Motor imagery of walking following training in locomotor attention.

The effect of 'the tango lesson'

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Abstract

The hypothesis of this study is that focusing attention on walking motor schemes could modify sensorimotor activation of the brain. Indeed, gait is a learned automated process, mostly regulated by sub-cortical and spinal structures. We examined the functional changes in the activity of the cerebral areas involved in locomotor imagery tasks, before and after one week of training consisting of physical and mental practice. The aim of the training was to focus the subject's conscious attention on the movements involved in walking. In our training subjects were asked to perform basic tango steps, which require specific ways of walking; each tango lesson ended with motor imagery training of the performed steps. The results show that training determines an expansion of active bilateral motor areas during locomotor imagery. This finding, together with a reduction of visuospatial activation in the posterior right brain suggests a decreased role of visual imagery processes in the post-training period in favor of motor-kinesthetic ones.

Introduction

Both cognitive and neurological similarities exist between imagined and executed actions. Time courses of imagined and executed movements are correlated (Jannerod, 1994; Decety and Jannerod, 1996) and the brain regions activated during imagined movements overlap with the brain regions of executed movements (Decety et al, 1994; for differences in connectivity networks see Solodkin et al, 2004). However, motor imagery tasks are affected by a theoretical caveat; in principle, two different strategies could be involved in motor imagery tasks: motor mental simulation of movements based on kinesthetic memory of corresponding executed movements, or visualization of corresponding effects of movements from visual kinematic imagery, without actual simulated movements (Sirigu and Duhamel, 2001). Classical motor imagery tasks possibly involve both motor and visual imagery. For instance, in mental rotation tasks a complex interaction between visual and motor imagery is hypothesized (Wexler et al, 1998). In sports psychology, motor training

2

often involves a visualization of oneself performing a motor action. As regards walking, Miyai et al (2001) have shown that brain activation during a locomotion task, revealed by near-infrared spectroscopy, is comparable to brain activation in a locomotor imagery task, investigated by fMRI. However, Jahn et al (2004) found considerable brain activation of the cerebral areas involved in visuospatial navigation, in a walking imagery task. Locomotion is based on a complex pattern of sequential movements based on both automatic spinal cord mechanisms (Dietz, 2003) and cortical and subcortical neurological control. In humans, walking is a learned automated process: people normally walk without being consciously aware of how they are walking. Indeed, the spinal control of locomotion prevents most kinesthetic feelings from accessing a conscious memory system. Thus, when imagining walking, recalling proprioceptive sensations is often difficult and we therefore tend to make use of visuospatial processes.

Motor learning of new motor skills and motor training for improving learned motor skills require motor attention and are able to produce changes in cortical motor representations. It has been demonstrated that during the learning of new skills, cortical regions associated with sensorimotor functions of the body parts most utilized for the skill gradually start to be represented over larger cortical territories (e.g. Karni et al, 1995; Pascual-Leone et al, 1994; Ioffe, 2004; Sanes, 2003). These effects of motor learning practice emerge also when tested with motor imagery tasks. Lacourse et al (2005) compared cerebral activation in imagined and executed sequential hand movements before and after one week of intensive physical practice. Their results showed that after practice imagined and executed movements elicited increasingly similar activation. The role of "motor expertise" in motor imagery is supported by an fMRI study of the motor imagery of golf players; it showed activation of motor and parietal cortices, supplementary motor area, cerebellum and vermis, and found a correlation between increased number of areas of activation and increased handicap of participants (Ross et al, 2003). As far as the lower limbs are concerned, only a few pilot studies have investigated brain activations following motor learning in normal subjects (Perez et al, 2004; Lafleur et al, 2002) and in patients with stroke (Dobkin et al, 2004). Reorganization in the motor cortex was also shown to occur after mentally practicing the corresponding movements (Pascual-Leone et al, 1995; for foot movements, Jackson et al, 2003). Functional changes of combined mental and physical practice while learning foot movements have recently been studied in a patient with stroke (Jackson et al, 2004).

