

# Step-by-Step: The Effects of Physical Practice on the Neural Correlates of Locomotion Imagery Revealed by fMRI

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**Abstract:** Previous studies have shown that mental imagery is a suitable tool to study the progression of the effect of practice on brain activation. Nevertheless, there is still poor knowledge of changes in brain activation patterns during the very early stages of physical practice. In this study, early and late practice stages of different kinds of locomotion (i.e., balanced and unbalanced) have been investigated using functional magnetic resonance imaging during mental imagery of locomotion and stance. During the task, cardiac activity was also recorded. The cerebral network comprising supplementary motor area, basal ganglia, bilateral thalamus, and right cerebellum showed a stronger activation during the imagery of locomotion with respect to imagery of stance. The heart beat showed a significant increase in frequency during the imagery of locomotion with respect to the imagery of stance. Moreover, early stages of practice determined an increased activation in basal ganglia and thalamus with respect to late stages. In this way, it is proposed the modulation of the brain network involved in the imagery of locomotion as a function of physical practice time. *Hum Brain Mapp* 31:694–702, 2010. © 2009 Wiley-Liss, Inc.

**Key words:** neurovegetative activity; motor system; basal ganglia; thalamus

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## INTRODUCTION

The validity of mental motor imagery as a tool to study motor representations is based on the similarity between temporal [Parsons, 1987] and kinematic [Parsons, 1994] properties of executed and imagined movements [Decety et al., 1991; Gerardin et al., 2000; Ionta et al., 2007]. Using transcranial magnetic stimulation (TMS), some studies

showed the specific influence of motor imagery on corticospinal excitability for the muscles whose movement was imagined [Fourkas et al., 2006], suggesting an overlap between the cortical motor components involved in execution and imagery [Cicinelli et al., 2006; Rossi et al., 1998]. The brain network recruited by mental imagery has been studied by functional magnetic resonance imaging (fMRI) [Lotze et al., 1999] and SPECT [Decety et al., 1990] and includes the parietal region, premotor areas, cerebellar vermis, and the basal ganglia.

A specific cerebral network is responsible for locomotion and its components such as foot extension and flexion [Sahyoun et al., 2004], ankle movements [Carey et al., 2004], and maintenance of stance [Ouchi et al., 1999]. This network includes supplementary motor area (SMA), striatum, visual cortex, dorsal brainstem, and cerebellum [Hanakawa et al., 1999]. In particular, some clinical studies

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highlighted the importance of the thalamus [Karnath et al., 2000] and basal ganglia [Martin and Hurtwitz, 1962] in the maintenance of the upright posture and locomotion, respectively. The network responsible for the execution of locomotion can be activated also by mental imagery of locomotion [Miyai et al., 2001]. The brain activity due to imagery is modulated by cognitive demand [Malouin et al., 2003] and is sensitive to real motor practice [Lacourse et al., 2005; van Mier et al., 1998]. Indeed, early and late stages of executed or imagined sequential foot movements modulate such cerebral activity [Lafleur et al., 2002].

Some neuroimaging studies used fMRI to investigate practice during long training sessions of hand motor tasks [Lacourse et al., 2004; Reinges et al., 2005] or focusing on fingers' representation [Nyberg et al., 2006; Olsson et al., 2008]. Those studies showed a greater activation of cortical and subcortical regions during imagery of novel movements with respect to the imagery of skilled movements, in particular, in premotor areas, cerebellum, and thalamus [Lacourse et al., 2005; Nyberg et al., 2006; Olsson et al., 2008]. Rapid changes in cortical representations over the motor cortex have been demonstrated using TMS after short periods of physical practice [Classen et al., 1998]. Whereas previous studies on very early changes in cortical representations dependent on practice used magnetoencephalography [Rossini et al., 1994; Spengler et al., 1997; Ziemus et al., 2000] and provided detailed temporal information. Nevertheless, the modulation of cerebral activity as a function of practice time is still poorly understood, especially when short periods are considered. In this framework, we planned an fMRI experiment based on the manipulation of the practice time and focusing on very early stages of practice.

