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Functional neuroanatomical networks associated with expertise in motor imagery

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Although numerous behavioural studies provide evidence that there exist wide differences within individual motor imagery (MI) abilities, little is known with regards to the functional neuroanatomical networks that dissociate someone with good versus poor MI capacities. For the first time, we thus compared, through functional magnetic resonance imaging (fMRI), the pattern of cerebral activations in 13 skilled and 15 unskilled imagers during both physical execution and MI of a sequence of finger movements. Differences in MI abilities were assessed using well-established questionnaire and chronometric measures, as well as a new index based upon the subject's peripheral responses from the autonomic nervous system. As expected, both good and poor imagers activated the inferior and superior parietal lobules, as well as motor-related regions including the lateral and medial premotor cortex, the cerebellum and putamen. Inter-group comparisons revealed that good imagers activated more the parietal and ventrolateral premotor regions, which are known to play a critical role in the generation of mental images. By contrast, poor imagers recruited the cerebellum, orbito-frontal and posterior cingulate cortices. Consistent with findings from the motor sequence learning literature and Doyon and Ungerleider's model of motor learning [Doyon, J., Ungerleider, L.G., 2002. Functional anatomy of motor skill learning. In: Squire, L.R., Schacter, D.L. (Eds.), Neuropsychology of memory, Guilford Press, pp. 225–238], our results demonstrate that compared to skilled imagers, poor imagers not only need to recruit the cortico-striatal system, but to compensate with the cortico-cerebellar system during MI of sequential movements.

Introduction

Motor imagery (MI) is a dynamic state during which a subject simulates an action mentally without any body movement (Jeannerod, 1994), and is subdivided into different modalities including visual and kinesthetic imagery. Visual imagery requires self-visualization of the movement from a first- or third-person perspective, while kinesthetic imagery requires one to "feel the movement". There is now ample evidence that MI and motor performance share the same neural networks (Decety et al., 1994; Gerardin et al., 2000). Lafleur et al. (2002) have also demonstrated that the cerebral plasticity that occurs following physical practice is reflected during MI. This relationship is called "functional equivalence" (Holmes and Collins, 2001), even though the neural substrates mediating these different types of MI and those activated during motor performance of the same action are not totally overlapping (Ruby and Decety, 2001; Sirigu and Duhamel, 2001; Binkofski et al., 2000; Solodkin et al., 2004).

Previous work has demonstrated that mental practice with MI can improve the performance and learning of a variety of motor tasks (for reviews, see Feltz and Landers, 1983; Guillot and Collet, 2008). The benefits of MI have been found, however, to differ depending upon the stages of the acquisition process and the subject's level of expertise (Hardy and Callow, 1999; Guillot et al., 2004). Other subject-dependent variables like the ability to create and manipulate accurate and vivid mental images have also been shown to influence the degree of improvement that can be seen following MI (Munroe et al., 2000). Indeed, the individual capacity to elicit efficient mental images is not universal, hence highlighting the importance to utilize appropriate psychological, behavioral and neurophysiological means to evaluate the subject's capacity in forming accurate motor images (Guillot and Collet, 2005b; Lotze and Halsband, 2006). To do so, researchers have used mental

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chronometry tests, which measure the ease/difficulty that subjects may encounter in preserving the temporal characteristics of the motor performance (for review, see Guillot and Collet, 2005a; Malouin et al., 2008). Many psychological questionnaires have also been validated to evaluate the individual MI abilities (e.g. Hall and Martin, 1997; Malouin et al., 2007). As responses to those questionnaires remain subjective, however, the use of physiological recordings that correlate with mental representations of actions has recently been proposed. In particular, activity of the autonomic nervous system has been shown to match MI in real time and to evaluate both MI accuracy and individual ability to form mental images (Roure et al., 1999; Guillot and Collet, 2005b).

Despite accumulated evidence that the benefits of MI are dependent upon the individual imagery abilities, there is still no data, however, with respect to the pattern of brain activations in subjects with good and poor MI abilities. Until now, the only neuroimaging study that indirectly touched upon (but did not address directly) this issue comes from Lotze et al. (2003) who compared professional musicians and beginners during both MI and motor performance of a violin concerto. Although the professionals reported using MI more often than the amateur violinists, this study focused more on identifying the brain structures related to the effects of the subject's expertise level in music than on their capacity to produce efficient MI. Furthermore, their participants were not subjected to rigorous MI testing procedures, as the MI abilities were only evaluated through a subjective and an *a posteriori* questionnaire. Thus, still to date, no study has looked at the cerebral networks associated with differences of expertise in MI.

In the present study, we aimed for the first time to identify the neural substrates mediating MI in good and poor imagers who were selected using a rigorous and quantitatively validated testing procedure including psychological tests, as well as behavioral and physiological measures. Based on the existing literature, it was expected that the neural substrates mediating MI would differ with respect to the accuracy and vividness of the mental images, even if good and poor imagers are showing a similar level of performance on tasks carried out physically. We thus hypothesized that, compared to poor imagers, greater activations in motor-related regions as well as in both the inferior and superior parietal areas would be observed during MI in subjects with good to excellent MI abilities. We also expected that fewer cerebral areas would be activated in good imagers, while a more distributed pattern of activity would be observed in the group of poor imagers. Finally, earlier neuroimaging studies have provided evidence that the cortico-striatal and the cortico-cerebellar anatomical systems contribute differently in motor learning, although they share functional interactions (e.g., Doyon and Ungerleider, 2002; Doyon et al., 2003; Doyon and Benali, 2005). Accordingly, we predicted that these two anatomical systems would contribute differently during MI of sequential movements in skilled and poor imagers.

Methods

In order to investigate the neural substrates mediating MI in good and poor imagers, we first tried to distinguish between subjects who were able to reach a high level of performance from those who were having trouble in using MI. As suggested by Guillot and Collet (2005b) and Lotze and Halsband (2006), a series of psychological, behavioral and neurophysiological tests were thus combined prior to the fMRI study to evaluate MI ability within a large sample of subjects. The fMRI experiment was then performed a few days later using a subset of those subjects. This study was approved by the Local Ethics Committee from the University of Montreal Geriatric Institute. All participants gave their informed consent and were paid for their participation.

Pre-selection

Participants

Fifty healthy right-handed volunteers (24 men: Mean age 26.4± 3.4, age range 21–34 and 26 women: Mean age 25.6±3.9, age range 20–35) without neurological or psychiatric complications participated in a pre-selection testing session.

