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Brain changes after learning to read and play music

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Abstract

Musically naive participants were scanned before and after a period of 15 weeks during which they were taught to read music and play the keyboard. When participants played melodies from musical notation after training, activation was seen in a cluster of voxels within the bilateral superior parietal cortex. A subset of these voxels were activated in a second experiment in which musical notation was present, but irrelevant for task performance. These activations suggest that music reading involves the automatic sensorimotor translation of a spatial code (written music) into a series of motor responses (keypresses).

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Introduction

When a child or adult starts to play the keyboard, a significant part of the initial musical training is devoted to learning to read musical notation. Musical pieces which, at first sight, appear meaningless in their written form, will eventually be translated into a recognizable melody. Just as written language becomes meaningful and even compelling to read, so does musical notation. But how does this happen? And what brain regions are recruited for this process in the aspiring pianist?

To date, there have been two neuroimaging studies involving music reading. One looked at the low-level perceptual aspect of music reading, contrasting passive viewing of music versus text (Nakada et al., 1998), and the other looked at how music reading interacts with the other processing components involved in musical performance (Sergent et al., 1992). The present study focuses on music reading as a translational process between the encoding of a stimulus (a note on the staff) and the execution of a motor response (a particular keypress). Specifically, we tested the hypothesis that music reading involves a sensorimotor translation in which the spatial information contained within musical no-

tation is used to guide selection of the appropriate motor response. The following consideration of the formal nature of musical notation, and some recent behavioral findings concerning the visuospatial nature of music reading (Stewart et al., 2003), will provide the rationale for this hypothesis.

Although western music, in its written form, may appear largely incomprehensible to the musical illiterate, it has a systematic organization: notes written vertically higher on the musical staff denote tones of a higher pitch. The systematic organization of musical notation is also seen with respect to keyboard layout. For instruments such as the piano, the keyboard layout is such that striking keys from left to right produces tones of successively higher pitch. Hence the written representation of musical notes on the vertical axis of the staff maps onto a representation of pitch as well as a representation of notes from left to right on the keyboard. Music reading for keyboard performance can therefore be envisaged as a visuospatial sensorimotor task, in which stimuli that vary along a vertical dimension are mapped onto the fingers, which strike horizontally arranged response elements. An empirical basis for proposing that the decoding of musical notation for keyboard performance is primarily visuospatial, involving a translation from a vertical to a horizontal dimension, comes from a recent musical Stroop study, performed in pianists and nonpianists. Pertur-

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EXPLICIT MUSIC READING

a) Pre-Training - Reading by Numbers

b) Post-Training - Reading by Notes

IMPLICIT MUSIC READING

c) Pre- and Post-Training - Visual Feature Detection Task

Fig. 1. Explicit and implicit music reading tasks. The explicit music reading task was different, pre-training versus post-training, for the learners (a,b). The nonlearners performed the number to finger mapping task in both scanning sessions. For both learners and nonlearners, the implicit music reading task was identical, pre-training and post-training (c).

bation of the systematic relationship between the vertical position of a note on the staff and its corresponding position on the keyboard significantly affected the performance of pianists, but not nonpianists (Stewart et al., 2003).

The assumption that sight-reading for keyboard performance involves a sensorimotor translation based upon spatial dimensions leads us to predict that it will activate the superior parietal cortex. Electrophysiological (Andersen et al., 1987; Lacquaniti et al., 1995; MacKay and Mendonca, 1995; Sakata et al., 1985) and lesion studies (Crowne et al., 1992; Petrides and Iversen, 1979; Pu et al., 1993) in the monkey have established a role for posterior parietal cortex in coordinated visuomotor behavior such as reaching and grasping and parietal damage in humans can lead to visuomotor impairments such as an inability to use visual information in the guidance of eye or hand movements (Jeanerod et al., 1994) and failure to perform reaching movements on the basis of mirror reversed cues (Ramachandran et al., 1997). Neuroimaging studies have made it possible to fractionate different parts of the parietal cortex, according to their function and mental rotation (Alivisatos and Petrides, 1997), and mirror-reading tasks (Dong et al., 2000; Goebel et al., 1998; Kassubek et al., 2001; Poldrack

et al., 1998; Poldrack and Gabrieli, 2001) have pinpointed a specific role for the superior parietal cortex in mediating visuospatial sensorimotor transformations (Dong et al., 2000; Goebel et al., 1998; Kassubek et al., 2001; Poldrack et al., 1998; Poldrack and Gabrieli, 2001).

A key question regards how the artificial process of sight-reading for keyboard performance becomes a natural process. How do brain areas become recruited for such a skill? The present study was designed to look at music reading in a learning context. The advent of functional magnetic resonance imaging (fMRI) has permitted longitudinal studies of the neural correlates of skill acquisition. Music reading is a skill which lends itself to such an approach, since only a small fraction of the population are musically literate and many are motivated to learn. Thus a unique opportunity exists for investigating the acquisition of an artificial and culturally valued skill.

Surprisingly few studies have used fMRI to look at skill learning (Karni et al., 1995, 1998; Poldrack et al., 1998; Poldrack and Gabrieli, 2001; Toni and Passingham, 1999) and almost all such studies have measured changes in brain activation as a function of the improvement in task performance where task performance, pretraining, is already

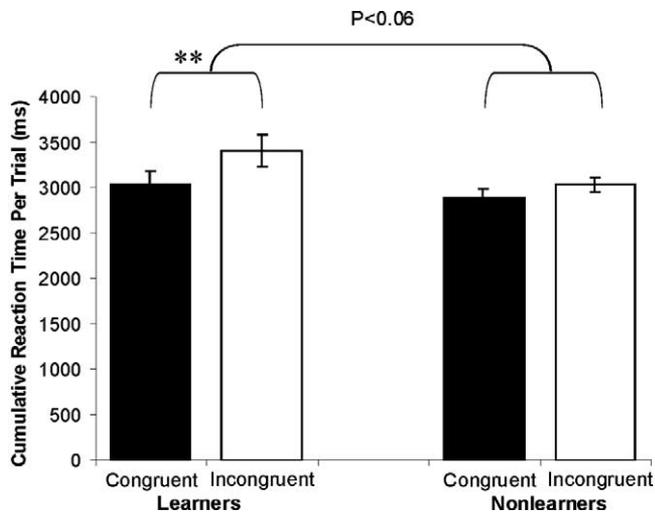


Fig. 2. Musical Stroop task as a measure of learning. In addition to assessment by an independent external examiner, participants' music reading skill was measured using a musical Stroop task (Stewart et al., 2003). Posttraining, a planned comparison showed a significant interference effect ($P < 0.01$) for the learner group only. The interaction between the learner and nonlearner groups approached significance ($P < 0.06$). (** $P < 0.01$).

above baseline. The present study, by contrast, measures functional brain changes before and after the acquisition of music reading skill from scratch. Such an approach presents unique experimental design issues. Studies which look at the neural correlates of improvement in an already existing skill can, and indeed must, use the same task, pre- and post-training. Studies of novel skill acquisition, by definition, cannot do this; if the participant is required to provide a meaningful behavioral response before and after training, different tasks must be used. However, this makes interpretation of the imaging data particularly challenging. How, for instance, is it possible to disentangle a post-training/pre-training activation change which is related to task differences from a post-training/pre-training activation change which is related to an effect of learning? The present study aims to solve this conundrum by using two different tasks, an explicit music reading task and an implicit music reading task.