The main point of this study is to verify the difference between a very well known behavior, achieved in memory and almost automatic, and a new behavior that is a perturbation of the same one. To this aim we chose locomotion, because it offers the opportunity to study a well-established motor behavior, which can be easily perturbed by a peripheral input and practiced again. In particular, we were interested in a differentiation between early and late stages of such a process; thus, our main hypothesis was that a larger cerebral network would be involved in the control of the new movements (early practice), in particular areas responsible for temporal and sequential organization of the single motor acts accomplishing the behavior, such as basal ganglia, thalamus, and cerebellum.

## MATERIALS AND METHODS

### Subjects

Twelve healthy male volunteers ranging in age from 22 to 29 years (average = 24.5-years-old; SD = 1.9) were enrolled in this study. All of them were right handed according to a revised version of Annett's hand preference

questionnaire [Annett, 1970; Briggs and Nebes, 1975]. In the questionnaire developed by Briggs and Nebes [1975], subjects are asked to rate on a five-point scale their hand preference when performing 12 specific actions, including precision and strength actions (e.g. to write, to hold a match when striking it, to throw a ball away, and to hammer a nail into wood). As described in an interview prior to the experiment, all the subjects were also right-footed. All of them were practicing some sports at the time of the experiment (soccer, box, and athletics) and during the debriefing at the beginning of the experiment, they declared to be already familiar with motor imagery tasks. The subjects were homogeneous for weight ( $70.2 \pm 3.8$  kg) and height ( $1.78 \pm 0.05$  m). All subjects gave their written informed consent according to the Declaration of Helsinki (World Medical Association Declaration of Helsinki [1997]). They were allowed to ask for a break at any time and paid for their participation. All subjects had normal vision and were naive about the purpose of the experiment. The general procedures were approved by the Ethical Committee of the University of Chieti "G. D'Annunzio."

### Imagery Ability

Before the fMRI session, subjects' imagery ability was evaluated using a modified version of the Movement Imagery Questionnaire-revised [Hall and Martin, 1997]. The purpose of the MIQ is to evaluate the subject's ability in both visual and kinaesthetic imagery. Subjects are asked to imagine to "see" and to "feel" each item (i.e. movement) and to rate how easy the imagination was. The modification consisted in a translation from English to Italian and in the inversion of the rating scale. In the original version, the values regarding the facility/difficulty in imagining a movement ranged from 7 (very easy) to 1 (very difficult) while in the revised version items "very easy to imagine" were labeled as 1 and "very difficult" as 7.

### Procedure

Subjects were asked to walk on a treadmill outside the scanner to enter the scanner and to imagine to walk using motor imagery. This procedure was repeated four times for all subjects, because the complete experiment included four conditions that varied in terms of the type of locomotion (Balanced, Non Balanced) and walking time (Long, Short). The four conditions consisted in (i) walking normally balanced for 20 min (Long-Balanced, LB); (ii) walking with a 3-cm-thick heel under the right foot for 3 min (Short-Non Balanced, SNB); (iii) walking with the heel for 20 min (Long-Non Balanced, LNB); (iv) walking without the heel for 3 min (Short-Balanced, SB). In particular, during the balanced conditions, participants were asked to walk normally (without any constraint), whereas during the unbalanced conditions a 3-cm high-polystyrene heel was applied under the participant's right foot and fixed with tape. The heel was new for

