*European Journal of Neuroscience, Vol. 26, pp. 3291–3302, 2007* doi:10.1111/j.1460-9568.2007.05894.x

# Assessment of sensorimotor cortical representation asymmetries and motor skills in violin players

Peter Schwenkreis,[1] Susan El Tom,[2] Patrick Ragert,[2] Burkhard Pleger,[1] Martin Tegenthoff[1] and Hubert R. Dinse[2]
[1]Department of Neurology, Ruhr-University Bochum, BG-Kliniken Bergmannsheil, Buerkle-de-la-Camp-Platz 1, D-44789 Bochum, Germany
[2]Institute for Neuroinformatics, Department of Theoretical Biology, Neural Plasticity Laboratory, Ruhr-University Bochum, D-44780 Bochum, Germany

*Keywords*: asymmetry, dipole source localization, motor performance, SEP, TMS mapping

## Abstract

As a model for use-dependent plasticity, the brains of professional musicians have been extensively studied to examine structural and functional adaptation to unique requirements of skilled performance. Here we provide a combination of data on motor performance and hand representation in the primary motor and somatosensory cortex of professional violin players, with the aim of assessing possible behavioural consequences of sensorimotor cortical asymmetries. We studied 15 healthy right-handed professional violin players and 35 healthy nonmusician controls. Motor and somatosensory cortex asymmetry was assessed by recording the motor output map after transcranial magnetic stimulation from a small hand muscle, and by dipole source localization of somatosensory evoked potentials after electrical stimulation of the median and ulnar nerves. Motor performance was examined using a series of standardized motor tasks covering different aspects of hand function. Violin players showed a significant right-larger-than-left asymmetry of the motor and somatosensory cortex, whereas nonmusician controls showed no significant interhemispheric difference. The amount of asymmetry in the motor and somatosensory cortices of musicians was significantly correlated. At the behavioural level, motor performance did not significantly differ between musicians and nonmusicians. The results support a use-dependent enlargement of the left hand representation in the sensorimotor cortex of violin players. However, these cortical asymmetries were not paralleled by accompanying altered asymmetries at a behavioural level, suggesting that the reorganisation might be task-specific and does not lead to improved motor abilities in general.

## Introduction

During the last two decades, there has been overwhelming evidence that extensive use or practice leads to substantial changes in the associated cortical representations; this has been referred to as training- and learning-induced cortical plasticity (for review, see Buonomano & Merzenich, 1998; Sanes & Donoghue, 2000; Dinse & Merzenich, 2002). After the first pioneering experiments conducted in animals (Jenkins *et al*., 1990; Recanzone *et al*., 1992; Nudo *et al*., 1996), the use of modern noninvasive imaging techniques in humans allowed the study of plastic changes in primary motor and somatosensory areas associated with the acquisition of perceptual and motor skills under experimental conditions (Pascual-Leone *et al*., 1994; Karni *et al*., 1995, 1998; Pleger *et al*., 2001; Dinse *et al*., 2003) as well as in 'naturalistically' designed studies, e.g. in Braille readers (Pascual-Leone *et al*., 1993; Pascual-Leone & Torres, 1993; Sterr *et al*., 1998) or racquet players (Pearce *et al*., 2000). These studies generally revealed an expansion of the cortical representation related to the acquisition of a defined skill, whereas a reduced use was linked to a reduction in the corresponding sensorimotor representation (Liepert *et al*., 1995; Coq & Xerri, 1999). As a particularly suitable model for training-induced cortical plasticity, the brains of musicians have been extensively studied to examine structural and functional adaptation to unique requirements of skilled performance as well as cerebral correlates of unique musical abilities such as absolute pitch (Pantev *et al*., 1998, 2001, 2003; Schlaug, 2001; Münte *et al*., 2002; Altenmüller, 2003). More specifically, as a possible sign of use-dependent plasticity, a number of atypical asymmetries have been described in musicians compared to nonmusicians using different imaging and behavioural approaches: a less pronounced left–right asymmetry of the posterior wall of the precentral gyrus was shown in right-handed keyboard players as compared to nonmusician controls (Amunts *et al*., 1997). The 'hand knob' in the precentral gyrus, which is associated with functional hand and finger movement representation, shows a left hemisphere advantage in keyboard players and a right hemisphere advantage in string players (Bangert & Schlaug, 2006), indicating a differential brain adaptation to different instruments. In addition, string players show an enlargement of the somatosensory cortical representation of the left hand dependent on the age at which they began studying their instrument (Elbert *et al*., 1995). In a behavioural study, professional string and keyboard players revealed a lesser degree of hand skill asymmetry than nonmusicians, regardless of which instrument they were playing (Jäncke *et al*., 1997).

However, most previous studies examined either the motor or the somatosensory system, and focused either on imaging or on behavioural data. The aim of the present study was to assess asymmetries of

*Correspondence*: Professor Dr Martin Tegenthoff, as above.
E-mail: martin.tegenthoff@ruhr-uni-bochum.de

*Received 5 May 2007, revised 9 September 2007, accepted 18 September 2007*

© The Authors (2007). Journal Compilation © Federation of European Neuroscience Societies and Blackwell Publishing Ltd

the hand representation in the somatosensory and motor cortex of violin players, and possibly related altered asymmetries in motor skills of arms, hands and fingers by providing a combination of behavioural and electrophysiological data obtained from professional violin players and nonmusician controls.

## Materials and methods

### *Personal data*

We investigated 15 healthy professional violin players (seven males and eight females, aged between 19 and 33 years; mean age 23.8 ± 4.5 years). In addition, 35 healthy nonmusicians (13 male, 22 female) with a mean age of 25.3 ± 5.7 years served as controls. They all gave their written informed consent. The protocol was approved by the ethical committee of the Ruhr-University Bochum, and conforms to The Code of Ethics of the World Medical Association (Declaration of Helsinki).

Handedness was assessed using the Edinburgh Handedness Questionnaire (EHQ; Oldfield, 1971). Previous studies showed a high congruence between self-rated hand dominance as provided by the EHQ and hand dominance based on tests of motor performance in young healthy subjects (Bishop *et al*., 1996; Corey *et al*., 2001; Henkel *et al*., 2001; Kalisch *et al*., 2006). According to the EHQ, all subjects tested in this study were right-handed.

By means of a questionnaire, information about the biography of the violinists was obtained, in particular about the duration of daily practicing and the age at which they began violin playing. All violinists were students at a conservatory, studying violin playing to be an orchestral musician. Musicians playing a second instrument (e.g. piano) on a similar level were excluded. Violinists had a history of regular violin training for between 14 and 27 years (mean 17.7 ± 3.6 years), and currently practiced daily for 2–6 h (mean 3.1 ± 1.2 h). Age at the beginning of regular violin training was between 5 and 10 years (mean 6.1 ± 1.5 years). Only three violinists began training after the age of 7, i.e. after the presumed sensitive period in childhood for the motor component of musical training (Watanabe *et al*., 2007).

Non-musician controls were matched with regard to the educational and socio-economic background of the violin players. None of the controls played an instrument as a hobby or was an extensive typist. Given the overwhelming reign of computers, all controls had some history of using computer keyboards.

None of the subjects participating in this study had a history of neurological or psychiatric disorders. Especially, none of the violin players ever suffered from motor disturbances such as focal dystonia.

### *Mapping of somatosensory evoked potentials (SEPs)*

In all 15 violin players we recorded SEPs after electrical stimulation of the median and ulnar nerve at the wrist of both hands. Results obtained in the violin players were compared to the results obtained in a control group of healthy nonmusicians (one male and seven females, aged between 20 and 35 years, mean 24.1 ± 5.1 years). Electrical stimulation was performed using a Digitimer Stimulator DS9A, with a pulse duration of 0.1 ms and a repetition rate of 3 Hz. Stimulation intensity was adjusted to 2.5× sensation threshold. Recordings were made using a 32-channel electroencephalography system (Neuroscan, El Paso, USA) from 32 scalp positions evenly positioned over both hemispheres according to the 10–20 system. The Fz electrode was used as a reference. The electrical potentials (band-pass filtered between 1 and 1000 Hz, sampling rate 5000 Hz) were recorded in epochs from 30 ms before to 100 ms after the stimulus. A total of 1600 stimulus-related epochs were registered for each side. After registration, the epochs were digitally filtered (band-pass filter 20–500 Hz, 24 dB/Oct), referenced to a common average, and averaged using Scan 4.1 software (Neuroscan). Further analysis was performed in a standardized manner using ASA software (ANT Software, Enschede, The Netherlands). For the source reconstruction of the N20 SEP component we used a spherical three-shell head model that was fitted to the individual electrode positions, which were measured with a 3-D digitizer in each subject (Polhemus Fastrak, Colchester, USA). Electrical source reconstruction then was performed using a single rotating dipole model. Therefore, global field power (GFP) was calculated, and the N20 SEP component was fixed at the maximum of the first peak, at ∼20 ms. The N20 component was chosen as it is known to be generated in area 3b of the primary somatosensory cortex (Baumgartner *et al*., 1991; Scherg & Buchner, 1993). Reliability and validity of this method has already been demonstrated in previous studies, and the spherical head model has been shown to be equal to a MRI-based boundary element head model for electrical source reconstruction in the primary somatosensory cortex (Kristeva-Feige *et al*., 1997; Yvert *et al*., 1997; Schaefer *et al*., 2002; Dinse *et al*., 2003). Coordinates of the dipole locations were given relative to a 3-D head coordinate system. The origin of this coordinate system was set at the midpoint of the medial–lateral axis (*y*-axis), which joins the centre points of the entrance to the acoustic meati of the left and right ear (positive towards the left ear). The posterior–anterior axis (*x*-axis) was orientated from the origin to the nasion (positive towards the nasion) and the inferior–superior axis (*z*-axis) was perpendicular to the *x*-*y* plane (positive towards the vertex). The polar angle of the dipole locations was computed. Additionally, maximal dipole strength and goodness of fit (GOF) for the calculated dipole solutions were assessed. A dipole solution was considered stable if the GOF was > 95%. The polar angle difference and the Euclidean distance between the N20 dipole locations after median and ulnar nerve stimulation were used as a parameter describing the extension of the cortical hand representation in the primary somatosensory cortex. Mixed peripheral nerves such as the ulnar and median nerve contain a large proportion of proprioceptive fibers (e.g. muscle afferents), which essentially contribute to the earliest SEP component (N20) due to their fast conducting properties (Desmedt & Brunko, 1980). Therefore the analysis of SEPs after mixed peripheral nerve stimulation provides information about the processing of proprioceptive and cutaneous input.

