

RESEARCH ARTICLE

Motor imagery training: Kinesthetic imagery strategy and inferior parietal fMRI activation

Florent Lebon¹ | Ulrike Horn² | Martin Domin² | Martin Lotze² 

¹CAPS, U1093 INSERM, Université de Bourgogne Franche-Comté, Faculté des Sciences du Sport, Dijon F-21078, France

²Functional Imaging Unit, Department of Diagnostic Radiology and Neuroradiology, University Medicine, University of Greifswald, Greifswald, Germany

Correspondence

Martin Lotze, M.D., Functional Imaging Unit, Center for Diagnostic Radiology and Neuroradiology, University of Greifswald, Walther-Rathenau-Str.46, D-17475 Greifswald, Germany.
Email: martin.lotze@uni-greifswald.de

Funding information

Burgundy Regional Council; the European Funds for Regional Development, Grant/Award Number: 2013-9201AAO050S04153; Deutsche Forschungsgemeinschaft (DFG), Grant/Award Number: LO795/28-1; State of Mecklenburg Vorpommern

Abstract

Motor imagery (MI) is the mental simulation of action frequently used by professionals in different fields. However, with respect to performance, well-controlled functional imaging studies on MI training are sparse. We investigated changes in fMRI representation going along with performance changes of a finger sequence (error and velocity) after MI training in 48 healthy young volunteers. Before training, we tested the vividness of kinesthetic and visual imagery. During tests, participants were instructed to move or to imagine moving the fingers of the right hand in a specific order. During MI training, participants repeatedly imagined the sequence for 15 min. Imaging analysis was performed using a full-factorial design to assess brain changes due to imagery training. We also used regression analyses to identify those who profited from training (performance outcome and gain) with initial imagery scores (vividness) and fMRI activation magnitude during MI at pre-test (MI_{pre}). After training, error rate decreased and velocity increased. We combined both parameters into a common performance index. FMRI activation in the left inferior parietal lobe (IPL) was associated with MI and increased over time. In addition, fMRI activation in the right IPL during MI_{pre} was associated with high initial kinesthetic vividness. High kinesthetic imagery vividness predicted a high performance after training. In contrast, occipital activation, associated with visual imagery strategies, showed a negative predictive value for performance. Our data echo the importance of high kinesthetic vividness for MI training outcome and consider IPL as a key area during MI and through MI training.

KEYWORDS

fusiform gyrus, inferior parietal lobe, kinesthetic imagery, mental training, motor imagery, prediction of training gain, visual imagery

1 | INTRODUCTION

Motor imagery (MI) practice, which is the repetition of an imagined action, is considered as a relevant intervention in various disciplines such as sport, medicine, psychology, education, and music (Schuster et al., 2011). It has been shown that MI does not only improve motor sequencing (Gentili, Han, Schweighofer, & Papaxanthis, 2010), aiming (Kim et al., 2014), and motor timing (Pascual-Leone et al., 1995) but also strength (Lebon, Collet, & Guillot, 2010; Ranganathan, Siemionow, Liu, Sahgal, & Yue, 2004; Yue & Cole, 1992). Behaviorally, MI training shows a comparable training curve to execution training (Gentili et al., 2010).

It has been suggested that MI and movement execution mostly share neural substrates (Jeannerod, 2001; Sharma & Baron, 2013). MI recruits a fronto-parietal network and subcortical and cerebellar regions

(for an ALE meta-analysis, see Héту et al., 2013). Therefore, some of the changes that can be expected after MI training might be deduced from knowledge on the representational changes after motor execution training. In general, motor skill learning is indicated by performance improvement of the sensorimotor system and by changes in the associated cortical and subcortical representation. With repetitive actual training, performance becomes more precise and automatic. This goes along with changes in functional representation such as reduced BOLD-response in the network investigated, with a focus on contralateral cortical and ipsilateral cerebellar representation, and with a switch from cortical to subcortical representation (Dayan & Cohen, 2011; Hund-Georgiadis & Yves Von Cramon, 1999; Jäncke, Shah, & Peters, 2000; Lotze, Braun, Birbaumer, Anders, & Cohen, 2003; Robertson, 2007; Walz et al., 2015).

Although some studies examining MI training exist, results are not entirely consistent. A PET study with foot movement sequence training demonstrated comparable changes as after execution (EX) training (Jackson, Lafleur, Malouin, Richards, & Doyon, 2003). An fMRI study with finger sequence training also showed similar activation changes in several sensorimotor structures following MI and EX training but striking differences in other regions (Lacourse, Turner, Randolph-Orr, Schandler, & Cohen, 2004): EX training led to increased striatal and decreased cerebellar activation, whereas MI training led to increased cerebellar, premotor, and striatal activation. Another study investigating finger sequences found the premotor regions only to be activated by EX training (Olsson, 2008). MI training might well rely on different neural substrates than EX training.

Several regions seem to be particularly crucial for MI: a network comprising dorsal premotor cortex (dPMC), inferior parietal lobule (IPL), and parts of the frontal gyrus is specific to MI when compared with EX (Sharma & Baron, 2013; Zapparoli et al., 2013). Parietal and premotor sites have also been shown to be important for MI when comparing with other planning processes without movement simulation (Johnson, 2002). In addition, MI modulates the parieto-motor connectivity (Lebon, Lotze, Stinear, & Byblow, 2012b) and consistently, continuous theta-burst stimulation over the left IPL was capable to successfully inhibit MI training of finger sequence learning (Kraeutner, Keeler, & Boe, 2016). Furthermore, the posterior parietal cortex seems to be coding different imagery strategies (Pelgrims, Andres, & Olivier, 2009).

However, higher visual representation sites have also been described to contribute to MI. Activation of the fusiform gyrus is modulated by MI training of sequential finger tapping tasks (Olsson, 2008; Zhang et al., 2011). It is still under debate which areas underlie the process of successful MI training and whether the initial representation of MI processes can be used to explain the motor performance after training.

