

# Neural and Behavioral Outcomes Differ Following Equivalent Bouts of Motor Imagery or Physical Practice

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## Abstract

■ Despite its reported effectiveness for the acquisition of motor skills, we know little about how motor imagery (MI)-based brain activation and performance evolves when MI (the imagined performance of a motor task) is used to learn a complex motor skill compared to physical practice (PP). The current study examined changes in MI-related brain activity and performance driven by an equivalent bout of MI- or PP-based training. Participants engaged in 5 days of either MI or PP of a dart-throwing task. Brain activity (via fMRI) and performance-related outcomes were obtained using a pre/post/retention design. Relative to PP, MI-based training did not drive robust changes in brain activation and was

inferior for realizing improvements in performance: Greater activation in regions critical to refining the motor program was observed in the PP versus MI group posttraining, and relative to those driven via PP, MI led only to marginal improvements in performance. Findings indicate that the modality of practice (i.e., MI vs. PP) used to learn a complex motor skill manifests as differences in both resultant patterns of brain activity and performance. Ultimately, by directly comparing brain activity and behavioral outcomes after equivalent training through MI versus PP, this work provides unique knowledge regarding the neural mechanisms underlying learning through MI. ■

## INTRODUCTION

Substantial evidence indicates that reliable changes of brain activation result from motor skill learning (Dayan & Cohen, 2011; Doyon & Benali, 2005; Ungerleider, Doyon, & Karni, 2002). With repeated practice, novices move along the expertise continuum, realizing improvements in performance coincident with brain activity that is decreased in magnitude, particularly in cortical areas, and more strongly lateralized (contralateral) to the effector used in the task (Dayan & Cohen, 2011; Nakata, Yoshie, Miura, & Kudo, 2010; Yarrow, Brown, & Krakauer, 2009). Although our knowledge of how performance and brain activation patterns evolve as learning occurs is derived almost exclusively from studies employing physical practice (PP), the “gold standard” to learn a motor skill, motor imagery (MI; the imagined performance of a motor task), is often used during assessments of brain activation as many complex motor skills cannot be performed in the various neuroimaging environments (e.g., fMRI, magnetoencephalography; see Baeck et al., 2012; Wei & Luo, 2010, for examples). MI is thought to be a useful facsimile to PP given the notion they share similar neural representations, with MI facilitating a simulation of the movement (i.e., motor simulation theory; e.g., O’Shea & Moran, 2017; Grèzes & Decety, 2001; Holmes & Collins,

2001; Jeannerod, 1994). However, one unknown factor related to motor skill learning is how the modality in which the individual practices (MI vs. PP) modulate changes in both performance and MI-based brain activity. Specifically, despite evidence showing the effectiveness of MI in motor skill learning (e.g., Di Rienzo et al., 2016; Schuster et al., 2011; Driskell, Copper, & Moran, 1994), we know comparatively little about the evolution of performance and MI-based brain activation patterns when this modality of practice is used to facilitate learning of a complex motor skill (Frank & Schack, 2017; Ruffino, Papaxanthis, & Lebon, 2017). Furthermore, as PP is more consistently associated with activation of cerebellar and cortical motor regions implicated in the modification and execution of motor programs, and MI is more consistently associated with activation of frontal and parietal regions critical to visuomotor transformation and generation of the motor program, the type of encoding that occurs during PP and MI-based learning may differ (see Frank & Schack, 2017; Ingram, Kraeutner, Solomon, Westwood, & Boe, 2016; Annett, 1995, for examples).

In line with the motor simulation theory, recent work indicates that expertise is reflected in patterns of MI-based brain activation (Kraeutner, McWhinney, Solomon, Dithurbide, & Boe, 2018; Debarnot, Sperduti, Di Rienzo, & Guillot, 2014; Chang et al., 2010; Milton, Solodkin, Hluatík, & Small, 2007). For instance, when varsity athletes performed MI of their sport-specific skills compared with a

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novel task for which they had no expertise, a decrease in recruitment of bilateral frontal and parietal regions was observed (Kraeutner et al., 2018). Similarly, when comparing brain activation during MI of a sport-specific skill between novices and the varsity athletes, more focal patterns of activation (i.e., decreased recruitment of bilateral regions involved in motor planning) were observed in the varsity athletes (i.e., the experts; Kraeutner et al., 2018). In contrast, no differences in patterns of brain activation were observed when the varsity athletes and novices performed MI of a task for which both groups lacked expertise (Kraeutner et al., 2018). This evidence demonstrates that alterations to the motor representation associated with skill learning are reflected in MI-related brain activation (e.g., Kraeutner et al., 2018; DeBarnot et al., 2014; Chang et al., 2010), but no conclusions can be drawn with regard to the extent to which practice modality contributed to the achieved level of expertise, as the extent to which MI was used to facilitate learning is unknown.

Longitudinal training studies using PP have demonstrated changes in brain activity during MI (Bar & DeSouza, 2016; Baeck et al., 2012; Lacourse, Orr, Cramer, & Cohen, 2005). In a task involving shooting, Baeck et al. (2012) demonstrated increased activation in parietal and frontal regions (including the SMA) during MI after novices trained with PP. A similar methodology was used with professional dancers acquiring a new dance via PP (Bar & DeSouza, 2016), finding that MI-related activity within the SMA and auditory regions initially increased (i.e., during the early stages of training) but then decreased over the course of training. Lacourse et al. (2005) assessed MI-related brain activation before and after 1 week of PP of a sequence task, noting an increase in activation localized to frontal and parietal areas after training—areas known to be associated with control of visually guided actions (Binkofski & Buxbaum, 2013; Culham, Cavina-Pratesi, & Singhal, 2006; Rizzolatti & Matelli, 2003). In addition, decreased cerebellar and increased striatal activation was found after training, which is a typical pattern for motor learning (e.g., Censor, Dayan, & Cohen, 2014; Dayan & Cohen, 2011; Penhune & Doyon, 2002). As noted earlier, studies that employ only PP during training do not address the question of how the modality of practice used to learn the skill (i.e., MI vs. PP) affects performance outcomes and patterns of brain activity.

There is a body of work examining changes in brain activation after MI-based sequence learning that provides some insight into how the modality of practice used to learn the skill manifests in the resultant brain activity (Zhang et al., 2011; Jackson, Lafleur, Malouin, Richards, & Doyon, 2003; Pascual-Leone et al., 1995). MI-related brain activation was assessed before and after MI-based practice of a keypress sequence task (14 sessions; Zhang et al., 2011) and foot sequence task (five sessions; Jackson et al., 2003). After training, increased activity was observed in regions linked to generating or accessing the mental representation of a movement (in particular, cingulate cortex and precuneus; Zhang et al., 2011) as well

as to reward- or familiarity-based response selection (viz., OFC; Jackson et al., 2003; Elliott, Dolan, & Frith, 2000). Furthermore, Pascual-Leone and colleagues showed 5 days of mental practice of a piano-based sequence task that encompassed both motor and auditory imagery resulted in a significant expansion of task-related representations in the primary motor cortex, although the magnitude of the change and associated improvement in performance was inferior to that observed for PP (Pascual-Leone et al., 1995). One limitation of these studies is the exclusive use of sequence tasks that are limited in the range and complexity of motor skills and thus do not likely generalize to the learning of complex motor tasks (Wulf & Shea, 2002). Thus, how patterns of brain activation associated with learning a complex skill through PP versus MI is unclear.