Motor learning and motor training involve a more accurate kinesthetic control of movements and, in principle, a more accurate ability as regards motor simulation in motor imagery tasks. As regards locomotion, a conscious effort has to be made in order to be aware of the movements of the legs and feet when walking. For these reasons, we believe that locomotor practice should be primarily aimed at focusing the patient's attention on walking motor schemes. The present study explores the effect of training in normal subjects that focuses the subject's conscious attention on the movements involved in walking. Some studies have investigated variations in attention to movement through different approaches: varying the automaticity of a movement sequence or thinking about each movement as it is being made (Jueptner et al 1997); directing attention away from a movement by using a distractor task (Johansen-Berg and Matthews, 2002; Passingham, 1996); using motor learning where subjects have to generate new responses, monitor movement outcomes, rehearse mentally and keep track of previous moves (Passingham, 1996). All studies confirm that the neural systems supporting motor learning depend on the availability of attentional processes. Rowe and collaborators (2002) clearly showed that under attention directed to the action there is increased activity in the prefrontal cortical regions; in particular, it seems that the dorsal prefrontal cortex exerts a cognitive control on action production by mediating the effect of attention on premotor cortical activity.

The training adopted in the present study combined motor learning and motor imagery. In particular, subjects attended basic tango lessons, each lesson ending with a motor imagery rehearsal of the performed steps. The tango was chosen for the intrinsic characteristics of the attention posited on the movements of the lower limbs: steps have to be performed along two pairs of virtual parallel lines, the two pairs being perpendicular to each other, so that only forward-back and right-left directions are allowed; the steps are similar to those of normal walking and the emphasis is on the precision of foot and leg movements. The constraints on locomotor directions and the attention required to perform the steps accurately make the tango a suitable form of training for bringing the subject's conscious awareness onto walking.

Methods

In order to investigate the effect of motor and motor imagery training on motor areas, we devised an fMRI paradigm involving locomotor imagery.

Subjects

Twelve right-handed and right-footed healthy volunteers (five women and seven men; age range = 20.8-34.9, mean age = 27.5 years) took part in the experiment. Limb dominance was determined according to the Edinburgh Handedness Inventory (Oldfield, 1971), to which specific items were added regarding foot preference (Chapman et al, 1987). The ability to form mental images was evaluated by the Vividness of Visual Imagery Questionnaire (VVIQ; Marks, 1973) and the Vividness of Movement Imagery Questionnaire (VMIQ; Isaac et al, 1986); the latter was modified in that motor representations were required in a first rather than third person perspective. All subjects had at least a sufficient ability to form visual and motor images. Exclusion criteria included history of neurological or developmental illness, mental disorders, drug or alcohol abuse, current use of medications known to alter neurological activity. No subject had attended tango lessons before the experiment. All subjects gave informed written consent. The fMRI study was performed at the Ospedale Koelliker in Turin (Italy).

Three males and three females were assigned to the experimental group; the remaining subjects were part of the control group. As regards the vividness of visual and motor imagery, there were no statistical differences between the two groups. The experimental group underwent combined physical and mental training, while the control group underwent no training at all.

Training

Subjects attended a training session every day for 5 consecutive days. Each training session lasted 1 hour and consisted of two parts: in the first 45 minutes basic tango steps were practiced; in the last 15 minutes the practiced steps were rehearsed through the use of motor imagery. Lessons were progressive in difficulty. At the beginning of each lesson subjects were asked to walk for five minutes timing their steps to the music, which was tango music. After this warm-up period, subjects practiced tango steps: the *academic basic* during the first two lessons and the *turn* in the last two lessons. The *academic basic* is a sequence of eight steps. The man takes one step backward starting with the right foot, one step left, three regular steps forward ending with his feet together. Then he takes another step forward starting with the left foot, one step right ending again with his feet together. The *turn* consists of a three-step sequence along a circular track around the partner. It can start with any one of the steps in the sequence: one step forward, one step left/right and one

