



Review

The neural network of motor imagery: An ALE meta-analysis

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ABSTRACT

Motor imagery (MI) or the mental simulation of action is now increasingly being studied using neuroimaging techniques such as positron emission tomography and functional magnetic resonance imaging. The booming interest in capturing the neural underpinning of MI has provided a large amount of data which until now have never been quantitatively summarized. The aim of this activation likelihood estimation (ALE) meta-analysis was to provide a map of the brain structures involved in MI. Combining the data from 75 papers revealed that MI consistently recruits a large fronto-parietal network in addition to subcortical and cerebellar regions. Although the primary motor cortex was not shown to be consistently activated, the MI network includes several regions which are known to play a role during actual motor execution. The body part involved in the movements, the modality of MI and the nature of the MI tasks used all seem to influence the consistency of activation within the general MI network. In addition to providing the first quantitative cortical map of MI, we highlight methodological issues that should be addressed in future research.

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1. Introduction

Remember the days when you were still a child stuck in a classroom, imagining being elsewhere, maybe fighting a blaze as a fireman, dancing on the world's biggest stages or perhaps for some, conducting intriguing science experiments. Imagining doing something is an important cognitive process that is used throughout our lifespan. Motor imagery (MI), which refers to the act of imagining a specific action without actually executing it, has fascinated scientists from a wide range of domains including sport sciences, psychology and neuroscience. However, its study has been challenging due to its covert nature: how can we measure something related to the motor domain in someone who is explicitly asked not to move? If the measure of behavioral parameters such as the temporal characteristics of imagined movements (through mental chronometry paradigms) and physiological signals provided a very interesting window into this process (see (Collet et al., 2011) for an overview), it is the development of brain imaging techniques such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) that brought scientists ever closer to “seeing how” people are doing MI. These technological advances were paralleled by a booming interest in the study of MI as can be seen by the important increase in publications related to MI since 1995 (see Fig. 1). With these new tools, neuroscientists are now at

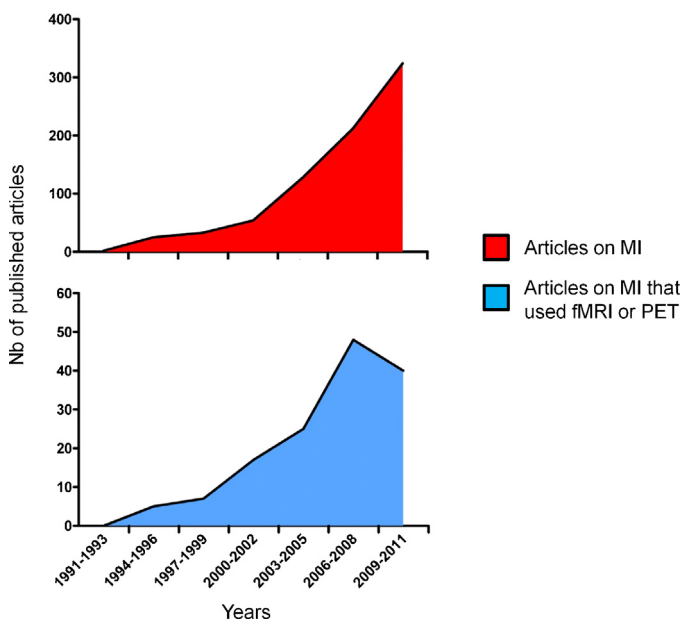


Fig. 1. Progression of the number of publications on motor imagery. Upper graph: number of published articles on motor imagery between 1995 and 2011. Lower graph: number of published articles on motor imagery which used functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) between 1995 and 2011. Data was collected through an online search on the PubMed database (<http://www.ncbi.nlm.nih.gov/pubmed/>) using the terms “motor imagery” for the upper graph and “motor imagery” and “fMRI” or “PET” for the lower graph.

the forefront of the scientific challenge of understanding how our brain subserves the act of imagining movements.

Motor imagery has been defined as the conscious mental simulation of actions involving our brain's motor representations in a way that is similar to when we actually perform movements (Jeannerod and Decety, 1995). This has led many to suggest that MI and motor execution rely on similar neural structures and processes (Grezes and Decety, 2001; Jeannerod, 2001; Jeannerod and Decety, 1995; Munzert et al., 2009). Numerous studies have tried to verify this claim by identifying the neural substrate of MI using neuroimaging techniques. An exhaustive overview of the results from these studies was presented more than 10 years ago by Grezes and Decety (2001) who suggested that MI recruits the primary motor cortex, premotor cortex (PMc), supplementary motor area (SMA), anterior cingulate cortex (ACC), inferior and superior parietal lobules (IPL/SPL) and the cerebellum (CB).

However, one has to be careful when trying to describe the network underlying a brain function by combining results from individual neuroimaging studies using a descriptive (as opposed to quantitative) approach such as the one used by Grezes and Decety (2001). Indeed, the statistical power of fMRI and PET studies remains relatively low, in part because of their small sample sizes (see (Yarkoni, 2009) for a commentary on this topic). Furthermore, as neuroimaging data is particularly sensitive to task and control condition selection, which often varies across studies, results obtained with a contrast approach (Task A > Control condition) are difficult to generalize. Thus, trying to get a precise and clear view of which regions are “truly” involved in the general process of MI by looking separately at data from individual studies is often impractical and potentially misleading. Large-scale synthesis methods are now available and offer new opportunities to probe and make sense of the immense data produced by the imaging community (e.g., Eickhoff et al., 2009; Wager et al., 2009; Yarkoni et al., 2011). Hence the aim of this paper is to use a meta-analytic approach to map the regions involved in MI and to assess the modulating effects of specific methodological variables that have already been topics of interest in the field of MI.

Previous work have already investigated the influence of variables such as which body parts the participants are imagining moving (Ehrsson et al., 2003; Szameitat et al., 2007) or the modality/strategy of MI (i.e., kinesthetic vs. visual MI) they use (Guillot et al., 2009). Another variable that has been less documented but could be of interest for the study of MI is the influence of the MI task the participants are instructed to complete. Indeed, if most studies have asked their participants to imagine single actions, others have instructed their participants to imagine motor sequences (often simple or complex series of finger movements). Others, instead of explicitly asking their participants to perform motor imagery, instruct them to identify the laterality of a limb shown in different orientations: a task thought to be solved using motor imagery. Since relatively few studies have looked at each of these variables, clear conclusion on how they influence brain activity during MI is still sparse. Furthermore, taken separately, each of these studies was done with relatively small samples. Meta-analyses make possible

the study of these modulating variables at a much larger scale as they combine and simultaneously analyze the findings from several studies (and thus use much larger samples). Also, meta-analyses can consider data from a study even if this particular study did not directly look at the variable. For example, trying to get a sense of the influence of the modality of MI, each study that used kinesthetic MI will be compared to each study that used visual MI even if these studies did not compare the two modalities directly.

As most reviews on MI have discussed results from neuroimaging studies using a descriptive approach, there is a great need for a fresh and quantitative look at the work that has been conducted on MI using fMRI and PET. First, results from this meta-analysis should offer answers to important questions in the field. Indeed, the involvement of the primary motor cortex is still a subject of debate and the differences/similarities in the involvement of the motor system during different types of MI remains an open question. Furthermore, looking at the methodological characteristics of a large sample of studies will highlight possible shortcomings related to MI research and offer possible methodological changes that could benefit future work on MI. Lastly, as MI is increasingly proposed as a possible rehabilitation tool to train the motor system (Flor and Diers, 2009; Jackson et al., 2001; Malouin and Richards, 2010; Mulder, 2007), and even to gain access to patients in neurovegetative states (Cruse and Owen, 2010), an empirical description of the neural system supporting MI should offer clinical neuroscientists useful normative data, for instance to study neural activation during MI in clinical populations, or to assess the efficacy of training programs using MI.

Based upon the work by Grezes and Decety (2001), it is expected that studies on MI should consistently report activity in regions involved in the actual production of movements such as the SMA, the PMc, IPL, SPL and the CB, and that variations in the type of MI performed should modulate the extent of this activation.

2. Methods

2.1. Article selection

Articles were obtained through an online search of the PubMed database (<http://www.ncbi.nlm.nih.gov/pubmed/>) using the terms “fMRI” or “PET” and “motor imagery” during the month of September 2011. In addition, reference sections of the reviewed articles were carefully inspected to identify additional articles of interest. Selected articles had to: (1) use either fMRI or PET; (2) present data on a MI task; (3) report activations in the form of stereotaxic coordinates of foci based on either the MNI or Talairach template; (4) present data from healthy participants. Peak results could be obtained with a contrast approach (e.g., MI vs. Rest) or with parametric analyses. For articles which used contrast analyses, the control condition could not consist of an active motor task, an action observation task or another MI task involving motion (e.g., MI of the right hand vs. MI of the left hand). Only articles which reported whole brain results were selected. Articles were rejected if they only used a region of interest (ROI) approach as this technique focuses on predefined regions and therefore do not report all activation clusters. Coordinates that were reported in Talairach space were transformed into MNI coordinates using the linear transformation developed by Lancaster (Lancaster et al., 2007). The complete list of articles meeting the inclusion criteria is presented in Supplementary Table 1.

2.2. Meta-analyses

To get a broad view of the brain regions involved in MI, we first performed a *general* meta-analysis on all studies. This general

meta-analysis, although very informative, does not take into account the methodological differences between the studies, some of which may represent moderating or confounding variables. Therefore, we also performed additional meta-analyses in order to investigate the influence of some of these variables: the body part involved in the imagined movement; the MI modality; and the nature of the MI task the participants were instructed to complete. All articles were categorized based on these variables (see Supplementary Table 1).

The different body parts of imagined movements were: upper-limb movements and lower-limb movements. Gait was included in lower-limb movements but was also assessed independently. Movements of the upper limb were further categorized as transitive (with or towards objects) or intransitive (no object involved). As very few studies used whole body movements and these movements greatly varied across studies, this category was not analyzed separately.

The modality of MI could either be kinesthetic or visual. Kinesthetic MI requires individuals to “feel the movement”, i.e. to perceive the sensations normally associated with its execution such as muscle stretching and contractions, whereas visual MI requires individuals to self-visualize the execution of the movement (Guillot et al., 2009).

As for the nature of the MI tasks, during most studies subjects were instructed to imagine a given movement (e.g., imagine yourself using a pen). As it can easily be considered as the most common MI task we named it Pure MI. Tasks requiring the production of motor sequences were excluded from this category. Indeed, such tasks require individuals to focus explicitly on the specific sequential order of movements (which is often not naturalistic) in addition to the movements per se. On the contrary, individuals performing Pure MI need only to focus on the motoric aspects of the movements. In order to investigate the possible modulating effect of instructions focusing on the “sequence” parameter we looked at studies that used motor sequence tasks and compared them to studies that used Pure MI tasks. In other studies participants were asked to complete the laterality judgment task (LJT). In this task subjects have to report the laterality of body parts presented in different angular orientations. MI is thus implicitly triggered as individuals generally mentally rotate their own limb in order to match the observed body part and assess if it matches the body part they chose to rotate (right or left) (Parsons, 1994, 2001). We consider this as implicit motor imagery as no instruction is given to the participants on how to complete this task. Note that tasks in which subjects had to identify which type of grip would be preferable to grasp a handle presented in different orientations were also included in the LJT category, as they are very similar to the LJT and also do not explicitly instruct subjects to perform MI (e.g., Johnson et al., 2002a). As the instructions for Pure MI clearly indicate to the participants that they have to perform MI, this task was compared to the LJT to determine whether regions activated during motor imagery vary according to whether implicit or explicit instructions are used.