To address the limitations of previous research, and particularly the lack of studies examining learning of complex motor skills that link performance outcomes to brain activation driven via different modalities of practice (e.g., MI and PP), this study directly compares changes in brain activity and performance outcomes (i.e., accuracy, consistency, and kinematics) before and after 5 days of training of a dart-throwing task via MI or PP. In addition to assessing performance at the pretraining and post-training time points, learning was assessed via a retention test administered a minimum of 24 hr after the final training session. We hypothesized that, for both MI- and PP-based training, there would be increased activity in cerebellar and contralateral motor regions, with the effect being attenuated for MI versus PP. We hypothesized that performance would improve after both MI- and PP-based training (as demonstrated via increased accuracy and consistency), although these improvements would be less for MI versus PP. Finally, owing to prior work suggesting differences in the type of encoding that occurs during MI- and PP-based learning (e.g., Frank & Schack, 2017; Kraeutner, Ingram, & Boe, 2017; Ingram et al., 2016; Kraeutner, Keeler, & Boe, 2016), we expected that robust kinematic changes would occur only after training via PP.

## METHODS

### Participants

Twenty-four participants (right-handed, as determined by a score of  $\geq 40$  on the Edinburgh Handedness Inventory [Oldfield, 1971]) were recruited from the local and university community. The Nova Scotia Health Authority research ethics board approved the study. All participants were healthy, reported normal hearing, were free of neurological disorders, had no contraindications to MRI, and each provided written informed consent. All participants engaged in five training sessions of the dart-throwing task involving either PP (PP group) or imagined practice (MI group). All participants underwent fMRI before (pretraining) and

after (posttraining) the five training sessions to obtain brain activity during MI of the dart-throwing task.

### Experimental Design

At the outset of the experiment, after the informed consent and screening process, participants completed the Motor Imagery Questionnaire-Revised Second Version (MIQ-RS) to characterize each individual's ability to perform MI (Gregg, Hall, & Butler, 2010; Gregg, Hall, & Nederhof, 2005), as previous work has shown questionnaires (including the MIQ-RS) to reflect processes critical to imagery ability (Kraeutner, Eppler, Stratas, & Boe, 2020). The MIQ-RS is a self-report questionnaire that assesses the vividness and intensity of both the visual and kinesthetic dimensions of MI, with increasing scores indicative of higher imagery quality (Gregg et al., 2005, 2010).

### Training Sessions

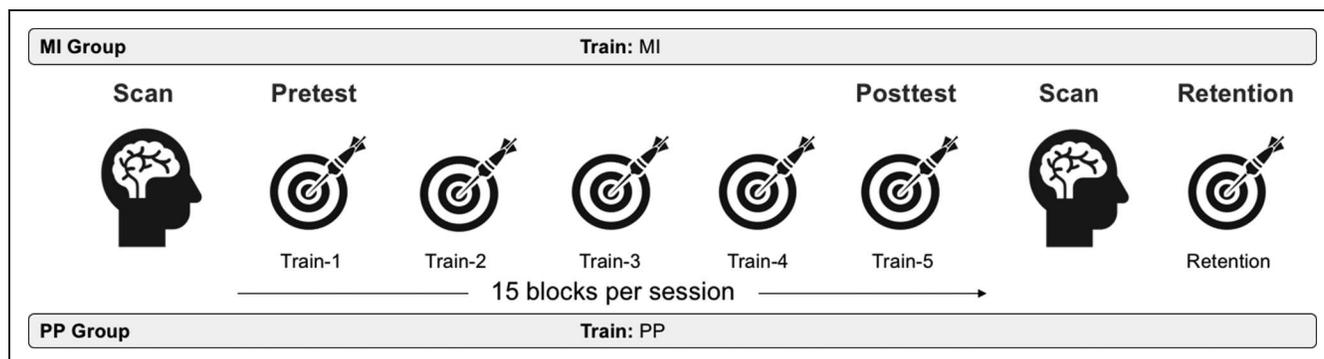
Each training session (Figure 1) lasted ~20 min and involved 15 blocks, with six dart throws per block (i.e., 90 dart throws per session, established via prior work examining learning of a dart task [Querfurth, Schücker, de Lussanet, & Zentgraf, 2016; Didier, Li, & Magill, 2013; Spittle & Kremer, 2010; Kremer, Spittle, McNeil, & Shinnars, 2009; McDonald, van Emmerik, & Newell, 1989; Mendoza & Wichman, 1978]). Dart throwing was performed in accordance with World Darts Federation regulations (World Darts Federation, 2017). Specifically, a competition bristle dartboard was set to regulation height (1.73 m from ground to bull's-eye) and distance (2.37 m from throwing line). Participants were instructed to aim at the bull's-eye and to limit their throws to flexion and extension movements at the elbow in the sagittal plane. Participants performed, or imagined performing, the dart throws (depending on group; PP or MI) with their dominant (right) arm. At the outset of training, participants watched a 5-min video that familiarized them to the task and provided exemplar performances from male

and female performers from both the third- and first-person perspectives.

For the PP sessions, participants threw nickel/brass-tipped darts that weighed 22 g. Participants were prompted by the experimenter to take a break at the end of each block. For the MI sessions, elements from the PETTLEP model of imagery were incorporated to ensure similarity with the PP sessions (Holmes & Collins, 2001). Specifically, participants were instructed to perform kinesthetic MI (i.e., first-person perspective with an emphasis on the polysensory aspect of the task; Schuster et al., 2011; Stinear, Byblow, Steyvers, Levin, & Swinnen, 2006) with their eyes closed. Kinesthetic MI was chosen as this type of MI is proposed to show greater functional equivalence with PP than other forms of imagery and thus better facilitate skill learning (e.g., Callow, Jiang, Roberts, & Edwards, 2016; Stinear et al., 2006; Holmes & Collins, 2001). Instructions on how to perform this type of MI (i.e., to focus on the feeling of the movement) were provided at the onset of each session. An auditory script was delivered via noise-canceling headphones, directing the participants to attend to sensory information related to task performance (e.g., the feel of the dart in one's hand, how long the movement takes, the position of one's body). Following the instructions, the auditory script guided participants through the training session, prompting the participants to imagine picking up the darts and to begin each block when ready. Participants were given 30 sec to complete each block of imagined throws (i.e., similar to the time it took to complete each block of physical throws) and were cued via the auditory script to open their eyes and take a break at the end of each block. Furthermore, participants performed the MI standing in front of the dart board at the toe line, with their arms relaxed at their sides, such that these sessions were not influenced by any physical exposure to the task.

### Test Blocks

To obtain our task-related performance outcomes, all participants engaged in a physical test block lasting



**Figure 1.** Timeline of the experimental design. Participants engaged in five training sessions of either PP- or MI-based practice of a dart-throwing task. Participants completed three physical testing sessions in a pre/post design (i.e., before the start of training on Day 1 or after training on Day 5, with an additional retention test), as well as two fMRI sessions pretraining/posttraining to capture changes in brain activation.

~15 min in a pre/post design, with an additional retention test administered after the posttraining scan (i.e., at least 24 hr but no more than 72 hr after the posttest; Figure 1). Each test block was composed of 18 dart throws, performed in three blocks of six (similar to parameters employed in Querfurth et al., 2016; Tyč & Boyadjian, 2011; Lohse, Sherwood, & Healy, 2010). The final location of each dart was digitized (Polhemus Fastrak) relative to the board in the order that they were thrown and stored for offline analysis. During the test blocks, video was recorded via a Canon Powershot SX280 HS (Canon Canada, Inc.) mounted on a tripod and placed perpendicular to the throwing line, to capture participant kinematics in the sagittal plane and stored for offline analysis.