### *Mapping of motor evoked potentials (MEPs) using transcranial magnetic stimulation (TMS)*

Ten out of 15 violin players (three males and seven females, aged between 19 and 33 years; mean age 24.9 ± 5.0 years) were subjected to MEP mapping, and their results were compared to the data obtained in a control group of 12 healthy nonmusicians (five male and seven female, aged between 19 and 42 years; mean 29.8 ± 6.9 years). Five musicians did not agree to participate in this part of the study. TMS was applied with a Magstim 200 HP device (The Magstim Company, Whitland, Dyfed, UK) to assess the motor output map of the first dorsal interosseus (FDI) muscle. We used a figure-of-eight coil (outside diameter 8.7 cm, peak magnetic field strength 2.2 T, peak electric field strength 660 V/m), which predominantly stimulates neural structures under its centre. MEPs were recorded with surface electrodes from the FDI muscle consecutively on both sides and stored on an electromyography

© The Authors (2007). Journal Compilation © Federation of European Neuroscience Societies and Blackwell Publishing Ltd

(EMG) device (Neuropack 8; Nihon Kohden, Tokyo, Japan). The bandpass filter was 20 Hz to 2 kHz and the gain 0.1–1 mV per division. The TMS pulses were delivered while the subjects were seated comfortably in a chair. During the whole mapping procedure, muscle relaxation was monitored by recording EMG activity of the FDI muscle with surface electrodes (gain 0.1 mV per division). Motor threshold was determined at rest to the nearest 1% of the stimulator output, and was defined as the minimum intensity which produced five motor evoked potentials >50 μV out of 10 trials. Threshold was determined over the scalp position were TMS previously elicited the highest amplitude. Starting at this scalp position and using a stimulation intensity of 110% of the motor threshold, the motor cortex was examined systematically in rostral, dorsal, medial and lateral direction in steps of 1 cm until no further MEP could be elicited. The positions were identified with the help of a tight-fitting cap with a coordinate system on it (1 × 1 cm width). Cz was identified as the intersection of the interaural line and the connection between nasion and inion, which made it possible to localize the coordinates relative to Cz. The *x*-coordinate was used to indicate the distance in anterior–posterior direction relative to Cz, and the *y*-coordinate to indicate the distance in medial–lateral direction. Coordinates of Cz were defined as 0/0. During the whole mapping procedure the coil was held tangentially to the head in an anterior–posterior direction, with the grip pointing backwards. Eight stimuli were applied to each position of the grid, and the averaged peak-to-peak MEP amplitude was considered for further statistical analysis. Amplitudes <10 μV were regarded as zero value. Afterwards, we calculated the sum of all MEP amplitudes (SOA) of the motor output map, and its amplitude-weighted centre of gravity (COG). The *x* and *y* coordinates of the COG were derived from the distribution of MEP amplitudes within the motor output area. They were calculated according to the formulae $[\Sigma(x \times z)/\Sigma z]$ and $[\Sigma(y \times z)/\Sigma z]$, with *x* and *y* as positions along the *x* and *y* axes, and *z* as the amplitude at this position (Liepert *et al*., 1999). Additionally, the number of positions from which MEPs could be elicited was used as a marker for the area size of the motor output map, each position equalling 1 $cm^2$.

### *Motor performance*

Several different fine motor skills of the left and right arms, hands and fingers were assessed by testing steadiness, aiming, tapping, and peg-board performance. Seven violin players (three males and four females, aged between 20 and 33 years; mean age 23.6 ± 4.4 years) participated in these tests. The results for the violin players were compared to results obtained in 17 healthy nonmusicians (10 female and seven male, aged between 19 and 34 years).

The different subtests were applied using the commercially available 'MLS' of the Vienna Test System (Dr G. Schuhfried Ges.m.b.H., Mödling, Austria), consisting of a standardized metal worktop (300 × 300 × 15 mm) with holes and contact fields for the different subtests (Kalisch *et al*., 2006) (Fig. 1A). Two contact pencils are connected to the sides of the worktop. The number and duration of contacts between pencils and test board are measured by closing electrical circuits (5 V, 20 mA). Data are transferred via an interface to a computer for analysis.

Each task was explained by reading a standardized instruction sheet, and then the task was demonstrated to ensure that the subjects fully understood what they had to do. While the subjects sat in front of the board, support of the test arm was not permitted except for the tapping task. All subtests were performed consecutively with the right and the left hand.

#### *Steadiness*

This test examined the ability to obtain a prescribed arm–hand position and to maintain it for a defined time period. The subjects were instructed to hold the tip of a test pencil perpendicularly into a hole of diameter 8.5 mm without touching the wall (Fig. 1B). Each contact with the wall within a 32-s testing period was counted as an error. The number of errors and the duration of the contacts (errors) were measured.

#### *Aiming*

This test examined the ability to accomplish fast arm–hand movements for small targets. Twenty contact fields with a diameter of 5 mm

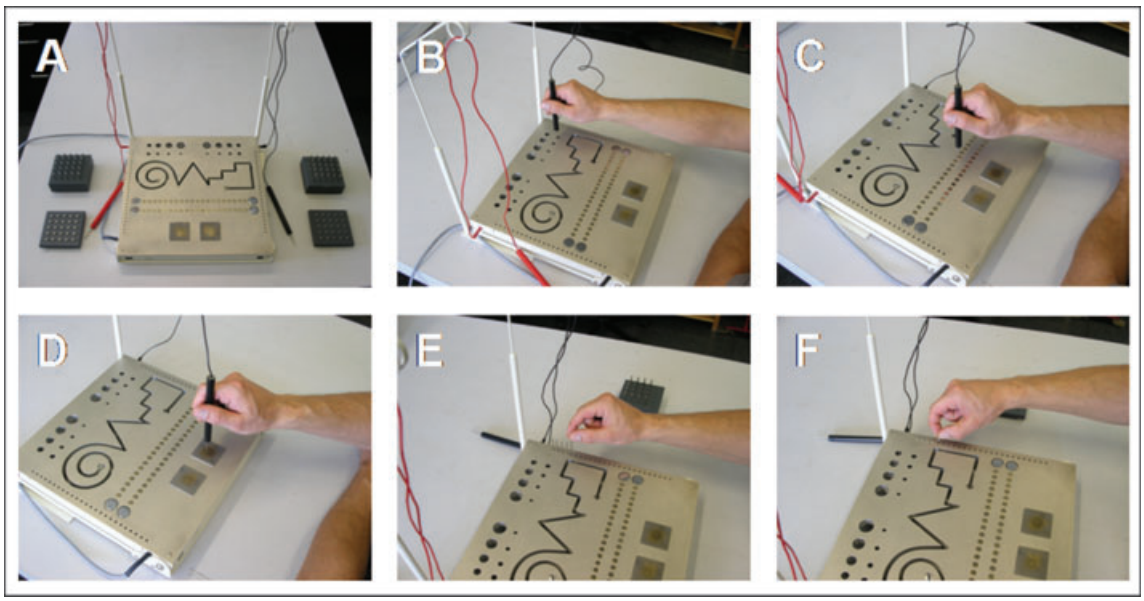


FIG. 1. Assessment of fine motor skills. (A) A commercially available test series of fine motor skills was used to assess the motor performance of both hands. (B) 'Steadiness' examined the ability to obtain a prescribed arm–hand position and to maintain it for a defined time period. (C) 'Aiming' examined the ability to accomplish fast arm–hand movements for small targets. (D) 'Tapping' examined the ability to perform very fast, repetitive wrist–finger movements with little emphasis on precision of movement. (E) Long and (F) short peg-board tests examined the dexterity of the hand and fingers.

© The Authors (2007). Journal Compilation © Federation of European Neuroscience Societies and Blackwell Publishing Ltd

each separated by 4 mm between adjacent fields were linearly arranged on the worktop. The subjects were instructed to hit these 20 fields one after the other with the tip of a test pencil as fast as possible, starting on the right and ending on the left side, avoiding contacts with the worktop outside the contact fields (Fig. 1C). Total performance time (duration), the number of errors (hits outside the contact fields) and the error duration were measured.

*Tapping*

This test examined the ability to perform very fast, repetitive wrist–finger movements with little emphasis on precision of movement. Subjects were instructed to hit a 40 × 40 mm contact field with the tip of a test pencil as often and fast as possible within a 32-s testing period (Fig. 1D). In this task, support of the forearm was allowed. The number of hits within the testing period was measured.

*Long and short peg board*

These tests examined the dexterity of the hand and fingers. The subjects were instructed to put 25 long pegs (length 50 mm, diameter 2 mm) from a box into 25 linearly arranged holes on the worktop as fast as possible (Fig. 1E). The box was placed at a distance of 10 cm from the right margin of the worktop. The time for completing the task was measured. In a second test, an identical task had to be performed with short pegs (length 10 mm, diameter 2 mm; Fig. 1F).

Using the left hand, the steadiness, the aiming and the tapping subtest had to be performed in exactly the same manner as for the right hand, i.e. starting on the right in the aiming subtest. In the peg-board subtests, the box was placed at a distance of 10 cm from the left margin of the worktop.

### Statistical analysis

An ANOVA for repeated measurements was calculated, with 'hand' (right vs. left) as within-subject factor and 'group' (violinists vs. controls) as between-subjects factor, to analyse the different parameters obtained by SEP mapping, MEP mapping and assessment of motor performance. The Greenhouse–Geisser procedure was used with epsilon-corrected degrees of freedom if data showed significant deviations from sphericity. Paired and unpaired *t*-tests were used for *post hoc* analysis if the ANOVA revealed a significant interaction. For these *t*-tests, the significance level was adjusted by dividing it by the number of comparisons ($0.05/4 = 0.0125$; Bonferroni correction). Before using these parametric tests, normality was tested using the Kolmogorov–Smirnov test, and homogeneity of variances was confirmed by a Levene test. If these prerequisites for conducting parametric tests were not fulfilled, nonparametric tests were used (Wilcoxon signed-rank test for within-group comparisons, Mann–Whitney *U*-test for between-group comparisons), also using a Bonferroni-corrected significance level.