The explicit music reading task (Fig. 1a and b), by definition, could not be given in an identical format, before and after training, since music reading was only possible after training. The implicit music reading task (Fig. 1c), however, was identical, before and after training. While training-related activation changes seen in the implicit music reading task can be attributed to learning, given the identical nature of the task, pre- and post-training, any activation changes occurring in the explicit task will be more equivocal as they may, at least partially, be attributable to the different nature of the pre-training versus the post-training task. However, if training-related changes in activation are seen in an overlapping area across the two tasks, it is parsimonious to consider that such changes are learning-related.

Methods

Participants

We recruited two groups of 12 participants each. One group (comprising the learners) responded to an advertisement asking for individuals with no music reading or playing experience to take part in two scanning sessions and undertake 15 weeks of musical training. The second group of participants (comprising the nonlearners) responded to a different advertisement which asked for individuals who were similarly lacking in musical experience to take part in two scanning sessions (with no training element in between). The nonlearners provided a control for nonspecific changes in activation which may relate to factors such as increased familiarity with the scanning environment during the second scanning session, physiological differences in arousal, differences in participants' head position, or slight variations in scanner hardware characteristics (McGonigle et al., 2000). Participants were screened for previous musical training (either formal or self-taught) using a self-report questionnaire. A second stage of selection required participants to attempt to play a set of simple melodies on a keyboard, using the right hand. The starting point of each melody was given before the start of each trial.

Training

Participants were provided with an electronic keyboard (Yamaha, PSS26), a keyboard tutorial book, and a music theory manual and exercise book. They were required to attend a 90-min music lesson once a week for 15 weeks. Lessons were given by an experienced music teacher and followed a standard method of teaching whereby music reading was taught in conjunction with practical keyboard skills. Practical keyboard skills and music theory were taught to Grade 1 (Associated Board, UK) level. Participants engaged in regular structured keyboard practice between lessons and completed music theory exercises which were assigned and marked by the teacher. Participants were taught in groups of three or four. Progress was not uniform across all participants and extra tuition was given where required in an attempt to equate the final level of proficiency across the group. This extra training amounted to an additional two lessons (each 90 min) for two of the subjects.

Measurement of skill acquisition

After the training was complete, an external music teacher examined participants individually on keyboard skills (scales, a prepared piece from the Grade 1 syllabus, and sight reading). Participants also sat a Grade 1 music theory examination. A more cognitive measure of music reading ability was obtained using a musical Stroop task (Stewart, submitted) in which music reading ability skill was measured indirectly by ascertaining the degree to which