step backward. Between each step the dancer has to pivot around the partner on his pivot foot, keeping his balance on just one foot. The trainer arranged the turn sequence so that the same steps were taught to both males and females. The third lesson, the central one, was used to rehearse the sequence that had been learned previously. During all the exercises, the trainer focused subjects' attention on the position of their feet, on proprioceptive inputs coming from the leg muscles (quadriceps and adductors) and on tactile sensations of foot-floor contact. Instead, no attention was placed on the correct position of the hands; thus, subjects were free to embrace their partner in the way they felt most comfortable. At the end of the tango exercises, the trainer asked the subjects to lie down and relax. To induce relaxation the trainer guided the subjects' imagination through a sequence of soothing landscape pictures (e.g. sunset) using background piano music. Then the trainer asked the subjects to progressively relax each part of their body, from head to foot, drawing their attention to their body perceptions. Once the subjects were relaxed, the trainer asked them to visualize the sequence of steps they had learned during the lesson. The trainer described the sequence verbally and counted the step cadence aloud. The trainer's verbal description was aimed at recalling the foot and leg sensations the subjects had felt during the tango lesson. Each sequence was repeated several times, depending on its length: 5 times for the academic basic and 10 times for the turn.

Procedures

Subjects underwent two fMRI scanning sessions one week apart. For the experimental subjects, the first scan was before the training period and the second one after it. In particular, starting two days after the first functional scanning session, subjects attended a training session every day for 5 consecutive days; the second scanning session was performed the day after the last lesson. Immediately before each scanning session, subjects were individually instructed on the task they were going to perform during the scan. The experimenter showed a 12-sec video in which an actor, filmed from a first person perspective, walked forward placing his feet on two parallel red lines drawn on the floor, at a speed of about 1.50 Hz (3 steps every 2 seconds). At the end of the video, subjects were asked to close their eyes and imagine they were walking along two parallel lines, at a self-paced frequency similar to the one shown in the video; subjects were urged to imagine themselves from a first person perspective, to feel their legs and feet and to concentrate on their movements so as to proceed straight ahead, step by step. Subjects watched the video and

tried the task three consecutive times. The experimenter then explained that the task was to be alternated with rest periods during which subjects had to imagine/feel themselves lying down and relaxing. Subjects tried the alternating conditions for 1 min. At the end of this warm-up period, subjects were asked how well they had managed to perform the task, using a three point Likert scale (very well, fairly well and badly): two subjects said 'badly' and were then excluded from the study.

Paradigm, task and stimuli

Paradigm: locomotor imagery. In the active condition, subjects imagined they were walking along two parallel lines at a normal speed; in the rest condition, they imagined they were lying down. The lights were dimmed and subjects kept their eyes closed, as it has been suggested that eye closure improves imagination (Marx et al, 2003). Subjects' legs were slightly raised and supported by pillows; sandbags were placed on both legs in order to limit leg movements. The stimuli were auditory and consisted in an audio-recorded voice saying 'Lie down' in the rest condition and 'Walk' in the active condition.

The paradigm was performed using a block design with 12 s of rest alternating with 12 s of the active condition. Each paradigm consisted of a total of 25 blocks (13 rest conditions, 12 active conditions); during each block 4 functional volumes were scanned. Each paradigm lasted 5 min. The paradigm was generated by the E-Prime software (Psychology Software Tools, Inc., Pittsburgh, PA, USA). The audio stimuli were transmitted through earphones. The stimuli were presented by IFIS-SA^{TM} (MRI Device Corporation, Waukesha, WI, USA), which also synchronized the presentation of the stimuli with the fMRI scanner.

Image acquisition

Data acquisition was performed on a 1.5 Tesla Philips Intera with a Sense high field high resolution head coil (MRIDC) optimized for functional imaging. Functional T_2-weighted images were acquired using echoplanar (EPI) sequences, with a repetition time (TR) of 3000 ms, an echo time (TE) of 60 ms and a 90° flip angle. The acquisition matrix was 64 x 64; the field of view (FoV) was 256 mm. For each paradigm, a total of 100 volumes were acquired. Each volume consisted of 25 axial slices, parallel to the anterior-posterior (AC-PC) commissure line and covering the whole brain; the slice thickness was 4 mm with a 0.5

mm gap. Two scans were added at the beginning of functional scanning and the data discarded to reach a steady-state magnetization before acquisition of the experimental data.