### MRI Acquisition

Structural and functional MRI data were acquired on a 3-T GE MRI (GE Medical Systems, with a 32-channel radio-frequency head coil). A 3-D T1-weighted anatomical image was acquired using an inversion-recovery-prepped fast spoiled gradient recalled echo sequence (inversion time = 450 msec, repetition time [TR] = 4.0 msec, echo time (TE) = 1.33 msec, flip angle = 9°, field of view [FOV] = 25.6 cm, 256 × 256, 184 sagittal slices at 1-mm thickness, autocalibrating reconstruction for Cartesian imaging [ARC] phase acceleration = 1, ARC slice acceleration = 1). A T2-weighted anatomical image was acquired using a 3-D CUBE sequence (inversion time = 400 msec, TR = 4200 msec, TE = 101 msec, echo train length = 140, 25.6-cm FOV, 256 × 256, 184 sagittal slices at 1-mm thickness, ARC phase acceleration = 1.5, ARC slice acceleration = 1). Functional MRI data were acquired using a 2-D multiband EPI sequence (TR = 950 msec, TE = 30 msec, flip angle = 60°, 21.6-cm FOV, 72 × 72, 3-mm thick slices, 224 volumes, MUX acceleration factor 3 slice direction, ARC acceleration factor 2 in-plane; Stanford Center for Cognitive and Neurobiological Imaging, <http://cni.stanford.edu>). Additional EPI reference scans with matching parameters except phase-encode blip direction reversal were acquired to facilitate field distortion correction (Smith et al., 2004; Andersson, Skare, & Ashburner, 2003).

The fMRI experiment included four runs performed in a block design. Each run began and ended with a rest block and included two imagery blocks of the darts task alternating with rest blocks. Each imagery block lasted 28.5 sec, during which participants were asked to imagine performing six dart throws, similar to a single block during the training/testing sessions. The start of each block was cued visually. Participants performed kinesthetic imagery with their eyes closed, and an auditory tone cued participants to the end of each imagery block. Each rest block lasted 19 sec during which participants were asked to rest quietly with their eyes open. After the completion of each run, participants completed an MI manipulation check where they were asked to rate both their engagement and quality of imagery on a scale of 1 (*not engaged; poor quality*) to 5

(*extremely engaged; excellent quality*). To ensure that the resultant brain activation could be attributed to MI uncontaminated by movement (Kraeutner, Gionfriddo, Bardouille, & Boe, 2014), we visually monitored each run for the presence of overt movement. Visual monitoring was employed as we were unable to obtain a measure of muscle activity (e.g., electromyography) during the fMRI session. Stimuli were delivered using Presentation software (Neurobehavioral Systems, Inc.), synchronized to MRI data acquisition. Stimuli were presented on a mylar screen positioned across the scanner bore via an LCD projector, which participants viewed via an angled mirror. Before beginning the functional runs, participants were familiarized with the task and type of MI (first person, kinesthetic) via an auditory script and a 30-sec clip depicting the darts task.

### Behavioral Analysis

#### Imagery Ability and Manipulation Checks

To ensure similarity in the ability to perform MI across groups, MIQ-RS scores were tabulated across participants for each imagery condition (kinesthetic and visual) and a 2 (imagery condition) × 2 (group) mixed ANOVA was conducted to assess the between-group effects of imagery condition on MIQ-RS score. In addition, responses for both manipulation checks during the neuroimaging sessions were averaged across participants for each run and scan to ensure similarity in imagery performance across groups. Separate 2 (Time Point) × 2 (Group) mixed ANOVAs were conducted on each outcome measure (engagement, quality) to assess the between-group effects on task engagement and imagery quality.

#### Performance Outcomes

Performance was measured in terms of accuracy (radial error [RE]) and consistency (bivariate variable error [BVE]; Querfurth et al., 2016; Sherwood, Lohse, & Healy, 2014; Schorer, Jaitner, Wollny, Fath, & Baker, 2012; Lohse, Sherwood, et al., 2010; Edwards et al., 2007; Hancock, Butler, & Fischman, 1995). For the above noted outcome measures, the bull's-eye was considered the point of origin (0,0), and deviations in the  $x$  and  $y$  plane from the point of origin were obtained from the digitized data. The first throw of each block during the test sessions was considered warm-up and omitted from further analyses (i.e., leaving 15 total throws per test session). For both performance and kinematic outcomes, outliers were identified as throws that exceeded 3  $SDs$  above the mean for each participant across sessions and were removed from further analyses.

#### Kinematics

Video data were analyzed using Dartfish Pro motion analysis software (Dartfish HQ) to derive shoulder angle,

**Table 1.** Behavioral Data (Mean and *SD*) for Performance Outcomes

			<i>Test Session</i>				
			<i>Pretest</i>	<i>Posttest</i>	<i>d (Pre vs. Post)</i>	<i>Retention</i>	<i>d (Pre vs. Retention)</i>
RE (cm)	MI		8.70 (3.89)	8.93 (5.08)	0.05	8.37(5.41)	-0.07
	PP		8.04 (4.05)	5.96 (1.41)	-0.69	5.75(1.27)	-0.76
BVE (cm)	MI		9.69 (4.72)	8.58 (3.84)	-0.26	8.30(3.33)	-0.34
	PP		9.19 (4.92)	5.72 (1.24)	-0.97	5.97(1.15)	-0.90
<i>Kinematic variable</i>							
Shoulder (°)	Maximum flexion	MI	63.0 (4.4)	65.7 (3.3)	-0.61	66.2 (4.4)	0.00
		PP	68.0 (5.2)	70.8 (2.8)	-1.01	70.4 (3.2)	-0.92
	Release	MI	80.4 (5.3)	80.8 (5.7)	0.09	83.6 (4.2)	-0.33
		PP	82.8 (4.5)	85.3 (3.9)	-0.39	83.2 (3.6)	-0.58
Elbow (°)	Maximum flexion	MI	36.2 (2.6)	36.9 (2.8)	0.24	37.3 (2.7)	0.10
		PP	35.5 (3.1)	38.0 (2.7)	-0.36	37.6 (2.8)	-0.30
	Release	MI	92.4 (13.4)	96.1 (12.9)	-0.16	96.0 (12.3)	-0.38
		PP	96.9 (11.9)	95.2 (11.2)	-0.18	96.5 (10.2)	-0.43
Time (sec)	Preparation	MI	4.4 (1.4)	4.5 (1.3)	-0.32	4.3 (1.1)	-0.47
		PP	3.8 (1.0)	3.52 (0.89)	-0.14	3.9 (1.0)	0.03
	Release	MI	0.18 (0.03)	0.17 (0.03)	-0.07	0.17 (0.03)	0.06
		PP	0.21 (0.03)	0.16 (0.03)	-0.46	0.16 (0.02)	-0.89
Angular velocity <sup>a</sup> (°/sec)	MI	334.5 (95.2)	365.6 (115.4)	0.30	370.7 (111.1)	0.35	
	PP	289.1 (95.7)	350.9 (121.9)	0.55	359.8 (103.8)	0.68	

Effect sizes conducted to characterize changes in performance (posttest minus pretest and retention minus pretest) are included. Improvements in performance are noted by negative effect sizes reflecting a decrease in error (RE and BVE) and kinematic variability and by positive effect sizes reflecting an increase in angular velocity.

