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Unlike overt movement, motor imagery cannot update internal models

Juliet M. Rowe [a,b], Shaun G. Boe [a,b,c,d,*]

[a] Laboratory for Brain Recovery and Function, Dalhousie University, Halifax, NS, Canada
[b] School of Physiotherapy, Dalhousie University, Halifax, NS, Canada
[c] School of Health and Human Performance, Dalhousie University, Halifax, NS, Canada
[d] Department of Psychology and Neuroscience, Dalhousie University, Halifax, NS, Canada

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ABSTRACT

In overt movement, internal models make predictions about the sensory consequences of a desired movement, generating the appropriate motor commands to achieve that movement. Using available sensory feedback, internal models are updated to allow for movement adaptation and in-turn better performance. Whether internal models are updated during motor imagery, the mental rehearsal of movement, is not well established. To investigate internal modelling during motor imagery, 66 participants were exposed to a leftwards prism shift while performing actual pointing movements (physical practice; PP), imagined pointing movements (motor imagery; MI), or no pointing movements (control). If motor imagery updates internal models, we hypothesized that aftereffects (pointing in the direction opposite the prism shift) would be observed in MI, like that of PP, and unlike that of control. After prism exposure, the magnitude of aftereffects was significant in PP (4.73° ± 1.56°), but not in MI (0.34° ± 0.96°) and control (0.34° ± 1.04°). Accordingly, PP differed significantly from MI and control. Our results show that motor imagery does not update internal models, suggesting that it is not a direct simulation of overt movement. Furthering our understanding of the mechanisms that underlie learning through motor imagery will lead to more effective applications of motor imagery.

1. Introduction

Despite similarities, motor imagery – the mental rehearsal of a movement – is principally different from physical practice because sensory feedback is absent during the imagination of movement, as there is no overt movement. Nevertheless, motor imagery has long been considered the mental simulation of overt movement (Jeannerod, 2001; O'Shea & Moran, 2017), providing a basis for its efficacy in driving skill acquisition and use in numerous applications including neurorehabilitation (Agostini et al., 2021; Caligiore et al., 2017; de Vries & Mulder, 2007; Stevens & Stoykov, 2003; Zimmermann-Schlatter et al., 2008). If motor imagery is truly as analogous to overt movement as motor simulation theory suggests, then motor imagery should use internal models, a process dependent on sensory feedback and critical for motor control and learning. Internal models consist of *forward models*, responsible for making predictions about the sensory consequences of a desired movement, and *inverse models*, responsible for using the current and desired state of the body to choose appropriate motor commands to execute a desired movement (Wolpert et al., 1995). In overt movement, sensory information about the current state of the body is compared to the desired state of the body and used to update the internal model for motor adaptation and improved performance. While the process of updating internal models and adapting to new environments is well documented in overt movement (Flanagan & Wing, 1997; Kawato, 1999; Krakauer et al., 1999; Shadmehr & Mussa-Ivaldi, 1994; Shadmehr et al., 2010), little is known about internal modelling during motor imagery.

In 2004 Grush proposed motor emulation theory, suggesting that motor imagery is the conscious perception of forward modelling: motor imagery uses a copy of the motor command (i.e., the efference copy) to make predictions about the sensory consequences of movements without reliance on sensory feedback. Contrary to the belief that motor imagery is fully a simulation of overt movement, motor emulation theory describes the forward model as a closed loop where the accuracy of the forward model's predictions cannot be influenced by the act of imagining a movement via motor imagery (Grush, 2004). Said another way, motor emulation theory would suggest that practice by motor imagery cannot update the predictions of the forward model. Motor

* Corresponding author at: School of Physiotherapy, Dalhousie University, Rm 407, 4th Floor Forrest Building, 5869 University Avenue, PO Box 15000, Halifax, NS B3H 4R2, Canada.

E-mail address: s.boe@dal.ca (S.G. Boe).

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emulation theory has had limited support up to 2018 when Kilteni and colleagues showed the first evidence that motor imagery can recruit forward models. In their experiment using self-generated touch, they demonstrated that forward models can predict the expected tactile feedback for self-touch leading to sensory attenuation in the motor imagery group, like that of the physical practice group (Kilteni et al., 2018). These findings support the idea that motor imagery involves internal modelling but does not answer the question of whether these internal models can be updated – a process critically dependent on sensory feedback.

