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The musician's brain: functional imaging of amateurs and professionals during performance and imagery

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Abstract

We compared activation maps of professional and amateur violinists during actual and imagined performance of Mozart's violin concerto in G major (KV216). Execution and imagination of (left hand) fingering movements of the first 16 bars of the concerto were performed. Electromyography (EMG) feedback was used during imagery training to avoid actual movement execution and EMG recording was employed during the scanning of both executed and imagined musical performances. We observed that professional musicians generated higher EMG amplitudes during movement execution and showed focused cerebral activations in the contralateral primary sensorimotor cortex, the bilateral superior parietal lobes, and the ipsilateral anterior cerebellar hemisphere. The finding that professionals exhibited higher activity of the right primary auditory cortex during execution may reflect an increased strength of audio–motor associative connectivity. It appears that during execution of musical sequences in professionals, a higher economy of motor areas frees resources for increased connectivity between the finger sequences and auditory as well as somatosensory loops, which may account for the superior musical performance. Professionals also demonstrated more focused activation patterns during imagined musical performance. However, the auditory–motor loop was not involved during imagined performances in either musician group. It seems that the motor and auditory systems are coactivated as a consequence of musical training but only if one system (motor or auditory) becomes activated by actual movement execution or live musical auditory stimuli.

Keywords: Music; Motor learning; Imagery; String players; fMRI

Introduction

Motor skill performance requires the need to overcome the numerous degrees of freedoms (Bernstein, 1967), acquisition of well-coordinated body movements, and the sequencing of movements in appropriate trajectories within the temporal demands of the task and its physical constraints. Such complexity is well demonstrated in musical training and performance. Particularly, in learning to perform a piece of music on an instrument, one has to coordinate the required hand and finger movement sequences within a strictly defined temporal structure. The process of achieving skilled performance relies on visual, auditory, and somatosensory feedback and integration, as well as long-term rehearsal. Given the multimodal nature and intensity of musical training, musicians are ideal subjects for the investigation of the various aspects of complex skill acquisition.

With continued practice in motor skills, performances become more precise and automatic and one gains dexterity as well as flexibility in adapting to changes and task demands. This often results in increased electromyography (EMG) amplitudes of the target muscles and a more precise coordination of movements (Seitz and Roland, 1992) in-

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cluding the suppression of associated movements of the other hand during unilateral movement execution (Rjintjes et al., 1999). Such behavioral modifications that accompany motor skill acquisition and long-term practice have been found to manifest structural (Schlaug et al., 1995; Schlaug, 2001; Amunts et al., 1997) and functional changes within the brain (Elbert et al., 1995; Pantev et al., 1998, 2001).

Functional magnetic resonance imaging (fMRI) studies investigating the performance of sequential finger movements reported that professional pianists, in comparison to nonmusicians, showed decreased motor activations within the supplementary motor area (SMA), the premotor cortex (PMC), and the ipsilateral primary motor cortex (iM1) during movement performances of varying complexities (e.g., Hund-Georgiadis and von Cramon, 1999; Jaenke et al., 2000). These authors proposed that prolonged musical training and efficiency in playing an instrument is associated with the liberation of additional resources for other aspects of artistic and motor performance. Furthermore, the idea of reduced effort following increased motor training has also been echoed by Krings et al. (2000).

On the contrary, Karni et al. (1995, 1998) observed a subsequent enlargement of cortical activity in the contralateral primary motor cortex (cM1) during learning (and repetition) of rapid finger movement sequences within the period of a few weeks (after an initial decrease) that persisted for 4 weeks to several months posttraining. Correspondingly, Seitz et al. (1994) also found that cM1 and bilateral PMC were more intensely activated as movement trajectories became increasingly well rehearsed. With increased training experience, the contribution of the dorsolateral prefrontal lobe, known to be involved in early phases of motor training (Sakai et al., 1997; Pascual-Leone et al., 1996), decreases. These prefrontal activations have been observed to be prominent during learning but not during well-rehearsed performances (Jueptner et al., 1997a, 1997b), which are observed to recruit the parietal regions (e.g., Sadato et al., 1996; Sakai et al., 1998). In particular, the inferior parietal lobe (inferior to the intraparietal sulcus; BA 39, 40) is found to be predominantly active during movements in relation to one's own body (Halsband et al., 2001), and the superior parietal lobe has been described to be involved in the storage of graphomotor trajectories (Seitz et al., 1997). As such, rather than being stored only in the cM1, once acquired, representations of movement sequences might be more widely distributed across additional motor areas such as the PMC and parietal areas (Penhune and Doyon, 2002).

In fact, Shadmehr and Holcomb (1997) described a shift of activation sites from a predominance in the prefrontal regions to the PMC (lateral BA 6), superior posterior parietal (BA 7), and cerebellar structures within 6 h of practice, underlining the importance of the training duration on the resulting activations. Interestingly, these changes are also observed within cerebellar activation sites, which decreased with continued practice over several days to 4 weeks (e.g., Penhune and Doyon, 2002), a time frame much longer than the training duration employed in Shadmehr and Holcomb's (1997) study. Furthermore, a decrease in cerebellar activation after continued practice is found to be followed by an increase of activation within the basal ganglia (e.g., Doyon et al., 1996). Consequently, such observations have encouraged the assumption that early motor learning may depend predominantly on a cerebello-cortical network while automation may rely more on a striato-cortical circuit (Doyon et al., 2002).

As motor sequences and the timing of such sequences in playing music on an instrument are acquired, new associative connections between different sensory inputs are formed. Studies in developmental aspects of musical skill acquisition have observed cross-modality functional coupling with musical training. In particular, the combined auditory feedback and motor training on the piano results in the coactivation of cortical auditory and sensorimotor hand regions in either pure auditory or silent motor tasks (Bangert et al., 2001). It might be that such cross-modal coactivations will be strengthened with increased musical training.

While learning to play an instrument has led one to focus mainly on the overt, observable behavioral aspects of skill acquisition, the benefits of mental imagery in motor skill learning is becoming increasingly appreciated in the literature (Yue and Cole, 1992; Langheim et al., 2002). In essence, imagery can be differentiated into sensory (such as visual or auditory) and motor imagination. Furthermore, motor imagery and motor performance are correlated and are believed to activate similar neural structures (e.g., Jeannerod, 1995; Beisteiner et al., 1995). In accordance with this hypothesis, fMRI studies investigating imagery of finger and hand movements (Leonardo et al., 1995; Sabbah et al., 1995; Porro et al., 1996; Lotze et al., 1999) demonstrated activation of the SMA, the PMC, and the cerebellum but also the cM1. Given that professional musicians employ imagery during training, we are interested in whether increased motor imagery experience (cf. amateurs) might result in changes in brain activations manifested during imagined motor performances.