In the same session, a set of three-dimensional high-resolution T_1-weighted structural images was acquired for each participant. This data set was acquired using a Fast Field Echo (FFE) sequence, with a repetition time (TR) of 25 ms, the shortest echo time (TE) and a 30° flip angle. The acquisition matrix was 256 x 256; the field of view (FoV) was 256 mm. The set consisted of 160 sagittal contiguous images covering the whole brain. The in-plane resolution was 1 x 1 mm and slice thickness was 1 mm (1 x 1 x 1 mm voxels).

Data analysis

Imaging data were analyzed using Brain Voyager QX (Brain Innovation, Maastricht, Holland). Functional data of each subject were preprocessed as follows. 1) Mean intensity adjustment of the global intensity of the repeatedly measured images of a slice: for each slice, the average intensity across the first image was computed; for each subsequent scan of the same slice, the mean intensity was computed and then scaled to the same average slice intensity. 2) 3D motion correction adjusted small head movements: all volumes were aligned spatially to the first volume by rigid body transformations, using a trilinear interpolation algorithm. 3) Slice scan time correction allowed a whole volume to be treated as a single data point: the sequentially scanned slices comprising each volume were interpolated in time, using a sinc interpolation algorithm. 4) Spatial data smoothing was performed using a 3D Gaussian kernel with full width half maximum (FWHM) of 4 mm. 5) Temporal filters removed drifts due to scanner and physiological noise: linear trend removal, and non-linear trend removal using a temporal high pass filter to eliminate frequencies lower than 3 cycles in time course. In addition, temporal smoothing was performed to improve the signal-to-noise ratio by removing high frequency fluctuations: a Gaussian kernel with full width half maximum (FWHM) of 2.8 sec was used for this purpose.

After preprocessing, a series of steps were performed in order to allow for precise anatomical locations of brain activity to facilitate intersubject analysis. First, each subject's slice-based functional scans were coregistered with their 3D high-resolution structural scan. This process involved mathematical coregistration exploiting slice positioning stored in the headers of the raw data, as well as fine adjustments that were computed by comparing the data sets on the basis of their intensity values; if needed, manual adjustments

were also performed. Second, each subject's 3D structural data set was transformed into Talairach space (Talairach and Tournoux, 1988): the cerebrum was translated and rotated into the anterior-posterior commisure plane and then the borders of the cerebrum were identified. Third, using the anatomical-functional coregistration matrix and the determined Talairach reference points, each subject's functional time course was transformed into Talairach space and the volume time course was created.

For each paradigm, the following procedure was performed. A multi-subject multi-study design matrix was specified and each defined box-car was convolved with a pre-defined hemodynamic response function (HRF) to account for the hemodynamic delay (Boynton, 1996). A statistical analysis using the General Linear Model with separate study predictors was performed on the group to yield functional activation maps during the pre- and post-tests separately. All voxels activated in the pre-test and those activated in the post-test were combined to create a mask excluding the rest of the cerebrum and cerebellum; this mask was used to compute the General Linear Model comparing post-test activations with pre-test activations in the group of subjects. Since we have used the same data set for mask definition and subsequent statistical tests, we have avoided circularity by using orthogonal contrasts; indeed, the sum of the element-wise multiplication of the contrast values results in zero. In these statistical comparisons, correction for multiple independent tests was performed using the false discovery rate (FDR) (Benjamini & Hochberger, 1995; Genovese et al, 2002), with a q value of 0.05, leading to a p value ≤ 0.004.

