Title
Prioritized verbal working memory content biases ongoing action.

Journal
Journal of Experimental Psychology Human Perception & Performance, 46(12)

ISSN
0096-1523

Authors
Miller, Jacob A
Kiyonaga, Anastasia
Ivry, Richard B
et al.

Publication Date
2020-10-22

DOI
10.1037/xhp0000868

Peer reviewed

J Exp Psychol Hum Percept Perform. Author manuscript; available in PMC 2022 April 22.

Prioritized verbal working memory content biases ongoing action

Jacob A. Miller[1,*], **Anastasia Kiyonaga**[1,*], **Richard B. Ivry**[1,2], **Mark D'Esposito**[1,2]

[1]Helen Wills Neuroscience Institute, University of California, Berkeley - 175 Li Ka Shing Center, MC#3770, Berkeley, CA, 94720

[2]Department of Psychology, University of California, Berkeley - 175 Li Ka Shing Center, MC#3770, Berkeley, CA, 94720

Abstract

Working memory (WM) holds information temporarily in mind, imparting the ability to guide behavior based on internal goals rather than external stimuli. However, humans often maintain WM content for a future task while performing more immediate actions. Consequently, transient WM representations may inadvertently influence ongoing (but unrelated) motor behavior. Here, we tested the impact of WM on adult human action execution and examined how the attentional or "activation" state of WM content modulates that impact. In three dual-task experiments, verbal WM for directional words influenced the trajectory and speed of hand movements performed during WM maintenance. This movement bias was also modulated by the attentional state of the WM content. Prioritized WM content strongly influenced actions during WM maintenance, while de-prioritized WM content was less influential. In sum, WM can unintentionally shape ongoing motor behavior, but the behavioral relevance of WM content determines the degree of influence on motor output.

Keywords

Working memory; dual-task; action control; attention; output gating

---

As humans engage in complex cognition, our thoughts can inadvertently influence our interactions with the environment. Imagine, for instance, accidentally typing out or saying the wrong word aloud in conversation because it was currently on your mind. Here, we test the idea that such everyday cognitive slips emerge from the typically adaptive processes by which working memory (WM) guides behavior. WM maintains temporary mnemonic representations that can support perceptual continuity and attentional orienting, but a core function of WM is also to steer goal-directed actions (Fuster & Alexander, 1971; van Ede,

---

Corresponding authors: Jacob A. Miller (jacob_miller@berkeley.edu), Anastasia Kiyonaga (akiyonaga@ucsd.edu), 210 Barker Hall, UC Berkeley, Berkeley, CA.

[*]equal contributions

Author contributions
A.K. developed the study concept. J.A.M. and A.K. developed the study design with input from R.B.I. and M.D.. J.A.M. collected and analyzed the data under the supervision of A.K.. J.A.M. and A.K. drafted the manuscript, and R.B.I. and M.D. provided feedback and revisions. All authors approved the final version of the manuscript for submission.

Chekroud, Stokes, & Nobre, 2019). Recent studies have begun to highlight the influential role of WM in preparing volitional motor responses (Belopolsky & Theeuwes, 2011; Zokaei, Board, Manohar, & Nobre, 2019), as well as the reciprocal role of motor systems in supporting WM maintenance (Hanning, Jonikaitis, Deubel, & Szinte, 2016; Ohl & Rolfs, 2017). While WM is classically described as a system for short-term information storage, some theories assert that it would be better construed as intention to perform an action (Fuster, 1990, 2004, 2015; Postle, 2006; Theeuwes, Belopolsky, & Olivers, 2009). If that is the case, then WM content may bias ongoing motor behavior, even when the content is not directly task relevant. The current study tests the boundaries of the linkage between WM and action control. We investigate whether WM impacts action execution during maintenance, and how that impact is modulated by task goals.

WM maintenance can bias visual attention toward related content in the environment, even at the expense of the current task (Soto, Hodsoll, Rotshtein, & Humphreys, 2008). However, this influence of WM can be strategically modulated (Carlisle & Woodman, 2011; Kiyonaga, Egner, & Soto, 2012). For instance, when one among several WM items is flagged as relevant (i.e., ‘retro-cued’), attended WM items evoke more detectable neural traces with fMRI or M/EEG (LaRocque, Lewis-Peacock, & Postle, 2014; Wolff, Jochim, Akyurek, & Stokes, 2017), and such prioritized content biases visual attention more strongly (Mallett & Lewis-Peacock, 2018; Olivers, Peters, Houtkamp, & Roelfsema, 2011; van Moorselaar, Theeuwes, & Olivers, 2014). These findings align with a biased competition account of visual attention, wherein visual representations compete for attention in a weighted manner (Desimone & Duncan, 1995). This model further predicts that WM should have a similar influence on competing response systems. That is, if actively maintained WM content biases perceptual representations that guide attention, it may also bias motor preparation representations that guide action (Meiran, Cole, & Braver, 2012; Oberauer, 2010; Theeuwes et al., 2009). Yet we often maintain WM content that is relevant for a future goal while engaged in more immediate actions. As a result, actively maintained WM representations may bias ongoing (but unrelated) motor behavior.

While prioritized WM content is considered to be in a privileged, active state (Zokaei, Manohar, Husain, & Feredoes, 2014), deprioritized content is relatively less immediately relevant and is considered “unattended” (LaRocque et al., 2014; Lewis-Peacock, Drysdale, Oberauer, & Postle, 2011). It may be maintained with lower activity levels (Bays & Taylor, 2018) or in a distinct latent format (Rose et al., 2016; Sprague, Ester, & Serences, 2016), but the cognitive, neural, and behavioral status of this deprioritized content is currently unclear (Mallett & Lewis-Peacock, 2018; Manohar, Zokaei, Fallon, Vogels, & Husain, 2019; Nobre & Stokes, 2019; Park, Sy, Hong, & Tong, 2017). If deprioritized content is maintained at a quantitatively lower level of activation, it may exert a diminished but still measurable influence on behavior. If, on the other hand, it is maintained in a qualitatively distinct state, it may be prevented from spilling over into behavior. Internally oriented attention processes modulate visual WM performance (Souza & Oberauer, 2016), and are theorized to modulate the nature of visual WM representations (Stokes, 2015; van Loon, Olmos-Solis, Fahrenfort, & Olivers, 2018; Wolff, Ding, Myers, & Stokes, 2015). Here, we test the idea that such attentional prioritization processes should also determine how WM information influences ongoing motor behavior. In other words, we ask whether relative WM priority levels drive (sometimes erroneous) actions that occur during maintenance. We therefore employ an intervening motor task as a behavioral "probe" into the activation state of the WM content.

In theories of motor function, goal-potentiated frontal cortical representations feed into a basal ganglia gating mechanism whereby only the most active representations surpass the threshold to drive actions (Ivry & Spencer, 2004). The behavioral influence of WM has been theoretically attributed to a similar output gating function (Wallis, Stokes, Cousijn, Woolrich, & Nobre, 2015). In this model, attentional selection transforms WM representations from suspended internal maintenance into a behavior-driving state (Myers, Stokes, & Nobre, 2017). The presumed gating system also tracks the utility of WM representations, defining which ones should be selected (Chatham & Badre, 2015; Cools, Ivry, & D'Esposito, 2006). If the activity state of WM content determines such a gating process, task-irrelevant representations could be gated out when they are activated above threshold. While output gating has typically been considered to result from volitional selection of WM content, it could theoretically sometimes drive incorrect actions. However, in a complex task, multiple rules must be tracked and segregated for successful behavior, and this may be accomplished through hierarchical control functions which regulate gating behavior (Badre & Nee, 2018). Here, we also examine how item-level attentional selection (which may promote output gating) interacts with task-level goal maintenance functions to control WM-guided behavior.

Patients with frontal lesions sometimes display contextual *action slips,* like sprinkling salt into tea instead of on food (Schwartz, 1995). These deficits may be an exaggerated form of the everyday slips humans commit when thought content unintentionally infiltrates behavior. But what determines which representations surpass the action threshold? And how might an adaptive WM process interact with contextual task demands? To experimentally formalize action slips, we created scenarios wherein hand movements were executed during WM maintenance. In this dual-task setting, cued movement directions could be either compatible or incompatible with the meaning of the maintained content. We manipulated the predictive relationship between WM and motor goals across a task context (i.e., varying the proportion of compatible trials), as well the attentional priority level of WM content for trial-by-trial WM goals (i.e., retro-cueing). Across three experiments, this study examines whether WM maintenance biases intervening motor action, and if so, how task context and behavioral relevance influence this bias.

