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RESEARCH ARTICLE

Control of Movement

Linking motor working memory to explicit and implicit motor learning

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Abstract

Explicit and implicit components of motor learning have been widely studied, but the extent to which movement information encoded and maintained in working memory (Motor Working Memory; MWM) contributes to motor learning remains unclear. Building on recent work pointing to separate effector-independent (abstract) and effector-specific (limb-bound) information formats in MWM, we conducted a correlational study in which human participants completed both a MWM task and a visuomotor rotation task. We observed that: *1*) the fidelity of effector-independent MWM was selectively correlated with the degree of explicit visuomotor learning, and *2*) the fidelity of inferred effector-specific MWM was selectively correlated with the degree of implicit visuomotor learning. Together, these results point to a possible relationship in which different formats of motor information stored in WM may contribute to distinct components of long-term motor learning, shedding light on a novel cognitive-motor interaction.

NEW & NOTEWORTHY Working memory is important for motor learning, yet its role beyond visuospatial domains remains unclear. Here, we examine whether and how non-visual Motor Working Memory (MWM) is related to long-term motor learning. Specifically, we identified selective correlations between effector-independent MWM and explicit motor learning processes, and between effector-specific MWM and implicit motor learning processes. These findings extend prior research relating visuospatial working memory to motor learning and highlight distinct MWM mechanisms supporting different learning processes.

adaptation; intermanual transfer; motor learning; skill learning; working memory

INTRODUCTION

Motor skills are typically associated with procedural memory, a long-term memory system that refines and stabilizes behaviors through the gradual process of motor learning. Behavioral and neurophysiological studies have also pointed to a separate, short-term form of motor memory—“Motor Working Memory” (MWM)—which may also contribute to skilled motor behavior (1). In contrast to other domain-specific working memory systems, such as visual working memory, the concept of a dedicated MWM system in the brain has only recently begun to receive attention. Thus, many basic questions about the role of MWM in motor behavior remain unanswered, even though MWM may be a critical substrate of cognitive-motor interactions. Here, we attempt to address one such open question: how might MWM relate to motor learning?

Importantly, both MWM and motor learning are not unitary processes and contain dissociable subcomponents. Current models of motor learning highlight two main processes: *1*) an explicit process, dominant during early stages of learning, which is characterized by deliberate decision-making and the application of cognitive strategies about how to move; and *2*) an implicit process, which involves slow, unconscious error-driven recalibration of movements to gradually adapt internal sensorimotor mappings (2–9).

Similarly, MWM also has dissociable components, as we have argued in recent work (10). Before describing those components, we first define MWM. Working memory (WM) in general involves the active maintenance and manipulation, on a seconds-to-minutes timescale, of information in a mental workspace (11–14). Motor WM applies this concept to motor information, and is defined as a WM subsystem that encodes, integrates, and maintains movement features, and

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which is not fully reducible to visuospatial or somatosensory WM (1).

Initial support for a movement-specific working memory system came from studies investigating how people perform short-term recall of arm movements without visual feedback. This work revealed classic WM effects, including capacity constraints, interference effects, and short-term forgetting, when people tried to recall movements seconds after executing them (15–21). Movements that are planned and executed by subjects, as opposed to movements administered passively (e.g., via an experimenter or robotic device moving the arm), are better maintained in MWM, suggesting that afferent somatosensory input is not the only feature encoded into MWM (22). WM-like effects are also seen for movements without salient spatial trajectories, such as hand gestures (21) and grip forces (23), suggesting that MWM is not reducible to a specialized form of spatial WM.

Neurophysiological evidence also points to a distinct MWM system: research in nonhuman primates has revealed retrospective short-term memory traces that encode recently completed eye movement trajectories, manifested as persistent neural firing in the dorsolateral prefrontal cortex (dlPFC) (24, 25). And recent neuropsychological work in humans shows that lesions to sensorimotor cortex can lead to selective deficits in maintaining observed movements in WM, but do not affect WM capacity for nonmotor content (26). In addition, neural recordings in humans point to separable motor and visual WM codes in the brain during memory maintenance (27, 28). Taken together, previous work points to the existence of a dedicated MWM system that flexibly integrates and maintains afferent and efferent motor information within a short-term memory buffer (1).

As noted earlier, MWM, like motor learning, has dissociable components. Recent findings from our laboratory suggest that MWM encodes movement-related information in at least two formats: effector-specific and effector-independent codes (10). Effector-specific information refers to content that is mapped to the particular body parts involved in an action, potentially including features of afferent somatosensory information and efferent motor commands. In contrast, effector-independent information captures abstract movement features that can be flexibly transferred across limbs (e.g., from your right arm to your left) or even across individuals, as in the case of imitation (29, 30). For instance, when learning a new dance move, one encodes not only how the action feels in specific limbs (effector-specific), but also the world-referenced spatiotemporal trajectory of the movement itself (effector-independent), which could in theory be mapped onto untrained effectors. Using a novel MWM task combined with an intermanual transfer manipulation, our recent study demonstrated that much of people's ability to recall reaching movements over short timescales likely relies on effector-independent information, and that this information is maintained separately from somatosensory or visuospatial WM (10).

With these previous findings in hand, here we investigated correlations between MWM and motor learning by isolating the distinct subcomponents of both memory systems. We hypothesized that: *1*) individual differences in effector-independent MWM fidelity would selectively correlate with the degree of explicit motor learning, and *2*) individual differences in effector-specific MWM would correlate positively with the degree of implicit motor learning. To test these hypotheses, we designed a correlational study using two tasks: a visuomotor rotation (VMR) task designed to dissociate explicit and implicit motor learning, and a non-visual MWM task designed to dissociate effector-specific and effector-independent components. Our hypotheses were grounded in theoretical models of motor learning and previous empirical findings linking various working memory capacities to different learning mechanisms. First, explicit learning in VMR tasks primarily involves deliberately "re-aiming" movements to counteract performance errors, a computation that requires remembering successful actions over short timescales and, putatively, spatial reasoning about the perturbed environment (3, 9, 31–33). Although effector-independent MWM appears to be functionally distinct from visuospatial working memory (1, 10), both effector-independent MWM and explicit motor learning systems likely encode abstract, spatial information that can be flexibly transferred across different effectors (9, 34, 35). We therefore reasoned that effector-independent MWM might correlate with explicit motor learning.