Separate meta-analyses were performed to determine the regions consistently activated by each of these categories (e.g., upper-limb movements in general, transitive upper-limb movements, LJT, kinesthetic MI, etc.). For each variable of interest, maps were also compared to identify overlaps and differences in the regions of consistent activation. As these comparisons have very seldom been investigated, we had no specific hypothesis about the results. However, it is more than plausible that, depending on the task, regions playing a role in motor control and/or programming will show differences in consistency of activation. Furthermore, our analyses may reveal that known differences between the networks involved during the production of different types of movements (e.g., between upper and lower-limb movements), are also observed during MI.

Table 1
Details of analyses and sub-analyses.

Meta-analyses	Nb of experiments	Nb of subjects	Nb of foci
General MI	81	1096	1070
MI of upper-limb mvts	54	705	732
Transitive mvts	22	280	325
Intransitive mvts	31	408	406
MI of lower-limb mvts	14	255	197
Gait	11	225	173
MI of whole body mvts	7	86	65
Kinesthetic MI	19	223	279
Visual MI	5	58	54
Laterality judgment task	10	121	99
MI of motor sequence	14	209	261
Pure MI	38	461	413

Details on the number of experiments, number of subjects and foci for each meta-analysis are presented in Table 1.

2.3. The activation likelihood estimation (ALE) technique

To carry out the meta-analyses we used the revised version of the ALE approach for coordinate-based meta-analysis of neuroimaging results described by Eickhoff et al. (2009). The algorithm identifies areas showing convergence of activations across the different experiments and tests if this convergence is higher than would be expected under a null-distribution reflecting a random spatial association between experiments. ALE treats reported foci as 3D Gaussian probability distributions thus capturing each focus' specific spatial uncertainty, which mainly depends on between-template and between-subject variance (Eickhoff et al., 2009). The parameters (width) of the probability distributions have thus been empirically determined based on these two sources of variance (see (Eickhoff et al., 2009)) and are weighted by the number of subjects in each experiment.

In the first step of the ALE analysis, for each experiment, a 3D modeled activation (MA) map is computed where, for every voxel, the probability of an activation being exactly at that location is calculated. To do so, for each experiment, all the activation foci are modeled as probability distributions as described earlier. Then, the probability associated with each voxel is calculated by taking the union of the probability values for all the foci. Therefore, the MA map corresponds to the summary of each experiment's results taking into account the spatial uncertainty associated with the reported coordinates.

The second step consists in merging all the MA maps (one for each experiment) by taking the voxel-wise union of the probability values to produce an ALE map. This map contains information about the convergence of results for each voxel, which is represented by a "true" ALE score. This analysis is restricted to voxels with a minimum of 10% probability of containing grey matter based on the ICBM tissue probability maps (Evans et al., 1994). The "true" ALE scores are then compared to a null-distribution reflecting a random spatial association between experiments. This null-distribution is obtained through a permutation procedure where a random grey-matter voxel from each experiment's MA map is selected, the probability associated with each voxel is extracted and a single ALE score is calculated through the same approach as mentioned before. This procedure is iterated by selecting new sets of random voxels to produce a null-distribution of ALE scores. Each "TRUE" ALE score is then compared to the ALE scores obtained under this null-distribution yielding a non-parametric p value that is transformed into a Z score.

In the present paper, the threshold was set at $p < 0.001$ uncorrected with an extent-threshold of 120 mm^3 based upon previous similar ALE papers (albeit on different topics such as action observation) which used and justified these parameters (Grosbras et al.,

2011). To identify common regions involved in two different meta-analyses, conjunction analyses (intersection between significant ALE maps) were performed. Note that conjunction analyses may result in seemingly contradictory results where common bilateral consistent activation is found in region A even if only one of the ALE maps included bilateral activation in this region. This is due to the fact that the reported peaks for the other map may be located in another specific region (e.g., B) even though the cluster extends onto A. When conducting the conjunction analyses, these larger clusters only partially overlap, in this example in region A, resulting in a bilateral conjunction peak in this region without "bilateral" peaks in A for each ALE map. Subtractions analyses (see (Eickhoff et al., 2009) for details) were used to assess differences between meta-analyses. For the subtraction analyses, we used an uncorrected threshold of $p < 0.005$, extent-threshold of 120 mm^3 . All resulting areas were labeled using the SPM Anatomy toolbox (Eickhoff et al., 2007, 2005).

3. Results

3.1. Number of articles and brief description

Our search resulted in 75 articles that corresponded to our inclusion criteria. The median size of their samples was 12 subjects (range: 5–60). Twelve articles used PET while the remainder used fMRI. Twenty five articles used rest as the control condition, 13 used a fixation condition (cross or scrambled image), six used a visual imagery condition (imagining a moving or static object), one used both a visual imagery and fixation condition, eight used a motor imagery of static self condition, and 22 used another form of control condition which included visual or auditory discrimination tasks or other cognitive tasks. For details see Supplementary Table 1.

3.2. General MI

The meta-analysis looking at the general pattern of consistent activations during MI revealed several large clusters spanning over both hemispheres (see Fig. 2). In the frontal lobes, regions consistently activated were bilateral inferior frontal gyri (IFG; including the pars opercularis), precentral gyrus (PcG), middle frontal gyrus (MfG), the SMA and regions of the anterior insula. In the parietal lobes, the bilateral SPL and supramarginal gyrus (SMG) in addition to the left IPL were consistently activated. Subcortical regions consistently activated included the left putamen, right thalamus and pallidum. Finally, area VI (bilateral) and the vermis of the CB were found to be consistently activated. Coordinates for all peak activations can be found in Table 2.

3.3. MI of different body parts

3.3.1. MI of the upper limb

MI of the upper limbs showed consistent activations in similar clusters than general MI (see Fig. 3; Table 3). Again, results showed bilateral activations within the IFG, including the pars opercularis (activation in pars triangularis was only seen in the left hemisphere), PcG, MfG, the SMA, anterior insula and right middle cingulate cortex. In the parietal lobes, activations were consistently found in bilateral SPL, SMG, and precuneus (PreC), in addition to the right postcentral gyrus (PocG) and left IPL. Consistent activations were also found in the CB (lobule VI) bilaterally and in the left putamen and right pallidum.

Taking a closer look at the possible modulating role of transitivity (see Fig. 4; Table 3), the ALE analysis focusing on MI of transitive movements produced consistent bilateral activations in the IFG, including the pars opercularis (activation in pars triangularis was

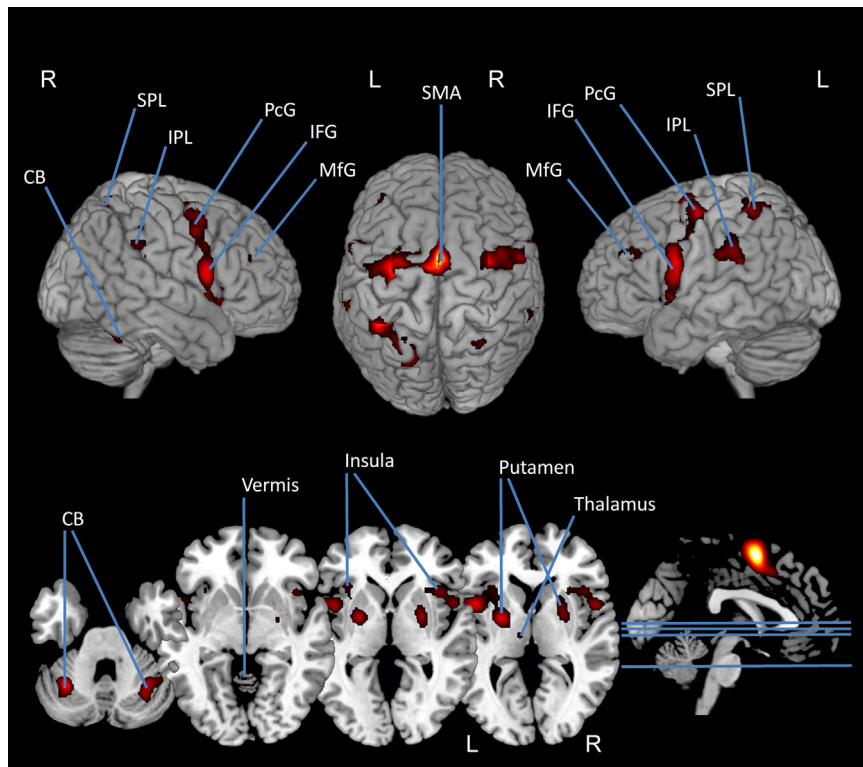


Fig. 2. Regions consistently activated during motor imagery. Map resulting from the ALE meta-analysis. The results are superimposed on a template brain (in MNI coordinate space) using MRIcron (<http://www.mccauslandcenter.sc.edu/micron/micron/>). CB: cerebellum; IPL/SPL: inferior/superior parietal lobule; PcG: precentral gyrus; IFG: inferior frontal gyrus; MfG: middle frontal gyrus; SMA: supplementary motor area.