When examining the different regions involved in MI training, several aspects such as imagery strategy or quality might be associated with these functional representations. Imagery strategies are related, in part, to the sensory modalities employed to imagine the action: kinesthetic (feeling of the movement), visual (with first and third-person perspective), or haptic (feeling of the pressure between fingertips during finger sequence). Solodkin, Hlustik, Chen, and Small (2004) and Guillot et al. (2009) reported overlapping but partially distinct networks for imagery strategies. When comparing them directly, they showed that kinesthetic imagery activates primarily motor associated structures (primary motor cortex (M1), dPMC, IPL and supplementary motor area (SMA), cerebellum), whereas visual imagery activates primarily the occipital regions (BA 17, 18) and the superior parietal lobule (SPL). Using transcranial magnetic stimulation, Stinear, Byblow, Steyvers, Levin, and Swinnen (2006) found a greater involvement of the corticospinal tract during MI when using kinesthetic compared to visual modality. It has been proposed that kinesthetic strategies are associated with forward modeling of a motor response and are therefore especially useful for training motor paradigms (Ridderinkhof & Brass, 2015). With respect to the utilization of different MI strategies Fery (2003) demonstrated that visual imagery is better for tasks that emphasize form while kinesthetic

imagery is better for tasks that emphasize timing or coordination of the two hands.

Imagery ability may also account for motor learning with MI. However, the direct influence of imagery vividness on motor improvement following MI practice is still in debate (Avanzino et al., 2015; Goss, Hall, Buckolz, & Fishburne, 1986; Lebon, Byblow, Collet, Guillot, & Stinear, 2012a; Lovell & Collins, 2001; Vergeer & Roberts, 2006). Vividness of imagery, which is how clearly one imagines a movement, is usually measured via questionnaires, the participants attributing a score to the clarity of their imagined movement.

In this study, we aimed at examining the MI training process of a finger sequence. We investigated associations between fMRI activation measured prior to MI training and kinesthetic or visual imagery strategies and their corresponding effect on motor performance. We further hypothesize that those areas involved in movement ideation and kinesthetic imagery should be highly predictive for performance gain and training outcome in the sequence task at hand, whereas those associated with visual imagery strategies should not.

2 | MATERIALS AND METHODS

2.1 | Participants

Forty-eight healthy participants (age average: 26 ± 3 years; 31 females, 17 males) were recruited via a student webpage of the Greifswald University campus. All participants were strictly right-handed (84 ± 14.57) according to the diagnostic criteria of the Edinburgh Handedness Inventory (Oldfield, 1971) and had no neurological impairments. The motor imagery score according to the revised version of the Movement Imagery Questionnaire (MIQ-R) (Hall & Martin, 1997) was completed before starting the experiment.

The study was approved by the ethical committee at the University Medicine Greifswald (BB39/10) and all participants gave informed consent prior to participation.

2.2 | Protocol and paradigm

Participants were instructed to actually move (during tests) or to imagine moving (during tests and training) the fingers of the right hand in a specific order in time with a 2 Hz blinking dot visible on a screen. One trial consisted in repeating the given sequence for 30 s: 2-4-3-5-5-3-4-2 (2 = index, 3 = middle finger, 4 = ring finger, 5 = little finger). All participants were carefully instructed and explored the assignment of the sequence before the pre-fMRI session. The experimenter first showed the finger sequence pressing the keypad with the corresponding fingers outside of the scanner. When the screen was blue, the participants were instructed to stay still. When the screen turned green, after a countdown to inform on the next trial, they started the sequence. To ensure they understood the sequence, the participants performed finger movements for 12 s (i.e., 24 finger taps). Participants were positioned supine in the MRI scanner and were given a four-finger key pad (Lumitouch, Photon Control Inc., San Francisco, USA) adapted for the right hand. During actual execution (EX), the key

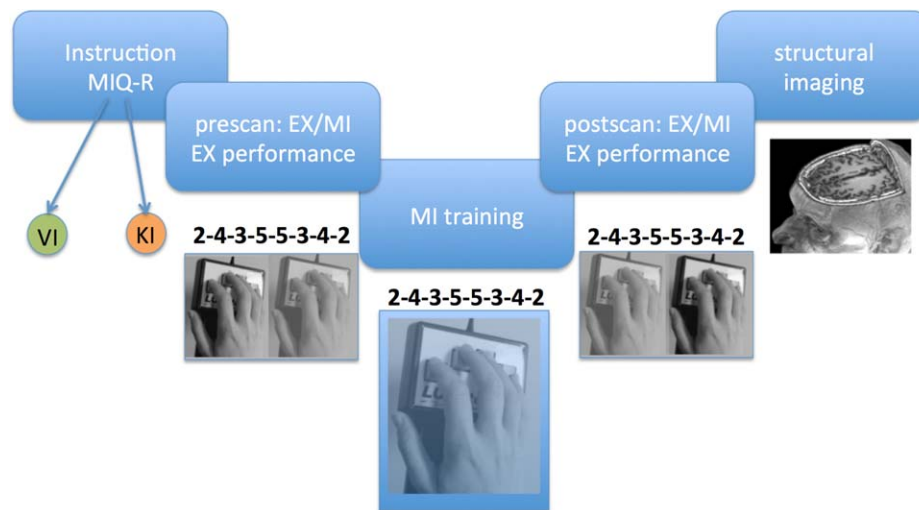


FIGURE 1 Experimental procedure. After being given instructions about the experiment and the finger sequence tapping, and after filling in the MIQ-R (visual (VI) and kinesthetic imagery (KI) score), the participant was placed in the MRI and performed a short prescan including the execution (EX) and mental imagery (MI) task. These scans and performance recorded during EX served as precondition. To control for possible extension movements during the MI task, the participant wore a virtual reality glove. During the 15-min training, participants imagined the sequence for about 150 times. At post-test, we assessed performance gain during EX task, and we performed a post-training scan including the EX and MI task. The experimental session ended with a structural T1-weighted image [Color figure can be viewed at wileyonlinelibrary.com]

presses were measured via dual photoelectric barriers and transferred by optical fibers to an electronic processor outside the scanner. The sequences of keystrokes were stored in log-files and were evaluated a posteriori. During imagined trials (MI), the participants were instructed to imagine the same finger sequence, without moving, combining kinesthetic and visual (first person perspective) imagery strategies. We ensured that participants stayed motionless with the 5DT Data Glove Ultra (Fifth Dimension Technologies).

Task instructions were presented using Presentation (Neurobehavioral Systems, Albany, USA) and were projected on a screen, which could be observed via a double mirror system affixed to the head coil.