The current study aimed to combine the ecological validity of a musical task with monitoring cortical activations manifested during the actual and imagined performance of this task. More specifically, it is of interest whether there might be (1) manifestations of differential neural activity with reference to musical experience, training onset, and training stages. To this end, our particular hypotheses are that increased musical training might lead to an increased focus on the contralateral M1 (Seitz et al., 1994; Hund-Georgiadis and Cramon, 1999; Jaenke et al., 2000), a decreased activation of the ipsilateral M1 (e.g., Hund-Georgiadis and Cramon, 1999), and alterations of cerebellar activations as a consequence of training onset (e.g., Penhune and Doyon, 2002); (2) manifestations of economization in professionals—of fewer activated brain areas for the same task; and (3) evidence of auditory coactivation during silent performance of musical sequences as previously observed in EEG studies (Bangert et al., 2001).

Methods

Subjects

Sixteen healthy right-handed subjects participated in the fMRI study, which was approved by the local ethics committee: Eight right-handed professional violinists (two female, six male; age range: 35–53 years) enlisted from either a German or a Swiss Philharmonic or Chamber orchestra and eight right-handed amateurs (six females, two males; age range, 18–65 years, not significantly different from the professional group) were recruited through announcements within the University of Tübingen. Handedness was assessed by the Edinburgh Handedness Inventory (Oldfield, 1971) and informed consent was given prior to the study.

Within the group of subjects studied, professionals began musical training, on average, at the age of 6.75 years until present without interruption; amateurs at the age of 9.50 years, pausing for 11.14 years on average. On the whole, professionals spent 35.63 years (SD = 6.37) playing their instruments, while amateurs spent 12.03 years (SD = 3.59), ($t(14) = 9.14$; $P < 0.001$). Professionals also engaged more hours in practice (in the past 3 months): 30.87 h per week (SD = 3.95) compared to the 1.45 h per week (SD = 1.60), ($t(9.24) = 19.52$; $P < 0.001$) of the amateurs. In addition, unlike the amateurs, all professionals reported extensive use of imagined musical performance during their training routine.

Musical task

The first 16 bars of Mozart's violin concerto in G major (KV216), a familiar piece that is part of every professional violinist's performance repertoire and is not too challenging for amateurs, were selected as the task to be performed in both execution (EM) and imagery (IM) conditions. The selected section of the solo part of the concerto demands highly dexterous finger and hand movement coordination (1) to execute the strictly defined rhythm sequences, (2) to bring into synchrony the hand and fingers during vibrato, and (3) to realize trills with the quick repetitive movements of one finger alone. In addition, without auditory or visual feedback during scanning, the selected section of Mozart's concerto had to be well-rehearsed and stored in memory.

Subjects were required to execute only the left hand fingering movements (EM), keeping their right hands and arms as relaxed as possible, or to imagine themselves performing the same movements (IM) without any actual physical movements. The professionals did no additional training of the piece the week before the experiment because they already could play it very well. The amateurs did a training of the selected part with their violin starting one week before scanning. However, given the limited space in the scanner, movement execution on a real violin was not feasible. To overcome this problem, subjects performed their finger tapping movements (together with whole hand displacement) on their chests, which substituted the violin fingerboard. This transference—trained only on the scanning day—was perceived as natural and the training was terminated once subjects could tap the correct rhythm with the correct placements of their fingers, as verified by the attending professional violinist (G.S.).

With respect to the imagination task, subjects were required to imagine the physical performance of their fingers as vividly as possible without any actual movements. The imagination (IM) task training followed after the execution (EM) task training 90 min before scanning time, using the same auditory (concert recording) and visual (musical score) materials. Therefore IM training included not only kinesthetic but also visual and auditory material. Muscle activation was controlled employing EMG feedback prior to the actual fMRI measurement. While professionals required only some 10 min of training (given their familiarity with the chosen piece and motor imagery), amateurs needed roughly an hour before they were confident in executing and imagining the correct finger movements. fMRI scanning was performed immediately after the training. Concentration and vividness of imagery of movement, of pitch, and of rhythm during the fMRI-scanning were assessed with a visual analogue scale (VAS; from 0 = "not at all" to 10 = "very good") after the fMRI scanning.

EMG measurement

Prior to and during the fMRI scanning, the activation of finger extensors of both hands was monitored via surface EMG recordings using an EMG system appropriate for measurements in the fMRI environment (IED system, Hamburg). The lower arm extensors of both hand sides were measured with two channels prior to and during fMRI using superficial silver chloride electrodes. The signals were amplified by a factor of 100, filtered with 200-Hz lowpass and 2-Hz highpass filters, and transformed into a light signal which is sent to a PC for data visualization and storage using DASYLAB. A frequency analysis was performed to assess EMG differences between sessions and subjects using BRAIN VISION (Version 1.03). EMG amplitudes of frequencies between 2 and 200 Hz were averaged for each condition and subject. Subsequently, the differences between activations (EM, IM) and rest for all subjects of each condition were subjected to multivariate analysis of variances (MANOVA) using STATVIEW. Bivariate correlations of demographic data, VAS scoring, and EMG data were calculated using SPSS.

fMRI measurement

Functional magnetic resonance imaging of cerebral blood oxygen level dependent (BOLD) signal changes was performed and echo planar MR images were acquired using a Siemens 1.5-T scanner (SIEMENS Vision, Erlangen, Germany), employing the following sequences: sequence repetition time (TR), 8 s; signal (echo)-gathering time (TE), 59 ms; field of view (FOV), 250 mm; matrix size, 96 × 128; scan time, 6.4 s. For each scan, 36 axial slices (slice thickness, 3 mm; interslice gap, 1 mm), encompassing the whole brain, were acquired. Using a block design of six scan measurements for every active (EM or IM) and every rest period, alternating four times, a total of 48 whole brain volumes were measured for each task condition. Subjects each performed the EM and IM task conditions twice, the order of which being counterbalanced across subjects.

fMRI data evaluation

Evaluation of activation maps was performed with the statistical parametric mapping program (SPM'99, Wellcome Department of Neurology). After discarding the first 2 images to suppress T1 saturation effects, the remaining 46 whole brain volume images from seven professionals and seven amateurs (one subject from each group participated as pilot-study subjects) of each task condition were realigned to the third image of each session (task condition) to correct for interscan head movements. Coregistration, using the anterior commissure as the reference, and spatial normalization to SPM stereotactic template were then applied to each subject's data, allowing for (within) group analysis. The normalized images were smoothed with a 6-mm full-width-at-half-maximum (FWHM) Gaussian kernel to increase the signal-to-noise-ratio.