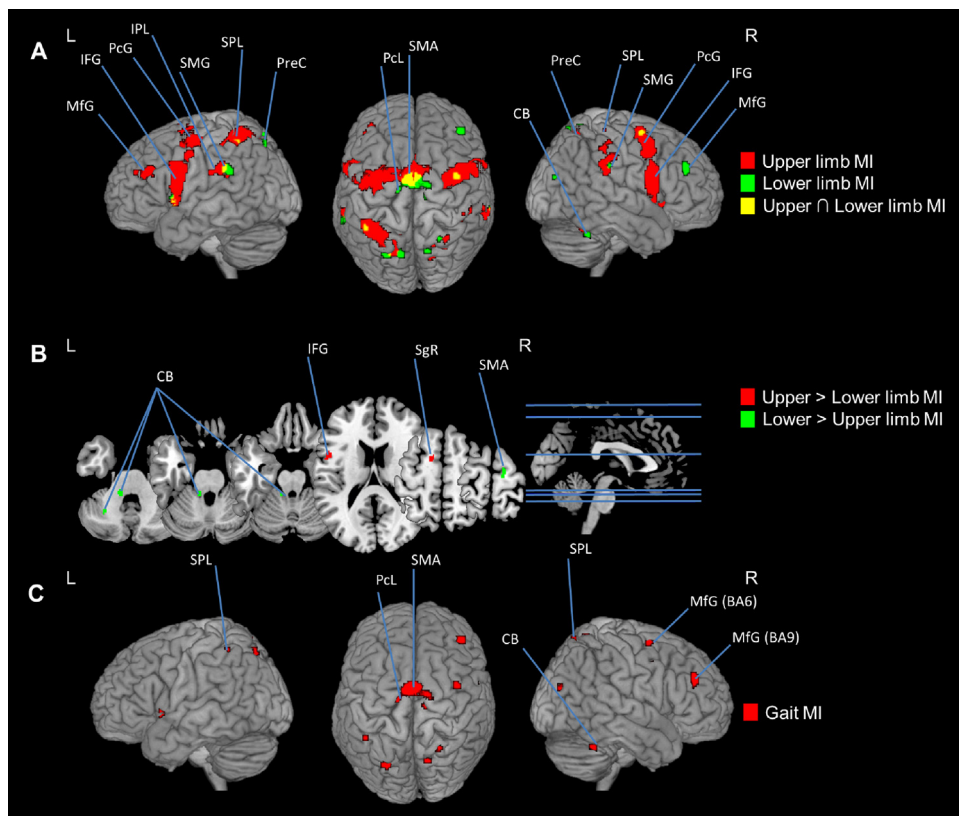


Fig. 3. Regions consistently activated during motor imagery of the upper and lower limbs. A: Maps of consistent activations while subjects imagined movements of the upper (red) or lower (green) limbs. Note that movements of the lower limb include gait. Regions consistently activated by both types of movements are shown in yellow. B: Results of the subtraction analysis: regions with more consistent activity during motor imagery of upper limbs are shown in red and of lower limbs in green. C: Regions consistently activated while imagining gait movements. MI: motor imagery; SMG: supramarginal gyrus; PreC: precuneus; Pcl: paracentral lobule; SgR: subgyral region. See Fig. 2 for other conventions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

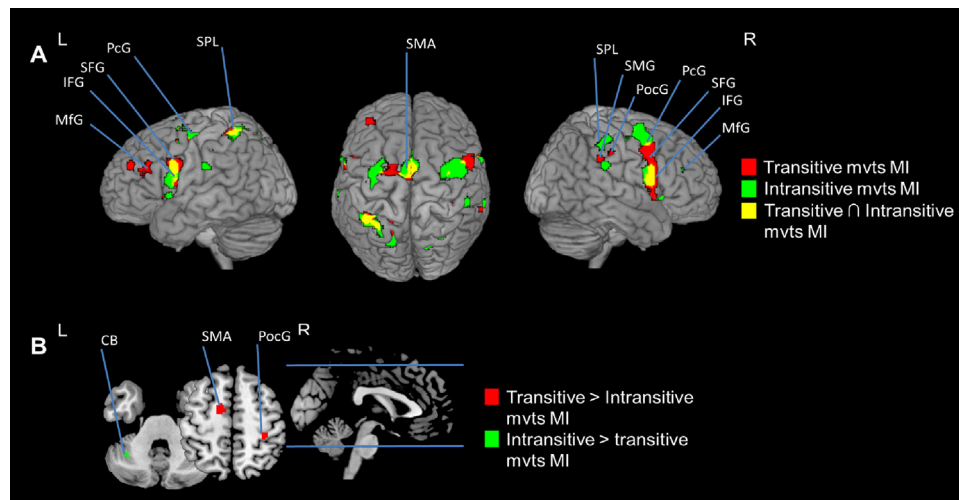


Fig. 4. Regions consistently activated during motor imagery of transitive and intransitive upper-limb movements. A: Maps of consistent activations while subjects imagined transitive (red) or intransitive (green) movements. Regions consistently activated by both types of movements are shown in yellow. B: Results of the subtraction analysis: regions with more consistent activity during motor imagery of transitive movements are shown in red. PcG: postcentral gyrus; SFG: superior frontal gyrus. See Figs. 2 and 3 for other conventions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 2

Peaks of consistent activations during motor imagery. IPC: inferior parietal cortex; HIP2/HIP3: intraparietal areas.

Location	Cytoarchitectonic location	MNI coordinates		
		x	y	z
General MI				
L cerebellar vermis		-2	-50	-6
L cerebellum (Lobule VI)		-32	-56	-30
L inferior frontal gyrus (p. opercularis)	44	-52	8	12
L inferior frontal gyrus (p. opercularis)	44	-56	8	24
L inferior parietal lobule	hIP3	-38	-42	50
L insula lobe (anterior)		-28	16	8
L insula lobe (anterior)		-34	24	0
L middle frontal gyrus	9	-40	36	28
L precentral gyrus	6	-26	-2	58
L precentral gyrus	6	-50	-2	42
L putamen		-26	-2	4
L SMA	6	-2	2	58
L superior parietal lobule	7A	-20	-66	54
L superior parietal lobule	7A	-26	-58	58
L supramarginal gyrus	IPC (PF)	-54	-36	26
L supramarginal gyrus	IPC (PF)	-60	-32	32
L supramarginal gyrus	IPC (Pfp)	-62	-24	28
L thalamus		-10	-16	4
R cerebellum (Lobule VI)		32	-62	-28
R cerebellum (Lobule VI)		34	-56	-30
R inferior frontal gyrus (p. opercularis)	44	58	10	14
R inferior frontal gyrus (p. opercularis)	44	50	8	4
R insula lobe (anterior)		40	18	0
R middle frontal gyrus	6	32	0	54
R middle frontal gyrus	6	48	-2	56
R middle frontal gyrus	9	40	38	22
R precentral gyrus	6	56	2	44
R precentral gyrus	44	54	8	32
R precentral gyrus	44	46	4	40
R putamen		26	0	2
R superior parietal lobule	7PC	26	-56	64
R superior parietal lobule	7A	26	-62	50
R supramarginal gyrus	hIP2	46	-36	44
R supramarginal gyrus	IPC (PF)	60	-38	34

only found in left hemisphere), PcG, superior frontal gyrus (SfG), MfG, and SMA. Consistent activations in the left SPL, IPL, anterior insula, and putamen, and in the right SMG, were also found. Results for MI of intransitive movements showed consistent bilateral activations in the IFG, including the pars opercularis, PcG, MfG, SPL, SMG, and SMA, left hemisphere activation in the CB (lobule VI), IPL, thalamus, and putamen, and right hemisphere activation in the middle cingulate cortex (MCC), pallidum, PocG, rolandic operculum and anterior insula. The conjunction between the two ALE maps (see Fig. 4; Table 4) revealed common and consistent bilateral activations in the IFG, including the pars opercularis, IPL, PcG, SMA, left SPL, putamen, and right MfG. When directly assessing differences due to transitivity with a subtraction analysis (see Fig. 4; Table 4), more consistent activations were found during MI of transitive movements in the left SMA, and right PocG. The inverse comparison revealed more consistent activations in the left CB (lobule VII a Crus I) during intransitive MI.

The type of movement, and specifically the «non-lateralization» of the movement, is in part responsible for the «non-lateralization» of the premotor cortex as shown by Szameitat et al. (2007). The use of the dominant vs. non-dominant hand would not produce any difference of activation, however, the complexity of the movement and his signification would lead to a difference. This difference of activation would also be applicable to the parietal cortex. Indeed, one possibility to explain the lateralization of the IPL in the results would be the methods used in the studies included. Task requiring more skills imply a greater activation of inferior region of the parietal cortex, including a greater activation of the inferior IPL. Simple grasping tasks then imply a greater activation of posterior IPL and the junction between the IPL and SPL. In the meta-analysis, studies having complex movement tasks are in minority what could in part explain this greater activation bilateral of the SPL compared to a unilateral activation of the IPL. Moreover, this over-representation of simple tasks could be responsible for the incapacity to discriminate ipsi- and contra-lateral activity of the SPL.

3.3.2. MI of the lower limb

The ALE meta-analysis for the lower-limb MI (see Fig. 3; Table 3) showed consistent activations in the SMA and CB (lobule VI bilaterally, left lobules V, I–IV right lobule VII Crus I) bilaterally, left activations in the paracentral lobule, SMG, SPL, PreC, and putamen, and

Table 3
Peaks of consistent activations during motor imagery of upper and lower-limb movements, transitive and intransitive movements and gait. See Table 2 for conventions.

Location	Cytoarchitectonic location	MNI coordinates		
		x	y	z
Upper-limb MI				
L cerebellum (Lobule VI)		-34	-54	-30
L inferior frontal gyrus (p. opercularis)	44	-52	6	12
L inferior frontal gyrus (p. triangularis)	45	-42	34	26
L inferior parietal lobule	2	-40	-42	50
L insula lobe (anterior)	44	-44	8	4
L insula lobe (anterior)		-30	16	6
L middle frontal gyrus		-26	-2	56
L precentral gyrus	6	-38	0	50
L precentral gyrus	6	-34	-16	54
L precentral gyrus	44	-56	6	28
L precentral gyrus	6	-52	-4	42
L precuneus	7A	-14	-58	60
L putamen		-24	0	2
L SMA	6	-2	2	58
L superior parietal lobule	7A	-18	-66	54
L supramarginal gyrus	IPC (PFcm)	-52	-34	24
L supramarginal gyrus	IPC (PF)	-60	-32	32
L supramarginal gyrus	IPC (Pfp)	-64	-24	28
R cerebellum (lobule VI)		32	-58	-28
R claustrum		30	20	-2
R inferior frontal gyrus (p. opercularis)	44	56	10	12
R inferior frontal gyrus (p. opercularis)	44	54	10	22
R insula lobe (anterior)		38	18	0
R middle cingulate cortex	6	6	16	44
R middle frontal gyrus	6	32	-2	56
R middle frontal gyrus	44	44	6	52
R pallidum		24	2	2
R postcentral gyrus	IPC (PFt)	52	-24	40
R postcentral gyrus	2	50	-30	52
R precentral gyrus	44	46	4	42
R precuneus	7A	14	-60	62
R superior parietal lobule	7A	28	-62	50
R superior parietal lobule	7P	14	-70	50
R superior parietal lobule	7PC	26	-56	64
R supramarginal gyrus	2	38	-36	44
R supramarginal gyrus	IPC (PF)	66	-32	28
R supramarginal gyrus	IPC (PF)	60	-36	34
Transitive upper-limb MI				
L inferior frontal gyrus (p. opercularis)	44	-52	6	12
L inferior frontal gyrus (p. triangularis)	45	-44	30	24
L inferior parietal lobule	hIP3	-38	-42	46
L inferior parietal lobule	7PC	-40	-46	60
L insula lobe (anterior)		-30	18	4
L middle frontal gyrus		-38	46	28
L precentral gyrus	3b	-52	6	30
L precentral gyrus	6	-38	0	48
L putamen		-20	6	6
L SMA	6	-4	0	60
L superior frontal gyrus	6	-24	-6	60
L superior parietal lobule	7PC	-32	-52	60
L superior parietal lobule	7A	-16	-58	60
R cingulate gyrus		24	40	-6
R inferior frontal gyrus (p. opercularis)	44	54	10	12
R inferior frontal gyrus (p. opercularis)	44	54	10	22
R postcentral gyrus	9	34	-34	52
R postcentral gyrus	IPC (PFt)	52	-24	40
R precentral gyrus	6	52	8	44
R middle frontal gyrus	6	28	-4	56
R supramarginal gyrus	IPC (PF)	60	-36	34
Intransitive upper-limb MI				
L cerebellum (lobule VI)		-34	-52	-30
L inferior frontal gyrus (p. opercularis)	44	-44	10	4
L inferior frontal gyrus (p. opercularis)	44	-58	8	20
L inferior parietal lobule	2	-40	-42	50
L middle frontal gyrus	6	-28	0	56
L precentral gyrus	6	-34	-16	54
L precentral gyrus	6	-38	0	50
L putamen		-26	0	2
L SMA	6	0	2	58
L SMA	6	-6	8	44
L superior parietal lobule	7A	-18	-66	54
L superior parietal lobule	7A	-28	-58	58

