# Multimodal functional imaging of motor imagery using a novel paradigm

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# Multimodal functional imaging of motor imagery using a novel paradigm

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ABSTRACT

Neuroimaging studies have shown that the neural mechanisms of motor imagery (MI) overlap substantially with the mechanisms of motor execution (ME). Surprisingly, however, the role of several regions of the motor circuitry in MI remains controversial, a variability that may be due to differences in neuroimaging techniques, MI training, instruction types, or tasks used to evoke MI. The objectives of this study were twofold: (i) to design a novel task that reliably invokes MI, provides a reliable behavioral measure of MI performance, and is transferable across imaging modalities; and (ii) to measure the common and differential activations for MI and ME with functional magnetic resonance imaging (fMRI) and magnetoencephalography (MEG). We present a task in which it is difficult to give accurate responses without the use of either motor execution or motor imagery. The behavioral results demonstrate that participants performed similarly on the task when they imagined vs. executed movements and this performance did not change over time. The fMRI results show a spatial overlap of MI and ME in a number of motor and premotor areas, sensory cortices, cerebellum, inferior frontal gyrus, and ventrolateral thalamus. MI uniquely engaged bilateral occipital areas, left parahippocampus, and other temporal and frontal areas, whereas ME yielded unique activity in motor and sensory areas, cerebellum, precuneus, and putamen. The MEG results show a robust event-related beta band desynchronization in the proximity of primary motor and premotor cortices during both ME and MI. Together, these results further elucidate the neural circuitry of MI and show that our task robustly and reliably invokes motor imagery, and thus may prove useful for interrogating the functional status of the motor circuitry in patients with motor disorders.



## Introduction

Motor imagery (MI) is an internal rehearsal of simple or complex motor movements without overt physical action (Annett, 1995; Jeannerod, 1995; Porro et al., 1996). Although difficult to describe verbally, MI involves kinesthetic and visual imagery and is characterized by vivid mental representations of movement execution from a first-person perspective (Munzert et al., 2009; Porro et al., 1996). Motor imagery plays a critical role in motor skill learning and sports training (Brouziyne and Molinaro, 2005; Murphy, 1994), as well as in prosthesis control (Hochberg et al., 2006) and motor rehabilitation in patients with motor disorders (Dijkerman et al., 2004; Kimberley et al., 2006; Sharma et al., 2006). Such ample clinical and neurophysiological applications of MI emphasize the necessity for deeper understanding of the neural mechanisms engaged in motor imagery.

The last two decades have yielded a number of imaging studies investigating the neural correlates of motor execution (ME) and MI, as well as their functional overlap, using various techniques, such as positron emission tomography (PET; e.g., Decety et al., 1994; Naito et al., 2002; Roland et al., 1980; Stephan et al., 1995), electroencephalography (EEG; e.g., Beisteiner et al., 1995; Rodriguez et al., 2004; Thayer and Johnson, 2006), functional magnetic resonance imaging (fMRI; e.g., 2Lotze et al., 1999; Porro et al., 1996; Roth et al., 1996), and magnetoencephalography (MEG; e.g., Lang et al., 1996; Nagakawa et al., 2011; Schnitzler et al., 1997). Convergent evidence shows that during ME the motor and premotor cortices, i.e., the primary motor cortex (M1), supplementary motor area (SMA), pre-supplementary motor area (pre-SMA), and ventral and dorsal premotor cortices (vPMC and dPMC, respectively) are modulated by the cerebello-thalamo-cortical loop. Other essential ME areas include the basal ganglia, primary somatosensory cortex (S1), and posterior parietal cortex—specifically, the superior and inferior parietal lobules (SPL and IPL, respectively).

Some studies report that the neural correlates of MI substantially overlap with those subserving ME (Jeannerod, 2001; Lotze and Halsband, 2006), especially within the neural circuits involved in the early stages of motor control (i.e., motor planning). These circuits include the supplementary motor area, premotor areas, and posterior parietal cortex. In light of these findings, Jeannerod (2001) proposed that ME and MI are functionally equivalent in that the neural processes are shared but in MI overt production of movement is inhibited. However,

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a substantial number of studies have reported contradictory results. For instance, while several studies show consistent and even somatotopic activations of the primary motor cortex (Porro et al., 1996; Stippich et al., 2002), others fail to show any involvement of M1 in motor imagery (Roland et al., 1980; Stephan et al., 1995). Lotze and Halsband (2006) and Sharma et al. (2006) argue that the involvement of M1 during motor imagery is dependent on the intensity and the complexity of the imagined movement and emphasize the importance of task selection, training, and imaging techniques. Similarly, studies differ with respect to activation of SMA during motor imagery. Although it is generally found that pre-SMA is active during movement selection and preparation (Gerardin et al., 2000; Lotze et al., 1999; Roland et al., 1980), conflicting results pertain to the role of posterior SMA. On the one hand, posterior SMA has been found active during ME (Deiber et al., 1991; Stephan et al., 1995), but on the other hand, several authors claim that posterior SMA may be central to the *inhibition* of overt movement in MI (Kasess et al., 2008; Solodkin et al., 2004). Research findings also diverge in the degree of vPMC and dPMC activations during motor imagery (Lotze and Halsband, 2006; Munzert et al., 2009). vPMC is argued to be critical for action execution, action observation (Rizzolatti et al., 1996), and sensory guidance of movement, whereas dPMC is proposed to be essential in learning of associations between sensory stimuli and specific movements; thus utilizing somatosensory strategies (Binkofski et al., 2000; Vry et al., 2012). Finally, some researchers have argued that motor imagery is supported by a distributed neural system that relies more on sensory planning and preparation (i.e., activity in parietal and temporal areas) than executive motor processes (i.e., activity in primary motor cortices; Annett, 1995).

