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Opinion

Motor working memory

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Working memory (WM) is crucial for planning, reasoning, and learning, and is one of the most extensively studied topics in cognitive psychology and neuroscience. However, the concept of a WM subsystem for motor content – or 'motor working memory' (MWM) – is generally neglected, even though MWM likely plays an important role in everyday action. Here, we synthesize evidence that the brain both prospectively and retrospectively maintains motor content in WM and propose that MWM carries out multiple key computational functions in motor control and skill learning. A focused research program on MWM is overdue and will deepen our understanding of the links between cognition and action.

Highlights

Working memory (WM) for motor content – 'motor working memory' (MWM) – has been neglected as a distinct working memory construct but is likely crucial for flexible and adaptive motor behavior and skill learning.

We synthesize behavioral and neural evidence that the brain can hold motor information in working memory.

We describe how information can be maintained and manipulated in MWM both prospectively, during deferred motor planning, or retrospectively, following movement execution.

We propose that – much like other forms of working memory – MWM likely relies on a distributed neural circuit that includes sensorimotor cortex and the prefrontal cortex.

Movements in mind: motor working memory

Motor skill learning is often framed as the product of extended practice leading to gradual gains in performance. While this is certainly the primary road to mastery, other processes contribute as well. Consider honing your tennis serve: After performing a serve and seeing how the ball went long, or did not spin as much as expected, you can rapidly correct for this on the next try by deliberately remembering what you did and adjusting accordingly. Or consider learning a difficult new dance move: You try and fail, then explicitly imagine the commands needed for the next (hopefully less embarrassing) attempt. These examples illustrate how improving motor performance is not limited to implicit, incremental learning – you can also leverage a working memory of movements you recently made, or plan to make in the near future.

Working memory (WM) involves the active storage and manipulation – on a seconds-to-minutes timescale – of information in a mental workspace [1]. A classical view posits multiple WM subsystems that are at least partly separable in the brain and behavior [2–4], including spatial WM (memory for spatial locations of stimuli [5,6]), visual working memory (memory for visual features of scenes and objects [7,8]), verbal working memory (a system for active rehearsal of verbal information [9]), and additional forms of sensory WM (e.g., for auditory or somatosensory content [10,11]). More contemporary theoretical accounts go beyond content-specific storage in WM, emphasizing the role of attention [2,12,13] in domain-general operations such as prioritization and updating of a range of possible WM contents [14]. Variants of these newer perspectives go as far as to argue that most, if not all, cortical circuits have the capacity to transiently store information in a WM-like format in the service of short-term goals [13].

Despite this theoretical progress, the format and function of *motor* content in WM have received little attention. In our view, 'motor working memory' (MWM) should be considered a distinct psychological and neural construct (Figure 1). We define MWM as a working memory system dedicated to encoding features of movement, which is informed by, but not reducible to, sensory WM (e.g., visuospatial or somatosensory). We believe that, to date, the evidence supports an early conjecture made by Mary Smyth and colleagues [15] that 'working memory may have to have a special subsystem to handle patterns of bodily movement', later echoed by Baddeley [16], who argued that WM may include a 'movement-based system' that goes beyond sensory WM.

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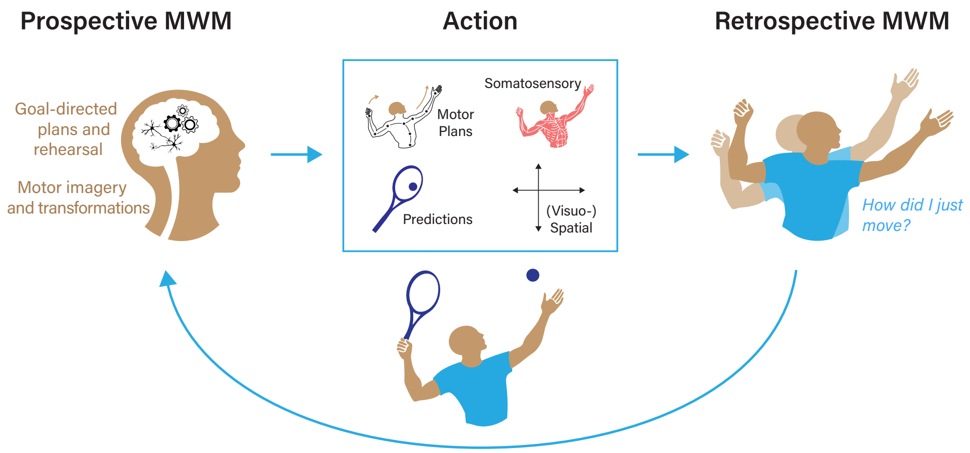

