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The unusual symmetry of musicians: Musicians have equilateral interhemispheric transfer for visual information

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Abstract

Previous behavioural research has shown that spatial attention is bilaterally represented in musicians, possibly reflecting more equal neural development between the hemispheres. We investigated this theory electrophysiologically with another measure that has shown asymmetry, interhemispheric transfer time (IHTT). Sixteen right-handed musicians and 16 matched non-musicians responded to stimuli presented to the left and right visual fields while 128-channel EEG was recorded. IHTT was calculated by comparing the latencies of occipital N1 components between hemispheres. Non-musicians showed significantly faster IHTT in the right-to-left direction than in the left-to-right direction and a shorter N1 latency in the left than in the right hemisphere. In contrast, the musician group showed no directional difference between hemispheres in IHTT, and no hemispheric difference in latency. These results indicate that musicians have more bilateral neural connectivity than non-musicians, reflected in an unusual lack of asymmetry. It is suggested that plastic developmental changes caused by extended musical training in childhood result in equally efficient connections to both hemispheres.

Keywords: Electroencephalography; Corpus callosum; Transfer time; Cerebral laterality; Musical training; Plasticity

Musicians are quickly becoming the subject of neuroscientific interest, as accumulating evidence indicates that their brains may differ anatomically and cognitively from those with little or no musical background. It is fairly well established, for example, that musical training in childhood results in anatomical white and grey matter plasticity (Amunts et al., 1997; Bengtsson et al., 2005; Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Schlaug, Jäncke, Huang, Staiger, & Steinmetz, 1995). Concurrently, a number of reports claim musicians have enhanced, or atypical cognition. Brochard, Dufour, & Despres (2004) found that adult musicians had faster reaction times than non-musicians on a visuospatial discrimination task and suggested that musicians may have enhanced visuospatial abilities due to developed music score reading skills. Schellenberg (2004, 2006) described positive benefits of long-term musical training on cognitive abilities including general IQ. Furthermore, Nering (2002) investigated 10 sets of monozygotic twins, in which only one of each set received biweekly private piano lessons for 7 months. Prior to musical training, the twins did not differ on measures of verbal, mathematical or spatial abilities, or language comprehension and general IQ, but after training the 'lessons' group had significantly higher scores.

Lateralization of cognitive functions may also differ 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, Yazgan, & 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, our earlier research showed that musicians bisected lines to the right of centre, and were also more accurate overall than non-musicians (Patston, Corballis, Hogg, & Tippett, 2006). In addition, when discriminating on which side of a vertical line a dot had been presented, musicians performed more equally to stimuli presented on both sides than did non-musicians, whose performance was significantly worse

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for dots appearing on the right side of the line (Patston, Hogg, & Tippett, 2007). 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 plastic changes at the neural level, in both white and grey 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 reorganisation in these musicians (Elbert et al., 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 et al. (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 years than those whose training began after age 7 years. 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 (Münte, 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). In this paradigm, stimuli are presented to each visual field individually and the latencies of occipital ERPs (N1) in the hemisphere contralateral (direct pathway) to the stimuli are subtracted from that in the hemisphere ipsilateral (callosal pathway). This methodology allows us firstly, to compare IHTT in the two directions, left-to-right and right-to-left, and secondly, to assess the absolute latency of the N1 in each hemisphere.

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, Snyder, & Hillyard, 1976). For example, Peeke, Callaway, Jones, Stone, and Doyle (1980) reported shorter N1 latencies and more errors for participants who were sleep deprived or 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 grey 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, we electrophysiologically assessed IHTT and absolute latency of the N1 in musicians and non-musicians. We expected to see faster right-to-left than left-to-right transfer in non-musicians, consistent with previous research (Barnett & Corballis, 2005; Barnett 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 (Patston et al., 2006, 2007), we anticipated that the asymmetry between left-to-right and right-to-left transfer would be less evident in musicians, and perhaps absent altogether. In addition, we were interested in exploring whether any N1 absolute latency differences arose between the hemispheres and/or groups.

1. Method

1.1. Participants

Two groups of adults, musicians ($N=16$, 8 female) and 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. The musician group had a mean age of 25.31 years (S.D. = 5.92) and all members had received at least 8 years of music lessons ($M=13.44$ years, S.D. = 4.07) and could read music. All musicians were right handed and had a mean laterality quotient of 92.19 (S.D. = 12.42), as established by the Edinburgh Handedness Inventory (Oldfield, 1971), and a mean of 17.63 years of education (S.D. = 2.68). 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 ($N=1$).

The non-musician group had a mean age of 23.31 years (S.D. = 5.25) and members had very little (less than 2 years) or no formal music training and could not read music. All non-musicians were right handed with a mean laterality quotient of 87.87 (S.D. = 12.64) and 16.81 years of education (S.D. = 3.15). Groups were matched for age, $t(30)=1.01$, $p=.32$, laterality quotient, $t(30)=.98$, $p=.34$, and years of education, $t(30)=.79$, $p=.44$. General exclusion criteria included epilepsy, left handedness, and formal music training for more than 2 years but less than 8 years.