Additionally, Pearson's correlation coefficient was calculated in order to detect any possible relationship between different neurophysiological parameters and between neurophysiological and psychophysical parameters. Significance was assumed at the $P = 0.05$ level. For all statistical tests, the SPSS 14.0 software package (SPSS software, Munich, Germany) was used.

## Results

Five out of 15 violin players underwent all examinations, i.e. SEP mapping, TMS mapping and assessment of motor performance. Five violin players underwent only SEP and TMS mapping, and two only SEP and assessment of motor performance. In three musicians, only SEP mapping was performed. In the control group, eight subjects underwent only SEP mapping and 10 only MEP mapping, and in 15 subjects only the motor performance was assessed. Two control subjects participated in the MEP mapping and in the assessment of motor performance. In general, both the SEP and the MEP mapping revealed an interhemispheric asymmetry of the sensorimotor hand representation in violin players, which did not exist in nonmusician controls. However, the right-handed subjects showed a side-to-side asymmetry in motor performance which did not differ between violin players and control subjects. In detail, the results were as follows:

### SEP mapping after median and ulnar nerve stimulation

After electrical stimulation of both the median and the ulnar nerve, a stable dipole solution for the N20 SEP component was obtained in all 15 violin players, using a single equivalent dipole model. For the Euclidean distance between the N20 dipole localizations obtained after stimulation of the left median and the left ulnar nerve, ANOVA revealed a significant effect of the factor 'hand' ($F_{1,21} = 7.987$, $P = 0.010$), but not of the factor 'group' ($F_{1,21} = 0.758$, $P = 0.394$), with a significant interaction between the two factors ($F_{1,21} = 7.987$, $P = 0.022$). *Post hoc* testing indicated a significant right–left difference in the violin players (Euclidean distance: right hand, 5.7 ± 1.9; left hand, 8.8 ± 3.4 mm; $P = 0.002$) but not in the controls (Euclidean distance: right hand, 6.2 ± 2.9; left hand, 6.4 ± 3.5 mm; $P = 0.641$; Figs 2, 3 and 5A). Similarly, for the difference of the polar angles, there was a significant effect of the factor 'hand' ($F_{1,21} = 8.363$, $P = 0.009$), but not of the factor 'group' ($F_{1,21} = 0.511$, $P = 0.483$), with a significant interaction between the two factors ($F_{1,21} = 5.293$, $P = 0.032$). Again, a right–left difference was only observed in violin players (right hand, 1.9° ± 0.9°; left hand, 3.7° ± 1.5°; $P = 0.002$), but not in controls (right hand, 2.4° ± 1.5°; left hand, 2.6° ± 1.6°; $P = 0.545$; Fig. 5B).

Additionally, ANOVA showed a significant 'hand' effect for the *y*-coordinate ($F_{1,21} = 8.943$, $P = 0.007$) and the polar angle ($F_{1,21} = 5.518$, $P = 0.029$) of the N20 dipole after stimulation of the median nerve. The effect of the factor 'group' and the interaction between the two factors were not statistically significant, indicating a more medial localization of the N20 dipole after left median nerve stimulation in all participating subjects (Table 1).

After stimulation of the ulnar nerve, there was also a significant 'hand' effect for the *y*-coordinate ($F_{1,21} = 18.155$, $P = 0.001$), with a significant interaction between 'hand' and 'group' ($F_{1,21} = 5.696$, $P = 0.026$). Similarly, there was a significant 'hand' effect for the polar angle of the ulnar N20 dipole ($F_{1,21} = 12.821$, $P = 0.002$), with a significant interaction between 'hand' and 'group' ($F_{1,21} = 5.261$, $P = 0.032$). For the dipole strength of the ulnar N20 dipole, there was also a significant 'hand' effect ($F_{1,21} = 11.299$, $P = 0.003$), with a significant interaction between 'hand' and 'group' ($F_{1,21} = 5.667$, $P = 0.027$). *Post hoc* testing revealed a more medially located N20 dipole with a smaller polar angle after stimulation of the left ulnar nerve in the violin players, and a left-smaller-than-right asymmetry of the dipole strength only in the controls (Table 1).

Taken together, these results indicate an asymmetry of the hand representation in the primary somatosensory cortex of violin players which is mainly due to a medial extension and enlargement of the left-hand representation.

© The Authors (2007). Journal Compilation © Federation of European Neuroscience Societies and Blackwell Publishing Ltd

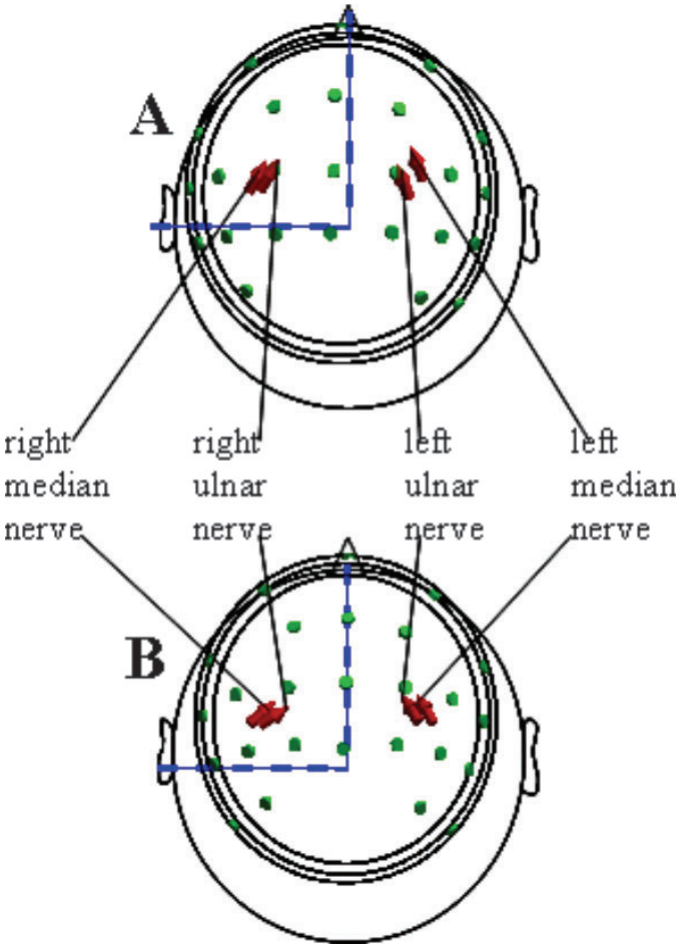


FIG. 2. SEP mapping (individual subject). Shown are the individual data of (A) J.V., a 25-year old female violin player, and of (B) J.A., a 24-year old female control subject. The arrows indicate the dipole positions and orientations of the N20 SEP component after stimulation of the right and left median and ulnar nerves. A spherical three-shell head model which was fitted to the individual electrodes is used. Electrodes are represented by the points. Note the larger distance between the N20 dipoles on the right hemisphere of the violinist after stimulation of the left ulnar and median nerves. In contrast, the distances between the N20 dipoles of the control subject were almost symmetrical.

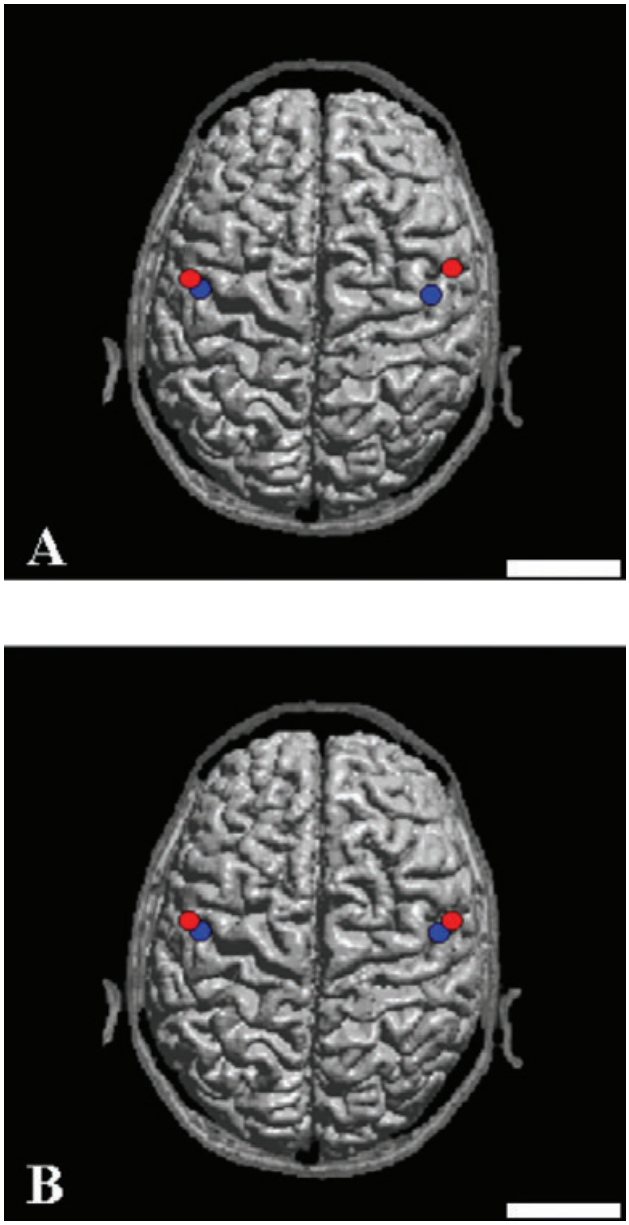


FIG. 3. SEP mapping (group data). Schematic projection of the average N20 dipole location after stimulation of the median nerve (red) and ulnar nerve (blue) in (A) right-handed violin players and (B) control subjects onto an MRI surface reconstruction. Note the greater distance on the violinists' right hemisphere (left hand stimulation) compared to the left hemisphere (right hand stimulation). In the control subjects, this interhemispheric difference was lacking.