Physiological measure of MI

One major innovation in this study was the use of physiological measures of the autonomic nervous system (ANS) to test the subject's abilities to produce MI. Higher brain functions may be investigated through ANS effectors activity at the peripheral level (Hugdahl, 1996), as central operations (planning and programming) are paralleled by ANS responses, hence representing non-conscious physiological mechanisms of mental processes (Collet et al., 1999). This quantitative measure of MI is now well-established, and ANS patterns have even been found to differentiate between good and poor imagers (Roure et al., 1999; Guillot et al., 2004). Among ANS effectors, sweat glands are innervated by sympathetic endings only. An increase of the subjects' level of arousal (such as during MI) elicits sweat release and, consequently, a decrease in skin resistance (SR). Indeed, electrodermal variations are under the unique control of the sympathetic branch, hence guaranteeing that they are not elicited by the antagonist effect of the sympathetic and the vagal endings. This autonomic parameter was recorded using two 30 mm^2 unpolarizable Ag/AgCl electrodes (Clark Electromedical Instruments, Ref. E243) placed on the second phalanx of the second and third digits of the non-dominant hand, and held by adhesive tape (Fowles et al., 1981). A conductive paste (TECA ref: 822-201210) was used to improve skin/electrode contact. Resistance was recorded with the constant current method (Boucsein, 1993) with a density of 0.5 $\mu A/mm^2$. As response amplitude depends on the pre-stimulation value (Furedy and Scher, 1989), a more reliable index was taken without referring to that initial value (tonic level). The Ohmic Perturbation Duration (OPD) was measured at the beginning of the sudden drop elicited by MI and was ended when the slope, while recovering basal level, showed no fluctuation and resembled the one observed before stimulation (Vernet-Maury et al., 1995). Response latency referred to the time lapse from the onset of the stimulus to the initiation of the response. Any response onset within 1–3 s following stimulus onset was thus considered to be elicited by that stimulus (Levinson and Edelberg, 1985). Each trial was separated from the next by a rest period (lasting at least 20 s), in order for the physiological measure to recover its baseline level, and subjects were acoustically isolated.

Behavioral tasks

In addition to the ANS procedure described above, several tests were combined to evaluate MI ability in our group of subjects. First, each participant completed the revised version of the Movement Imagery Questionnaire (MIQ-R, Hall and Martin, 1997). The MIQ-R is made up of 8 items that evaluate both inter-subject differences in visual imagery (4 items) and kinesthetic imagery (4 items), as well as within-subject differences (visual versus kinesthetic imagery). Participants were requested to read descriptions of the movement to be performed physically, and then to imagine themselves performing the same movement. They were then asked to rate the difficulty to imagine each movement using a 7-point rating scale. Second, and

simultaneously to the measure of the ANS responses, the temporal congruence between real and imagined actions was evaluated. To do so, the participants were asked to physically perform and imagine, in a way that was comfortable for them, 3 motor actions that required the ability to use both visual and kinesthetic imagery: i) a sequence of 16 rhythmic steps performed within a square drawn on the floor, ii) a series of 5 consecutive complete flexion-extensions (squats) of the lower limbs and iii) the maintenance of a sitting position for 12 s with their back against the wall and their knees bent at 90°. Subjects had to perform the actions using visual imagery first, and then using kinesthetic imagery. The ability to preserve the temporal characteristics between the physical execution of the movement and during MI was measured, as it is thought to be a reliable method to evaluate the subjects' MI abilities (Guillot and Collet, 2005a; Malouin et al., 2008). Subjects were required to start and stop the timer upon mental initiation of the first body movement as well as at the end of the sequence, respectively. In the third task, there were no explicit movement (isometric contraction). Yet, the temporal congruence was measured using a chronometric evaluation requiring subjects to feel the movement and estimate the duration of the motor sequence simultaneously. Finally, to verify that they performed MI as they were instructed to, participants were required to describe the nature of the images they attempted to form after the MI session and to score their effort using a 4-point rating scale (1 = very difficult to imagine/feel and 4 = very easy to imagine/feel).

Motor imagery quality

On the basis of the measures mentioned above, four well-established data were used to evaluate the final individual MI abilities.

(1) *ANS score*. The number of SR responses was first calculated and represented on a 0–12 scale: 0 indicating a lack of SR response on each MI trial during the 3 motor tasks described above, and 12 indicating that each MI trial elicited a SR response. In addition, the subject's level of arousal was assessed through SR basal tonic evolution across the MI session. In fact, the level of arousal during MI has been found to be comparable to that recorded during the actual execution of movements, and consequently it has been suggested that subjects should be able to increase their arousal level, just as they would do during the physical performance (for review, see Guillot and Collet, 2008). To give equal importance to these two factors, however, the evolution of the arousal level was graded between −5 (subjects relaxed throughout MI), −2 (increased relaxation by steps), 0 (no adjustment, the activation level remaining stable during MI), +2 (increased activation by steps during MI) and +5 (increasing activation regularly). Thereby, the ANS score consisted of the sum of the two preceding measures (number of SR responses + arousal level score): the minimal score subjects could obtain being −5, and the maximal score being 17.
(2) *MIQ-R score*. This measure was calculated by adding the scores assigned by the subjects to each MI test-item. The minimal score subjects could obtain was 8, and the maximal score was 56.
(3) *Auto-estimation score*. This score was the mean of all ratings given by the subjects on a 4-point scale, when evaluating the vividness of each MI trial during the 3 motor tasks described above.
(4) *Mental Chronometry score*. This score was the mean of the absolute time differences between the actual and imagined trials during the 3 motor tasks. This difference score was subtracted from the global imagery score as it was inversely proportional to the subjects' ability to preserve the temporal characteristics of movement during MI, suggesting therefore a difficulty to imagine the action.

Following the recommendations of Roure et al. (1999), a global imagery score was finally calculated for each participant, using this simple formula: (ANS score + MIQ-R score + Auto-estimation score) − (Mental chronometry score).

Participants in the fRMI study

Among the 50 volunteers who took part in the pre-selection study, only 28 were selected for the fMRI experiment. They were separated in two groups (good and poor imagers) as defined by at least one SD above or below their average global imagery score. The first group was composed of 13 subjects with good MI abilities (6 men: Mean age 25.5 ± 2.4 years and 7 women: Mean age 23.9 ± 2.8 years), while 15 subjects (6 men: Mean age 26.5 ± 4.1 years and 9 women: Mean age 25.4 ± 3.8 years) were assigned into the poor imager group. None of the subjects were a musician or a professional typist in order to eliminate subjects with pre-existing skills requiring highly coordinated finger dexterities.

Finger sequence task

Participants were first asked to learn a sequence of eight moves using fingers 2 to 5 of the left hand, until they were able to perform them explicitly from memory within a 6 s-period. The order of finger movements was pseudo-randomly selected such that each finger was used twice in the sequence. The subjects' performance was assessed inside and outside the scanner by using a 4-keys keyboard (Electrical Geodesics, Eugene, OR) that was MR-compatible. The keyboard allowed recording of the subjects' response accuracy and timing. Participants were required to keep their fingers on the keys to minimize amplitude variation and the amount of force required to press the keys. They were instructed to tap the sequence at a comfortable and self-paced speed, while making as few errors as possible. Speed tests, however, were also scheduled to check that the participants were able to correctly perform and imagine the movement within a period not exceeding 6 s.

After being introduced to the sequence and on each run (total = 6 runs), participants were scanned in 3 conditions (physical execution, MI and perceptual control), which were always separated by rest periods of 10 s following a block-design:

(1) *Physical execution*. The participants executed the finger sequence explicitly learned before the scanning session using the 4-key keyboard.
(2) *Motor Imagery.* The subjects were required to imagine the finger sequence without any movement, using the first-person perspective.
(3) *Perceptual control condition* (*CTRL*). The subjects were specifically instructed to remain motionless while listening to distinct high and low tones sounds (see below). This control condition was chosen to control for the same "start" and "stop" sound signals that were used in the other experimental conditions.