In contrast, implicit motor learning involves the fine-tuning of movement kinematics to gradually (and unconsciously) counteract sensory prediction errors (6, 8). Critically, implicit motor learning does not reliably transfer across limbs and is thought to be closely related to somatosensory processing (34, 36–38). Thus, we reasoned that the fidelity of effector-specific MWM may correlate with the observed degree of implicit motor learning. Our correlational study was designed to test these specific hypotheses.

MATERIALS AND METHODS

Participants

The study was reviewed and approved by Yale University's Institutional Review Board, and all participants provided written informed consent before participation. A total of 34 participants were recruited through a psychology pool and received class credit for their participation. Two participants were excluded due to incomplete data collection, and one participant was excluded for aberrant explicit learning behavior (i.e., negative explicit learning in the VMR task, which was also less than three standard deviations from the mean explicit learning observed across the sample). Of the remaining 31 participants, 17 were females, with a mean age of 18.8 ± 0.75 yr (SD), and 27 participants were right-handed, as assessed by the Edinburgh Handedness Inventory (39).

Apparatus

Both tasks were conducted using a Kinarm End-Point Lab (BKIN Technologies Ltd., Kingston, ON, Canada), equipped with a low-friction, two-joint robotic arm fitted with a cylindrical handle that enabled planar reaching movements by passively guiding participants or being actively guided by them. Participants were seated in an adjustable chair with their feet on the ground in two outlined boxes, discouraging them from moving their legs throughout the experiment.

The hand not holding the robot's handle at any given moment rested flat on a mousepad on the workspace table. Participants sat with their foreheads resting against a soft pad mounted to a horizontal LCD monitor. The monitor was mounted parallel to the table, facing a semi-silvered mirror, allowing them to comfortably view the presented instructions and visual stimuli while preventing them from seeing their hands below the mirror. Furthermore, participants wore a fabric bib around their necks, which was fastened to the mirror and fully occluded their upper bodies. An experimenter remained in the room for the duration of the study to monitor participants' adherence to instructions and postural requirements.

Motor Working Memory Task

The only visual stimuli participants received throughout the MWM task were text prompts that appeared outside the reaching workspace. At no point did participants see their hands, arms, or any indication of their arm position, nor did they receive any performance feedback throughout the task. The MWM task was always completed before the VMR task. Participants first completed a five-trial practice block (excluded from analysis) to become accustomed to the robot and ask any task-related questions. Once the experimenter was confident that the participant understood the instructions, they proceeded to complete two experimental blocks of 48 trials each. Participants were allowed to rest briefly between blocks but remained seated throughout.

Each trial consisted of three phases: encoding, maintenance, and retrieval (Fig. 1*A*). Before each trial, participants were instructed to grasp the robot's handle with their right hand, which then guided them to the "home" position, located ∼13 cm from their chest along the midline. During the encoding phase, participants were passively guided by the robot in outward reaching trajectories to four different locations, returning to the home position between each movement. While moving, a number was displayed above the workspace, indicating the current movement in the sequence (e.g., participants saw "#1" during the first movement, "#2" during the second, and so on). Each movement lasted 800 ms. At the end of each outward movement, the robot paused for 1 s before returning to the home position, where the hand rested for an additional 1 s between movements. There were 12 possible invisible targets 9 cm from the home position, evenly spaced between 15° and 165°. Target locations were pseudorandomly selected to ensure equal sampling throughout the task, with no repetitions within a trial and a minimum angular difference of ±25° between consecutive movements in a given sequence.

After encoding the four movements, participants were required to maintain all four movements in working memory for 3 s. During this period, they were instructed to either *1*) "Switch hands," in which case they would grasp the handle with their opposite (left) hand, or *2*) "Wait," keeping their right hand on the handle without letting go. Following the 3-s maintenance phase, participants were prompted to recall one of the four movements (e.g., "Recall movement #1") using whichever hand was currently grasping the handle. To recall a movement, they executed an outward-reaching motion that matched their memory of the cued movement trajectory in the workspace (non-mirrored), then paused at the recalled movement's end point. The robot registered their final location after 500 ms of dwell time before guiding them back to the home position. Participants were not informed in advance which movement they would be asked to recall or whether they would need to switch hands during maintenance. The specific movement probed for recall (i.e., the first, second, third, or fourth movement from the encoding sequence) was randomly selected and equally sampled.

A previous study from our laboratory demonstrated that this hand-switching paradigm is an effective method for dissociating effector-specific and effector-independent contributions to motor working memory (10). When participants were instructed to recall a movement from working memory using the same hand they had used to encode it (the "Same" condition), they could, in theory, use both effector-specific (e.g., somatosensory) and effector-independent (e.g., abstract spatial trajectory) information to inform recall. However, when participants switched hands (the "Switch" condition) and recalled movements with the opposite hand, effector-specific information was no longer applicable, meaning they could rely only on effector-independent information to inform recall (Fig. 1*A*).

Visuomotor Rotation Task

Visuomotor rotation tasks are widely used to assess error-based motor learning and to measure the simultaneous contributions of implicit and explicit motor learning processes (8). Participants attempted to move a small white visual cursor, representing their hand position (0.15 cm radius), through a green target (0.5 cm radius) (Fig. 1*C*). A circular home position landmark (0.5 cm), the target, and, on most trials, the cursor was the only visual feedback provided during the task. As in the MWM task, participants could not see their hands or the robotic arm. On each trial, the target was positioned at either 0°, 60°, 120°, or 180°, located 9 cm from the central home position. Participants saw one target per trial, and target locations were randomly selected and equally sampled throughout the task. For each movement, participants were instructed to reach through the target with a fast, straight, ballistic movement. At the end of the movement, the robot guided them back to the home position. If participants waited more than 500 ms after the target appeared, they were instructed to initiate their movement sooner in the next trial. If their movement took more than 500 ms to cross the target radius, they were asked to move faster.