2.2.1 | Scanning sessions (pre- and post-training)

During the two scanning sessions, which is before and after the mental training, the participants performed two actual execution trials and three imagined trials with an intertrial interval (baseline) of 20 s. The execution block lasted 2 min (20 s baseline–30 s execution–20 s baseline–30 s execution–20 s baseline) and the imagery block 170 s (20 s baseline–30 s imagery–20 s baseline–30 s imagery–20 s baseline–30 s imagery–20 s baseline). During pretest, the actual execution block was performed before the imagery block, whereas during post-test, the order was inverted. The measurement procedure is shown in Figure 1.

2.2.2 | Motor imagery training session

MI training was performed inside the scanner without actual scanning for an overall period of 15 min and 30 s. We asked the participants to imagine the finger sequence in time with a 2 Hz blinking dot visible on a screen. We tested the temporal congruence of the imagined finger sequence, i.e., imagery accuracy: During MI training, participants were verbally asked four times, at a specific time point, to tell the experimenter the digit he/she was currently imagining moving. We collected

the responses and compared it to the expected movement, calculated from the 2 Hz frequency. For each response, we scored 2 points when temporal congruence was perfect, 1 point when shifted from the expected position at most by 2 taps, and 0 point when shifted by at least 3 taps. Therefore, the minimal and maximal accuracy scores were 0 and 8, respectively. In total, two blocks of 10 trials (1 trial = 30 s) were trained with 15-s rest between trials and 1-min rest between blocks, summing up to about 150 finger sequences. After each trial of 30 s, we asked the participants to score the imagery vividness with a 7-point Likert scale (1 = very hard to imagine the movement; 7 = very easy to imagine the movement; 2–6 = intermediate scores). As for pre- and post-tests, we checked that participants were motionless with a virtual movement glove (Data Glove Ultra 5DT, Pretoria, South Africa) connected via glass fiber technology for online monitoring and offline analysis.

2.3 | Functional imaging measurement

A 3 T Siemens Magnetom Verio (Siemens, Erlangen, Germany) equipped with a 32-channel head coil was used to acquire both a T1-weighted structural volume of the whole head (MP-Rage; 176 sagittal slices, voxel size: 1 mm × 1 mm × 1 mm) and T2*-weighted echo-planar images (EPI; TR = 2000 ms, TE = 30 ms, flip angle 90°, 34 axial slices, voxel size of 3 mm × 3 mm × 3 mm, field of view (FOV) 192 mm). 3-D echo planar images were obtained for the pre- and post-measurements, the first 2 dummy volumes in each session being discarded to allow for T1 equilibration effect. In detail, for each participant, 60 execution EPI-volumes and 85 imagery volumes were measured during the preassessment and during post-training assessment each. We used a rubber foam head restraint to avoid head movements.

2.4 | Statistical analysis

2.4.1 | Behavioral data

We assessed motor performance with the variables *error* defined as number of incorrect and omitted button presses and *velocity* defined as the averaged inter time interval (ITI) between finger taps in milliseconds. We compared these variables between pre- and post-tests with Wilcoxon paired tests as the data were not normally distributed ($p < .05$, Shapiro–Wilk test). We then joined errors and velocity into a combined performance variable (weighted velocity). For this purpose, we divided the velocity at pre- and post-test by the respective percentage of correctly performed sequences. We also used Wilcoxon paired-test between pre- and post-test. To assess the performance improvement, we further determined the performance gain as (weighted velocity pre – weighted velocity post)/weighted velocity pre \times 100. We also compared the averaged ITI to the reference ITI—i.e., 500 ms—using a signed rank Wilcoxon tests to evaluate the deviation from the reference ITI.

We used linear regressions to predict motor performance (weighted velocity) observed at post-test and the performance gain (weighted velocity improvement) based on the motor imagery score assessed before MI training (MIQ-R: kinesthetic imagery score = KI, and visual imagery score = VI).

To test the gender effect, we first measured the percentage of improvement between the pre- and post-session for errors, velocity and weighted velocity. Then, we used a Mann–Whitney *U* test for each variable with gender as the independent variable.

2.4.2 | MRI and fMRI data

fMRI data were analyzed with the Statistical Parametric Mapping software (SPM12; Wellcome Department of Cognitive Neurosciences, London, UK) running under Matlab 7.1 (MathWorksInc; Natick, MA; USA). Spatial preprocessing included realignment to the first scan, unwarping, coregistration to the T1 anatomical volume images. Unwarping of geometrically distorted EPIs was performed using the FieldMap Toolbox. T1-weighted images were segmented to localize the grey and white matter and the cerebrospinal fluid. This segmentation was the basis for spatial normalization to the Montreal Neurological Institute (MNI) template, which was then resliced and smoothed with a $6 \times 6 \times 6$ mm full-width at half-maximum Gaussian Kernel filter to improve the signal-to-noise ratio. To correct for low-frequency components, a high-pass filter with a cutoff of 128 s was applied.

Statistical analysis was performed using the general linear model as implemented in SPM12. The MI and EX conditions were modeled as separate regressors with onsets as described in the paradigm section and for each time point (pre and post) separately, resulting in 4 sessions. No additional regressors were added. Comparisons between condition and time were performed with the full factorial design at the second level. This included the main effect for the conditions at each time point (EX_{pre} , MI_{pre} , EX_{post} , MI_{post}) and their interactions (for condition: $MI_{pre} - EX_{pre}$, $MI_{post} - EX_{post}$; for time: $EX_{post} - EX_{pre}$, $MI_{post} - MI_{pre}$). For thresholding, we applied both a correction without a priori assumptions ($p_{FWE} < .05$ corrected for the whole brain volume)

and a more liberal ROI correction for anatomically defined areas (also $p_{FWE} < .05$ but ROI restricted) if we had certain assumptions on which areas would be implicated given by the literature and the activation would not survive the whole-brain correction. We expected the following areas to be implicated in MI in general: IPL, SPL, dPMC, SMA, cerebellum, and BA44 (Héту et al., 2013). The EX condition was expected to show activation in similar areas although the comparison EX – MI was expected to display stronger activation representations especially in sensorimotor areas (Sharma & Baron, 2013) at each time point. The comparison MI – EX was expected to display stronger activation in IPL, dPMC, and BA44 (Sharma & Baron, 2013; Zapparoli et al., 2013). The areas to be implicated in MI training cannot easily be inferred from the literature as only few MI training studies exist. Therefore, we used a whole-brain correction to examine the effect of time in the MI condition.

