1.59
M15	M	34	69	-5.52	0.21	0.16	3.21	1.20	4.53
M16	M	18	100	-0.46	2.06	0.20	1.17	5.91	0.95
M17	F	42	90	-2.60	-2.82	1.14	-5.13	1.86	-1.36
M18	F	35	81	-0.59	-1.38	-0.57	0.26	2.33	1.48
M19	M	23	100	0.95	2.60	-0.44	3.83	8.88	5.59
M20	M	20	81.8	0.31	1.46	0.76	0.65	2.91	3.07

* indicates position of lines on page

Appendix F: Raw Data for Study 4

Participant number	Sex	Age (Years)	Laterality Quotient	Years of Education	Matrix Reasoning task	Easy Right Side RT	Hard Right Side RT	Easy Left Side RT	Hard Left Side RT	Easy Right Side Acc	Hard Right Side Acc	Easy Left Side Acc	Hard Left Side Acc
N1	M	20	100	15	17	628	467	271	296	85	45	100	85
N2	M	25	100	17	14	523	583	408	502	95	70	100	90
N3	F	18	100	12	11	221	246	222	254	95	65	100	85
N4	F	24	81.8	19	15	314	471	469	443	85	75	90	55
N5	M	20	90.9	16	17	297	339	319	334	100	90	100	65
N6	M	20	52.4	16	15	283	390	222	229	85	50	100	100
N7	M	21	72.7	16	17	273	396	233	371	95	65	100	90
N8	F	27	77.8	16	17	784	742	807	741	90	50	95	80
N9	F	18	90.5	15	11	532	610	509	581	70	45	85	70
N10	F	26	100	13	14	246	233	206	200	35	35	100	90
N11	M	26	81.8	18	17	217	415	221	283	100	80	100	100
N12	F	23	100	16	17	651	642	615	717	85	50	85	70
N13	F	24	100	13	17	676	639	719	611	70	45	85	85
N14	F	20	87.0	15	17	533	547	536	577	70	40	95	90
N15	F	21	90.0	16	17	352	264	261	272	95	60	95	90
N16	F	20	71.4	15	15	536	584	566	567	65	40	95	80
M1	F	21	100	16	14	341	382	415	374	95	60	90	70
M2	F	28	100	23	18	182	295	183	264	90	45	100	65
M3	F	25	64.7	17	17	281	336	297	337	100	95	100	85
M4	F	20	81.8	15	16	514	623	468	576	100	60	100	85
M5	F	23	100	17	17	208	268	217	226	95	65	95	95
M6	F	18	57.1	14	14	184	194	203	593	80	55	100	75
M7	F	19	100	14	14	273	337	433	313	100	90	100	90
M8	F	19	71.4	15	17	163	177	155	187	95	65	90	40
M9	F	22	90.5	17	16	192	260	202	232	95	70	100	90
M10	F	18	100	14	15	325	417	302	468	100	100	100	100
M11	M	20	100	15	17	421	492	363	423	95	45	95	95
M12	M	18	100	13	16	236	289	255	436	100	85	95	70
M13	M	20	81.8	15	17	274	333	267	314	100	60	100	90
M14	M	22	100	17	18	216	324	346	311	100	60	95	80
M15	M	21	73.9	16	15	327	395	366	383	95	45	90	65
M16	M	24	100	14	17	197	294	160	264	100	55	100	95