Experiment 1: Block-wise WM-relevance manipulation

Methods

Participants.—Participants were recruited from the Berkeley community, gave informed consent in accordance with the University of California Berkeley Institutional Review Board (IRB), and received either course credit or $20 per hour for participation. We aimed to recruit 30 participants for each experiment. This sample size was estimated from previous experiments that used a WM dual-task structure and a similar statistical comparison (e.g., congruent vs. incongruent Stroop trials; Kiyonaga & Egner, 2014). We expected a similar effect size, around Cohen's d = 0.7, for our primary effect of WM compatibility. With alpha = 0.05, this would yield a power of 0.96. Individuals were excluded if accuracy was below

60% or responses were entered on fewer than $\frac{2}{3}$ trials for either the motor or WM tasks. Experiment 1 was administered to 32 participants, but 3 were excluded for failing to meet the accuracy threshold. Therefore, analyses included 29 participants (9 male; mean age = 20.0 y, range = 18–24).

Task overview.—The goal was to simulate an everyday situation where information is maintained for future use while performing immediate actions. We therefore interleaved a verbal delayed recognition test with a simple motor task (Fig. 1a). On each trial, participants were instructed to remember a directional word (‘up,’ ‘down,’ ‘left,’ or ‘right’). Then, during the WM delay, they were visually cued to move the mouse and click on a target located at one of four cardinal screen positions (top, bottom, left, or right). After the motor task, participants were tested on their memory for the sample word. The meaning of the verbal WM content could be either compatible (e.g., remember ‘left’, click inside leftward box) or incompatible (e.g., remember ‘left’, click inside rightward box) with the direction of the cued hand movement. The task therefore required maintenance of multiple rules and representations for WM and motor components, which were sometimes in conflict with each other.

To examine how the priority level of WM representations might modulate their influence over behavior, we developed three variations of this basic task. Experiment 1 manipulated the relative value of the WM content across block conditions by varying the predictive utility of WM to the motor task. That is, the ratio of compatible to incompatible trials was varied across three task block contexts. Experiment 2 manipulated the trial-by-trial priority status of individual WM items to the WM test—with retro-cues to shift attention among simultaneously remembered items—while keeping the WM relationship to the motor task unchanged. Experiment 3 combined elements of Experiments 1 and 2, to examine the contributions of modulating WM at the level of task goals vs. item representations. All data and code are available on the Open Science Framework: https://bit.ly/2RlYRm5

Stimuli and procedure.—All tasks were programmed using Psychtoolbox functions (Brainard, 1997) (http://psychtoolbox.org/) in Matlab (https://www.mathworks.com/), along with custom scripts to track mouse positions. Participants sat ~60 cm from a 23 in. screen. The WM stimuli consisted of directional words (‘up,’ ‘down,’ ‘left,’ or ‘right’), presented in black (visual angle ~ 1.2°) on a neutral grey background (RGB: [128,128,128]). Every trial began with a 2 sec intertrial interval (ITI). Then a WM sample word appeared centrally for 1 sec. After a total delay of 5 sec, a WM probe word (selected from the same set as the WM samples) appeared centrally underneath a question mark. The WM task was to make a keyboard button press indicating whether the probe word was a match (‘S’ key) or non-match (‘D’ key) to the WM sample. Match and non-match WM probes were equally likely (50% match / 50% non-match) in all experiments.

During the WM delay, participants completed a manual action task. A central filled colored square (i.e., the cue) was flanked by unfilled square boxes (i.e., the targets) at each of four locations: to the top, bottom, left, and right of center. The central square could be one of four colors (RGB: green = [122,164,86], pink = [198,89,153], orange = [201,109,68], blue = [119,122,205]), which were chosen to be maximally distinct, matched on saturation and brightness, and color-blind friendly (http://tools.medialab.sciences-po.fr/iwanthue/). Each color was instructed to cue one of four screen locations: green *= left,* pink *= right,* orange *= up,* blue *= down*. The target boxes were equidistant from the central color cue and each other (size ~ 3.7°, distance from center ~ 9.3°). The motor task was to move the mouse and click inside the target box at the location cued by the color. The motor task therefore required a symbolic transformation from color to location, which was meant to engage the goal representation circuitry involved in gating motor behaviors (O'Reilly & Frank, 2005; Oliveira & Ivry, 2008). The motor task epoch ended when a cursor click was recorded in any of the target locations, or when a 2 sec response deadline passed.

The sequence of one complete dual-task trial started with a 2 sec ITI, followed by a 1 sec WM sample display, then a 2 sec fixation delay. After this first delay, the motor task display appeared for 2 sec, followed by another fixation delay of 1 sec, and then finally the WM probe display for 2 sec (Fig. 1a, left). There were two primary trial types: compatible trials, wherein the meaning of the WM word matched the cued direction of movement, and incompatible trials, wherein the WM word was paired with any of the three non-matching movement cues. The ratio of compatible to incompatible trials was manipulated across a given task block. Blocks contained either 80%, 50%, or 20% compatible trials (Fig. 1a, right). In "high compatibility" blocks (80% compatible), the WM sample meaning usually helped the motor task, as it corresponded to the directional goal of the upcoming movement. In "middle compatibility" blocks (50% compatible), the WM content was equally likely to be helpful or harmful to the motor task on any given trial. In "low compatibility" blocks (20% compatible) the WM sample meaning usually differed from the motor task target, and was therefore unhelpful. To minimize probabilistic learning effects, participants were explicitly informed about the percentage of compatible trials at the start of each block.

In order to learn the color-direction response mapping, participants practiced at least 12 trials of the motor task before each experiment. Then participants completed one 6-trial practice block of each condition (with feedback for motor and WM response accuracy) before completing three 30-trial experimental blocks of each condition (without feedback; 9 blocks total). Participants therefore completed 90 trials in each block condition and 135 trials of each compatibility condition across blocks (72 incompatible/18 compatible trials across "low compatibility" blocks, 45 incompatible/45 compatible trials across "middle compatibility" blocks, and 18 incompatible/72 compatible trials across "high compatibility" blocks). The first block was always middle compatibility (50% compatible), while the predictability conditions occurred in random order for the remaining blocks. The difference in motor behavior on compatible vs. incompatible trials—or the 'compatibility effect'—will serve here as an operational index of the influence of WM over ongoing action.

Movement trajectory analysis.—Mouse positioning data was tracked across the motor task to assess the influence of WM content on the direction of hand movements. To define when hand movement trajectories were curved away from the target location, we created a circle around the start position with a radius of ¼ the distance to the target. Trajectories were considered precise if they first crossed that boundary within 45° of the correct response axis, but were classified as *course adjustments* if they crossed that boundary at a wider angle than 45° before terminating at the correct target (Fig. 1b). All cursor trajectories were rotated to a common axis for comparison. Because the number of compatible and incompatible trials varied across block conditions in Experiment 1, we calculated the proportion of corrected movements as the number of *course adjustments* divided by the total trial number of that type. Finally, to test if course adjustment trajectories were biased specifically toward the direction held in WM, we analyzed trajectory data for each incompatible trial and categorized whether the exit angle of the initial movement matched the direction held in WM. We tested the proportion of trials matching the WM direction against 33.3%—the probability of moving randomly into one of the non-target directions on an incompatible trial. This is a conservative comparison, as the chance of randomly moving toward any of the four possible movement targets would be 25%.

Movement speed measures: *Movement initiation*—also sometimes referred to as 'reaction time'—was defined as the time from the onset of the color cue until the cursor first crossed a radius of 30 pixels from the starting position. *Movement duration*—also sometimes referred to as 'movement time'—was defined as the amount of time after movement initiation until a click was made within one of the movement targets.

Quality control criteria.—Trials were excluded if no WM probe response was made. For analyses of motor response speeds, outlier trials were excluded if a measurement was greater than 3 standard deviations away from the participants' mean, or if the motor task response was inaccurate. In Experiment 1, 2.8% of total trials were excluded as response speed outliers, 1.2% as nonresponse trials, and 2.7% as response errors.

Analysis strategy: For all measures, we conducted a 2 (*trial compatibility*: compatible vs. incompatible) × 3 (*block predictability*: low vs. middle vs. high compatibility) repeated measures ANOVA. To decompose any significant interactions, we conducted one-way ANOVAs of block predictability separately for compatible and incompatible trials. All ANOVA main effects and interactions are reported with the generalized-eta-squared (η_G^2) effect size measure. This estimate indexes the proportion of variability in the outcome measure associated with a given variable and generalizes across within- and between-subjects designs (Fritz, Morris, & Richler, 2012). All post-hoc t-tests are reported with the Cohen's d effect size and a bootstrapped (n = 10,000 bootstraps) 95% confidence interval for the Cohen's d value.

Results

WM accuracy.—For all experiments, WM probe accuracy was > 90% correct, confirming that participants completed the task as instructed. Neither trial compatibility nor block conditions significantly modulated WM probe accuracy (SI Exp. 1 Results). As our goal was to assess the influence of WM over motor behavior, the remaining analyses examine motor task performance.

Movement accuracy and action slips.—We first examined whether WM content impacted the direction of cued hand movements. Mouse clicking accuracy (% correct of click location) was reliably worse on incompatible (96%) vs. compatible trials (98.5%), $F(1,28) = 26.3$, $p < .001$, $\eta_G^2 = .08$. When the meaning of the WM content was incompatible with motor goals, participants entered more responses at the wrong target location. However, there was neither a main effect of block predictability, $F(2,56) = 0.94$, $p = .47$, $\eta_G^2 = .006$, nor an interaction between factors, $F(2,56) = 0.77$, $p = .40$, $\eta_G^2 = .003$.