each participant to prevent potential deformation and changes in thickness due to use. We assumed that a short condition should always be after a long condition, thus two orders of conditions were counterbalanced across subjects: six subjects performed the task with the order LNB-SB-LB-SNB; six subjects followed the order LB-SNB-LNB-SB. The speed of walking was controlled by the treadmill, which was constantly operating at 2.7 km/h. Given the effectiveness of kinaesthetic/motor imagery on motor pathways' activation with respect to the lack of such a specific influence of visual imagery [Fourkas et al., 2006], during the real locomotion subjects were trained to focus on all the proprioceptive information relative to all the muscles and body parts involved in the locomotion. The experimenter was standing nearby and asked them to concentrate on one body part at once, guiding them through the focusing process with fast verbal reminders indicating the body part and the sensation to be noticed. In this way, subjects were asked to notice and rate the muscular contraction, stretching, weight distribution, fatigue, heating, pain, and, in particular, the differences between the same left and the right body part, for all the mentioned body segments. The left and right foot plantar, toes, heels, hamstrings, tibial muscles, frontal and posterior thighs, pelvises, lower-back, mid-back, upper-back, shoulders, and neck were progressively taken into account. After each session of real locomotion, subjects were asked to enter the scanner and imagine walking as in the condition just experienced on the treadmill. They had to use motor imagery based on the sensations they perceived during the previous locomotion. During the fMRI sessions, subjects alternated motor imagery of themselves while walking in the condition they just experienced (30 s) and imagery of themselves staying still in the upright stance position (rest condition, 30 s). The alternation between task (imagery of walking) and rest (imagery of stance) was driven by vocal instructions given by the experimenter to the subjects through a microphone. The participants' legs' potential uncontrolled movements were continuously monitored by the experimenters by on-line visual inspection. Four blocks were used for the imagery of both locomotion and stance. As a physiological evidence of motor imagery [Decety et al., 1991], heart beat was measured during imagery sessions. A semi-structured imagery questionnaire was administered after the fMRI session to investigate the imagery strategy used by each subject. The questionnaire was designed to disclose the strategies used to solve the task, collecting introspective information on the task just done. The procedure consisted of a written interview in which people described all the contents of their imagery, focusing on visual or kinaesthetic aspects and on the imagery perspective used (egocentric or allocentric).

### fMRI Recording

BOLD contrast functional imaging was performed with a SIEMENS MAGNETOM VISION scanner at 1.5 T by

means of T2\*-weighted echo planar imaging free induction decay sequences with the following parameters: TR 3 s, TE 60 ms, matrix size  $64 \times 64$ , FOV 256 mm, in-plane voxel size  $4 \times 4$  mm, flip angle  $90^\circ$ , slice thickness 5 mm, and no gap. A standard head coil was used, and the subject's head was fixed with foam pads to reduce involuntary movement. Functional volumes consisted of 26 transaxial slices parallel to the AC-PC line including the whole brain. The experimental paradigm was a block design alternating a state of gait mental simulation of 30 s (corresponding to the acquisition of 10 functional volumes) with a control state having the same duration (stance mental simulation). For each run, 85 volumes were acquired starting with a task period. A high-resolution structural volume was acquired at the end of the session via a 3D MPRAGE sequence with the following features: sagittal, matrix  $256 \times 256$ , FoV 256 mm, slice thickness 1 mm, no gap, in-plane voxel size  $1 \times 1$  mm, flip angle  $12^\circ$ , TR = 9.7 ms, TE = 4 ms.

### Data Analysis

Raw data were analyzed by means of the BrainVoyager QX software (Brain Innovation, The Netherlands). Because of the T1 saturation effects, the first five scans of each run were discarded from the analysis. Preprocessing of functional scans included motion correction and removal of linear and nonlinear trends from voxel time series. A three-dimensional motion correction was performed by means of a rigid body transformation to match each functional volume to the reference volume (the sixth volume, because the first five volumes were discarded to avoid the T1 saturation effect), estimating three translation and three rotation parameters. These parameters were stored in log files and inspected to check that the estimated movement was not larger than 2 mm or  $2^\circ$  (approximately half a voxel) for each functional run. Preprocessed functional volumes of a subject were coregistered with the corresponding structural data set. The final coregistration transformation in BrainVoyager QX was determined concatenating an initial alignment matrix obtained using the Siemens position parameters of the functional and structural images with a fine-tuning alignment matrix obtained by means of an intensity-driven alignment algorithm. Structural and functional volumes were transformed into the Talairach space [Talairach and Tournoux, 1988] using a piecewise affine and continuous transformation. Functional volumes were resampled at a voxel size of  $3 \times 3 \times 3$  mm. Statistical analysis was performed using the general linear model (GLM) [Friston et al., 1995] with correction for temporal autocorrelation [Woolrich et al., 2001]. To account for the hemodynamic delay, the boxcar waveform representing the rest and task conditions was convolved with an empirically founded hemodynamic response function