Table 3 (Continued)

Location	Cytoarchitectonic location	MNI coordinates		
		x	y	z
L superior parietal lobule	7PC	−30	−52	62
L supramarginal gyrus	IPC (Pfp)	−64	−22	28
L thalamus		−16	−10	8
R claustrum		30	20	0
R inferior frontal gyrus (p. opercularis)	44	56	8	20
R insula lobe (anteior)		38	18	0
R middle cingulate cortex	6	6	16	44
R middle frontal gyrus	6	34	0	56
R middle frontal gyrus	6	42	4	54
R middle frontal gyrus	9	40	38	22
R pallidum		24	0	0
R postcentral gyrus	2	50	−30	52
R precentral gyrus	44	44	4	40
R precentral gyrus	6	40	−12	52
R rolandic operculum	44	58	8	14
R superior parietal lobule	7A	28	−62	50
R superior parietal lobule	7P	14	−70	50
R supramarginal gyrus	hIP2	48	−36	44
R supramarginal gyrus	IPC (PF)	68	−32	28
Lower-limb MI				
L cerebellum (lobule VI)		−30	−54	−34
L cerebellum		−12	−36	−32
L cerebellum (lobule I–IV)		−10	−36	−24
L cerebellum (lobule V)		−6	−50	−8
L middle frontal gyrus	6	−28	−6	42
L paracentral lobule	6	−14	−12	66
L precuneus	7P	−12	−70	60
L putamen		−24	−2	8
L superior parietal lobule	7A	−24	−70	52
L supramarginal gyrus	IPC (PF)	−60	−38	30
R cerebellum (lobule VI)		30	−62	−28
R cerebellum (lobule VI)		34	−52	−32
R cerebellum (lobule VIIa crus I)		44	−50	−32
R cingulate gyrus	31	26	−42	36
R middle frontal gyrus	9	42	40	30
R middle frontal gyrus	6	38	0	62
R SMA	6	2	−4	64
R SMA	6	10	−18	70
R SMA	6	12	−10	70
Gait MI				
L cerebellum (lobule VI)		−30	−54	−34
L cerebellum		−12	−36	−32
L cerebellum (lobule I–IV)		−10	−36	−24
L cerebellum (lobule V)		−6	−50	−8
L middle frontal gyrus	6	−28	−6	42
L paracentral lobule	6	−14	−12	66
L putamen		−26	−2	10
L SMA	6	−6	−4	68
L superior parietal lobule	7A	−24	−70	52
R cerebellum (lobule VI)		30	−62	−28
R cerebellum (lobule VI)		34	−52	−32
R cerebellum (lobule VII a crus I)		44	−50	−32
R cingulate gyrus	31	26	−42	36
R claustrum		30	20	6
R middle frontal gyrus	9	42	40	30
R middle frontal gyrus	6	38	0	62
R SMA	6	2	−4	64
R SMA	6	10	−18	70
R SMA	6	12	−10	70
R superior parietal lobule	7A	22	−56	66

right MfG. Focusing on gait (see Fig. 3; Table 3), consistent bilateral activations were measured for the SMA, CB (lobule VI bilateral, left lobule I–IV, right lobule VII Crus I), and SPL with left activation in the paracentral lobule and putamen, and right activation in the MfG.

3.3.3. Comparing upper and lower-limb MI

Conjunction between the ALE maps of upper and lower-limb MI (see Fig. 3; Table 4) revealed consistent activations bilaterally

in the SMA, SMG, and CB (lobule VI), in the left IFG (including pars opercularis), IPL, SPL, anterior insula, and putamen, and in the right MfG. Contrasting both modalities of MI (see Fig. 3; Table 4) showed that upper-limb MI was associated with more consistent activation in left IFG (pars opercularis) and subgyral region while lower-limb MI was associated with more consistent activation in the right SMA and left CB (lobules I–IV and VII a Crus I).

Table 4

Peaks of consistent activations for various conjunction and subtraction analyses. See Table 2 for conventions.

Locations	Cytoarchitectonic location	MNI coordinates		
		x	y	z
Upper \cap lower-limb MI				
L cerebellar vermis		–2	–50	–8
L cerebellum (lobule VI)		–32	–54	–32
L inferior frontal gyrus (p. opercularis)	44	–52	10	2
L inferior parietal lobule	2	–42	–46	54
L insula lobe (anterior)		–28	16	8
L putamen		–26	–2	6
L SMA	6	0	–2	62
L superior parietal lobule	7A	–22	–68	52
L supramarginal gyrus	IPC (PF)	–60	–34	32
R cerebellum (lobule VI)		30	–62	–28
R middle frontal gyrus	6	36	0	60
R middle frontal gyrus	6	28	–4	52
R supramarginal gyrus	hIP2	48	–36	42
Upper > lower-limb MI				
L IFG (pars opercularis)	44	–48	8	18
L subgyral	6	–14	2	56
Lower > upper-limb MI				
L cerebellum		–11	–34	–31
L cerebellum (lobule I–IV)		–11	–38	–29
L cerebellum (lobule VII a crus I)		–31	–56	–39
L cerebellum		–28	–52	–38
R SMA	6	11	–18	71
R SMA	6	12	–12	69
Transitive \cap intransitive mvts MI				
L inferior frontal gyrus (p. opercularis)	44	–52	6	12
L inferior parietal lobule	hIP3	–38	–42	50
L precentral gyrus	6	–26	–2	58
L precentral gyrus	44	–56	6	28
L precentral gyrus	6	–38	0	50
L putamen		–22	4	4
L SMA	6	–2	2	60
L superior parietal lobule	7PC	–30	–54	60
R inferior frontal gyrus (p. opercularis)	44	56	8	12
R inferior frontal gyrus (p. opercularis)	44	56	10	22
R inferior parietal lobule	hIP2	42	–38	46
R middle frontal gyrus	6	30	–4	56
R precentral gyrus	6	46	8	–48
Transitive > intransitive mvts MI				
L SMA	6	–14	–4	58
L SMA	6	–12	–8	54
R postcentral gyrus	3	33	–33	53
Intransitive > transitive mvts MI				
L cerebellum (Lobule VII a Crus I)		–37	–54	–32
Kinesthetic \cap visual MI				
L insula lobe (anterior)		–42	8	4
L precentral gyrus	6	–42	–8	54
L putamen		–28	–6	10
L SMA	6	–2	4	68
L SMA	6	–6	0	64
R putamen		24	8	4
Kinesthetic > visual MI				
No cluster found				
Visual > kinesthetic MI				
No cluster found				
Pure MI \cap LJT				
L inferior parietal lobule	2	–38	–38	48
L middle frontal gyrus	6	–26	–4	56
R middle frontal gyrus	6	30	–4	56
Pure MI > LJT				
L SMA	6	0	–6	64
L SMA	6	0	8	60
L SMA	6	–1	–6	70
L supramarginal gyrus	IPC (PFcm)	–52	–42	24
L supramarginal gyrus	IPC (PFcm)	–46	–40	24
R SMA	6	4	–1	59
R SMA	6	1	–8	62

Table 4 (Continued)

Locations	Cytoarchitectonic location	MNI coordinates		
		x	y	z
LJT > Pure MI				
R middle frontal gyrus	6	32	4	58
R postcentral gyrus	2	30	-48	62
R postcentral gyrus	2	32	-44	62
R postcentral gyrus	3b	30	-40	62
R superior parietal lobule	7A	26	-60	70
R superior parietal lobule	7PC	32	-53	70
Pure MI \cap motor sequence MI				
L inferior frontal gyrus (p. opercularis)	44	-58	10	12
L inferior parietal lobule	2	-40	-44	50
L insula lobe (anterior)	44	-44	8	4
L precentral gyrus	6	-28	-4	56
L precentral gyrus	6	-34	-16	54
L precentral gyrus	44	-56	8	28
L putamen		-22	4	4
L SMA	6	-2	2	58
L superior parietal lobule	7A	-32	-52	60
R inferior frontal gyrus (p. opercularis)	44	56	10	22
R inferior frontal gyrus (p. opercularis)	44	58	10	12
R inferior parietal lobule	hIP2	42	-38	46
R middle frontal gyrus	6	30	-4	56
R precentral gyrus	44	44	6	50
Pure MI > motor sequence MI				
No cluster found				
Motor sequence MI > Pure MI				
L inferior parietal lobule	IPC (PF)	-46	-46	54
L inferior parietal lobule	2	-45	-41	49
L middle frontal gyrus	6	-24	2	55
L postcentral gyrus	OP4	-64	-10	18
L putamen		-27	-2	0
L superior parietal lobule	7A	-18	-68	53
L superior parietal lobule	7A	-17	-66	48
R inferior parietal lobule	hIP2	40	-44	44
R middle cingulate cortex		10	16	40
R middle frontal gyrus	6	28	7	56
R precentral gyrus	6	34	-8	54
R precuneus	7P	14	-72	48
R supramarginal gyrus	hIP2	49	-36	39
R supramarginal gyrus	IPC (PF)	54	-34	46
R superior parietal lobule	7P	22	-71	48

3.4. The modality of MI

Kinesthetic MI consistently activated bilaterally the SMA, IPL, PcG, and CB (left lobule VII, right lobule VI), left IFG (including pars opercularis and triangularis), SMG, temporal pole, putamen, and anterior insula, and right Rolandic operculum, angular gyrus, PreC and pallidum (see Fig. 5; Table 5). Results for visual MI showed consistent activations in bilateral SMA, left PcG, lingual gyrus, and CB (lobule V), and right MfG and PocG (see Fig. 5; Table 5). Conjunction between kinesthetic and visual MI revealed consistent activations in the left PcG, SMA, and anterior insula and bilaterally in the putamen (see Fig. 5; Table 4). Contrasting the two modalities of MI did not reveal any significant difference between ALE maps.

3.5. The nature of the MI task

3.5.1. LTJ task vs. Pure MI

Next, we compared the LJT (implicit MI task) to the Pure MI task (explicit MI task) (see Fig. 6; Table 5). As the proportion of studies on lower limb/gait MI was very different for the LJT and the Pure MI (no study on lower-limb movement for the LJT vs. around 1/3 for Pure MI), we decided to only look at studies on MI of the upper limb for both types of tasks. The LJT consistently activated regions

in bilateral SPL, PcG, left IPL, and CB (lobule VII), in addition to right MfG and putamen. Pure MI consistently activated regions in bilateral SMA, PcG, IFG (including pars opercularis but only left pars triangularis), IPL, SPL, and PocG, in the left SMG and MfG, and in the right caudate and CB (lobule VI). The conjunction of the LJT and Pure MI showed consistent activation in bilateral MfG and left IPL. The LJT consistently activated more right SPL, MfG, and PocG while Pure MI consistently activated more bilateral SMA and the left SMG (see Fig. 6; Table 4).