The order of administration of each of the experimental and control conditions was counterbalanced across each run. Instructions for each condition were given on a computer screen that could be seen through a mirror embedded within the head-coil. After

reading the instructions, the subjects were required to close their eyes. Each period of the experimental and control conditions (lasting 30 s) were composed of five trials and two separate sounds were used to indicate the beginning of each trial (high tones) and the end of a run (low tones), using MR-compatible headphones (MR confon HP-SI01, Germany). At the end of the sequence (following the low pitch tone), subjects were requested to open their eyes and to remain in a resting, awake state until the next assignment.

Before the scanning session began, all of the participants were given a few trials until they physically performed 5 successive correct finger sequences. They were also asked to perform 5 MI trials to become familiar with the presentation of the auditory stimuli and the apparatus itself.

Functional Imaging

Blood oxygen level-dependent (BOLD) signal was registered using a 3-T whole-body TRIO system (Siemens, Erlangen, Germany) located at the "Unité de Neuroimagerie Focntionnelle, Institut Universitaire de Gériatrie de Montréal". The head of the subject was immobilized by using foam cushions. The protocol lasted 90 min and included (i) one scout to localize the functional axial slices, 6 functional runs and one high resolution anatomical scan [sagittal T1-weighted; repetition time (TR): 13 ms; echo time (TE): 4.92 ms; 1 slab divided into 160 slices; matrix size: 256×256; voxel size: 1×1×1 mm^3; partial Fourier imaging 7/8; bandwidth 140 Hz per voxel; slice orientation: sagittal] and (ii) 43 oblique axial gradient echo-planar imaging (EPI) images [repetition time (TR): 4.5 s; echo time (TE): 30 ms; 90°; bandwidth: 1 562 Hz per pixel; field of view (FOV): 192×192 mm^2; voxel size: 1.5×1.5×2.5 mm^3; partial Fourier imaging 6/8; matrix size: 128×128]. For each series, 75 EPI volumes were acquired over 5 min and 37 s.

Behavioral recordings

Behavioral dependent variables (key pressed, movement frequency, total sequence speed and reaction times) were automatically recorded based on the subjects' responses using a home-made MATLAB-written routine. For each participant, this software compared the sequence of key presses produced by the subject to that of the correct sequence template to be performed, and thus detected any discordance between the real and expected taps within the given sequence.

Data analysis

Kolmogorov–Smirnov tests were first carried out to verify whether the behavioral data from our sample of subjects followed a normal distribution. The behavioural results were then compared using both t-tests and analyses of variance (ANOVAs) with repeated measures. Functional data analyses were performed with SPM2 (Wellcome Department of Cognitive Neuroscience, London). Motion correction in the functional images was done first using the SPM realignment. This estimates a set of 6 rigid-body transformation parameters for each image by finding the parameters that minimize the mean squared difference between it and a reference image. The middle image of the last run of the scanning session was used as the reference image for each subject. The anatomical image was realigned to the mean functional image with the SPM coregister method (Collignon et al., 1995). The functional and anatomical images were then normalized to the MNI coordinates (avg152-T1.mnc template with a final voxel size of 1.5×1.5×2.5 mm^3) using the 4th degree B-spline interpolation method, and finally into the standard proportional stereotaxic space of Talairach and Tournoux (1988). The scans were smoothed using a Gaussian kernel set at 8-mm full width at half-maximum (FWHM). Statistical analysis was done using the General Linear Model (GLM) to describe the data in terms of experimental and confounding effects, as well as residual variability. Six regressors of no interest corresponding to the movement were used (x, y, z, pitch, roll and yaw). We also used the Hemodynamic Response Function (HRF) with time derivative for these regressors of interest. Single subject analyses were first performed with a first-level, fixed effect analysis, which use within-subject variance. Then group analyses were done with random-effects analyses, which involved taking the contrasts of parameters estimated from a first-level (fixed-effect) analysis and entering them into a second-level (random-effect) analysis. To identify the location of brain areas involved in each task, one sample t-tests were used to contrast i) the physical and MI conditions with the perceptual control condition, and ii) the physical condition against the MI condition. Comparisons of the functional data were assessed at a statistical threshold ($p<0.001$) uncorrected for multiple comparisons. In these maps, activated clusters were considered significant if their spatial extent was >10 voxels. The data of the results section are presented as mean (standard deviation values).

Results

Pre-experiment

MIQ-R

When comparing the two groups selected for the fMRI experiment ($n=28$), the MIQ-R scores were significantly different ($t=5.6$, $p<0.001$), mean MIQ-R scores being 45.7 (2.7) in the good imagers and 38.6 (5.2) in the poor imager groups. The minimal and maximal scores were 42 and 50 in good imagers and 27 and 46 in poor imagers, respectively. Interestingly, there was no significant difference between men and women scores ($t=0.7$, $p>0.05$, NS).

Mental chronometry

The average time difference between the physical and the imagined trials did not reach significance between the two groups ($t=-1.1$, $p>0.05$, NS). In the good imager group, this difference was 2.22 s (1.5), while it was 3.08 s (2.4) in poor imagers. Also, there was no significant gender difference ($t=-0.82$, $p>0.05$, NS).

Auto-estimation

Compared to the poor imagers, subjects with good MI abilities assigned a significantly higher score when evaluating the vividness of their MI on the 4-point scale ($t=2.34$, $p<0.05$). Mean scores were 2.68 (0.5) and 3 (0.2), respectively. Again, no gender effect was found ($t=0.6$, $p>0.05$, NS).

ANS activity

The mean SNV score (number of responses + arousal level score) strongly differed between the two groups ($t=8.29$, $p<0.0001$), the mean scores being 7.08 (3.9) in good imagers and −2.4 (2) in poor imagers. Again, there was no significant difference between men and women on this score ($t=0.07$, $p>0.05$, NS). A representative comparison of SR response between good and poor imagers is presented in Fig. 1.

Global imagery score

The global imagery scores were 53.4 (4.7) in good imagers and 33.9 (6.2) in poor imagers, this difference reaching significance ($t=9.3$, $p<0.0001$). No gender effect was found ($t=0.6$, $p>0.05$,