[Boynton et al., 1996]. No spatial or temporal smoothing was performed in this analysis.

To search for activated areas that were consistent for the entire group of subjects, a random-effect statistical group analysis was performed. In this analysis, the time series from each run and subject was normalized (% signal change normalization). The group statistical maps were thresholded at  $P < 0.05$ , corrected for multiple comparisons. The correction for multiple comparisons was performed using a cluster-size thresholding algorithm [Forman et al., 1995] based on Monte Carlo simulations and implemented in the BrainVoyager QX software. A threshold of  $P < 0.004$  at the voxel level and an estimate of the spatial correlation of voxels was used as input in the simulations, yielding a minimum cluster size of nine voxels to obtain statistical maps thresholded at a standard alpha level ( $P < 0.05$ , corrected for multiple comparisons). Thresholded statistical maps were then superimposed on the Talairach transformed structural scan of one of the subjects, for the localization of significantly activated areas. Regions of interests (ROIs) in SMA, bilateral thalamus, basal ganglia, and right cerebellum were determined by considering the mask obtained from voxels activated at any postural condition. The Talairach coordinates of each ROI were determined considering the centroid of the related cluster of activation. The mean time course of the fMRI signal from voxels belonging to a given ROI was derived and analyzed for each subject to compare the responses during the different postural conditions. Subjects' responses were characterized by evaluating the BOLD signal intensity variation in each ROI. The relative signal variation between baseline (rest period) and activation (motor imagery period) was calculated from the fitted parameters of the GLM:  $\text{BOLD \% change} = (\text{beta} * 100) / \text{baseline}$ , where beta represents the estimated amplitude of the variation of the fMRI signal. The regional comparison of activation was undertaken by means of the analysis of variance (ANOVA) for repeated measures. The dependent variable of the ANOVA analysis was the relative variation of the BOLD signal between the motor imagery and rest conditions. The ANOVA factors were locomotion (balanced vs. nonbalanced), and practice (short vs. long). For all the ANOVA calculations, Mauchly's test was used to evaluate the sphericity assumption. The number of degrees of freedom was corrected by means of the Greenhouse-Geisser procedure, and the Newman-Keuls test was used for post hoc comparisons.

## RESULTS

### Questionnaires

Subjects' mean rating of visual [2.0 (SD = 0.5) of 7.0] and kinaesthetic [1.75 (SD = 0.5) of 7.0] imagery of the revised Movement Imagery Questionnaire suggested that before the scanning session, they were already able to pro-

duce a "clear image" and experienced a "vivid sensation" when imagining the different movements. In the postscan interview, subjects reported to have used egocentric motor imagery to fulfill the task, with particular reference to their own body, focusing on the recalling of proprioceptive information experienced during the actual walking session before the fMRI session.

### Neurovegetative Response

Variations of heart beat during imagery of locomotion were analyzed by means of a three-way repeated measures ANOVA with practice (long vs. short), locomotion (balanced vs. nonbalanced), and task (imagery of locomotion vs. imagery of stance) as main factors. Post hoc analyses were carried out using the Newman-Keuls test ( $P < 0.05$ ). This analysis showed a significant main effect of task [ $F(1,11) = 9.74$ ;  $P < 0.009$ ]. Whereas the main effect of practice [ $F(1,11) = 0.39$ ;  $P > 0.54$ ] and locomotion [ $F(1,11) = 0.15$ ;  $P > 0.69$ ] nor any interaction were not statistically significant (all  $P > 0.45$ ). The main effect of task was accounted for by an increase of the heart beat rate during imagery of walking with respect to the imagery of stance (see Fig. 1).