3.5.2. MI of motor sequence vs. Pure MI

MI of motor sequences (simple or complex) consistently activated bilaterally the SMA, MfG, IFG (including pars opercularis), SMG, SPL, and putamen, in addition to left PcG, IPL, thalamus, and CB (lobules VI and VII), and right MCC, PocG, angular gyrus and anterior insula (see Fig. 6; Table 5). The conjunction of MI of motor sequence and Pure MI showed bilateral activations in the SMA and IFG (including pars opercularis), in the left PcG, IPL, SPL, anterior insula and putamen, in addition to right activations in the MfG and IPL. MI of motor sequence had more consistent activation in bilateral MfG and IPL, SPL, left putamen, PocG and right PcG, PreC, SMG and MCC, while the inverse comparison yielded no significant difference (see Fig. 6; Table 4).

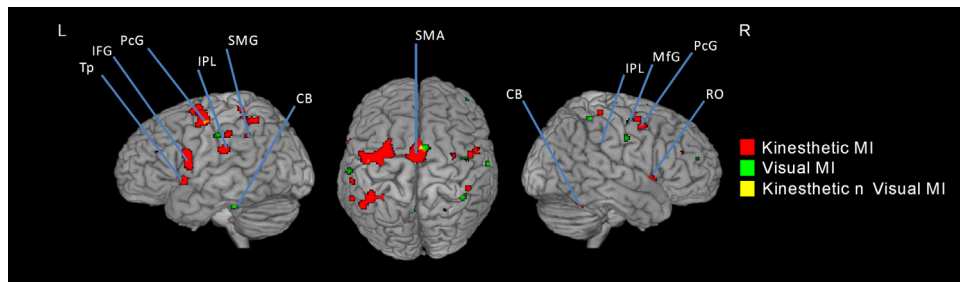


Fig. 5. Regions consistently activated during kinesthetic and visual motor imagery. A: Maps of consistent activations while subjects used kinesthetic (red) or visual (green) motor imagery. Regions consistently activated by both types of movements are shown in yellow. Tp: temporal pole; RO: rolandic operculum. See Figs. 2–4 for other conventions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

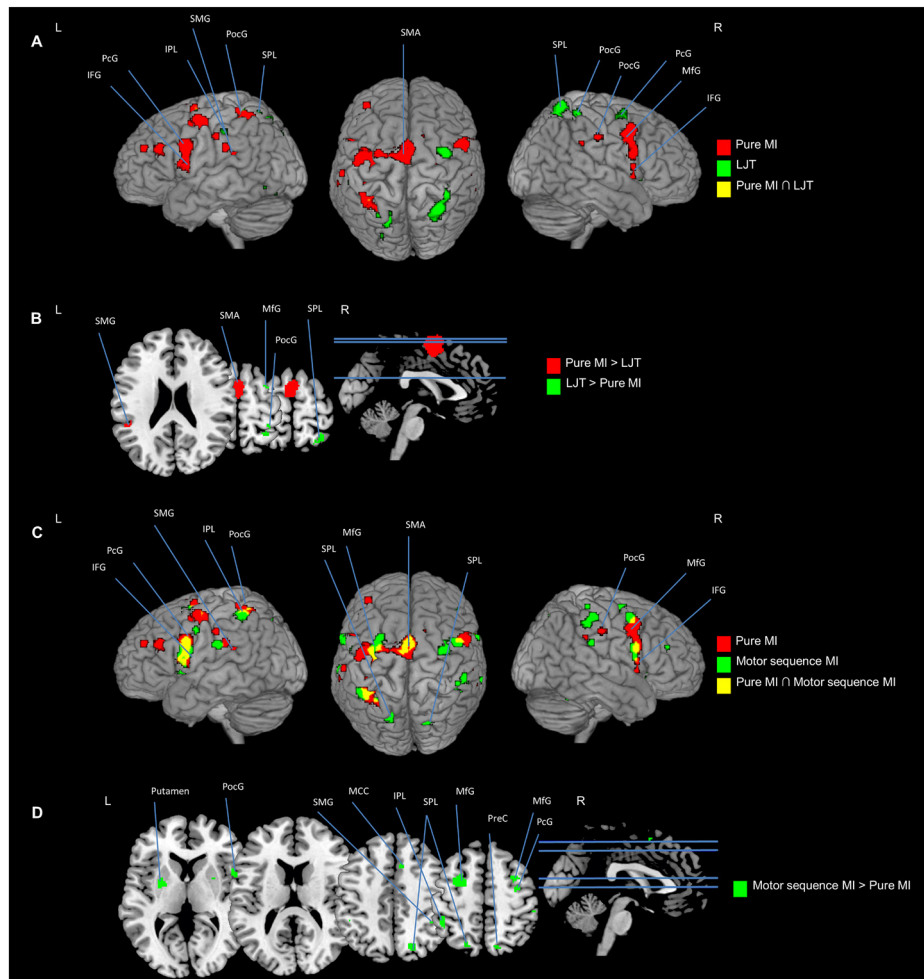


Fig. 6. Regions consistently activated during Pure motor imagery, motor imagery of motor sequences and the laterality judgment task. A: Maps of consistent activations during Pure motor imagery tasks (red) or the laterality judgment task (LJT) (green). Regions consistently activated by both types of movements are shown in yellow. B: Results of the subtraction analysis: regions with more consistent activity during Pure motor imagery are shown in red and during the LJT in green. C: Maps of consistent activations during Pure motor imagery tasks (red) or tasks using imagery of motor sequences (green). Regions consistently activated by both types of movements are shown in yellow. D: Results of the subtraction analysis: regions with more consistent activity during motor imagery of motor sequences than Pure motor imagery are shown in green. See Fig. 2 for conventions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 5

Peaks of consistent activations during kinesthetic, visual motor imagery, pure motor imagery, the laterality judgment task (LJT) and imagery of motor sequences. See Table 2 for conventions.

Location	Cytoarchitectonic location	MNI coordinates		
		x	y	z
Kinesthetic MI				
L cerebellum (Lobule VIIa Crus I)		−32	−60	−30
L inferior frontal gyrus (p. opercularis)	44	−52	8	10
L inferior frontal gyrus (p. opercularis)	44	−58	8	20
L inferior frontal gyrus (p. triangularis)	45	−38	36	26
L inferior parietal lobule	2	−40	−42	50
L inferior parietal lobule	40	−50	−52	56
L insula lobe (anterior)	44	−44	8	2
L precentral gyrus	6	−28	−2	58
L putamen		−26	−2	4
L SMA	6	−2	2	60
L supramarginal gyrus	IPC (Pfp)	−62	−22	26
L temporal pole	22	−56	12	−4
R angular gyrus	7A	26	−64	48
R cerebellum (Lobule VI)		32	−62	−30
R inferior parietal lobule	hIP2	40	−44	48
R pallidum		26	−2	0
R precentral gyrus	6	54	2	50
R precuneus	7P	20	−70	46
R rolandic operculum	44	50	8	2
R SMA	6	6	10	48
Visual MI				
L cerebellum (lobule V)		−28	−36	−28
L lingual gyrus	18	−12	−68	−4
L precentral gyrus	6	−38	−6	46
L SMA	6	0	4	68
R middle frontal gyrus	6	42	−8	54
R postcentral gyrus	3b	40	−32	52
R SMA	6	6	4	68
R SMA	6	12	2	62
LJT				
L cerebellum (Lobule VIIa Crus I)		−38	−54	−30
L inferior parietal lobule	2	−50	−28	44
L postcentral gyrus	2	−40	−36	50
L superior frontal gyrus	6	−24	−2	54
L superior parietal lobule	7A	−18	−66	54
R middle frontal gyrus	6	34	0	56
R postcentral gyrus	1	34	−40	62
R postcentral gyrus	3b	34	−34	56
R putamen		28	20	0
R superior frontal gyrus	11	30	46	−26
R superior parietal lobule	7PC	28	−54	66
R superior parietal lobule	7A	26	−62	56
Pure MI				
L inferior frontal gyrus (p. opercularis)	44	−52	8	12
L inferior frontal gyrus (p. triangularis)	45	−44	30	26
L inferior parietal lobule	2	−38	−44	48
L middle frontal gyrus	6	−28	−6	58
L middle frontal gyrus	9	−38	46	28
L postcentral gyrus	5	−42	−42	66
L precentral gyrus	6	−40	−4	52
L precentral gyrus	44	−52	8	32
L SMA	6	−2	2	58
L superior parietal lobule	7PC	−38	−48	60
L superior parietal lobule	7A	−26	−60	54
L supramarginal gyrus	PFcm	−50	−38	24
L supramarginal gyrus	IPC (PF)	−62	−30	30
R caudate nucleus		18	14	6
R cerebellum (lobule VI)		32	−56	−24
R inferior frontal gyrus (p. opercularis)	44	54	10	24
R inferior frontal gyrus (p. opercularis)	44	50	8	4

Table 5 (Continued)

Location	Cytoarchitectonic location	MNI coordinates		
		x	y	z
R inferior frontal gyrus (p. opercularis)	44	50	10	10
R inferior frontal gyrus (p. opercularis)	44	56	10	10
R inferior parietal lobule	2	40	−36	46
R postcentral gyrus	2	56	−22	38
R precentral gyrus	44	52	10	46
R SMA	6	4	8	50
R superior frontal gyrus	6	28	−6	58
Motor sequence MI				
L cerebellum (lobule VI)		−34	−54	−32
L cerebellum (lobule VIIa Crus I)		−32	−58	−32
L inferior frontal gyrus (p. opercularis)	44	−44	10	4
L inferior parietal lobule	2	−42	−42	50
L middle frontal gyrus	6	−28	−2	56
L precentral gyrus	6	−34	−18	52
L precentral gyrus	44	−60	8	20
L putamen		−26	0	2
L SMA	6	0	4	58
L superior parietal lobule	7A	−18	−68	52
L supramarginal gyrus	IPC (PFop)	−64	−22	28
L thalamus		−16	−10	8
R angular gyrus	7A	26	−64	48
R inferior frontal gyrus (p. opercularis)	44	56	8	22
R inferior frontal gyrus (p. opercularis)	44	58	10	12
R insula lobe (anterior)		36	20	−10
R middle cingulate cortex	6	6	16	42
R middle frontal gyrus	44	44	6	52
R middle frontal gyrus	6	32	−4	52
R middle frontal gyrus	9	40	38	22
R pallidum		24	2	2
R postcentral gyrus	2	50	−30	52
R superior parietal lobule	7P	16	−70	50
R supramarginal gyrus	hIP2	46	−38	44

4. Discussion

By combining the results from previous fMRI and PET studies, our general ALE meta-analysis provides a quantitative map of the brain regions involved in MI. Further meta-analyses offer evidence that certain methodological variables can modulate which parts of the general MI network is recruited.