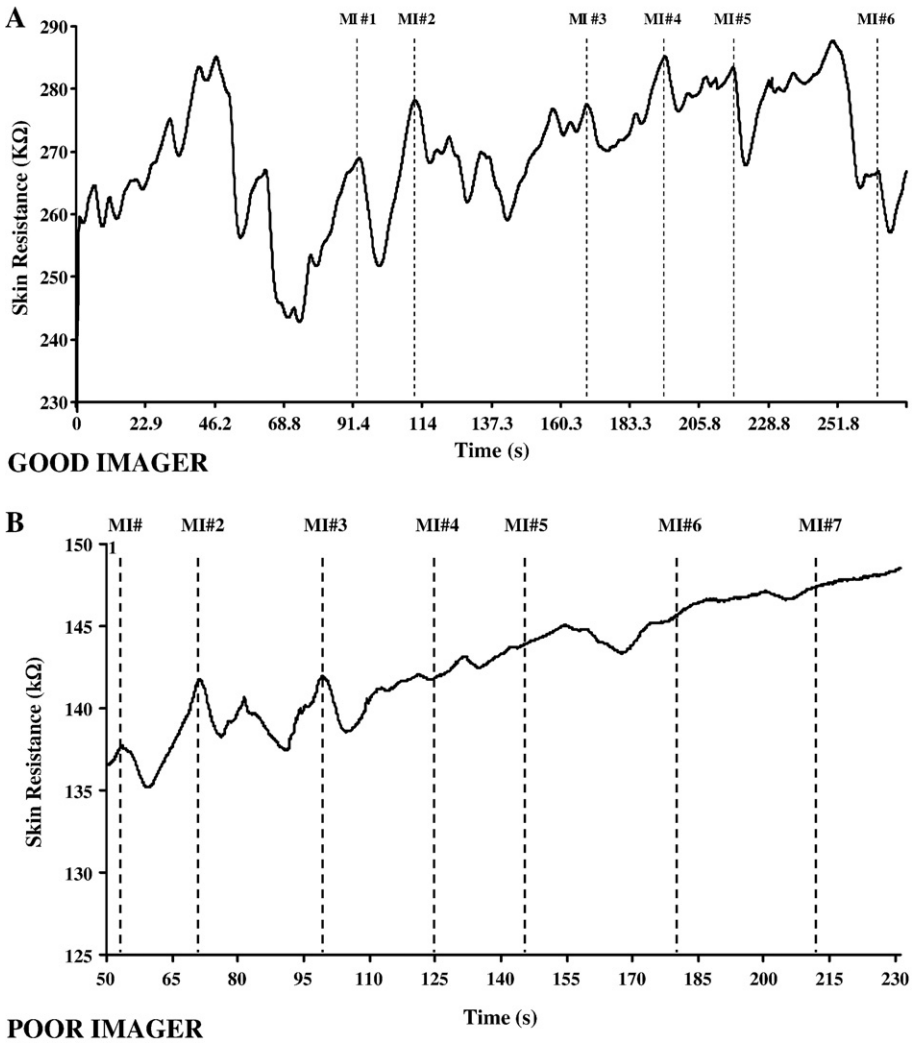

Fig. 1. Skin resistance responses during motor imagery. In the good imagers (A), a response (indicated by the dotted line) is recorded during each motor imagery trial, hence attesting to mental work. Conversely, in the poor imagers (B), skin resistance responses related to motor imagery are recorded during the initial trials only. Responses then tend to disappear or to be delayed, attesting difficulties in forming clear representation of action. The strong increase in skin resistance throughout the session also indicates that the subject is relaxed. MI = motor imagery.

NS), and thus there was no need to subdivide the subject's group by gender for the functional analyses.

fMRI experiment

Behavioral data

During the first run, the subjects' mean time to perform the 8-item finger sequence was 3.7 s (0.8). Over the 6 functional runs, they took on average 3.4 s (0.7) to physically complete the sequence. An analysis of variance with repeated measures showed that the subjects significantly improved their performance from run to run ($F_{1,26}=13.5$, $p<0.001$), with a mean completion time of 3.02 s (0.12) during the last run. There was no group effect nor interaction Group x Run effect, however ($F_{1,26}=0.2$, $p>0.05$, NS), hence demonstrating that the two groups did not differ in their ability to learn the sequence of movements. Similarly, the mean number of correct responses increased from run to run ($F_{1,26}=7.7$, $p<0.001$), without any group effect ($F_{1,26}=0.7$, $p>0.05$, NS), nor any interaction.

fMRI data

Physical execution vs. perceptual control condition. When the physical execution and the perceptual control conditions were contrasted, both groups manifested a similar network of activation, even though the extent of the significant activity was unexpectedly wide in poor imagers (Table 1, Fig. 2). Within the motor-related regions, both groups showed increased bilateral activity in lateral and medial premotor cortices (BA 6) and in both the anterior (lobule V) and posterior (lobule VI) cerebellar hemispheres. The right primary (BA 4) motor cortex was also recruited. While the data showed bilateral activations in the ventral premotor cortex (BA 44) in the good imagers, peaks of activations were located only in the left hemisphere in the poor imagers. Furthermore, lobules III and IV of the anterior cerebellum were activated in the good imagers. In the basal ganglia, both groups showed bilateral activations of the putamen. Bilateral activations in the globus pallidus were also found in the poor imager group, whereas the good imagers showed only

Table 1
Coordinates of peak activations for the physical execution and the motor imagery conditions versus the perceptual control condition

Anatomical areas	Hemisphere	Good imagers								Poor imagers							
		PE vs. PC				MI vs. PC				PE vs. PC				MI vs. PC			
		x	*y*	*z*	*t*-value	*x*	*y*	*z*	*t*-value	*x*	*y*	*z*	*t*-value	*x*	*y*	*z*	*t*-value
Occipital cortex																	
Primary visual area (BA 17)	L									−10	−95	0	5.44				
Pre-striate cortex (BA 18)	R					12	−73	−4	6.26								
Pre-striate cortex (BA 19)	L									−30	−82	−11	4.04				
Parietal cortex																	
Inferior parietal lobule (BA 40)	L	−51	−30	32	3.36	−62	−24	26	5.66	−40	−38	49	10.55	−51	−31	49	6.42
	R	39	−32	57	4.02	45	−34	49	6.17	63	−24	26	8.33	46	−39	43	6.42
	L					−42	−41	43	5.41	−53	−29	51	6.07				
	R					65	−36	27	4.47	34	−35	54	7.28				
	R									48	−30	32	6.3				
Superior parietal lobule (BA 1−3)	L	−61	−19	34	4.27					−45	−29	−51	5.57				
	R	38	−24	48	5.99												
Superior parietal lobule (BA 5)	L									−36	−40	60	5.72	−36	−41	60	5.99
	R	38	−40	60	4.39					27	−41	66	6.18				
Superior parietal lobule (BA7)	L	−10	−60	50	3.36	−12	−53	63	7.44	−12	−59	53	7.86	−10	−59	53	8.17
	R	22	−45	69	3.72	22	−59	55	7.67	4	−61	56	6.18	24	−47	66	5.92
	L					−48	−9	50	6.59					−24	−57	61	5.83
	R					10	−61	58	4.29	18	−51	63	5.86	9	−63	56	4.7
Motor and premotor cortex																	
Primary motor cortex (BA 4)	R	33	−26	57	6.71					38	−23	56	11.77	51	−6	44	7.17
	R									51	−2	19	4.75				
Lateral premotor area (BA6)	L	−59	5	27	6.8	−55	3	30	7.71	−26	−6	50	9.69	−56	2	33	10.5
	R	32	−16	59	6.17	51	1	25	8.52	42	−11	61	11.11	30	−6	50	6.93
	L	−42	−7	50	4.96	−46	7	53	7.47	−55	3	30	8.74	−26	−7	50	8
	R					32	1	50	4.87	61	5	27	8.08	55	−2	39	6.78
	L					−26	−3	55	5.55								
Medial premotor area (BA 6)																	
Pre-SMA	L	−8	10	35	5.3	−4	20	40	7.16	−6	5	47	6.93				
	R	14	−9	50	5.56	3	11	46	8.33	12	3	52	4.79				
SMA proper	L	−3	−7	61	7.37	−6	−6	7	13.7	−3	−7	62	7.27	−9	−11	61	8.56
	R	3	−6	61	4.48	6	−3	61	6.44	3	−5	53	12.47				
Ventral premotor cortex (BA 44)	L	−46	0	6	5.03	−56	9	16	5.64					−59	6	11	7.14
	R	44	−32	54	4.5	55	5	16	9.9	44	3	8	7.64	56	15	11	6.54
Prefrontal cortex																	
Rostral prefrontal area (BA 10)	R									53	43	−2	5.47				
Orbito-frontal cortex (BA 13)	L													−33	20	7	7.24
	R													34	18	7	5.82
Orbito-frontal cortex (BA 47)	L					−48	15	−1	5.13								
	R									38	15	−8	4.94				
Limbic regions																	
Cingulate cortex (BA 24)	L					−10	13	32	4.82	−8	5	36	6.70	−6	4	41	7.63
	R													10	5	36	7.94
	L													−55	1	22	7.42
Subcortical regions																	
Lateral Globus Pallidus	L					−20	−6	3	7.05	−24	−17	4	7.34				
	R	20	−6	0	5.74	20	−8	0	6.02	20	−3	−2	9.53	24	−13	3	8.2
Anterior putamen	L									−24	1	8	9				
	R									26	1	11	9.33				
Posterior putamen	L	−24	−5	−7	3.36	−27	−2	3	5.7	−26	−7	9	8.73	−26	−6	6	7.7
	R	27	−8	3	3.94	28	−2	−5	5.18					26	−3	6	7.3
Cerebellum																	
Anterior (lobule III)	L	−8	−40	−18	4.47												
Anterior (lobule IV)	R	2	−54	0	5.43												