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Figure 1. Motor working memory (MWM) in action. A putative MWM system plays a role in prospectively planning, imagining, and manipulating voluntary movements in a flexible mental workspace, as well as retrospectively storing a short-term memory of recently executed movements by integrating movement features (e.g., motor plans, somatosensory and visuospatial state estimates, etc.) to afford rapid movement refinement and learning.

Integrating motor control with core cognitive functions like WM will be crucial for any successful theory of intelligent, adaptive behavior [17–19]. And clarifying what kinds of information the mind uses to deliberately plan, recall, and refine movements over short timescales should lead to a better understanding of a range of sophisticated human motor skills, from social mimicry and speech, to music, dance, and athletics. In the following we outline how WM for recently completed movements bears classic signatures seen in nonmotor domains (e.g., capacity limitations, domain-specificity, etc.). We draw on both behavioral and neural evidence to describe this form of retrospective MWM. Then, we discuss behavioral and neural evidence supporting prospective MWM, which allows for the short-term maintenance and manipulation of motor information. Finally, we discuss the behavioral functions of MWM, from reinforcement learning to motor imagery and imitation.

Retrospective MWM: remembrance of movements past

Core features of working memory include a limited capacity short-term buffer, vulnerability to interference, and some degree of domain-specificity for specific contents (e.g., visual). Is there evidence for a MWM system that shares these features?

Several papers in the 1960s through the 1980s demonstrated that people retrospectively store details of movements in short-term memory [15,20–28]. In these and similar studies, human subjects actively or passively make reaching movements along a track or with a mechanical handle to various distances or at various angles, or remember novel sequences of pre-trained hand postures. After a typical delay interval of several seconds, subjects then attempt to precisely recall previous movements using the same limb. The majority of such tasks are performed with limited visual input to rule out visual memory confounds, and do not repeatedly train movements to rule out long-term learning effects.

Performance in these tasks displays the signature temporal and capacity constraints of WM: recall performance is limited both by the time interval between encoding and recall [20,22] and the degree of cognitive load [28,29]. These WM signatures are also seen when people are asked to recall novel hand postures [15,30] and even nonspatial kinematic dimensions, like precise grip forces [25,31], suggesting that complex kinematic details may be stored in WM.

For the most part, these previous studies did not differentiate between WM for motor output representations versus sensory inputs [11,32,33]. We argue that MWM is not reducible to sensory WM (e.g., somatosensory or visuospatial). Instead, MWM integrates afferent and efferent information to maintain a representation of the action itself, including prospective motor plans (Figure 1). (By 'motor plans' we mean neural content during movement preparation that specifies movement features, such as kinematics or trajectory shape, rather than perceptual properties of a movement goal [34].) Evidence for output-related content in MWM could come in two forms: (i) active movement planning should enhance memory performance beyond what can be explained by passively encoded sensory states, and (ii) motor memories should be resilient to dual-task interference from sensory WM.

With respect to the first point, previous findings have indeed demonstrated that self-generated movements (i.e., movements chosen and planned by the subject) are recalled more precisely than passively administered movements [21,28]. Speculatively, it may be that case that information related to actively planning a movement can be maintained in working memory and retrieved at recall. These findings are also consistent with the idea that efference copy (internally reproduced representations of outgoing motor commands, or, potentially, motor plans [35]) may contribute to motor memory [36].