Subsequently, contrast images of each group were generated by voxel-wise t statistic calculation via estimation of a prespecified model (a simple delayed box-car reference vector, describing the alternating periods of activity and rest for each condition across subjects, and convolved with the canonical hemodynamic response function) with a highpass filter of 191 s. Statistical analysis, comparing voxel-wise activity (EM or IM) and rest periods, were performed (fixed-effect statistics). Whole volume correction with a height threshold of $P < 0.05$ and no additional spatial threshold was applied to generate an overview of the brain activity (activations and deactivations) in the two conditions (see Fig. 2). Activated pixels surviving the criteria were superimposed on the Montreal Neurological Institute (MNI) render brain.

The prominent deactivations in frontal and parietal regions, corresponding to observations by Gusnard and Raichle (2001), posed difficulties for direct comparisons of activations in different conditions within and between groups (i.e., professionals vs amateurs). Therefore exclusive masking, comparing only suprathreshold activation sides between groups (amateurs and professionals) or task condition (imagery versus execution), was applied with masking threshold of 0.05 and the same intensity threshold of $P < 0.05$ was used to correct for the whole measurement volume. The coordinates of highest activated voxel of significant activation sides were transformed from the SPM-MNI space to the Talairach coordinates (Talairach and Tournoix, 1988) using the MATLAB conversion program "mni2tal" written by Matthew Brett (MRC Cognition and Brain Sciences Unit, Cambridge, England). Thereafter, the corresponding Brodmann's areas were compared to an automated version implemented in the "talairach daemon" (http://ric.uthscsa.edu/td_applet/) before being labeled. For those areas associated with our a priori hypotheses (cM1, iM1, and cerebellum), the z values of the highest activated voxel within preselected anatomical regions (bilateral precentral gyri and bilateral anterior cerebellar hemispheres) were correlated with(a) demographic data, (b) VAS scoring, and (c) EMG data using SPSS-rendered bivariate correlations.

Results

EMG measurements

During movement performance, professionals generated larger EMG amplitudes compared to amateurs (normalization to the resting period; MANOVA; $F(1) = 5.38$; $P < 0.05$; for hand*condition*group) and this effect is significant only for the left hand (condition*group: $F(1) = 6.1$; $P < 0.05$; right hand, $F(1) = 2.4$; NS; see Fig. 1B). In addition, EMG amplitudes during left-hand performance correlated positively with the training time per week ($r = 0.68$; $P < 0.05$) and during lifetime ($r = 0.62$; $P < 0.05$). In agreement with our premise that there should not be any actual muscle activities during IM, there were no observable differences in EMG amplitudes between rest and motor imagery in either subject group. As such, these EMG data could be excluded from further analysis.

VAS ratings

Apart from the fact that professional violinists are found to have higher ratings for vividness of imagined movement ($t(14) = 3.36$; $P < 0.05$), there were no overall significant differences between subgroups in all ratings given the corrections for multiple testing (e.g., rhythm ($t(7.77) = 3.15$; $P = 0.056$; see Fig. 1C). In addition, vividness of imagined rhythm and pitch are both positively correlated with duration (and frequency) of training per week (rhythm: $r = 0.65$; $P < 0.01$; pitch; $r = 0.54$; $P < 0.05$) and lifetime (rhythm: $r = 0.68$; $P < 0.005$; pitch: $r = 0.64$; $P < 0.05$).

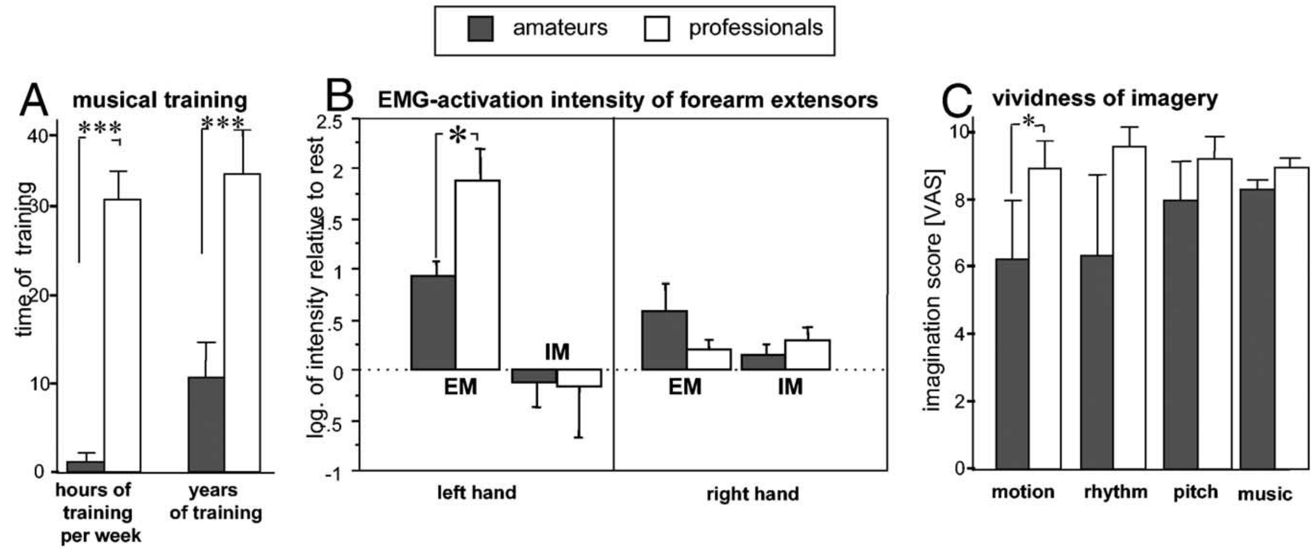

Fig. 1. Duration of musical training, EMG data, and vividness of imagery. The standard deviations are indexed with a line in each part of the figure. (A) Musical training between amateurs and professionals differed highly significantly in years of lifetime training ($t(14) = 9.14$; $P < 0.001$) and hours of training per week ($t(9.24) = 19.52$; $P < 0.001$). (B) During movement execution (EM) professionals generated higher EMG amplitudes than amateurs ($F(1) = 5.38$; $P < 0.05$), although there were no differences in EMG amplitudes between rest and motor imagery in both groups. (C) Amateur and professional musicians differed significantly in their vividness of imagery for the movement ($t(14) = 3.36$; $*P < 0.05$).

fMRI measures

Executed movements

Activation. In general, both groups manifested very similar activations, which were more widely distributed in the amateurs, compared to the more circumscribed activities observed in professional violinists (refer to Fig. 2, red). Within the sensorimotor regions, apart from professionals with only contralateral motor cortex activations in the hand area compared to the bilateral primary motor cortical activities in amateurs, both groups manifested activations in bilateral somatosensory and secondary motor areas (SMA, PMC), including bilateral anterior and posterior cerebellum. Moreover, amateurs' iM1 activation correlated positively but not significantly ($r = 0.61$; NS) with associated motor activity of the right hand as measured by EMG monitoring. Similarly, both amateurs and professionals also exhibited comparable activities in the bilateral superior parietal lobes, the left anterior superior temporal lobe, and right Heschl's gyrus. Within the prefrontal regions, apart from similar activation in the left frontal operculum, amateurs showed activations in bilateral middle and orbital frontal areas where professionals had none. Interestingly, activity in the basal ganglia (left caudate nucleus) was seen only in the amateurs. In addition, two notable correlations could be established about the professional group: first, the average EMG amplitude during EM correlated with the cM1 BOLD effect intensity ($r = 0.82$; $P < 0.05$; highest activated voxel) and second, the earlier professionals began music training the higher were the activations observed within their ipsilateral cerebellar hemispheres ($r = 0.67$; $P < 0.05$) during EM.