### fMRI

A significant activation ( $P < 0.05$ , corrected for multiple comparisons) was observed for the group during imagery of locomotion in precentral gyrus (BA6), corresponding to SMA, for both long and short practice. The activation of

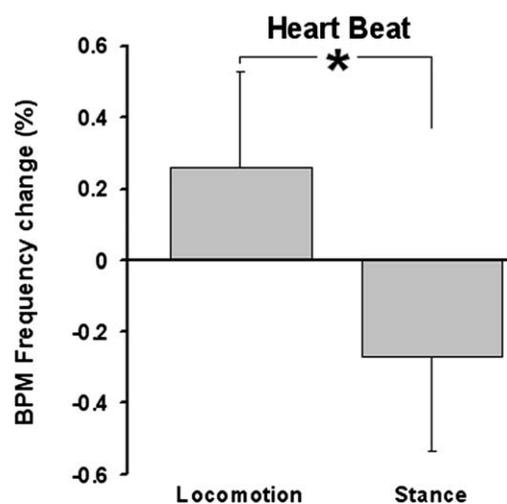


Figure 1.

Heart beat frequency changes as a function of the imagery conditions. During imagery of locomotion, the number of beats per minute was higher than during imagery of stance. Error bars are standard errors.



Figure 2.

(a) Results of the random-effect group analysis showing the activated areas during the motor imagery task in the short-time walking conditions. (b) Talairach coordinates of cortical and cerebellar structures significantly activated during the motor imagery task (lower panel). The group statistical maps were thresholded at  $P < 0.05$ , corrected for multiple comparisons.

Localization	Right hemisphere			Left hemisphere				
	$t$	$df = 11$	Talairach coordinates	$t$	$df = 11$	Talairach coordinates		
			$x$ $y$ $z$			$x$ $y$ $z$		
Precentral Gyrus (BA6)	-	-	-	5.14	-6	-8	61	
Globus Pallidus	5.12	21	-7	6	-	-	-	
Thalamus	5.61	9	-13	5	6.24	-15	-7	8
Cerebellum	5.64	33	-54	-24	-	-	-	

right globus pallidus, bilateral thalamus, and right cerebellum was observed during imagery of locomotion after periods of short practice. The activation maps obtained from the group analysis superimposed on an individual (Talairach transformed) structural image are shown in Figure 2a. Talairach coordinates of the clusters' centroids of activation in precentral gyrus (BA6), globus pallidus, thalamus, and cerebellum are listed in Figure 2b. Individual responses in each activated area were then compared across conditions by means of ANOVA, as described in the section below.

The fMRI data relative to long and short practice were analyzed considering the ROI's resulting from the group analysis as separate functional subregions. A two-way ANOVA design was used to evaluate the influence on the relative BOLD changes (dependent variable) of the factors practice (long vs. short) and locomotion (balanced vs. nonbalanced). A statistically significant main effect was observed for practice in right globus pallidus [ $F(1,11) = 8.6$ ;  $P < 0.014$ ], right thalamus [ $F(1,11) = 11.9$ ;  $P < 0.005$ ], and left thalamus [ $F(1,11) = 10.4$ ;  $P < 0.008$ ]. Notably, the BOLD signal in SMA and right cerebellum did not differentially modulate as a function of practice. The factor locomotion (all  $P > 0.26$ ) and the interaction between locomotion and practice (all  $P > 0.24$ ) did not reach significance in any of the selected ROI. Post hoc analysis carried out on significant effects showed that BOLD response during imagery session after short practice periods was larger than after long practice in right thalamus ( $P < 0.026$ ), left thalamus ( $P < 0.036$ ), and right globus pallidus ( $P < 0.014$ ) (see Fig. 3).