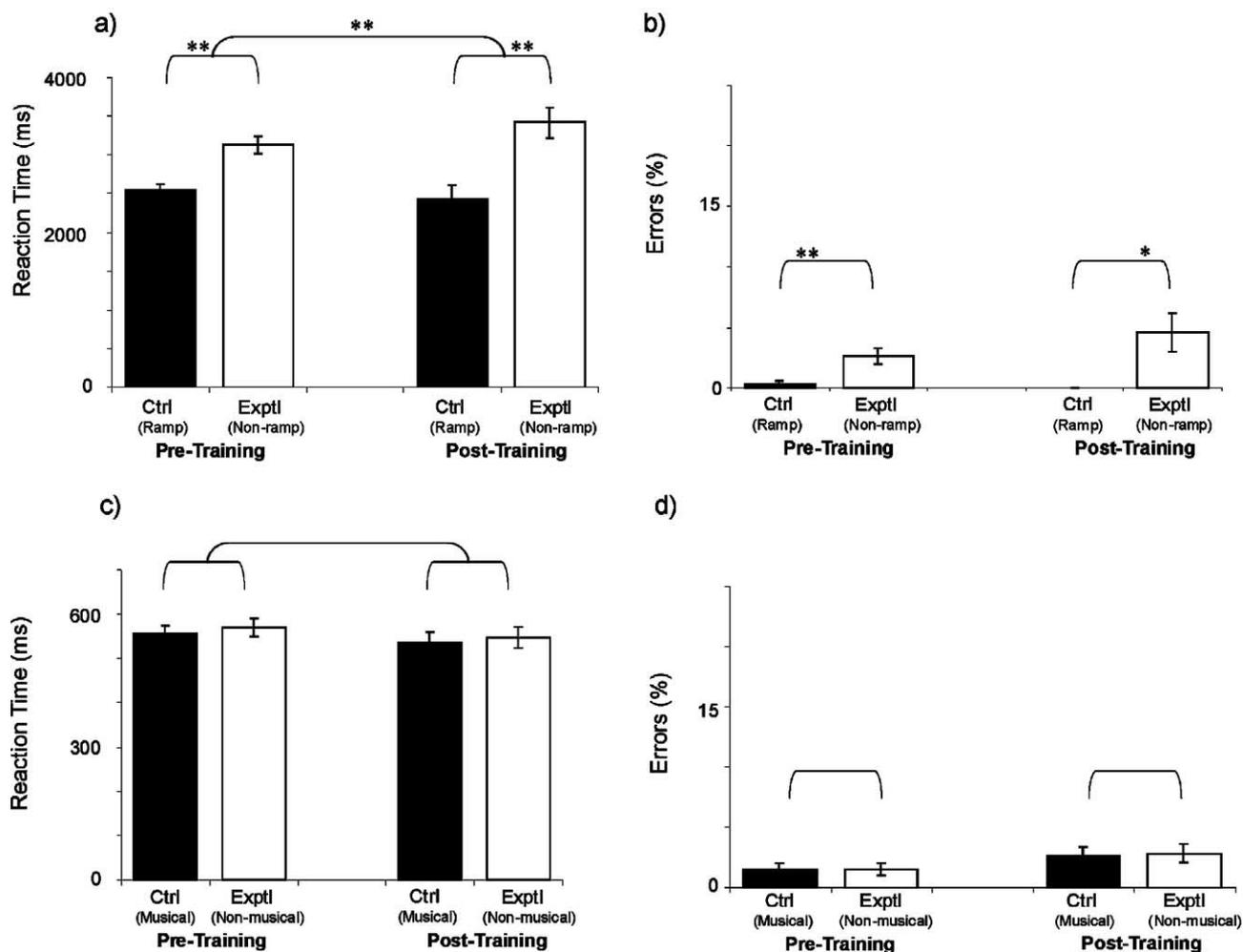


Fig. 3. Behavioural data from explicit and implicit music reading tasks. Explicit music reading (a, b). Participants were faster and more accurate in producing a sequence of keypresses in response to control (ramp) trials, compared to experimental (non-ramp) trials, both for reading by numbers and for reading by notes ($P < 0.01$). The control/experimental difference in reaction time was significantly greater for reading by notes ($P < 0.01$). Implicit music reading (c, d). Participants did not differ in speed or accuracy between control and experimental trials. There was no effect of training on either reaction time or error percentage and no interaction between trial type (control/experimental) and stage (pre-/post-training).

musical notation for pitch interferes with the required number to finger mapping.

Tasks used during scanning

Explicit music reading task

This task required participants to produce a series of keypresses in response to the appearance of a sequence of five musical notes (Fig. 1a). Pre-training, these musical notes were labeled with numbers (1–5), enabling participants to make a simple number to finger mapping. After training, these labels were replaced with nonsense symbols, requiring participants to decode the musical notes using their newly acquired musical literacy. The nonlearners, who could not read music, performed the explicit music reading task using numbers during both scanning sessions. Both the pre-training and the post-training tasks incorporated a control for low-level visual and motor elements. The appear-

ance of an ascending or descending pattern of notes prompted participants to execute a simple ramp sequence of keypresses from the thumb to the little finger (ascending) or vice versa (descending). Thus stimulus and response elements were maintained across experimental, nonramp trials and control, ramp trials but the control trials were sufficiently overlearned as to minimize the visuomotor translation required.

Implicit music reading task

This task was based on an implicit text reading paradigm (Price et al., 1996). The rationale of our task was that the mere presence of musical notation, post-training, may result in implicit decoding of the irrelevant musical notation in musical trials which would be reflected in an activation change. The task was identical before and after training. It comprised a visual feature detection task in which the target (a vertical stem which protruded above or below the hori-

Table 1
Talairach coordinates of activations relating to a training effect (significant at the $P < 0.001$ uncorrected level, extent threshold five voxels) in the explicit and implicit music reading tasks

	Talairach coordinates			Z score
	x	y	z	
Explicit music reading task				
Region				
Right superior parietal cortex	18	-72	57	3.71
Right medial superior parietal cortex	15	-69	48	3.68
	9	-66	57	3.49
Left superior parietal cortex	-12	-66	60	3.37
Left fusiform gyrus	-36	-69	-9	3.59
Implicit music reading task				
Region				
Left supramarginal gyrus	-63	-30	27	4.84
	-48	-24	21	3.52
Right frontal pole	39	57	6	3.64
Left inferior frontal sulcus	-57	12	30	4.10

zontal stave) could form part of a musical stimulus (musical trial) or a nonmusical stimulus (nonmusical trial), constituting experimental and control trials, respectively. Participants indicated whether the target was ascending or descending, using an arbitrary up/down mapping to the index and middle fingers. Musical trials were visually and motorically matched with nonmusical trials but only the musical trials were musically interpretable.

Experimental design

Participants were scanned while they performed the explicit music reading task and the implicit music reading tasks in two separate runs. Participants also performed an additional two tasks, the results of which are not reported here. The order of the runs was counterbalanced across participants. A blocked design was used. Each task comprised 6 control and 6 experimental blocks, presented alternately, and interspersed with rest blocks (12 in total). Control blocks and experimental blocks lasted 30 s; rest blocks lasted 15 s. For the explicit music reading task, control and experimental blocks comprised 6 trials of 5 s each. Each rest block (presentation of a blank stave, no response required) contained 3 trials of 5 s each. Stimuli were presented for 4.5 s. Participants fixated on a cross hair in the center of the screen for the remainder of the trial (0.5 s). For the implicit music reading task, control and experimental blocks consisted of 20 trials of 1.5 s each. Each rest block (presentation of a blank stave, no response required) contained 10 trials of 1.5 s each. Stimuli were presented for 1 s. Participants

fixated on a cross hair for the remainder of the trial (0.5 s). Each run lasted 9 min in total.

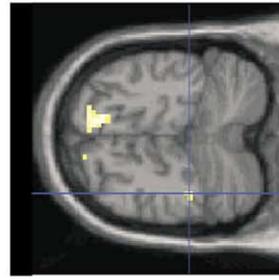
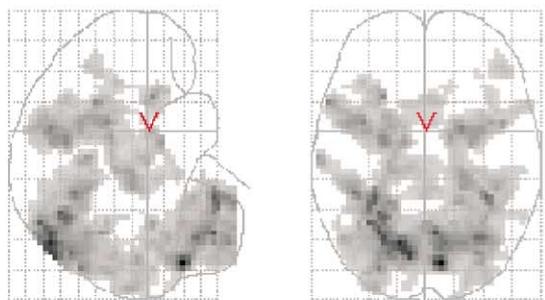
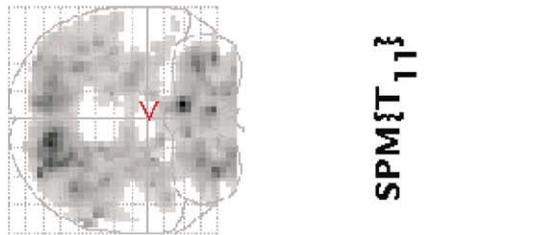
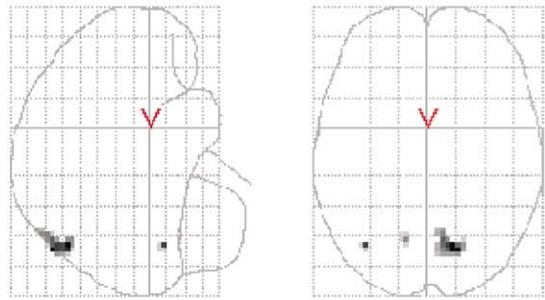
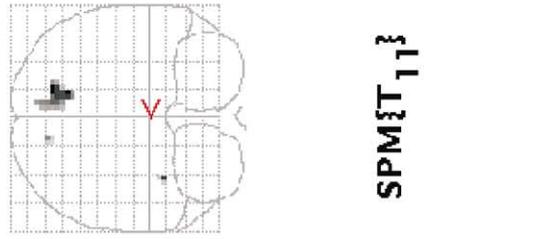
Imaging parameters