There is a number of potential explanations for these disparate results; for instance the diverse variety of brain mapping techniques, mental training procedures, instructions, analysis tools, tasks that have been employed to invoke MI, as well as inadequate behavioral monitoring (Gao et al., 2011; Munzert et al., 2009; Oosterhof et al., 2012; Porro et al., 1996). Motor imagery is exclusively an internal process and therefore is fundamentally difficult to control and monitor. Ideally, empirical paradigms should provide some measure of imagery success, maximizing the consistency and continuity of imagery engagement and vividness. However, studies differ substantially in the tasks used to invoke MI, pre-experimental training, movement monitoring, and reported imagery strategies. The classical paradigms for MI involve simple hand and finger movements, e.g., hand/finger flexion (Gerardin et al., 2000; Lotze et al., 1999); button pressing (Guillot et al., 2009; Kasess et al., 2008); finger-to-thumb opposition (Porro et al., 1996; Roland et al., 1980; Solodkin et al., 2004), joystick movement (Deiber et al., 1991; Stephan et al., 1995); or target tracing (Binkofski et al., 2000). These tasks are problematic for two main reasons. Firstly, because of their simple, repetitive, and predictable nature, they may result in the fluctuation of attention and vigilance levels during long testing blocks (e.g., Porro et al., 1996). Secondly, most do not include any behavioral measure of MI performance (Lotze and Halsband, 2006) and are thus unable to independently confirm that participants actually engage in MI as instructed. Confirmation of MI often relies on rather indirect measures, e.g., physiological indices of heart and respiratory rates, which have been proposed to increase during MI (Decety et al., 1991); or duration of MI, which is argued to positively correlate with duration of ME (Decety and Michel, 1989).

More recently, Hanakawa et al. (2003, 2008) aimed to rectify some of the early methodological limitations, introducing an external behavioral measure in a sequential movement and imagery (SMI) task. In the SMI task, participants learn a simple sequential tapping sequence and are cued to the first finger of the tapping sequence, as well as to the number of taps to be executed or imagined. The critical point of the behavioral response is at the end of the task period when a question mark appears and the participants are asked to report the next finger in the tapping sequence. Albeit an elegant design, a few methodological issues are evident, for instance the visual presentation of the stimuli, verbal report of the target response, or presenting experimental conditions in separate imaging runs. The purpose of the current study was to design and test a novel MI paradigm, which has (i) a behavioral outcome measure that directly and objectively indexes success in the imagery task, (ii) an unpredictable auditory cueing sequence that promotes sustained imagery vigilance, (iii) a randomized order of all experimental conditions within each testing run, conducive to a direct comparison of experimental conditions in the analysis, and, (iv) which is suitable, in its exact experimental layout, for testing with various imaging modalities, such as fMRI, EEG, or MEG. We report the neural activity associated with task performance in a group of participants measured using fMRI. To demonstrate the cross-modal applicability of the paradigm, we also report brain responses from a complementary imaging technique, magnetoencephalography (MEG). The easy transferability of the paradigm across testing modalities has clinical and empirical benefits. For instance, clinically the EEG or MEG environment may be more suitable than fMRI to claustrophobic individuals, children, or noise-sensitive individuals. Empirically, the spatial resolution of fMRI is superior to that of MEG, whereas the temporal resolution of MEG is near perfect, superior to that of fMRI. Thus, the results of our study converge complementary spatio-temporal information relevant to motor execution and motor imagery.

## Methods

### *Participants*

Fourteen young adults (age range = 18–31; mean age = 25 years; SD = 4.2; 7 females) participated in the study. All participants were strongly right-handed (Oldfield, 1971), had normal or corrected-to-normal vision, and had no history of neurological impairment or psychiatric illness. All participants provided written informed consent approved by the Macquarie University Human Research Ethics Committee.

### *Task*

Participants were required to perform the following conditions: execution of specific finger movements with the right or left hand, imagination of specific finger movements with the right or left hand, and rest (see Fig. 1).

#### *Motor execution*

The fingers of each hand were assigned numbers (1 = thumb, 2 = index finger, 3 = middle finger, 4 = ring finger, 5 = little finger). Starting from a default position (i.e., resting their arms alongside the body, with the ventral surface against the plinth, to minimize elbow flexions during the task, and keeping their arms and hands completely relaxed, with their fingers extended but relaxed), participants were presented with a random sequence of 4 or 5 spoken digits and were asked to either slowly curl in the respective finger or extend it again to the default position if the same digit occurred again. At the end of each cue sequence, participants saw a picture of a hand and were asked to decide whether their final finger configuration was the same or different from that of the displayed hand. They indicated "yes" by slightly moving the toes of their right foot or "no" with the toes of their left foot. An examiner outside the testing room manually recorded the responses. We chose a toe response to minimize interference with both the behavioral and neural aspects of the finger-moving task.

#### *Motor imagery*

In the MI condition, participants performed the same task but instead of actually moving their fingers they were asked to imagine performing the movements. Participants were trained prior to the study on motor imagery (see the Training section below) and were explicitly and repeatedly instructed to maintain the vividness of motor

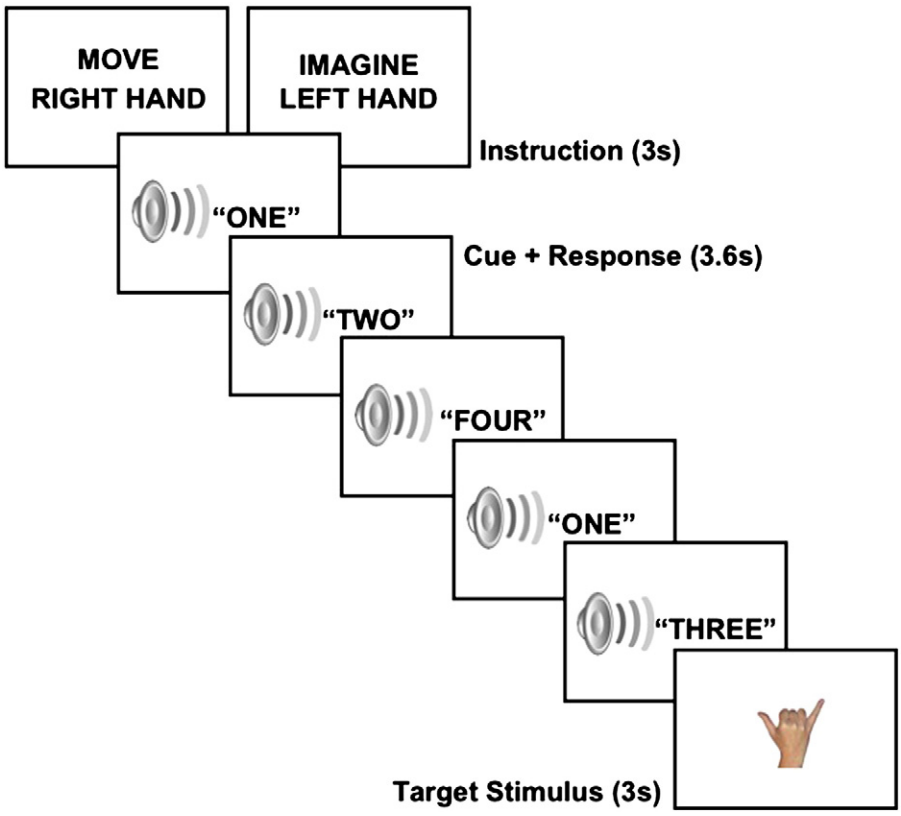


**Fig. 1.** Task layout. In each trial, participants were instructed to either move or imagine moving the fingers of their right or left hand (two example instructions shown), starting from a default position of all fingers extended. They curled in or extended specific fingers according to sequentially presented auditory cues. At the end of a cue sequence, participants were asked to indicate whether the configuration of their fingers matched the configuration of the displayed target hand. In the example shown, the correct response is 'Yes'.