Three studies investigating motor imagery and internal models have demonstrated evidence for updating internal models during motor imagery practice. First, Michel et al. (2013) exposed participants to 15° rightward shifting prisms while participants practiced reaching movements either physically (prisms-active), through motor imagery (prisms-imagery), or neither (prisms-stationary). Results showed that participants in the prisms-imagery group pointed in the opposite horizontal direction as the prism shift, a phenomenon known as *aftereffects*, like that of the prisms-active group, and unlike that of the prisms-stationary group. This finding suggests that practice through motor imagery can result in adaptation to the prism environment despite the absence of sensory feedback during imagined reaching movements (Michel et al., 2013). Second, Rannaud Monany et al. (2022) showed that internal models are updated during motor imagery-based practice in microgravity conditions. Results demonstrated that participants who practiced imagined arm swinging movements during microgravity exposure carried over increased duration of the same imagined arm swinging movement during normal gravity conditions compared to (1) participants who were exposed to microgravity but did not practice motor imagery and (2) participants who were never exposed to microgravity conditions (Rannaud Monany et al., 2022). Third, Fleury et al. (2023) investigated whether adaptation to a prism environment can be transferred between pointing and throwing skills. Results showed that participants with high motor imagery abilities (MI+ group) demonstrated significant pointing aftereffects and significant transfer effects from pointing to throwing. However, the pointing aftereffects observed for the MI+ group were not significantly different from those observed in the MI− group (participants with low motor imagery abilities) and the inactive (INA) group. Further, the transfer effects observed were not significantly different from those of the INA group (Fleury et al., 2023). Ultimately, these three studies provide some evidence for updating internal models, and consequently for motor adaptation, resulting from motor imagery-based practice. However, the context in which this evidence was generated needs to be considered.

Low sample size, the lack of a comparator group, limited prism exposure, and dividing a motor imagery group into two smaller subgroups, are four methodological issues that may have impacted the conclusions arrived at. First, all three studies were likely underpowered as each had small samples ($n \leq 10$) with no reported effect sizes, and none reported a power analysis based on an estimated effect size. Collectively these issues make it challenging to replicate the studies. Second, Rannaud Monany et al. (2022) did not include an experimental group to demonstrate the expected results of updating internal models during microgravity (i.e., a group that demonstrates that arm swinging movements would increase after exposure). Third, Michel et al. (2013) and Fleury et al. (2023) conducted less than half of the recommended prism exposure trials, suggesting that true adaptation is unlikely to have occurred. Lastly, Fleury et al. (2023) divided their motor imagery group into MI+ (top 10 motor imagery ability scores) and MI− (bottom 10 motor imagery ability scores), despite already excluding participants with the lowest motor imagery ability scores (average scores below 4 on the revised Motor Imagery Questionnaire (MIQ-R)). This raises the issue of creating groups that are not different from one another, evidenced by scores of 6.51 ± 0.41 and 5.65 ± 0.59 on the MIQ-R for the MI+ and MI− groups, respectively. In the absence of a significant difference in aftereffects between the MI+ and MI− groups, it would be interesting to know if aftereffects would have been observed if the motor imagery group was kept whole. Given these limitations, we question whether motor imagery truly can update internal models in the absence of sensory feedback.

In prism adaptation tasks, like that used in the studies by Michel et al. (2013) and Fleury et al. (2023), only participants in physical practice groups have explicit knowledge of errors during the reach and point movement. In contrast, during motor imagery, participants receive no feedback on their performance because the movement is imagined, and thus covert. It is interesting then that prior research observed aftereffects in participants performing motor imagery during prism adaptation, given these participants did not have an error signal that would lead to updating of the internal model and in-turn sensory re-alignment and adaptation of the movement. It is important to note that while Fleury et al. (2023) observed aftereffects in the MI+ group, these aftereffects were not significantly different from the MI− and INA groups. This suggests that the magnitude of aftereffects in the MI+ group was so small that it was not significantly different from the groups that did not exhibit aftereffects. Thus, it is unlikely that merely having vision of their hand was sufficient for sensory realignment and subsequent updating of internal models.

Our current understanding of motor imagery-based skill acquisition and the basis for using motor imagery in practical applications rests on the idea that motor imagery is a mental simulation of overt movement. If this is the case, then motor imagery practice should update internal models like that of overt movement despite sensory feedback, known to be critical for updating internal models, not being available in motor imagery. While prior literature provides some support for updating internal models during motor imagery, methodological limitations raise concern about the validity of the findings. Here we sought to confirm or refute these prior findings by exploring updating of internal models during motor imagery. To do so, participants were exposed to leftward shifting prisms while performing actual pointing movements (physical practice), imagined pointing movements (motor imagery), or no pointing movements (control). If motor imagery updates internal models, we hypothesized that the motor imagery group would demonstrate aftereffects (pointing in the direction opposite of the prism shift, i.e., rightwards) like that of the physical practice group and unlike that of the control group.

2. Materials and methods

2.1. Participants

We recruited 67 participants from the university community. The required sample was determined using a power analysis with G*Power software. Previous work reported a large effect for aftereffects in prism adaptation during physical practice of a reach and point task ($d = 0.95$; McIntosh et al., 2019). No previous research has reported effect sizes for prism adaptation during motor imagery-based practice. That being said, prior research has demonstrated that the magnitude of aftereffects is less for motor imagery than overt movement (Fleury et al., 2023; Michel et al., 2013). Thus, we anticipated a smaller, yet still large, effect size of $d = 0.8$. To have an 80 % chance of detecting a large effect ($f = 0.40$) between groups in a two-way analysis of variance (ANOVA), a total of 66 participants (22 per group) was required. Of the 67 participants recruited, one was excluded due to a software error that precluded them from completing the experiment. Participants ranged from 18-65 years of age, with 35 females and 3 left-handed individuals.