<sup>a</sup>Effect sizes calculated for angular velocity were conducted on the mean values observed for each time point, and thus a positive effect size is indicative of an increase in angular velocity across practice sessions.

elbow angle, throwing time, and preparation time (Sherwood et al., 2014; Lohse, Sherwood, et al., 2010). Shoulder and elbow flexion angles were measured at the point of maximum elbow flexion (i.e., also termed the “take back”) and the point of release for each dart throw, with anatomical markers placed on the acromion process, olecranon, and highest point of the iliac crest in line with the coronal plane of the body (for shoulder angle) or styloid process of the throwing arm (for elbow angle). Throwing time was defined as the time between maximum elbow flexion to the point of release. Preparation time was defined as the time between the point of release (i.e., of trial *N*) to maximum flexion of the subsequent throw (i.e., of trial *n* + 1; see Lohse,

Sherwood, et al., 2010). Mean and *SD* values are reported for these kinematic variables, but like Lohse, Sherwood, et al. (2010), only *SD* (calculated across trials per test session for each participant) was used in the group-level analyses (described below) as we were interested in assessing changes in kinematic variability. Angular velocity, defined as the angle at maximum flexion subtracted from the point of release and divided by the throwing time, was also calculated (Lohse, Sherwood, et al., 2010). For angular velocity, we assessed changes in the absolute values (i.e., mean values) instead of its variability for each group, consistent with prior literature suggesting that increased angular velocity is associated with expert performance of throwing tasks (Hansen, Rezzoug, Gorce, &

**Table 2.** Linear Mixed Effects Conducted to Assess Changes Related to RE

Predictors	RE (cm)		
	Estimates	CI	<i>p</i>
(Intercept)	13.48	6.39, 20.57	<b>&lt;.001</b>
PP group	-0.32	-2.93, 2.29	.811
Posttest	0.23	-1.08, 1.54	.729
Retention	-0.34	-1.65, 0.97	.613
Male	-2.79	-5.34, -0.25	<b>.032</b>
Age	-0.16	-0.44, 0.12	.252
PP group: Posttest	-2.31	-4.18, -0.44	<b>.015</b>
PP group: Retention	-2.05	-3.92, -0.18	<b>.032</b>
Random effects			
$\sigma^2$	35.84		
$\tau_{00}$ participant	7.15		
ICC <sub>participant</sub>	.17		
Observations	953		
Marginal $R^2$ / conditional $R^2$	.082/.235		

Values that reached statistical significance ( $p < 0.05$ ) are indicated in **bold**.

Isableu, 2012) and that precision of speed is a critical factor underlying throwing consistency in darts (Smeets, Frens, & Brenner, 2002).

### Group-Level Analyses

A linear mixed effects model conducted using the LME4 package (Bates, Maechler, & Bolker, 2015) was used to assess changes related to RE as a function of group, time point, and their interaction with participant entered as a random effect. The base model was significantly improved through inclusion of age and sex (as measured using Akaike information criterion; Akaike, 1974); thus, terms for age and sex were included in the final model. Linear mixed effects modeling was employed to account for both random and fixed effects, thus allowing for greater control over the sources of variability and increased sensitivity of the analysis. This same analysis could not be applied to BVE or kinematic variability, as these outcomes are calculated across throws within a session. Thus, mean values for BVE and kinematic variability were determined for each participant at each test session (pre/post/retention), and separate 2 (Group)  $\times$  3 (Time Point) mixed ANOVAs were conducted for each measure to assess the between-group effects of training. Before statistical analyses, these data were tested for normality and homogeneity of variance using Shapiro–Wilk and Bartlett’s

tests. Data that did not meet the assumptions of ANOVA were analyzed using nonparametric tests.

Effect sizes were also calculated within each group for each outcome measure to characterize the extent to which performance improved over the course of training. Specifically, we computed effect sizes between the pretest/posttest and pretest/retention test within each group. All statistical analyses were performed using R (R Project for Statistical Computing), with an a priori alpha of .05 denoting significance.

### fMRI Preprocessing and Analysis

Preprocessing and statistical analyses were performed using the Oxford Centre for Functional MRI of the Brain’s (FMRIB) software library (FSL v.5.0.10; FMRIB Oxford, www.fmrib.ox.ac.uk/fsl) and fMRI Expert Analysis Tool (FEAT) Version 5.0.10 (Smith et al., 2004; part of FSL). Preprocessing of the anatomical T1 and T2 scans included registration-based skull-stripping to template brain MNI152\_T1\_1 mm using FLIRT and FNIRT.

fMRI preprocessing included motion correction with MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002), field inhomogeneity-induced distortion correction with reverse-phase encoded blips using TOPUP (Andersson et al., 2003), brain extraction using BET (Smith, 2002), spatial smoothing using a Gaussian kernel (FWHM 5 mm), and high-pass temporal filtering at 0.01 Hz to remove low-frequency noise. Functional images were then rigid-body spatially coregistered (using 6DOF) to the processed anatomical image using FLIRT and combined with the nonlinear registration to MNI152\_1 mm with a voxel size of 3 mm for a group comparison of individual fMRI results.

Individual statistical activation maps were calculated within each run using a general linear model with FEAT with motion outliers included as confounds, determined from a contrast of imagery (darts) versus rest computed for each run (first-level analysis). A second-level analysis combined all runs in a fixed effects model to produce contrast of parameter estimate (COPE) maps for each individual and time point (pre/post).

High-level group analyses were carried out using FLAME (FMRIB’s Local Analysis of Mixed Effects) model with FEAT. All analyses used a corrected cluster threshold of  $z > 2.0$  and a significance threshold of  $p < .05$ , corrected for FWE. To assess the impact of training modality on resultant patterns of MI-related brain activity, a between-group comparison was conducted on the averages of the lower-level COPE maps for each group at the posttraining scan, with a performance outcome (BVE) added as a covariate to account for resultant differences in performance across participants regardless of equal practice of the task. We adjusted for BVE as consistency is shown to be a more stable measure than accuracy and less influenced by external factors (e.g., time of day, fatigue; Kumar et al., 2017; Edwards et al., 2007; Edwards,

**Table 3.** MNI Coordinates of Local Maxima Resulting from Between-group Comparisons Conducted at Each Time Point

<i>Anatomical Region</i>	<i>MNI Coordinates (mm)</i>			<i>Z Score</i>	
	<i>x</i>	<i>y</i>	<i>z</i>		
<b>Pretraining</b>					
MI > PP	R Cerebellum (Lobule VI)	24	-59	-34	3.25
	R Cerebellum (Lobule VIIb)	26	-77	-47	3.38
	R Cerebellum (Lobule VIIb)	33	-69	-47	3.08
	R Cerebellum (Lobule VIII)	22	-59	-37	3.13
	R Cerebellum (Crus I)	39	-88	-32	2.85
	R Cerebellum (Crus II)	28	-90	-40	3.12
PP > MI	-	-	-	-	-
<b>Posttraining</b>					
MI > PP	-	-	-	-	-
PP > MI	L Superior temporal pole	-36	27	-26	3.73
	L Middle temporal gyrus	-67	-10	-2	3.53
	L Superior temporal pole	-46	3	-15	3.4
	L Middle temporal gyrus	-64	-12	-7	3.33
	L Superior temporal pole	-55	12	-10	3.27
	L Superior temporal pole	-56	9	-7	3.27
	L Cerebellum (Lobule VI)	-26	-59	-29	3.22
	L Cerebellum (Lobule VI)	-27	-62	-20	3.1
	L Cerebellum (Lobule IV/V)	-4	-59	-18	3.06
	L Anterior cingulate	0	8	26	3.39
	L Medial frontal gyrus	-11	34	35	2.81
	L Anterior cingulate	-9	33	18	2.73
	L Precentral gyrus	-30	-16	76	3.23
	L SMA	-11	-5	73	3.22
	L SMA	-8	0	81	3.21
	L Paracentral lobule	-16	-20	77	3.13
	R Cerebellum (Lobule IV/V)	10	-46	-7	3.2
	R Cerebellum (Vermis IV/V)	4	-58	-16	3.1
	R Cerebellum (Lobule IV/V)	11	-50	-7	2.93
	R Anterior cingulate	10	12	30	2.81
	R SMA	2	-3	58	2.73
	R SMA	2	3	52	2.71
	R Superior frontal gyrus	16	-3	74	3.11
	R Superior frontal gyrus	27	-5	68	3
Positive BVE effect	-	-	-	-	-
Negative BVE effect	L Superior parietal lobule	-18	-51	51	3.52
	L Superior parietal lobule	-17	-51	53	3.51