A 2-T Siemens Vision system (Siemens, Erlangen, Germany) was used to acquire T2* weighted echoplanar (EPI) slices (64×64 grid, each slice, $3 \times 3 \text{ mm}^2$, TE = 40 ms) with blood oxygenation level dependent (BOLD) contrast. A trajectory based reconstruction sequence was used (Josephs et al., 2000). Each EPI image comprised 40 axial slices taken every 3.5 mm (2 mm thick with a 1.5-mm gap) which were positioned to cover the whole brain. Both tasks consisted of 185 whole brain acquisitions, the first five of which were not analyzed. Volumes were acquired continuously with an effective repetition time of 3.04 s/vol. Volumes were realigned, resliced using sinc interpolation, and normalized to an EPI template based on the Montreal Neurological Institute reference brain of $3 \times 3 \times 3 \text{ mm}$ voxels in Talairach space using nonlinear basis functions. The EPI volumes were smoothed with an 8-mm full width at half maximum isotropic Gaussian kernel.

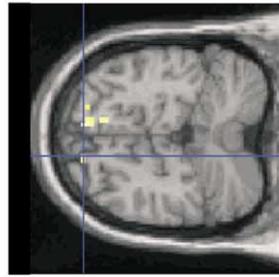
Statistical analysis

Both the explicit music reading and the implicit music reading tasks were analyzed separately for the pre-training and post-training sessions. Data were analyzed with the Statistical Parametric Mapping Software (SPM99, Wellcome Department of Cognitive Neurology, London; <http://>

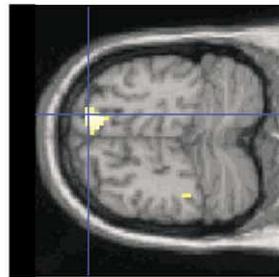
Fig. 4. Imaging data, explicit music reading. (a) Glass brain statistical parametric map (SPM) relating to the common trial effect for reading by numbers (pre-training) and reading by notes (post-training) (b) Glass brain statistical parametric map (SPM) relating to the training effect (reading by notes minus reading by numbers). (c, d, e) Axial sections (top) and plots of the mean percentage signal change, relative to the grand mean over all voxels (bottom) corresponding to each of the voxels which showed a significant training effect. (c) Right superior parietal cortex; (d) left superior parietal cortex; (e) left fusiform gyrus.