Behavioral signatures of retrospective MWM

The main body of evidence for a dedicated MWM system are findings showing that short-term memory of movements is notably resistant to dual-task interference. Verbal interference and articulatory suppression tasks do not significantly disturb the fidelity of short-term motor memories [20,27,37], suggesting independence between verbal versus bodily WM representations. Moreover, when subjects maintain a sequence of novel hand gestures in WM, visually encoding a sequence of spatial targets during the memory delay period, or even pointing to those targets with the same effector that encoded the initial gestural movements, only minimally interferes with recall of the gestural movements [15,38]. This lack of visual and somatosensory dual-task interference helps distinguish MWM as its own construct and suggests that MWM may 're-code' information from various sensory sources into a more integrated, abstract action representation.

We recently built on these results [39]. Using a task where subjects encoded and later recalled reaching movements, we observed classic set size effects, where holding multiple movements in memory led to worse recall of single movements [7]. Second, by having participants switch hands between encoding and recall on a subset of trials, we dissociated limb-specific versus limb-independent memory codes. Strikingly, recalling a remembered movement with a different limb only weakened memory in select contexts, supporting the idea that MWM recodes effector-specific somatosensory information into a more abstract, effector-independent format. Finally, using a dual-task we found that visuospatial WM load had no discernible effect on MWM performance, further reinforcing a distinction between motor and visuospatial WM systems.

A separate body of dual-task experiments also invokes MWM: in these studies, people are asked to encode and remember verbally instructed movement sequences (e.g., 'Touch the red cup, pick up the green key,' etc.). These tasks have revealed an 'enactment advantage,' where physically performing instructed movements at encoding or recall leads to substantially better performance versus only verbally encoding or recalling the instructions [40–43]. Similarly, physically drawing pictures of memory items boosts their eventual recall [44]. Planning and performing other task-irrelevant movements during encoding reduces or even abolishes the enactment advantage, suggesting that storing instructed movements in WM while planning and executing similar volitional movements draw on the same cognitive resources [40,42,45]. Importantly, these interference effects are not observed when secondary tasks do not require similar motor planning processes [46].

Neural signatures of retrospective MWM

A neural signal that reflects retrospective MWM content should show distinct (i.e., decodable) patterns of population activity for different motor memories well after a movement is completed [2]. Several lines of evidence support the existence of such patterns of activity.

Seminal work in the neurobiology of working memory had monkeys remember the location of visual stimuli and, after a brief delay, report those memories with eye movements [47]. Variants of these study designs disentangle signals related to remembering spatial locations versus preparing eye movements [47,48]. While these and similar studies have been foundational in characterizing the neural mechanisms of visuospatial WM, motor information is often treated as a confound. However, several studies have targeted retrospective neural representations of motor information in WM.

First, in tasks where animals (monkeys and rodents) have to remember specific responses across trials (e.g., saccading or nose-poking right versus left), retrospective memory for oculomotor and postural response-related information is seen in key areas implicated in WM, including dorsolateral prefrontal cortex (dlPFC) [49–52]. While compelling, these putative neural correlates of MWM (e.g., an eye movement to the left) might be confused with spatial working memory for the movement goal (e.g., the leftward target location).

A recent study addressed this confound, revealing retrospective short-term motor memory representations [53]: when monkeys made saccades to cued targets and then fixated those targets for a variable interval, persistent retrospective representations of the preceding saccade were decodable in dlPFC, with precise coding specificity for the previous motor command. This activity persisted even seconds after the saccade was complete, demonstrating that dlPFC post-saccadic responses exhibit classic WM signatures – persistent, decodable, internally generated mnemonic activity [54]. Using clever control experiments in which different saccades were made to an identical target location, the authors discovered that persistent oculomotor memory traces in the dlPFC encoded the kinematics of the preceding movement – the trajectory of the saccade – not the end location. Interestingly, neural activity reflecting MWM traces was stronger following rewarded versus unrewarded movements, an effect also echoed in studies of visual WM [7,55]. These compelling results suggest that retrospective representations of motor output are flexibly maintained in the neocortex, similar to sensory information [5,54,56].

Retrospective MWM for observed and imitated actions

Additional neural evidence for retrospective MWM comes from neuroimaging and neuropsychological studies in humans. For the former, observing actions and storing them in WM activates sensorimotor circuits, not just standard visual WM circuits [57–59]. This has led some to speculate that visually observed actions might be maintained in WM in an 'embodied' format to support social imitation [57,60]. Indeed, researchers have observed that visually encoded actions attain special status in WM relative to standard visual WM stimuli like abstract shapes [57,61].