All participants were over the age of 17, with normal or corrected-to-normal vision and no self-reported neurological injury or disease that would preclude their participation. The Edinburgh Handedness Inventory (Oldfield, 1971) was used to assess participants' handedness, and the Kinesthetic and Visual Imagery Questionnaire used to assess participants' imagery ability. Participants self-reported their age and sex. Ethical approval was obtained from the Dalhousie University Social

Sciences and Humanities Research Ethics Board, and all participants provided written, informed consent prior to their participation.

2.2. Questionnaires

2.2.1. Edinburgh Handedness Inventory

The Edinburgh Handedness Inventory is a screening tool for handedness that consists of 10 activities of daily living (Oldfield, 1971). Participants were asked to report their preferred hand for each activity of daily living. A score of greater than +40 indicates right-handedness; a score of less than −40 indicates left handedness; and a score of between −40 and +40 indicates ambidexterity. Scores from the Edinburgh Handedness Inventory were used to determine handedness for the experimental task. In the case of ambidexterity, participants chose their preferred hand for the experiment.

2.2.2. Kinesthetic and Visual Imagery Questionnaire

The Kinesthetic and Visual Imagery Questionnaire (KVIQ) is used to assess the vividness and sensation intensity of the visual and kinesthetic dimensions of motor imagery, respectively (Malouin et al., 2007). During the KVIQ, participants performed five movements physically, via third-person visual motor imagery, and via first-person kinesthetic motor imagery. These five movements include (1) forward shoulder flexion, (2) thumb-fingers opposition, (3) forward trunk flexion, (4) hip abduction, and (5) foot tapping. The visual and kinesthetic dimensions of motor imagery are evaluated on a self-report rating scale from 1 to 5. In the visual dimension, a score of 1 represents imagining no image at all, while a score of 5 represents an image as clear as seeing. In the kinesthetic dimension, a score of 1 represents imagining no movement sensation, while a score of 5 represents imagining movements as intense as overt movement. The KVIQ is a reliable tool with high internal consistency in healthy subjects (Malouin et al., 2007) and has previously been shown to be an excellent predictor of motor imagery performance (Kraeutner, Eppler, et al., 2020).

2.3. Experimental task

Participants were seated comfortably in a chair facing a desk with a keyboard positioned at the end of the desk, nearest to the participant, and a touchscreen monitor (PCT2485 Touch LED LCD Monitor, Planar, Hillsboro, OR) placed behind the keyboard (Fig. 1). The touchscreen was angled slightly towards the participant by propping up the back of the screen to improve visibility. The participants rested their non-dominant arm in their lap and placed their dominant index finger on the spacebar of the keyboard. Participants performed a custom reach and point task programmed in Python (Version 3.9.13) on the touchscreen monitor using their dominant hand. There were three trial types: physical practice, motor imagery, and control. During physical practice trials, participants pressed and held the spacebar until after a 400–600 ms delay a 10 mm diameter circular target appeared randomly at one of three locations on the touchscreen monitor (centre of screen, 10 % to the left of centre, 10 % to the right of the centre); participants then released the spacebar and reached and pointed to the target as quickly and accurately as possible. Upon touching the screen, the target would disappear and the pixel coordinates of the location of the screen contact was recorded alongside total movement time (time from presentation of the target to screen contact). During motor imagery and control trials, participants pressed and held the spacebar until after a 400–600 ms delay the target appeared randomly at one of the three locations on the touchscreen monitor. Participants kept their finger pressed on the

Fig. 1. Experimental setup. A) Participant pressing the spacebar with their dominant index finger, presenting the circular target on the touchscreen tablet. B) Participant reaching and touching the target with their dominant index finger.

spacebar while imagining reaching and pointing to the target (motor imagery trials) or imagining a line drawing itself straight from the center of the target to the participant's dominant index finger (control trials). When participants were finished the trial, they released the spacebar and the target disappeared from the screen, ending the trial. Total movement time in motor imagery and control trials was recorded as the time from presentation of the target to release of the spacebar. For the motor imagery trials, participants were specifically instructed to "imagine what it would look like and feel like to reach forward and touch the target", thus participants used first-person visual and kinesthetic imagery.

The experiment involved four blocks: familiarization, baseline testing, prism exposure, and final testing. During familiarization, participants completed physical practice trials while wearing goggles with clear, non-prism lenses (3M^{TM} 47110 Over-The-Glass Impact Resistant Clear Safety Glasses, London, ON, Canada). These practice trials were closed loop, where participants viewed their starting hand position, movement trajectory, and terminal hand position. During baseline and final testing, participants completed physical practice trials while wearing PLATO goggles (Translucent Technologies, Toronto, ON, Canada). Participants viewed their starting hand position, but after viewing the target on the screen, the PLATO goggles closed when the participants removed their finger from the spacebar to reach for the target. This occluded the participant's vision of their movement trajectory and terminal hand position (open-loop trials). Finally, during prism exposure, participants completed either physical practice, motor imagery, or control trials. Participants wore the same clear goggles as in familiarization, but with 35 diopter prism lenses attached (The Fresnel Prism and Lens Co., Bloomington, MN). These lenses shifted the visual field 17° to the left, as per the recent *meta*-analysis recommendations for prism studies (McIntosh et al., 2019). These trials were closed loop, where all participants viewed their starting hand position, and participants completing physical practice trials also viewed their movement trajectory and terminal hand position (not applicable to motor imagery and control trials, as the participants' dominant finger never left the spacebar).