Appendix G: Raw Data for Study 5

Participant number	Sex	Age (years)	Laterality Quotient	Years of Education	LVF Left hem Ab	LVF Right hem Ab	Right-to-left IHTT	RVF Left hem Ab	RVF Right hem Ab	Left-to-right IHTT	IHTT Difference*
N1	M	21	100	15	214	205	9	194	220	26	17
N2	F	24	100	19	188	170	18	181	197	16	2
N3	F	25	100	20	219	201	18	192	221	29	11
N4	F	40	87.5	26	153	152	1	149	172	23	22
N5	F	21	71.4	16	202	186	16	153	199	46	30
N6	F	20	77.8	16	209	185	24	178	205	27	3
N7	M	21	88.9	17	232	212	20	168	216	48	28
N8	M	29	83.3	20	220	216	4	176	208	32	28
N9	M	22	66.7	14	204	180	24	140	208	68	44
N10	M	22	100	15	204	184	20	188	212	24	4
N11	M	21	100	16	196	192	4	168	220	52	48
N12	M	19	66.7	14	216	200	16	204	268	64	48
N13	F	22	100	17	223	197	26	149	223	74	48
N14	F	20	100	15	205	189	16	160	206	46	30
N15	M	27	81.8	15	157	152	5	166	235	69	64
N16	F	19	81.8	14	218	216	2	150	213	63	61
M1	F	25	100	20	208	184	24	196	205	9	15
M2	F	21	81.8	17	221	192	29	187	215	28	1
M3	F	27	100	23	190	183	7	168	187	19	12
M4	M	41	100	18	201	192	9	181	209	28	19
M5	M	34	69	15	191	149	42	144	202	58	16
M6	F	22	100	17	214	151	63	171	193	22	41
M7	F	25	100	19	184	162	22	192	197	5	17
M8	M	17	82	13	212	209	3	184	210	26	23
M9	M	25	100	16	198	184	14	179	204	25	11
M10	M	20	100	15	204	195	9	178	212	34	25
M11	F	28	100	22	204	188	16	188	208	20	4
M12	F	21	73.3	16	219	215	4	212	216	4	0
M13	F	19	100	15	242	220	22	214	234	20	2
M14	M	26	100	18	214	171	43	173	209	36	7
M15	M	28	69	19	193	160	33	158	192	34	1
M16	M	26	100	19	216	209	7	198	212	14	7

* Absolute values shown

Appendix H: Raw Data for Study 6

Participant number	Sex	Age (years)	Laterality Quotient	Years of Education	LVF-RH RT	LVF-LH RT	RVF-RH RT	RVF-LH RT	LVF-RH Acc	LVF-LH Acc	RVF-RH Acc	RVF-LH Acc
N1	M	21	100	15	440	476	427	493	91	92	89	92
N2	F	24	100	19	422	418	443	449	99	100	100	99
N3	F	25	100	20	358	357	341	365	100	99	98	98
N4	F	40	87.5	26	327	320	322	318	100	99	100	100
N5	F	21	71.4	16	350	327	348	331	100	100	100	100
N6	F	20	77.8	16	321	345	307	340	100	100	100	100
N7	M	21	88.9	17	371	343	359	352	100	100	100	98
N8	M	29	83.3	20	246	240	241	247	100	100	100	100
N9	M	22	66.7	14	251	253	246	256	100	100	97	100
N10	M	22	100	15	268	268	262	262	100	100	100	100
N11	M	21	100	16	312	316	314	333	100	100	98	97
N12	M	19	66.7	14	280	267	292	295	100	100	97	100
N13	F	22	100	17	298	302	292	309	100	100	100	100
N14	F	20	100	15	314	315	299	314	98	100	100	100
N15	M	27	81.8	15	280	293	265	279	97	96	98	95
N16	F	19	81.8	14	280	293	265	279	100	99	98	100
M1	F	25	100	20	340	348	333	346	100	100	100	100
M2	F	21	81.8	17	332	323	320	308	99	100	100	100
M3	F	27	100	23	327	310	319	319	100	100	100	100
M4	M	41	100	18	346	375	347	358	99	100	100	100
M5	M	34	69	15	335	335	331	347	100	100	100	100
M6	F	22	100	17	280	290	285	299	100	99	100	100
M7	F	25	100	19	349	347	337	340	100	100	100	100
M8	M	17	82	13	272	270	263	256	98	97	98	95
M9	M	25	100	16	469	412	449	418	100	100	100	100
M10	M	20	100	15	319	325	323	328	100	100	100	99
M11	F	28	100	22	291	278	302	277	100	100	100	100
M12	F	21	73.3	16	293	285	274	277	100	100	100	100
M13	F	19	100	15	332	355	325	347	100	100	100	100
M14	M	26	100	18	304	314	305	308	100	100	100	100
M15	M	28	69	19	297	293	292	293	100	100	100	100
M16	M	26	100	19	320	316	320	320	99	99	100	100

Appendix I: Musician Instruments Studies 1 and 4

Participant number	Age of training onset	Number of instruments	Voice	Piano**	Percussion**	Recorder**	Clarinet**	Trumpet**	French Horn	Violin	Cello	Flute	Guitar
M1	5	2	14	16*									
M2	4	1								19*			
M3	8	2		10*								6	
M4	5	3	8	15*						14			
M5	6	3	2	18*						10			
M6	5	4		6*				5	5		5		
M7	8	4		6	1	4*						6	
M8	5	3		15*	7			5					
M9	5	4	9	8*							6	15	
M10	5	4	10	13*		2	10						
M11	6	3	10	15*	10								
M12	5	3	8	14*									3
M13	7	2	12	14*									
M14	6	3	4							17*			8
M15	8	3	8	5*						9			
M16	8	4	3	3*			5						
Frequency:			11	14	3	2	2	2	1	5	2	3	2