Deactivation. Likewise, deactivations in both groups were similar and mainly observed within the dorso-medial frontal and parietal regions (see Fig. 2A; green).

Masking between groups: professionals (EM) vs amateurs (EM). While the right, contralateral M1 and the left, ipsilateral anterior cerebellum were more strongly activated in professionals, amateurs manifested stronger BOLD signals in the ipsilateral M1, the contralateral anterior cerebellum, bilateral premotor and somatosensory cortices, and the supplementary motor area (refer to Fig. 3A, Table 1A). Furthermore, activity within the frontal regions (bilateral middle and orbital frontal gyri) including the left frontal operculum and that within the basal ganglia (left caudate nucleus) were manifested only in amateurs. Finally, while it was the anterior superior temporal gyrus (BA22, 38) that was more strongly activated in the amateurs, professionals manifested more prominent primary auditory cortex (A1/Heschl's gyrus) activity during the motor performance of the musical task.

Imagined musical performance

Activation. Unlike the EM condition, BOLD signals were quite distinct in each group (refer to Fig. 1B, red, for an overview). Amateurs manifested sparsely clustered but widely distributed activity, with particular prominence in bilateral lateral frontal, inferior opercularis, the primary and supplementary motor, parietal, anterior temporal, and posterior lateral cerebellar regions. On the other hand, BOLD-signals in professionals were observed in few but specific clusters within left M1, SMA, bilateral posterior cerebellum, bilateral superior and left inferior parietal cortices, and the right superior opercular part of the inferior frontal gyrus.

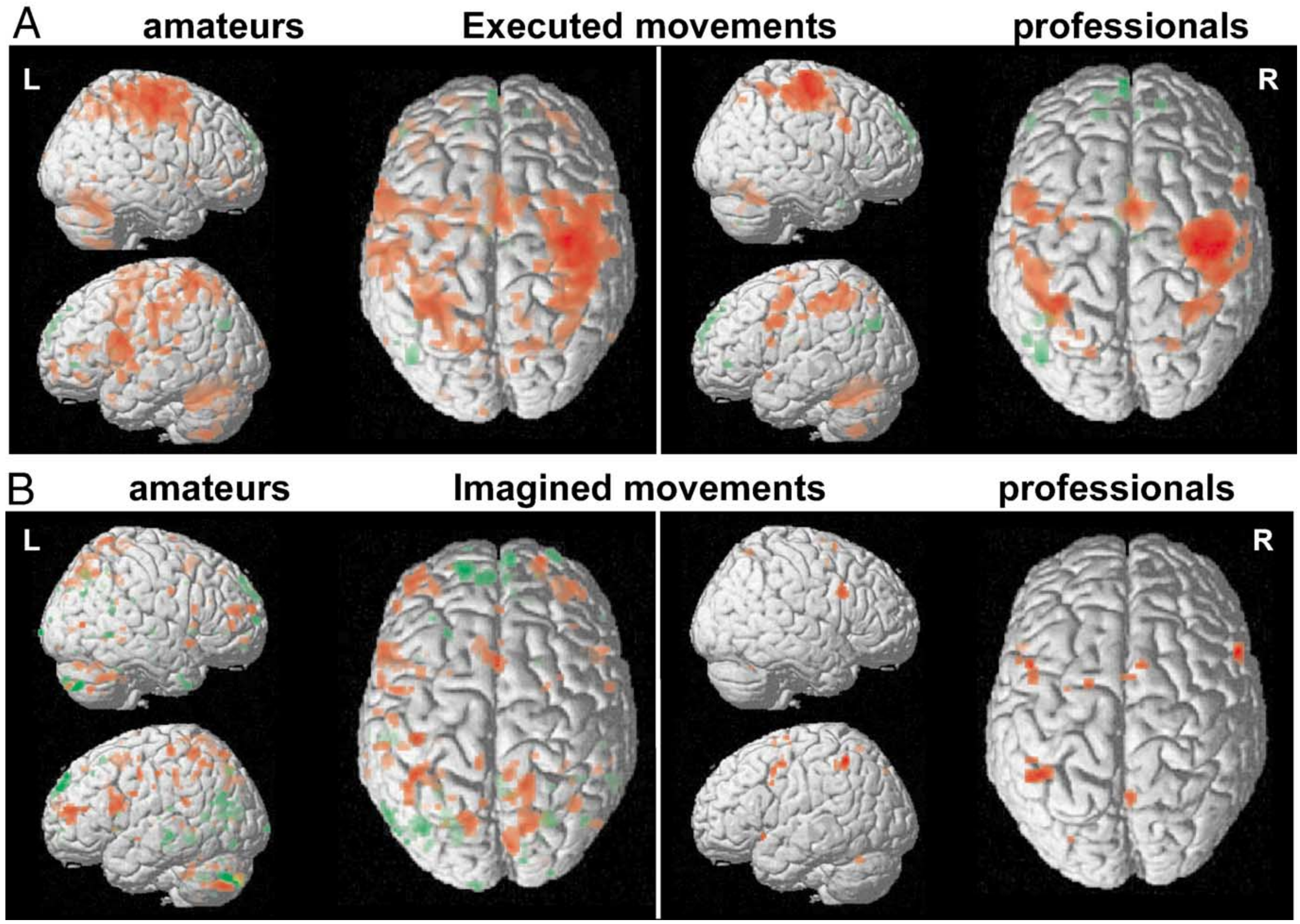

Fig. 2. Within-group-analysis: fMRI activation maps during executed (A) and imagined (B) left-hand performance of the musical sequence in the group of amateurs (left) and the professional musicians (right). The 3D-segmented top view and the left and right lateral view are shown. Increased BOLD effect during the task is coded red, while decreased BOLD effect is coded green. (A) Executed performance. Both groups manifested very similar activations, being more distributed in the amateurs, compared to the more circumscribed activities observed in professional violinists. Deactivations in both groups were present mainly in the medio-dorsal prefrontal and in the left inferior parietal lobe. (B) Imagined musical performance. Amateurs (left) manifested sparsely clustered but widely distributed activity, with particular prominence in bilateral lateral frontal, inferior opercularis, primary and supplementary motor, parietal, and anterior temporal and posterior lateral cerebellar regions, whereas those in professionals (right) were observed in few but specific clusters within right M1, SMA, bilateral posterior cerebellum, bilateral superior and left inferior parietal cortices, and right superior opercular part of the inferior frontal gyrus.