We were further interested in associating brain areas with KI and VI scores. We conducted linear regression analyses of the MI_{pre} BOLD magnitude in these preselected regions and the imagery quality (KI and VI scores) to assess the correlates of the two imagery modalities. As the kinesthetic imagery representation has been shown to display more motor-related characteristics and the visual imagery network to display more visual characteristics (Guillot et al., 2009; Solodkin et al., 2004), we further added M1, BA17, and BA18 to the list of hypothesized areas in this analysis.

Again using linear regressions, we aimed to predict motor performance after training (weighted velocity post) and performance improvement (weighted velocity improvement) with BOLD-magnitude in ROIs in the MI_{pre} task. We only used whole-brain correction in this analysis as hypotheses from the literature for MI training prediction are rare.

Anatomical assignment was performed using ANATOMY (http://www.fz-juelich.de/inm/inm-1/DE/Home/home_node.html) if cytoarchitectonic mapping was available or anatomical labeling (AAL) (Tzourio-Mazoyer et al., 2002) as implemented in the WFU-Pick Atlas toolbox for SPM12.

3 | RESULTS

3.1 | Motor performance after MI training

MI training was effective in terms of sequence accuracy and velocity: the number of errors decreased from 2.94 ± 4.16 to 0.93 ± 2.94 ($Z = 4.04$, $p < .001$; Figure 2a) and the averaged ITI decreased from 530 ± 97 to 480 ± 73 ms ($Z = 3.73$, $p < .001$; Figure 2b). In addition, the variance of ITI decreased significantly (pretest = 6.8 ± 4.2 , post-test = 5.4 ± 3.5 ; $Z = 2.62$; $p = .008$) indicating a more stable performance after training. The score of weighted velocity showed a performance gain following mental training ($+9.32 \pm 13.37\%$), with the weighted velocity being greater at post-test in comparison to pretest ($Z = 4.26$, $p < .001$). These findings show that the participants generally increased their motor performance after mental training.

Note that averaged ITI at pretest was above the reference ITI of 500 ms ($\chi^2 = 982.75$, $p < .001$), while at post-test, it was below this reference ($\chi^2 = 549.97$, $p < 0.001$).

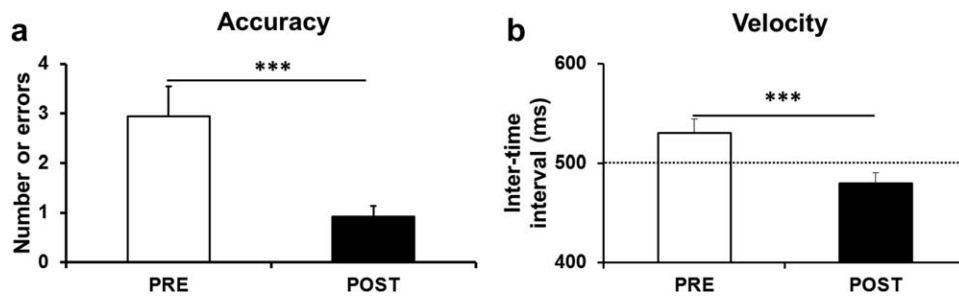


FIGURE 2 Effect of MI training on the actual performance of the finger sequence. Number of errors (a) and velocity of tapping (b) decreased between pre- and post-test (** $p < .001$)

We found no effect of gender for the behavioral variables (errors: $Z = 0.74$, $p = .45$; velocity: $Z = -0.77$, $p = .43$; weighted velocity: $Z = 0.47$, $p = .63$).

3.2 | Imagery quality

The motor imagery score (MIQ-R) was on average 43 ± 7.79 and showed differences between visual (22.7 ± 4.7) and kinesthetic modalities (20.3 ± 4.4 , $Z = 3.58$, $p < .001$). During MI training, participants estimated the vividness of the imagined finger sequence on a 7-point Likert scale with a mean score of 5.3 ± 0.9 . Also, measured imagery accuracy during training was on average 6.6 ± 1.2 on a scale from 0 to 8 (0, no temporal congruence; 8, perfect temporal congruence) demonstrating strong involvement in the imagery training.

The MIQ subscales were used to predict the motor performance after training ($F(2,45) = 5.02$, $p = .01$, $R^2 = .18$). Interestingly, KI, but not VI, predicted weighted velocity after training (KI: $\beta = -0.43$; $p = .007$; VI: $\beta = 0.008$; $p = .96$). To assess the gain by training, these subscales were also used to predict the motor performance improvement. No significant regression equation was found ($F(2,45) = 1.55$, $p = .22$, $R^2 = 0.064$).

3.3 | fMRI activations

Overall, movement execution and MI at pretest showed high similarity in their activation map, including bilateral M1/S1, dPMC, SMA, left

secondary somatosensory cortex (S2) and superior parietal lobe, and bilateral cerebellar hemispheres (for the top view, see Supporting Information, Figure 1).

3.3.1 | Effect of condition

During MI_{pre} , participants showed higher left inferior parietal activation than during EX_{pre} (Table 1A and Figure 3a (orange)). This representation was confirmed for the calculation of the effect of condition during the post-test measurement. MI_{pre} also showed increased fMRI activation when compared to EX_{pre} in the left STS/middle temporal gyrus and the left SPL.

In comparison to MI_{pre} , EX_{pre} showed increased activation in the contralateral primary sensorimotor cortex (Table 1B), ipsilateral anterior cerebellar hemisphere, contralateral cerebellar hemisphere, the motor cingulate, and ipsilateral primary sensorimotor cortex. Bilateral rolandic operculum/S2 was also increasingly active during EX_{pre} compared to MI_{pre} (Table 1). Again, this pattern was confirmed for the post-test measurement comparison ($EX_{post} - MI_{post}$).