Movement landing positions (i.e., final click location) were highly accurate overall (97%), but the shape of movement trajectories may also be biased by WM content. For instance, incompatible trials could result in curved paths that are skewed toward the direction that matches what is held in WM. Mouse movement tracking can therefore provide a more sensitive probe into the decision processes and action execution that are influenced by ongoing cognition. Indeed, the proportion of movement *course adjustments* was ~15% greater on incompatible versus compatible trials, $F(1,28) = 45.0$, $p < .001$, $\eta_G^2 = .18$ (Fig. 1c). The direction of initial movement on these course adjustment trials was also most likely to match the meaning of the word held in WM, $t(28) = 3.1$, $p = .005$, $d = 0.57$, rather than being driven by general conflict processes that might impair behavior overall (Fig. S1). However, while this compatibility effect was descriptively largest in high compatibility blocks and smallest in low compatibility blocks, there was neither a main effect of block predictability, $F(2,56) = 0.3$, $p = .72$, $\eta_G^2 = .0006$, nor an interaction between factors, $F(2,56) = 2.4$, $p = .10$, $\eta_G^2 = .006$. In sum, action execution was biased by the meaning of WM content, but was insensitive to the block WM compatibility context. When the meaning of the WM content was incompatible with motor goals, it produced circuitous hand movement trajectories in the WM-matching direction.

Movement speeds.—Multiple subprocesses may be influenced by the compatibility of the current WM content, or its relevance to the motor task. We therefore examined distinct measures of movement *initiation* and *duration*. A main effect of trial compatibility, $F(1,28) = 42.8$, $p < .001$, $\eta_G^2 = .04$, indicated that movements were initiated more slowly when the cued movement was incompatible with the WM sample (53 ms difference). A main effect of block predictability, $F(2,56) = 20.1$, $p < .001$, $\eta_G^2 = .03$, indicated that movements were also initiated more slowly overall in contexts when WM content was less likely to help motor performance. Moreover, there was an interaction between compatibility and predictability factors, $F(2,56) = 3.88$, $p = .026$, $\eta_G^2 = .003$. Separate follow-up ANOVAs for both trial types revealed effects of block predictability (compatible: $F(2,56) = 18.1$, $p < .001$, $\eta_G^2 = .05$; incompatible: $F(2,56) = 8.21$, $p < .001$, $\eta_G^2 = .01$). However, paired comparisons to the middle compatibility condition indicated that compatible movements were initiated faster in high compatibility blocks, $t(28) = 5.6$, $p < .001$, $d = 0.46$, $CI_{95\%}$ [0.25, 0.79], but no different in low compatibility blocks, $t(28) = 1.0$, $p = .32$, $d = 0.09$, $CI_{95\%}$ [−0.09, 0.29]. While incompatible trials were also initiated faster in high (vs. middle) compatibility blocks, $t(28) = 2.1$, $p = .04$, $d = 0.15$, $CI_{95\%}$ [0.01, 0.31], they were initiated more slowly in low compatibility blocks, $t(28) = 2.47$, $p = .02$, $d = 0.12$, $CI_{95\%}$ [0.03, 0.26]. These differences translated into a compatibility effect (i.e., incompatible - compatible RT) that was significantly greater in high compatibility blocks than in low compatibility blocks, $t(28) = 2.76$, $p = .01$, $d = 0.52$, $CI_{95\%}$ [0.20, 0.85], (Fig. 1d, left).

Movement duration also showed main effects of trial compatibility, $F(1,28) = 33.7$, $p < .001$, $\eta_G^2 = .07$, and block predictability, $F(2,56) = 5.01$, $p = .010$, $\eta_G^2 = .004$. However, while movement *initiation* was overall speeded by a higher frequency of compatible trials, *movement duration* was slowed instead. There was also an interaction between trial and block factors, $F(2,56) = 8.44$, $p < .001$, $\eta_G^2 = .008$, where follow-up ANOVAs revealed an effect of block predictability only for incompatible trials, $F(2,56) = 11.3$, $p = .001$, $\eta_G^2 = .02$ (but not compatible, $F(2,56) = 1.1$, $p = .35$, $\eta_G^2 = .002$). Incompatible movement times were relatively longer in high compatibility blocks (vs. middle compatibility), $t(28) = 3.83$, $p < .001$, $d = 0.26$, $CI_{95\%}$ [0.12, 0.41], but low compatibility blocks were unaffected, $t(28) = 0.7$, $p = .49$, $d = 0.04$, $CI_{95\%}$ [−0.10, 0.16]. Like *movement initiation*, the compatibility effect was greater in the high compatibility block condition compared to middle compatibility blocks, $t(28) = 3.82$, $p < .001$, $d = 0.56$, $CI_{95\%}$ [0.29, 0.82] (Fig. 1d, right). Whereas the effect in *movement initiation* was driven by speeding on compatible trials, this effect in *movement duration* was driven by slowing on incompatible trials. That is, the influence of WM on movement speeds was strongest when WM content was most relevant to the motor task, although trial compatibility affected *movement initiation* and *duration* times differently. Even in low compatibility blocks alone, however, there was still a robust compatibility effect for both *movement initiation*, $t(28) = 5.56$, $p < .001$, $d = 0.33$, $CI_{95\%}$ [0.20, 0.50], and *movement duration*, $t(28) = 2.87$, $p = .008$, $d = 0.35$, $CI_{95\%}$ [0.12, 0.65]. To examine whether this effect might stem from a strategic carryover from high compatibility blocks when WM content was helpful, we analyzed the compatibility effect only for low compatibility (20%) blocks that were administered *before* any high compatibility (80%) blocks. The *movement initiation* benefit was present even when participants had not yet experienced any high compatibility (80%) blocks, $t(12) = -2.85$, $p = .014$, $d = 0.26$, $CI_{95\%}$ [0.08, 0.52]. Therefore, WM content biased motor behavior before it would have been reinforced as useful for the manual task.

Finally, to address whether incompatible WM content truly slowed the rate of movement execution (rather than requiring time to redirect initially deviant movement paths), we analyzed response speeds after excluding *course adjustment* trials (SI Exp. 1 Results). Even precise movements were overall slowed by incompatible WM content, but the predictability between the WM content and the motor task only modulated *movement initiation* (not *duration*). In other words, the extended incompatible *movement durations* in high compatibility blocks may be explained by the longer movement paths on course adjustment trials.

Experiment 1 Discussion

Motor behavior was influenced by WM content: movement accuracy, precision, initiation, and duration were all worse when remembered words were incompatible with the intended direction of movement. Even when WM content was irrelevant to the immediate task (i.e., low compatibility blocks), it still sometimes translated into motor output. These findings mirror the attentional biasing effects of visual WM content (Desimone & Duncan, 1995; Soto et al., 2008), suggesting that this visual cognitive framework may also be applied to understand how verbal WM content interacts with ongoing demands, and moreover, how

WM content biases overt manual actions. Recent theoretical work has further described a strong functional link between visual WM and planned actions (van Ede, 2020). The current findings empirically support the notion that WM may be best understood as intention to perform an action (Theeuwes et al., 2009), extrapolating from this framework to show that the linkage may promote some unplanned influences of WM as well. Such an incidental influence of WM content has previously been labeled as “automatic,” because it occurs even when the content is detrimental to ongoing processing (e.g., Soto et al., 2008). However, it could instead stem from a strategic tendency to apply WM content toward current behavior because it is typically relevant to immediate goals and would be generally adaptive to do so.

Indeed, movement speeds revealed that task context can adaptively modulate this WM influence over motor behavior. Movements were initiated faster when WM was likely to predict movement direction, but slower when it was unlikely to help. Block-level WM utility to the motor task may have lowered the decision threshold to trigger a movement, as if the WM content were gated into an action-facilitating state. However, this facilitation ultimately produced more time-consuming movement paths when WM turned out to be incompatible—i.e., slower *movement duration* in high compatibility blocks—as the motion was triggered toward the wrong location and required course adjustment to reach the target.

Here, WM content is in competition for selection with motor rules, and the likelihood for selectively gating out the WM content (rather than the correct motor rule) might theoretically increase when WM is more likely to aid motor performance (Badre, 2012). However, theories of hierarchical control also predict varying levels of segregation between representations for multiple concurrent task rules (Verbruggen, McLaren, Pereg, & Meiran, 2018). Here, when the context dictated that WM would likely help, it could have increased the relative weighting of the WM rule, making it more difficult to segregate from motor goals. This would facilitate motor behavior when the two are compatible but promote interference when incompatible, like we observed here. That is, these results may reflect control limitations in a task with competing nested rules and demands (Braem et al., 2019), rather than a modulation of gating thresholds, per se.