The task consisted of four types of blocks: baseline, rotation, catch, and washout. A schedule of these trials is shown in Fig. 1*D*. The experiment began with 39 baseline trials (the 40th baseline trial was not recorded due to a software error). During baseline trials, participants received continuous online cursor feedback as they reached through a target. Following the baseline block, the rotation block commenced. In rotation trials, the cursor feedback was rotated ±45° relative to the reach direction, with the rotation direction counterbalanced across participants. Participants thus had to learn to counteract this 45° discrepancy to restore accurate performance. During the rotation blocks, participants received online feedback on their cursor position. The rotation

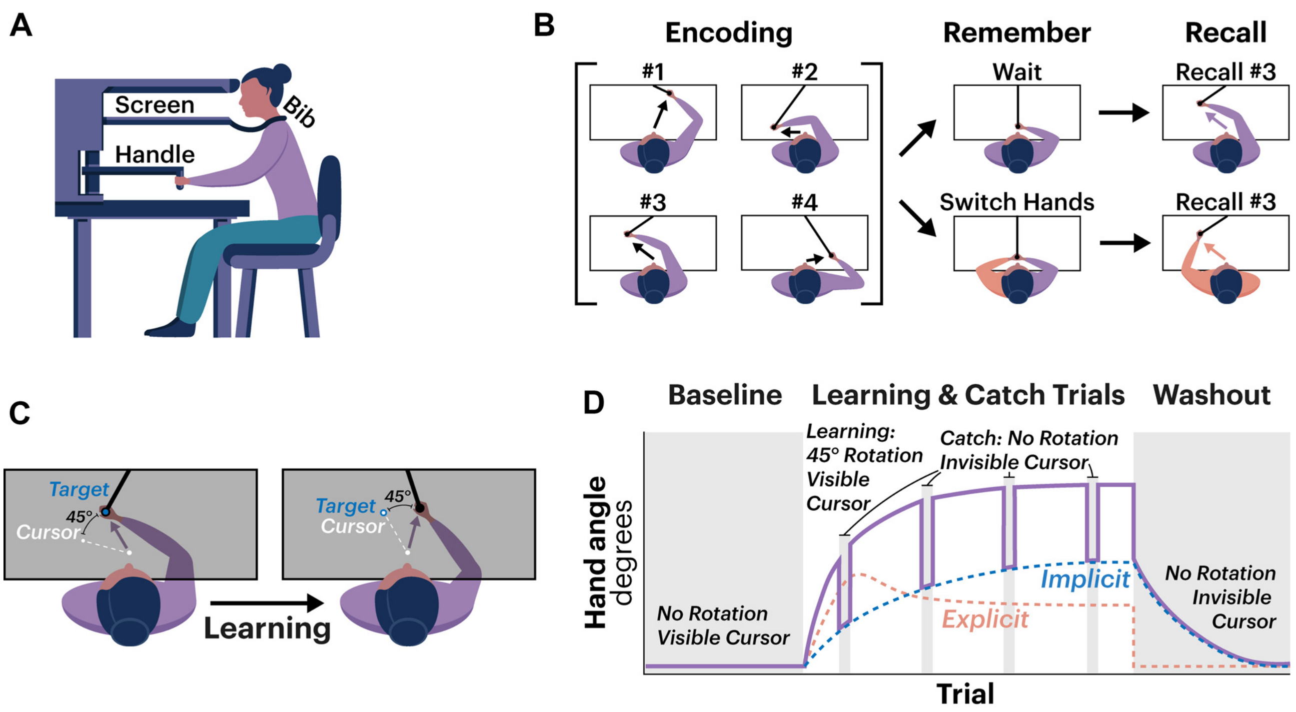

Figure 1. Motor working memory and visuomotor learning task design. *A*: experimental setup used in both tasks: participants were seated at a table with their heads resting on a headrest and their eyes directed toward a screen that displayed visual stimuli while blocking any view of their hands and arms. The rest of the upper body was occluded by an opaque bib. *B*: motor working memory (MWM) task: during the encoding phase, participants were passively guided to four locations by the robotic arm, returning to a home position between movements. During each movement they saw a number corresponding to the current movement's position in the sequence order. While maintaining this information in memory, participants were instructed either to wait or to switch the hand grasping the handle. Finally, they were prompted to recall one of the movements using whichever hand was currently on the handle. *C*: visuomotor rotation (VMR) task: during the learning phase, participants were instructed to make rapid, straight movements to direct a cursor through a target. In rotation trials, the cursor was rotated 45° relative to their movement direction. Participants adjusted their movements to compensate for the cursor rotation. *D*: schedule of trial types in the VMR task and multiple learning processes: The VMR task consisted of four trial types. Participants first completed a baseline phase, during which they moved toward the targets while receiving veridical cursor feedback on their hand position. In the subsequent learning phase, the cursor was rotated relative to the hand position (as described in *C*), requiring participants to adapt their movements. During the learning phase, participants experienced four catch-trial periods in which they were instructed to move directly toward the target without compensating for rotation; during these trials, no cursor feedback was provided. This method isolated implicit motor adaptation, allowing for the dissociation of explicit and implicit contributions to learning (see MATERIALS AND METHODS). Finally, in the washout phase, participants performed trials identical to the catch trials, allowing for the measurement of the final implicit learning state.

phase consisted of five 32-trial blocks, totaling 160 rotation trials.

Crucially, we also included four brief "catch" blocks interspersed throughout the rotation phase. Each catch block consisted of four trials, one for each target location, presented in a random order. Before each catch block, participants were instructed to abandon any strategy they had been using to move the cursor to the target in the rotation trials, and instead reach directly toward the target. During these trials, participants did not see their cursor. Without error feedback and without the use of any explicit aiming strategy, the catch blocks served as a measure of participants' implicit learning. Explicit learning was then inferred by subtracting movement angles in catch blocks from those in neighboring rotation trials. This approach, known as the exclusion method, has been shown to be an effective and straightforward technique for dissociating explicit and implicit motor learning (40).