2. Stimuli and apparatus

Stimuli were circular white/black checkerboards with a diameter of 3° of visual angle that appeared for 100 ms against a grey 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 kΩ. Data were acquired using a common reference electrode (Cz), positioned anatomically, and later re-referenced to the average.

EEG was segmented into epochs 140 ms pre-stimulus onset to 360 ms post-stimulus onset, and those contaminated by eye movement (blink threshold set at 70 μV detected by electrodes

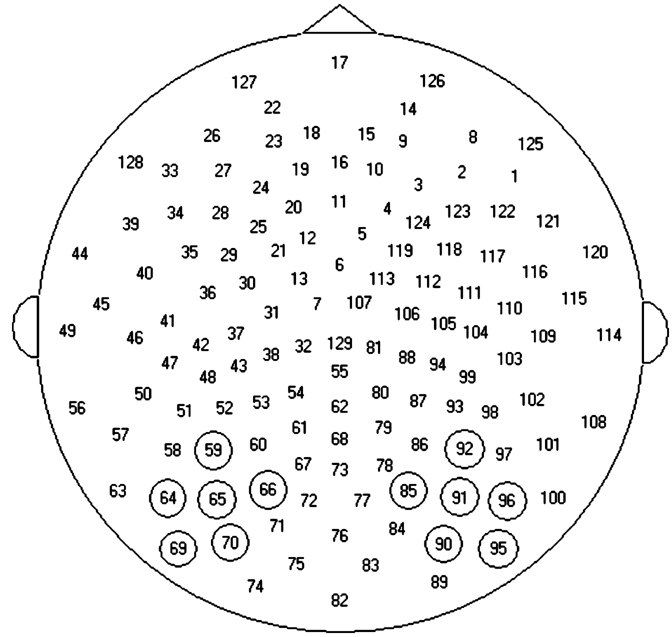

Fig. 1. Diagram of electrode positions for Electrical Geodesic 128-electrode net. Circles indicate electrode clusters used for the right and left hemispheres.

128 (left) and 125 (right)) were discarded. The percentage of epochs remaining for musicians was 78.84 (S.D. = 24.73) for the LVF and 79.70 (S.D. = 24.02) for the RVF, and for non-musicians was 75.71 (S.D. = 23.69) for the LVF and 75.17 (S.D. = 24.23) for the RVF. Independent samples t-tests revealed no difference between the groups for either the LVF, $t(30)=.92$, $p=.72$, or the RVF $t(30)=.85$, $p=.60$. 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 140 ms 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 Fig. 1. 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.

3. Procedure

Participants were tested in a quiet, electrically shielded Faraday chamber and were seated 57 cm from a 15 in. SVGA computer monitor (640 × 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. 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.

4. Results

4.1. 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) as the between-subjects factor. Data were averaged across hands.

The grand mean waveforms for N1 elicited to LVF and RVF stimuli are shown in Fig. 2 for musicians and non-musicians. The ANOVA for IHTT did not reveal a significant main effect of group, $F(1,30) = 2.28$, $p = .14$, but a main effect of direction showed right-to-left transfer to be significantly faster than left-to-right transfer, $F(1,30) = 23.85$, $p < .001$. More importantly, there was an interaction between group and direction, $F(1,30) = 17.85$, $p < .001$. 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 ($p = .65$; see Fig. 3). In addition, musicians showed significantly faster transfer in the left-to-right direction in comparison to non-musicians ($p = .002$), but not significantly slower transfer in the right-to-left direction in comparison to non-musicians ($p = .11$).

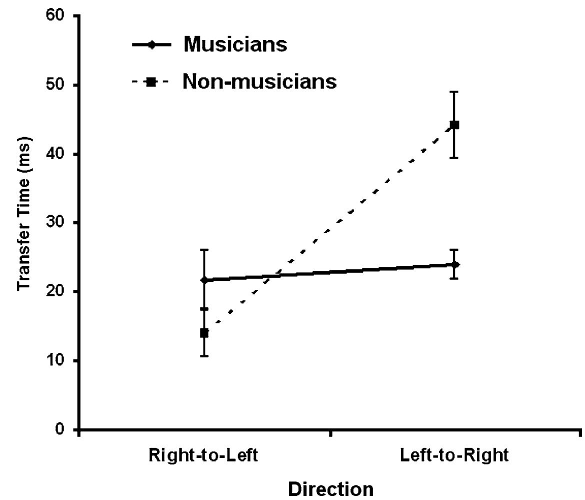

Fig. 3. Mean IHTT for each direction averaged across hands for musicians and non-musicians. Error bars represent standard error of the mean.