Experiment 2: Probabilistic retrocue manipulation

Methods

Rationale.—Experiment 1 showed that the effect of WM content on motor behavior is modulated by its predictive relationship to movement goals. However, if this influence of WM does indeed stem from the activation state of the WM content—rather than simply the likelihood that the WM content will be useful—then prioritized WM content should bias actions, even when there is no relationship between WM and motor task components. Therefore, in Experiment 2, we manipulated the priority level of individual WM representations among competing alternatives. Two WM samples were presented, and trial-by-trial retrocues indicated which sample was most likely to be probed. Across all blocks of the experiment, compatible and incompatible trials were equally likely. Whereas Experiment 1 may have modulated the tonic weighting between higher order WM vs. motor task goals (i.e., compatible trials are more likely, therefore WM > motor), explicit cueing in Experiment 2 should instead acutely modulate the weightings between concurrently maintained WM stimuli (i.e., ‘left’ is more likely to be tested, therefore ‘left’ > ‘right’). If the activation state of WM content determines its degree of influence on behavior, then a prioritized (i.e., retrocued) WM item should influence ongoing actions more than a de-prioritized (i.e., uncued) item, even when both are equally likely to aid motor task performance.

Participants.—A new set of 31 participants was recruited using the same guidelines and IRB approval as in Experiment 1. 28 participants were included in Experiment 2 analyses (14 male; mean age = 20.2 y, range = 18–26) after 3 exclusions for below threshold accuracy (60%).

Procedure.—Experiment 2 employed the same basic dual-task structure as Experiment 1, with a few key adjustments (Fig. 2a). Rather than a single WM sample, two WM sample words were presented sequentially for 250 ms each, separated by a 500 ms ISI. After a 1,500 ms delay, a cue (*1*, *2*, or *X*) was displayed. A *1* or *2* served as an informative retrocue, indicating that either the first or second WM sample word was most likely to be probed. An *X* designated that the two sample words were of equal priority, as either word was equally likely to be tested (this is often referred to in the literature as a ‘neutral’ condition). Following a second delay of 2,000 ms, participants completed the same motor task as in Experiment 1. Before the WM probe, a probe cue appeared for 1,500 ms to indicate which item was being tested (*1* or *2*). Then the match/non-match WM probe word appeared centrally until a response, for up to 2,000 ms. Regardless of which item was retrocued earlier in the trial, the task was to compare the probe word to the corresponding WM sample: the 1st WM sample if the probe cue was a *1*, and the 2nd sample if the probe cue was a *2*. Retrocues were 90% valid, meaning that the WM sample that was cued earlier in the trial was probed on 9 out of 10 trials. Therefore, either a *1* or *2* should attentionally prioritize the cued item (and relatively de-prioritize the uncued item), whereas an *X* should result in equal priority for both items.

Three compatibility conditions were defined based on which WM item was retrocued. On *compatible* trials, the retrocued WM item was congruent with the movement direction. On *incompatible* trials, the retrocued item was incongruent with the movement direction. On *equal priority* trials, neither item was retrocued, Therefore, trials labeled *compatible* or *incompatible* only occurred when there was an informative retrocue. Retrocues only informed which WM item would be probed, but provided no information about the motor task. *Compatible*, *incompatible*, and *equal priority* trials were equally distributed in random order within each experimental block (i.e., each occurred on 1/3 of trials). Moreover, retrocue validity (i.e., whether the retrocued item was probed at the end of the trial) was unrelated to trial compatibility. In Experiment 2, therefore, the proportion of compatible trials remained constant across the experiment.

Because there were two WM sample items, they could either both be incompatible with the movement direction, or one could be compatible while the other was incompatible. *Equal priority* trials were evenly split so that one item was compatible on half of trials, while both items were incompatible on the other half of trials. For *incompatible* trials, the uncued item was selected equally often from the remaining three words, which resulted in a compatible uncued item on 1/3 of incompatible trials. However, this experiment was not optimized to examine these compatibility sub-conditions, so analyses collapse across them to maximize trial numbers in each condition (but see Experiment 3). Participants completed one 8-trial practice block (with performance feedback), before completing at least 6 experimental blocks of 36 trials (without feedback). Each participant therefore completed at least 72 trials per condition (*compatible* / *incompatible* / *equal priority* trials) across the session.

Quality control criteria.—As with Experiment 1, nonresponse trials for the WM probe, outliers for the motor response speed (> 3 s.d. from subject mean), and inaccurate motor task responses were excluded. In Experiment 2, 3.2% of total trials were excluded as response speed outliers, 1.6% as nonresponse trials, and 2.8% as response errors.

Analysis strategy.—We performed one-way ANOVAs, with a factor of *cued compatibility* (*compatible* vs. *equal priority* vs. *incompatibl*e), on all measures. We then decomposed any significant effects of compatibility by calculating and comparing difference scores from the *equal priority* condition, where a ‘benefit’ reflects relatively faster or more precise responses, and a ‘cost’ reflects relatively slower or less precise responses. To determine if the influence of compatibility was reflected across each subject’s distribution of response times (rather than being driven by a small number of trials on either end of the RT distribution), we analyzed the slopes of response time decile distributions (SI Exp. 2 Methods).

Results

WM accuracy.—WM probe accuracy was high (~92% correct) and was unaffected by *compatibility*, $F(2,54) = 0.4$, $p = .67$, $\eta_G^2 = .002$. To ensure that participants used the retrocue as expected, we examined the effect of retrocue validity on WM probe performance. Accuracy was better when participants were validly probed on memory for the cued item (94.7%), compared to when they were invalidly probed on memory for the uncued item (85.4%), $t(27) = 4.1$, $p < .001$, $d = 0.98$, $CI_{95\%}$ [0.61, 1.36]. Therefore, participants prioritized the cued item as expected but still remembered the uncued item well above chance.

Movement accuracy and action slips.—Overall movement accuracy was high (~97%) and marginally influenced by *cued compatibility*, $F(2,54) = 2.6$, $p = .08$, $\eta_G^2 = .03$, in that performance was best for compatible and worst for incompatible trials. Movement precision was also influenced by the compatibility between WM and movements goals, $F(2,54) = 7.4$, $p = .001$, $\eta_G^2 = .01$, as course adjustment errors were least frequent on compatible trials and most frequent on incompatible trials. This difference in the proportion of course adjustments also emerged as a benefit of compatible trials (relative to *equal priority*), $t(27) = 2.4$, $p = .022$, $d = 0.14$, $CI_{95\%}$ [0.02, 0.27], and a marginal cost of incompatible trials, $t(27) = 1.9$, $p = .069$, $d = 0.14$, $CI_{95\%}$ [0.00, 0.31] (Fig. 2b, right). When prioritized WM content was compatible with action goals, movement precision was improved, but when the two were incompatible, movement trajectories were more roundabout and required adjustment to arrive at the target.

Movement speeds.—The compatibility of the cued WM item influenced *movement initiation*, $F(2,54) = 8.3$, $p < .001$, $\eta_G^2 = 0.008$, and *duration*, $F(2,54) = 5.0$, $p = .01$, $\eta_G^2 = .005$. There was a significant benefit of compatible cueing to *movement initiation*, $t(27) = 3.3$, $p = .003$, $d = 0.20$, $CI_{95\%}$ [0.06, 0.39], but no cost of incompatible cueing, $t(27) = 1.2$, $p = .25$, $d = 0.06$, $CI_{95\%}$ [−0.06, 0.17] (Fig. 2c, *left*). Conversely, there was a significant cost of incompatible cueing to *movement duration*, $t(27) = 2.4$, $p = .024$, $d = 0.10$, $CI_{95\%}$ [0.02, 0.21], but no benefit of compatible cueing, $t(27) = 1.2$, $p = 0.24$, $d = 0.07$, $CI_{95\%}$ [−0.04, 0.18] (Fig. 2c, *right*). When prioritized WM content matched the goals of a motor task, movement initiation was speeded, but when WM matched a motor task distractor, the movement itself took longer. This compatibility effect was reflected across the entire RT distribution (SI Exp. 2 Results, Fig. S2), rather than being driven by a small number of trials at the edges of the distribution.

Experiment 2 Discussion

While Experiment 1 manipulated the utility of WM content to the motor task, Experiment 2 used retrocues among two WM samples to manipulate their relative value to the WM test. Retrocues modulate neural signatures of WM representations (LaRocque et al., 2014), as well as pupil responses to WM content (Zokaei et al., 2019), and they are theorized to transform WM content into an “output-driving” state (Myers, Stokes, et al., 2017). We therefore predicted that retrocues would modulate the behavioral impact of WM, even on a task with a distinct goal from the WM task. As predicted, when multiple items were maintained in WM, the prioritized item influenced ongoing manual actions (and was also remembered better). Like Experiment 1, however, movement speeds suggested that prioritized WM content ignited movements toward WM-compatible locations, but resulted in circuitous and slower movement paths on incompatible trials.