3.3.2 | Effect of MI training

Over time, the fMRI representation during executed movements remained unchanged. In contrast, MI training changed the representation of MI between pre- and post-test: we observed a strong increase over training in the IPL (BA 39) of the left hemisphere (Table 2A and

TABLE 1 Effect of condition

Region	BA	Side	t	MNI coordinates		
				x	y	z
(A) $MI_{pre} - EX_{pre}$						
Inferior parietal lobe (IPL)	40	L	5.58 ^a	-42	-57	54
STS (superior temporal sulcus)	21	L	5.04 ^a	-63	-51	6
Superior parietal lobe (SPL)	7	L	4.85 ^b	-36	-63	54
(B) $EX_{pre} - MI_{pre}$						
Primary sensorimotor cortex	1-4	L	9.50 ^a	-33	-24	36
Primary sensorimotor cortex	1-4	R	5.49 ^a	36	-12	63
Cingulate gyrus	24	R	5.03 ^a	3	0	42
Anterior cerebellar hemisphere	Larsell lobule IV-VII	R	7.87 ^a	15	-51	-18
Anterior cerebellar hemisphere	Larsell lobule IV-VII	L	7.51 ^a	-21	-51	-21
Rolandic operculum/S2	43	L	7.23 ^a	-45	-21	18
Rolandic operculum/S2	43	R	4.81 ^a	48	-18	21

^a $p < .05$; FWE-corrected for the whole volume.

^b $p < .05$; FWE-corrected for the ROIS.

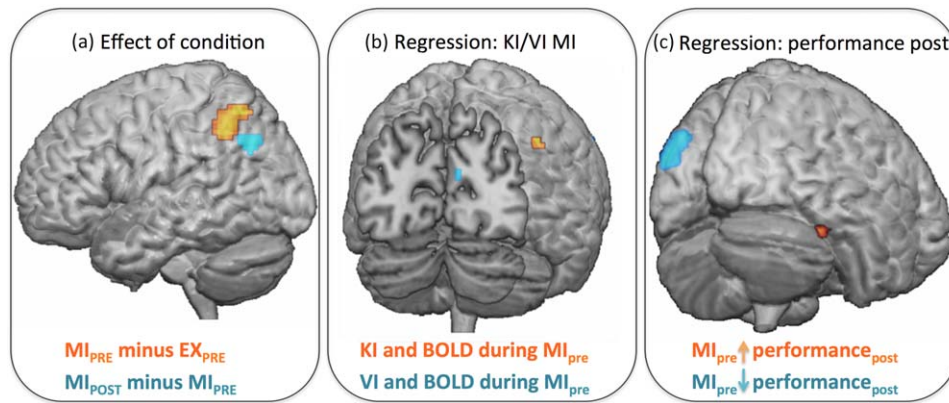


FIGURE 3 (a) Effect of condition and training. The effect of condition ($MI_{pre} - EX_{pre}$) showed a left-sided inferior parietal and medial temporal fMRI activation (orange). The effect of training ($MI_{post} - MI_{pre}$) showed a strong effect in the left inferior parietal lobe (blue). Statistical threshold: $p < .05$; FWE corrected for the whole volume. (b) Associations between fMRI activation during MI_{pre} and motor imagery score for kinesthetic (KI) and visual (VI) imagery. KI (orange) was positively associated with fMRI activation in right inferior parietal lobe during the MI_{pre} task. In contrast, VI (blue) was positively associated with fMRI activation in right visual striate. The statistical threshold has been adjusted to $p < .05$; FWE corrected per ROI. (c) Outcome prediction by fMRI activation during MI_{pre} . High performance after training (weighted velocity scores) could be predicted by high initial right fusiform activation (orange) during MI. Low performance after training could be predicted by high initial left occipital activation (blue) during MI_{pre} . Statistical threshold: $p < .05$; FWE corrected for the whole volume [Color figure can be viewed at wileyonlinelibrary.com]

Figure 3a (blue)) but also an effect in the left precuneus, ventromedial prefrontal cortex, and left middle temporal gyrus. $MI_{pre} - MI_{post}$ (decrease over training) showed an effect in the left anterior cerebellar hemisphere (Table 2B). The parietal effect of condition and training is demonstrated in Figure 3a.

3.3.3 | Linear regression analysis of fMRI activation

We calculated associations between the KI- or the VI-score (MIQ-R) and activation magnitude during MI_{pre} . The initial KI score was highly positively associated with right inferior parietal lobe activity during MI_{pre} ($t = 4.02$; $p_{FWE \text{ per ROI}} = 0.02$; coordinates: 48, -54, 39; Figure 3b, orange). In contrast, VI was positively associated with fMRI activation during MI_{pre} in the bilateral visual cortex (BA 18) ($t = 3.49$; $p_{FWE \text{ per ROI}} = 0.001$; coordinates: 9, -75, 21) activation (Figure 3b, blue).

3.3.4 | Outcome prediction with MI_{pre} activation

High performance after training (low weighted velocity post) could be predicted by MI_{pre} activation in the right fusiform gyrus (Figure 3c; $t = 5.24$; $p_{FWE} = 0.036$; coordinates: 42, -42, -24). Low performance

after training (high weighted velocity post) was associated with an initially high occipital lobe activation (Figure 3c; $t = 5.28$; $p_{FWE} = .032$; -15, -99, 24). We also tried to predict the performance improvement but neither the whole-brain regression analysis nor the ROI analysis with hypothesized regions showed an association with the improvement in weighted velocity.

4 | DISCUSSION

In this study, we observed positive effects of MI training on velocity and error rate in a finger sequence task. The post-training performance defined by a combined score including velocity and error rate could be predicted by KI ability before training. A high KI ability was represented by strong activation of the right IPL during MI before training. In contrast, high initial occipital activation during MI was associated with high initial visual imagery intensity (VI ability), which did not predict any training outcome. In fact, the initial activation of another occipital area directly predicted a low motor performance after training.

TABLE 2 MI-effect over training

Region	BA	Side	t	MNI coordinates		
				x	y	z
(A) Increase over training: $MI_{post} - MI_{pre}$						
Inferior parietal lobe (IPL)	39	L	6.24 ^a	-48	-66	36
precuneus	7	L	6.24 ^a	0	-54	33
Ventromedial PFC (vmPFC)	10	L	5.95 ^a	0	51	9
Middle temporal gyrus	21	L	5.60 ^a	-63	-12	-15
(B) Decrease over training: $MI_{pre} - MI_{post}$						
Anterior cerebellar hemisphere	Larsell lobule IV-VII	L	5.14 ^a	-27	-63	-27

^a $p < .05$; FWE-corrected for the whole volume.