Deactivation. While no significant deactivation was found in professionals, amateurs manifested scattered deactivations (refer to Fig. 2B, green). These were found bilaterally within the anterior and posterior cerebellum, angular gyrus, anterior superior temporal gyrus, and middle prefrontal gyrus. Additionally, deactivations found within the right hemisphere included the supramarginal gyrus, superior parietal lobe, and caudate nucleus. Increased BOLD signals in the left frontal operculum and left somatosensory regions were also manifested exclusively in amateurs during rest.

Masking between groups: professionals (IM) vs amateurs (IM). Professionals clearly manifested more prominent BOLD signals that clustered within the sensorimotor regions (left M1-premotor cortex, supplementary motor area, and left posterior cerebellum), bilateral superior and left inferior parietal lobes, and the right superior pars opercularis as well as the left anterior superior temporal lobe (refer to Fig. 3B, Table 1B). On the other hand, amateurs showed stronger activations in many sensorimotor regions (left M1, left PMC, SMA) including bilateral somatosensory cortices and bilateral posterior cerebellum. Furthermore, bilateral (posterior and inferior) parietal and (opercular and dorsolateral) prefrontal lobes including the anterior cingulate were also more prominently activated in amateurs. Both groups showed anterior left temporal activation but the amateurs manifested theirs more posterior–superiorly. Basal ganglia activity dominated by the right caudate nucleus was once again exclusive only to amateurs.

Within-group comparisons: executed vs imagined movements (EM vs IM). EM–IM: Within the sensorimotor regions, more prominent activities during movement execution by amateurs included bilateral primary cortices, left premotor and right somatosensory cortices, and supplementary motor area, as well as bilateral anterior and left inferior

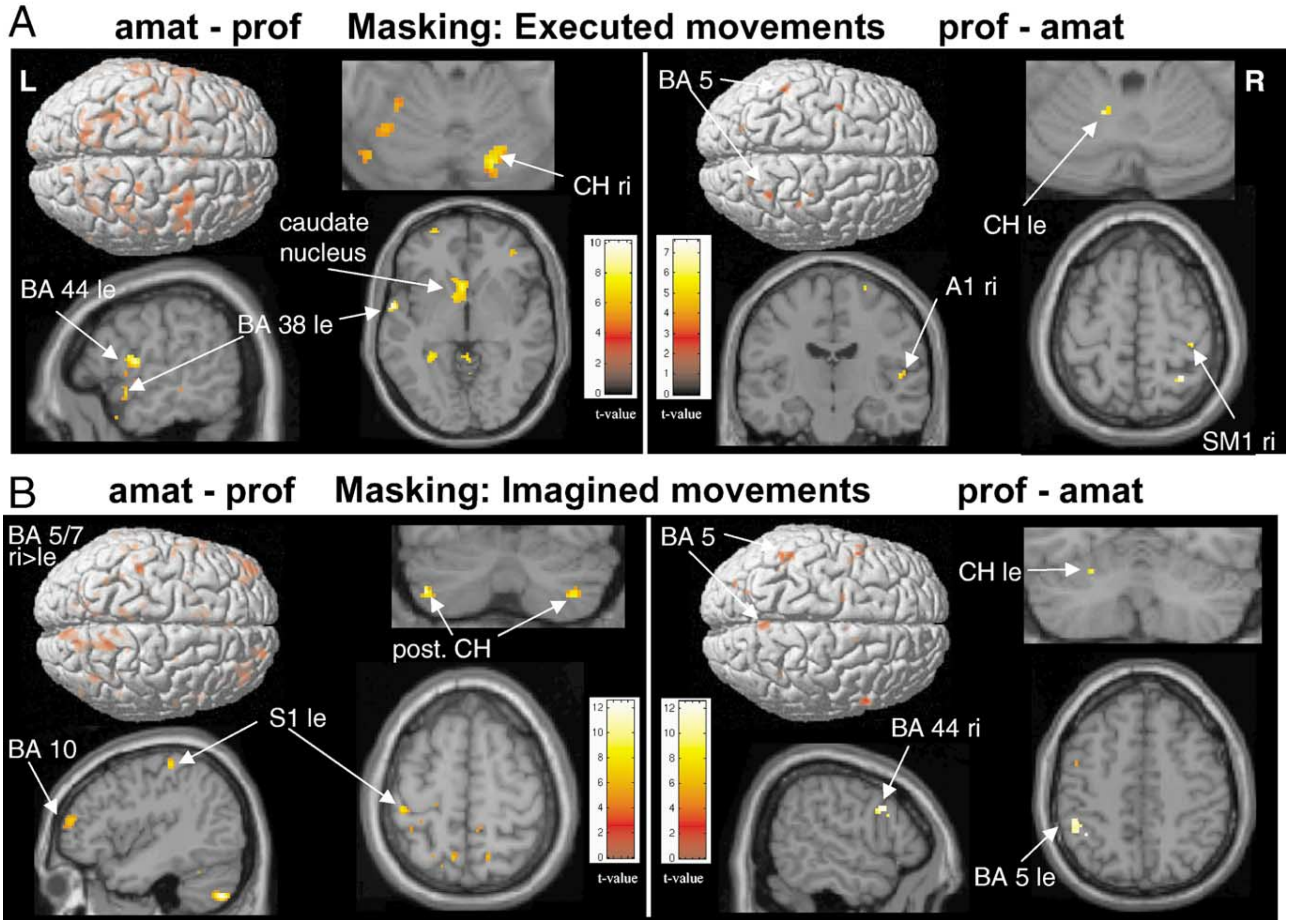

Fig. 3. Between-group analysis. Exclusive masking between activation maps of amateurs and professionals. The top view of the segmented SPM. One subject brain and slices are shown for the results of each masking. Only main areas are illustrated. Intensity of activations (*t* values) projected to anatomical slices are color-coded (red: low intensity; yellow/white: high intensity). (A) Executed movements. Amateurs manifested an increase of activation in secondary motor areas (SMA, PMC), bilateral superior parietal lobe, ipsilateral M1/S1, right (contralateral) cerebellar hemisphere (CH ri), left caudate nucleus, left superior anterior temporal lobe (BA 38), and left opercular part of gyrus frontalis inferior (BA 44). Professionals exhibited higher activation in right (contralateral) SM1 and right primary auditory cortex (A1 ri), left (ipsilateral) anterior cerebellar hemisphere (CH le), and bilateral BA 5. (B) Imagined movements. Amateurs (left) manifested higher activation particularly within the prefrontal cortex (BA 10) but also in bilateral BA 5 and 7, left S1, and bilateral posterior cerebellar hemispheres. Professionals (right) exhibited increased activity within the superior parietal lobe (BA 5), the left (ipsilateral) cerebellar hemisphere, and the right pars opercularis of the inferior frontal gyrus (BA 44 ri).