imagery throughout the experiment. All participants also completed the Vividness of Visual Imagery Questionnaire (Marks, 1973) to ensure that they were able to engage imagery and would be able to perform the task according to instructions. The range of the vividness scores was 55–73 (out of 80); mean score = 65; SD = 6.3. A cut-off value of 50 was used for inclusion.

*Experimental design*

Prior to the experiment, participants underwent a 30-minute training session (described in the Training section below). During the experiment, each participant took part in two identical brain-imaging sessions in the same day, first measured by MEG and then by fMRI. Electromyographic (EMG) measurements were acquired during the MEG session to ensure that there was no muscle activation during imagery trials. Two MEG compatible surface electrodes were attached to the *extensor digitorum* of each arm following the procedure described in Burgar et al. (1997) and recorded using a BrainProducts MEG-compatible polygraphic system (BrainProducts GmbH, Gilching, Germany). EMG was acquired using a sampling rate of 1000 Hz and a filter bandpass of 20–500 Hz. Sample EMG data are included in the Supplementary materials. Due to the lack of technical equipment in the MRI suite, we were unable to collect EMG data during the fMRI session. However, an experimenter observed participants' hands closely via a scanner camera aimed at participants' hands during the entire scanning session to ensure that participants did not move their fingers during MI conditions. Although we believe that we controlled immobility sufficiently, ultimately measuring EMGs during both imaging sessions would have been optimal.

The experimental design consisted of four functional runs and four experimental conditions in a $2 \times 2$ within-subjects design with factors of hand (left/right) and task (execution/imagery). We used a blocked design, with four trials of one condition presented in sequence, followed by a 21-second block of rest, followed by the next condition. The order of conditions was counterbalanced across subjects, but identical for MEG and fMRI. At the beginning of each session, an instruction was presented for 3 s, followed by a sequence of four or five spoken digits. Each auditory cue was presented for 1 s and followed by a response period of either 2.6 or 3.5 s, depending on whether five or four cues were presented, respectively. The number of presented auditory cues was varied to reduce predictability of the sequence length. During each response period, participants either moved or imagined moving the cued finger. At the end of each trial, a visual target picture was presented for 4 s, during which time participants responded whether their finger configuration corresponded to the target configuration, using toe movements. After each imaging session, participants were debriefed and asked about their performance on the task. All participants reported sustained vigilance on imagery conditions, especially in the light of the counterbalanced design and length of each condition block (e.g., "Each condition felt really short, so I had no problem focusing on the particular task, especially with the intermixed rest blocks that allowed me to prepare for the next condition").

*Training*

Each participant was trained on the task 48 h prior to the experiment and asked to practice at home in a supine position prior to coming in for testing. The training procedure consisted of an introduction and one practice block for each of the four conditions. In the introduction, the purpose of the task was explained. Special emphasis was placed on the vividness of sustained imagery, as well as inhibition of any movement during the imagery trials. In each of the four practice blocks, the participants completed 10 trials, equal in length and layout to those in the actual experiment. The training started with the execution conditions (first right, then left hand), followed by imagery conditions (first

right, then left hand), so that the participants could imagine the movement of their own fingers as it was just executed in the preceding conditions. Specific instructions given to the participants were: "We would like you to imagine your own hand and fingers in your mind and focus on slowly curling in or extending your fingers according to the given auditory cues. In your mind, move your fingers deliberately slowly." Participants' performance was monitored by the experimenter who, when necessary, paused the practice and reiterated the task requirements. All participants gave verbal feedback on their motor imagery experience. When the participants performed according to the instructions and were comfortable with the timing of the movements or imagined movements, the next block of practice trials was initiated. The training session took 30 min on average. On the day of testing, the imagery instructions were re-iterated prior to each imaging session and participants gave verbal feedback on the vividness of imagery after each scanning session.

### *fMRI data acquisition & preprocessing*

Anatomical and functional images were acquired at the Macquarie University Hospital, Sydney, using a 3 Tesla Siemens Magnetom Verio scanner with a 12-channel head coil. Anatomical images were acquired using an MP-RAGE sequence (208 axial slices, TR = 2000 ms, TE = 3.94 s, FOV = 240 mm, voxel size = 0.9 $mm^3$, TI = 900, flip angle = 9°). Brain activation was assessed using the blood oxygenation level-dependent (BOLD) effect (Ogawa et al., 1990) with optimal contrast. Functional images were obtained using a whole head T2*-weighted echo-planar image (EPI) sequence (40 axial slices with interleaved acquisition, 0.5 mm gap, TR = 3000 ms, TE = 30 ms, flip angle = 90°, FOV = 260 mm, voxel size = 2.5 $mm^3$).

The acquired images were preprocessed using the Statistical Parametric Mapping software (SPM8; http://www.fil.ion.ucl.ac.uk/spm). The images were firstly corrected for the acquisition time delay among different slices, realigned onto the mean image for head-motion correction, and then spatially normalized into a standard stereotaxic space with voxel size of 2 $mm^3$ using the Montreal Neurological Institute (MNI) EPI template. Finally, a spatial smoothing filter was employed for each volume by convolving it with an isotropic Gaussian kernel (FWHM = 6 mm).