Even in a task context where WM goals have no predictive relationship to action goals (unlike Experiment 1), activated WM content can influence actions. Because Experiment 2 manipulated the relative priority status of two concurrently-maintained WM items, the findings suggest that the activation state of WM determines its sway over behavior. Theories of visual WM and attention have proposed that the activation status of a visual WM representation should determine whether it biases externally oriented visual attention (Olivers et al., 2011). The current findings suggest that this theoretical framework can be applied to understand the relationship between verbal WM and motor behavior as well.

However, retrocues were 90% valid in Experiment 2, which could have encouraged multiple strategies, like dropping the uncued item from memory entirely, or actively maintaining both items in case the uncued one were tested. Therefore, the distinction in attentional state between cued and uncued WM items was still ambiguous. In order to test competing theories about whether or not uncued (i.e., “unattended”) WM content influences behavior, we devised an additional experiment in which uncued WM content always had to be maintained for later use. Experiment 3 will therefore provide a stronger manipulation of attentional prioritization within WM, so we can test the impact of attended versus “unattended” WM content and clarify the conditions that trigger WM biasing of action.

Experiment 3: Double retrocue manipulation

Methods

Rationale.—This third (and final) experiment combines elements of Experiments 1 and 2 to examine the contributions of several distinct modes of WM modulation and influence over actions. Experiment 1 manipulated the task-level predictive relationship between WM and motor goals, while Experiment 2 manipulated the item-level likelihood that a given stimulus would need to be remembered. Experiment 3 combines these two manipulations, in a between-subjects design, to examine whether they evoke distinct or overlapping influences on behavior. This experiment again used a trial-by-trial retrocue procedure, but the task-level predictability between WM and motor goals was also manipulated between groups. Experiment 3 further employed two 100% valid retrocue phases (Fig. 3a). Thus, the cued item was known with certainty to be the one that should be prioritized in the first phase, but the uncued item still had to be retained because it was likely to become relevant again in the second phase. This allowed us to additionally test whether an unprioritized item imparts any trace on concurrent behavior when it may become relevant later.

Participants.—Two new groups of participants were recruited using the same guidelines and IRB approval as Experiments 1 and 2. After 3 exclusions for below threshold accuracy (60%), Experiment 3 analyses included 30 (out of 30) participants in a “middle compatibility” group condition (12 male; mean age = 20.8 y, range = 18–30), and 29 (out of 32) participants in a “low compatibility” group condition (7 male; mean age = 20.9 y, range = 18–30).

Procedure.—Like Experiment 2, two WM sample words were presented on each trial. After a delay of 1,500 ms, a retrocue (*1, 2,* or *X*) was displayed, but informative retrocues (*1* or *2)* were 100% valid indicators of which item would be probed, while an *X* indicated *equal priority*. After a second delay of 2,000 ms, participants completed the same motor task as in Experiments 1 and 2. Then the WM probe word appeared centrally until a response or a 3,000 ms deadline. On informative retrocue trials, participants compared the probe to the cued item. On *equal priority* trials, participants indicated whether the probe matched either item in WM. After an intermediate delay of 1,500 ms, the second trial phase began and participants were presented with another retrocue, motor task, and WM probe (Fig. 3a). Phase 2 followed the same structure and timing as Phase 1. After the second probe, a fixation cross appeared to indicate the start of a new trial. Participants completed one 8-trial practice block (with feedback), before completing 7 experimental blocks of 24 trials (without feedback).

The retrocue conditions (*1, 2,* or *X*) were evenly distributed, counterbalanced within each block and across trial phases, and each equally likely in the first and second phases. Like Experiment 2, the compatibility conditions are labeled depending on which of the two WM items was cued. However, the ratio of compatible to incompatible trials across the experiment was manipulated between groups. One experimental group was administered a version where, like Experiment 2, *compatible*, *incompatible*, and *equal priority* trials occurred equally often. Therefore 1/3 of all trials were compatible, and any given trial was equally likely to be one of the three conditions. Because half of all informatively cued trials were compatible, this is most akin to the middle (50%) compatibility condition from Experiment 1 and is therefore referred to as the "middle compatibility" group. The other group was administered a lower compatibility task version, wherein only one quarter of informatively cued trials were compatible, and therefore only 1/6 of all trials were compatible. This condition is referred to as the "low compatibility" group (Fig. 3b, *right*). Within a group, the proportion of compatible trials remained fixed across blocks. However, because incompatible trials could be categorized into subtypes that had an unequal distribution (described below), and the longer running time of the two-phase trial necessitated fewer trials per block, the incompatible subtypes could not be evenly divided for each block. Therefore, trial numbers of each condition were slightly variable across blocks and participants (+/−1 occurrence of each trial type in each block). In total, participants in the "middle compatibility" group completed 56 trials (+/− 7) per condition (*compatible* / *incompatible* / *equal priority* trials). Participants in the "low compatibility" group completed 28 compatible trials, 84 incompatible, and 56 equal priority trials.

In addition to assessing performance on the compatibility conditions that were tested in Experiment 2, here the experiment was designed to also test the behavioral impact of deprioritized or "unattended" WM content. On trials where the cued item was incompatible, the uncued item was selected from one of the three remaining words and could therefore be either compatible or incompatible with the movement direction. The label "fully incompatible with WM" will be used to describe trials where both the cued and uncued WM items were incompatible (2/3 incompatible trials), while "compatible with uncued WM" will be used to described trials where the cued item was incompatible but the uncued item was compatible (1/3 incompatible trials). The label "compatible with active WM" will describe trials where the cued item is compatible and the uncued item is necessarily incompatible, as it is impossible to have more than one compatible item in this task design. If deprioritized WM items have any impact on behavior, then "compatible with uncued WM" trials—when an unprioritized WM item is compatible with the movement direction—should be faster than "fully incompatible with WM" trials.

Quality control criteria.—As with Experiments 1 and 2, nonresponse trials for the WM probe, outliers for the motor response speed (> 3 s.d. from subject mean), and inaccurate motor task responses were excluded. Because Experiment 3 included two motor and WM phases, trimming criteria applied to both trial phases. In the "middle compatibility," group, 6.1% of total trials were excluded as response speed outliers, 0.3% as nonresponse trials, and 3.6% as response errors, while in the "low compatibility" group, 5.9% were excluded as response speed outliers, 0.5% as nonresponses, and 4.6% as response errors.

Analysis strategy: We first analyzed the compatibility conditions that were tested in Experiment 2, to assess whether the basic compatibility effects replicated in this modified task design. We conducted 3 (*trial compatibility*: compatible, equal priority, incompatible) × 2 (*task group*: middle vs. low compatibility) repeated measures ANOVAs on all Phase 1 performance measures. Trial type was modeled as a within-subjects factor and task compatibility as a between-subjects factor. We decomposed any significant interactions with follow-up one-way ANOVAs of trial compatibility, separately for each task group. Like Experiment 2, we further decomposed any main effects by examining benefits and costs (relative to *equal priority* trials). This task employed a second retrocue and motor phase in order to ensure that uncued WM content was still remembered for the later test. Although we had no hypotheses about performance in Phase 2, we also ran a full model of the experiment that included task phase. However, the task phase factor showed no main effects or interactions with either compatibility or task group (SI Exp. 3 Results). We also examined whether Phase 1 item priority levels impacted Phase 2 motor behavior, categorizing trials based on the interaction between Phase 1 and Phase 2 attentional states (SI Exp. 3 Results, Fig. S4). There were no significant effects of changing priority status, therefore the primary analyses below focus on Phase 1 alone.

To test the impact of deprioritized WM content, we calculated difference scores from the *equal priority* condition for each compatibility sub-condition. We conducted 3 (*trial compatibility*: compatible with active WM, compatible with uncued WM item, fully incompatible with WM) × 2 (*task group*: middle vs. low compatibility) repeated measures ANOVAs on these difference scores, for each movement speed measure. We also decomposed any significant interactions with follow-up one-way ANOVAs of trial compatibility, separately for each task group. One participant was excluded from this analysis because too few trials remained in the "compatible with uncued WM item" condition (the least frequent trial type) after removal of outliers and motor errors.

Results

WM accuracy.—WM probe accuracy was high in trial Phase 1 (92.4%), and showed an interaction between compatibility and task group, $F(2,114) = 3.24$, $p = .04$, $\eta_G^2 = .01$, but no main effects (compatibility: $F(2,114) = 1.05$, $p = .35$, $\eta_G^2 = .003$, task group: $F(1,57) = 0.08$, $p = .78$, $\eta_G^2 = .001$). This interaction was likely driven by a trending effect of compatibility in the low compatibility task group, $F(2,56) = 2.75$, $p = .07$, $\eta_G^2 = .01$, although there were no significant differences between any of the main trial types on Phase 1 WM accuracy. On trial Phase 2, WM probe accuracy was also high (93.1%), but with no main effect compatibility, $F(2,114) = 0.4$, $p = .65$, $\eta_G^2 = .001$, task group, $F(1,57) = 0.8$, $p = 0.4$, $\eta_G^2 = .01$, or interaction, $F(2,114) = 0.1$, $p = .49$ $\eta_G^2 = .0001$. Therefore, participants did retain both WM items for the second WM test.