**Table 3.** (continued)

Anatomical Region	MNI Coordinates (mm)			Z Score
	x	y	z	
L Precuneus	-18	-51	51	2.91
L Lingual gyrus	-8	-59	53	3.34
L Lingual gyrus	-19	-78	0	3.32
L Lingual gyrus	-21	-78	1	3.32
L Lingual gyrus	-21	-80	0	3.31
L Calcarine	-20	-74	0	3.07
R Superior parietal lobule	21	-66	64	3.45
R Angular gyrus	40	-60	30	3.32
R Superior parietal lobule	27	-56	66	3.02
R Lingual gyrus	19	-77	-1	3.05

Instances in which no significant differences in activation were noted are indicated by dashed lines.

Lindsay, & Waterhouse, 2005). To characterize changes in brain activation driven by each modality of training, averages of the lower-level COPE maps for each time point were compared within groups.

## RESULTS

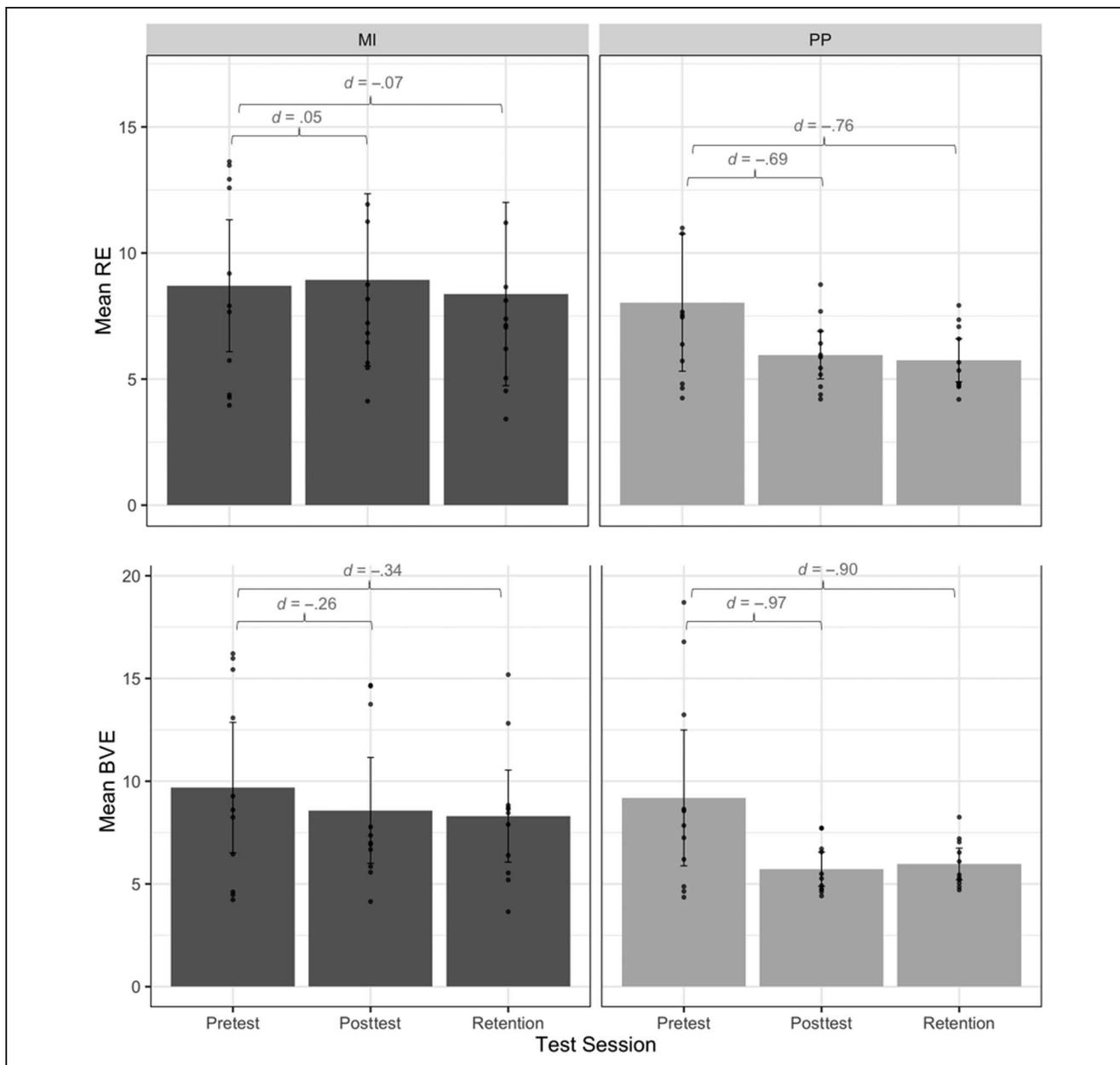
Two participants were excluded from the study (one from the MI group because they did not complete the first MRI session and subsequently dropped out and one from the PP group for excess head motion during scanning that exceeded our exclusion criteria of 2.0 mm), leaving 22 participants (PP group:  $n = 11$ , eight women, aged  $24.6 \pm 4.7$  years; MI group:  $n = 11$ , seven women, aged  $24.5 \pm 4.2$  years) for the final analyses. Furthermore, one participant from the MI group had only engaged in two of the three blocks during each testing session, and kinematic data from another participant from this group were not included in the analysis as they did not remain perpendicular to the camera throughout testing, precluding analysis. Both groups demonstrated similar MI ability, evidenced by MIQ-RS scores in both the visual and kinesthetic imagery conditions (see Supplementary Table 1<sup>1</sup>). Neither the main effect for Group,  $F(1, 20) = 3.34, p = .08$ , or Imagery Condition,  $F(1, 20) = 0.33, p = .57$ , was significant, and the interaction between Group and Imagery Condition was not significant,  $F(1, 20) = 0.67, p = .42$ . Engagement in, and quality of, imagery was also similar between groups at both time points, as evidenced by responses to our manipulation checks during both neuroimaging time points (Supplementary Table 1). For engagement, neither the main effect for Group,  $F(1, 20) = 0.13, p = .72$ , or Time Point,  $F(1, 20) =$

$0.74, p = .40$ , was significant, and the interaction between the two was also not significant,  $F(1, 20) = 1.28, p = .27$ . For quality, neither the main effect for Group,  $F(1, 20) = 1.81, p = .19$ , nor Time Point,  $F(1, 20) = 0.003, p = .96$ , was significant, and the interaction between the two was not significant,  $F(1, 20) = 0.68, p = .42$ . All data pertaining to the MIQ and manipulation checks are included as supplementary materials (Supplementary Table 1).

## Performance Outcomes

Means and standard deviations for all behavioral outcomes are reported in Table 1. Table 2 shows results from the linear mixed effects analysis conducted to assess changes related to RE. Interactions between group and time point were significant at both the posttest and retention, indicating that PP led to greater improvements in RE relative to an equivalent bout of MI (Table 2). As data for BVE did not meet the assumptions of ANOVA, separate Kruskal–Wallis rank sum tests were conducted to analyze the between-group effects at each time point. No between-group differences existed for BVE ( $H = 0.01, p = .92$ ) at the pretest, but BVE was shown to differ between the PP and MI groups at the posttest ( $H = 4.6, p = .03$ ) and retention ( $H = 4.6, p = .04$ ).