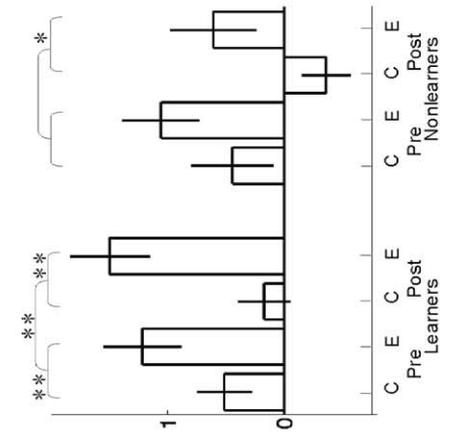
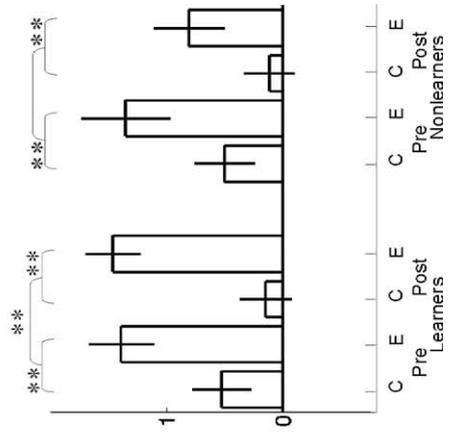
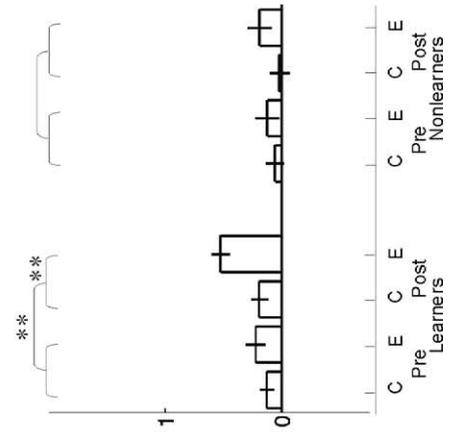
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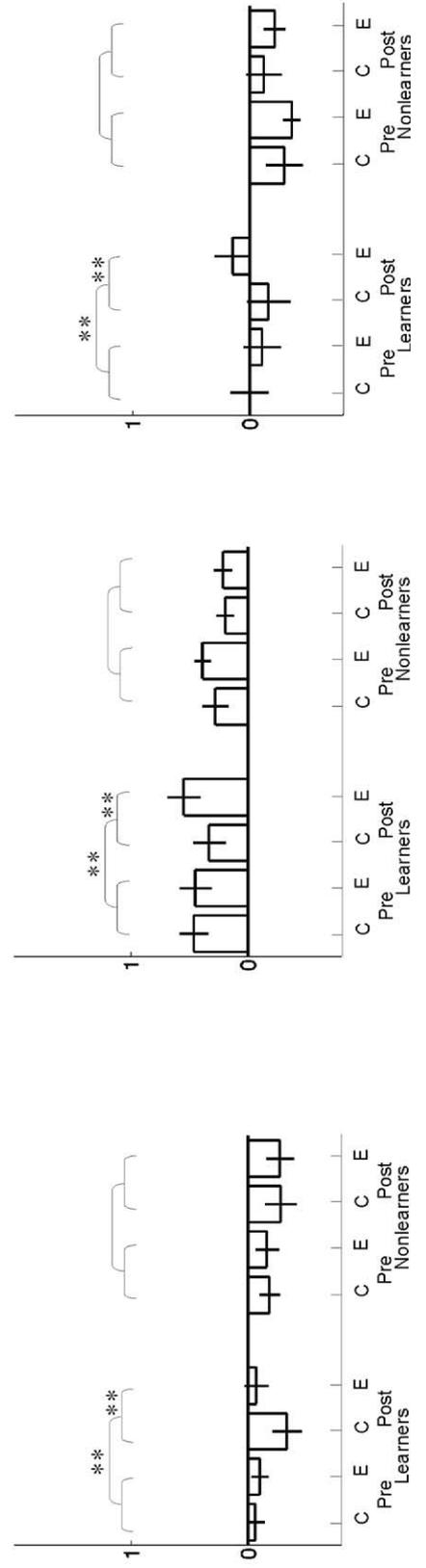
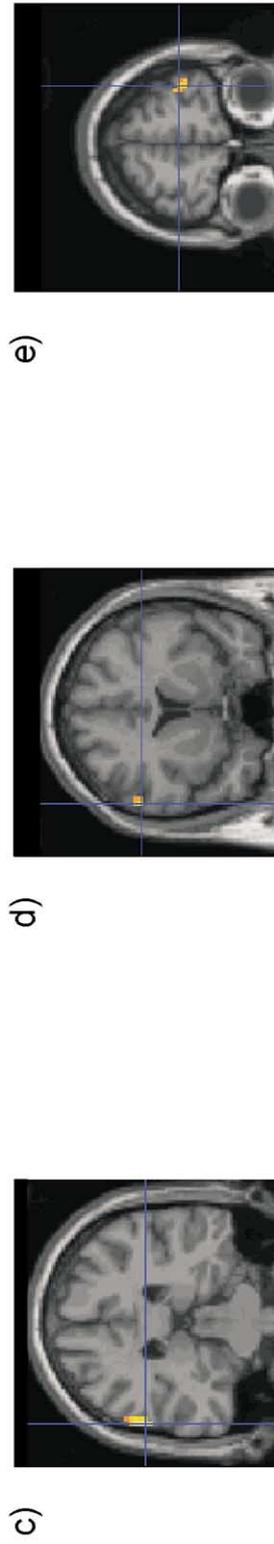
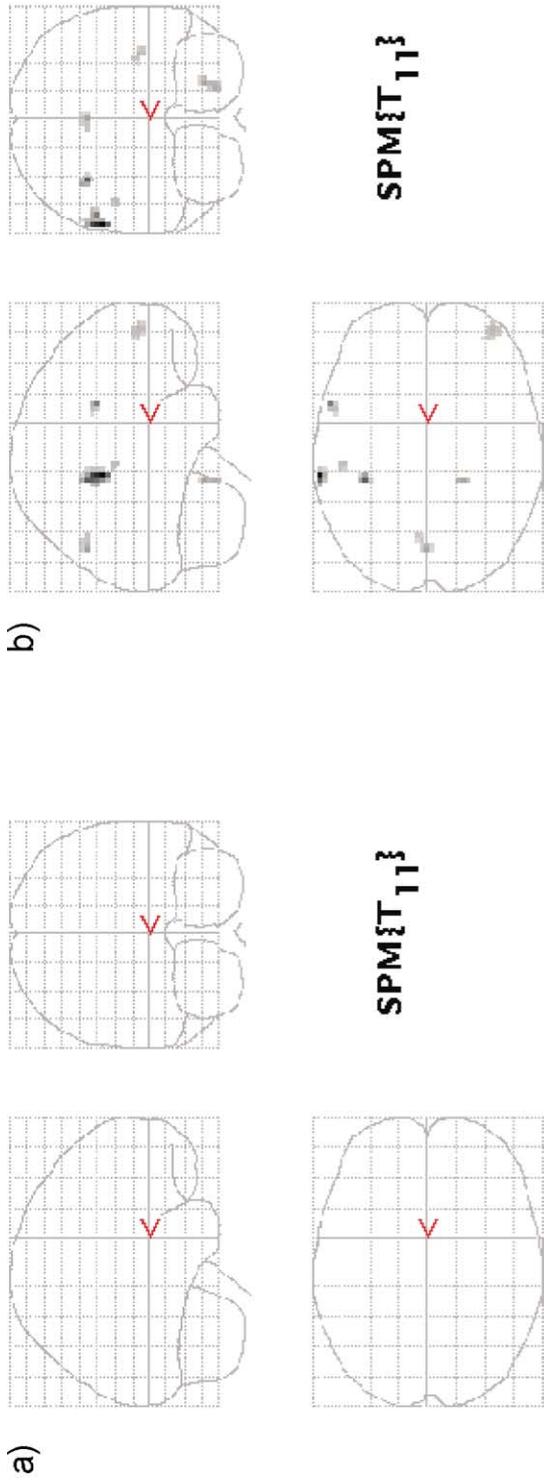


d)



c)





fil.ion.ucl.ac.uk/spm). Population inferences were made through a two-stage procedure. In the first stage, the data were analyzed participant by participant. The volumes acquired during each condition were treated as a time series. The BOLD response to the stimulus onset for the experimental and control blocks was modeled as a boxcar function convolved with a hemodynamic response function. The rest blocks were not modeled. These functions, plus six rigid body deformation parameters, derived from the realignment stage and a constant term, were used as participant-specific covariates in a general linear model. Parameter estimates for each covariate were calculated from the least mean squares fit of the model to the time series at each voxel.

The following terms have been defined so that they can be used as a short hand for the contrasts which we refer to throughout the remainder of the paper.

Trial effect

A voxel shows a trial effect if there is statistically greater activity for experimental trials versus control trials.

Training effect

A voxel shows a training effect if there is statistically greater trial effect, post-training versus pre-training (i.e., an interaction between control/experimental trials and pre-/posttraining).

Planned contrasts across covariates were performed for each participant, generating a contrast image of the Trial Effect for each participant. These contrast images were used in the second, random-effects analysis. Contrast images for each participant were compared between scanning sessions (posttraining–pretraining) using a paired *t* test and treating participants as a random variable in order to derive statistical parametric maps (SPMs) of the *Z* statistic (thresholded at $P < 0.001$ uncorrected), relating to the training effect. Inclusive masking of SPMs revealed commonalities in the trial effect across pre-training and post-training sessions. Each SPM was thresholded at $P < 0.01$ to give a combined $P < 0.0001$. To look at commonalities in the training effect across the two tasks, contrast images relating to the training effect were produced for each participant. Inclusive masking of the SPMs revealed commonalities in the training effect across the two tasks, using a combined threshold of $P < 0.0001$.