## DISCUSSION

### Early Stages of Practice

In this study, we provide neurophysiological evidence (fMRI) in favor of the modulation of a specific cerebral network as a function of physical practice and in line with introspective reports and neurovegetative measurements as controls. A general activation during imagery of locomotion when compared with imagery of stance (in both postural conditions) was observed in SMA, bilateral thalamus, right globus pallidus, and right cerebellum. But a stronger activation during early stages with respect

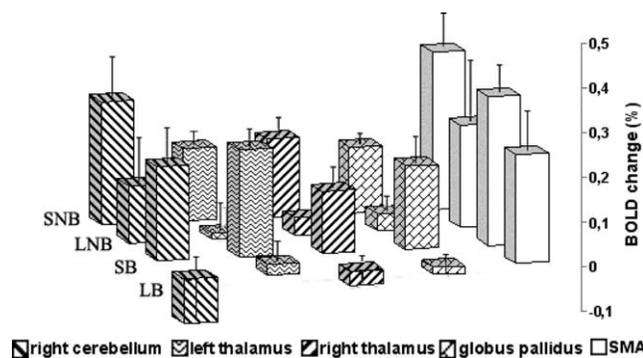


Figure 3.

BOLD responses (averaged across subjects) in the activated areas during imagery of locomotion in the four conditions (LB, long balanced; SB, short balanced; LNB, long not balanced; SNB, short not balanced). Error bars are standard errors.

to late stages was found only in bilateral thalamus and right globus pallidus. This pattern of activation was present during the imagery of both balanced and unbalanced locomotion. In the comparison between novel hand sequential movements and the same sequences after a 5-day long training (30 min a day), a larger and bilateral thalamic activation has been found during the imagery of novel with respect to skilled movements [Lacourse et al., 2005]. Our data extend these results to another body part and to a different (and shorter) training time, suggesting an involvement of subcortical structures in the initial phases of movements, aspecifically with respect to the body part. Basal ganglia together with thalamus are particularly involved in timing and sequence planning of motor acts. We suggest that when the movement becomes progressively better known, even after only 20 min of practice, it is already integrated into the body schema and the activity of those last areas decreases, delegating the control of the movement to higher structures.

In line with Jahn et al. [2004], thalamic activation was observed during imagery of locomotion. In addition, we manipulated the practice time for different kinds of locomotion. In line with the results obtained by Lacourse et al. [2004] with the imagery of hand movements, we observed a bilateral activation of the thalamus during imagery of locomotion after short practice. The thalamus is also involved in visuomotor association processes (see Murray et al. [2000] for review) and most of the signals coming from subcortical structures and directed to primary motor cortex pass through it [Kandel et al., 2000]. It is activated during the first stages of visuomotor association, and its activity decreases when the task is progressively well practiced [Landau et al., 2004]. As revealed by a PET study, during dorsiflexion of the left foot without any previous practice, thalamus is IPSI-laterally activated, while after a 1-h practice, the activation is bilateral [Lafleur et al., 2002]. However, its role in mental imagery is still under discussion. The thalamus was more active during imagery of the upright standing posture with respect to imagery of walking, whereas no thalamic activation was observed during imagery of running [Jahn et al., 2004]. On the other hand, a PET signal increase was recorded in the thalamus during both the execution and the imagery of finger movements [Deiber et al., 1998]. Furthermore, an fMRI study revealed a bilateral activation in the thalamus during a finger tapping task, whereas a contralateral activation was observed during the same task after a training lasting 1 week [Lacourse et al., 2004]. In conclusion, the reason why the shift between uni- and bilateral activation of the thalamus shows an opposite behavior when comparing motor imagery [Lacourse et al., 2004] and execution [Lafleur et al., 2002] is still an open debate.