2.4. Experimental protocol

Prior to the onset of the study, participants were randomly assigned to one of three experimental groups: a physical practice group (PP), a motor imagery practice group (MI), or a control group. Participants first provided written informed consent, completed the Edinburgh Handedness Inventory, and were administered the KVIQ. The investigator oriented each participant to the reach and point task prior to starting the experimental blocks. Familiarization consisted of 40 self-paced closed-loop physical practice trials over approximately three minutes. Here, 'self-paced' was operationalized as allowing participants to initiate trials at their own discretion and take as long of breaks as needed between blocks. Participants were instructed to reach and point to the target as quickly and accurately as possible. Next, participants performed the baseline testing block, consisting of 10 self-paced open-loop physical practice trials. The prism exposure block consisted of 250 self-paced closed-loop physical practice, motor imagery, or control trials (10 blocks of 25 trials) over approximately 15 min. During this block participants were instructed that they may experience dizziness or headaches and if this were the case, they were allowed to remove the prism goggles between blocks; if prism goggles were to be removed, participants were further instructed to keep a fixed gaze on the touchscreen monitor. Final testing consisted of 10 self-paced open-loop physical practice trials over approximately one minute. An overview of the experimental protocol is shown in Fig. 2.

2.5. Data analysis

The primary outcome measure was the magnitude of aftereffects during the final test block. Aftereffects are characterized by the distance of the participant's finger from the center of the circular target in the x (horizontal) direction, measured in mm, in the final test block. This

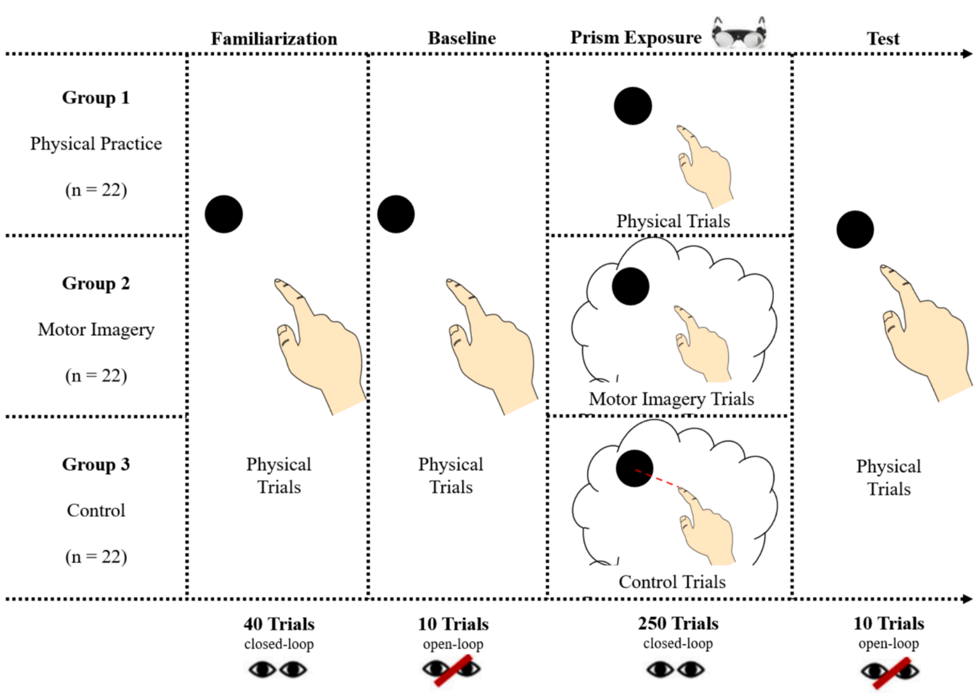

Fig. 2. *Schematic of experimental procedure.* In the familiarization block, all groups performed 40 closed-loop physical trials of the reach and point task. In the baseline block, all groups performed 10 open-loop physical trials of the same task. In the prism exposure block, the physical practice group was instructed to perform 250 closed-loop physical trials of the reach and point task; the motor imagery group was instructed to perform 250 closed-loop motor imagery trials of the reach and point task; and the control group was instructed to perform 250 closed-loop control trials. In the final test block, all groups performed 10 open-loop physical trials of the reach and point task.

distance is converted from mm to visual angle. A two-way ANOVA was used to determine if internal models can be updated during motor imagery, as indicated by 1) the magnitude of aftereffects (between-group analysis); and 2) the presence of aftereffects (within-group analysis). The two-way ANOVA model included factors of group (PP, MI, and control) and time point (baseline and test) and the outcome variable was the average aftereffects for each group. Post-hoc analyses were used to determine significant differences between groups, time point, and the interaction of group and time point. Effect sizes were calculated to characterize the magnitude of the effect. Statistical analyses were performed using open-source statistical software 'R' (Version 4.2.2) with $\alpha = 0.05$ denoting significance.