To localize activations, we used two different approaches, depending on the locations of the active clusters (cerebrum or cerebellum). Activated clusters were determined using the automated routines in Brain Voyager. A home-made script in Matlab (the MathWorks, Inc.) was created to probe the Brodmann.voi file provided with Brain Voyager 2000 (prior to this the Brodmann.voi file was split into two files, one for the right hemisphere and the other for the left hemisphere) and the shared voxels between the Brodmann areas and the clusters of activation were reported. This procedure is similar to that suggested by Tzourio-Mazoyer et al (2002), except that it is based on the Brodmann area boundaries, and thus the results do not take into account the voxels a priori located in the white matter. The intersected regions of interest were read in Brain Voyager, and the statistical values for the local maxima of each region were determined. As regards Brodmann Area 6, we also wanted to obtain a quantitative estimate of the activated voxels in the dorsal premotor cortex (premotor area) and in the supplementary motor area (preSMA and SMA proper). To do

this, we used the Brodmann area and lobe templates provided in the Brodmann.voi and Gyri.voi files in Brain Voyager 2000. In particular, for the premotor area, we intersected the precentral gyrus areas with BA6, while for the supplementary motor area we took the activated clusters in the medial wall of the BA6 within the following boundaries: genu of corpus callosum (anteriorly); paracentral lobule (posteriorly); cingulate gyrus (inferiorly). We then recorded the local maxima value provided by Brain Voyager for each of these clusters. For cerebellar regions, we did not perform any further intersection, and simply reported the statistical values of the local maxima in the activated cluster.

Home-written scripts have been made available on-line (http://www.neurocogsci.net). To label anatomical structures we used the Talairach Daemon (Lancaster et al, 1997; Lancaster et al, 2000), a digitalized version of the Talairach atlas, available on-line (http://ric.uthscsa.edu/resources/talairachdaemon). The results of all automated procedures were reviewed for accuracy of localization by an expert neuroradiologist.

Results

Motor imagery pre-training results

As imagery of locomotor tasks has been studied little so far, before considering the effect of training, we report the results for this paradigm in the pre-test condition. Activations were found bilaterally in the primary motor area (leg/foot), premotor area, supplementary and pre-supplementary motor areas, prefrontal cortex (medial frontal cortex BA 8; dorsolateral inferior frontal cortex BA 9), cingulate gyrus, insula, primary somatosensory areas, paracentral lobule (BA 5/31), inferior parietal lobule (BA 40), precuneus and cerebellum. Moreover, in the right hemisphere, activations were in the cuneus and lingual gyrus; in the left hemisphere, activations were found in the inferior frontal gyrus (BA 44), superior parietal lobule and hippocampus. Table 1 details these results.

Insert Table 1 about here

Table 1. Results of the motor imagery task in the pre-test condition. The table indicates the Talairach coordinates of local maxima of cortical and cerebellar structures showing significant ($p < 0.05$, corrected for multiple comparisons) activity. Increased activations (+) and decreased activations (-) are specified in the first column.

Effect of training

In the control group no difference of activation emerged when comparing the first and second fMRI scans. In the experimental group, a comparison of imaging data obtained before and after training revealed the activations (increased hemodynamic responses in the post-test) and deactivations (reduced hemodynamic responses in the post-test) described below. Activations were found bilaterally in the supplementary motor area and in the premotor area. Furthermore, in the left hemisphere, activations are in the primary motor area, primary somatosensory area, superior and inferior parietal lobule (BA 7; 40) and in the superior temporal gyrus (BA 22). Deactivations were found in the right hemisphere, in the lingual gyrus, fusiform gyrus, anterior and posterior cerebellum.

For explorative purposes, during the last lesson some measurements of improved skills were obtained in the experimental group: the trainer assessed each participant's performance using a 5 point Likert scale, and three different parameters. Subjects showed improvements on all the assessed parameters: sequence learning +3.75 (SD= 0.43), clearness of movements +1.87 (SD= 1.05), coordination +2.25 (SD= 0.96).

Insert Figure 1 about here

Figure 1. Results for the post-test condition munus pre-test condition during locomotor imagery. The table indicates the Talairach coordinates of local maxima of cortical and cerebellar structures showing significant (p < 0.05, corrected for multiple comparisons) activity. Increased activations (+) and decreased activations (-) are specified in the first column. Note that in this comparison positive t-values indicate an increased activation in the post-test condition compared to the pre-test condition, and negative t-values indicate a decreased activation in the post-test condition compared to the pre-test condition.