The present results relating to globus pallidus are in line with other studies demonstrating involvement of basal ganglia in the motor imagery of an unpracticed motor task

[Jueptner et al., 1997] and suggesting a connection between cerebellum, basal ganglia and SMA for the initiation and transient phases of movements. Basal ganglia activation is somatotopically organized [Maillard et al., 2000; Scholz et al., 2000] and observed in both imagined and executed movements [Gerardin et al., 2000], especially under complex environmental conditions [Nutt et al., 1993]. Basal ganglia, connected to SMA [Nutt et al., 1993] and responsible for temporal encoding of motor events [Macar et al., 2004], play an important role in the execution of non-skilled movements [Jueptner et al., 1997]. This kind of practice-dependent involvement of basal ganglia in motor control has been demonstrated for motor imagery of actions such as a golf swing [Ross et al., 2003], but the precise nature of the involvement remains unclear. On one hand, it seems that basal ganglia activity *decreases* as a function of the automatization of a movement [Jahn et al., 2004]; on the other hand, there is evidence of automatization-related *increases* in activity, manifesting as stronger activation of the IPSI-lateral caudate nucleus and CONTRA-lateral putamen during imagery with respect to execution in the early stages of motor learning [Lacourse et al., 2005].

### Effects of Imagery

In our paradigm, most of the postural manipulation (and imagery effort) was on relief of the right leg (the heel was under the right foot). The significant right cerebellar activity during motor imagery of locomotion after short practice when compared with imagery of stance is in line with previous studies on the imagery of different motor behaviors and that found a cerebellar activation IPSI-lateral to the limb involved in the imagined movement [Luft et al., 1998; Naito et al., 2002], whereas cerebellar activation after long practice showed a large variability across subjects and was not significant at the group level. Cerebellum is connected to SMA via the basal ganglia [Hoshi et al., 2005]. It is involved in motor imagery, even if with a weaker activity with respect to the execution of the same movement [Lafleur, 2002; Nair et al., 2003]. Cerebellum has also been shown to play an important role in the motor imagery of slow movements [Jahn et al., 2004] and in the organization of movement sequences: indeed, it is recruited during imagery of playing tennis [Decety et al., 1990; Ryding et al., 1993], dancing [Sacco et al., 2006], standing, walking, and running [Jahn et al., 2004], playing golf [Ross et al., 2003]. Our task required a sharp imagined coordination, and this is probably why we found cerebellar activation in all conditions.

The activity in the precentral gyrus (SMA) was weakly modulated by the extent of practice and by the different postural conditions, supporting the idea that SMA is always involved in the simulation of motor acts [Dechent et al., 2004; Lotze et al., 1999] and in the inhibition of

competing motor plans [Serrien et al., 2005; Toma et al., 1999]. The activity of SMA during sustained imagery of different walking conditions (walking and walking with obstacles) does not change with the difficulty increase between the conditions [Malouin et al., 2003]. These and our results lead to suggest that the contribution of SMA during a sustained motor imagery task is constant.

All subjects included in this study reported that they used an egocentric perspective, supporting in this way the idea that they used motor mechanisms [Ruby and Decety, 2001]. Moreover, the heart beat measured during the fMRI session in this study, was modified by the imagery task, with a higher frequency during the imagery of locomotion with respect to the imagery of stance. Those are data in line with the modulation of vegetative responses already observed in previous studies [i.e. Decety et al., 1991]. Mental imagery is usually hard to control, but in the present case the heart beat frequency enhancement during the imagery of locomotion but not during imagery of stance is a clear sign that subjects were actively performing the imagery task.

## CONCLUDING REMARKS

This fMRI study investigated the neural correlates of motor practice during early and late stages of such a process using motor imagery. To our knowledge, this is the first study that used fMRI in combination with introspective and neurovegetative responses to investigate and compare very early with later stages of motor practice. Our working hypothesis has been confirmed by the experimental evidence of a large cerebral network activated during the motor imagery only after early stages of locomotion practice. In particular, globus pallidus and bilateral thalamus showed an increased activity during early stages of motor practice when compared with late stages.

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