### *MEP mapping of the FDI muscle*

An MEP mapping of the FDI muscle was performed in 10 violin players and in 12 nonmusician controls. For the area, ANOVA showed a significant influence of the factor 'hand' ($F_{1,20} = 5.172$, $P = 0.034$), and a significant interaction between 'hand' and 'group' ($F_{1,20} = 9.987$, $P = 0.005$), whereas the influence of the factor 'group' was statistically not significant ($F_{1,20} = 0.001$, $P = 0.970$). *Post hoc* analysis showed a significantly greater area of the motor output map of the left FDI muscle than of the right FDI in violin players, but not in controls (Table 2, Figs 4 and 5C). In addition, for the *y*-coordinate of the COG there was also a significant influence of the factor 'hand' ($F_{1,20} = 8.295$, $P = 0.009$), and a significant interaction between 'hand' and 'group' ($F_{1,20} = 13.794$, $P = 0.001$), but no significant influence of the factor 'group' ($F_{1,20} = 0.035$, $P = 0.854$). The COG of the left FDI motor map was significantly more laterally localized than the right FDI motor map in the violin players, but not in the controls (Table 2, Fig. 5D).

The results indicate an asymmetry of the FDI representation in the motor cortex of violin players, which is mainly based on an enlargement and lateral extension of the left FDI representation.

### *Motor performance*

Analysing the motor performance in violin players and controls, ANOVA revealed a significant influence of the factor 'hand' on the task duration in the long peg-board task ($F_{1,22} = 6.397$, $P = 0.019$; Fig. 6) and on the number of hits in the tapping task ($F_{1,22} = 58.061$, $P = 0.001$; Fig. 6). There was a tendency towards an increased

© The Authors (2007). Journal Compilation © Federation of European Neuroscience Societies and Blackwell Publishing Ltd

TABLE 1. Results of SEP mapping

| Subjects (*n*) | N20 dipole coordinates (mm) | | | Polar angle of the N20 dipole (°) | Dipole strength (nAm) | GOF (%) |
|---|---|---|---|---|---|---|
| | *x* (anterior–posterior) | *y* (medial–lateral) | *z* (cranial–caudal) | | | |
| Violinists (15) | | | | | | |
| Median nerve | | | | | | |
| Left | 25.0 ± 6.7 | 34.9 ± 4.9 | 96.5 ± 4.6 | 24.3 ± 2.0 | 8.7 ± 3.9 | 97.4 ± 1.3 |
| Right | 23.0 ± 5.0 | 40.7 ± 4.3 | 96.0 ± 3.7 | 26.1 ± 2.2 | 9.9 ± 4.6 | 97.5 ± 2.1 |
| Ulnar nerve | | | | | | |
| Left | 22.5 ± 6.0 | 29.0 ± 4.0* | 99.5 ± 7.7 | 20.6 ± 1.6* | 6.7 ± 2.2 | 97.4 ± 2.1 |
| Right | 21.9 ± 5.0 | 37.9 ± 5.5* | 98.2 ± 5.5 | 24.2 ± 2.8* | 7.1 ± 2.8 | 97.5 ± 1.3 |
| Control group (8) | | | | | | |
| Median nerve | | | | | | |
| Left | 24.5 ± 7.7 | 35.9 ± 8.6 | 92.6 ± 4.7 | 25.5 ± 3.2 | 9.2 ± 3.3 | 98.6 ± 0.4 |
| Right | 23.8 ± 7.5 | 38.1 ± 4.4 | 92.8 ± 4.2 | 26.1 ± 2.0 | 10.2 ± 2.8 | 98.4 ± 0.4 |
| Ulnar nerve | | | | | | |
| Left | 23.3 ± 8.5 | 31.6 ± 7.1 | 95.4 ± 7.0 | 22.9 ± 3.2 | 5.9 ± 1.2* | 98.5 ± 0.5 |
| Right | 24.0 ± 8.1 | 34.1 ± 5.1 | 96.4 ± 6.8 | 23.7 ± 2.6 | 7.9 ± 1.7* | 98.1 ± 1.2 |

Values are mean ± SD. *$P < 0.01$, side-to-side difference (paired *t*-test). GOF, goodness of fit.

TABLE 2. Results of TMS mapping

| Subjects (*n*) | Motor threshold (%) | Area ($cm^2$) | SOA (μV) | COG coordinates (cm) | |
|---|---|---|---|---|---|
| | | | | *x* (anterior–posterior) | *y* (medial–lateral) |
| Violinists (10) | | | | | |
| Left hand | 41.4 ± 12.8 | 16.7 ± 3.7* | 2570.4 ± 2181.5 | 1.7 ± 0.6 | 5.4 ± 0.5* |
| Right hand | 37.4 ± 7.5 | 12.1 ± 3.3* | 2107.1 ± 1969.7 | 1.5 ± 0.6 | 4.9 ± 0.6* |
| Control group (10) | | | | | |
| Left hand | 40.7 ± 7.1 | 14.1 ± 4.6 | 1414.8 ± 905.6 | 1.3 ± 0.7 | 5.2 ± 0.6 |
| Right hand | 40.6 ± 6.8 | 14.8 ± 4.4 | 1471.7 ± 1262.0 | 1.0 ± 0.9 | 5.2 ± 0.7 |

Values are mean ± SD. *$P < 0.01$, side-to-side difference (paired *t*-test).

number of hits in the tapping task in the violin players compared to the controls; this, however, failed to reach statistical significance ($F_{1,22} = 4.257$, $P = 0.051$ for the factor 'group'). A significant interaction between 'hand' and 'group' did not exist in the tapping task ($F_{1,22} = 0.375$, $P = 0.547$).

For the error number and the error duration in the aiming task, the prerequisites for conducting parametric tests were not fulfilled and therefore nonparametric tests were used. The left-to-right differences of the error number and the error duration did not significantly differ between violin players and controls (Mann–Whitney *U*-test, $P = 0.494$ for the number of errors and $P = 0.631$ for the error duration). Over both groups, there were significantly more errors (Wilcoxon signed-rank test, $P = 0.004$; Fig. 6), and a significantly longer error duration (Wilcoxon signed-rank test, $P = 0.002$) when the aiming task was performed with the left than with the right hand.

The results indicate that right-handed violin players and control subjects showed a right-better-than-left performance in a number of motor tasks, regardless of the study group to which they belonged.

### *Correlations*

In 10 violin players both MEP and SEP mapping was performed. We therefore performed a linear correlation analysis between different right–left quotients of parameters describing either motor or sensory cortical map characteristics. We found that the right–left quotients of the area of the FDI motor map assessed by MEP mapping were correlated with the right–left quotients for the Euclidean distance between the N20 dipoles obtained for stimulation of the median and ulnar nerves ($r = 0.808$, $P = 0.005$; Fig. 7A). Similarly, the right–left quotients of the area of the FDI motor map were correlated with the polar angle difference of the N20 dipoles of the median and ulnar nerve ($r = 0.913$, $P < 0.001$; Fig. 7B). These data indicate that the asymmetry in the primary somatosensory cortex was paralleled by an asymmetry in the primary motor cortex, and that subjects with a more extended asymmetry of the hand representation in primary somatosensory cortex (S1) also showed a more extended asymmetry in primary motor cortex (M1). We found no correlation between right–left quotients of parameters describing cortical maps and right–left quotients of motor performance parameters. We also found no relationship between cortical asymmetries or motor performance and the age at beginning of violin training, the years of regular violin training or the hours of daily practice.

## Discussion

Our main finding was a significant interhemispheric asymmetry in right-handed violin players, which was due to an enlargement of the left hand representation in S1 and M1, and which contrasted with the symmetrical representations in age-matched right-handed controls. At the behavioural level, however, this difference did not result in a different motor performance in violin players in general as compared

© The Authors (2007). Journal Compilation © Federation of European Neuroscience Societies and Blackwell Publishing Ltd

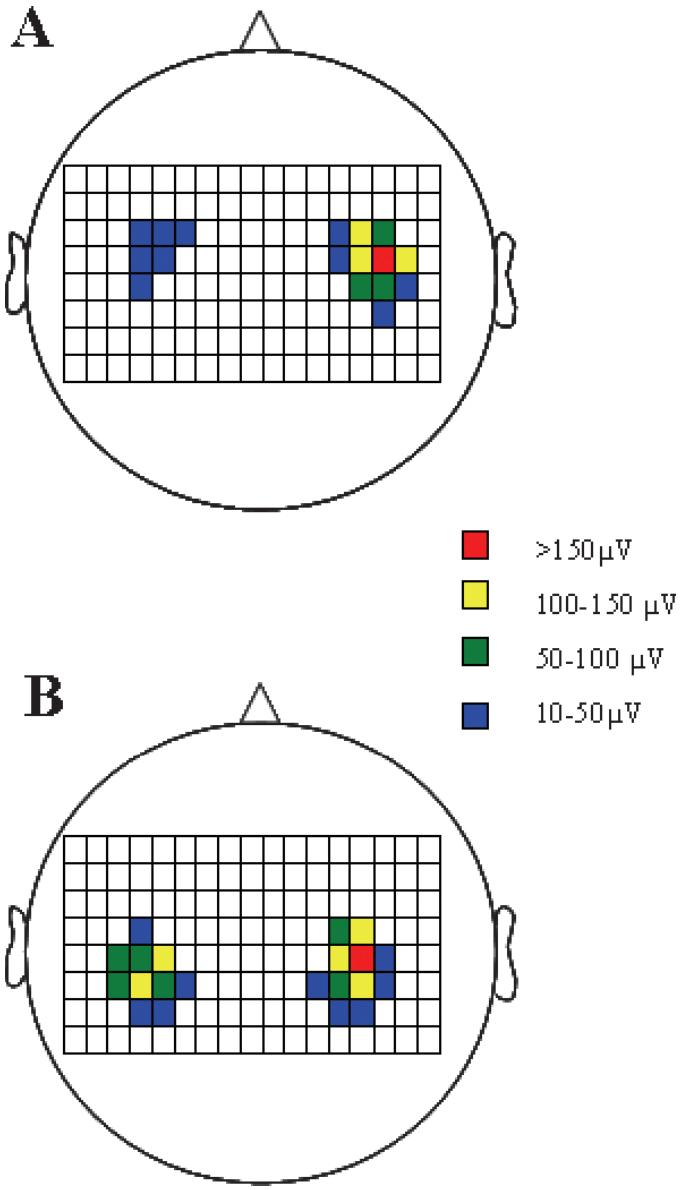


FIG. 4. TMS mapping (individual subject). Shown are the individual data of (A) J.V., a 25-year old female violin player (see Fig. 2), and of (B) A.B., a 25-year old female control subject. Filled squares represent the positions from which motor evoked potentials could be evoked in the contralateral FDI muscle, and the amplitudes are coded with different colours. Note the larger motor output map recorded from the left FDI of the violinist, which is also situated more laterally, whereas the motor output maps of the control subject are almost symmetrical.

to healthy controls, with a right-better-than-left performance in a number of motor tasks which was independent of the group.