Effect sizes calculated within each group (i.e., between test sessions) to characterize improvements in performance revealed a moderate (RE) and large (BVE) effect of training within the PP group (Table 1) at both the posttest and retention. Within the MI group, no difference was noted when comparing RE across time points (i.e., either pre/post or pre/retention); however, a small effect for BVE indicated an improvement in consistency as a result of training (Table 1) at both the posttest and



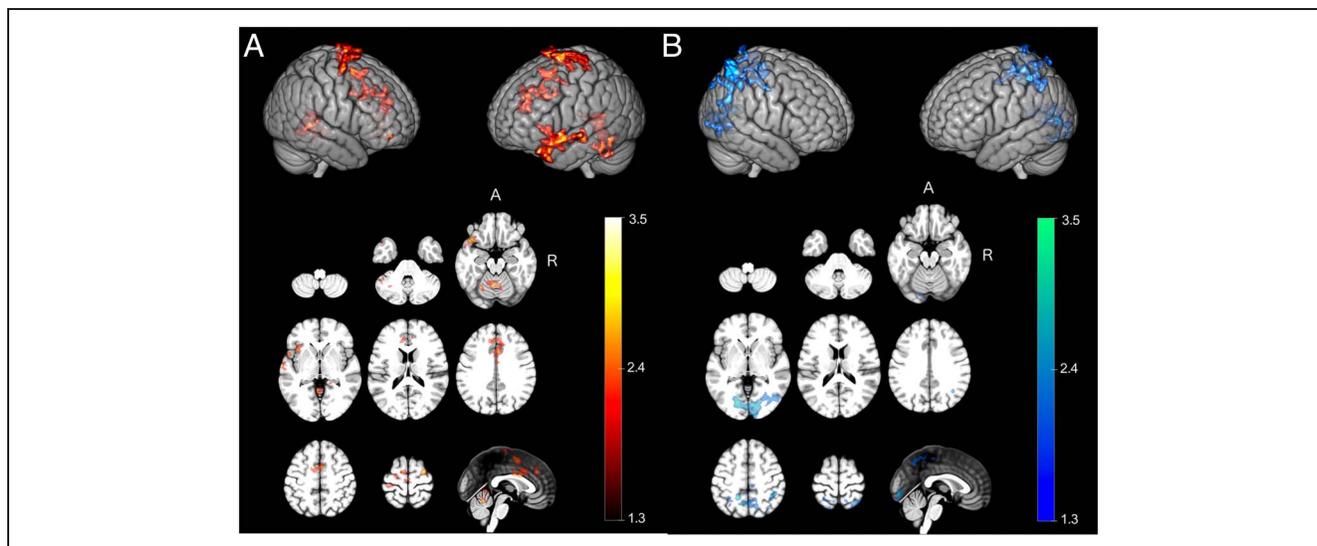
**Figure 2.** Changes in performance outcomes. Mean RE (top) and BVE (bottom) are shown across the pre/post/retention tests for each group. Individual participant means are overlaid, with error bars denoting 95% confidence intervals (see Table 1 for mean values and standard deviations). Effect sizes characterizing improvements in performance (Cohen's *d*) are shown for each group. Whereas the PP group demonstrated improvements in mean RE and BVE across sessions, the MI group only demonstrated improvements in BVE.

retention. Changes observed in performance outcomes across groups are depicted in Figure 2.

### Kinematics

Means and standard deviations for the kinematic variables are reported in Table 1. With the exception of angular velocity, the kinematic data did not meet the assumptions of ANOVA, and therefore separate Kruskal–Wallis rank sum tests were conducted to analyze between-group effects at each time point. No significant differences between groups at each time point were

observed (pre/post/retention). Results from this analysis are included as supplementary materials (Supplementary Table 2). The 2 (Group)  $\times$  3 (Time Point) ANOVA conducted on angular velocity ( $^{\circ}/\text{sec}$ ) revealed no main effect of Group,  $F(1, 19) = 0.29, p = .60$ , and no significant interaction,  $F(1.56, 29.60) = 0.86, p = .41$  (corrected using Greenhouse–Geisser estimates of sphericity). However, a significant main effect of Time Point was observed,  $F(1.56, 29.60) = 8.35, p < .01$  (corrected using Greenhouse–Geisser estimates of sphericity), indicating that angular velocity increased after training regardless of modality. Effect sizes, calculated to characterize the change in



**Figure 3.** (A) Differential effects on resultant MI-based brain activity after training after PP versus MI where the color bar represents the z-max value. Activated voxel clusters remaining after subtraction of the map of activations of the MI group from the PP group, accounting for BVE. Activation was localized to regions including the SMA, ACC, cerebellum, contralateral precentral and middle temporal gyri, and ipsilateral superior frontal gyrus. (B) Correlation between brain activity and performance, where the color bar represents the z-max value. During MI, BVE correlates negatively with brain activity localized to bilateral parietal cortices and lingual gyri. Clusters shown reached a cluster-corrected threshold ( $z > 2.0$ ;  $p < .05$ ), FWE-corrected for number of comparisons, and are shown overlaid on the MNI template.

**Table 4.** MNI Coordinates of the Local Maxima Resulting from Comparisons Conducted to Assess Within-group Differences in MI-related Brain Activation After Training of the Dart-Throwing Task

<i>Anatomical Region</i>	<i>MNI Coordinates (mm)</i>			<i>Z Score</i>	
	<i>x</i>	<i>y</i>	<i>z</i>		
<i>PP group</i>					
Post > pre	L Middle temporal gyrus	-66	-14	-4	4.51
	L Thalamus	-4	-20	-7	4.38
	L Middle temporal gyrus	-62	-4	-8	4.34
	L Anterior cingulate	-14	49	-3	3.54
	L Middle frontal gyrus (orbital)	-18	57	-16	3.53
	L Medial OFC	-10	56	-1	3.36
	R Supramarginal gyrus	44	-39	22	4.53
	R Supramarginal gyrus	46	-39	24	4.45
	R Supramarginal gyrus	49	-39	25	4.43
	R Medial frontal gyrus	6	38	54	3.65
	R Medial OFC	9	59	0	3.51
	R Medial frontal gyrus	15	49	2	3.46
Pre > post	-	-	-	-	-
<i>MI group</i>					
Post > pre	-	-	-	-	-
Pre > post	-	-	-	-	-

Instances in which no significant differences in activation were noted are indicated by dashed lines.

variance across sessions as stated above, revealed a decrease in kinematic variability in the PP group after training across all of our variables of interest (pre/post or pre/retention), with the exception of preparation time (Table 1). Interestingly, elbow angle at the point of release only showed a decrease in kinematic variability from the pretest to retention. In contrast, only kinematic variability of the shoulder angle at maximum flexion, preparation time, and angular velocity showed changes from pretest to posttest in the MI group (Table 1). From the pretest to retention, however, changes were observed for the shoulder and elbow angle at the point of release as well as preparation time (Table 1).