Discussion

As far as motor imagery pre-training results are concerned, they are in line with those obtained in previous PET (Malouin et al, 2003) and fMRI (Jahn et al, 2004) locomotor related studies. All activated regions are part of a well documented network associated with the mental representation of motor actions (Decety et al, 1994; Stephan et al, 1995). Although the role of the primary motor cortex in motor imagery is controversial,

it has been demonstrated that this area is involved in sensory processing for the purpose of upcoming movement generation, as well as in mental operations of sensorimotor representations (Hanakawa et al, 2003). Moreover, transcranial magnetic stimulation over the primary motor area impairs the imagination of movements (Ganis et al 2000). The premotor area contributes to the preparation of sequential movements (Leonardo et al, 1995; Rizzolatti et al, 1988) and it is involved in dynamic visuospatial imagery (Lamm et al, 2001). Supplementary and pre-supplementary motor areas (SMA and pre-SMA) are linked with the intention and anticipation of the action. Stimulation of the SMA in humans reportedly generates an urge for or anticipation of movements (Fried et al, 1991). The pre-SMA is known to become active not only when subjects voluntary generate movements (Thaler et al, 1995) but also during simulation of movement without actual execution (Lotze et al, 1999). Recently, it has been suggested (Lau et al, 2004a; 2004b) that the pre-SMA reflects the representation of intention, as it's activity is enhanced when subjects consider their intention to move rather than their actual movement. Bilateral activation of both the ventral and the dorsal parts of the prefrontal cortex has been found in many imagining experiments. In particular, when comparing bipedal standing with eyes closed versus eyes open, it has been found that there is activation in medial BA 8 (Ouchi et al, 1999), and that the frontal eye field and the supplementary eye field are activated during imagined saccade without eye movement (Bodis-Wollner et al, 1997). That seems to fit well with the specific features of our experiment, where subjects lay with their eyes closed imagining bipedal movements in space. Furthermore, dorsolateral inferior frontal cortex BA 9 has been demonstrated to be responsible for response inhibition (for a review see Aron et al, 2004), which is essential during a motor imagery task. Evidence that Broca's region (BA 44) subserves imagery of motion was provided in a combined cytoarchitectonic and fMRI study (Binkofski et al, 2000), that also showed a left-hemispheric dominance for egocentric movements. The anterior cingulate cortex provides an interface for motor control, drive and cognition (Busher et al, 2000; Paus, 2001); in particular, the dorsal areas 24c'/32' are closely linked with cognitive-motor functions (Vogt et al, 1992). The insula appears to play a role in cognitive control, task coordination and working memory (Derrfuss et al, 2004), and, together with the hippocampus, it is involved in mental navigation along memorized routes (Ghaem et al, 1997). Activations in the anterior parietal lobe have been reported in previous works. Porro and his collaborators (1996) stressed the role of the primary somatosensory cortex in motor imagery, especially in tasks involving the recall of sensations of a

proprioceptive nature: such sensations are indeed required in our paradigm. Area 5 supports the important role of somatosensory-motor integration and it is regarded as a higher-order somatosensory area mostly devoted to analyzing proprioceptive information such as location of body parts (Hanakawa et al, 2003). Activation in the posterior parietal regions, such as superior (BA 7) and inferior parietal lobules (BA 40), is in agreement with previous data on cerebral activation during hand movement (Decety et al, 1994; Stephan et al, 1995; Grafton et al, 1996). The fact that activation in the parietal lobule is more extensive in the left hemisphere has already been found and explained (Gerardin et al, 2000): only lesions of the left parietal lobe can produce bilateral apraxia (De Renzi et al, 1982; Heilman et al, 1982) and motor imagery impairment for both hands (Sirigu et al, 1996). More precisely, the superior parietal lobule appears to be related to attention and memory requirements (Nair et al, 2003). The precuneus is involved in the retrieval of visuomotor sequences (Fletcher et al, 1995) and in the imagination of motor actions in space (Ogido et al, 2000; Ruby & Decety, 2001). As far as the posterior regions are concerned, the cuneus and the lingual gyrus seem to be related to the perception of walking biological motion (Buchel et al, 1998; Servos et al, 2002). Finally, the cerebellum has been associated with internally simulated movement sensations during motor imagery (Naito et al, 2002).