The cortical findings are in line with previous study results (Elbert *et al*., 1995; Hashimoto *et al*., 2004; Bangert & Schlaug, 2006) which also demonstrated an atypical cortical asymmetry resulting from an increased representation of the left hand in the somatosensory and motor cortex of string players. However, these results seem to contradict results obtained by MR morphometry in keyboard players, who were found to have a more symmetrical intrasulcal length of the precentral gyrus, whereas here the nonmusician controls exhibited a pronounced left-larger-than-right asymmetry (Amunts *et al*., 1996; Amunts *et al*., 1997). In agreement with previous TMS mapping studies (Wilson *et al*., 1993; Cicinelli *et al*., 1997), a similar left-larger-than-right asymmetry of the motor cortex did not exist in our control group, and was also lacking in the study of Bangert & Schlaug (2006), who used the 'hand knob' as an anatomical marker for the hand representation in the motor cortex. This emphasizes the complementary character of different structural and functional markers obtained by different electrophysiological and imaging techniques, which might be indicative of different underlying physiological processes. Further, in the study by Amunts *et al*. (1997), some of the musicians were keyboard players who additionally played string instruments. It has been argued that this might have confounded the results as instrument-specific cortical asymmetries have been described for the motor cortex, with a right hemisphere advantage in string players and a left hemisphere advantage in keyboard players (Bangert & Schlaug, 2006). The same confounding factor might have contributed to the finding of a less lateralized speech-related modulation of motor cortical outputs in musicians, considering the heterogeneity of the instruments played by the musicians in this study (Lin *et al*., 2002).

There has been overwhelming evidence that functional and structural organization of the brain in musicians substantially differs from that in nonmusicians (Gaab & Schlaug, 2003; Schmithorst & Holland, 2003). It has been shown that multisensory information is processed in a qualitatively different way in trumpet players than in nonmusicians (Schulz *et al*., 2003), and that primary and secondary motor areas are activated to a lesser degree during bimanual coordination in concert pianists than in nonmusicians (Jäncke *et al*., 2000; Krings *et al*., 2000; Haslinger *et al*., 2004). In professional musicians, motor and auditory networks are more closely linked than in nonmusicians (Zatorre *et al*., 2007), with the motor cortex being activated by auditory stimuli (Bangert *et al*., 2006; D'Ausilio *et al*., 2006). Different motor areas show a greater response to rhythm perception in musicians than in nonmusicians (Grahn & Brett, 2007). This audio–motor interaction might even be specific to the individual instrument (Drost *et al*., 2007) Moreover, an fMRI study demonstrated audio–motor coupling to occur in nonmusician subjects when they were trained to play a novel piano piece over 5 days, putting emphasis on its relationship to the individual's motor experience (Lahav *et al*., 2007). Differences in white-matter architecture have been described in musicians compared to nonmusicians (Schmithorst & Wilke, 2002) and an increased grey-matter volume has been found in professional keyboard players, extending from the premotor region to the primary somatosensory cortex and into the anterior parietal lobe, using voxel-based morphometry (Gaser & Schlaug, 2003a,b). In behavioural studies, professional pianists had not only lower spatial discrimination thresholds at the top of the index finger but also a significantly larger gain after Hebbian learning induced by a coactivation protocol, pointing to enhanced learning abilities as compared to nonmusician controls (Ragert *et al*., 2004). Similar findings were reported in the motor system (Hund-Georgiadis & von Cramon, 1999); these might be related to an enhanced motorcortical excitability and synaptic plasticity (Rosenkranz *et al*., 2007).

In musicians, deliberate practice is thought to be the main factor in the acquisition and maintenance of extraordinary musical skills (Ericsson *et al*., 1993; Krampe & Ericsson, 1996). Besides, there is evidence that musicians who began their training before the age of 7 years have long-lasting benefits for performance later in life, which suggests a sensitive period in development for the motor component of musical training (Watanabe *et al*., 2007). The fact that, in several studies, a correlation has been established between

© The Authors (2007). Journal Compilation © Federation of European Neuroscience Societies and Blackwell Publishing Ltd

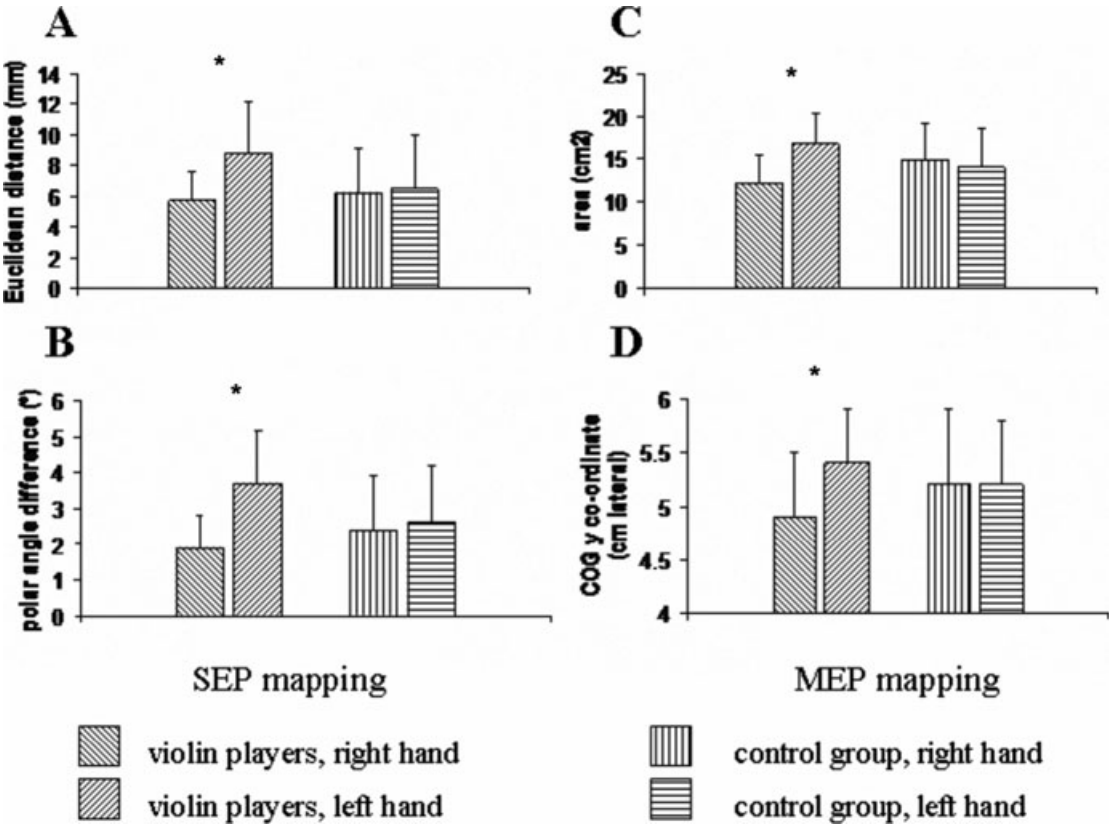


FIG. 5. Results of the SEP and MEP mapping in violin players and controls. Shown are (A) the Euclidean distance between the N20 dipole after stimulation of the median and ulnar nerve, (B) the polar angle difference between the N20 dipole after stimulation of the median and ulnar nerve, (C) the area of the motor output map of the first dorsal interosseus muscle and (D) the *y*-coordinate of the COG of the motor output map which indicates the position in medial–lateral direction. Note the significant right–left difference for these parameters in violin players (*$P < 0.01$, paired *t*-test), which was not observed in nonmusician controls.

the extent of structural and functional differences of the brain and the age at which the training started and/or the amount of training argues against the possibility that these differences are pre-existing and the cause, rather than the consequence, of practising music (Münte *et al*., 2002; Zatorre *et al*., 2007). Therefore, the asymmetry of the hand representation in M1 and S1, which was seen in our study, might be a consequence of an increased use of the left hand in the violin players, and therefore can be considered an example of use-dependent plasticity. There are a variety of studies which stress the impact of motor skill acquisition or perceptual learning on the functional organization of the brain (Karni, 1996). Extensive training of elementary finger tapping movements over several weeks changed the pattern of motor cortex excitability in healthy subjects (Koeneke *et al*., 2006). An increased representation of the reading hand in M1 and S1 was found in Braille readers (Pascual-Leone & Torres, 1993; Pascual-Leone *et al*., 1993; Sterr *et al*., 1998), and skilled racquet players showed an interhemispheric asymmetry in M1 as revealed by TMS mapping of the FDI muscle (Pearce *et al*., 2000). In contrast, reduced use such as an immobilization of a leg over several weeks led to a reduced M1 representation (Liepert *et al*., 1995). It has been shown that such use-dependent plasticity does not only occur on the level of synapses or cortical maps but can even lead to changes of the brain's macroscopic structure (Draganski *et al*., 2004).