Table 1 (*continued*)

Anatomical areas	Hemisphere	Good imagers								Poor imagers							
		PE vs. PC				MI vs. PC				PE vs. PC				MI vs. PC			
		x	*y*	*z*	*t*-value	*x*	*y*	*z*	*t*-value	*x*	*y*	*z*	*t*-value	*x*	*y*	*z*	*t*-value
Subcortical regions																	
Cerebellum																	
Anterior (lobule V)	L	−14	−50	−13	5.8	−18	−53	−20	10.87	−4	−59	−5	10.28				
	R					12	−53	−15	5.67	1	−55	0	8.03				
	L									−28	−33	−26	4.8				
Posterior (lobule VI)	L	−28	−48	−18	7.78	−36	−46	−23	8.31								
	R					34	−52	−23	10.28	27	−55	−20	11.48	32	−52	23	8.03
	L	−22	−65	−12	8.09	−22	−63	−17	7.17	−24	−57	−15	14.67	−26	−56	−20	9.13
	R	38	−65	−17	4.82	9	−68	−14	5.61					21	−69	−12	5.88
Posterior (Lobule VIIb)	L					−36	−46	−28	8.69								
	L					38	−52	−35	4.43								
Posterior (Crus I)	L	−48	−62	−20	4.24												
Posterior (Crus I)	R					34	−52	−27	12.46								

The table shows the Talairach coordinates of significant fMRI activity clusters which are reported in millimeters, relative to the anterior commissure (Talairach and Tournoux, 1988). In this table, as well as the other tables and figures, differences in activation were considered significant when reaching a $p<0.001$ value, $k>10$ voxels. BA = Brodmann area; L = left; R = right; PE = Physical Execution; PC = Perceptual Control; MI = Motor Imagery; SMA = supplementary motor area.

right activations of this structure. Interestingly, the posterior part of the putamen was activated in the good imagers, while the anterior region was recruited in the poor imagers. In the prefrontal regions, a set of active voxels was seen in the left cingulate cortex (BA 24) and in the orbito-frontal regions (BA 10, 47) in the poor imagers.

In the parietal lobe, an activation of BA 5 was found on the right, while bilateral activations in the primary sensory cortex (BA 1–3) as well as in both inferior (BA 40) and superior (BA 7) parietal lobules were observed in the good imagers. In the poor imager group, a distributed activation of these structures was recorded, including the

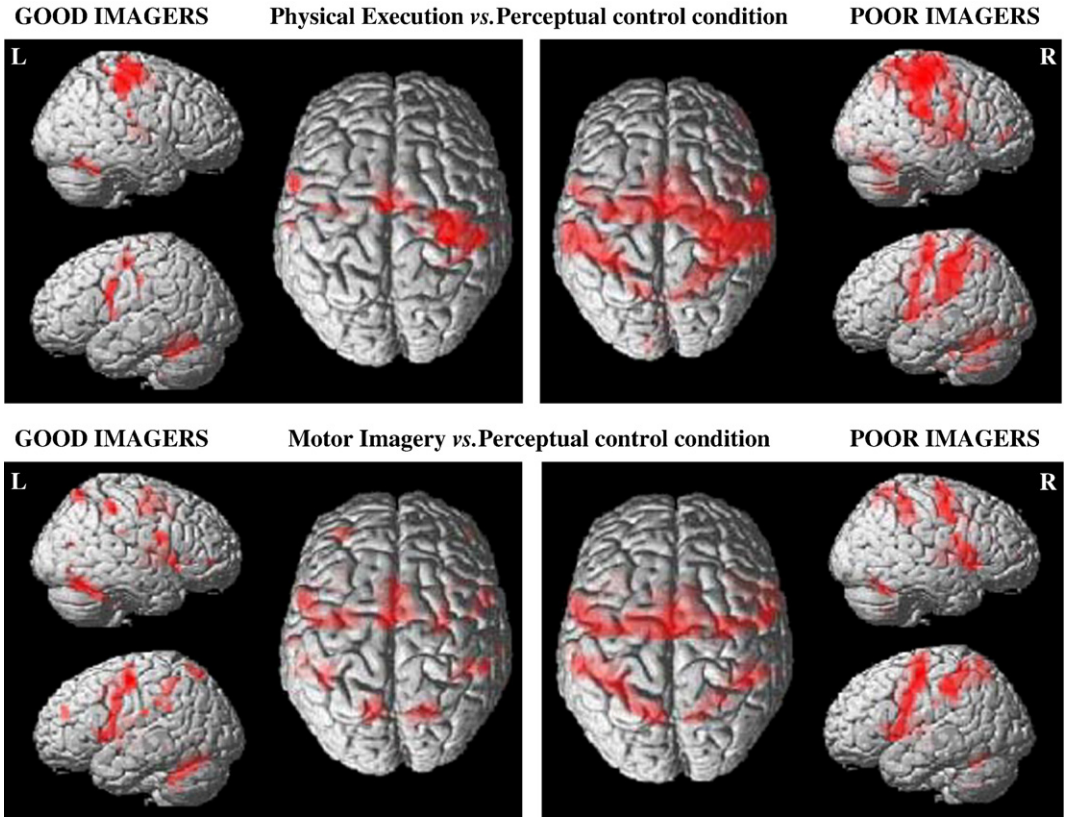

Fig. 2. fMRI activation maps during physical execution (upper row) and motor imagery (lower row) of left-hand movements in both good and poor imager groups. The 3-D segmented view and the left and right lateral views of the brain are shown. When the physical execution and the motor imagery conditions were contrasted with the perceptual control condition, both groups showed similar activations, which were more distributed in the poor imager group than in the good imager group. Furthermore, the poor imagers revealed more widely distributed activity within the left hemisphere than the good imagers, independently of the experimental conditions. L = left; R = right.

left primary sensory cortex (BA 1–3) as well as the inferior (BA 40) and superior (BA 5, 7) parietal lobules bilaterally. Finally, the poor imagers revealed an increase in activity in the left occipital cortex (BA 17, 19).