As far as the effect of training is concerned, our data suggest that locomotor training affects the reorganization of the cortical areas involved in locomotion: while in the control group no difference emerged in the comparison between the first and second scans, in the experimental group significant modifications in the motor circuits resulted in the post-training scan. In line with our expectations, the main result was a greater activation of the premotor and the supplementary motor areas, as well as the primary motor and somatosensory areas of the dominant hemisphere. These findings are in accord with previous experiments on motor learning (Hlustik et al, 2004; Grafton et al, 1998). Moreover, the role of the supplementary motor area in learning has already been confirmed in studies involving animals and patients: in monkeys, neurons of the supplementary motor cortex encode sequences of discrete movements (Mushiake et al, 1990; Aizawa et al, 1991), and patients with supplementary motor cortex lesions show impairments in sequential movements (Halsband et al, 1993). As far as the inferior parietal lobule is concerned, some studies (Lafleur et al, 2002; Jackson et al, 2003) have underlined its role both in the early stages and in subsequent phases of foot motor

learning, suggesting that this structure is crucial for establishing the cognitive strategies and motor routines involved in executing sequential foot movements, as well as in the development of a long-lasting representation of the sequence. The activation of the superior temporal gyrus in the post-training condition could be due to the spontaneous use of musical imagery (Kraemer et al, 2005): after-scan participants' comments confirm that some of them mentally rehearse the tango music while imagining they are walking.

The left hemisphere dominance we detected is in line with previous works on motor control, motor sequence learning and motor attention. Recent studies in patients with lateralized hemispheric damage, and transcranical magnetic stimulation studies in healthy volunteers have demonstrated the dominant role of the left hemisphere in shifting the focus of motor attention from one movement in a sequence to the next (Winstein and Pohl, 1995; Rushworth et al, 1997, 1998; Schluter et al, 1998; 2001). Moreover, some authors have shown that learning movements with the non-dominant left foot leads to an extension of the activations in the left hemisphere: for instance, Lafleur and collaborators (2002) found that the brain regions associated with learning sequential movements of the left foot were predominantly located in the ipsilateral (left) hemisphere. This may be due to the fact that the neural representation of movements executed using the non-dominant limb may be less lateralized than that of those performed with the dominant one. This interpretation is consistent with findings from previous studies, which reported ipsilateral activations in left motor regions when subjects executed finger movements with the non-dominant hand but not with the dominant (right) hand (Kawashima et al, 1993; Kim et al, 1993; Ziemann and Hallet, 2001).

Considering cerebellar activity, its decreased activity in the post-training scan is in accord with previous studies on motor learning (Jackson et al, 2003; Lacourse et al, 2004; Lafleur et al, 2002). These studies showed an increased activity in the cerebellum in the early stages (1 hour) of motor acquisition, but the same regions were no more significantly activated during later (6 hours) stages of practice.

Finally, a deactivation in the lingual and fusiform gyri was found. In an fMRI motor imagery study of different locomotor activities (walking and running) Jahn et al (2004) found an activation in the parahippocampal and fusiform gyri in walking imagery vs imagined lying down. They interpreted their findings as visuospatial navigational correlates. In our finding of pre-training walking imagery vs rest, a significant activation of the posterior brain could be associated with visual imagery processes (activation of the bilateral parietal lobe and precuneus and right activations of the right cuneus and lingual gyri (Ganis et al,

2004). Therefore, posterior right brain deactivation in post-training imagery tasks could represent a decreased involvement of visual imagery processes in relation to visuospatial navigational aspects of locomotion.

Concluding remarks

In order to study the role of conscious motor attention in locomotor imagery, in this work a motor attentional training scheme was devised as a combination of motor and cognitive practice. The aim of our investigation was not to specify the single contribution of physical vs. mental training.