Determination of sample size, data exclusions (if any), manipulations, and measures are reported in full. Experimental code, data, and analysis code are openly available in the Open Science Framework repository (https://osf.io/6tv5m/?view_only=f1a3d858c4004ffb8fc4b0b386f429ce). Programming languages and version numbers are reported. The study was not pre-registered.

3. Results

3.1. Participants

The analysis included 66 participants (n = 22 in each of the PP, MI, and control groups). Table 1 presents the mean and standard deviation of age and KVIQ scores for each group. We confirmed motor imagery ability through the KVIQ: the mean scores for the visual and kinesthetic components of the KVIQ were not significantly different amongst groups [visual: $F(2,63) = 0.91$, $p > 0.05$, $\eta^2 = 0.028$; kinesthetic: $F(2,63) = 0.98$, $\eta^2 = 0.030$, $p > 0.05$] and these values were within the previously reported range for healthy controls (Malouin et al., 2007).

3.2. Movement time

Total movement time during exposure trials for all groups was visually inspected to check for participants' compliance with performing motor imagery (Fig. 3). Visual inspection indicated that movement times were different across groups. Specifically, movement times in the MI group were consistently longer than the PP group, an expected finding given prior literature demonstrating the time to imagine a movement is typically slower than overt execution (Dahm & Rieger, 2016; Guillot & Collet, 2005). Our assumption that participants were engaging in motor imagery is based on several observations: 1) the MI group's movement times were consistent across the 250 prism exposure trials; 2) their movement times were greater than zero, and exceeded what would be a typical reaction time had they just pressed the space bar following the cue to start the trial; and 3) their movement times were different from those of the control group. Collectively, these three observations would indicate that the MI group was engaging in the task – if they were not, we would expect considerable variability in the movement times within this group, as one would not expect each participant to engage in some other task that resulted in the same movement time, or alternatively that participants in this group would just press the space bar immediately, resulting in a movement time equivalent to a simple reaction time. Moreover, the difference in movement times between the MI and control groups suggest that the MI group was engaging in a task unique from that of the controls.

Table 1
Participant descriptive statistics including age and KVIQ scores.

Group	Age		KVIQ-V		KVIQ-K	
	M	*SD*	*M*	*SD*	*M*	*SD*
PP	24.8	9.7	19.5	5.3	21.0	5.2
MI	29.7	11.9	20.2	4.3	20.4	4.3
Control	25.2	5.2	21.6	3.6	22.4	2.9

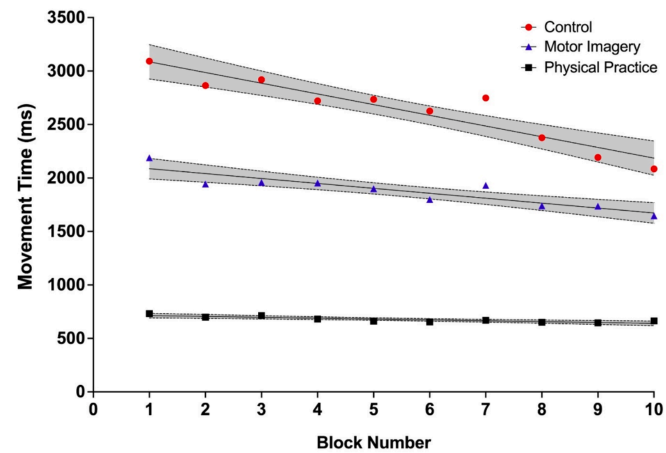

Fig. 3. Average movement time (ms) across blocks (of 25 trials) during prism exposure for control, motor imagery, and physical practice groups. The solid line represents the line of best fit depicting the relationship between movement time and block number. The shaded area around the lines for each group indicates the 95% confidence interval.

3.3. Aftereffects

There was a large and significant main effect of group [$F(2, 63) = 51.56$, $p < 0.001$, $\eta^2 = 0.528$] and time point [$F(1, 63) = 167.80$, $p < 0.001$, $\eta^2 = 0.457$] (Fig. 4). There was also a large and significant interaction effect of group and time point [$F(2,63) = 103.49$, $p < 0.001$, $\eta^2 = 0.510$]. Post-hoc analyses with a Tukey adjustment demonstrates that there was a significant difference in final test and baseline visual angle in the PP group, in that the final test visual angle ($M = 4.73°$, $SD =$