Movement accuracy.—Movement accuracy was high in trial Phase 1 (95.2%), but with no main effects of *cued compatibility*, $F(2,114) = 1.5$, $p = .23$, $\eta_G^2 = .004$, or task group, $F(1,57) = 0.6$, $p = .45$, $\eta_G^2 = .008$, nor an interaction, $F(2,114) = 1.6$, $p = .21$, $\eta_G^2 = .005$. Accuracy was slightly worse in Phase 2 (95.8%), but was unaffected by *cued compatibility*, $F(2,114) = 0.5$, $p = .59$, $\eta_G^2 = .002$, or task group, $F(2,114) = 1.9$, $p = .17$, $\eta_G^2 = .03$, and with no interaction, $F(2,114) = 2.2$, $p = .11$, $\eta_G^2 = .007$. Because of a programming error, cursor trajectory data are missing for Experiment 3, and the remaining analyses focus on movement speeds.

Movement speeds.—There were no main effects of task group for either *movement initiation,* $F(1,57) = 0.2$, $p = .67$, $\eta_G^2 = .002$, or *duration,* $F(1,57) = 1.0$, $p = .31$, $\eta_G^2 = .02$, indicating that performance was comparable across groups. Replicating Experiment 2, however, there were strong effects of compatibility on both movement *initiation* and *duration,* which were reflected across the entire RT distribution for *initiation* (SI Exp. 3 Results, Fig. S2). Movement *initiation* displayed a main effect of compatibility, $F(2,114) = 13.6$, $p = < .001$, $\eta_G^2 = .02$, as well as an interaction with task group $F(2,114) = 4.4$, $p = .01$, $\eta_G^2 = .007$ (Fig. S3). Follow-up one-way ANOVAs indicated that the compatibility effect was only present in the middle compatibility group, $F(2,58) = 13.0$, $p = < .001$, $\eta_G^2 = .04$, but not the low compatibility group, $F(2,58) = 2.1$, $p = .13$, $\eta_G^2 = .006$. In the middle compatibility group, there was a significant benefit of compatible cueing to *movement initiation*, $t(28) = 3.9$, $p < .001$, $d = 0.49$, $CI_{95\%}$ [0.23, 0.73], but no cost of incompatible cueing, $t(28) = 1.13$, $p = .27$, $d = 0.09$, $CI_{95\%}$ [−0.07, 0.24], much like Experiment 2.

Likewise, movement *duration* displayed a main effect of compatibility, $F(2,114) = 5.1$, $p = .008$, $\eta_G^2 = 0.007$, as well as an interaction with task group, $F(2,114) = 4.7$, $p = .01$, $\eta_G^2 = .007$. follow-up one-way ANOVAs indicated that the compatibility effect was only present in the middle compatibility group, $F(2,58) = 10.1$, $p < .001$, $\eta_G^2 = .02$, but not the low compatibility group, $F(2,58) = 1.17$, $p = .32$, $\eta_G^2 = .004$. Also like Experiment 2, there was no significant benefit of compatible cueing to *movement duration*, $t(28) = 0.9$, $p = .37$, $d = 0.09$, $CI_{95\%}$ [0.12, 0.31] but there was a cost of incompatible cueing, $t(28) = 3.6$, $p = .001$, $d = 0.28$, $CI_{95\%}$ [0.11, 0.51], in the middle compatibility group (Fig. S3). Therefore, for the middle compatibility group, the dissociable pattern of benefits and costs between movement *initiation* and *duration* replicated Experiment 2. However, these benefits and costs disappeared in the low compatibility task context, when WM content was unlikely to aid motor performance (1/6 of all trials).

These compatibility effects also persisted when the "total" compatibility of the WM sample set was held constant. That is, we repeated these ANOVAs including only trials where the WM sample contained at least one compatible item (i.e., *incompatible* trials where the uncued item was compatible, and *equal priority* trials where one of the 2 items was compatible). There were still main effects of compatibility on *movement initiation*, $F(2,114) = 4.0$, $p = .02$, $\eta_G^2 = .01$, and *movement duration*, $F(2,114) = 3.1$, $p = .05$, $\eta_G^2 = .007$ (SI Exp. 3 Results). Therefore, given trials that included both a compatible and an incompatible item, movement speeds were driven by which of the two were prioritized (Fig. 3d).

Additional analyses of each compatibility sub-condition provided further insight into the costs and benefits of WM content at different levels of attentional priority. We analyzed movement speed difference scores from *equal priority* trials as a function of whether (1) the cued WM item was compatible, (2) the uncued WM item was compatible, or (3) both WM items were incompatible (Fig. 3b). For *movement initiation*, there was a main effect of trial compatibility, $F(2,112) = 9.4$, $p < .001$, $\eta_G^2 = .06$, as well as an interaction between compatibility and task group, $F(2,112) = 3.0$, $p = .05$, $\eta_G^2 = .02$ (Fig. 3c, *left*). Follow-up tests showed that, in only the middle compatibility task group, there was a strong *initiation* benefit when the hand movement direction was compatible with the active (cued) WM item, $t(28) = 4.0$, $p < .001$, $d = 0.51$, $CI_{95\%}$ [0.24, 0.77]. There was also a marginal benefit compared to *equal priority* trials when the movement was compatible with the uncued WM item, $t(28) = 0.3$, $p = .051$, $d = 0.28$, $CI_{95\%}$ [0.05, 0.55], and no effect when both WM items were incompatible, $t(28) = 2.0$, $p = .78$, $d = 0.05$. Although there was a small benefit of a compatible uncued item (compared to equal priority), however, this condition did not differ from fully incompatible trials, $t(28) = 1.9$, $p = .07$, $d = 0.26$, $CI_{95\%}$ [0.03, 0.53]. Moreover, *movement initiation* was still significantly faster when the cued WM item was compatible, compared to the uncued item, in the middle compatibility group alone, $t(28) = 2.0$, $p = .05$, $d = 0.23$, $CI_{95\%}$ [0.05, 0.38], and combined across both task groups, $t(58) = 2.6$, $p = .01$, $d = 0.21$, $CI_{95\%}$ [−0.01, 0.48] (Fig. 3d).

To further probe a possible impact of relatively unattended WM content, we also tested whether *equal priority* trial performance varied according to the compatibility of the sample set. Indeed, *movement initiation* was faster on trials when the equal priority WM set included one compatible item versus two incompatible WM items, although neither was cued as most relevant – both for the middle compatibility group, $t(29) = 2.8$, $p = .009$, $d = 0.24$, $CI_{95\%}$ [0.06, 0.40], and marginally for the low compatibility group, $t(28) = 2.0$, $p = .06$, $d = 0.23$, $CI_{95\%}$ [−0.01, 0.50].

Finally*, movement duration* also displayed a main effect of compatibility when examining these trial sub-type difference scores, $F(2,112) = 5.3$, $p = .006$, $\eta_G^2 = .03$, as well as an interaction between compatibility and task group, $F(2,112) = 9.4$, $p < .001$, $\eta_G^2 = .06$ (Fig. 3c, *right*). As with the earlier experiments and analyses, in the middle compatibility group there was no benefit (relative to equal priority trials) when the movement direction was compatible with the active (cued) WM item, $t(28) = 0.8$, $p = .43$, $d = 0.08$, $CI_{95\%}$ [−0.03, 0.40]. However, there were costs when the WM content was fully incompatible with the movement direction, $t(28) = 3.3$, $p = .003$, $d = 0.29$, $CI_{95\%}$ [0.11, 0.56] as well as when the movement was compatible with the uncued WM item (but the cued item was still incompatible) $t(28) = 2.7$, $p = 0.01$, $d = 0.28$, $CI_{95\%}$ [0.09, 0.55]. In the case of movement duration, the unattended compatible content did not appear to impart any benefit. Again, these costs of incompatible cuing were eliminated in the low compatibility task group, when WM content was unlikely to aid motor performance on average.

Experiment 3 Discussion

Like Experiment 2, compatible WM content facilitated *movement initiation* while incompatible content slowed the motion itself (relative to equal priority trials). Here, we also show that deprioritized WM content can modestly influence action in certain contexts. *Movement initiation* was faster when there was a compatible item in the WM set (vs. two incompatible items), even if that item was not cued as relevant (either uncued or equal priority). Rather than an all-or-none influence of attentional prioritization, remembered items at lower priority may be maintained in a state that still influences behavior, but to a lesser extent than fully prioritized WM content. However, *movement duration* times were unaffected by deprioritized content, suggesting that accessory WM items may influence decision processes to start actions, but only prioritized content influences execution of the action itself.