posterior cerebellum (refer to Table 1C). Professionals on the other hand exhibited higher contralateral primary motor activity, more activation within bilateral primary somatosensory cortices, right superior premotor cortex, supplementary motor area, and left posterior and anterior cerebellum. Within the parietal region, professionals manifested stronger right superior parietal activity, while amateurs showed increased activation in the left superior parietal lobe. Both groups exhibited more BOLD signals in the left anterior superior temporal lobe as well as the right Heschl's gyrus (A1). In addition, amateurs showed increased BOLD effect in the prefrontal lobe (bilateral orbitofrontal, right middle frontal, left frontal operculum), the amygdala, the thalamus, and the basal ganglia (left caudate nucleus).

IM–EM: Stronger activations during imagined movement performance (cf. EM) were observed in bilateral posterior cerebellum, supplementary motor area, contralateral somatosensory cortex, and left inferior premotor cortex for amateur violinists (refer to Table 1D). Similarly, enhanced activities were also manifested bilaterally in the inferior parietal lobes and the left (frontal opercularis and dorsolateral) prefrontal areas in amateurs. In addition, left anterior superior temporal gyrus was more prominently activated during IM compared to EM for amateurs. Interestingly, professionals manifested more BOLD signal activation only within the left superior and inferior parietal lobes and the SMA during imagined movement performance.

Discussion

This study aimed to investigate how superior musical performance in professional violinists (cf. amateurs) might be manifested in fMRI BOLD signals, how executed and

Table 1

Region	BA/Larsell	Amateurs–professionals				Professionals–amateurs			
		t value	*x*	*y*	*z*	*t* value	*x*	*y*	*z*
(A) Differences between groups during movement execution									
Sensorimotor									
Left precentral gyrus, iM1	4	6.79	−26	−18	65				
Left postcentral gyrus, iS1	1,2,3	7.90	−50	−16	39				
Left premotor cortex	6	8.09	−34	9	55	5.68	−36	3	51
Right precentral gyrus, cM1	4					6.94	38	−26	58
Right postcentral gyrus, cS1	1,2,3	8.82	36	−38	63				
Right premotor cortex	6	9.44	29	11	55				
Supplementary motor area	6	7.48	2	14	45				
Left anterior cerebellar hem.	HV					6.30	−10	−53	−18
Right sup. post. cerebellar hem.	HVIc	8.00	18	−74	−13				
Right inf. post. cerebellar hem.	HVIII	7.63	10	−58	−42				
Parietal lobe									
Left superior ant. parietal	5					5.96	−48	−38	50
Left superior post. parietal	7	7.23	−38	−54	51				
Right superior post. parietal	7	7.79	14	−62	49	7.60	32	−48	59
Prefrontal lobe									
Left inf. frontal gyrus (opercular)	44	9.20	−59	13	20				
Left middle frontal gyrus	10	6.49	−32	43	9				
Right middle frontal gyrus	10	6.55	34	49	12				
Temporal lobe									
Left sup. anterior temporal lobe	22, 38	10.10	−59	−2	−2				
Right gyrus of Heschl, A1	41					5.33	50	−15	8
Basal ganglia									
left nucleus caudatus		7.61	−2	13	−2				
(B) Differences between groups during movement imagination									
Sensorimotor									
Left postcentral gyrus, iS1	1,2,3	8.33	−40	−26	58				
Left inferior premotor cortex	6	7.20	−57	−1	26	6.18	−50	10	40
Right postcentral gyrus, cS1	1,2,3	8.91	14	−49	69				
Supplementary motor area, SMA	6					6.03	−18	0	66
Left post. cerebellar hemisphere	HVIc					5.68	−24	−59	−17
Left post. inf. cerebellar hem.	HVIIAcrII	12.55	−42	−72	−35				
Right post. inf. cerebellar hem.	HVIIAcrII	10.72	40	−58	−29				
Parietal lobe									
Medial superior parietal	7					6.05	2	−55	60
Left superior parietal	5.7	8.33	−40	−26	58	5.05	−22	−67	55
Left inf. parietal	40	7.86	−55	−40	20	5.96	−48	−46	48
Right superior parietal	5,7	7.72	14	−69	50	5.11	38	−46	56
Right inf. parietal	39	9.28	40	−60	45				
Prefrontal lobe									
Left inf. frontal gyrus (opercular)	44	6.79	−57	11	16				
Left dorsolateral prefrontal	10	7.40	−32	45	11				
Right inf. front. gyrus (opercular)	44	6.40	53	16	16	7.11	57	13	27
Right dorsolat. prefrontal lobe	10	8.72	38	47	12				
cingular gyrus	24	7.41	−10	17	27				
Temporal lobe									
left anterior sup. temporal	22, 38	5.60	−59	−2	7	5.71	−51	15	−6
right anterior sup. temporal	22, 38	5.7	49	13	11				
Basal ganglia									
right caudate nucleus		5.29	16	10	9				
(C) Differences between movement imagination and execution: Execution masked with imagination									
Sensorimotor									
left precentral gyrus, iM1	4	6.79	−25	−18	65				
left postcentral gyrus, iS1	1,2,3					7.16	−50	−27	51
left inferior premotor cortex, PMC	6	8.53	−54	6	35				
right precentral gyrus, cM1	4	16.17	38	−10	63	12.95	32	−14	65
right postcentral gyrus, cS1	1,2,3	11.11	36	−38	61	9.18	46	−30	53

Table 1 (*continued*)