Finally, the experiment concluded with a 40-trial washout block. The instructions and feedback for these trials were identical to those of the catch trials. This block measured the final state of implicit learning and its gradual decay.

Analysis

Data preprocessing was performed using MATLAB (MathWorks, 2024), and all analyses were conducted in R (R Core Team, 2024). For statistical tests, all reported t tests are two-tailed, paired tests with an α level of 0.05. In our key correlational analyses, we report both Pearson and Spearman correlation coefficients (for completeness), also using an α level of 0.05.

For the MWM task, participant performance was assessed using two metrics: variability in memory errors and absolute memory errors, both in the angular and extent dimensions (see RESULTS). Variability was quantified using the interquartile range (IQR) of angular errors, chosen for its robustness to outliers given the limited number of trials in some data subsets (see RESULTS). This approach follows previous studies on both hand localization and working memory variability (41, 42). Because our study was primarily correlational, we included multiple MWM metrics to evaluate the robustness of any observed correlations. We additionally computed reaction time (RT) by taking the interval between the cue to recall the reach and the onset of movement from the start position.

For the VMR task, behavior was quantified by computing participants' hand angles relative to the start position at the moment they crossed the invisible ring defined by the start position (the ring's center) and the target location. Three key VMR metrics were calculated: *1*) Total learning, defined as the mean hand angle for the last three trials at each target location in the final rotation block (12 trials total); *2*) Explicit learning, indirectly measured by subtracting the last catch block (a measure of implicit learning) from total learning; and *3*) Total implicit learning (early aftereffects), calculated as the average hand angle for the first three trials at each target location in the washout block.

In addition to the three participants excluded (see *Participants*), individual trials were removed from analysis in each task based on performance. In the MWM task, 98 trials (3.3% of all data) were excluded for having an angular error over ±90°, suggestive of a memory lapse, hand slip, or swap error. In the VMR task, 51 trials (0.6% of total data) were removed for having a hand angle exceeding ±3 standard deviations from the block's mean hand angle.

RESULTS

Motor Working Memory Task

Participants ($n = 31$) in our study performed two tasks: a motor working memory (MWM) task and a visuomotor rotation adaptation task (Fig. 1). Building on our recent finding (10) that MWM is composed of two distinct representational codes, effector-independent and effector-specific, we hypothesized that these codes would correlate, respectively, with two dissociable components of visuomotor learning: explicit strategic learning and implicit motor adaptation. Such a finding would provide evidence for a link between well-known mechanisms of long-term motor learning and short-term motor memory processes.

To dissociate effector-specific and effector-independent contributions to MWM, participants passively encoded four movements and were then asked to recall one of them using either the same hand (Same condition) or the opposite hand (Switch condition; see MATERIALS AND METHODS and Fig. 1*A*). We reasoned that in the Same condition, both effector-specific and effector-independent information could contribute to recall performance. However, in the Switch condition, where participants switched effectors (hands) between encoding and recall, only effector-independent information could influence recall performance.

The results of the MWM experiment replicated our previous finding that the benefit of using the same hand for encoding and recall is limited to the most recently encoded movements [Fig. 2; Hillman et al. (10)]. Two metrics were used to quantify MWM performance, angular variability (IQR) in report errors and absolute angular errors (see MATERIALS AND METHODS). For IQR, a significant difference between Switch and Same errors was observed when the fourth (last-encoded) movement was cued for recall [$t(29) = 2.28$, $P = 0.029$, $d = 0.41$]. However, no significant differences were found when the first [$t(29) = 0.84$, $P = 0.409$, $d = 0.15$], second [$t(29) = 0.56$, $P = 0.579$, $d = 0.10$], or third [$t(29) = 1.46$, $P = 0.155$, $d = 0.26$] encoded movements were recalled. For the mean of absolute angular errors, a significant difference between Switch and Same errors was observed for the fourth [$t(29) = 4.62$, $P = 0.0001$, $d = 0.83$] and third [$t(29) = 2.21$, $P = 0.035$, $d = 0.40$] movements, but not for the first [$t(29) = 1.34$, $P = 0.191$, $d = 0.24$] or second [$t(29) = 1.26$, $P = 0.216$, $d = 0.23$] movements.

These results align with our recent findings, which demonstrate that working memory for recently encoded movements exhibits attenuated interlimb transfer, whereas movements encoded earlier undergo successful transfer (10). Our previous work attributed this pattern to interference at the encoding limb rather than passive temporal decay. Specifically, we found evidence that as additional movements are made, they interfere retroactively with the effector-specific (but not effector-independent) memory (Fig. 2).

Effector-independent information is presumably available in all trial conditions (Switch and Same); therefore, isolating effector-specific contributions to performance is more complicated. To approximate effector-specific MWM, two methods were used: *1*) an "effector-specific benefit" was calculated by subtracting the Same condition's performance error from that of the Switch condition (note that subtracting the Switch from Same would not calculate benefit, as the comparison is based on error). This difference was measured only for the fourth movement, as it was the sole position that showed a reliable difference between the Same and Switch conditions across both MWM metrics. *2*) A second, sequence-dependent "fourth-movement" metric was quantified by calculating the difference between performance error in the fourth position and that of the other three positions within the Same condition. As previously mentioned, evidence suggests that as new movements are executed, they retroactively interfere with or "wash out" previously stored effector-specific information (10). Therefore, by comparing the fourth movement, which shows the most reliable effector-specific benefit, with the other three movements, effector-specific information can be approximated. Since this measurement is derived only from the Same condition, it has the added advantage of not being subject to performance disruptions that could arise from the act of switching hands during memory maintenance.

All three of these variables, effector-independent MWM and the two estimates of effector-specific MWM, were then correlated with key measures from the visuomotor rotation learning task (implicit and explicit) to examine potential relationships between MWM codes and error-based motor learning. We discuss this analysis in our cross-task correlation section.

Visuomotor Rotation Task

The same participants who performed our MWM task also completed a standard visuomotor rotation (VMR) task. Participants readily adapted to the 45° visuomotor rotation (Fig. 3*A*), reaching an asymptotic hand angle of 36.21° ± 5.51° [$t(29) = 36.63$, $P < 2.2e\text{-}16$, $d = 6.58$].