Results

Measurement of skill acquisition

None of the participants showed any signs of previous musical training, either via self-report or via their perfor-

mance on a simple music reading task. After 15 weeks of musical training in keyboard skills and music theory (90 min per week), an independent music teacher examined the participants in the learner group and confirmed that they had all reached a standard of keyboard skill equivalent to Grade 1, Associated Board, UK. The attainment of Grade 1 Keyboard requires demonstration of the ability to play a set piece with two hands simultaneously, to play a short piece from sight, and to execute designated scales and arpeggios. Additionally, participants' knowledge of music theory was judged to be of Grade 1, Associated Board standard, as indexed by their performance on a written music theory test. The attainment of Grade 1 Theory requires the ability to derive note names and timing information from musical notation, to understand key signatures and time signatures, to construct certain scales, and to be familiar with musical terms and symbols. The assessment of music reading ability, using a musical Stroop task (Stewart et al., 2003), showed that, posttraining, the learner group exhibited a significant interference effect ($P < 0.01$) when musical notation was incongruent with the required number to finger mapping. Participants in the nonlearner group showed no such interference (Fig. 2).

Behavioural data during scanning

Reaction times and errors for each participant were calculated, pre- and posttraining, for both music reading tasks. For the explicit music reading task, the cumulative response time (total time taken to make all five keypresses across a single trial) was calculated for trials in which all keypresses were correct (Fig. 3a and b). Participants were faster to produce a sequence of keypresses on control (ramp) trials compared to experimental (nonramp) trials, both for reading by numbers (pre-training) and reading by notes (post-training) (both $P < 0.01$). Analysis of variance revealed that this control/experimental difference in reaction time was significantly greater for reading by notes ($P < 0.01$), owing to an increase in reaction time for experimental trials based on notation. Participants were also more accurate in their production of a sequence of keypresses on control trials compared to experimental trials, both for reading by numbers ($P < 0.001$) and for reading by notation ($P < 0.01$). It was not possible to test for an interaction since the error data was not normally distributed and only nonparametric tests could be used.

For the implicit music reading task, simple reaction time and error percentages were calculated for each trial type (Fig. 3c and d). There was no difference in reaction time or percentage error between experimental trials and control trials. Similarly, there was no effect of training on either

Fig. 5. Imaging data, implicit music reading. (a) Glass brain statistical parametric map (SPM) relating to the common trial effect, pre-training and post-training. (b) Glass brain statistical parametric map (SPM) relating to the training effect. (c, d, e) Axial sections (top) and plots of the mean percentage signal change (bottom) corresponding to each of the voxels which showed a significant training effect. (c) Left supramarginal gyrus; (d) left inferior frontal sulcus; (e) right frontal pole.

reaction time or error percentage and no interaction. As might be expected, given the relative simplicity of the feature detection task, the acquisition of music reading skill had no measurable behavioral effect on performance.

fMRI data

We defined our the following contrasts of interest a priori:

Trial Effect: experimental trials–control trials

Training Effect: (experimental trials–control trials, post-training)–(experimental trials–control trials, pre-training)

We do not report deactivations for experimental trials versus control trials (the reverse of a trial effect as defined above) nor do we report changes in post-training versus pre-training (the reverse of a training effect) since these were not planned comparisons. However, the results of these contrasts can viewed at <http://www.icn.ucl.ac.uk/members/Stewa169/>.

Talaraich coordinates of activations, significant at the $P < 0.001$ (uncorrected) level and surviving an extent threshold of five voxels, are displayed for all voxels which showed a training effect (Table 1). Regions which did not show an equivalent trial effect, pre-training, across learners and nonlearners, were excluded, even if they showed a training effect.

Learning to play a melody: explicit music reading task

Inclusive masking revealed a common trial effect, pre-training and post-training, in the bilateral cerebellum, parietal cortex, caudate nucleus, and middle frontal gyrus (Fig. 4a). The extensive commonality seen in the trial effect, pre- and post-training, is thought to arise because the cognitive demands differed between experimental and control trials in a similar way, across both scanning sessions. Experimental trials required participants to make an unpredictable sequence of keypresses, dependent on the presentation of a number (pre-training) or a note (post-training). Control trials, in contrast, required participants to perform an over-learned sequence of keypresses which, although contingent on the stimulus display, did not require a number-by-number or a note-by-note visuomotor translation to arrive at the correct sequence.

A training effect (greater trial effect, posttraining minus pretraining) was seen in superior parietal cortex, including the intraparietal sulci, bilaterally, as well as an area in left fusiform gyrus (Fig. 4b). An examination of the mean percentage signal change for the maxima of these regions (Fig. 4c,d, and e) revealed a trial effect which, although it was significant at pretraining, was even greater at posttraining. A control group of nontrained participants, who were scanned twice using the same interscan interval, performed the reading by numbers task on both occasions. They showed the

expected trial effect in both scanning sessions but no training effect.

Effect of exposure to musical notation: implicit music reading task

Inclusive masking revealed no common trial effect, pre-training and post-training (Fig. 5a).

A training effect was seen in the left supramarginal gyrus, left inferior frontal sulcus, and right frontal pole (Fig. 5b). An examination of the mean percentage signal change for the maxima of these regions (Fig. 5c,d, and e) revealed that all voxels exhibited the same relative pattern: a trial effect that was restricted to the post-training session. The nonlearner group showed no activation difference between the experimental and control trials, at either scanning session. The inclusion of data from the nonlearner group is informative in the interpretation of the mean percentage signal change. The voxel shown in Fig. 5c, for instance, shows a pattern which, without comparison with the nonlearner group, would be interpreted as an interaction arising because of a deactivation in the control/nonmusical trials, posttraining. The nonlearners, however, show that there is a general deactivation for both experimental and control trials in the second scanning session, thus requiring the pattern of signal change seen in the learner group to be interpreted in terms of relatively less deactivation for experimental, as opposed to control trials.

Activations common to both explicit and implicit music reading

Inclusive masking revealed common training effects across the explicit and implicit music reading tasks. Only two cerebellar regions in the left hemisphere survived the extent threshold of five voxels; however, the striking bilaterality of some of the subthreshold activations caused us to relax the extent threshold to the single voxel level, revealing a common training effect in the bilateral superior parietal cortex, medial superior parietal cortex, and left postcentral gyrus. The medial superior parietal region also survived $P < 0.001$ (uncorrected) in both the implicit and the explicit tasks separately (Fig. 6).