Two main findings arose from our study after motor attention training. First, bilateral motor and premotor activation and no activation in the prefrontal cortex occur; we hypothesized that, while attention mainly involves prefrontal regions, typically related to cognitive effortful processes, trained attention produces a greater activation in more posterior frontal regions, such as the primary motor area, the supplementary motor area and the somatosensory areas, which are specifically involved in motor production. Second, a decreased involvement of the posterior visuospatial areas occurs; this finding could demonstrate more genuine motor mental processes in motor imagery after training.

One limitation is that, having only performed two fMRI measurements and since training was of limited temporal duration, it is not possible to determine whether the detected cerebral and cerebellar changes are critical in the early stages of cognitive focusing or whether they represent long-lasting features related to some sort of 'attention to locomotor movements'.

These findings support the idea that locomotor attention training increased motor simulation processes in locomotor imagery tasks. Such results give us some suggestions for neurological rehabilitation. Indeed, they are in favor of the use of motor practice and motor imagery in the rehabilitation of brain-injured paretic patients, as many authors have already proposed (see for example Jackson et al, 2004; Malouin et al, 2004). In particular, re-acquisition of motor schemes could be facilitated by protocols involving specific physical and cognitive exercises able to focus patients' conscious attention on the movements they are performing or trying to perform.

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Table 1

Table 1

Localization (Brodmann area)	RIGHT HEMISPHERE				LEFT HEMISPHERE			
	t value	Talairach coordinates			t value	Talairach coordinates		
		x	y	z		x	y	z
+ Prefrontal cortex (8; 9)	6.338	46	5	28	7.790	-51	2	25
+ Inferior frontal gyrus (44)					6.832	-51	2	21
+ Precentral gyrus (4)	6.256	56	-19	34	7.069	-51	-12	42
+ Precentral gyrus (6)	7.848	51	-1	34	9.230	-54	-1	31
+ Medial frontal gyrus (6)	10.314	3	-10	55	10.514	-2	-13	55
+ Anterior cingulate gyrus (24; 32)	7.586	6	8	43	8.290	-3	-1	47
+ Insula (13)	6.745	39	-1	17	7.260	-39	-4	16
+ Hippocampus					5.681	-30	-30	-5
+ Postcentral gyrus (3)	5.632	56	-16	30	7.623	-51	-13	46
+ Postcentral gyrus (2)	6.850	55	-19	31	6.957	-39	-25	43
+ Paracentral lobule (5; 31)	6.040	3	-40	58	7.465	-9	-40	55
+ Superior parietal lobule (7)					7.267	-30	-58	49
+ Inferior parietal lobule (40)	7.597	39	-34	42	8.571	-51	-34	37
+ Precuneus (7; 31)	6.444	-15	-45	55	5.722	-8	-61	22
+ Cuneus (17)	6.319	15	-82	7				
+ Lingual Gyrus (18; 19)	6.276	26	-74	-5				
+ Cerebellum	6.533	18	-61	-13	5.977	-12	-61	-8

Figure 1
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Localization (Brodmann area)	RIGHT HEMISPHERE				LEFT HEMISPHERE			
	t value	Talairach coordinates			t value	Talairach coordinates		
		x	y	z		x	y	z
+ Precentral gyrus (4)					4.528	-39	-16	53
+ Medial frontal gyrus (6)	5.395	3	-22	61	5.745	-1	-22	64
+ Precentral gyrus (6)	7.931	30	-16	61	4.491	-50	-1	37
+ Postcentral gyrus (2)					5.498	-52	-25	37
+ Superior parietal lobule (7)					5.100	-30	-54	58
+ Inferior parietal lobule (40)					4.902	-39	-40	49
+ Superior temporal gyrus (22)					5.014	-64	-43	19
- Lingual Gyrus	-4.772	15	-85	4				
- Fusiform Gyrus	-5.473	34	-70	-11				
- Anterior cerebellum [culmen]	-4.012	9	-55	-5				
- Posterior cerebellum [declive]	-3.941	19	-64	-14				