4.1 | Outcome of training, predictive value of KI capacity, and associated fMRI activation

We observed a training effect for finger sequence training for velocity and error rate which could be predicted by KI scores before training. A strong association between KI strategies and motor timing outcome has been reported before (for timing of bimanual movements: Fery, 2003). KI strategies have been associated with forward modeling of a motor response making them useful for training motor paradigms (Ridderinkhof & Brass, 2015). In this study, we showed that this KI self-assessment was associated with inferior right IPL activation intensity. Associations with KI scores during MI have been reported before (Gerardin et al., 2000; Guillot et al., 2009; Lorey et al., 2011; Solodkin et al., 2004) supporting the specific role of this area in movement ideation. In addition, these studies suggest a role of bilateral M1 underlining the role of the dorsal loop in those with good KI capacities (Guillot et al., 2009; Solodkin et al., 2004). Here bilateral M1 did not reach significance thresholds after ROI correction for the linear regression with the KI (right: $t = 3.22$; coordinates: 45, -3, 33; $p_{FWE} = 0.50$; left: $t = 3.06$; coordinates: -36, -15, 48; $p_{FWE} = 0.63$). This might be based on a weaker effect for the regression analysis of non-KI-directed MI performance in comparison to clear instructions for the KI technique in other studies.

4.2 | Inferior parietal representation and MI

We found a strong effect for inferior left IPL fMRI activation increase for the effect of condition ($MI_{pre} - EX_{pre}$) and the effect of time ($MI_{post} - MI_{pre}$). The most compelling evidence for the left sided IPL function for MI is the finding that patients with damage in this area (BA 40, BA 39) show deficits in the ability to use MI, and here especially for predicting the duration of a movement (Sirigu et al., 1996). Another evidence is that inhibiting repetitive magnetic transcranial stimulation (rTMS) over this area in healthy volunteers decreases motor outcome for implicit learning through MI training (Kraeutner et al., 2016). Especially, the visuospatial processes seem to be impaired by continuous theta-burst TMS over that area. However, not only the left inferior parietal lobe is highly important for mental imagery performance: rTMS functional lesions applied 400–600 ms after stimulus onset over the right parietal lobe can also decrease performance in implicit MI tasks (Harris & Miniussi, 2003). In this study, we found an association between right IPL activation and KI. Right parietal lobe activation have been reported in numerous MI studies (Binkofski et al., 2000; Gerardin et al., 2000; Kultz-Buschbeck et al., 2003; Lacourse, Orr, Cramer, & Cohen, 2005; Sharma, Jones, Carpenter, & Baron, 2008); for an ALE-review, see Héту et al. (2013). In addition, the right IPL has been associated with movement ideation: perioperative direct cortical stimulation of this area (BA 40/39) triggered a strong desire to move the contralateral hand, arm, or foot (Desmurget & Sirigu, 2009). Previous virtual lesion studies of the right parietal lobe demonstrated degraded accuracy of MI (Fleming, Stinear, & Byblow, 2010). In a recent study, the activation pattern within the parietal lobe (but also the premotor cortex) was associated with imagined action content (Pilgramm et al.,

2016)—again increase in demand to remember the movement pattern increases recruitment within processing resources.

4.3 | Changes over training

Our MI training showed an effect on performance for both velocity and error rate. However, the effect of training induced fMRI activation was completely different to those observed after an active training paradigm: Dayan and Cohen (2011) described that skill improvement reflect motor memory consolidation, which has been identified as an intermediate stage between fast and slow learning (Doyon & Benali, 2005). We found specific changes in the MI condition over training with increased fMRI activation in the left IPL, left precuneus, and left medial temporal gyrus. Changes in these parieto-temporal areas centered on the left hemisphere are not present in an execution training (Dayan & Cohen, 2011; Lotze et al., 2003; Walz et al., 2015). More commonly, we found a decrease in left (contralateral) anterior cerebellar activation. This is comparable to some findings described during executed long-term repetitive motor training (Dayan & Cohen, 2011; Walz et al., 2015) and also to another study investigating effects of MI-training on finger sequence performance (Olsson, 2008).

Furthermore, the representation of movement execution did not change over time after MI training. It is possible that the training paradigm specifically modulates only fMRI activation during the trained task (MI) but not during the actual execution (EX) but due to the relatively short duration of EX condition no final statement can be provided.

4.4 | Occipital activation and VI versus fusiform activation and performance outcome prediction

Occipital (BA 17, 18) fMRI activation during MI_{pre} was associated with VI - a finding underlining those of others (Guillot et al., 2009; Solodkin et al., 2004). Overall, a high primary visual activation seems to be associated with poor outcome in MI training as we observed after linear regression of performance outcome (weighted velocity) with fMRI activation during MI_{pre} . Therefore, a high visual imagery content associated with high occipital fMRI activation is possibly a bad strategy for mental training of finger sequences. This seems to be true also for other fields of imagery expertise: high occipital recruitment has been observed in aged persons who performed worse in a behavioral mental chronometry test than younger ones (Zapparoli et al., 2013).

In contrast, fusiform gyrus activation during MI before training predicted good motor outcome. Higher visual imagery strategies, as for instance imagining finger sequences or numbers indicating the finger sequence seem to be helpful for performing the sequence with high velocity (Ishai, Ungerleider, & Haxby, 2000). Others already reported a modulation of the fusiform gyrus during mental training of a sequential finger tapping task before (Zhang et al., 2011). In another study, left fusiform gyrus activation increased after mental training of finger sequence over a longer training duration (72 min over 6 weeks) (Olsson, 2008). These authors interpreted the function of the fusiform gyrus as a formation of a visual memory for the motor procedure.

This study has some limitations which should be mentioned. First, we did not investigate a control population of a nontrained sample to control for habituation effects. In a mental training finger sequence study, including a nontrained group, Avanzino et al. (2015) showed an increase in movement rate of about 14% and 7% in the MI and control group, respectively. In their study, the participants performed 300 imagined finger movements in one session. We might expect comparable effects of mental training in our study, as the participants showed a performance increase of about 9% after 150 imagined finger movements. Also, recruiting a high number of participants in the MI group allowed us to differentiate those who benefited more from MI training. Second, using more complex finger sequences may be even better suited to investigate error rate as there was a floor effect in a number of participants after the 15-min training period.