As described in the MATERIALS AND METHODS, the "exclusion" method was used to isolate implicit learning by instructing participants to abandon any cognitive

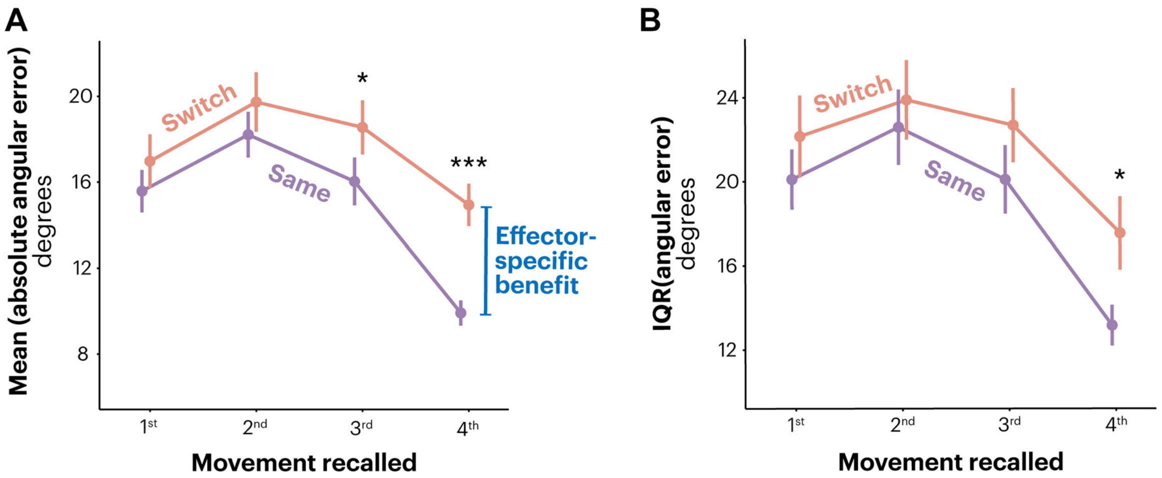

Figure 2. Motor working memory (MWM) results. Movements on the *x*-axis are ordered by sequence position, where "1st" represents the first movement encoded (and thus the oldest). The *y*-axis reflects participants' errors in each condition, measured as either the average absolute angular error (*A*) or variability (*B*), as the interquartile range (IQR) of angular errors. The difference between these conditions indicates the advantage of using the same hand for recall, referred to as the effector-specific benefit. Error bars represent the standard error of the mean (SEM). $*P < 0.05$; $***P < 0.005$.

strategy, reach directly to the displayed targets, and receive no visual feedback on exclusion trials. This approach allowed explicit learning to be quantified through simple subtraction by deducting implicit learning from the measured hand angles on neighboring standard nonexclusion trials.

The dissociation of explicit and implicit learning was successful (Fig. 3*B*), demonstrating robust contributions of both components to the overall learning curve. Asymptotic explicit learning reached 11.51° ± 7.52° [$t(29) = 8.51$, $P < 1.7e\text{-}9$, $d = 1.53$], whereas asymptotic implicit learning, measured over the first three cycles (12 trials) of the washout phase (early aftereffects), reached 19.83° ± 6.36° [$t(29) = 17.37$, $P < 2.2e\text{-}16$, $d = 3.12$]. These two measures of explicit and implicit learning served as the primary motor learning metrics in our correlation analyses. Asymptotic measures were used to examine the overall tradeoff between the two processes at the individual level.

Cross-Task Correlations

With respect to correlations across tasks, we had two primary hypotheses: first, that effector-independent MWM would selectively correlate with explicit motor learning, and second, that effector-specific MWM would selectively correlate with implicit motor learning. To test the first hypothesis, we computed participants' average MWM performance in the Switch condition (collapsing across all four movements of the encoding sequence) using both variability (IQR) and average absolute angular error metrics. We then correlated these metrics with total explicit learning from the VMR task. We observed significant negative between-subject correlations between errors in effector-

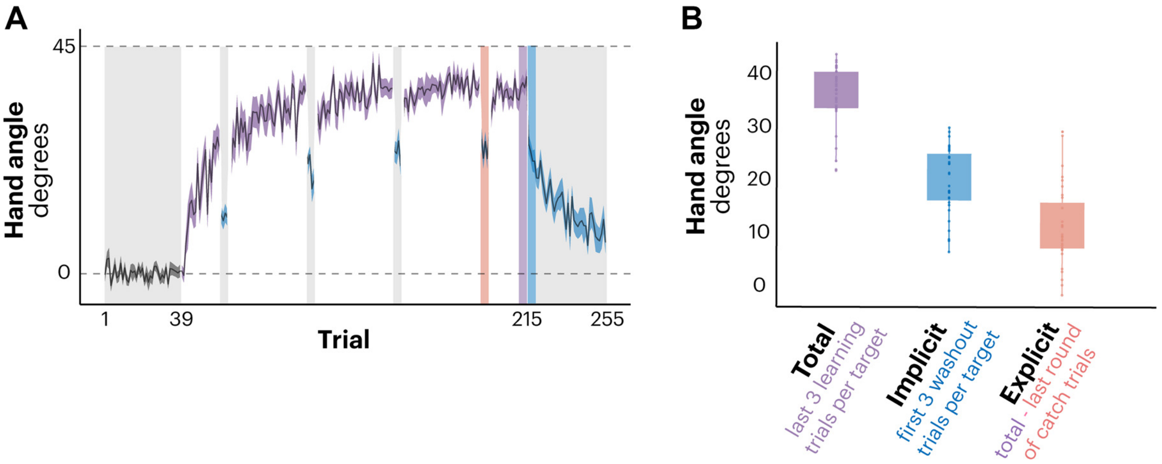

Figure 3. Visuomotor rotation (VMR) results. *A*: the mean hand angle per trial for each experimental condition (green = baseline; purple = learning phase; blue = catch trials and washout phase). Error shading reflects the standard error of the mean (SEM). *B*: total learning was calculated as the average of the last three learning trials per target (12 trials total). Implicit learning was measured using the first three washout trials per target. Explicit learning was determined by subtracting the final round of catch trials from the total learning metric. Box plot height shows confidence intervals and dots show individual subjects.

independent MWM and total explicit motor learning (Fig. 4; variability: $r_{\text{Pearson}} = -0.44$, $P = 0.013$; $r_{\text{Spearman}} = -0.46$, $P = 0.01$; mean absolute angular error: $r_{\text{Pearson}} = -0.41$, $P = 0.024$). These results support our first prediction, that explicit VMR learning would correlate with abstract, effector-independent MWM.