## fMRI

Table 3 reports the Montreal Neurological Institute (MNI) coordinates of activation observed for between-group comparisons, accounting for BVE. To identify a priori group differences in MI-based brain activation, we initially compared activation maps between groups for the pretraining scan. Greater activation, localized to the ipsilateral cerebellum, was observed for the MI group (MI > PP; Table 3). Between-group comparisons at the post-training scan, accounting for BVE, revealed additional activation for the PP group (PP > MI), localized to regions including the SMA, ACC, cerebellum, contralateral precentral and middle temporal gyri, and ipsilateral superior frontal gyrus (Figure 3). No additional activation was observed for the MI group (i.e., MI > PP). Negative correlations between BVE and MI-related activity were found in regions including bilateral parietal cortices and lingual gyri (Table 3, Figure 3).

Table 4 reports the MNI coordinates of activation resulting from within-group comparisons. Within-group comparisons revealed additional activation in contralateral ACC and middle temporal gyrus, ipsilateral inferior parietal lobule (localized to the supramarginal gyrus), and bilateral medial OFC within the PP group when comparing the posttraining to pretraining scans (posttraining > pretraining; Table 4). No decreases in activation were observed (pretraining > posttraining) for the PP group. No significant differences in activation were observed from pretraining to posttraining within the MI group.

## DISCUSSION

The current study sought to determine how the modality of practice used to learn a complex motor skill manifests in the pattern of MI-based brain activity and performance by directly comparing an equal amount of MI- or PP-based training of a complex motor skill. Contrary to our hypotheses, no significant increases in brain activation were driven by MI-based practice. Consistent with our hypotheses, however, we observed greater activation in the PP versus MI group during MI of the dart-throwing task at the posttraining scan, encompassing regions known to

be active during MI (Hardwick, Caspers, Eickhoff, & Swinnen, 2018; Kraeutner et al., 2014; Burianová et al., 2013; Héту et al., 2013; Hanakawa, Dimyan, & Hallett, 2008) and to underlie skilled motor performance and control (Rizzolatti, Cattaneo, Fabbri-Destro, & Rozzi, 2014; Binkofski & Buxbaum, 2013; Hardwick, Rottschy, Miall, & Eickhoff, 2013; Dayan & Cohen, 2011; Rizzolatti, Luppino, & Matelli, 1998). Furthermore, despite both groups engaging in the same amount of training, performance improvements in MI were marginal relative to the improvement in performance observed for PP. In particular, in contrast to robust changes across all outcome measures driven via PP-based training, MI-based training only resulted in small changes related to consistency (albeit to a lesser extent than PP) and few of our kinematic outcomes. MI-based training did not result in improved accuracy, and repetitive movements remained inconsistent within a session as evidenced by the lack of a global decrease in kinematic variability. Below, we discuss our findings in the context of prior work examining MI-based brain activation and the neural networks underlying expertise.

## Modality-specific Differences

Why MI did not result in changes closer to the magnitude observed for PP is attributable to a difference in the mechanism underlying learning between the two modalities related to the absence of sensory information about task performance (e.g., Ingram, Solomon, Westwood, & Boe, 2019; Bonassi et al., 2017; Frank & Schack, 2017; Kraeutner, Ingram, & Boe, 2017; Ingram et al., 2016; Land et al., 2016; Lohse, Healy, & Sherwood, 2010). After PP, but not MI-based training, we observed greater SMA and cerebellar activation, regions critical in the error detection/correction process that is needed for modification of the motor program. It is well established that the SMA is a key substrate in motor planning and execution (Flash & Bizzi, 2016; Dayan & Cohen, 2011; Nachev, Kennard, & Husain, 2008; Tanji & Shima, 1996; Tanji & Kurata, 1982), with increases in SMA activity observed as long-term learning occurs (Dayan & Cohen, 2011). It is thought that the SMA generates a preparatory state for the impending (and forthcoming) movements, ultimately relaying the motor command to the primary motor cortices for output to the effectors (Cunnington, Windischberger, & Moser, 2005; Tanji & Shima, 1996; Tanji & Kurata, 1982; Roland, Larsen, Lassen, & Skinhøj, 1980). Furthermore, prior work suggests the SMA transforms the desired kinematics to be used in the task to the set of forces exerted by the effectors (termed the “kinematics-to-dynamics transformation”; Padoa-Schioppa, Li, & Bizzi, 2002, 2004; Li, Padoa-Schioppa, & Bizzi, 2001). Accordingly, we attribute the lack of SMA activation observed in the MI group post-training relative to PP to the absence of sensory information (i.e., it is covert), in that the dynamics of the movement are likely not being encoded or altered within the motor program.

Output of cerebellar neurons is modulated by discrepancies between predicted and feedback representations in internal models (Brooks & Cullen, 2013), whereby the predicted consequences of the movement (efference copy) are compared to actual movement outcomes (reafference) in a forward model to update the motor program (Popa, Hewitt, & Ebner, 2012; Bastian, 2006; Wolpert, Miall, & Kawato, 1998; Miall & Wolpert, 1996). Integral in error detection/correction, it follows that increases in bilateral cerebellar activation are typically observed in early (i.e., “fast”) stages of PP-based motor learning when error magnitude is large and substantial alterations to the motor program are made (e.g., Dayan & Cohen, 2011; Lacourse, Turner, Randolph-Orr, Schandler, & Cohen, 2004; Seitz et al., 1994). In contrast, MI may instead rely on an alternative internal comparison to facilitate learning as theorized by prior work, in which the predicted consequences of the movement are compared to a simulated feedback representation of the movement (Ingram et al., 2019; Kilteni, Andersson, Houborg, & Ehrsson, 2018; O’Shea & Moran, 2017). Specifically, although one may postulate that removing sensory feedback during PP leads to similar outcomes as MI, prior work demonstrating that MI leads to greater improvements in performance relative to a PP group that did not receive visual feedback after 5 days of practice of a complex skill suggests otherwise (Ingram et al., 2019). Yet, although updates to the motor program are indeed made via MI (Ingram et al., 2019; Kraeutner, MacKenzie, Westwood, & Boe, 2016; Gentili, Han, Schweighofer, & Papaxanthis, 2010; Gentili, Papaxanthis, & Pozzo, 2006), it is likely that any discrepancy observed between the predicted consequences and simulated feedback representation is diminished relative to when feedback is derived from actual sensory information, leading to a lessened reliance on the cerebellum for error detection/correction (i.e., a lack of cerebellar activation observed after MI- vs. PP-based training), as only slight alterations to the motor program are made and, in turn, only marginal changes in performance are realized (i.e., decreased variability of few kinematic outcomes, coupled with improvements related to consistency, but not accuracy, of the dart throw was observed after MI-based training). We therefore suggest robust improvements in performance were not realized because MI is missing the richness of both the ongoing encoding and sensory feedback (which results from overt execution) such that insufficient updates to the motor program are made within each bout of practice.

Importantly, although we might expect greater improvements in performance to result from MI-based training given results observed in prior work, it is critical to consider the extent to which the efficacy of MI in learning a complex motor skill may depend on prior sensory information. Indeed, the greatest gains in performance driven by MI are observed when MI is incorporated with PP (McNeill, Toth, Harrison, & Campbell, 2019; Di Rienzo

et al., 2016; Smith, Wright, & Cantwell, 2008) or when participants have high physical exposure to the task throughout the experiment (i.e., extensive PP during familiarization or test sessions; Zhang et al., 2011; Jackson et al., 2003; Glisky, Williams, & Kihlstrom, 1996; Pascual-Leone et al., 1995). For instance, although MI was shown to drive significant improvements in performance on a complex skill (stabilometer task), participants performed an equivalent number of physical test trials as MI trials embedded throughout training (Glisky et al., 1996). Similarly, Pascual-Leone and colleagues had participants in their mental practice group physically perform 20 repetitions of the sequence to be learned at the end of each practice session, limiting the degree to which the improved performance and expansion of the task-related regions in primary motor cortex can be attributed solely to mental practice (Pascual-Leone et al., 1995). In contrast, in studies whereby physical exposure to the complex motor skill is limited (see Frank, Land, Popp, & Schack, 2014, and Romano-Smith, Wood, Coyles, Roberts, & Wakefield, 2019, for examples), improvements in performance because of MI were observed only after a high (i.e., 18 sessions across 6 weeks; Romano-Smith et al., 2019) versus low (Ingram et al., 2019; Frank et al., 2014) dose of practice, indicating that the marginal alterations to the motor program induced by MI may not translate to behavioral effects after five practice sessions, as in the current study.