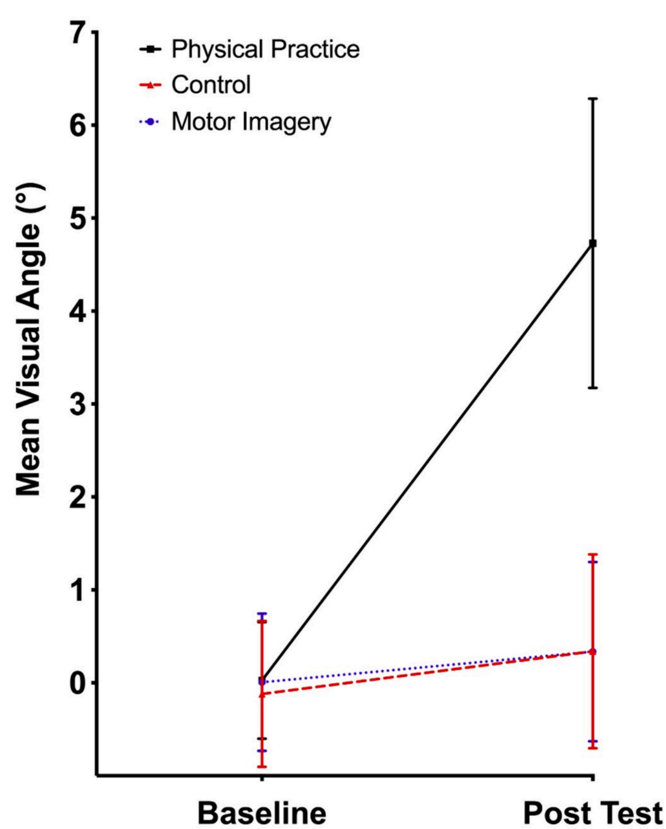

Fig. 4. Mean visual angles scores (°) at baseline and final testing for control, motor imagery, and physical practice groups. Error bars represent standard deviation.

1.56°) was significantly greater than the baseline visual angle (M = 0.026°, SD = 0.63°). There were no significant differences between the final test and baseline visual angles in either the MI or control groups. Further, there was a significant difference between the PP group and MI group during the final test block, as the visual angle for the PP group (M = 4.73°, SD = 1.56°) was significantly greater than that of the MI group (M = 0.34°, SD = 0.96°). Visual angle for the PP group (M = 4.73°, SD = 1.56°) was also significantly different from that of the control group (M = 0.34°, SD = 1.04°) during the final test block. Lastly, no significant difference was found between the MI group and the control group during the final test block, $p = 1.00$.

4. Discussion

Our findings amplify the growing body of evidence suggesting that motor imagery is *not* functionally equivalent to overt movement, contrary to motor simulation theory, the prevalent and dominant theory of motor imagery (Jeannerod, 2001; O'Shea & Moran, 2017). Below we discuss our findings, that motor imagery cannot update internal models like that of overt movement and discuss how it relates to contemporary theories of motor imagery. Further, we discuss the likely factors that contribute to the differences in the nature of learning between motor imagery and overt movement.

In line with prior research, and as per our hypothesis, the PP group demonstrated aftereffects, indicating updating of internal models during overt movement (McIntosh et al., 2019). No aftereffects were observed in the control group, suggesting that prism exposure alone was not enough to update internal models. Lastly, contrary to prior literature, no aftereffects were observed in the MI group, indicating that internal models were not updated during motor imagery. These results provide evidence that motor imagery alone is not sufficient to adapt movements to new environments, and thus differs from overt movement.

The best explanation for the absence of aftereffects in the MI group, and consequently the lack of updating internal models, is that the MI group had no explicit knowledge of their errors, and in-turn no sensory information with which to update the internal model. The PP group in the current study received terminal sensory feedback for all their reaching movements under prism exposure, allowing for the explicit knowledge of their errors (i.e., they appeared to be pointing leftward of the target). Conversely, the MI group received no actual terminal sensory feedback during prism exposure and thus, to adapt to the prism environment, the MI group needed to *implicitly* learn to adapt to the prism environment. Given that the current study did not observe aftereffects in the MI group, we conclude that merely viewing the starting hand in the motor imagery group is not sufficient for sensory realignment and subsequent updating of internal models. Indeed, prism adaptation results from an interplay of explicit and implicit learning where (1) during strategic control, early adaptation is driven by explicit knowledge of errors, allowing for rapid correction of movement errors and (2) during sensory realignment, true adaptation occurs through a slow process driven by implicit learning where internal models update and adapt to the new prism environment; aftereffects are the result of this slow implicit process of adaptation (Prablanc et al., 2020). Thus, motor imagery may rely on explicit knowledge of errors during the strategic control stage of prism adaptation to update internal models, and consequently generate aftereffects.

The finding here that internal models are not updated during motor imagery raises the question of what accounted for the difference in results from prior work. It is likely that methodological issues contributed to the different outcomes, including low sample size, lack of a comparator group, prism exposure, and dividing a motor imagery group into two smaller sub-groups.