Discussion

Robert Schumann's "Melodie," one of the first pieces in his "Piano Album Fur Die Jugend" (Schumann, 1849), comprises a tune played by the five fingers of the right hand. Even this simple exercise demonstrates pleasing musical patterns. In the present study, we confined ourselves to the most simple of five finger exercises, played from musical notation and, in order to isolate the processes involved in the translational component of this newly learned skill, removed the sound aspect of musical production. We asked

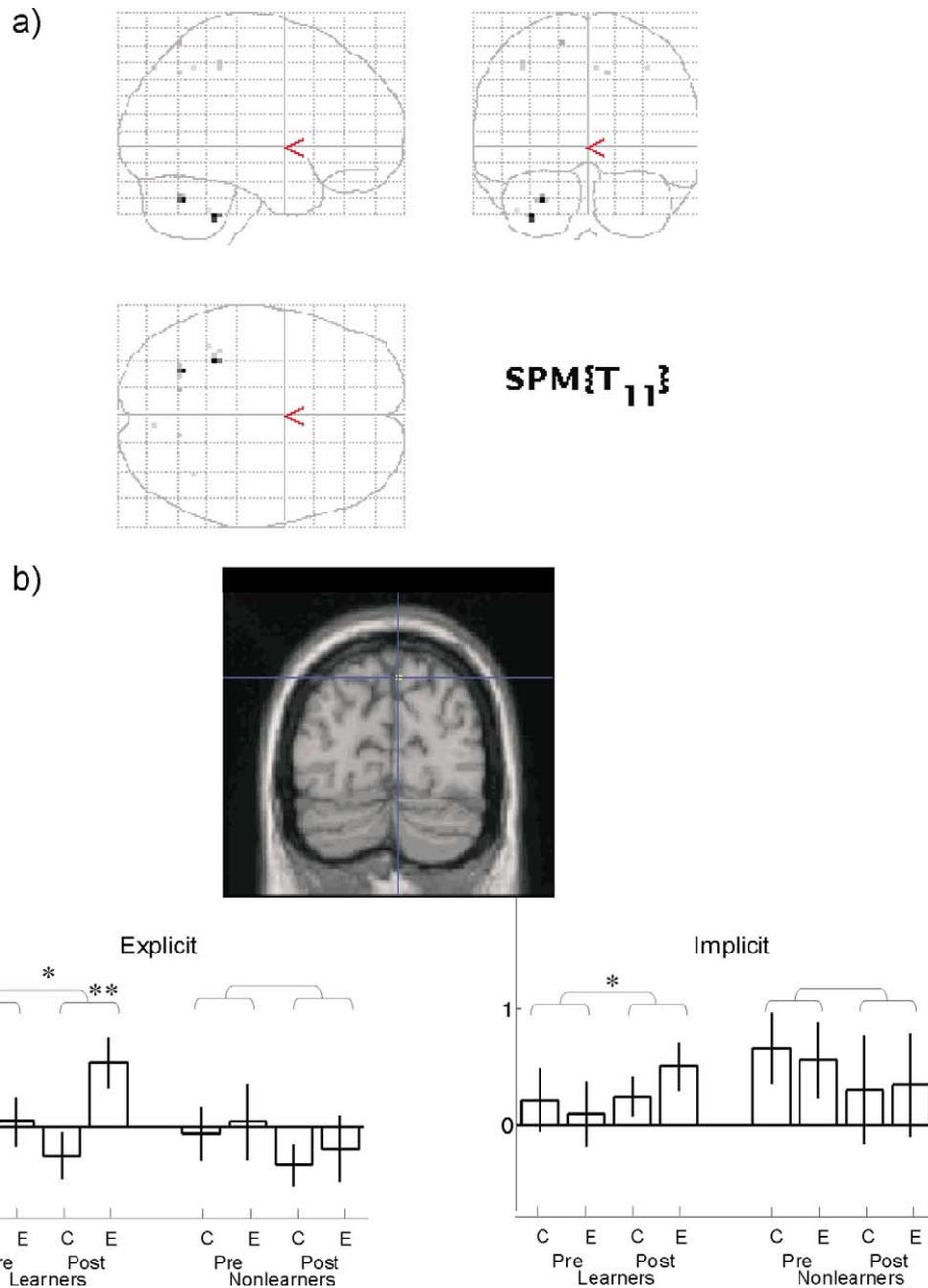


Fig. 6. Imaging data, a common training effect: explicit and implicit music reading. (a) Glass brain statistical parametric map (SPM) relating to a common training effect across explicit and implicit music reading tasks. (b) Axial section (top) through an area in medial superior parietal cortex which, as well as showing a common training effect across both tasks, survived $P < 0.001$ in each task separately; plots of the mean percentage signal change of this voxel (bottom) in the explicit and implicit music reading tasks.

the following question: which brain areas would show functional change after the acquisition of musical literacy?

Learning to play a melody: explicit music reading task

When our learners used their newly acquired skill of sight-reading, they showed activation in bilateral superior parietal cortex. A group of nonlearners, who were also scanned twice, using an equivalent interscan interval, did

not show any difference in this brain region, thus ruling out the possibility that the changes were due to nonspecific factors associated with being scanned twice.

Why is this part of cortex recruited in our aspiring pianists? In the introduction, we argue that music reading is essentially visuospatial. The dorsal visual processing stream, within which superior parietal cortex resides, is known to be important for coding of spatial, as opposed to the featural, aspects of visual stimuli (the “what”/“where”

distinction”) (Damasio and Benton, 1979; Gross, 1973; Maunsell and Newsome, 1989; Mishkin and Ungerleider, 1982; Pohl, 1973). A distinction has also been made between the visual perception of objects versus the control of action toward those objects (the “what”/“how” dichotomy) (Goodale and Milner, 1992). Whether the distinction made is one of “what versus where or “what versus how,” sight-reading for keyboard performance falls within the class of behaviors that the dorsal stream is known to subserve. First, the information relevant for performance is contained in the position of the note on the staff (“where”); second, musical performance relies on the use of this positional information to guide selection of the appropriate keypress (“how”).

An activation similar to one found in the present study, in right superior parietal cortex, was also seen in a PET study of musical sight-reading. Performance of the main task (sight reading, playing, and listening) by professional pianists activated the right superior parietal cortex, but this region was not activated in the reading-alone or listening-alone condition (Sergent et al., 1992). The replication of this finding in our study, using fMRI as opposed to PET and novice pianists as opposed to professionals, suggests that the common activation across the two studies is likely to reflect the specifically visuospatial translational element of music reading and, furthermore, that such activation may be independent of skill level.