Region	BA/Larsell	Amateurs–professionals				Professionals–amateurs			
		t value	*x*	*y*	*z*	*t* value	*x*	*y*	*z*
right sup. premotor cortex, PMC	6	9.68	30	11	57				
left ant. cerebellar hem.	HV	14.27	−18	−50	−18	12.46	−18	−50	−19
left inf. posterior cerebellar hem.	HVIII	8.65	−28	−59	−44	8.19	−20	−62	−42
right ant. cerebellar hem.	HV	9.18	34	−61	−19				
vermis	V	11.95	−2	−63	−11	10.42	−4	−61	−14
Parietal lobe									
left superior parietal	7	8.91	−36	−46	57				
right superior parietal	7					7.20	32	−46	59
Prefrontal lobe									
left orbitofrontal lobe	11	7.54	−26	58	−6				
right orbitofrontal lobe	11	7.32	36	44	−17				
right amygdala		5.58	22	−8	−13				
Temporal lobe									
left anterior sup. temporal	22	10.10	−60	−2	−2	6.08	−52	9	−11
right gyrus of Heschl, A1	41	5.24	44	−17	10	5.33	50	−15	8
left gyrus of Heschl, A1	41	5.76	−53	−17	8				
Thalamus		7.06	14	−19	1				
Basal ganglia									
left caudate nucleus		7.61	−2	13	−2				
(D) Differences between movement imagination and execution: Imagination masked with execution									
Sensorimotor									
left inf. premotor cortex	6	6.75	−59	1	26				
right postcentral gyrus, cS1	1,2,3	8.51	14	−49	69				
supplementary motor area	6	7.09	−4	14	51	5.11	−16	1	66
left post. cerebellar hem.	HVIIAcrII	10.71	−42	−72	−35				
right post. cerebellar hem.	HVIIAcrII	10.50	40	−58	−29				
Parietal lobe									
left sup. parietal	7					6.00	−48	−48	50
left inf. parietal	39/40	7.86	−55	−40	20	5.42	−28	−77	44
right inf. parietal	40	5.52	40	−43	24				
Prefrontal lobe									
left inf. frontal gyrus (opercular)	44	6.46	−55	18	12				
left dorsolateral prefrontal	10	7.18	−42	49	10				
Temporal lobe									
left anterior sup. temporal	22	4.98	−59	−2	7				

imagined motor performance of the same musical task might differ, and whether differential BOLD signals observed in professional and amateur violinists allow additional insights to changes in neural activity with continued motor training. The observations support the notion that musical production involves not only the motor areas but also other functional systems (Altenmueller, 2001) such as the somatosensory, auditory, emotional, temporal, and memory loops. There is clear evidence of differential brain activations in the two groups of musicians during executed as well as imagined performances: In general, professional violinists manifest fewer clusters of BOLD signals. Amateurs on the other hand, showed a more widely distributed sensorimotor representation in both hemispheres of the cortex and the cerebellum, weaker activations in A1, and increased prefrontal activation. Furthermore they manifested activations within the basal ganglia where professionals exhibited none. Since the deactivations in most tasks were located in regions which have been previously described to be deactivated during visual, motor, and language tasks (Gusnard and Raichle, 2001), we will not further discuss these results, which may reflect unspecific effects not related to the particular musical task.

Executed musical performance

Professionals manifested more focused motor representations within the cM1 and the ipsilateral anterior cerebellar hemisphere, whereas amateurs exhibited bilateral motor representations with an increase of activation in iM1 and the contralateral cerebellar hemisphere. Interestingly, in the professional group—who continued musical training without interruption—activation intensity in the ipsilateral cerebellar hemisphere during EM increased if musical training began early in life. This correlation of activation and early start of training may be in close relation to a previous observation of a correlation of morphological changes in the cerebellum observed only in musicians with early onset of musical training (Schlaug, 2001). Activations within the right precentral gyrus, for which an anatomical enlargement has also been previously shown (Amunts et al., 1997), correlated with the EMG amplitude for the left finger extensors during musical performance. Consistent with previous observations (Hund-Georgiadis and von Cramon, 1999; Jaenke et al., 2000; Krings et al., 2000), increased lateralization in M1, which follows increased training, paralleled the decreased activations in the SMA, the bilateral PMC, and the contralateral cerebellar hemisphere. Compared to amateurs, the professionals demonstrated increased activation in the contralateral M1 during executed musical performance. This finding is in line with previous reports demonstrating an increase of cM1 activation after extensive motor training (Karni et al., 1995, 1998; Seitz et al., 1994) and may also be related to an enlargement of the intrasulcal depth of the central sulcus in the vicinity of the motor hand area in the nondominant hemisphere observed in professional musicians (Amunts et al., 1997).

Moreover, a more focused recruitment of motor areas was not associated with decreased EMG amplitudes during musical execution. In fact, the professionals revealed increased EMG amplitudes compared to the amateur group. In particular, the left hand EMG amplitude during motor execution correlated positively with the training time, underlining the interrelationship between performance and training as previously described (Sloboda, 1996). In addition, the finding that amateurs showed a trend for higher right hand EMG amplitudes (Fig. 1B) together with increased ipsilateral M1 activation during EM is concurrent with observations that additional associated movements of the right hand are common in less trained subjects (Rjintjes et al., 1999) and higher iM1 activities are prominent during the early phase of motor learning (Andres et al., 1999). Furthermore, we observed that amateurs in our study manifested an increased BOLD effect within the bilateral dorsolateral prefrontal regions, underlining the role of prefrontal areas for the acquisition of motor skills before a level of automation is reached (Sakai et al., 1997; Pascual-Leone et al., 1996).

It is intriguing that activity within the basal ganglia is manifested only in amateurs during both conditions. Seitz and Roland (1992) have previously observed increased basal ganglia activity, and particularly within the caudate nucleus (Jueptner et al, 1997b), during early phases of motor skill acquisition and reasoned that this enhancement is important for the formation of the final “motor program.” More recently, Penhune and Doyon (2002) found increased basal ganglia (and frontal) activity during late phases of learning. They proposed that the basal ganglia could be involved in transforming learned associations between sensory inputs and required motor responses into more automatic and smooth actions. This might explain why basal ganglia activity is not manifested in professionals, since in their case both EM and IM are presumably well-rehearsed and internalized. Moreover, it has also been proposed that activities in the caudate nuclei could be associated with cognitive processes (Jeannerod, 2001) and/or temporal structuring (Rao et al., 2001), processes which less skilled individuals might rely on before movements can be generated more automatically when required.

Activations within the right primary auditory cortex (BA 41; Heschl’s gyrus) as well as the left auditory association area BA 42 were observed in both amateurs and professionals during EM, although professionals showed higher activity in the right primary auditory cortex. The right auditory cortex has been implicated to be dominant for perceiving pitch, harmony, timbre, and to a certain extent melody (see Tramo, 2001; Zatorre and Samson, 1991); recently, it has also been observed to be activated during piano playing (Parsons, 2001). As such, the higher activation manifested within this area in professionals may indicate an increased recruitment of these stored auditory associations. It is interesting that this auditory activation in professionals is centered in the core of the auditory cortex (see Figs. 2A and 3A, right) whereas amateurs manifested more posterior activations, found in the belt area (see Fig. 2A, left; for the differentiation of the auditory core and belt area refer to Wessinger et al., 2001). The activations in the primary auditory cortex and the belt area were observed only during EM and were absent during IM in both groups. Although we did not perform an analysis of connectivity, the fact that both activation sites are lacking if movement execution had to be avoided during our IM task suggests that the auditory–motor coactivation exists only in the presence of actual performance or real-world stimuli (e.g., physically moving or actual hearing of auditory stimuli).