Prior work showing that expertise also modulates improvements driven by MI, when exposure to PP across the study is low, further indicates that the efficacy of MI depends on prior sensory information related to the skill (McNeill et al., 2019). After dividing participants into groups based on prior experience with a toe-abduction task, Mulder, Zijlstra, Zijlstra, and Hochstenbach (2004) showed that improvements were only shown after MI for participants who had prior experience with the task. Furthermore, improvements on a golf (bunker) shot driven by MI were observed in a study involving experienced ( $\geq 10$  years) golfers (Smith et al., 2008), yet no improvements were observed after MI-based practice of a golf putt in novices with no prior golf experience (Frank et al., 2014). Interestingly, greater behavioral effects have resulted after MI-based practice in experts versus novices when MI is performed while holding the object used in the MI task (i.e., providing sensory information, Zhang et al., 2018; Wang et al., 2014), despite numerous reports of enhanced cortical activation during both transitive (object-based) and intransitive MI (Li, Wang, Xu, Li, & Xie, 2015; Bisio, Avanzino, Ruggeri, & Bove, 2014; Héту et al., 2013). Taken in the context of the current study, in which participants had low physical exposure to the task and performed imagery with their arms relaxed at their side—mitigating the presence of any relevant muscle activity during the session or sensory feedback during MI—the substitution or presence of task-related sensory information likely impacted the

efficacy of MI. However, future research is required to address this line of inquiry.

### Expertise and MI-related Brain Activation

As previously mentioned, evidence generated primarily from cross-sectional studies has shown that MI-based brain activation associated with novice versus expert performance is more diffuse; additional recruitment of bilateral posterior parietal and visual regions is associated with novice performance when experts versus novices performed imagery of their sport-specific skill (e.g., Chang et al., 2010; Olsson & Nyberg, 2010; Olsson, Jonsson, et al., 2008) and when experts performed imagery of a novel task versus their sport-specific skill (Kraeutner et al., 2018). However, these studies did not permit control over the modality in which the expertise was achieved, nor the amount of training engaged in (across the experts). In extending this prior work, we showed that improvements in performance after a controlled amount of training, regardless of modality, were negatively correlated with activation encompassing bilateral posterior parietal regions and visual regions (localized to lingual gyri and calcarine sulci). Our findings may reflect that participants were still relying on a visual image at the posttraining scan, despite being instructed and oriented to perform kinesthetic imagery, as recruitment of visual areas during MI is typically linked to visual but not kinesthetic imagery (Hétu et al., 2013; Solodkin, Hlustik, Chen, & Small, 2004). Furthermore, posterior parietal and visual regions are thought to be key in generating an initial motor representation or a “new” image of the skill to be learned, as there is no existing motor representation to access (Dayan & Cohen, 2011; Olsson & Nyberg, 2010; Olsson, Jonsson, Larsson, & Nyberg, 2008; Olsson, Jonsson, & Nyberg, 2008). Thus, relying on a visual image may be necessary until adequate exposure to the task has occurred to activate motor pathways and properly perform kinesthetic imagery.

### Limitations

As prior work employing sequence tasks has demonstrated changes in brain activity driven by MI-based training, it is important to consider why we did not observe robust changes in MI-related brain activation after 5 days of MI-based training. As the stages of learning depend on the nature of the task, the fast stage of learning of a sequence task may persist for a number of minutes (Dayan & Cohen, 2011), resulting in a robust change in brain activation after multiple sessions that indicate a shift to the slow stage of learning (Zhang et al., 2011; Jackson et al., 2003). In contrast, we employed a multiarticular complex motor skill whereby the fast stage of learning may persist for a number of months (Dayan & Cohen, 2011), and participants were likely still in this stage at the posttraining scan (evidenced by imperfect accuracy and consistency at the retention test, regardless of

group). Furthermore, that we did not observe statistically significant changes in core motor regions in our within-group analyses is likely due in part to our participants performing MI in the scanner and that these increases may only occur after longer term practice, as shown in Bar and DeSouza (2016). Although the associated lack of changes in brain activation driven by 5 days of training via MI is supported by performance outcomes, robust learning did not occur in the MI group—it may well be that a proportionately larger amount of MI-based training (similar to Romano-Smith et al., 2019) would result in performance improvements and coincident changes in brain activation patterns akin to those driven by PP. Furthermore, it is important to note that we captured kinematic outcomes in 2-D; thus, future work should consider employing more sensitive kinematic outcomes (i.e., in 3-D) when pursuing this unexplored area of research.

Alternatively, methodological limitations should be taken into consideration. Twenty-two participants with 44 imaging sessions were included in final analyses. Although the sample size is consistent with the vast majority of neuroimaging literature, a larger sample may have resulted in greater statistical power. Furthermore, BOLD is (indirectly) reflective of an increased use of neural substrates, yet fMRI is limited by its low temporal resolution and the ability to measure direct electrophysiological activity (Sutton, Ouyang, Karampinos, & Miller, 2009). Although neuronal activity is upregulated during repeated MI-based practice, resulting in lasting changes in the activation pattern during MI of that task (Zhang et al., 2011; Jackson et al., 2003), the extent to which neuronal upregulation occurs in regions associated with skilled motor practice is reduced in magnitude and sustained for a shorter duration than that of PP (evidenced by studies employing direct electrophysiological measures, see Duann & Chiou, 2016; Kraeutner et al., 2014; Burianová et al., 2013, for examples). Thus, any changes in neuronal activation realized in the current study may be too minimal or not sustained long enough and may therefore go undetected by fMRI (Kraeutner et al., 2014; Pfurtscheller & Neuper, 1997).

Finally, we opted to conduct our pretraining scan before familiarizing participants to MI and completing the pretraining testing to provide a true baseline (i.e., a baseline not confounded by any prior exposure to the task). Differences in imagery strategy and/or aspect of the task focused on during the pretraining scan, indicated by the increased ipsilateral cerebellum activation for the MI versus PP group at this time point, may have thus arisen as participants were not yet oriented to the polysensory aspects of the task (although they were instructed to perform kinesthetic MI). However, our primary aim was to examine patterns of brain activation associated with learning (i.e., posttraining) through MI relative to PP, and thus potential differences in imagery strategy at the pretraining scan were unlikely to affect our findings.

## Conclusion

Here, we showed that, relative to PP, MI-based training did not drive robust changes in brain activation and was inferior for realizing improvements in performance: Greater activation in regions critical to refining the motor program was observed in the PP versus MI group post-training, and MI led to smaller improvements in performance relative to PP. Together, our findings indicate that the refinement of the motor program is less robust in MI owing to a difference in the mechanism underlying learning in the absence of sensory information. Ultimately, the current study provides unique knowledge regarding how the modality of practice (i.e., MI vs. PP) used to learn a complex motor skill manifests in resultant patterns of brain activity, as well as differences in performance.

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## Note

1. Supplementary materials for this paper can be retrieved from <https://www.dropbox.com/sh/trq4zre3zh10hj7/AADHkXdnwJOW4RV0yTTgFIha?dl=0>.

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