The presence of fusiform activity in the explicit music reading task was not predicted. Fusiform cortex occupies the ventral, as opposed to the dorsal, stream of visual processing. However, the activation of classic object recognition areas in tasks that are presumed to be visuospatial in nature is not unprecedented. An fMRI study of mirror reading (Goebel et al., 1998) found joint activation in superior parietal areas and an area in left lateral occipital cortex which is close to the fusiform activation seen in the present study. In that study, a high correlation was found between activation in lateral occipital cortex and an area in left intraparietal sulcus, suggesting the existence of crosstalk between ventral and dorsal stream structures. On the basis of monkey lesion work (Cowey and Gross, 1970), it has been argued that both the ventral and the dorsal streams are necessary for some mental rotation tasks (Walsh and Butler, 1996). Anatomical studies in the monkey, demonstrating the existence of corticocortical projections from intraparietal sulcus and area 7a to area TE and TEO in the inferotemporal cortex (Andersen et al., 1990), provide an anatomical basis for functional communication between the two streams.

Effect of exposure to musical notation: implicit music reading task

Since the implicit music reading task did not involve, or require, sight-reading, differences in activation, related to the presence of task-irrelevant musical notation, after training, must reflect an effect of learning at an implicit level. Such differences were obtained in the left supramarginal

gyrus, left inferior frontal sulcus, and right frontal pole. Unlike the explicit music reading task, in which the training effect was characterized by a relative increase in the trial effect across the two scanning sessions, the training effect observed in the implicit music reading task was characterized by a trial effect that was present only after training. The training effect was independent of any behavioral change in the performance of the feature detection task (Fig. 3c and d).

An explanation of the activation change in supramarginal gyrus rests on the following argument. During the course of training, participants learned to make specific keypresses in response to particular musical notes. We suggest that the visual appearance of musical notes, posttraining, may be automatically and unconsciously interpreted as an instruction to act. For the purposes of performing the feature detection task (up/down discrimination of a visual target), preparation of the learned musical response would be inappropriate and would be overridden by the preparation and execution of the task-relevant motor response. While the preparation and execution of the task-relevant response was common across both the pre- and the post-training sessions, the implicit preparation of a music-specific motor response would have only occurred post-training.

The left supramarginal gyrus is thought to be important in processes related to “motor intention.” While a network of areas including the posterior parietal cortex of the right hemisphere have been demonstrated to subserve visual attentional processes (Corbetta, 1993, 1998; Corbetta et al., 1993), imaging and TMS studies have highlighted the importance of more anterior parietal cortex of the left hemisphere for motor orienting (Godschalk and Lemon, 1989; Rushworth et al., 2001a, 2001b, 2001c), a hypothesis that is supported by observations that patients with damage to left inferior parietal cortex have difficulty in performing a number of different movements one after another (Harrington and Haaland, 1992; Kimura, 1993; Rushworth et al., 1997), as well as having problems in the representation and awareness of movements (Sirigu et al., 1999).

The left lateralized inferior frontal activation, in the vicinity of Broca’s area, also commonly appears in studies of motor response preparation (Krams et al., 1998; Rushworth et al., 2001a, 2001b, 2001c). This area is believed to be the homolog of an area known as F5 in the macaque which is interconnected with area 7b, the homolog of the human supramarginal gyrus. While the supramarginal gyrus is believed to be important in response preparation per se, the involvement of the inferior frontal region may be specific to response preparation characterized by a “standard” stimulus-response mapping, where standard refers to a spatial correspondence between stimulus and response (Krams et al., 1998) such as the kind of mapping used in reading music notation.

The involuntary effect of musical literacy, as reflected in activation changes in the implicit music reading task, is also seen behaviorally (Fig. 2). The musical Stroop task, a measure of music reading skill, showed that, post-training, the

reaction time to perform an explicit task (mapping from numbers to fingers) was increased when the numbers were superimposed on incongruent musical notes. Thus, although no behavioral changes were seen, post-training, in the feature detection/implicit music reading task (presumably because the task was very easy), training-related changes in performance of the Stroop task lend support to the notion that activation changes seen in left supramarginal gyrus in the implicit music reading task may reflect response preparation. The absence of a similar activation in the explicit music reading condition may be explained by the fact that, in this task, both control and experimental trials required explicit preparation and execution of a motor response.

Additional evidence that the presentation of musical stimuli can elicit implicit activation of motor-related cortical areas comes from studies within the auditory domain. Trained pianists have been shown to have an involuntary increase in motor cortex activity when listening to piano pieces and performing a decoy task requiring detection of a wrong note in a piece of familiar music (Hauelsen and Knosche, 2001). The decoy task was designed to emphasize the perceptual rather than the production components of musical processing, thus ensuring that any motor-related activations were genuinely involuntary. Activation of the primary motor cortex during an explicitly perceptual task supports the idea that music listening, as well as music reading, can implicitly affect the musical production system. The sight-reading PET study of Sergent et al. also activated supramarginal gyrus although this was related to the combination of score reading and music listening as compared to score reading alone, a finding that was interpreted to suggest that supramarginal gyrus was involved in a visual–auditory mapping process. However, activation of the supramarginal gyrus in our study is not consistent with such a view since there was no auditory component. An alternative explanation for the involvement of supramarginal gyrus in Sergent's study may be that score reading alone was not sufficient to activate motor preparatory systems but the conjunction of musical information from visual and auditory modalities was suprathreshold for eliciting music production-related activity in the supramarginal gyrus.

Commonalities in the training effect: explicit and implicit tasks

In the introduction, we argued that a common training effect (a post-training/pre-training activation change in the same brain region across both explicit and implicit tasks) could be confidently interpreted to be specifically learning related. In the present study, specific learning effects were seen in several areas, including the bilateral superior parietal cortices. The presence of a training effect in the superior parietal cortex is of particular interest. We have suggested that the training effect shown by this area in the explicit task reflects a visuospatial sensorimotor translation between the

notes on the staff and the appropriate keypresses. The fact that this region also showed a training effect in the implicit task leads us to conclude that the mere presence of musical notation may result in a similar translation even when such translation does not result in motor execution.

Conclusion

The activation in superior parietal cortex seen in the explicit music reading task, after training, supports the hypothesis that music reading involves a sensorimotor translation in which the spatial characteristics of musical notation are used to guide selection of the appropriate keypress. The activation of the left supramarginal gyrus in the implicit music reading task, in conjunction with the Stroop interference seen after training, suggests that after 15 weeks, musical notation is automatically processed. The common activation of superior parietal cortex across the two tasks reflects an effect which is specific to the acquisition of music reading skill and is independent of the particular tasks used. The study serves to illustrate the power that culture has in shaping brain function and illustrates one approach by which neuroimaging can be used to capture and delineate such changes.

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