Within the temporal lobe, the increased activation in the anterior superior temporal lobe in amateurs may be interpreted as an increase of recruitment of temporal processing modules (Liégeois-Chauvel et al., 1998). However, the anterior temporal region is also known to be involved in the retrieval of different types of stored information (autobiographic: Brunet et al., 2000; semantic: Tsukiura et al., 2002) and its activities are not correlated with the amount of training or executed or imagined musical performance. This region was suggested to be part of a cortical memory network that serves the sensory processing and development of motor responses involved in learning to play an instrument (Bangert et al., 2001). Unfortunately, the low spatial resolution offered by the EEG technique in Bangert et al.’s study does not allow one to delineate the anatomical basis for its suggested role.

Notwithstanding, the duration of training not only influences the quality of motor performance in musicians but also their artistic skills (Sloboda, 2000). It could therefore be assumed that our group of professional musicians might also be more expressive in their performance of the violin concerto. Sergent (1993) previously postulated that the enhanced somatosensory and auditory feedback during performance on the instrument (e.g., strings of the violin) facilitates the online modification of movements and related sound production to meet the intended performance plan. As such, sensory feedback and close internal monitoring of the plan must be continuously activated. It can therefore be assumed that an increased sensorimotor coupling is particularly important for the quality of musical performance.

These processes depend on associative feedback–feedforward connections between sensory (somatosensory and auditory) and supervising areas that establish the internal image and plan of the intended movement(s). The more musicians are involved in motor performance the less resources can be recruited for expressive–artistic features of the musical play or the correction of possible discrepancies between the intended and the actual performance.

Additionally, the presence of limbic activations (within the bilateral orbitofrontal lobes and the right amygdala) in amateurs after exclusive masking (EM–IM) could reflect their apprehension and anticipatory anxiety during their task performances in the scanner. It is plausible that due to their lack of public performances, such an experimental situation can be rather daunting.

Imagined musical performance

Experienced musicians are known to employ motor imagery to improve their performance as well as to memorize the aesthetic–emotional concept of the musical piece. Furthermore, it has also been reported that motor imagery improves the dynamics of motor performance, e.g., movement trajectories (Yágüez et al., 1998). Consequently, the vividness of movement imagery was higher in the professional group, with rhythm and pitch imagination scores correlating positively with lifetime and weekly training (refer to Fig. 1C). In order to understand the importance of imagery in musical performance in our group of professional musicians, we asked them to score (using an a posteriori questionnaire with VAS) the frequency of use, the content, and the importance of IM for performance improvement. They scored on average, 5.76 (±3.38) of 10 for frequency of use even though the most difficult parts of the piece were trained predominantly using imagery (mean score: 7.01 ±2.34). Imagination of sequential finger movements was rated on average 6.91 (±2.68), while the use of sound imagery rated 8.58 (±0.97). It is noteworthy that professionals indicated that they are almost always (8.05 ±2.35) able to improve their musical play by IM. Although professionals reported frequent use of this technique and amateurs denied using imagery in their practice, further quantification of imagery used per week and over lifetime was not possible.

It has been previously suggested that the complex spatial and timing components of musical performance may be coordinated by a network involving the lateral cerebellar, superior parietal, and superior frontal regions during covert musical rehearsal (Langheim et al., 2002). In the present study, both IM and EM induced activations in multiple motor areas such as the PMC, SMA, the cerebellum, and the bilateral parietal lobes (see also Farah, 1995), underlining the concept that motor imagery shares the same neuronal substrates as executed movements (Jeannerod et al., 1994).

In direct comparison, professionals recruited very few cerebral areas, whereas amateurs again manifested a widely distributed activation map, which is also reflected in their lower scores for vividness of imagined movement. Whereas many cortical areas exhibited increased activity during IM in the amateur group compared to the professionals, some discrete increases are also observed in the professional group, e.g., the SMA, the superior PMC, more anterior areas (Larsell's lobule HVI) in the left cerebellar hemisphere, and bilateral superior parietal areas (see Fig. 3B). A more focused activation of superior left parietal and anterior ipsilateral cerebellar regions in the professional group may indicate more efficient recruitment of stored sensorimotor engrams. This view is supported by the role of the superior parietal lobe for storage of movement kinematics (e.g., Seitz et al., 1997) and by the proposed cerebellar involvement in motor automation (Lang and Bastian, 2002). Moreover, during IM, professional musicians revealed more anterior cerebellar activations (c.f. amateurs), which are found close to the EM activations in the cerebellar somatosensory hand area (see Fig. 3B and Grodd et al., 2001), suggesting a recruitment of stored movement programs of sequential finger movements during imagery.

In the present study, the lack of significant activations during IM within the cM1 in the professional musicians was observed (Fig. 2B). A similar observation has also been reported by Langheim et al. (2002), who examined musicians with an average lifetime training of 19.6 years (compared to the 12 years of training in the amateurs and the 35.6 years of training in the professionals in our study). It is also noteworthy that whereas all musicians reported using IM in Langheim et al.'s study, only the group with a high lifetime of musical experience in our study used IM.

Furthermore, in accordance with the observations of Langheim et al. (2002) and earlier studies (e.g., Zatorre et al., 1996) the right primary auditory cortex was not activated during imagery of musical performance, although subjects of our study indicated high imagery vividness of pitch and music during IM (see Fig. 1C). This result leads us to hypothesize that primary motor and auditory areas become tightly coupled with executed activities during musical training. When one primary area is activated, the other also coactivates. This view is in agreement with Bangert et al.'s (2001) study of silent piano playing and pure auditory musical tasks. Furthermore, this may explain why the auditory processes (which were active during EM) are not recruited in the absence of actual motor execution.

In summary, this study has sought to investigate the neural activity manifested during executed and imagined musical motor performance in professional and amateur violinists. The findings are consistent with previous studies and highlight the view that prolonged musical (or motor) training is associated with enhanced efficiency, reduced effort, and increased spontaneity and flexibility in skill transference (with respect to different environments and task demands, e.g., the substituted violin fingerboard). In particular, it has shown that musical accomplishment is manifested in a cortical network that seems to originate from a more diffuse network (cerebello-cortical, striato-cortical, cortical–cortical), before becoming more refined and circumscribed with practice. Furthermore, even though the primary motor and auditory cortices may play the most important role in highly overtrained musical performance, they have been shown not to be activated during imagined musical performance.

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