Numbers in instrument columns represent number of years instrument was played

* indicates first childhood instrument

** indicates bimanual midline instrument

Frequency of sample playing: only one instrument = 1
 more than one instrument = 15
 more than two instruments = 12
 more than three instruments = 5

 at least one bimanual midline instrument = 14
 no bimanual midline instruments = 2

Appendix J: Musician Instruments Study 2

Participant number	Age of training onset	Number of instruments	Voice	Piano**	Percussion**	Recorder**	Clarinet**	Oboe**	Saxophone**	Trombone	Violin	Cello	Flute	Guitar
M1	5	2	14	16*										
M2	11	1		16*										
M3	4	3	11	11*										3
M4	8	2		10*									6	
M5	5	1		13*										
M6	5	3	2	5*								11		
M7	7	2		18*				3						
M8	4	1									19*			
M9	7	2		7	10*									
M10	5	4	9	8*								6	15	
M11	9	3	3	4	16*									
M12	6	3	2									12*		2
M13	7	2		3*									9	
M14	4	2		16*		8								
M15	13	1			17*									
M16	5	2		17*	10									
M17	7	2	12	14*										
M18	4	2		14*								15		
M19	6	2		14*					5					
M20	8	4	3	3*					6			5		
Frequency:			8	17	2	2	1	1	1	1	1	5	3	2

Numbers in instrument columns represent number of years instrument was played

* indicates first childhood instrument

** indicates bimanual midline instrument

Frequency of sample playing:

only one instrument = 4

more than one instrument = 16

more than two instruments = 6

more than three instruments = 2

at least one bimanual midline instrument = 18

no bimanual midline instruments = 2

Appendix K: Musician Instruments Study 3

Participant number	Age of training onset	Number of instruments	Voice	Piano**	Organ**	Harpsichord**	Percussion**	Recorder**	Clarinet**	Trumpet**	Saxophone**	Guitar	Bass Guitar	Piano Accordion	Violin	Cello	Flute
M1	5	2	14	16*													
M2	11	1		16*													
M3	4	3	11	11*							3						
M4	8	2		10*													6
M5	4	5	20	28*						21	25	15					
M6	7	4	15	10*				1								3	
M7	8	3	8	5											9*		
M8	7	1											13				
M9	8	4		6*		1	4										6
M10	5	3		15*		7			5								
M11	5	4	9	8												6	15*
M12	5	4	30	32*				2	11								
M13	5	4	10	13*				2	10								
M14	6	3	10	15*		10											
M15	7	3	5	11*			4										
M16	5	3	8	14*							3						
M17	7	2	20	8*													
M18	8	5	2	10*	10	10		3						9			
M19	6	2	9	16*													
M20	7	2	12	14*													
Frequency:			15	19	1	1	3	5	3	1	1	3	1	1	2	2	3

Numbers in instrument columns represent number of years instrument was played

* indicates first childhood instrument

** indicates bimanual midline instrument

Frequency of sample playing: only one instrument = 2

more than one instrument = 18

more than two instruments = 13

more than three instruments = 7

at least one bimanual midline instrument = 19

no bimanual midline instruments = 1

Appendix L: Musician Instruments Studies 5 and 6

Participant number	Age of training onset	Number of instruments	Voice	Piano**	Percussion**	Recorder**	Clarinet**	Oboe**	French Horn	Violin	Cello	Double Bass	Flute	Guitar
M1	9	4	3	11*					3	4				
M2	5	3	10	3*						11				
M3	7	4	12	11*							2	4		
M4	5	3	2	5*							11			
M5	7	3	5	11*	4									
M6	5	4	9	8							6		15*	
M7	7	2		18*				3						
M8	7	2		7	10*									
M9	9	3	3	5	16*									
M10	4	1		13*										
M11	4	1								19*				
M12	10	2				11*								
M13	5	3		2	2*								7	
M14	5	7	3	9*	1	3	18*						1	
M15	7	2		21*										11
M16	9	1		9*										
Frequency:			8	14	1	5	2	1	1	3	3	1	3	1

Numbers in instrument columns represent number of years instrument was played

* indicates first childhood instrument

** indicates bimanual midline instrument

Frequency of sample playing:

only one instrument = 3

more than one instrument = 13

more than two instruments = 9

more than three instruments = 4

at least one bimanual midline instrument = 15

no bimanual midline instruments = 1