4.1. General MI

By including all the studies for our main meta-analysis, we sought to identify the general network of MI. This ALE meta-analysis revealed that a large fronto-parietal network is involved when we imagine ourselves moving. In addition we found that MI consistently activates subcortical and cerebellar regions. Consistent with the view that MI is the activation of motor programs without motor output, our results showed that several cortical areas playing a role during actual motor behaviors are also consistently activated during MI.

4.1.1. Premotor cortex

Premotor regions such as the IFG and SMA, known to be involved during motor execution, were found to be consistently activated during MI. Work in primates has shown that the ventral and dorsal premotor cortices (vPM/dPM) play important roles in the planning, preparation and execution of motor acts (see (Hoshi and Tanji, 2007) for a review). Imagined and executed movements often

require a similar amount of time to be performed (Guillot and Collet, 2005) suggesting that they are produced through analogous computational steps in the brain. This implies that imagined movements also include a planning/preparation phase before being simulated. Our results, showing consistent activation in premotor areas are in line with this assumption. Moreover, the fact that strokes to the left frontal lobe can impair performance in a MI task (Johnson, 2000) whereas MI capabilities are preserved in stroke patients with an intact premotor cortex (Johnson et al., 2002b) also supports the functional role of the premotor cortex during MI. The SMA, another region of the premotor cortex, was also shown to be consistently activated during MI. The SMA has been proposed as playing a role in complex condition–action associations (where an action Y is prompted by a condition X), self/internally generated movements or actions that require sequences of movements (Nachev et al., 2008). Others (e.g., Leek and Johnston, 2009) have put forward the possibility that the SMA is involved in visuo-spatial transformations such as those required during mental rotation tasks (of objects). Indeed, these tasks can sometimes be completed by using a motor simulation approach and the SMA seems to play an important role when this is the case (Zacks, 2008). Thus, the consistent activation within the SMA during MI found in the general meta-analysis could be related to the processing of complex information related to movement initiation/sequence and/or visuo-spatial transformation. The exact nature of the role of the SMA during MI may depend on the type of MI performed. For example, Pure MI instructions (imagine doing a movement) may be associated with motor programming/planning processes whereas the IJT (implicit MI instructions) in which the visual presentations of the limb have to be rotated could recruit the SMA for visuo-spatial transformation purposes. However, this hypothesis still needs to be tested.

4.1.2. Parietal cortex

Parietal regions such as the IPL, the SMG and the SPL were also found to be consistently activated during MI. In line with those results, which suggest an important role of the parietal cortex during MI, deficits in MI tasks have been observed in patients with damage to this region (Sirigu et al., 1996) and after virtual lesions to the SMG in healthy adults (Pelgrims et al., 2009). The parietal cortex is an important sensory integration hub and its different subregions projecting to various brain areas including the premotor and motor cortex play important roles during motor execution (e.g., see Fogassi and Luppino, 2005; Wise et al., 1997). Indeed, the central role of the parietal cortex in voluntary motor behaviors is apparent in patients with apraxia after parietal damage (generally to the left hemisphere). These patients show important motor deficits when, for instance, they are asked to imitate or when they have to produce actions (often pantomimes) on verbal command even if they do not show any proper motor or sensory deficit (Heilman and Rothi, 1993). Furthermore there is some evidence that apraxic patients are impaired on MI tasks (Buxbaum et al., 2005; Ochipa et al., 1997) possibly because both pantomimes and MI rely on internal models and stored representations in the parietal lobes ((Buxbaum et al., 2005); but see (Goldenberg, 2009; Sunderland et al., 2012) for a conflicting explanation for apraxia).

The parietal cortex is especially important for the online control of movements when visual information is available. Indeed, the posterior parietal cortex (PPC) which includes the IPL and SPL, is involved in visuomotor transformation processes (Torres et al., 2010) and is very important in visually guided motor tasks, particularly the left parietal cortex (Mutha et al., 2011). MI rarely involves the processing of visual information (note the exception of imagined movements that have to be done towards a real object) hence consistent activation within these regions during MI is probably not related the visual guidance of the imagined movement. The role of

the parietal cortex has been recently extended beyond its role in visually guided motor tasks to other higher cognitive and motor functions (Culham and Valyear, 2006; Fogassi and Luppino, 2005). For example, fMRI data have revealed that the SPL is involved in reaching without visual input (Filimon et al., 2009), and in updating and maintaining the postural representation of the upper limb when visual input is absent (Parkinson et al., 2010). Furthermore, the left parietal cortex has been linked to motor attention processes (i.e., preparation and redirection of movements and movement intentions; (Rushworth et al., 2003)). The PPC also seems to code for the goals of actions (Fogassi et al., 2005; Tunik et al., 2007). Hence, the consistent activations within the parietal cortex observed during MI are likely to reflect such higher cognitive functions. Indeed, imagining a movement would require one to access the goal of the movement (e.g., reaching to drink from a cup), prepare the simulated movement and while imagining it, update its postural representations.

There is evidence that the IPL contains several motor representations (Cooke et al., 2003) organized somatotopically (Rozzi et al., 2008). Moreover, there is a large body of evidence that these representations are “activated” not only during one’s voluntary movements but also when one observes someone else’s actions (Caspers et al., 2010; Chong et al., 2008; Gazzola and Keysers, 2009; Grosbras et al., 2011; Héту et al., 2011; Turella et al., 2009). Indeed, the parietal cortex (especially the anterior intraparietal area (AIP) and the IPL) is the proposed parietal node of the fronto-parietal mirror neuron system responsible for the correspondence between observed and executed movements (Cattaneo and Rizzolatti, 2009; Grafton, 2009; Rizzolatti and Craighero, 2004). Therefore, whereas motor representations in the parietal cortex are activated from external (visual) inputs during action observation, the consistent activation we have found in the parietal cortex during MI may correspond to the internal recruitment of these motor representations.

Work on primates has shown that several of the fronto-parietal regions identified by our meta-analysis are connected to each other and form functional ensembles active during motor execution (e.g., see reviews by (Rizzolatti and Luppino, 2001; Tanji and Hoshi, 2008; Wise et al., 1997) (connection between IPL and IFG); (Tanji and Hoshi, 2008; Wise et al., 1997) (connection between SPL and dorsal premotor cortex (PMd/BA6)). A study by Solodkin et al. (2004) in humans has shown that these regions are functionally connected to each other during motor execution but also during kinesthetic MI. The importance of the left PMd, IPL and SPL in the functional network supporting MI was also recently shown using a conditional Granger causality approach (Gao et al., 2011). This same approach was used to highlight that the SMA is functionally connected to the IPL, SPL, PMd, primary somatosensory cortex (S1) and primary motor cortex during MI (Chen et al., 2009). These different results suggest that the fronto-parietal regions identified by our meta-analysis do not work in isolation but form a functional network during MI.

4.1.3. Outside the fronto-parietal regions

Our results also showed consistent activation within the basal ganglia, the putamen and pallidum, regions that have been linked to the selection of motor programs during motor execution (Grillner et al., 2005). In line with the importance of the basal ganglia during MI, patients suffering from Parkinson’s disease, which affects principally this region (Obeso et al., 2008), show several impairments on MI tasks (Frak et al., 2004; Helmich et al., 2007; Heremans et al., 2011). During motor behaviors, the basal ganglia receive input from several cortical areas as well as from the thalamus, also shown to be consistently activated during MI. Our meta-analysis also revealed that various parts of the CB such as the vermis and lobules VI and VII were consistently activated during MI. The CB, through its connections to the PPC, is involved in the execution of various types of

movements (Prevosto et al., 2010). In line with our findings, lesions to the CB are known to impair MI (Battaglia et al., 2006; Gonzalez et al., 2005; Grealy and Lee, 2011). Our results thus suggest that MI also relies on the processing of information in various regions outside of the fronto-parietal network of MI, regions that are known to play a role in motor execution. It therefore seems that MI is not restricted to the simple activation of motor representations within the premotor and parietal cortex but rather, much like during motor execution, requires further processing of these representations. This may include motor initiation and/or motor selection, probably supported by the basal ganglia, and motor control supported by the CB.

The theoretical view suggesting that MI is supported (at least in part) by the motor system (Crammond, 1997; Jackson et al., 2001; Jeannerod and Decety, 1995; Lotze and Halsband, 2006) has been the most influential in the recent years. This is not surprising as this proposition is both anatomically and computationally economic: why have a completely different network for simulating movements when we have a perfectly good one for executing them? This assumption is also deeply rooted in our personal experience of MI: anyone who tries to imagine an action can “feel” the similitude between the imagined and real movement. Our meta-analysis adds to the large empirical support for the shared neural network between MI and motor execution. It is important to note that because we did not include in our meta-analyses studies that focused on motor execution per se, we did not directly compare the networks supporting MI and motor execution. Several studies have demonstrated that MI and motor execution although sharing similar neural underpinning, do have some anatomical (e.g. (Deiber et al., 1998; Frak et al., 2004; Gerardin et al., 2000; Hanakawa et al., 2003; Higuchi et al., 2007)) and functional connectivity differences (Gao et al., 2011; Solodkin et al., 2004). Nevertheless, by combining the results from more than 80 experiments (from 75 papers) and showing that regions known to play a role during motor execution are consistently activated during MI, we provide strong evidence that MI is performed by accessing and processing motor representations in various parts of the motor system.

4.1.4. The case of the primary motor cortex

Interestingly, even though MI and motor execution seem to rely on similar structures, our study suggests that the primary motor cortex is not consistently activated during MI. This result is important as there is a lasting controversy surrounding the involvement of the primary motor cortex during MI (see (Lotze and Halsband, 2006; Madan and Singhal, 2012; Munzert et al., 2009; Sharma et al., 2006)). Several authors have fueled this debate by citing on the one hand some studies in which primary motor cortex activation was found during MI and on the other hand studies which did not, implicitly suggesting that an equivalent number of articles supported each position. As mentioned before, such qualitative evaluation of the neuroimaging literature may be misleading. Indeed, examining the 122 experiments (from 75 papers) considered in our study, only 22 (from 16 papers) reported primary motor cortex activation during MI (18%) (see Fig. 7; Supplementary Table 2). This shows that, quantitatively ($\chi^2(1) = 46.848, p < 0.001$), very few experiments have found primary motor cortex activity during MI and therefore previous reviews may in fact have overstated this controversy. Nonetheless, it is important to stress that our results do not demonstrate that the primary motor cortex is absolutely not involved during MI but simply that current fMRI and PET studies have not found consistent activation within the primary motor cortex. In fact, numerous transcranial magnetic stimulation (TMS) studies have provided strong evidence that MI can increase the excitability of the primary motor cortex (see (Loporto et al., 2012; Munzert et al., 2009) for reviews). This increase in excitability is assumed to be caused by activation of premotor (Loporto et al.,

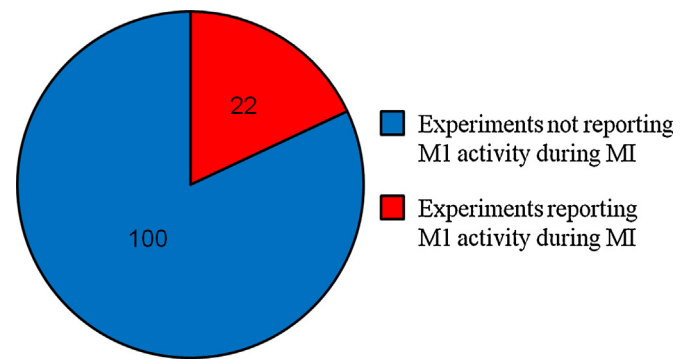


Fig. 7. Proportion of neuroimaging experiments on motor imagery where activity in the primary motor cortex (M1) was found.