4.2. Absolute latency of the N1

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

The main effect of hemisphere was significant, $F(1,30) = 10.85$, $p = .003$, reflecting longer latency in the right hemisphere ($M = 187.53$, S.E. = 3.69) than in the left hemisphere ($M = 176.22$, S.E. = 3.28). While the main effect for group was not significant, $F(1,30) = .47$, $p = .50$, there was a hemisphere by group interaction, $F(1,30) = 6.49$, $p = .016$. Post

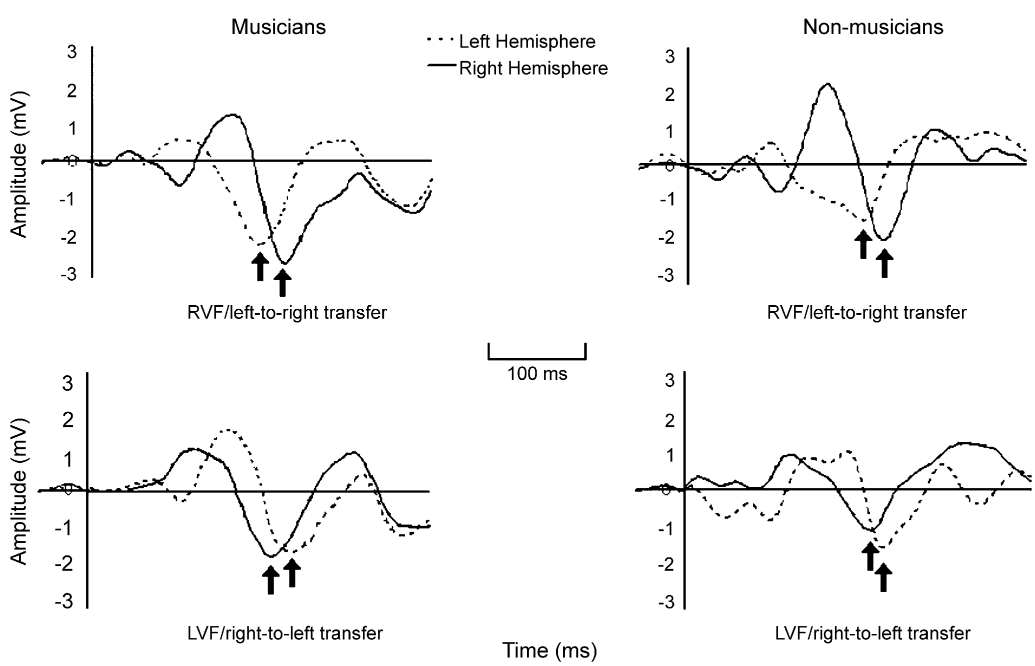

Fig. 2. Grand mean waveforms averaged across hands in right and left hemisphere occipital electrode clusters for musicians and non-musicians recorded during stimulus presentation in the RVF and LVF.

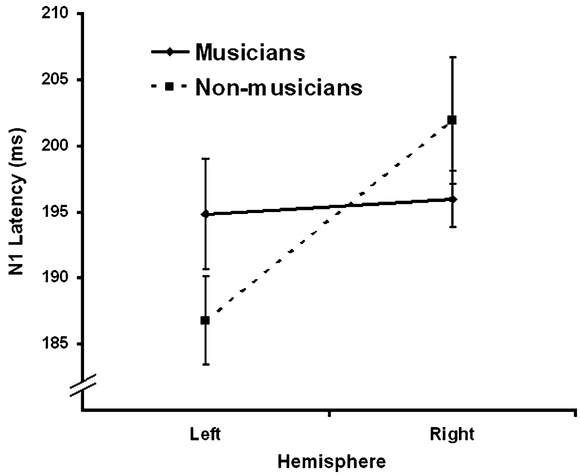

Fig. 4. Mean absolute latency for direct pathways averaged across hands for each hemisphere for musicians and non-musicians. Error bars represent standard error of the mean.

hoc 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 Fig. 4). Also, latency in the left hemisphere approached being significantly slower in musicians than in non-musicians ($p = .06$), but there was no difference between groups in the right hemisphere ($p = .54$).

5. Discussion

Using the latencies of N1 responses to measure IHTT, we found that musicians did not exhibit the usual directional asymmetry. As expected from previous studies (Barnett & Corballis, 2005; Barnett 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 Fig. 3 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 hemispheric latency 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 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 (Patston et al., 2006, 2007). Here, we propose 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 (13/16) of the musicians in this sample 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 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), 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 abnormal myelin production and subsequent hemispheric equilaterality, regardless of whether myelination is decreased or increased relative to normal.

A major consideration in research involving musicians and non-musicians is the issue of investigating a group that is self-selected. It is possible that children with biologically more balanced neural connections may have more success in their progression of music lessons, and may, therefore, be more 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, 1966 as cited in Rowley, 1988). There is also convincing evidence, however, 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 an increased number of hippocampal cells compared with rats reared in isolation (Kempermann, Kuhn, & Gage, 1998). 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, 1998) have shown enhanced activation of the primary motor cortex following daily practice of a finger opposition task. These results strongly suggest that specific plastic 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.

In conclusion, we found 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, our findings suggest that the brains of musicians differ from those of non-musicians in ways other than those related to music itself.

6. Competing interests

The authors declare that they have no competing financial interests.

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