Causal evidence from neuropsychology also points to a distinct MWM system that can be selectively disrupted. A recent study [60] found that stroke patients diagnosed with apraxia had selective WM deficits related to encoding and imitating observed motor actions, but not other content (e.g., numerical digits). Such disruptions of MWM might be a feature of apraxia that contributes to some patients having difficulty imitating abstract movement trajectories [62,63].

Another relevant neuropsychological study [30] found that individuals born without hands have selective deficits visually encoding manual actions and storing them in WM, but no such deficits for visual WM stimuli unrelated to action. These findings are taken to imply that WM for observed bodily movements might rely, at least in part, on one's own experience performing or imitating those movements [64,65], perhaps via activation of long-term memory. Taken together, the neuropsychological evidence points to causal effects of both cortical lesions and motor experience on MWM fidelity.

Prospective MWM: a workspace for future movements

Nonmotor WM theories emphasize that WM functions not only to recall past information, but also to prospectively guide future behavior [12]. We now highlight behavioral and neural evidence supporting an analogous prospective role for MWM.

Behavioral signatures of prospective MWM

We propose that MWM may often be important for maintaining the motor plans that precede action [12,66–69]. While MWM is likely not engaged when movements are overlearned or do not require complex trajectories (e.g., a direct reach to a visible object) [34], behavioral studies have demonstrated that in many contexts motor planning shares core features with WM, including (i) comparable capacity constraints, (ii) active maintenance and manipulation of contents in accordance with task goals, and (iii) evidence of chunking.

First, motor planning, especially for complex or novel movements, is often cognitively demanding and taxes WM resources [70,71]. Moreover, tasks requiring subjects to plan newly-learned movement sequences show that motor planning capacity constraints echo WM capacity constraints seen in nonmotor domains – people appear to be able to plan, at most, around three or four movements into the future [72].

Other research has suggested that people sequentially prepare multiple potential motor plans as different movement options are presented, and that these plans can be restructured dynamically in memory [73]. These results have led some to argue that multiple action plans can be maintained online [74] and manipulated according to task goals, a core feature of WM. The idea of holding multiple parallel motor plans in mind before movement execution was introduced by neural studies in nonhuman primates showing evidence for simultaneous representations of competing movement plans in sensorimotor cortex [75]. While this idea has been challenged by evidence pointing to only single motor plans being represented at a given time [76,77], the tasks used in these studies [75,77] have differed in their memory demands. Speculatively, it may be the case that having to internally maintain a memory trace of multiple potential movements leads to multiple plans being represented in MWM, while having access to salient direct cues about movement goals biases the brain to represent single movement plans.

Another key signature shared between motor planning and WM is 'chunking.' Chunking involves the compression of items into meaningful units to increase the amount of information that can be held in WM. Both in classic WM contexts (e.g., remembering a phone number) and, critically, in the planning of learned motor sequences [78], people chunk sequential information to relieve WM load [79,80]. Moreover, people also appear to compress visuomotor information into structured memory representations to guide rapid motor memory retrieval [81].

Taken together, this evidence suggests that MWM is not merely retrospective (i.e., remembering what movement just happened), but plays a prospective role in guiding flexible and adaptive motor planning.

Neural signatures of prospective MWM

In WM tasks that require motor responses, areas of the brain typically linked to movement execution also prospectively represent motor information. This includes the primary motor cortex for reaching movements [82,83] and prefrontal regions for eye movements [48]. Kinematic features of movements that are executed after a WM delay (e.g., their direction and velocity) can often be decoded from sensorimotor cortical activity during the delay period [84], reflecting true motor content in these deferred planning representations [34].

Motor plans can also be dissociated from other types of WM representations long before movement initiation. In recent work using scalp electrophysiology, motor plans and visuospatial working memories could be separately decoded throughout a WM delay period [68]. These results demonstrate that the brain can simultaneously store sensory and motor codes during memory maintenance [12,67,68,85]. Recent work using functional neuroimaging echoes these findings, showing flexible deployment of either a sensory code (in visual regions) or motor code (in motor and premotor cortex) during a WM delay [69].