2012) and/or parietal regions (Feurra et al., 2011) which project to M1. Increases in excitability without overt signs of activation measured with fMRI/PET are somewhat of a paradox. However, this situation is similar to what is reported in action observation/mirror neuron research where action observation is known to increase the excitability of the primary motor cortex even though there are very few evidence that it activates this region (see the commentary by (Taschereau-Dumouchel and Héту, 2012)). One possible reason for increases in the primary motor cortex excitability without primary motor cortex BOLD signal increase during MI or action observation is that current fMRI/PET technology is not sensitive enough to pick up the subtle changes in excitatory/inhibitory processes that can be assessed with TMS. Contrary to electroencephalography and TMS, which have good temporal resolution, fMRI and PET have difficulty measuring very rapid changes in brain activity. In fact, if any change in the primary motor cortex activity is actually produced during MI, it may be too rapidly suppressed for current fMRI/PET approaches to pick it up. In line with this possibility, Kasess et al. (2008) have recently found that the SMA exerts an inhibitory influence on the primary motor cortex during kinesthetic MI (see (Raffin et al., 2012) for similar results in amputees). In addition to this temporal resolution issue, changes in activity in the primary motor cortex may be quantitatively too small to be picked up by the fMRI/PET analysis methods (i.e., whole brain analysis) used in the studies reviewed here. One way to boost the sensitivity of fMRI techniques is by performing small volume corrections on regions of interest (ROI). Using such an approach, Sharma et al. (2008) have indeed found activity in the primary motor cortex during MI. The fact that most studies on MI (and all studies in our sample) have used a whole brain approach which is less sensitive than ROI analyses may explain why our meta-analysis did not reveal consistent activity in the primary motor cortex. Nevertheless it is important to point out that the participants in Sharma and colleagues' study were selected for their high MI capability. This suggests that individual differences could also explain why primary motor cortex activity is not consistently found during MI. Indeed, in some papers that reported no group activation in the primary motor cortex, single-subject analyses clearly showed primary motor cortex activity in some participants (Dechent et al., 2004; Gerardin et al., 2000). Examples of individual characteristics that could influence the quality of MI and hence its underlying brain activity are motor expertise (Chang et al., 2011; Milton et al., 2008), age (Personnier et al., 2010; Saimpont et al., 2010, 2009; Schuster et al., 2011; Skoura et al., 2009), sex (Schuster et al., 2011), and experience/practice (Guillot et al., 2008; Jackson et al., 2003; Lafleur et al., 2002; Malouin and Richards, 2010). The impact of these factors on the involvement of the primary motor cortex during MI still needs to be directly addressed by the scientific community.

Other methodological factors may also play a role in the presence/absence of primary motor cortex activity during motor imagery. First, there is evidence that the instructions given to the participants may exert such a modulating influence. TMS data suggest that kinesthetic MI can increase the primary motor cortex excitability more than visual MI (Fourkas et al., 2006) suggesting that the instructions on the modality of MI to perform may modulate the involvement of the primary motor cortex. However, in a fMRI study that specifically looked at the differences between kinesthetic and visual MI, both modalities activated the primary motor cortex when compared to a rest condition, and the direct comparison of the two MI modalities yielded no significant difference in primary motor cortex activity (Guillot et al., 2009). It is important to point out that in most other experiments reviewed here in which participants were instructed to use kinesthetic MI (20 out of 25), no primary motor cortex activation was found. Furthermore, none of our focused meta-analyses that looked at the regions involved in specific types of MI found consistent activity in the primary motor cortex. These different results greatly reduce the probability that activity in the primary motor cortex depends on the type of MI performed.

Turning our attention to the control of overt movement, MI is often described as the mental simulation of action *without* motor output. Thus, most researchers consider that if the participant's muscles are activated, he or she is *not* doing MI, or at least he/she is not doing it in the right way. The gold standard for controlling muscle activity is measuring the electromyographic (EMG) activity. However, acquiring reliable EMG data in a scanner is considerably complicated by the electromagnetic noise induced by the magnet. Hence, very few neuroimaging studies have controlled for muscle activity during MI (see (Bakker et al., 2008; deCharms et al., 2004) for studies which did record EMG during scanning sessions). It therefore remains possible that participants in studies where primary motor cortex activity is reported contracted their muscles. Other techniques to control for overt movements include visual inspection or the use of a recording glove (e.g., see (Sharma et al., 2008)). However, both approaches are only sensitive to movement *per se* and not to muscle activity without movement and are thus less reliable than EMG recording. Clearly, future research will need to use more rigorous methods to control for overt movement in order to specify the role of the primary motor cortex during MI.

4.2. MI for movements of different body parts

When visually comparing the maps of consistent activation produced by the general meta-analysis and the meta-analysis focused on MI of upper-limb movements, one can clearly see that both meta-analyses resulted in very similar networks. This is not surprising as the majority of experiments (54 out of 81) that were included in the general meta-analysis focused on this type of movement. In a similar way, our results also showed that lower-limb MI including gait and MI of gait *per se* showed striking similarities, most probably because of the important number of articles on gait within the lower-limb sample (11 out of 14 experiments). Interestingly however, MI of lower-limb movements including gait seems to rely on a very different cerebral network than MI of upper-limb movements. While imagining upper-limb movements showed large clusters of consistent activation in the premotor cortex including the IFG, MfG, and PcG, MI of lower limb mainly involved the SMA, CB, putamen, and parietal regions. This is in line with the presence of various upper-limb movement representations in the premotor cortex (Graziano, 2006). As for lower-limb MI, involvement of the CB is supported by data showing that atrophy of its anterior part (where we found consistent activation during lower-limb MI) can produce gait related impairments (see (Thach and Bastian, 2004)).

Mammalian locomotion is thought to rely on the activation, by commands coming from the midbrain and brainstem, of specific neural networks within the spinal cord called central pattern generators (CPG) (Kiehn, 2006). Furthermore, a recent study in humans using [¹⁸F]-FDG PET revealed that the mesial part of the primary motor and sensory cortices (which contains motor and sensory representations of the lower limbs), lingual, fusiform and parahippocampal gyri, occipital lobe, precuneus and the CB were activated during real locomotion (la Fougere et al., 2010). When compared to our results, these findings suggest that contrary to real locomotion, gait MI relies on the SMA, the PPC and putamen probably because MI requires more motor programming than real locomotion. One interpretation for this increased need for motor programming during MI is proposed by la Fougere et al. (2010). They suggest that MI of gait is more similar to gait modulation (e.g., transition phases from initiation to actual walking to termination), which implicates the SMA and necessitates processing by intermediate regions such as the basal ganglia, than actual locomotion, which is more automatic and during which motor commands are directly sent from the primary motor cortex to the CPG. The mesencephalic locomotor region composed of the pedunculopontine nucleus and cuneiform nucleus are also known to be involved during actual gait (Alam et al., 2011). The absence of consistent midbrain activity during MI of gait in our meta-analysis may be partially explained by a recent fMRI study which showed that activity in the cuneiform and dorsal pedunculopontine nuclei during MI of gait is related to changes in the speed of gait (slow vs. fast) instead of gait *per se* (MI vs. visual imagery) (Karachi et al., 2012). Current fMRI and PET techniques can hardly be used to study brain activity during actual locomotion as it cannot be performed in a scanner. This has led many neuroimaging researchers to use MI of gait as a proxy for actual locomotion. However, this approach relies on the assumption that MI and motor execution of gait are nearly identical. Very few studies have directly tested this hypothesis (see (la Fougere et al., 2010)). Although we did not compare MI and gait execution, our meta-analysis provides a map of the cerebral regions that showed consistent activation during MI of gait. When compared to the results of one of the few studies which studied actual gait (la Fougere et al., 2010), our findings suggest that there seem to be differences between MI and actual gait. This observation should however be verified in future studies looking at the similarities and differences between MI and motor execution of human locomotion.

Several of our everyday actions involve an object (transitive movements). To be performed appropriately, transitive movements not only require the activation of a motor program but also need the processing of the object's representation (size/shape, location in space, etc.). We also produce numerous actions that are not performed with or directed at objects (intransitive movements), for example when we raise our hand to answer a question or rotate our wrists during stretching exercises. One might argue that such actions are somewhat less complex than transitive actions as their execution does not require the processing of an object's representation. By directly comparing MI of transitive and intransitive movements, we showed that both types of movements involved the fronto-parietal network mentioned before: IFG, PcG, SMA, MfG, IPL, and SPL. These regions could thus contain the motor representations necessary for the programming of the upper-limb movements to be imagined. Activations of greater consistency for transitive vs. intransitive movements were mainly found in the frontal section of the MI network (SMA), suggesting that these regions may process the properties of the imaginary object. More consistent activation in frontal rather than parietal regions is somewhat surprising as the PPC is known to play a pivotal role in movement and object interactions such as during object reaching (Brochier and Umiltà, 2007). More consistent activation in frontal regions during MI of transitive movements may suggest increased computational load related to

motor programming and control for transitive movements rather than the processing of the objects' characteristics. A similar distinction between object-related and non-object-related actions has already been conducted in a meta-analysis on action observation (Caspers et al., 2010), a cognitive process that is supposed to activate motor representations in a way comparable to MI (Jeannerod, 2001). Similar to our results, Caspers and colleagues have shown more consistent activation in the premotor cortex (areas 6 and 44 in Caspers et al.; area 6 in the present study) during the observation of transitive than intransitive actions. Still, our results differ from theirs as Caspers and colleagues also found more consistent activation in the parietal regions and in the temporo-occipital cortex for object-related compared to intransitive actions while our results showed more consistent activation in the SMA. Thus, when compared to intransitive actions, *imagining* transitive actions seems to require more motor programming (activity within the premotor cortex) whereas *observing* transitive actions may require, in addition to motor programming, more processing of the object's characteristics (activity within the premotor AND parietal cortex). This raises the possibility that although MI and action observation are similar (both involve motor simulation in a certain way), when considering transitivity, the relative involvement of their networks differ. It is interesting to note that, unlike action observation research, which has put significant effort into studying the influence of transitivity (e.g. (Buccino et al., 2001; Caspers et al., 2010; Corina et al., 2007; Grosbras et al., 2011; Hétu et al., 2011; Koski et al., 2002; Menz et al., 2009; Newman-Norlund et al., 2010)), this question has seldom been directly addressed by MI researchers. Our understanding of MI could therefore benefit from empirical research directly comparing MI of transitive and intransitive movements.