5 | CONCLUSIONS

Our data echo the importance of high KI for MI training outcome for a precise finger sequence task. In addition, the IPL is the area associated with MI (in comparison to actual execution), with the increase of fMRI activation over time, and with KI ability. In contrast, occipital visual fMRI activation was associated with VI ability and predicted poor performance outcome. The role of fusiform gyrus for MI training of a finger sequence which was highly predictive for weighted velocity outcome needs further clarification.

ACKNOWLEDGEMENTS

FL was supported by a grant from the Burgundy Regional Council and the European Funds for Regional Development (2013-9201AAO050S04153). This work is part of a project supported by the German Research Foundation (DFG; LO795/28-1). UH was financed by a graduate scholarship from the State of Mecklenburg Vorpommern.

CONFLICT OF INTERESTS

The authors declare that there is no conflict of interest regarding the publication of this article.

ORCID

Martin Lotze  <http://orcid.org/0000-0003-4519-4956>

REFERENCES

- Avanzino, L., Gueugneau, N., Bisio, A., Ruggeri, P., Papaxanthis, C., & Bove, M. (2015). Motor cortical plasticity induced by motor learning through mental practice. *Frontiers in Behavioral Neuroscience*, *9*, 105.
- Binkofski, F., Amunts, K., Stephan, K. M., Posse, S., Schormann, T., Freund, H. J., ... Seitz, R. J. (2000). Broca's region subserves imagery of motion: A combined cytoarchitectonic and fMRI study. *Human Brain Mapping*, *11*, 273–285.
- Dayan, E., & Cohen, L. G. (2011). Neuroplasticity subserving motor skill learning. *Neuron*, *72*, 443–454.
- Desmurget, M., & Sirigu, A. (2009). A parietal-premotor network for movement intention and motor awareness. *Trends in Cognitive Sciences*, *13*, 411–419.
- Doyon, J., & Benali, H. (2005). Reorganization and plasticity in the adult brain during learning of motor skills. *Current Opinion in Neurobiology*, *15*, 161–167.
- Fery, Y.-A. (2003). Differentiating visual and kinesthetic imagery in mental practice. *Canadian Journal of Experimental Psychology*, *57*, 1–10.
- Fleming, M. K., Stinear, C. M., & Byblow, W. D. (2010). Bilateral parietal cortex function during motor imagery. *Experimental Brain Research*, *201*, 499–508.
- Gentili, R., Han, C. E., Schweighofer, N., & Papaxanthis, C. (2010). Motor learning without doing: Trial-by-trial improvement in motor performance during mental training. *Journal of Neurophysiology*, *104*, 774–783.
- Gerardin, E., Sirigu, A., Lehericy, S., Poline, J. B., Gaymard, B., Marsault, C., ... Le Bihan, D. (2000). Partially overlapping neural networks for real and imagined hand movements. *Cerebral Cortex (New York, N.Y. : 1991)*, *10*, 1093–1104.
- Goss, S., Hall, C., Buckolz, E., & Fishburne, G. (1986). Imagery ability and the acquisition and retention of movements. *Memory & Cognition*, *14*, 469–477.
- Guillot, A., Collet, C., Nguyen, V. A., Malouin, F., Richards, C., & Doyon, J. (2009). Brain activity during visual versus kinesthetic imagery: An fMRI study. *Human Brain Mapping*, *30*, 2157–2172.
- Hall, C. R., & Martin, K. A. (1997). Measuring movement imagery abilities: A revision of the Movement Imagery Questionnaire. *Journal of Mental Imagery*, *21*, 143–154.
- Harris, I. M., & Miniussi, C. (2003). Parietal lobe contribution to mental rotation demonstrated with rTMS. *Journal of Cognitive Neuroscience*, *15*, 315–323.
- Héту, S., Grégoire, M., Saimpont, A., Coll, M. P., Eugène, F., Michon, P. E., & Jackson, P. L. (2013). The neural network of motor imagery: An ALE meta-analysis. *Neuroscience and Biobehavioral Reviews*, *37*, 930–949.
- Hund-Georgiadis, M., & Yves Von Cramon, D. (1999). Motor-learning-related changes in piano players and non-musicians revealed by functional magnetic-resonance signals. *Experimental Brain Research*, *125*, 417–425.
- Ishai, A., Ungerleider, L. G., & Haxby, J. V. (2000). Distributed neural systems for the generation of visual images. *Neuron*, *28*, 979–990.
- Jackson, P. L., Lafleur, M. F., Malouin, F., Richards, C. L., & Doyon, J. (2003). Functional cerebral reorganization following motor sequence learning through mental practice with motor imagery. *NeuroImage*, *20*, 1171–1180.
- Jäncke, L., Shah, N. J., & Peters, M. (2000). Cortical activations in primary and secondary motor areas for complex bimanual movements in professional pianists. *Brain Research. Cognitive Brain Research*, *10*, 177–183.
- Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *NeuroImage*, *14*, S103–S109.
- Johnson, S. (2002). Selective activation of a parietofrontal circuit during implicitly imagined prehension. *NeuroImage*, *17*, 1693–1704. <http://linkinghub.elsevier.com/retrieve/pii/S1053811902912656>.
- Kim, W., Chang, Y., Kim, J., Seo, J., Ryu, K., Lee, E., ... Janelle, C. M. (2014). An fMRI study of differences in brain activity among elite, expert, and novice archers at the moment of optimal aiming. *Cognitive and Behavioral Neurology: Official Journal of the Society for Behavioral and Cognitive Neurology*, *27*, 173–182.
- Kraeutner, S. N., Keeler, L. T., & Boe, S. G. (2016). Motor imagery-based skill acquisition disrupted following rTMS of the inferior parietal lobule. *Experimental Brain Research*, *234*, 397–407.
- Kuhtz-Buschbeck, J. P., Mahnkopf, C., Holzknecht, C., Siebner, H., Ulmer, S., & Jansen, O. (2003). Effector-independent representations of