We performed an a priori power analysis that indicated 22 participants per group was needed to measure a large effect between groups. The 22 participants in the present work are more than twice the number of participants per experimental group in the prior literature, and we observed a large effect. Michel et al. (2013), Rannaud Monany et al. (2022), and Fleury et al. (2023) did not perform a priori or post-hoc power analyses, did not report effect sizes, and had a considerably smaller sample (n ≤ 10 per group). Comparing results between studies proves challenging owing to these differences, as the earlier work was likely underpowered, making replication difficult. This limitation is evident given the results of the current study.

In the present work, appropriate comparison groups were included by randomly assigning participants to (1) a PP group which was needed to demonstrate the expected effect – updating internal models with overt movement; (2) a MI group which was needed to demonstrate whether or not motor imagery practice can update internal models; and (3) a control group which was needed to demonstrate that prism exposure alone was not enough to show true adaptation. In contrast, Rannaud Monany et al. (2022) did not include a physical practice comparison group, meaning there was no experimental group to demonstrate the expected results of updating internal models during microgravity exposure (i.e., that arm swinging movement times would increase after exposure).

The prior work using prism exposure (Fleury et al., 2023; Michel et al., 2013) included less than half of the exposure trials in their prism adaptation paradigm recommended by the most recent *meta*-analysis detailing the observation of aftereffects following prism adaptation – i.e., 250 exposure trials over the duration of ~15 min (McIntosh et al., 2019). This low number of exposure trials decreases the certainty that the aftereffects observed in both studies reflected true adaptation. Conversely, the present work included the recommended number of exposure trials needed for true adaptation of the sensorimotor system to the new prism environment. Adhering to this recommendation provides confidence that the aftereffects observed in the PP group reflects true adaptation to the prism environment and, on the other hand, that the lack of adaptation in the MI group was not attributable to a methodological limitation.

Unlike the work of Fleury et al. (2023), the MI group was analyzed as one given all participants demonstrated good (or better) ability at performing imagery, and a correlation between motor imagery ability (as determined by the KVIQ) and presence of aftereffects was not significant ($t(20) = 1.5732$, $p > 0.05$, $r = 0.33$). This is of course in contrast to the approach of Fleury et al. (2023), who excluded participants with low motor imagery ability scores and divided the remaining participants into MI+ and MI− groups despite little difference in average motor imagery ability scores.

Ultimately, the methodological limitations described above makes comparing the current results to that of the prior literature difficult. The finding that motor imagery cannot update internal models still raises the question of how skill acquisition occurs via motor imagery. To answer this question, we look to Grush's motor emulation theory, physiological differences between motor imagery and overt movement, and theories of motor imagery that consider the perceptual-cognitive components of learning.

Motor emulation theory posits that learning through motor imagery occurs because it is the conscious perception of a forward model's sensory predictions, but this process of learning does not involve updating internal models (Grush, 2004). Specifically, Grush suggests that adaptation in behaviour (or 'motor output') occurs through a Kalman filter system where, during an action, this system estimates the accuracy of sensory input and necessarily adjusts the amount of correction applied to improve the accuracy of the internal model; the amount of correction is known as the Kalman gain. In the motor emulation theory motor imagery has a Kalman gain of zero, meaning that motor imagery *cannot* change the internal model's predictions. Accordingly, motor emulation theory provides an explanation for how we learn through motor imagery using internal models, an idea supported by Kilteni et al. (2018), while unequivocally stating that practice through motor imagery cannot update the predictions of the internal model, an idea supported by the findings of the current study. However, if this is true, then how can motor imagery influence or change behaviour to allow for skill acquisition? Highlighting the differences between motor imagery and overt movement may help us identify ways in which we can leverage motor imagery for skill acquisition.

Given the dominance of motor simulation theory, which indicates motor imagery is a simulation of overt movement, it is widely believed that motor imagery-based learning is the same as learning through overt movement. Despite this long-standing belief, this study and countless others have noted differences between motor imagery and overt movement, suggesting that motor imagery may influence behaviour *differently* than overt movement. For example, overt movement is consistently known to activate the neural regions associated with modification and execution of motor programs (i.e., cerebellar and cortical motor regions), whereas motor imagery more commonly activates regions associated with visuomotor transformation and generation of the motor program (i.e., frontal and parietal regions), with evidence suggesting they are critically important to motor imagery performance (Hardwick et al., 2018; Hétu et al., 2013; Kraeutner et al., 2017, 2016; McInnes et al., 2016; Oostra et al., 2016; Sirigu et al., 1996). In a longitudinal study in which participants trained on a dart-throwing task, motor imagery and overt movement were found to have different patterns of brain activity, and learning via motor imagery to be inferior to that occurring via overt movement (Kraeutner, Stratas, et al., 2020). For instance, compared to motor imagery, overt movement was shown to have greater activation of the cerebellum, a region critical for refining motor programs. The authors speculated that sensory feedback, available during overt movement, allowed for optimal error detection/correction to occur, accounting for the greater activation observed for the cerebellum during overt movement compared to motor imagery, and the superior outcomes for overt movement. The need for sensory feedback to adapt behaviour and learn motor skills via overt movement supports our findings, as the MI group did not have access to sensory information at the terminus of the imagined reach and point movement and consequently did not demonstrate any aftereffects. While the need for sensory feedback explains the current findings, how motor imagery drives adaptation and learning when this feedback is not available is still not clear. Perhaps being *aware* that errors have occurred is needed for motor imagery to effectively adapt to new environments, or perhaps motor imagery relies on something completely different, such as cognitive or perceptual representations of actions.