4.3. Importance of the modality of imagery on the MI network

Kinesthetic and visual MI are two different ways of imagining oneself moving. Behavioral data showing differences in performance between the two types of MI (Grangeon et al., 2011; Malouin et al., 2010) further support the view that they rely on different cognitive processes. Additionally, some attempts have been made at comparing the cerebral underpinnings of the two MI modalities (Binkofski et al., 2000; Guillot et al., 2009; Solodkin et al., 2004). Although these studies have suggested that kinesthetic and visual MI activate some common cerebral areas, their results have mostly highlighted the anatomical (Binkofski et al., 2000; Guillot et al., 2009) and functional (Solodkin et al., 2004) differences between their networks. Comparing the consistent activation maps produced by our meta-analyses on kinesthetic and visual MI revealed that both modalities share a small part of the general MI network (SMA, left PcG, insula and putamen). However, kinesthetic MI seems to involve a more extensive network as important clusters of activation were observed in the left premotor (mostly in the IFG and PcG/area 6) and parietal cortex (IPL, PreC) that were not obtained with visual MI. However, the subtraction analysis between kinesthetic MI and visual MI revealed no significant difference in activation consistency. This result has to be carefully considered as only five studies specifically instructed their participants to perform visual MI. Even if the meta-analysis algorithm should be able to accommodate for large differences between the number of experiments, such a small sample could nevertheless have impacted the results (see (Caspers et al., 2010) for a similar case). Looking at our results on visual MI, one could be surprised that the specific instruction to "imagine observing yourself moving" did not yield consistent activation in the occipital lobe. Indeed, from the five papers that used the visual modality, only one reported more activation in the occipital lobe compared to the control condition (listening to different sounds). Furthermore, there is some

evidence that injuries to the occipital lobe can produce impairments in visual imagery of objects (Ganis et al., 2003). Clearly, this intriguing result requires further investigation. Considering the fact that the only study reporting occipital activity during visual MI (Guillot et al., 2009) directly compared visual to kinesthetic MI, future research could try to explicitly distinguish the two modalities through more specific instructions to participants in order to maximize possible differences. One striking fact is that from the 75 papers reviewed here, only 20 (27%) specified the modality through which their participants performed MI (i.e., visual MI, kinesthetic MI, or both). Hence, this remains an important confounding factor in most studies. This is especially the case if one considers the results from the present study, which highlight important differences in the network involved in each type of MI. Furthermore, there are important individual differences in the ability to perform MI through each modality (some individuals are better at using kinesthetic than visual MI or vice versa) which can influence the tendency to use one modality over the other (Guillot et al., 2004). Thus, when no instruction is given, one cannot be certain of *how* an individual performs MI. We strongly suggest that future work should always carefully instruct their participants about the modality of MI to be performed and clearly report the exact instructions given to the participants in their methods.

4.4. The laterality judgment task

It is generally assumed that the LJT requires to mentally move one's own hand in order to match it with the hand-stimulus (Cooper and Shepard, 1975; de Lange et al., 2006, 2008; Parsons, 1987, 1994, 2001; Saimpont et al., 2009; Shenton et al., 2004). This assumption is notably based on chronometric data showing that subjects' response times in the laterality judgment task are proportional to the time taken by the subjects to physically move their hands in the position of the hand-stimuli (Parsons, 1987, 1994). Indeed, response times not only increase with the angular distance between the subjects' hand and the hand-stimulus but also with the biomechanical constraints that apply when one is actually trying to match one's hand with the stimulus (Parsons, 1987, 1994). During the LJT, participants are rarely asked explicitly to do MI (see (de Lange et al., 2008)). Thus, the LJT *implicitly* triggers MI of arm movements (Parsons et al., 1995). We compared the consistent activations found during the LJT to the ones observed during tasks where participants were explicitly asked to perform MI. We focused on MI of the upper limb or the whole body since the studies on the LJT in our sample used hands or whole body rotations (note that the vast majority of experiments on the LJT focused on hand rotation; 8/10). Contrary to what was expected, our results suggest that explicit and implicit MI rely on relatively different networks. Indeed, there were very few overlaps between the regions consistently activated during the LJT and Pure MI. Furthermore, the consistent activations for the LJT were mainly in the right hemisphere whereas Pure MI was associated with consistent bilateral activations. The LJT did not show consistent activation in the SMA and the only consistent activation in the premotor cortex was found in the right MfG. This is surprising as results from our meta-analysis on upper-limb MI clearly showed consistent activation in these regions and the SMA has been shown to be involved in visuo-spatial transformation tasks (Leek and Johnston, 2009). These large differences between Pure MI (explicit MI) and the LJT suggest that if subjects do indeed perform MI during the LJT, this MI is different (at least in its neural underpinning) from when one mentally simulates an upper-limb movement with explicit instructions to do so. One possible explanation is that for the LJT, participants imagine only their hand moving in space rather than doing the movement which would include participation of more parts of the upper limb such as the wrist, the forearm and even the elbow. If this is the case, the LJT may be more similar

to tasks where objects have to be mentally rotated by the participants. Zacks (2008) has conducted a meta-analysis on this topic and found that mental rotation of objects consistently activated the regions around the intraparietal sulcus, which is consistent with our results on the LJT. Contrary to our results however, Zacks also found consistent activation in the SMA, especially when the stimuli were pictures of hands: thus during the LJT. Considering that we looked at 10 studies which is twice the number used by Zacks, the activity within the SMA during the LJT seems less consistent than what was previously suggested by Zacks. Furthermore, the fact that behavioral data have consistently shown that response times during the LJT are influenced not only by the orientation of the stimuli, but also by biomechanical constraints (e.g. (Parsons, 1987, 1994; Saimpont et al., 2009)) leads us to believe that the LJT cannot be considered as an object rotation task.

The subtraction analysis between Pure MI and the LJT performed in the present study revealed that the LJT showed more consistent activations in the right SPL while more consistent activations were found in the SMA and SMG for the Pure MI tasks. These results suggest that the LJT may not require the motor preparation or control performed by the SMA and the IFG that is usually associated with MI but mostly relies on the representation within the parietal cortex. Indeed, in his meta-analysis, Zacks (2008) found that the SPL was consistently activated during mental rotation tasks including the LJT. Furthermore, a recent behavioral paper has suggested that the feeling of movement during the LJT is in fact an aftereffect related to the multisensory binding between the visual representation of the stimuli and the proprioceptive representation of the subject's hands (Viswanathan et al., 2012). As the SPL is known to contain postural representations of the upper limb (Parkinson et al., 2010; Pellijeff et al., 2006) and it has been repeatedly shown that subjects take into account their current upper-limb posture while solving the LJT (Conson et al., 2011; de Lange et al., 2006; Funk et al., 2005; Ionta et al., 2007; Lorey et al., 2009; Parsons, 1994; Shenton et al., 2004; Sirigu and Duhamel, 2001), it is not surprising that this region is consistently activated during the LJT.

Importantly, another possible explanation for the important differences between Pure MI and the LJT lies in the methods used to analyze the BOLD signal. Whereas most Pure MI studies used a whole brain contrast approach, most LJT use a parametric analysis in order to identify which region's activity is modulated by the varying angle of the presented hand. Hence, it is possible that parametric analyses result in a network of regions specifically associated with the amplitude of the movement and omits regions involved in the mental representation of the body. Nevertheless, our results raise some doubts on the exact nature of the processes involved during the LJT. Thus it would be important for researchers to investigate more thoroughly (and possibly using similar analysis techniques) the similarities and discrepancies between this task and MI per se. For example, comparing a LJT where participants are instructed to perform MI to the classical LJT where MI is implicitly engaged could shed some light on the exact strategy used by the participants. In light of the evidence presented here, one should also be careful when using MI and the LJT as two interchangeable or even equivalent concepts.

4.5. MI of motor sequence

Several researchers have used motor sequences to study MI. Motor sequences have also extensively been used in research on motor learning as performance on this type of task can easily be measured through several parameters (error rate, speed, etc.). Extensive data show the importance of the CB, striatum and parietal cortex during the acquisition, maintenance, and retrieval of motor sequences (Doyon, 2008). The CB, basal ganglia and SMA are also known to play a role in the preparation, execution and control of

sequential movements (Tanji, 2001). Furthermore, results from an ALE meta-analysis have revealed consistent bilateral activation in the dorsal and ventral premotor cortices, right IPL, and bilateral PPC during multi-finger tapping tasks (Witt et al., 2008). The network involved during the actual execution of motor sequences is similar to our results on MI of motor sequences, which revealed consistent activations in various regions of the premotor cortex and the PPC, the basal ganglia and the CB. This again suggests a striking similarity between motor execution and MI. The fact that motor execution and MI of motor sequences seem to recruit similar regions supports the idea that imagining a motor sequence requires similar computational steps as actually performing it.

The conjunction analysis between Pure MI and motor sequences revealed overlapping consistent activations in the lateral part of the premotor cortex (i.e., IFG) as well as in the SMA and the parietal cortex (IPL and SPL), suggesting that both types of MI rely on similar networks. However, several of these regions were more consistently activated during MI of motor sequences than Pure MI. This suggests that motor sequences may be more complex to imagine and require more motor programming than movements without the need for specific temporal organization. This formulation is consistent with a study by Kuitz-Buschbeck et al. (2003), in which they compared a finger pressing task to a finger-thumb opposition sequence to study the influence of complexity on MI (where the sequential movements were considered as more complex). The authors found that the sequential MI task was associated with greater activation in the precuneus, intraparietal cortex and precentral gyrus, regions that were shown to be more consistently activated by MI of motor sequence (vs. Pure MI) in our subtraction analysis.

Overall, our results indicate that the involvement of the brain networks activated during MI can depend on several factors such as the type of movement to be imagined, the MI modality and the instructions given to the participants. While the map of this network remains relatively constant (fronto-parietal in addition to subcortical regions), the relative importance of its components varies according to these factors, as revealed by our focused meta-analyses. These variations seem to depend on the nature of the information to be processed (e.g., motor representation, body representation, proprioceptive information) and the computational load (e.g., motor control or motor planning) necessary to complete the various types of MI.

5. Conclusion

Up to now, the description of the neural network supporting MI could only be inferred by examining the results from neuroimaging studies individually. Our ALE meta-analysis, by greatly reducing the influence of the many confounding factors associated with the diverse methods of previous fMRI/PET studies, provides the first quantitative map of the structures activated during MI. MI seems to rely on a network involving motor related regions including fronto-parietal areas and subcortical structures, supporting the view that MI and motor execution are very similar processes. Just as the literature on motor execution has grown from a gross description of the motor network to a deeper understanding of how several modulating factors influence its functioning, MI research will need to take a closer look at variables that most probably influence how our brain works when it imagines movements. The few variables examined in this paper are only a small fraction of the factors that could influence the quality of MI. The study of these factors could potentially help in optimizing how MI can be used, for examples, in rehabilitation or by athletes. Indeed, research on MI offers a unique window into how humans can intentionally recruit and manipulate internal representations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.neubiorev.2013.03.017>.

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