We now turn to our second hypothesis, which concerns the predicted relationship between effector-specific MWM and implicit motor adaptation. To test this prediction, we computed effector-specific MWM in two ways: first, by measuring participants' MWM "effector-specific benefit," and second, by examining a recency-based "pre-washout" effect in the Same trials. We used both angular variability and absolute error metrics for completeness and correlated these metrics with total implicit VMR learning (i.e., average early aftereffects; see MATERIALS AND METHODS).

Overall, the results supported our hypothesis (Fig. 5), though they were more mixed than our findings on effector-independent MWM and explicit motor learning. For the fourth-movement measure of effector-specific MWM, we observed a correlation between the angular variability and implicit motor learning ($r_{\text{Pearson}} = -0.46$, $P = 0.01$; though not reliable for the Spearman metric, $r_{\text{Spearman}} = -0.27$, $P = 0.138$), and a correlation between the average absolute angular error metric and implicit motor learning ($r_{\text{Pearson}} = -0.53$, $P = 0.002$; $r_{\text{Spearman}} = -0.46$, $P = 0.009$). For the effector-specific benefit measure of effector-specific MWM, we observed a significant negative correlation between angular variability and implicit learning ($r_{\text{Pearson}} = 0.38$, $P = 0.037$; $r_{\text{Spearman}} = 0.40$, $P = 0.025$), but did not see a reliable correlation when using the average absolute angular error metric ($r_{\text{Pearson}} = 0.24$, $P = 0.202$; $r_{\text{Spearman}} = 0.18$, $P = 0.323$). Although more variable than our explicit learning versus effector-independent MWM correlation results, these results do, in broad strokes, support our second prediction, that effector-specific MWM would correlate with implicit motor learning.

Control Analyses

It is possible that some of the observed correlations, particularly those related to explicit learning measures, could be driven by differences in general task engagement or executive functioning. That is, the degree of cognitive effort a participant puts into both tasks could lead to spurious correlations stemming from generic factors rather than potential shared underlying computations between the correlated measures.

As an initial control, we conducted a cross-task correlation analysis (Figs. 4 and 5), in which we substituted extent error for angular error as the metric of MWM performance (Supplemental Figs. S1 and S2). Extent error measures how much a participant over- or undershot the memory target during recall, regardless of angular deviation. We reasoned that because extent and angular error are thought to represent distinct features of spatial cognition and kinematic programming (43, 44) yet should be similarly influenced by general cognitive resources such as effort and attention, observing robust cross-task correlations as in Figs. 4 and 5 would support a generic effort interpretation of our findings, while null results would not.

No significant correlations were found between extent error in the MWM task (average error or error variability) and our motor learning metrics (all P values > 0.18; see Supplemental Figs. S1 and S2). Rather than reflecting a generic MWM capacity or effort, this suggests that the link between motor learning and MWM depends on the specific content being remembered; namely, angular information. These findings support our emphasis on angular error in the principal analysis, as it is the only dimension learned in the VMR task. Moreover, this aligns with previous research demonstrating dissociations in the motor system's representation of angular versus extent dimensions in reach planning (43). (Indeed, absolute angular and extent errors were uncorrelated in our data, $P = 0.26$.)

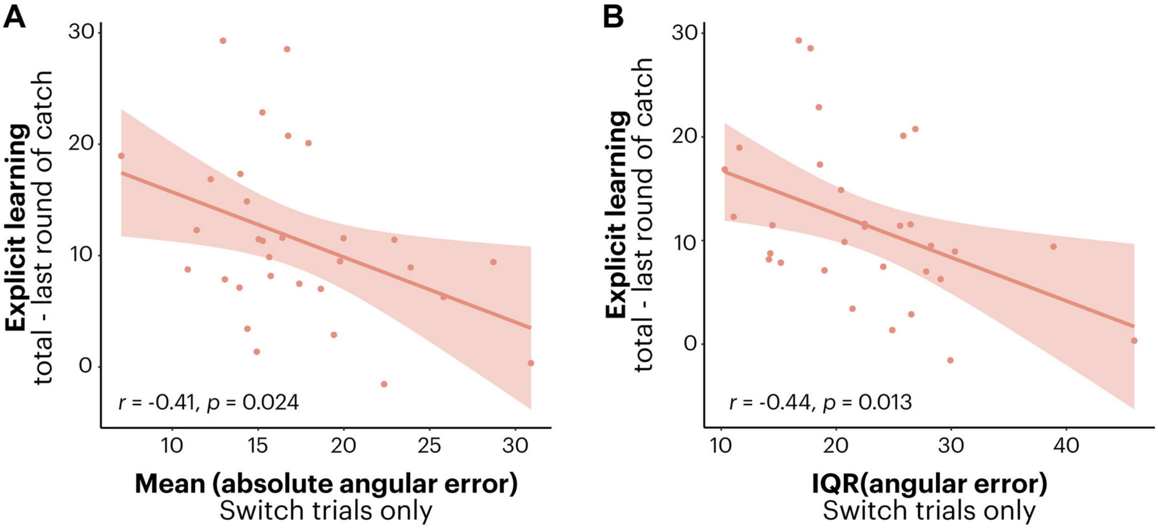

Figure 4. Explicit motor learning and effector-independent motor working memory (MWM) cross-task correlations. Explicit learning from the visuomotor rotation (VMR) task is represented on the *y*-axis. The *x*-axis displays error in the MWM task under Switch conditions (collapsed across all sequence positions), measured as either the average absolute angular error (*A*) or the variability of angular error (*B*).