### *fMRI data analysis*

Image data were analyzed with a multivariate method Partial Least Squares (PLS; McIntosh et al., 1996, 2004), which allows for the identification of regional activity change as a function of task demands (i.e., task PLS). This multivariate approach is similar to a principal component analysis (e.g., Friston et al., 1993) and assumes that brain function reflects the coordinated activity of groups of brain regions rather than the independent activity of any single brain region. In the current study, we used task PLS to examine changes in activity during the four experimental conditions to establish similarities and differences in the spatial pattern. Each analyzed block was 18 s long, commencing at the onset of the first auditory cue and ending before the target stimulus appeared. The output of PLS analysis is a set of latent variables (LVs), components that reflect cohesive patterns of brain activity related to the experimental design and account for maximum covariance between regional activity changes and task measure. A brain score was calculated for each participant, which is the product of the weighted value (salience) of each voxel and BOLD signals summed across the entire brain for each condition on a given LV. Salience indicates the degree to which a voxel is related to the LV and can be positive or negative, depending on the voxel's relation to the pattern of task-dependent differences identified by the LV.

The significance for each LV was determined by 500 permutation tests (McIntosh et al., 1996). In addition to the permutation tests, a second and independent step was to determine the reliability of the saliences (or weights) for the brain voxels characterizing each pattern identified by the LVs. To do so, we estimated the standard error of each voxel's salience on each LV by 100 bootstrap resampling steps (Efron and Tibshirani, 1985). Peak voxels with a bootstrap ratio (BSR; i.e., salience/standard error) > 3.0 were considered to be reliable, as these approximate $p < 0.005$ (Sampson et al., 1989).

### *MEG data acquisition & preprocessing*

Prior to MEG recordings, marker coil positions, electrode positions, and head shape were measured with a pen digitizer (Polhemus Fastrack, Colchester, VT). MEG recordings were obtained in a magnetically shielded room (Fujihara Co. Ltd., Tokyo, Japan) with the participants in a supine position, using the KIT-Macquarie MEG160 (Model PQ1160R-N2, KIT, Kanazawa, Japan). The recordings consisted of 160 coaxial first-order gradiometers with a 50 mm baseline (Kado et al., 1999; Uehara et al., 2003). MEG data were acquired using a sampling rate of 1000 Hz and a bandpass filter of 0.03–200 Hz. MEG data were co-registered to each individual's structural MRI scan (obtained during the fMRI session) using BESA MRI version 1.0 (BESA GMbH, Grafelfing, Germany). MEG artifacts, including blinks and eye-movements, were rejected using the artifact scan tool in BESA 5.2.7, which rejects trials based on abnormally high amplitudes or abrupt rises or falls in amplitude (gradients). For each subject and condition, at least 90% of trials survived artifact rejection.

### *MEG data analysis*

Statistical analyses of beta-band beamformer images were carried out in BESA Statistics 1.0 (BESA GMbH, Grafelfing, Germany). Data were analyzed in 3500 ms epochs with respect to the presentation of the acoustic cue for each finger movement, including a pre-cue period of 500 ms. Time-frequency analyses were carried out for each condition (i.e., left hand execute; left hand imagery; right hand execute; right hand imagery) using a frequency sampling of 2 Hz, a time sampling of 25 ms and a bandpass of 4–40 Hz. Beamforming was carried out using a baseline interval of −500 to 0 ms and a target interval of 500–1000 ms. The frequency range for beamforming analysis was selected from the maximum event-related desynchronization in the beta frequency range (13–30 Hz) in each individual participant. All contrasts were performed as 2-sided *t*-tests. Significance testing of the whole brain MEG images was computed using 1000 permutations and a cluster alpha of 0.05.

## Results

### *Behavioral performance*

A 2 (imagery/execution) × 2 (left hand/right hand) × 2 (fMRI/MEG) repeated-measures ANOVA of accuracy of responses revealed no significant main effect or interaction ($ps > 0.1$), suggesting that participants were equally able to do the task using imagery and execution, using either hand, and being tested in either imaging environment (see Fig. 2A). A second 2 (imagery/execution) × 2 (fMRI/MEG) × 4 (experimental runs) repeated-measures ANOVA of accuracy of responses revealed no significant main effect or interaction ($ps > 0.1$), demonstrating little effect of fatigue or practice over time (see Fig. 2B).

### *fMRI results*

The PLS analysis of the five conditions yielded two significant LVs. LV1 accounted for 69% of covariance in the data ($p < 0.001$) and reflected a pattern of activity related to the motor imagery and motor execution conditions in contrast with the fixation condition. This pattern reflected the spatial overlap of MI and ME and included bilateral activations in M1, S1, basal ganglia, insula, cerebellum, inferior frontal gyrus, middle frontal gyrus, posterior parietal cortex, and superior temporal gyrus.

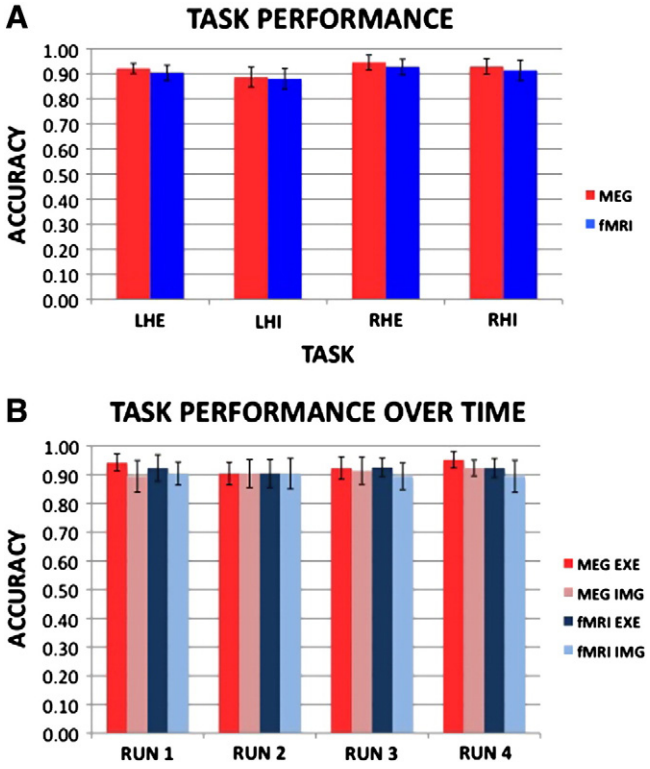


**Fig. 2.** Task performance. A) Accuracy scores for the four experimental conditions and two imaging modalities; B) Accuracy scores for the execution and imagery conditions (handedness collapsed) across the four MEG and four fMRI runs.