It is well established that motor imagery-based practice can result in improved performance outcomes and learning. Recent work by Ingram and colleagues demonstrated that over 5 days of training, participants training via motor imagery were able to learn a complex motor skill, and while the magnitude of learning was less than that of a group training via overt movement, it was significantly better than an overt movement group for which knowledge of results was withheld, and of a control group that merely attended to the stimulus (Ingram et al., 2019). Importantly, a follow-up study by the same authors explored how learning could occur in the absence of sensory feedback (Ingram et al., 2022). Here the authors showed the motor imagery group self-reported errors resulting from task performance, and like that observed for overt movement, the magnitude of the errors was influenced by the speed and complexity of the movement to be learned, both known drivers of error during physically executed movements. Participants reports of *explicit knowledge* of errors in this work supports the notion that this is required for motor adaptation to occur via motor imagery. Indeed, researchers have recently theorized that feedback simulated during motor imagery ('predicted effects' or 'simulated effects') are used in internal models to alter motor programs and thus learning of the movement (Dahm & Rieger, 2019; Rieger et al., 2023; Solomon et al., 2022). Considered in the context of motor emulation theory, it may be that this simulated feedback serves to alter the gain of the Kalman filter, in turn resulting in tuning of the internal model necessary for learning to occur. Future research should investigate the role of explicit knowledge of errors during motor imagery-based practice and prism adaptation, as this explicit knowledge may be needed to change the predictions of the internal model and subsequently affect behaviour and drive skill acquisition.

Finally, it is important to consider the possibility that skill acquisition through motor imagery-based practice simply does not involve updating internal models. Perhaps learning through motor imagery is more *perceptual-cognitive* than *motor* in nature. While both motor simulation theory and motor emulation theory support that motor imagery uses the motor regions of the brain, there are several other theories suggesting that motor imagery-based learning is more perceptual-cognitive in nature, such as the motor-cognitive model, the perceptual-cognitive model, and the effects imagery model to name a few (for a full review see Hurst & Boe, 2022). Most recently, Frank and colleagues proposed the perceptual-cognitive scaffolding theory suggesting that practice through motor imagery links the perceptual and cognitive representations of actions and refines the higher order representation networks, resulting in motor learning (Frank et al., 2023). This theory posits that skill level will influence motor imagery-based practice effects as learning truly motoric tasks should be more difficult when the individual has no prior physical practice experience. If this is the case, then this theory may explain why the MI group was unable to adapt to the prism environment, as the MI group would not have any perceptual or cognitive representations of the action in the prism environment to rehearse. Future research should compare individuals who have physical practice experience in a prism environment to individuals who do not, to examine whether motor imagery is more effective with prior physical experience.

Considerations. Participants in all groups were instructed to keep the prism lenses on during the prism exposure phase, but if participants experienced dizziness or nausea, they were allowed to remove the lenses during breaks between trials. Removal of prism lenses may promote de-adaptation, however we controlled for this risk by ensuring all groups received the same instructions, meaning that the removal of the prism lenses should not affect any one group more than the other. Additionally, participants were instructed to keep a fixed gaze on the screen to further minimize the risk of de-adaptation.

5. Conclusions

The current work demonstrates that motor imagery cannot update internal models to a prism environment, like that of overt movement. This adds to our understanding of motor imagery-based learning, as it suggests that motor imagery is not a simulation of overt movement. Our results align with the proposition that the absence of aftereffects in the MI group is best explained by the fact that the MI group had no explicit knowledge of errors, unlike that of the PP group which did demonstrate aftereffects. Motor emulation theory further suggests that motor imagery cannot update internal models, but this does not answer the question of how motor imagery can change behaviour to allow for skill acquisition. Recognizing the differences between motor imagery and overt movement, including a pattern of brain activation that is unique to motor imagery, provides context for how motor imagery can drive skill acquisition. Future research should investigate if explicit knowledge of errors is needed prior to motor imagery to update internal models to new environments. Despite motor imagery's promise for acquiring skills, it's efficacy in practical application is mixed: for instance, a recent *meta*-analysis demonstrates that the efficacy of motor imagery in promoting functional recovery in stroke rehabilitation is moderate at best (Barclay et al., 2020). This finding may be attributed, at least in part, to the assumption that motor imagery is a simulation of overt movement, and thus motor imagery is applied using the same principles. The knowledge that motor imagery-based learning may depend on mechanisms different from that of overt movement should be leveraged to improve its effectiveness in practical applications such as rehabilitation.

CRediT authorship contribution statement

Juliet M. Rowe: Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Shaun G. Boe:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

A link to the study data and code is provided in the methods section of the manuscript.

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