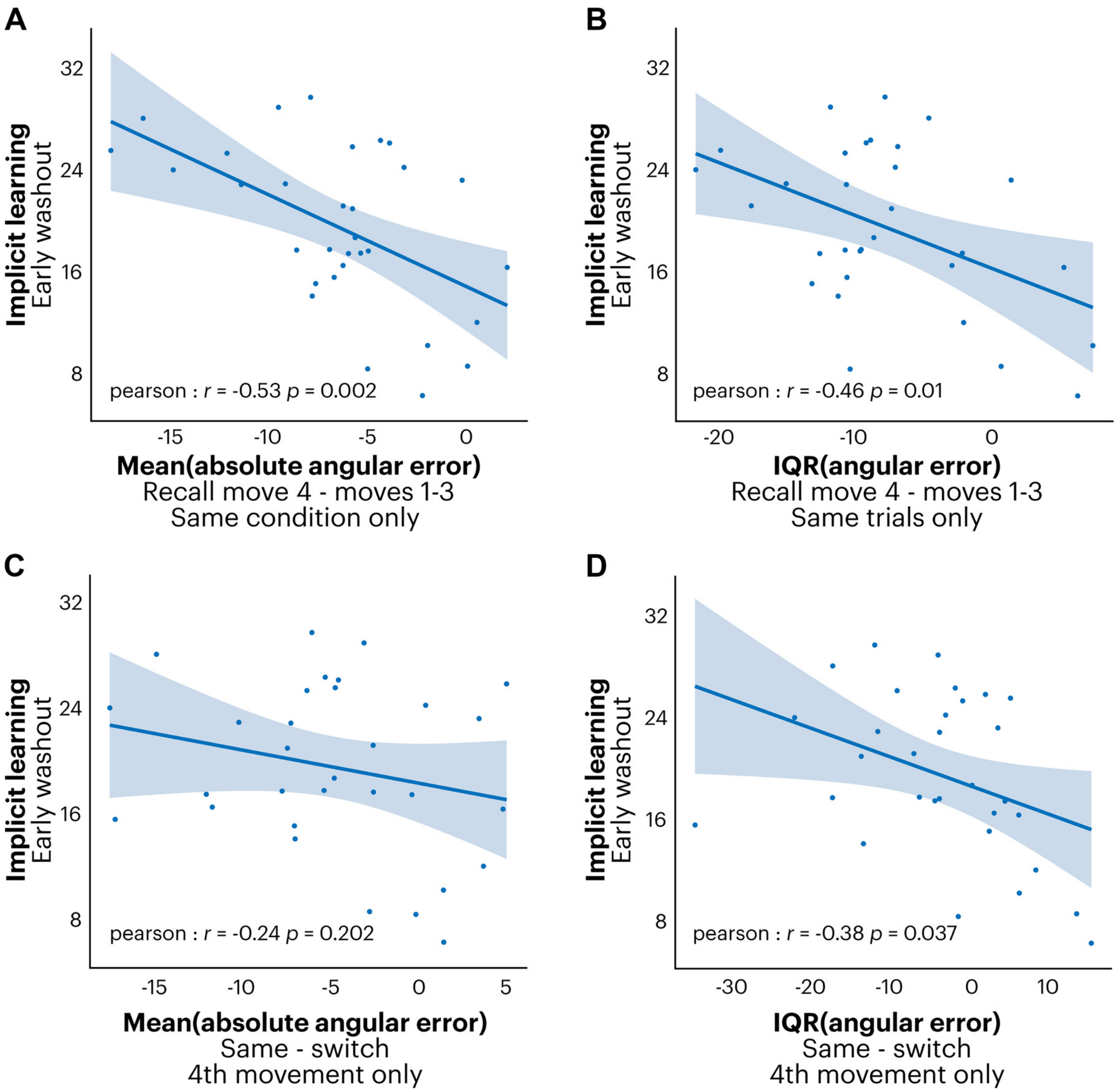

Figure 5. Implicit motor learning and effector-specific motor working memory (MWM) cross-task correlations. *Top*: effector-specific MWM was quantified as the difference in error between the fourth movement, which demonstrated an effector-specific benefit, and the first three movements within the Same condition. Error was measured using the average absolute angular error (*A*) and the variability of angular error (*B*). Since this calculation is based on error, a negative correlation signifies a positive relationship between implicit learning and effector-specific MWM. *Bottom*: The *x*-axis represents the difference in error between the Same and Switch hand conditions for the fourth movement in the MWM task, using both the average absolute angular error (*C*) and the variability of angular error (*D*). This difference reflects the advantage of recalling movements with the same hand (the effector-specific benefit; see Fig. 2*A*).

In a second set of control analyses, we examined response times (RTs) from the MWM task in relation to the same VMR task metrics (Supplemental Fig. S3). RTs could also index general effort, particularly in the MWM task, which had liberal RT constraints. For each MWM task condition, we computed median RTs and RT differences in the same manner as the MWM error metrics and correlated these values with explicit and implicit motor learning metrics. Similar to the extent error analyses, we found no significant correlations (all P values > 0.08, and all P values > 0.44 with the removal of a single outlier in the bottom panel, see Supplemental Fig. S3).

Taken together, the absence of significant correlations between VMR metrics and extent errors or RTs on the MWM task, both potential indices of general cognitive effort, suggests feature-specific associations between motor learning and effector-specific and effector-independent components of MWM.

DISCUSSION

In this study, we explored potential relationships between short-term memory for movements (motor working memory; MWM) (1) and motor learning. Specifically, we asked whether the capacity to hold effector-independent and effector-specific information in MWM is selectively correlated with explicit and implicit components of motor learning, respectively. We observed individual differences that supported these hypotheses: *1*) individuals with more robust explicit motor learning also exhibited greater memory fidelity in effector-independent MWM, and *2*) individuals with a high level of implicit motor learning also exhibited greater memory fidelity in effector-specific MWM. These results, although only correlative, add further support to the distinction between effector-specific and effector-independent representations in MWM (10), and may offer novel insights into how MWM could contribute to long-term motor learning processes.