Although the poor imagers manifested a wide distribution, the direct comparison of the two groups revealed that the good imagers showed stronger activation in the superior parietal lobule (BA 7) bilaterally and in the left posterior part of the putamen. Increased bilateral activity was further observed in the lateral (BA 6) and medial (SMA) premotor cortex, in the right ventral premotor cortex (BA 44), in the inferior parietal lobule (BA 40) bilaterally, and in the right anterior (dentate nucleus) and left posterior cerebellum (Crus 1), as shown by Table 2 and Fig. 3. The subtraction "poor imagers minus good imagers" showed no significant activation.

Motor imagery vs. perceptual control condition. When the perceptual control condition was subtracted from the MI condition (see Table 1, Fig. 2), both groups showed bilateral activations of the lateral (BA 6) and ventral premotor cortices (BA 44). In the poor imager group, activations were also observed in the right primary motor cortex (BA 4), in the left medial premotor cortex (SMA proper) and in the cingulate cortex (BA 24) bilaterally. In the good imager group, peaks of activations were located in the left cingulate (BA 24) and orbito-frontal regions (BA 13, 47), as well as in the SMA bilaterally. Within the other motor-related areas, both groups manifested bilateral activations of the posterior part of the putamen. The globus pallidus was activated bilaterally in the good imager group, but only in the right hemisphere in poor imagers. Finally, apart from a cluster of activation in the left anterior and bilateral posterior cerebellum (lobule VI) in the poor imager group, a large bilateral peak of activity in the cerebellar cortex, including both the anterior (lobule V) and posterior (lobules VI, VIIb and Crus I) hemispheres was observed in the good imagers. Finally, the inferior (BA 40) and superior (BA 7) parietal lobules were also recruited in both groups, bilaterally.

When the MI condition was contrasted with the perceptual control condition (Table 2, Fig. 4), the direct comparison between the two groups revealed a bilateral increased of BOLD activity in the good imager group within the superior parietal lobule (BA 7) and the lateral premotor cortex (BA 6). The left cingulate cortex (BA 24) and the right inferior parietal lobule (BA 40) were also recruited in good

Table 2
Coordinates of peak activations for the comparisons between good and poor imagers

Anatomical areas	Hemisphere	Good imagers vs. poor imagers							
		Physical execution vs. perceptual control				Motor imagery vs. perceptual control			
		x	*y*	*z*	*t*-value	*x*	*y*	*z*	*t*-value
Parietal cortex									
Inferior parietal lobule (BA 40)	L	−61	−30	26	3.61				
	R					46	−34	36	3.71
Superior parietal lobule (BA7)	L	−10	−60	50	5.36	−10	−61	53	4.08
	R	8	−54	50	5.16	8	−58	51	3.74
Premotor cortex									
Lateral premotor area (BA6)	L	−20	−9	63	4.65	−42	−12	33	3.85
	R					44	−10	39	3.68
	L	−46	−10	33	4.61	−20	−9	63	3.50
	L	−16	8	54	3.58				
Medial premotor area (BA 6) SMA proper	L	−3	−6	53	4.47				
	R	8	−12	53	4.17				
Ventral premotor cortex (BA 44)	R	44	16	10	4.16				
Limbic regions									
Cingulate cortex (BA 24)	L					−16	−6	45	3.94
Subcortical regions									
Posterior putamen	L	−24	−8	−9	5.39				
Cerebellum									
Dentate nucleus	R	18	−54	−25	3.77				
Posterior (Crus I)	L	−48	−62	−20	4.24				
		Poor imagers vs. good imagers							
		Physical execution vs. perceptual control				Motor imagery vs. perceptual control			
		x	*y*	*z*	*t*-value	*x*	*y*	*z*	*t*-value
Parietal Cortex									
Cuneus	R					4	−67	27	3.07
Limbic regions									
Posterior cingulate cortex (BA 23)	R					10	−72	12	3.93
Prefrontal cortex									
Rostral prefrontal area (BA 10)	L					−30	50	1	3.66
Subcortical regions									
Cerebellum									
Anterior (lobule V)	R					18	−39	−16	3.58
Posterior (lobule VI)	L					−9	−61	−18	3.42
Posterior (lobule VI)	R					18	−73	−17	3.71

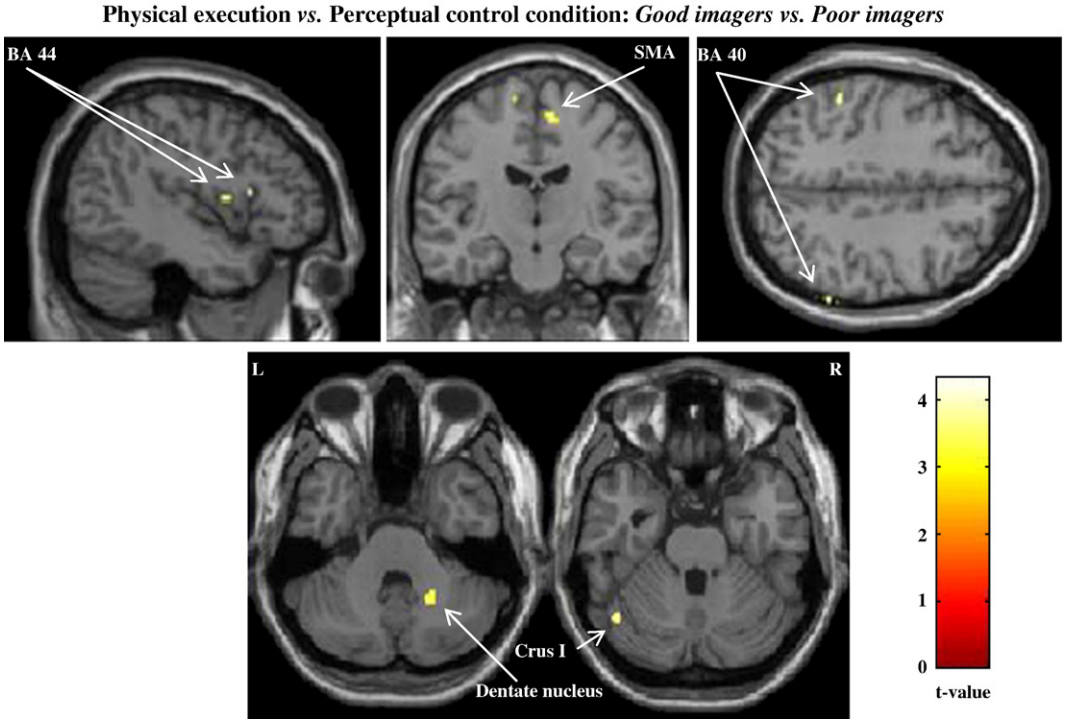

Fig. 3. Activation maps of the brain during physical execution vs. perceptual control condition. When the good imager group was contrasted to the poor imager group, selective activation was found in the right inferior frontal areas (BA 44; X=44), the right SMA (BA 6; Y=−12), as well as in the inferior parietal lobule, bilaterally (BA 40; Z=40), the right anterior (Dentate nucleus; Z=−25) and the left posterior (Crus I; Z=−20) cerebellum. BA = Brodmann area; L = left; R = right; SMA = supplementary motor area.

imagers. In contrast, only a few peaks of activity were seen in the poor imager group, including the left anterior (lobule V) and the right posterior cerebellum (lobule VI), as well as the orbito-frontal areas (BA 10) and the posterior cingulate cortex (BA 23).