Areas whose activity negatively correlated with the task conditions included left fusiform gyrus, right occipital gyrus, bilateral inferior parietal lobule, and posterior cingulate gyrus, reflecting the posterior nodes of the default mode network (e.g., Buckner et al., 2008; see Fig. 3 and Table 1).

LV2 accounted for 16% of covariance in the data ($p = 0.03$) and showed differentiation of the MI conditions from the ME conditions, reflecting activation differences between MI and ME. MI engaged bilateral occipital areas and inferior as well as superior frontal gyri, left parahippocampus, left inferior parietal lobule and supramarginal gyrus, and left dorsal premotor gyrus. ME, on the other hand, showed bilateral activity in the cerebellum, precuneus, putamen, and further activations in the right M1, postcentral gyrus, fusiform gyrus, and left superior temporal gyrus (see Fig. 4 and Table 2).

*MEG results*

Execution of the finger movements resulted in a robust event-related desynchronization (ERD) at MEG sensors located in the proximity of primary motor cortex (see Fig. 5). The movement-related ERD was maximal in the beta band (13–30 Hz) and low gamma band (30–40 Hz) from the beginning of the epoch to about 2000 ms. Group statistical analysis contrasting left execution versus right execution showed two significant clusters centered at right motor cortex (left execute<right execute, MNI coordinates 44, −18, 63, range = 0, $p<0.00001$) and left motor cortex (left execute<right execute, MNI coordinates −25, −32, 73, range = 0, $p<0.00001$). In other words, the left versus right contrast showed significantly greater beta band desynchronization for left hand movement in the right motor cortex and greater desynchronization for right hand movement in the left motor cortex.

A comparable ERD was elicited in the imagine condition, although it was smaller in magnitude and more restricted in frequency range and duration. The beamformer analysis localized the beta ERDs of both execution and imagery conditions to areas including the primary motor and premotor cortices (Fig. 6 and Table 3). Activations were in bilateral motor cortices with maximal amplitudes in the hemisphere contralateral to the hand being used or imagined. These results align with the fMRI results in showing that the same regions of primary and premotor cortex were activated in ME and MI conditions. The MEG results add

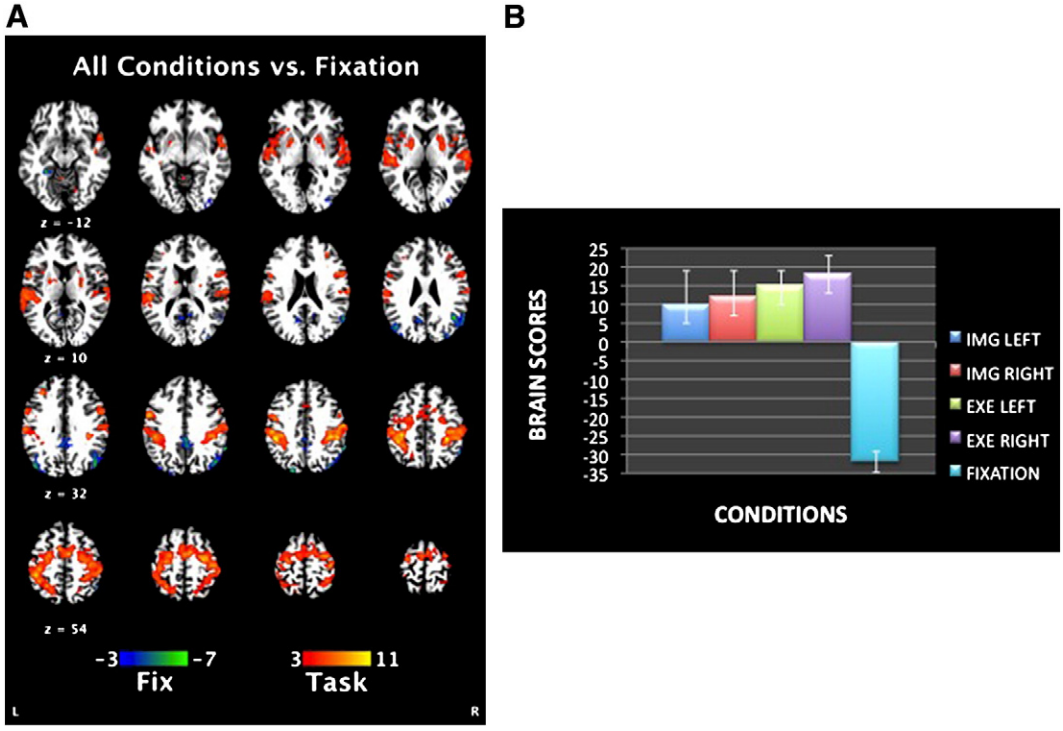


**Fig. 3.** Task PLS result 1: (A) A pattern of whole-brain activity depicting areas active during execution and imagery (yellow/red) vs. fixation (blue/green). (B) Brain scores related to whole-brain activity seen in (A) across the five conditions. Error bars denote 95% confidence intervals for correlations calculated from the bootstrap procedure.

**Table 1**
Overlap in activity during motor imagery and motor execution.

| Region | Hem | BA | MNI coordinates | | | Ratio |
|---|---|---|---|---|---|---|
| | | | *x* | *y* | *x* | |
| Task > fixation | | | | | | |
| Precentral gyrus (M1) | R | 4 | 28 | −14 | 58 | 13.66 |
| | L | | −30 | −18 | 58 | 9.04 |
| Postcentral gyrus (S1) | R | 1, 2, 3 | 32 | −34 | 48 | 13.38 |
| | L | | −46 | −34 | 42 | 15.30 |
| Pre-SMA/SMA proper | R | 6 | 6 | −4 | 54 | 10.62 |
| | L | | −8 | 4 | 52 | 9.65 |
| vPMC | R | 6 | 56 | 6 | 32 | 7.52 |
| | L | | −56 | 4 | 36 | 13.47 |
| dPMC | R | 6 | 32 | −6 | 70 | 8.38 |
| | L | | −28 | −12 | 68 | 9.96 |
| Inferior frontal gyrus | R | 44/45 | 52 | 10 | 20 | 6.91 |
| | L | | −56 | 8 | 18 | 7.97 |
| Posterior parietal cortex | R | 7 | 34 | −46 | 64 | 7.37 |
| | L | | −30 | −54 | 58 | 10.05 |
| Putamen | R | | 28 | −4 | 0 | 7.88 |
| | L | | −24 | 0 | 8 | 6.76 |
| vl thalamus | R | | 16 | −14 | 6 | 7.38 |
| Cerebellum | R | | 26 | −54 | −22 | 10.30 |
| | L | | −38 | −58 | −24 | 8.19 |
| Fixation > task | | | | | | |
| Fusiform gyrus | L | 37 | −32 | −36 | −16 | −8.20 |
| Occipital gyrus | R | 18 | 34 | −84 | 2 | −6.44 |
| IPL | R | 40 | 44 | −56 | 25 | −7.48 |
| | L | 40 | −46 | −72 | 30 | −6.70 |
| Posterior cingulate gyrus | R | 31 | 4 | −36 | 36 | −5.89 |