Effector-Independent MWM and Explicit Motor Learning

Prior research relating working memory to motor learning has been largely focused on examining the relationship between visual working memory and motor learning (3, 31, 45). Here, we found that a greater contribution of explicit processes during motor learning was correlated with lower error in effector-independent MWM. Given recent findings from our laboratory showing no interference between visuospatial load and effector-independent MWM, these results are distinct from previous work by identifying potentially "motor-specific" working memory processes as a distinct contributor to explicit motor learning (10).

Our results linking effector-independent MWM and explicit motor learning are also consistent with intermanual transfer research. Transfer studies have used visuomotor and force field adaptation tasks, in which one arm undergoes adaptation and the opposite arm is tested for residual learning. Recent work has demonstrated that explicit learning is largely effector-independent (transferable across limbs) (34, 46), which is fully consistent with our results. Furthermore, a study by van Mier and Petersen (47) found that participants who learned a maze by tracing showed significantly better transfer when tested with the opposite hand on an identical maze than on a mirrored one. This finding supports the MWM task design, where effector-independent MWM is assessed by replicating a non-mirrored movement on Switch trials.

Effector-Specific MWM and Implicit Motor Learning

We also found evidence supporting our secondary hypothesis, that implicit motor learning may leverage effector-specific information held in working memory. We observed a significant positive correlation between implicit learning and effector-specific MWM, measured as both the memory benefit afforded by using the same hand to recall movements, and a recency-based "fourth-movement" metric related to recalling the most recently encoded movement with the same hand. However, when using both our absolute error and variability MWM metrics, one of these correlations, between implicit adaptation and the absolute error in the same-hand benefit metric, was not statistically reliable (Fig. 5). Thus, the correlations observed between implicit adaptation and effector-specific MWM should be taken with a grain of salt.

Our finding that effector-specific MWM correlated with implicit motor learning is broadly consistent with other findings showing that, unlike explicit motor learning, implicit motor adaptation is highly effector-specific, exhibiting minimal (if any) transfer across limbs (34, 36, 48). Moreover, recent work on motor adaptation has uncovered a subcomponent of implicit motor learning that is susceptible to short-term forgetting ("temporally volatile" adaptation), biasing movements back to an unadapted state as time passes between trials (49, 50). Speculatively, these effects could relate to a possible reliance on some kind of implicit motor working memory cache. Although our previous study found a lack of strong temporal decay effects in our MWM tasks (10), those tasks involved no learning and were thus focused on an increase in memory error over time, not a drift back to a nonadapted motor memory. Future work could attempt to more directly relate our measures of working memory fidelity with temporally volatile implicit adaptation.

Previous work has highlighted a negative relationship between working memory recruitment and implicit motor processes (3), which may appear contrary to our results here (Fig. 5). We propose that the positive relationship we observed between implicit motor learning and effector-specific MWM challenges the conventional view that any use of working memory impairs implicit motor learning. Instead, it suggests that interference may stem not from using working memory in general, but from the specific content maintained within it. That is, working memory content related to recent movement features may be useful for implicit motor learning, while working memory content related to irrelevant visual or spatial stimuli may cause interference.

MWM: Eligibility Traces for Learning?

The correlations between effector-independent MWM and explicit learning we observed here may reflect the requirements of remembering an abstract motor plan across short timescales (35). This type of working memory process would be quite useful for retrieving and refining a consistent cognitive strategy during learning, and for linking those strategies to observed errors during performance monitoring (9, 35, 51). In the context of implicit motor learning, short-term memory of movements could help link observed sensory errors to preceding movements, especially under feedback delays (52, 53).

These proposed functions of MWM during learning are akin to the maintenance of an "eligibility trace," a key concept in reinforcement learning (54). That is, working memory can help the learner link recent actions held in memory (the "traces") with specific observed outcomes of their actions (55, 56). This key computation could be implemented by maintaining a persistent representation of recent action kinematics. Neural recordings in monkeys performing saccades provide some compelling neural evidence for this possible role of MWM. Studies have revealed robust post-saccade working memory traces of eye movement kinematics in the dorsolateral prefrontal cortex (24, 25), a key hub of the working memory system. It is plausible that these findings would generalize to other motor behaviors, like reaching. Future work could try to reveal in more detail the precise format and neural correlates of persistent working memory representations of actions that could be used to undergird motor learning.

Limitations

Although the current study provides evidence supporting a role for MWM in motor learning, several limitations should be acknowledged. First, the correlational design precludes any definitive conclusions about causality. That is, although we observed associations between MWM and visuomotor adaptation, we did not directly demonstrate the recruitment of working memory resources during motor learning. Future studies could employ experimental manipulations, such as introducing a MWM load during learning or using brain stimulation, to more directly test causal links between motor learning and effector-independent or effector-specific MWM.

Second, our measures of explicit learning and effector-specific MWM were derived indirectly, relying primarily on subtraction-based calculations. Although such approaches are widely used, they may introduce errors (40) or confounding influences from overlapping cognitive processes.

Finally, the relationships we observed between working memory and motor learning likely varies across different age groups and skill levels. For instance, athletes and musicians may attend to or retain different types of information in MWM, which could influence motor learning in distinct ways.

Conclusion

In sum, recent research suggests that motor learning is more than just long-term, incremental improvements in movement execution; various cognitive processes play key roles in motor learning (4). We believe that holding motor content in working memory is one such cognitive process (1). Our findings here suggest that MWM may play a role in multiple forms of motor learning.

DATA AVAILABILITY

Data will be made available upon reasonable request.

SUPPLEMENTAL MATERIAL

Supplemental Figs. S1–S3: https://doi.org/10.5281/zenodo.10206635.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

H.H. and S.D.M. conceived and designed research; H.H. and T.N.M. performed experiments; H.H. and T.N.M. analyzed data; H.H., T.N.M., and S.D.M. interpreted results of experiments; H.H. prepared figures; H.H. drafted manuscript; H.H. and S.D.M. edited and revised manuscript; H.H., T.N.M., and S.D.M. approved final version of manuscript.

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