Motor imagery vs. physical execution. When the MI and the physical execution conditions were compared in the good imager group, bilateral activations were located in the ventral premotor cortex (BA 44) and the pre-cuneus (BA 7), as shown by Table 3. Further increased activity was observed with a right hemispherical dominance in the lateral and medial premotor cortex (BA 6), in the orbital frontal and cingulate cortices (BA 9, 32, 47) and in the inferior parietal cortex (BA 39). In the poor imager group, apart from a set of active voxels in the right cingulate cortex (BA 32), left activations were located in the lateral premotor cortex (BA 6), the dorsolateral prefrontal cortex (BA 46) and the pre-cuneus (BA 7).

Discussion

This study aimed to investigate whether the neural substrate mediating MI might differ among participants showing high or poor MI ability, i.e. with respect to the accuracy and the vividness of the mental images. To check the compliance of the subjects with instructions and to ensure that they performed MI as they were instructed to, the participants were requested to describe the nature of the mental images they formed after the MI session and to score their effort using a 4-point rating scale. Further, and for the first time, individual MI abilities were assessed before the fMRI experiment, using well-established psychological tests, chronometric measures and physiological recordings of the ANS (Roure et al., 1999). The association of these complementary techniques has recently been found to be the most reliable procedure to control MI quality, hence guaranteeing the high/low MI abilities of the subjects (Guillot and Collet, 2005b; Lotze and Halsband, 2006).

Notably, the subjects' performance in the physical execution condition revealed that the two groups did not differ in their ability to learn the sequence of finger movements. Thus, this suggests that the differences in the pattern of functional activations seen in the groups are not due to unequal behavioral performance on the task, but rather to genuine distinctions in the neural substrates associated with good or poor abilities in MI. Furthermore, the fMRI findings of the present study support previous neuroimaging results and highlight the functional anatomy of MI. During MI, both good and poor imagers were found to recruit quite similar neural networks involving the inferior and superior parietal lobules, as well as the motor-related regions including the lateral and medial premotor cortex, the cerebellum and the putamen. The pattern of activation in these regions which overlaps those controlling overt movement, is consistent with the well-established results from neuroimaging experiments that investigated sequential finger-to-thumb opposition tasks (Roth et al., 1996; Gerardin et al., 2000; Porro et al., 2000; Binkofski et al., 2000; Ehrsson et al., 2003; Kuhtz-Buschbeck et al., 2003; Nair et al., 2003). However, inter-group comparisons revealed that good imagers manifested greater activation in the parietal and ventrolateral premotor regions, known to play a crucial role in the generation of mental images (Gerardin et al., 2000; Nair et al., 2003). In contrast, poor imagers recruited not only the orbito-frontal and the posterior cingulate cortices, but the cerebellum as well, possibly reflecting their difficulties in eliciting a vivid mental representation of sequential movements.

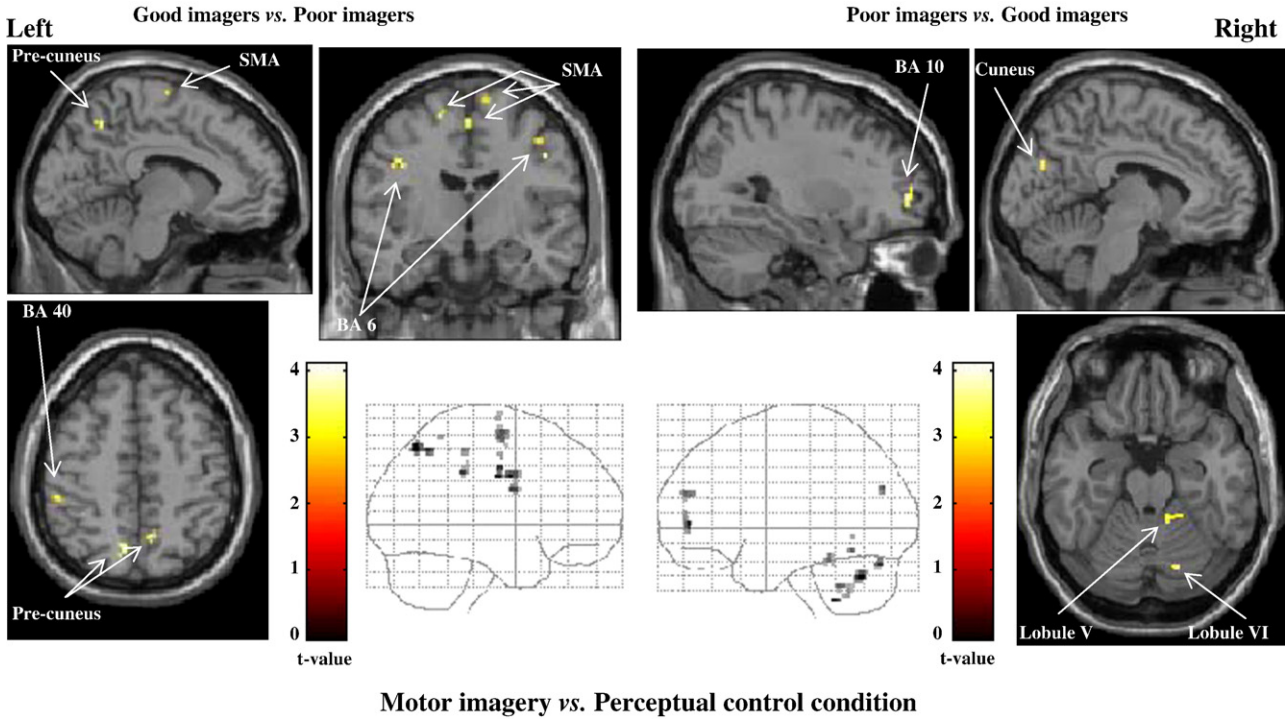

Fig. 4. Activation maps of the brain activations during motor imagery vs. perceptual control condition in good and poor imagers. When the good imager group was contrasted with the poor imager group (left), bilateral activations were observed in the pre-cuneus (BA 7; $X=10$ upper left and $Z=50$ lower), the lateral premotor cortex (BA 6; $Y=-8$) and the SMA (BA 6; $Y=-8$ upper right, $Z=50$ lower). Increased activity was also observed in the left inferior parietal lobule (BA 40; $Z=50$). Conversely, when the poor imager group was contrasted with the good imager group (right), activations were located in the left rostral prefrontal cortex (BA 10; $X=-30$), the right cuneus (BA 18; $X=12$), as well as in the right anterior (lobule V; $Z=-15$) and posterior (lobule VI; $Z=-15$) cerebellum.