An important issue in this study was the relationship between cortical sensorimotor asymmetries and functional asymmetries of fine motor skills. In order to address this question, we used a test battery examining different aspects of motor performance in both musicians and nonmusicians. However, there was no significant difference between right-handed violin players and right-handed nonmusician controls with respect to the right-better-than-left motor performance in a number of motor tasks. Furthermore, correlation analysis did not establish an individual relationship between motor performance and cortical representation in M1 and S1, as was demonstrated in previous studies for the two-point discrimination threshold and the cortical representation of the index finger in S1 (Pleger *et al*., 2001; Dinse *et al*., 2003). An improved performance, which was linked to an enlargement of the cortical map, has been reported to be present in several studies in animals and humans (Jenkins *et al*., 1990; Recanzone *et al*., 1992; Pascual-Leone & Torres, 1993). In these studies, generally the trained perceptual skill that induced the cortical map plasticity was improved. However, there was little information about the specificity of this phenomenon, i.e. whether there was a training-induced improvement of skills independent of the trained tasks. Our results suggest that the cortical asymmetry in string players as observed in our study might be an example of use-dependent plasticity which is specific to the trained motor abilities but does not lead to an accompanying asymmetry of motor abilities in general, as motor performance was not affected in a variety of tests which did not necessarily reflect the trained motor abilities in musicians. This lack of generalisation therefore has to be considered as an additional strong argument against the hypothesis that the cortical asymmetries could be pre-existing and the cause rather than the consequence of the musical practice. The results are in contrast to previous reports, which

© The Authors (2007). Journal Compilation © Federation of European Neuroscience Societies and Blackwell Publishing Ltd

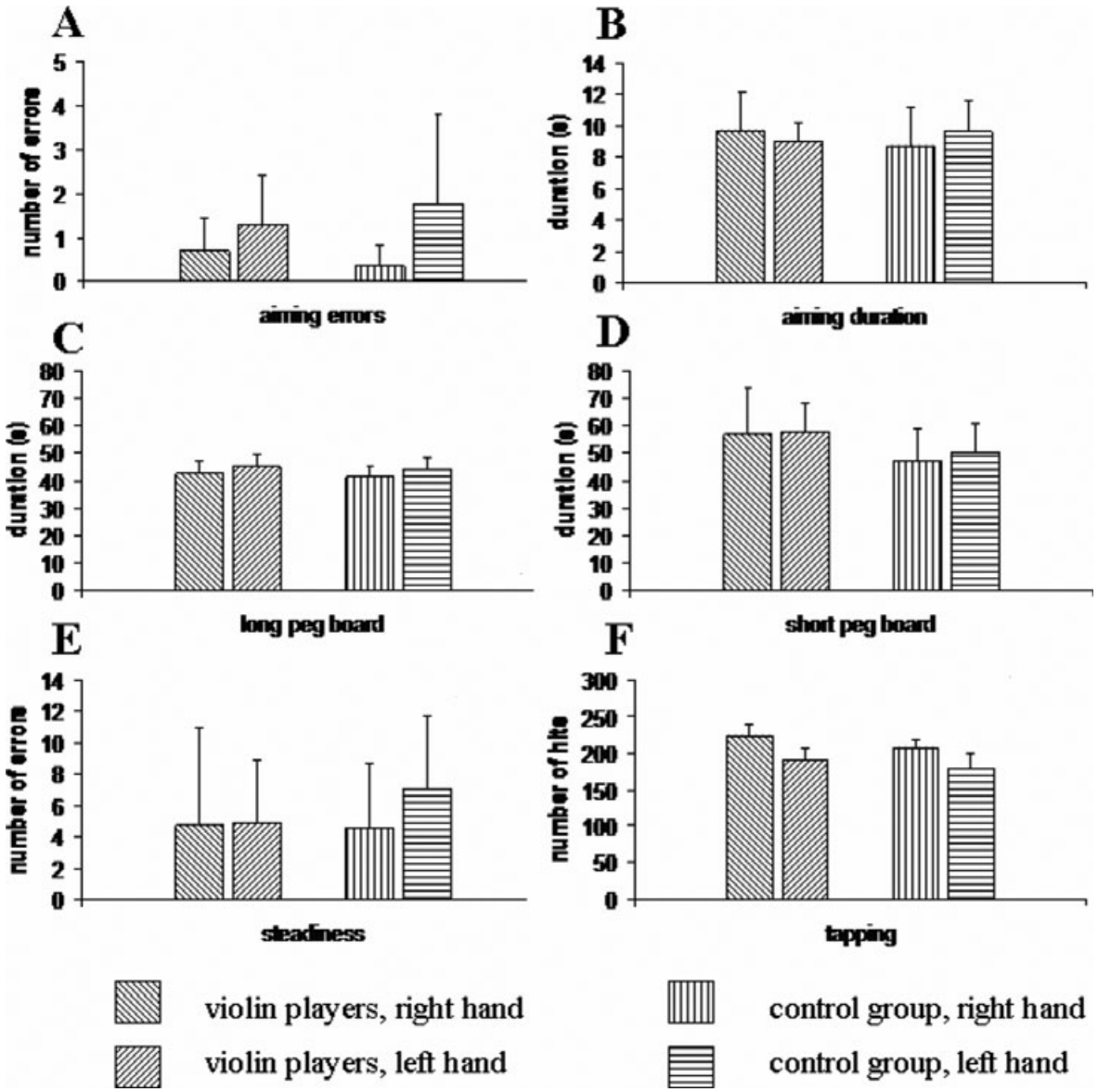


FIG. 6. Results of the different motor tasks in violin players and controls. Shown are (A and B) the right–left comparisons for the aiming task, (C and D) the long (C) and short (D) peg-board task, (E) the steadiness task and (F) the tapping task. Note the right–left differences for (A) the aiming errors, (C) the duration of the long peg-board task, and (F) the number of hits in the tapping task, which were independent of the group (musicians or nonmusicians).

described a reduced hand skill asymmetry in professional right-handed string players and piano players (Jäncke *et al*., 1997). The main reason for this difference might be the methodological differences in the tests of motor performance, and especially the differences between the tapping tasks used in the two studies. The index finger tapping task used by Jäncke *et al*. (1997) mainly examined the speed of isolated index finger movements, whereas the tapping task in our study was performed with a pencil, therefore mainly examining the speed of wrist–finger movements. Hence, the specifically trained motor abilities in musicians might more accurately be represented by the index finger tapping task than by the tapping task used in our study. On the other hand, although less pronounced than in nonmusicians, musicians still showed significant right-hand superiority in the study by Jäncke *et al*. (1997), suggesting that the difference between musicians and nonmusicians might be small and only detectable in larger groups of subjects.

In our study, we found a high congruence between the asymmetry in M1 and S1 with respect to the enlargement of the cortical representation of the left hand, which in string players is highly skilled with respect to the performance of complex motor tasks. In line with these results, we previously demonstrated in a series of experiments that repetitive training of a motor task consisting of a synchronized contraction of two limb muscles leads to plastic changes in M1 as well as in S1 (Tegenthoff *et al*., 1999, 2004; Schwenkreis *et al*., 2001; Pleger *et al*., 2003). These results were discussed with respect to a task-specific sensory (especially proprioceptive) input to S1, and to horizontal connections which closely link S1 to M1. Evidence for a close anatomical and functional relationship between S1 and M1 came from a number of animal studies (Lemon, 1981; Porter, 1991, 1997; Kaneko *et al*., 1994). They are in line with fMRI studies which showed a high functional connectivity between M1 and S1 in humans performing a tactile frequency discrimination task (Pleger *et al*.,

© The Authors (2007). Journal Compilation © Federation of European Neuroscience Societies and Blackwell Publishing Ltd

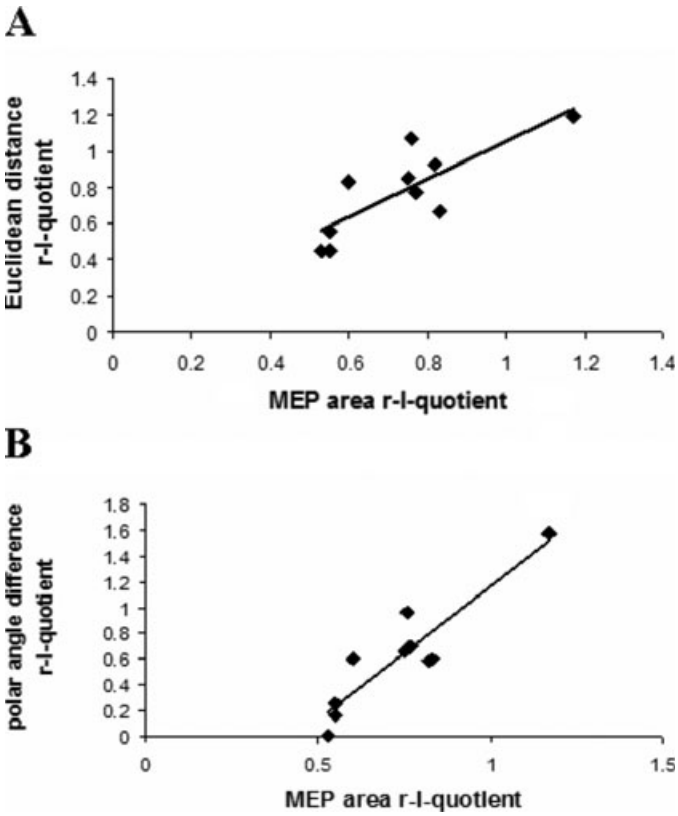


FIG. 7. Sensorimotor interaction. Correlation between the right–left quotients of (A) the Euclidean distance between the N20 dipole after median and ulnar nerve stimulation and the area of the motor output map of the FDI muscle for individual subjects (violin players), and between the right–left quotients of (B) the polar angle differences of the N20 dipoles and the areas of the motor maps. Correlation analysis revealed a significant linear correlation between interhemispheric asymmetries of the somatosensory and the motor cortices.