Studies in rodents looking at large-scale regional interactions in the brain during memory-guided action have also blurred the line between delayed motor preparation and WM [86]. Persistent delay period activity is maintained in frontal cortex via thalamocortical loops during delayed motor execution, and strikingly similar neural signatures are observed during nonmotor WM tasks [87,88]. These converging neural mechanisms have even led some, like Svoboda and colleagues, to remark that 'motor planning is a prospective form of short-term memory' [86].

Moreover, neural algorithms that separate movement planning from movement execution mirror neural algorithms seen in nonmotor WM tasks. Influential studies looking at population coding dynamics in sensorimotor cortex revealed orthogonal neural subspaces for planning versus executing movements [89]. Recent research has identified a highly similar orthogonalization phenomenon in the prefrontal cortex that differentiates WM content from sensory input [90].

To summarize the evidence for MWM, we see that: (i) actively remembering a recently executed movement generates domain-specific motor content in WM; (ii) remembering instructed or visually observed actions may rely on a distinct WM store; (iii) retrospective representations of recent movements are present in sensorimotor and prefrontal cortex during WM maintenance; and (iv) prospective representations of planned movements can be behaviorally expressed, and are neurally implemented, in a manner consistent with WM.

Functional roles for MWM

We have so far highlighted behavioral and neural evidence for a MWM subsystem involved in retrospectively remembering and prospectively planning movements. But for what specific tasks or computations is MWM useful? Below we propose specific functional roles for MWM in cognition and action.

Mental manipulation of motor plans

One defining characteristic of working memory is the manipulation of memory contents. There is plenty of evidence for manipulation of visual and verbal items in nonmotor WM [4]. There is also some evidence for manipulation of motor information in WM. In one classic study, monkeys were trained to reach either directly to a target or 90° away from a target [91]. Neurons in motor cortex were analyzed as a 'population vector' that related preparatory neural firing to the upcoming movement direction. In trials where monkeys simply planned a movement to the target, the population vector aligned to the target throughout the planning interval. However, in the 90° trials, the population vector initially pointed at the target before parametrically rotating from the target direction to the goal direction prior to the animal executing the correct rotated movement, suggesting mental rotation of an internal motor plan (though see [92] for an alternative explanation). Similar results have been seen in the oculomotor system [48].

Mental manipulation of motor plans is also seen behaviorally: In tasks where people learn to compute a rotated movement plan to counteract visuomotor errors (Box 1), movement response times scale linearly with the required degree of rotation, echoing classic signatures of mental rotation in the visual WM domain [93]. Mental manipulations of motor plans are key for success in such tasks and are thought to be one component of deliberate forms of motor control (e.g., volitionally adjusting an arrow shot to account for the wind; [19]). As mental rotation is considered a visual WM function [94], it is reasonable to believe that motor mental rotation is a motor WM function [95].

Motor imagery

Another intuitive function of MWM is acting as a substrate for motor imagery. Decades of research have suggested that motor imagery recruits brain regions related to motor execution, but also regions involved in attention and WM [96]. In an impressive recent study, researchers analyzed intracortical recordings in humans and found that both performing or simply imagining a movement produce remarkably similar planning dynamics in motor cortex [97]. In the visual domain, some have argued that visual WM acts as the substrate of visual imagery [98]. An analogy here could be made, where MWM acts as an internal buffer for imagery, rehearsal, and manipulation of future movements, all without driving movement execution [89].

Interactions between motor and nonmotor WM

Action plans in MWM may also interact with nonmotor working memory processes. For example, reach or saccade planning has been shown to boost visual encoding and support visual WM maintenance, specifically at the target of planned movements [99–101]. Moreover, planning to manually act on an object can change how its visual features are encoded and stored in visual WM [102,103]. Sensory information can also help guide the retrieval of different context-dependent motor memories [104–106]; for instance, the perceived density of an object influences

Box 1. MWM and sensorimotor adaptation

MWM may contribute to error-based motor learning, which involves refining movements so they match sensory predictions [19]. In typical sensorimotor adaptation tasks, individuals experience a perturbed visuomotor environment that induces errors (e.g., an imposed mismatch between movement commands and concurrent visual feedback). Sensorimotor adaptation tasks induce explicit forms of learning, where participants deliberately re-plan movements [112,113], and implicit forms of learning, where learners unconsciously alter movement kinematics to restore performance [113].