Experiment 3 further supports the hypothesis that WM activation status modulates its impact on action. When two items were maintained, the attended one preferentially drove ongoing behavior. Item-level WM priority status also interacted with the task-level WM predictive utility to movement goals. When WM goals had a neutral relationship to motor goals (middle compatibility group, 1/3 compatible trials total), item-level activation status of WM content exerted a strong influence over behavior. However, in a task context when WM content was unlikely to help motor behavior (low compatibility group, 1/6 compatible trials total), both costs and benefits from WM content were eliminated. This suggests that the temporally-extended, higher-order task goals may take precedence and control the impact of phasic item-level attentional modulation.

General Discussion

Here, we examined how transient WM representations shape ongoing actions. We tested whether WM content influences movements executed during maintenance, and we probed the flexibility of that influence by manipulating the task-relevance of WM to either motor or mnemonic goals. Movements were less accurate, less precise, initiated later, and completed more slowly when they were incompatible with WM content. Across all three experiments, motor benefits of compatible WM content manifested in accelerated decision processes, while costs of incompatible content manifested in imprecise and time-consuming actions. This effect on movement speeds depended on the priority level of WM representations, and was enhanced or diminished when WM content was predictably helpful or harmful to motor behavior, respectively. Visual WM content has long been shown to inadvertently influence perception and attention (Soto et al., 2008), and these findings now demonstrate that verbal WM exerts similar influences on motor behavior. However, rather than a monolithic effect on movement, WM content biases distinct stages of action execution in dissociable ways.

Theories of visual WM and attention have proposed that the ‘activation state’ of visual WM content will determine whether it incidentally biases perceptual and attentional processing (Olivers et al., 2011). A more recent proposal further distinguishes between neural and “functional” activation states, to suggest that the influence of WM will depend on its intended future use (Nobre & Stokes, 2019). The current results suggest that these frameworks can be applied to understand the incidental influence of verbal WM content on manual actions. These results support and augment theoretical conceptualizations of WM as intention or preparation for future actions (Fuster, 1990, 2004; Fuster & Alexander, 1971; Postle, 2006; Theeuwes et al., 2009). Here, verbal WM biases actions even when it is irrelevant (or detrimental) to the current task. This translation of WM content into (sometimes incorrect) actions confirms predictions of action control made by event coding theories, which propose a potentially automatic relationship between action selection and execution (Hommel, 2009). The present study also advances recent descriptions of a reciprocal influence between visual WM and planned motor behavior (van Ede, 2020), which can be observed in oculomotor (Hanning et al., 2016; Ohl & Rolfs, 2017; van Ede, Chekroud, & Nobre, 2019) and pointing movements (Heuer, Crawford, & Schubo, 2017). Here, we show that this framework may additionally extend to the influence between verbal WM and unplanned actions. Moreover, the task and trial-level modulations that we observed here also fit predictions from an intention-based reflexivity theory—that WM information in the focus of attention should exert the greatest influence over actions (Meiran et al., 2012). Therefore, several complementary theories of attentional and action control may be informed by the current findings.

While many studies have demonstrated the privileged status of attended WM content, the fate of unattended content remains debated (Myers, Chekroud, Stokes, & Nobre, 2017; Schneegans & Bays, 2017). Yet, unattended WM content evokes detectable neural traces in higher cortical regions (Christophel, Iamshchinina, Yan, Allefeld, & Haynes, 2018). Here, unprioritized (and presumably less active) WM content still modestly influenced movement initiation, suggesting that these representations may be sufficient to guide WM-based decisions. However, the results do show a graded influence of prioritization over WM content: uncued WM content influenced only movement initiation (not duration) and to a lesser extent than prioritized content. The observed distinction between movement initiation and duration also supports a theoretical mechanism whereby prioritization reduces the time to access a given representation in WM, as suggested by drift diffusion modeling (Shepherdson, Oberauer, & Souza, 2017). That is, the graded effect of WM priority may be specific to movement initiation time because it influences decision processes involved in triggering a movement, rather than the mechanics that influence the duration of the movement itself.

The current data show that the WM-action bias can be modulated by modulating item representations, but superordinate task goals can also influence that item-level bias. Earlier theories of procedural WM suggest that executive systems mediate the interaction between immediate goals and a task set (Oberauer, 2009, 2010). This is consistent with the current finding that higher-order WM task context determines the degree to which WM influences motor behavior. WM item selection (or output gating) may work in tandem with task-level control functions that segregate competing demands in complex tasks (Badre & Nee, 2018). That is, WM goals may be prioritized over motor goals when WM is likely to aid motor performance, biasing motor decision-making toward WM (e.g., Experiment 1, high compatibility condition). Moreover, when WM and motor goals are equally weighted and may compete (e.g., a middle compatibility condition), item-level attentional modulation may tip the balance in favor of prioritized WM content. When WM is unlikely to aid motor behavior across the task, however, representations for WM and motor rules may be well-segregated (Verbruggen et al., 2018), minimizing leakage of WM content into action execution (e.g., Experiment 3, low compatibility condition). These findings may therefore extend the application of output gating and hierarchical control models to complex scenarios where WM content can trigger incorrect actions.

It remains unknown at which representational level these interactions occur, or whether the WM compatibility effect generalizes between content with less explicit overlap. In an adaptive system, it seems most likely that this interplay would in fact depend on the content domains being sufficiently related. Likewise, classic work on interference between WM and reading demonstrates that verbal and spatial recall are processed in a modality-specific manner, with the highest levels of interference when competing information is presented in the same domain (Brooks, 1968). The present results and related work therefore point to WM-motor interactions that may occur at an abstract, executive control level. For example, in a multi-component model of working memory, the spatially-focused visuospatial sketchpad and the verbally-focused phonological loop only have direct connections through a central executive system (Baddeley & Logie, 1999; Repovs & Baddeley, 2006). It may also be the case that verbal WM content for directions (e.g., ‘left’) generates neural signals similar to those for actions themselves, for instance, via priming (Mollo, Pulvermuller, & Hauk, 2016), or that the demand here to transform the symbolic motor cue into a direction resulted in an interfering verbal representation. Alternatively, participants here may have recoded verbal directions into visuo-spatial representations. However, the WM response in this task had no directional content, and used a different effector from the manual task, so we would not expect the WM response preparation to influence the motor task response. Yet, a visuo-spatial representation may still have been the most efficient or preferred maintenance strategy. So, having established some of the boundaries of the interplay between verbal WM and motor behavior, additional work should tease apart where those boundaries manifest representationally.

While it may seem intuitive that more task relevant WM content would exert the greatest impact on behavior, the compatibility of WM content to motor goals was typically unknown or unlikely in most cases across these three Experiments. This was a simple WM task, performed with high accuracy, which should engage relatively modest attentional demands. Yet WM content imparted a dramatic influence on the course and speed of hand movements, producing a seemingly inadvertent impact over ongoing behavior. The modulation of this WM bias by task context, however, highlights the sensitivity of the system to temporally-extended regularities of the environment. Compatibility effects were consistently stronger when WM was most likely to help performance (on either the motor or WM task). Collectively, these results support the idea that occasional glitches in motor output stem from an adaptive WM system that adjusts to the correspondence between WM and other concurrent goals.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

References

Baddeley AD, & Logie RH (1999). Working Memory: The Multiple-Component Model Models of Working Memory (pp. 28–61).

Badre D (2012). Opening the gate to working memory. Proc Natl Acad Sci U S A, 109(49), 19878–19879. doi:10.1073/pnas.1216902109 [PubMed: 23144220]

Badre D, & Nee DE (2018). Frontal Cortex and the Hierarchical Control of Behavior. Trends Cogn Sci, 22(2), 170–188. doi:10.1016/j.tics.2017.11.005 [PubMed: 29229206]

Bays PM, & Taylor R (2018). A neural model of retrospective attention in visual working memory. Cognitive Psychology, 100, 43–52. doi:10.1016/j.cogpsych.2017.12.001 [PubMed: 29272732]

Belopolsky AV, & Theeuwes J (2011). Selection within visual memory representations activates the oculomotor system. Neuropsychologia, 49(6), 1605–1610. doi:10.1016/j.neuropsychologia.2010.12.045 [PubMed: 21315747]

Braem S, Bugg JM, Schmidt JR, Crump MJC, Weissman DH, Notebaert W, & Egner T (2019). Measuring Adaptive Control in Conflict Tasks. Trends Cogn Sci. doi:10.1016/j.tics.2019.07.002

Brainard DH (1997). The Psychophysics Toolbox. Spatial Vision, 10(4), 433–436. [PubMed: 9176952]

Brooks L (1968). Spatial and Verbal Components of the Act of Recall. Canadian Journal of Psychology, 22(5), 349–368.