When physical execution was contrasted to the perceptual control condition, the focus of activation was quite similar in the two groups. For the same level of performance, however, the poor imagers revealed a bilateral pattern of activations involving the motor system as well as the inferior and superior parietal lobules. Such activity in cortical motor control areas may be attributed to a greater neural effort needed to perform the correct finger sequence. Furthermore, good and poor imagers showed a functional dissociation in the basal ganglia and in the putamen in particular. While good imagers activated the posterior (sensorimotor) region of the putamen bilaterally, the poor imagers revealed bilateral activations in its associative regions. Despite some conflicting observations (Toni et al., 1998; Wu et al., 2004), the associative striatal regions have been found to be implicated in the early acquisition phase of sequential movements (Jueptner et al., 1997; Hikosaka, 2002; Lehericy et al., 2005), while the sensorimotor regions have been thought to play a more critical role in the long-term maintenance of this skilled behavior (Hazeltine et al., 1997; Doyon et al., 2002; Hikosaka, 2002). Such an interpretation is supported by Lehericy et al.'s (2005) study, in which they have reported a switch from the associative to the sensorimotor regions of the putamen during the early learning phase. Our results thus confirm the skill-learning model proposed by Doyon and Benali (2005), who have suggested that the long-lasting maintenance of a motor skill involves representational changes within the striatum.

Altogether, the results of the physical execution vs perceptual control conditions demonstrate that compared to poor imagers, good imagers show a more focused recruitment of the motor system as well as activations in the sensorimotor regions of the putamen. As such a pattern of results is often observed in well-trained individuals on sequential tasks, this suggests that good imagers are able to create a better representation of the sequence early in the acquisition process, and that they are capable of forming a more vivid mental representation of the movement than poor imagers.

Consistent with previous studies, the comparison between the MI and perceptual control conditions revealed similar brain activations in good and poor imagers, including activations in motor-related regions and both the inferior and superior parietal lobules (Gerardin et al., 2000; Solodkin et al., 2004; Lotze and Halsband, 2006). Again, however, the focus of activation seemed to be greater in the poor imagers than in the good imagers, highlighting the fact that the former need to recruit more mental resources in order to build a vivid representation of the movements. When the two groups were compared, the good imagers showed increased bilateral activations in the superior parietal lobule and the lateral premotor cortex, as well as in the left cingulate cortex, the right inferior parietal lobule and the right inferior prefrontal region. Such activations are consistent with the studies underlining the crucial role of the parietal and premotor cortices in the generation of mental images (Sirigu et al., 1996; Gerardin et al. 2000; Lafleur et al., 2002; Lotze and Halsband, 2006). By contrast, poor imagers showed exclusive activation of the posterior cingulate and orbito-frontal cortices, as well as both the anterior and posterior cerebellar hemispheres. The increased in activation in the frontopolar region involved in memory retrieval, and in the cingulate cortex that has strong reciprocal connections with the parahippocampal cortex, may be linked to the memorization process necessary while practicing a new sequence of movements known explicitly. More specifically, the orbito-frontal cortex is known to play a critical role in underlying memory formation (Frey and Petrides, 2002). Many

Table 3
Coordinates of peak activations for the motor imagery condition versus the physical execution condition

Anatomical areas	Hemisphere	Motor imagery vs physical execution			
		x	*y*	*z*	*t*-value
GOOD imager group					
Parietal cortex					
Inferior parietal cortex (BA 39)	R	36	−69	39	4.47
Superior parietal lobule	L	−23	−70	42	8.15
(pre-cuneus BA 7)	R	4	−62	54	5.28
Motor and premotor cortex					
Lateral premotor area (BA 6)	R	35	−5	54	4.17
Medial premotor area (BA 6)					
Pre-SMA	R	8	−5	63	3.86
Ventral premotor cortex (BA 44)	L	−44	2	7	4.02
	R	45	2	9	3.93
Prefrontal cortex					
Dorsolateral prefrontal area (BA 9)	R	42	11	34	4.08
Dorsolateral prefrontal area (BA 47)	R	41	16	−7	3.96
Limbic regions					
Cingulate cortex (BA 32)	R	14	29	26	4.53
POOR imager group					
Parietal cortex					
Superior parietal lobule (pre-cuneus BA 7)	L	−18	−64	46	3.84
Motor and premotor cortex					
Lateral premotor area (BA 6)	L	−35	−6	55	3.91
Prefrontal cortex					
Dorsolateral prefrontal area (BA 46)	L	−47	42	20	7.88
Limbic regions					
Cingulate cortex (BA 32)	R	10	12	35	3.81

studies have already reported that this area is involved in the learning of a motor sequence following MI (*e.g.* Lafleur et al., 2002; Jackson et al., 2003). Furthermore, such activations have been observed as the 8-item finger sequence is known explicitly by the subjects before the scanning session, hence improving the efficiency with which this sequence is associated with a specific and repeated pattern of movement.

Distinct contributions of the cortico-striatal and the cortico-cerebellar anatomical systems have been proposed in motor learning (e.g. Doyon and Ungerleider, 2002; Doyon and Benali, 2005). Although functional interactions between these anatomical systems are thought to be essential for the mediation of a new motor skill at the beginning of the learning process, a plethora of evidence indicates that the cerebellum is no more necessary when the sequence is well learned and has reached asymptotic performance (for review, see Doyon and Benali, 2005). Thus, although conjectural, the fact that poor imagers showed greater activations of the cerebellum than good imagers suggests that they do not only need to recruit the cortico-striatal system, but to compensate by activating in greater extent the cortico-cerebellar system during MI performance of sequential movements as well. This also suggests that compared to poor imagers, good imagers may have a more efficient recruitment of movement engrams.

Finally, though Lotze and colleagues (2003) did not investigate the neural substrates involved in good and poor imagers, their functional results in musicians speaks to this issue as the professionals violinists reported using MI more often than the amateurs. These authors reported that the professional musicians showed greater activations in the cerebellum during imagined performance of a musical concerto than amateur musicians. Such activations may be explained by the fact that in their experiment, the participants were required to consider the motor timing and outcomes of long movements. Thus, it is conceivable that such task characteristics required mental representations that taxed even more the motor system and the cerebellum, in particular.

The present findings have strong theoretical and practical implications for motor learning and neurorehabilitation. First, based on evidence demonstrating that mental practice with MI improves motor performance and facilitates motor learning (for review, see Guillot and Collet, 2008), and that it produces cerebral plasticity similar to that seen following physical practice of a motor task (Jackson et al., 2004), such technique could be used to train poor imagers to become more efficient with MI. Indeed, the pattern of activation recorded during MI in poor imagers should become close to that observed in the good imagers after MI training. The latter hypothesis awaits further experimental investigation, but could be tested by measuring the dynamic changes in cerebral activity through real-time fMRI. Second, MI can be employed as a therapeutic tool to prevent mis-repair by keeping the remaining well-functioning structures active and by improving neuronal plasticity, hence preserving motor functions (Pascual-Leone et al., 1995; Page et al., 2001; Johnson-Frey, 2004; Malouin et al., 2004). This requires, however, identifying the patient populations that could benefit most from this therapeutic approach, by investigating their abilities to generate mental images of movement after cortical or subcortical lesions (Jackson et al., 2001). As the neural networks mediating MI are not identical in good and poor imagers, it would therefore be crucial to evaluate the individual MI ability to determine the optimal training conditions for learning how to use mental practice with MI in neurological rehabilitation.

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