The relationship between MWM and explicit learning is straightforward. First, people could use MWM to mentally manipulate motor plans to quickly counteract errors [93,95]. Second, people efficiently 'cache' previously successful movement plans in memory across trials to speed learning [93,114]. Capacity constraints for this form of motor memory closely mirror capacity limitations in sensory WM (e.g., two to five items) [115,116]. Moreover, we recently observed that explicit learning in motor adaptation tasks is selectively correlated with an abstract limb-independent component of MWM, directly linking MWM to motor learning [117].

The first evidence for MWM signatures in implicit sensorimotor learning comes from adaptation studies pointing to distinct motor working memory stores for movement kinematics versus dynamics [118], or, alternatively, for different kinematic variables like position versus velocity [119]. Other evidence comes from elegant recent studies where it was discovered that during long temporal delays between trials, the degree of motor adaptation appears to decay back to an unadapted baseline state [120]. This is seen as reflecting a 'temporally volatile' component of motor adaptation and is consistent with a short-term motor memory trace that passively decays or is subject to interference. Whether this finding reflects the same form of MWM discussed in this review, or a separate memory process specific to sensorimotor adaptation, is unknown.

how one plans to lift it, suggesting that sensory contextual factors might be integrated into MWM representations [107]. Thus, one function of MWM may be to help integrate motor and nonmotor memory contents to guide adaptive actions [33,108–110].

Motor credit assignment

At a computational level, we propose that the core function of MWM is to assist with 'credit assignment'. Credit assignment is a fundamental concept in reinforcement learning, referring to the brain's ability to link outcomes to their preceding causes; for instance, to relate rewards and punishments to the actions that led to them. In the context of motor learning, a key candidate function of MWM could be to link rewards or errors not just to abstract action choices (e.g., selecting target A versus target B), but to the precise kinematic details of the preceding motor plans or commands (e.g., the reach curved 5° versus 10°) [111]. This would help bridge movement and feedback, especially when feedback is delayed.

This computation could be implemented in the brain by maintaining a persistent representation of recent movement details, perhaps through recruitment of a circuit that includes both sensorimotor and prefrontal cortices [52–54]. After performing a movement, the maintained trace could be compared to action outcomes to support (motor) reinforcement learning [11]. Recent observations of especially strong post-movement motor memory activity following rewarded versus unrewarded actions support this speculation [53].

Concluding remarks

From athletics and dance to knife skills and latte art, refining a motor skill requires consistently analyzing our performance after each movement. We believe this critical function – maintaining and manipulating motor information in mind over short time scales – is performed by a dedicated MWM system (see Outstanding questions). Moreover, we believe that MWM has both retrospective and prospective roles in behavior: retrospectively, integrated representations of actions can be stored in MWM following movement execution, after which actions can be refined to improve performance. Prospectively, MWM may allow for maintenance of motor information during movement preparation, such as when actions are deferred, mentally manipulated, or even imagined. In our view, MWM is a fundamental component of cognition and action.

Outstanding questions

How might MWM capacity or flexibility vary across people with different levels of expertise (e.g., athletes, musicians, etc.)?

What are the key nodes in the putative MWM neural circuit? Beyond sensorimotor cortex and prefrontal cortex, are subcortical areas (e.g., cerebellum, basal ganglia) also involved?

Might MWM be involved with an individual's ability to rapidly learn a novel brain-computer interface (BCI)?

Would successful computational models of MWM directly mirror current models of, for example, visual WM, or might they diverge in key ways?

Is MWM affected by aging in a manner similar to other forms of WM?

How might one's MWM system be leveraged to improve clinical outcomes related to motor performance, e.g., in stroke rehabilitation?

How conscious (or unconscious) is MWM?

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Declaration of interests

No interests are declared.

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