Abbreviations: Hem = hemisphere; BA = Brodmann area; R = right; L = left; Ratio = salience/SE ratio from the bootstrap analysis; *x* coordinate = right/left; *y* coordinate = anterior/posterior; *z* coordinate = superior/inferior; M1 = primary motor cortex; S1 = primary sensory cortex; SMA = supplementary motor area; vPMC = ventral premotor cortex; dPMC = dorsal premotor cortex; vl = ventrolateral; IPL = inferior parietal lobule.

information, which is not available in the fMRI data about the timing of these activations. Group statistical analysis contrasting left imagery versus right imagery confirmed significantly greater desynchronization for right hand imagery in the left motor cortex ($p < 0.00001$). The left hemisphere cluster included a maximum in primary motor cortex but had a larger spatial extent than was seen in the corresponding execute contrast, with the cluster extending into the parietal lobe. Interestingly, the *p* value for the left hand imagery contrast was considerably larger ($p = 0.09$), indicating less consistency of neural activation for left hand imagery compared to right hand imagery in this strongly right-handed group. However the location of the maximum for left hand imagery was identical to the location for left hand execution in right motor cortex (MNI coordinates 44, −18, 63).

## Discussion

The purpose of this study was to develop a novel motor imagery paradigm and to examine brain activation during motor execution and imagery using this task. The paradigm was designed to effectively invoke motor imagery, with an objective measure of success, and sustained intensity over time. To achieve this, we used relatively long trials, a block-design approach, randomized order of experimental conditions within each imaging run, and task in which there was a correct response, unlike many previous imagery studies (Porro et al., 1996; Roland et al., 1980; Solodkin et al., 2004). Unlike Hanakawa et al.'s (2003, 2008) task, which used visual stimuli to cue imagery, our task consists of non-repetitive sequences of auditory cues to which participants respond by moving or imagining movements of specific fingers of their right or left hand. Because the cue sequences vary in both timing and cue type, it is impossible to predict which fingers will be involved. Also, the possibility of repetition of digits, which reverses the finger position, requires constant maintenance of the mental image.

An important feature of the task is the ability to accurately gauge imagery performance by measuring the outcome of the imagery task—the comparison of the final postures of the imagined fingers with a target image. The benefits of accuracy monitoring in this task are twofold: (i) to attain an index of behavior, which provides information about significant fluctuations in performance due to confounding variables; and (ii) to increase and sustain participants' attention to the task and reduce

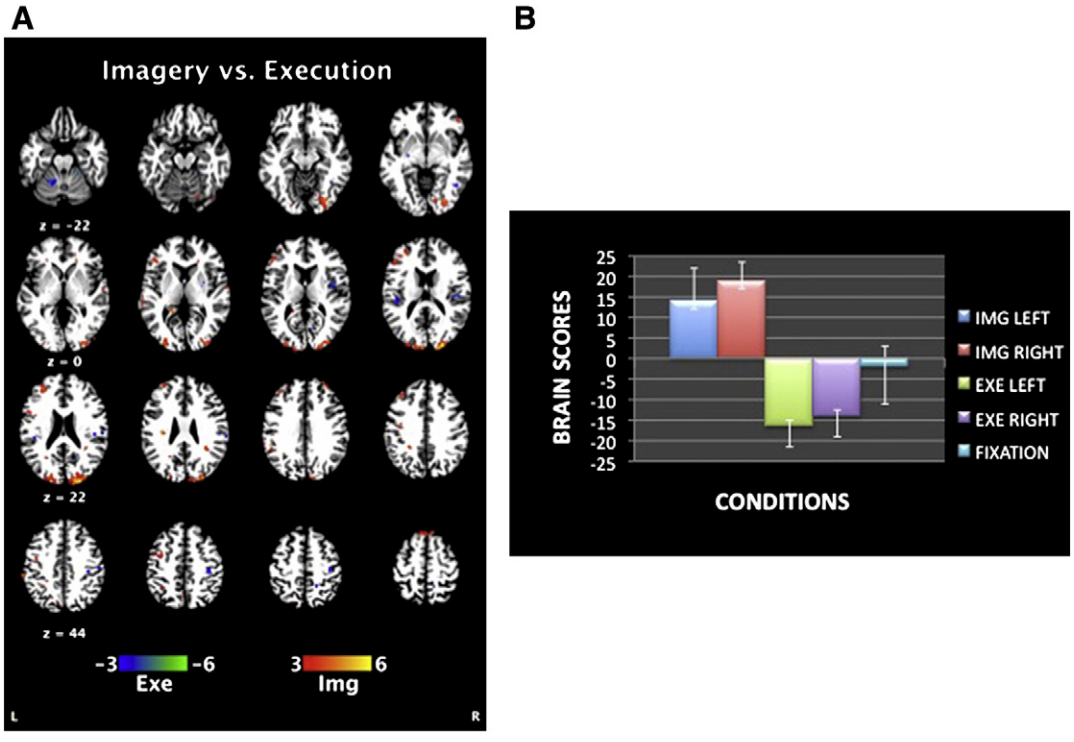


**Fig. 4.** Task PLS result 2: (A) A pattern of whole-brain activity depicting areas active during imagery (yellow/red) vs. execution (blue/green). (B) Brain scores related to whole-brain activity seen in (A) across the five conditions. Error bars denote 95% confidence intervals for correlations calculated from the bootstrap procedure.