2006), and which revealed a simultaneous activation of S1 and M1 during active movements (Rausch *et al*., 1998). This high functional connectivity between M1 and S1 might account for the asymmetry in the two cortices seen in the violin players we tested, and the SEP mapping method that was used to investigate S1 in our study (stimulation of mixed peripheral nerves which contain a high percentage of fast-conducting proprioceptive fibers) underlines the importance of the proprioceptive input in this process. Whereas our results reveal a static aspect of sensorimotor interaction, recently in a number of experiments a dynamic motor task-related adaptation of representational maps within S1 was demonstrated using neuromagnetic source localization (Braun *et al*., 2001; Schaefer *et al*., 2004, 2005). They showed an increased distance between the cortical representation of digit 1 and digit 5, which was only present during motor task performance and which depended on the complexity of the motor task (Wühle *et al*., 2006). Both the static and dynamic aspects of this sensorimotor interaction emphasize their importance for skilled motor performance.

To summarise, our results give evidence for a highly asymmetrical hand representation in string players as compared to nonmusicians, with a high congruence of changes in the primary somatosensory and motor cortex. However, these cortical asymmetries were not paralleled by accompanying altered asymmetries of motor skills in general, suggesting that the cortical asymmetries are the result of use-dependent plasticity as a specific consequence of extensive musical practice.

## Acknowledgements

This work was supported by grants from the Deutsche Forschungsgemeinschaft (grant numbers DI 334/10-4 and TE 315/2-1). We thank H. Richter for statistical advice.

## Abbreviations

COG, centre of gravity; FDI, first dorsal interosseus muscle; GFP, global field power; MEP, motor evoked potential; M1, primary motor cortex; SEP, somatosensory evoked potential; SOA, sum of amplitudes; S1, primary somatosensory cortex; TMS, transcranial magnetic stimulation.

## References

Altenmüller, E. (2003) Focal dystonia: advances in brain imaging and understanding of fine motor control in musicians. *Hand Clin.*, **19**, 523–538, xi.

Amunts, K., Schlaug, G., Jäncke, L., Steinmetz, H., Schleicher, A., Dabringhaus, A. & Zilles, K. (1997) Motor cortex and hand motor skills: structural compliance in the human brain. *Hum. Brain Mapp.*, **5**, 206–215.

Amunts, K., Schlaug, G., Schleicher, A., Steinmetz, H., Dabringhaus, A., Roland, P.E. & Zilles, K. (1996) Asymmetry in the human motor cortex and handedness. *Neuroimage*, **4**, 216–222.

Bangert, M., Peschel, T., Schlaug, G., Rotte, M., Drescher, D., Hinrichs, H., Heinze, H.J. & Altenmüller, E. (2006) Shared networks for auditory and motor processing in professional pianists: evidence from fMRI conjunction. *Neuroimage*, **30**, 917–926.

Bangert, M. & Schlaug, G. (2006) Specialization of the specialized in features of external human brain morphology. *Eur. J. Neurosci.*, **24**, 1832–1834.

Baumgartner, C., Doppelbauer, A., Deecke, L., Barth, D.S., Zeitlhofer, J., Lindinger, G. & Sutherling, W.W. (1991) Neuromagnetic investigation of somatotopy of human hand somatosensory cortex. *Exp. Brain Res.*, **87**, 641–648.

Bishop, D.V., Ross, V.A., Daniels, M.S. & Bright, P. (1996) The measurement of hand preference: a validation study comparing three groups of right-handers. *Br. J. Psychol.*, **87**, 269–285.

Braun, C., Heinz, U., Schweizer, R., Wiech, K., Birbaumer, N. & Topka, H. (2001) Dynamic organization of the somatosensory cortex induced by motor activity. *Brain*, **124**, 2259–2267.

Buonomano, D.V. & Merzenich, M.M. (1998) Cortical plasticity: from synapses to maps. *Annu. Rev. Neurosci.*, **21**, 149–186.

Cicinelli, P., Traversa, R., Bassi, A., Scivoletto, G. & Rossini, P.M. (1997) Interhemispheric differences of hand muscle representation in human motor cortex. *Muscle Nerve*, **20**, 535–542.

Coq, J.O. & Xerri, C. (1999) Tactile impoverishment and sensorimotor restriction deteriorate the forepaw cutaneous map in the primary somatosensory cortex of adult rats. *Exp. Brain Res.*, **129**, 518–531.

Corey, D.M., Hurley, M.M. & Foundas, A.L. (2001) Right and left handedness defined: a multivariate approach using hand preference and hand performance measures. *Neuropsychiatry Neuropsychol. Behav. Neurol.*, **14**, 144–152.

D'Ausilio, A., Altenmüller, E., Olivetti Belardinelli, M. & Lotze, M. (2006) Cross-modal plasticity of the motor cortex while listening to a rehearsed musical piece. *Eur. J. Neurosci.*, **24**, 955–958.

Desmedt, J.E. & Brunko, E. (1980) Functional organization of far-field and cortical components of somatosensory evoked potentials in normal adults. In Desmedt, J.E. (ed.), *Clinical Uses of Cerebral Brainstem and Spinal Somatosensory Evoked Potentials*. Karger, Basel, pp. 27–50.

Dinse, H.R. & Merzenich, M.M. (2002) Adaption of inputs in the somatosensory system. In Fahle, M. & Poggio, T. (eds), *Perceptual Learning.* MIT Press, Cambridge, pp. 19–42.

Dinse, H.R., Ragert, P., Pleger, B., Schwenkreis, P. & Tegenthoff, M. (2003) Pharmacological modulation of perceptual learning and associated cortical reorganization. *Science*, **301**, 91–94.

Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U. & May, A. (2004) Neuroplasticity: changes in grey matter induced by training. *Nature*, **427**, 311–312.

Drost, U.C., Rieger, M. & Prinz, W. (2007) Instrument specificity in experienced musicians. *Q. J. Exp. Psychol.*, **60**, 527–533.

Elbert, T., Pantev, C., Wienbruch, C., Rockstroh, B. & Taub, E. (1995) Increased use of the left hand in string players associated with increased cortical representation of the fingers. *Science*, **270**, 305–307.

© The Authors (2007). Journal Compilation © Federation of European Neuroscience Societies and Blackwell Publishing Ltd

Ericsson, K.A., Krampe, R.T. & Tesch-Römer, C. (1993) The role of deliberate practice in the aquisition of expert performance. *Psychol. Rev.*, **100**, 363–406.

Gaab, N. & Schlaug, G. (2003) Musicians differ from nonmusicians in brain activation despite performance matching. *Ann. NY Acad. Sci.*, **999**, 385–388.

Gaser, C. & Schlaug, G. (2003a) Brain structures differ between musicians and non-musicians. *J. Neurosci.*, **23**, 9240–9245.

Gaser, C. & Schlaug, G. (2003b) Gray matter differences between musicians and nonmusicians. *Ann. NY Acad. Sci.*, **999**, 514–517.

Grahn, J.A. & Brett, M. (2007) Rhythm and beat perception in motor areas of the brain. *J. Cogn. Neurosci.*, **19**, 893–906.

Hashimoto, I., Suzuki, A., Kimura, T., Iguchi, Y., Tanosaki, M., Takino, R., Haruta, Y. & Taira, M. (2004) Is there training-dependent reorganization of digit representations in area 3b of string players? *Clin. Neurophysiol.*, **115**, 435–447.

Haslinger, B., Erhard, P., Altenmüller, E., Hennenlotter, A., Schwaiger, M., Grafin von Einsiedel, H., Rummeny, E., Conrad, B. & Ceballos-Baumann, A.O. (2004) Reduced recruitment of motor association areas during bimanual coordination in concert pianists. *Hum. Brain Mapp.*, **22**, 206–215.

Henkel, V., Mergl, R., Juckel, G., Rujescu, D., Mavrogiorgou, P., Giegling, I., Moller, H. & Hegerl, U. (2001) Assessment of handedness using a digitizing tablet: a new method. *Neuropsychologia*, **39**, 1158–1166.

Hund-Georgiadis, M. & von Cramon, D.Y. (1999) Motor-learning-related changes in piano players and non-musicians revealed by functional magnetic-resonance signals. *Exp. Brain Res.*, **125**, 417–425.

Jäncke, L., Schlaug, G. & Steinmetz, H. (1997) Hand skill asymmetry in professional musicians. *Brain Cogn.*, **34**, 424–432.

Jäncke, L., Shah, N.J. & Peters, M. (2000) Cortical activations in primary and secondary motor areas for complex bimanual movements in professional pianists. *Brain Res. Cogn. Brain Res.*, **10**, 177–183.

Jenkins, W.M., Merzenich, M.M., Ochs, M.T., Allard, T. & Guic-Robles, E. (1990) Functional reorganization of primary somatosensory cortex in adult owl monkeys after behaviorally controlled tactile stimulation. *J. Neurophysiol.*, **63**, 82–104.

Kalisch, T., Wilimzig, C., Kleibel, N., Tegenthoff, M. & Dinse, H.R. (2006) Age-related attenuation of dominant hand superiority. *PLoS ONE*, **1**, e90.

Kaneko, T., Caria, M.A. & Asanuma, H. (1994) Information processing within the motor cortex. II. Intracortical connections between neurons receiving somatosensory cortical input and motor output neurons of the cortex. *J. Comp. Neurol.*, **345**, 172–184.

Karni, A. (1996) The acquisition of perceptual and motor skills: a memory system in the adult human cortex. *Brain Res. Cogn. Brain Res.*, **5**, 39–48.

Karni, A., Meyer, G., Jezzard, P., Adams, M.M., Turner, R. & Ungerleider, L.G. (1995) Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature*, **377**, 155–158.

Karni, A., Meyer, G., Rey-Hipolito, C., Jezzard, P., Adams, M.M., Turner, R. & Ungerleider, L.G. (1998) The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. *Proc. Natl Acad. Sci. USA*, **95**, 861–868.

Koeneke, S., Lutz, K., Herwig, U., Ziemann, U. & Jäncke, L. (2006) Extensive training of elementary finger tapping movements changes the pattern of motor cortex excitability. *Exp. Brain Res.*, **174**, 199–209.