- simple and complex imagined finger movements: A combined fMRI and TMS study. *The European Journal of Neuroscience*, 18, 3375–3387.
- Lacourse, M. G., Orr, E. L. R., Cramer, S. C., & Cohen, M. J. (2005). Brain activation during execution and motor imagery of novel and skilled sequential hand movements. *NeuroImage*, 27, 505–519.
- Lacourse, M. G., Turner, J. A., Randolph-Orr, E., Schandler, S. L., & Cohen, M. J. (2004). Cerebral and cerebellar sensorimotor plasticity following motor imagery-based mental practice of a sequential movement. *Journal of Rehabilitation Research and Development*, 41, 505.
- Lebon, F., Byblow, W. D., Collet, C., Guillot, A., & Stinear, C. M. (2012a). The modulation of motor cortex excitability during motor imagery depends on imagery quality. *European Journal of Neuroscience*, 35, 323–331.
- Lebon, F., Collet, C., & Guillot, A. (2010). Benefits of motor imagery training on muscle strength. *Journal of Strength and Conditioning Research*, 24, 1680–1687.
- Lebon, F., Lotze, M., Stinear, C. M., & Byblow, W. D. (2012b). Task-dependent interaction between parietal and contralateral primary motor cortex during explicit versus implicit motor imagery. *PLoS One*, 7, 7–12.
- Lorey, B., Pilgramm, S., Bischoff, M., Stark, R., Vaitl, D., Kindermann, S., ... Zentgraf, K. (2011). Activation of the parieto-premotor network is associated with vivid motor imagery—A parametric fMRI study. *PLoS One*, 6, 1–10.
- Lotze, M., Braun, C., Birbaumer, N., Anders, S., & Cohen, L. G. (2003). Motor learning elicited by voluntary drive. *Brain: A Journal of Neurology*, 126, 866–872.
- Lovell, G., & Collins, D. (2001). Speed of image manipulation, imagery ability and motor skill acquisition. *International Journal of Sport Psychology*, 32, 355–368.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9, 97–113.
- Olsson, C.-J. (2008). Learning by doing and learning by thinking: An fMRI study of combining motor and mental training. *Frontiers in Human Neuroscience*, 2, 1–7.
- Pascual-Leone, A., Nguyet, D., Cohen, L. G., Brasil-Neto, J. P., Cammarota, A., & Hallett, M. (1995). Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. *Journal of Neurophysiology*, 74, 1037–1045.
- Pelgrims, B., Andres, M., & Olivier, E. (2009). Double dissociation between motor and visual imagery in the posterior parietal cortex. *Cerebral Cortex (New York, N.Y. : 1991)*, 19, 2298–2307.
- Pilgramm, S., de Haas, B., Helm, F., Zentgraf, K., Stark, R., Munzert, J., & Krüger, B. (2016). Motor imagery of hand actions: Decoding the content of motor imagery from brain activity in frontal and parietal motor areas. *Human Brain Mapping*, 37, 81–93.
- Ranganathan, V. K., Siemionow, V., Liu, J. Z., Sahgal, V., & Yue, G. H. (2004). From mental power to muscle power - Gaining strength by using the mind. *Neuropsychologia*, 42, 944–956.
- Ridderinkhof, K. R., & Brass, M. (2015). How kinesthetic motor imagery works: A predictive-processing theory of visualization in sports and motor expertise. *Journal of Physiology, Paris*, 109, 53–63.
- Robertson, E. M. (2007). The serial reaction time task: Implicit motor skill learning? *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 27, 10073–10075.
- Schuster, C., Hilfiker, R., Amft, O., Scheidhauer, A., Andrews, B., Butler, J., ... Ettlin, T. (2011). Best practice for motor imagery: A systematic literature review on motor imagery training elements in five different disciplines. *BMC Medicine*, 9, 75.
- Sharma, N., & Baron, J.-C. (2013). Does motor imagery share neural networks with executed movement: A multivariate fMRI analysis. *Frontiers in Human Neuroscience*, 7, 1–8. <http://journal.frontiersin.org/article/10.3389/fnhum.2013.00564/abstract>.
- Sharma, N., Jones, P. S., Carpenter, T. A., & Baron, J. C. (2008). Mapping the involvement of BA 4a and 4p during Motor Imagery. *NeuroImage*, 41, 92–99.
- Sirigu, A., Duhamel, J.-R., Cohen, L., Pillon, B., Dubois, B., & Agid, Y. (1996). The mental representation of hand movements after parietal cortex damage. *Science (80-)*, 273, 1564–1568.
- Solodkin, A., Hlustik, P., Chen, E. E., & Small, S. L. (2004). Fine modulation in network activation during motor execution and motor imagery. *Cerebral Cortex (New York, N.Y. : 1991)*, 14, 1246–1255.
- Stinear, C. M., Byblow, W. D., Steyvers, M., Levin, O., & Swinnen, S. P. (2006). Kinesthetic, but not visual, motor imagery modulates corticomotor excitability. *Experimental Brain Research*, 168, 157–164.
- Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., ... Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *NeuroImage*, 15, 273–289.
- Vergeer, I., & Roberts, J. (2006). Movement and stretching imagery during flexibility training. *Journal of Sports Sciences*, 24, 197–208.
- Walz, A. D., Doppl, K., Kaza, E., Roschka, S., Platz, T., & Lotze, M. (2015). Changes in cortical, cerebellar and basal ganglia representation after comprehensive long term unilateral hand motor training. *Behavioural Brain Research*, 278, 393–403.
- Yue, G., & Cole, K. J. (1992). Strength increases from the motor program: Comparison of training with maximal voluntary and imagined muscle contractions. *Journal of Neurophysiology*, 67, 1114–1123.
- Zapparoli, L., Invernizzi, P., Gandola, M., Verardi, M., Berlinger, M., Sberna, M., ... Paulesu, E. (2013). Mental images across the adult lifespan: A behavioural and fMRI investigation of motor execution and motor imagery. *Experimental Brain Research*, 224, 519–540.
- Zhang, H., Xu, L., Wang, S., Xie, B., Guo, J., Long, Z., & Yao, L. (2011). Behavioral improvements and brain functional alterations by motor imagery training. *Brain Research*, 1407, 38–46.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Lebon F, Horn U, Domin M, Lotze M. Motor imagery training: Kinesthetic imagery strategy and inferior parietal fMRI activation. *Hum Brain Mapp*. 2018;39:1805–1813. <https://doi.org/10.1002/hbm.23956>