**Table 2**
Differences in activity during motor imagery vs. motor execution.

| Region | Hem | BA | MNI coordinates | | | Ratio |
|---|---|---|---|---|---|---|
| | | | *x* | *y* | *x* | |
| Imagery > execution | | | | | | |
| Middle occipital gyrus | R | 18 | 24 | −94 | 20 | 7.61 |
| | L | | −6 | −100 | 16 | 5.30 |
| Supramarginal gyrus | L | 40 | −52 | −46 | 32 | 5.04 |
| Inferior parietal lobule | L | 40 | −64 | −28 | 44 | 4.96 |
| Parahippocampal gyrus | L | 30 | −18 | −44 | 4 | 4.82 |
| Superior temporal gyrus | R | 22 | 64 | −8 | 4 | 4.98 |
| Superior frontal gyrus | R | 9 | 28 | 56 | 34 | 4.80 |
| | L | 6 | −2 | 36 | 60 | 4.65 |
| Inferior frontal gyrus | R | 47 | 50 | 42 | −6 | 4.14 |
| | L | 46 | −56 | 36 | 6 | 4.60 |
| dPMC | L | 6 | −52 | −2 | 46 | 4.10 |
| Execution > imagery | | | | | | |
| Precentral gyrus (M1) | R | 4 | 36 | −20 | 52 | −4.42 |
| Postcentral gyrus | R | 43 | 48 | −22 | 20 | −5.75 |
| Cerebellum | R | | 22 | −38 | −24 | −5.79 |
| | L | | −22 | −252 | −22 | −4.34 |
| Precuneus | R | 7 | 14 | −46 | 58 | −4.56 |
| | L | 7 | −24 | −50 | 70 | −4.54 |
| Putamen | R | | 26 | −8 | −2 | −4.54 |
| | L | | −28 | −14 | −4 | −4.79 |
| Fusiform gyrus | R | 37 | 38 | −54 | −10 | −7.33 |
| Superior temporal gyrus | L | 22 | −44 | −30 | 18 | −6.72 |

Abbreviations: Hem = hemisphere; BA = Brodmann area; R = right; L = left; Ratio = salience/SE ratio from the bootstrap analysis; *x* coordinate = right/left; *y* coordinate = anterior/posterior; *z* coordinate = superior/inferior; M1 = primary motor cortex; S1 = primary sensory cortex; dPMC = dorsal premotor cortex.

its fluctuations over time. We found no significant difference in accuracy across time (i.e., across the four experimental runs of each scan), suggesting that our task is robust to fatigue and practice effects. Together with participants' verbal reports of imagery maintenance and vividness during the two imaging sessions, the behavioral results seem to provide strong support for sustained attention on the MI conditions in this task.

The fMRI analyses conform with those of many previous studies in showing a substantial overlap of brain mechanisms activated by motor imagery and motor execution. These activations include both pre-SMA and SMA proper, ventral and dorsal premotor cortices, inferior frontal gyrus, posterior parietal cortex, putamen, ventrolateral thalamus, and cerebellum. These areas have been implicated in movement selection and preparation, sensory guidance of movement, and learning of associations between the stimulus and specific movements (Binkofski et al., 2000; Lotze et al., 1999; Rizzolatti et al., 1996; Roland et al., 1980; Vry et al., 2012). fMRI activations were also found in bilateral primary motor cortex, and the MEG results confirm that the imagery task activated primary motor cortex contralateral to the imagined hand. This is of considerable interest because a number of previous motor imagery studies have failed to show any consistent activation here and the role of primary motor cortex in MI remains controversial (e.g., Munzert et al., 2009). The present results seem to support the position that primary motor cortex is activated during MI and suggest that the inconsistent results of some of the previous studies may be attributable to use of tasks that are less robust and consistent in their ability to evoke MI.

In addition to the shared neural circuitry described above, our imagery task also elicited fMRI activations in brain regions that were unique to MI and ME. Imagery yielded activations in dorsal PMC and inferior frontal gyrus, two areas important in inhibition of response (Aron and Poldrack, 2006; Aron et al., 2003, 2004; Chambers et al., 2006; Xue et al., 2008). Dorsal PMC has been implicated in learning of the associations between a stimulus and response, i.e., learning not to move the fingers when presented with auditory cues, and inferior frontal gyrus has been shown to be essential for the general inhibition of responses,

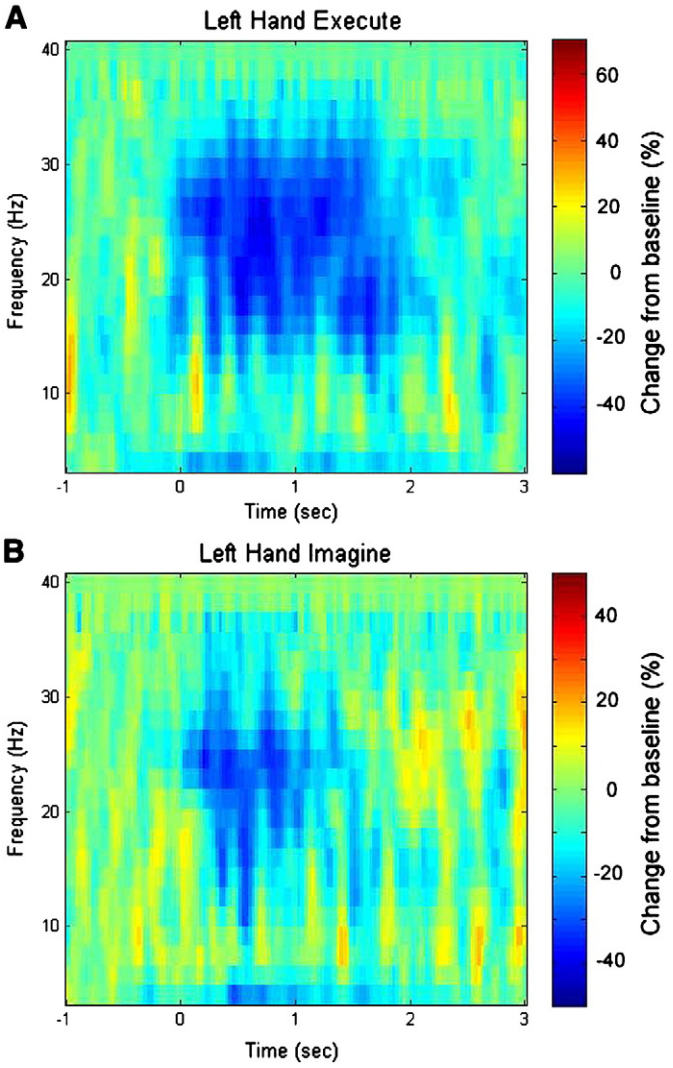


**Fig. 5.** Event-related spectral perturbations at a sensor in the proximity of the right primary motor cortex. A) Left ME condition; B) Left MI condition.