Krampe, R.T. & Ericsson, K.A. (1996) Maintaining excellence: deliberate practice and elite performance in young and older pianists. *J. Exp. Psychol. Gen.*, **125**, 331–359.

Krings, T., Topper, R., Foltys, H., Erberich, S., Sparing, R., Willmes, K. & Thron, A. (2000) Cortical activation patterns during complex motor tasks in piano players and control subjects. A functional magnetic resonance imaging study. *Neurosci. Lett.*, **278**, 189–193.

Kristeva-Feige, R., Grimm, C., Huppertz, H.J., Otte, M., Schreiber, A., Jager, D., Feige, B., Buchert, M., Hennig, J., Mergner, T. & Lucking, C.H. (1997) Reproducibility and validity of electric source localisation with high-resolution electroencephalography. *Electroencephalogr. Clin. Neurophysiol.*, **103**, 652–660.

Lahav, A., Saltzman, E. & Schlaug, G. (2007) Action representation of sound: audiomotor recognition network while listening to newly acquired actions. *J. Neurosci.*, **27**, 308–314.

Lemon, R.N. (1981) Functional properties of monkey motor cortex neurones receiving afferent input from the hand and fingers. *J. Physiol. (Lond.)*, **311**, 497–519.

Liepert, J., Tegenthoff, M. & Malin, J.P. (1995) Changes of cortical motor area size during immobilization. *Electroencephalogr. Clin. Neurophysiol.*, **97**, 382–386.

Liepert, J., Terborg, C. & Weiller, C. (1999) Motor plasticity induced by synchronized thumb and foot movements. *Exp. Brain Res.*, **125**, 435–439.

Lin, K.L., Kobayashi, M. & Pascual-Leone, A. (2002) Effects of musical training on speech-induced modulation in corticospinal excitability. *Neuroreport*, **13**, 899–902.

Münte, T.F., Altenmüller, E. & Jäncke, L. (2002) The musician's brain as a model of neuroplasticity. *Nat. Rev. Neurosci.*, **3**, 473–478.

Nudo, R.J., Milliken, G.W., Jenkins, W.M. & Merzenich, M.M. (1996) Use-dependent alterations of movement representations in primary motor cortex of adult squirrel monkeys. *J. Neurosci.*, **16**, 785–807.

Oldfield, R.C. (1971) The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, **9**, 97–113.

Pantev, C., Oostenveld, R., Engelien, A., Ross, B., Roberts, L.E. & Hoke, M. (1998) Increased auditory cortical representation in musicians. *Nature*, **392**, 811–814.

Pantev, C., Roberts, L.E., Schulz, M., Engelien, A. & Ross, B. (2001) Timbre-specific enhancement of auditory cortical representations in musicians. *Neuroreport*, **12**, 169–174.

Pantev, C., Ross, B., Fujioka, T., Trainor, L.J., Schulte, M. & Schulz, M. (2003) Music and learning-induced cortical plasticity. *Ann. NY Acad. Sci.*, **999**, 438–450.

Pascual-Leone, A., Cammarota, A., Wassermann, E.M., Brasil-Neto, J.P., Cohen, L.G. & Hallett, M. (1993) Modulation of motor cortical outputs to the reading hand of Braille readers. *Ann. Neurol.*, **34**, 33–37.

Pascual-Leone, A., Grafman, J. & Hallett, M. (1994) Modulation of cortical motor output maps during development of implicit and explicit knowledge. *Science*, **263**, 1287–1289.

Pascual-Leone, A. & Torres, F. (1993) Plasticity of the sensorimotor cortex representation of the reading finger in Braille readers. *Brain*, **116**, 39–52.

Pearce, A.J., Thickbroom, G.W., Byrnes, M.L. & Mastaglia, F.L. (2000) Functional reorganisation of the corticomotor projection to the hand in skilled racquet players. *Exp. Brain Res.*, **130**, 238–243.

Pleger, B., Blankenburg, F., Bestmann, S., Ruff, C.C., Wiech, K., Stephan, K.E., Friston, K.J. & Dolan, R.J. (2006) Repetitive transcranial magnetic stimulation-induced changes in sensorimotor coupling parallel improvements of somatosensation in humans. *J. Neurosci.*, **26**, 1945–1952.

Pleger, B., Dinse, H.R., Ragert, P., Schwenkreis, P., Malin, J.P. & Tegenthoff, M. (2001) Shifts in cortical representations predict human discrimination improvement. *Proc. Natl Acad. Sci. USA*, **98**, 12255–12260.

Pleger, B., Schwenkreis, P., Dinse, H.R., Ragert, P., Höffken, O., Malin, J.P. & Tegenthoff, M. (2003) Pharmacological suppression of plastic changes in human primary somatosensory cortex after motor learning. *Exp. Brain Res.*, **148**, 525–532.

Porter, L.L. (1991) Patterns of connectivity in the cat sensory-motor cortex: a light and electron microscope analysis of the projection arising from area 3a. *J. Comp. Neurol.*, **312**, 404–414.

Porter, L.L. (1997) Morphological Characterization of a Cortico-cortical relay in the cat sensorimotor cortex. *Cereb. Cortex*, **7**, 100–109.

Ragert, P., Schmidt, A., Altenmüller, E. & Dinse, H.R. (2004) Superior tactile performance and learning in professional pianists: evidence for meta-plasticity in musicians. *Eur. J. Neurosci.*, **19**, 473–478.

Rausch, M., Spengler, F. & Eysel, U.T. (1998) Proprioception acts as the main source of input in human S-I activation experiments: a functional MRI study. *Neuroreport*, **9**, 2865–2868.

Recanzone, G.H., Merzenich, M.M., Jenkins, W.M., Grajski, K.A. & Dinse, H.R. (1992) Topographic reorganization of the hand representation in cortical area 3b owl monkeys trained in a frequency-discrimination task. *J. Neurophysiol.*, **67**, 1031–1056.

Rosenkranz, K., Williamon, A. & Rothwell, J.C. (2007) Motorcortical excitability and synaptic plasticity is enhanced in professional musicians. *J. Neurosci.*, **27**, 5200–5206.

Sanes, J.N. & Donoghue, J.P. (2000) Plasticity and primary motor cortex. *Annu. Rev. Neurosci.*, **23**, 393–415.

Schaefer, M., Flor, H., Heinze, H.J. & Rotte, M. (2005) Dynamic shifts in the organization of primary somatosensory cortex induced by bimanual spatial coupling of motor activity. *Neuroimage.*, **25**, 395–400.

Schaefer, M., Muhlnickel, W., Grusser, S.M. & Flor, H. (2002) Reproducibility and stability of neuroelectric source imaging in primary somatosensory cortex. *Brain Topogr.*, **14**, 179–189.

Schaefer, M., Rothemund, Y., Heinze, H.J. & Rotte, M. (2004) Short-term plasticity of the primary somatosensory cortex during tool use. *Neuroreport.*, **15**, 1293–1297.

Scherg, M. & Buchner, H. (1993) Somatosensory evoked potentials and magnetic fields: separation of multiple source activities. *Physiol. Meas.*, **14** (Suppl. 4A), A35–A39.

Schlaug, G. (2001) The brain of musicians. A model for functional and structural adaptation. *Ann. NY Acad. Sci.*, **930**, 281–299.

© The Authors (2007). Journal Compilation © Federation of European Neuroscience Societies and Blackwell Publishing Ltd

Schmithorst, V.J. & Holland, S.K. (2003) The effect of musical training on music processing: a functional magnetic resonance imaging study in humans. *Neurosci. Lett.*, **348**, 65–68.

Schmithorst, V.J. & Wilke, M. (2002) Differences in white matter architecture between musicians and non-musicians: a diffusion tensor imaging study. *Neurosci. Lett.*, **321**, 57–60.

Schulz, M., Ross, B. & Pantev, C. (2003) Evidence for training-induced crossmodal reorganization of cortical functions in trumpet players. *Neuroreport*, **14**, 157–161.

Schwenkreis, P., Pleger, B., Höffken, O., Malin, J.P. & Tegenthoff, M. (2001) Repetitive training of a synchronised movement induces short-term plastic changes in the human primary somatosensory cortex. *Neurosci. Lett.*, **312**, 99–102.

Sterr, A., Muller, M.M., Elbert, T., Rockstroh, B., Pantev, C. & Taub, E. (1998) Perceptual correlates of changes in cortical representation of fingers in blind multifinger Braille readers. *J. Neurosci.*, **18**, 4417–4423.

Tegenthoff, M., Cornelius, B., Pleger, B., Malin, J.P. & Schwenkreis, P. (2004) Amphetamine enhances training-induced motor cortex plasticity. *Acta Neurol. Scand.*, **109**, 330–336.

Tegenthoff, M., Witscher, K., Schwenkreis, P. & Liepert, J. (1999) Pharmacological modulation of training-induced plastic changes in human motor cortex. *Electroencephalogr. Clin. Neurophysiol. Suppl.*, **51**, 188–196.

Watanabe, D., Savion-Lemieux, T. & Penhune, V.B. (2007) The effect of early musical training on adult motor performance: evidence for a sensitive period in motor learning. *Exp. Brain Res.*, **176**, 332–340.

Wilson, S.A., Thickbroom, G.W. & Mastaglia, F.L. (1993) Transcranial magnetic stimulation mapping of the motor cortex in normal subjects. The representation of two intrinsic hand muscles. *J. Neurol. Sci.*, **118**, 134–144.

Wühle, A.D., Fahlbusch, J.J. & Braun, C. (2006) Effects of motor activity on the organization of primary somatosensory cortex. *Neuroreport*, **17**, 39–43.

Yvert, B., Bertrand, O., Thevenet, M., Echallier, J.F. & Pernier, J. (1997) A systematic evaluation of the spherical model accuracy in EEG dipole localization. *Electroencephalogr. Clin. Neurophysiol.*, **102**, 452–459.

Zatorre, R.J., Chen, J.L. & Penhune, V.B. (2007) When the brain plays music: auditory–motor interactions in music perception and production. *Nat. Rev. Neurosci.*, **8**, 547–558.

© The Authors (2007). Journal Compilation © Federation of European Neuroscience Societies and Blackwell Publishing Ltd