particularly in the light of two or more possible response options (Aron and Poldrack, 2006; Aron et al., 2003, 2004; Chambers et al., 2006; Xue et al., 2008), i.e., not moving the fingers. In addition, motor imagery activated bilateral occipital gyrus, left inferior parietal lobule, parahippocampus, right superior temporal gyrus and superior frontal gyrus. These areas are part of a circuitry important for visuospatial imagery, processing and remembering of visual scenes, and representation of three-dimensional space (Aguirre et al., 1996, 1998; Epstein and Kanwisher, 1998; Epstein et al., 1999; Mullaly and Maguire, 2011). In contrast, motor execution activated right primary motor and sensory cortices, cerebellum, putamen, and posterior parietal areas. These areas are critical for somatosensory coordination that is largely absent in imagined movement.

## Conclusions

We present a novel experimental task with improved capabilities for inducing, maintaining, and measuring motor imagery in experimental participants. The design of the task provides a clear objective measure of successful motor imagery, making it useful for both neuroimaging and behavioral studies of healthy performance, and for investigating conditions where impairments involving imagery are suspected. Our neuroimaging results show activation of brain regions that have been

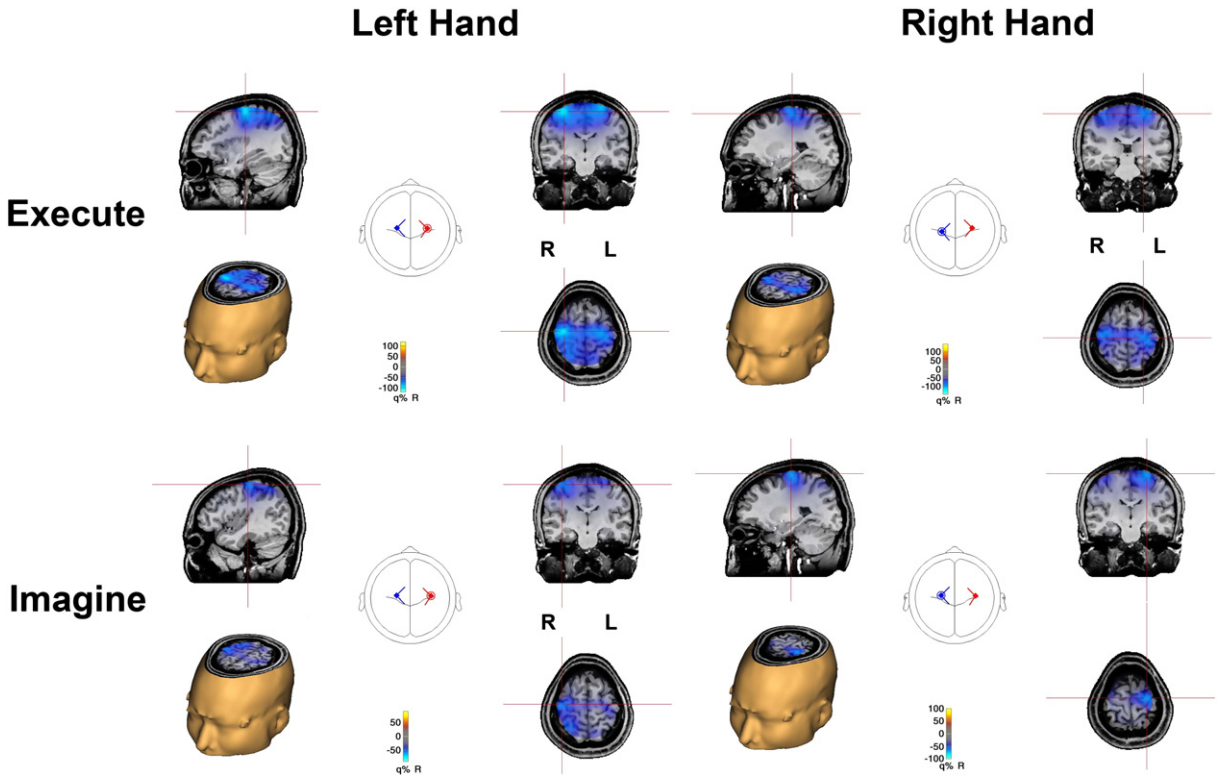


**Fig. 6.** Beamformer source maxima for the left and right ME and MI conditions.

implicated in motor imagery in many previous studies, and also show convincing activations of primary motor cortex, a region that has not been activated reliably in previous work and whose role in MI consequently remains controversial. The task can be implemented identically in diverse neuroimaging modalities, including fMRI and MEG. Thus, this new task will be useful in further elucidating the neural mechanisms and neural computations employed in imagery. The ability to consistently engage primary motor cortex in the absence of movement also has clear implications for the assessment of remaining cortical function, cortical reorganization, and functional plasticity in patients with paralysis or paresis following stroke or brain damage or disease. Finally, covert activation of primary motor cortex may prove useful in the search for brain signals that can reliably drive prosthetic devices via brain–computer interfaces.

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**Table 3**
Beamformer source maxima for motor imagery and motor execution.

| Condition | Hem | BA | MNI coordinates (mm) | | | q% |
|---|---|---|---|---|---|---|
| | | | *x* | *y* | *z* | |
| Left ME | L | 6 | −25 | −10 | 71 | −90 |
| | R | 6 | 37 | −10 | 62 | −97 |
| Left MI | L | 6 | −25 | −10 | 71 | −42 |
| | R | 4 | 44 | −10 | 62 | −54 |
| Right ME | L | 4 | −25 | −18 | 64 | −87 |
| | R | 6 | 37 | −10 | 62 | −86 |
| Right MI | L | 6 | −25 | −10 | 71 | −69 |
| | R | 6 | 44 | −10 | 62 | −43 |

Abbreviations: Hem = hemisphere; BA = nearest gray matter to source maximum; R = right; L = left; q% = magnitude change from baseline at source maximum; *x* coordinate = right/left; *y* coordinate = anterior/posterior; *z* coordinate = superior/inferior; ME = motor execution; MI = motor imagery.

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