Carlisle NB, & Woodman GF (2011). Automatic and strategic effects in the guidance of attention by working memory representations. Acta Psychol (Amst), 137(2), 217–225. doi:10.1016/j.actpsy.2010.06.012 [PubMed: 20643386]

Chatham CH, & Badre D (2015). Multiple gates on working memory. Curr Opin Behav Sci, 1, 23–31. doi:10.1016/j.cobeha.2014.08.001 [PubMed: 26719851]

Christophel TB, Iamshchinina P, Yan C, Allefeld C, & Haynes JD (2018). Cortical specialization for attended versus unattended working memory. Nat Neurosci, 21(4), 494–496. doi:10.1038/s41593-018-0094-4 [PubMed: 29507410]

Cools R, Ivry RB, & D'Esposito M (2006). The Human Striatum is Necessary for Responding to Changes in Stimulus Relevance. Journal of Cognitive Neuroscience, 18(12).

Desimone R, & Duncan J (1995). Neural mechanisms of selective visual attention. Annu Rev Neurosci, 18, 193–222. [PubMed: 7605061]

Fritz CO, Morris PE, & Richler JJ (2012). Effect size estimates: current use, calculations, and interpretation. J Exp Psychol Gen, 141(1), 2–18. doi:10.1037/a0024338 [PubMed: 21823805]

Fuster J (1990). Prefrontal Cortex and the Bridging of Temporal Gaps in the Perception-Action Cycle. Ann N Y Acad Sci, 608(1), 318–336. [PubMed: 2127512]

Fuster J (2004). Upper processing stages of the perception-action cycle. Trends Cogn Sci, 8(4), 143–145. doi:10.1016/j.tics.2004.02.004 [PubMed: 15551481]

Fuster J (2015). Anatomy of the Prefrontal Cortex The Prefrontal Cortex (5 ed.): Elsevier.

Fuster J, & Alexander G (1971). Neuron activity related to short-term memory. Science, 173, 652–654. [PubMed: 4998337]

Hanning NM, Jonikaitis D, Deubel H, & Szinte M (2016). Oculomotor selection underlies feature retention in visual working memory. J Neurophysiol, 115(2), 1071–1076. doi:10.1152/jn.00927.2015 [PubMed: 26581875]

Heuer A, Crawford JD, & Schubo A (2017). Action relevance induces an attentional weighting of representations in visual working memory. Mem Cognit, 45(3), 413–427. doi:10.3758/s13421-016-0670-3

Hommel B (2009). Action control according to TEC (theory of event coding). Psychol Res, 73(4), 512–526. doi:10.1007/s00426-009-0234-2 [PubMed: 19337749]

Ivry RB, & Spencer RM (2004). The neural representation of time. Curr Opin Neurobiol, 14(2), 225–232. doi:10.1016/j.conb.2004.03.013 [PubMed: 15082329]

Kiyonaga A, Egner T, & Soto D (2012). Cognitive control over working memory biases of selection. Psychon Bull Rev, 19(4), 639–646. doi:10.3758/s13423-012-0253-7 [PubMed: 22528872]

LaRocque JJ, Lewis-Peacock JA, & Postle BR (2014). Multiple neural states of representation in short-term memory? It's a matter of attention. Frontiers in Human Neuroscience, 8.

Lewis-Peacock JA, Drysdale A, Oberauer K, & Postle BR (2011). Neural Evidence for a Distinction between Short-term Memory and the Focus of Attention. Journal of Cognitive Neuroscience, 24(1), 61–79. [PubMed: 21955164]

Mallett R, & Lewis-Peacock JA (2018). Behavioral decoding of working memory items inside and outside the focus of attention. Ann N Y Acad Sci. doi:10.1111/nyas.13647

Manohar SG, Zokaei N, Fallon SJ, Vogels TP, & Husain M (2019). Neural mechanisms of attending to items in working memory. Neurosci Biobehav Rev, 101, 1–12. doi:10.1016/j.neubiorev.2019.03.017 [PubMed: 30922977]

Meiran N, Cole MW, & Braver TS (2012). When planning results in loss of control: intention-based reflexivity and working-memory. Front Hum Neurosci, 6, 104. doi:10.3389/fnhum.2012.00104 [PubMed: 22586382]

Mollo G, Pulvermuller F, & Hauk O (2016). Movement priming of EEG/MEG brain responses for action-words characterizes the link between language and action. Cortex, 74, 262–276. doi:10.1016/j.cortex.2015.10.021 [PubMed: 26706997]

Myers NE, Chekroud SR, Stokes M, & Nobre AC (2017). Benefits of flexible prioritization in working memory can arise without costs. Journal of Experimental Psychology.

Myers NE, Stokes MG, & Nobre AC (2017). Prioritizing Information during Working Memory: Beyond Sustained Internal Attention. Trends Cogn Sci. doi:10.1016/j.tics.2017.03.010

Nobre AC, & Stokes MG (2019). Premembering Experience: A Hierarchy of Time-Scales for Proactive Attention. Neuron, 104(1), 132–146. doi:10.1016/j.neuron.2019.08.030 [PubMed: 31600510]

O'Reilly R, & Frank MJ (2005). Making Working Memory Work: A Computational Model of Learning in the Prefrontal Cortex and Basal Ganglia. Neural Computation, 18.

Oberauer K (2009). Design for a Working Memory The Psychology of Learning and Motivation (pp. 45–100).

Oberauer K (2010). Declarative and Procedural Working Memory: Common Principles, Common Capacity Limits? Psychologica Belgica, 50(3), 277–308.

Ohl S, & Rolfs M (2017). Saccadic eye movements impose a natural bottleneck on visual short-term memory. J Exp Psychol Learn Mem Cogn, 43(5), 736–748. doi:10.1037/xlm0000338 [PubMed: 27762577]

Oliveira FTP, & Ivry RB (2008). The Representation of Action: Insights From Bimanual Coordination. Current Directions in Psychological Science, 17(2).

Olivers CN, Peters J, Houtkamp R, & Roelfsema PR (2011). Different states in visual working memory: when it guides attention and when it does not. Trends Cogn Sci, 15(7), 327–334. doi:10.1016/j.tics.2011.05.004 [PubMed: 21665518]

Park YE, Sy JL, Hong SW, & Tong F (2017). Reprioritization of Features of Multidimensional Objects Stored in Visual Working Memory. Psychological Science, 28(12).

Postle BR (2006). Working Memory as an Emergent Property of the Mind and Brain. Neuroscience, 139(1), 23–38. [PubMed: 16324795]

Repovs G, & Baddeley A (2006). The multi-component model of working memory: explorations in experimental cognitive psychology. Neuroscience, 139(1), 5–21. doi:10.1016/j.neuroscience.2005.12.061 [PubMed: 16517088]

Rose NS, LaRocque JJ, Riggall AC, Gosseries O, Starrett MJ, Meyering EE, & Postle BR (2016). Reactivation of latent working memories with transcranial magnetic stimulation. Science, 354(6316), 1136–1139. doi:10.1126/science.aah7011 [PubMed: 27934762]

Schneegans S, & Bays PM (2017). Neural Architecture for Feature Binding in Visual Working Memory. J Neurosci, 37(14), 3913–3925. doi:10.1523/JNEUROSCI.3493-16.2017 [PubMed: 28270569]

Schwartz MF (1995). Re-examining the Role of Executive Functions in Routine Action Production. Ann N Y Acad Sci, 769.

Shepherdson P, Oberauer K, & Souza AS (2017). Working Memory Load and the Retro-Cue Effect: A Diffusion Model Account. J Exp Psychol Hum Percept Perform. doi:10.1037/xhp0000448

Soto D, Hodsoll J, Rotshtein P, & Humphreys GW (2008). Automatic guidance of attention from working memory. Trends Cogn Sci, 12(9), 342–348. doi:10.1016/j.tics.2008.05.007 [PubMed: 18693131]

Souza AS, & Oberauer K (2016). In search of the focus of attention in working memory: 13 years of the retro-cue effect. Atten Percept Psychophys, 78(7), 1839–1860. doi:10.3758/s13414-016-1108-5 [PubMed: 27098647]

Sprague TC, Ester EF, & Serences JT (2016). Restoring Latent Visual Working Memory Representations in Human Cortex. Neuron, 91(3), 694–707. doi:10.1016/j.neuron.2016.07.006 [PubMed: 27497224]

Stokes MG (2015). ‘Activity-silent’ working memory in prefrontal cortex: a dynamic coding framework. Trends Cogn Sci, 19(7), 394–405. doi:10.1016/j.tics.2015.05.004 [PubMed: 26051384]

Theeuwes J, Belopolsky A, & Olivers CN (2009). Interactions between working memory, attention and eye movements. Acta Psychol (Amst), 132(2), 106–114. doi:10.1016/j.actpsy.2009.01.005 [PubMed: 19233340]

van Ede F (2020). Visual working memory and action: Functional links and bi-directional influences. Visual Cognition, 1–13. doi:10.1080/13506285.2020.1759744 [PubMed: 33574729]

van Ede F, Chekroud SR, & Nobre AC (2019). Human gaze tracks attentional focusing in memorized visual space. Nature Human Behaviour. doi:10.1038/s41562-019-0549-y

van Ede F, Chekroud SR, Stokes MG, & Nobre AC (2019). Concurrent visual and motor selection during visual working memory guided action. Nat Neurosci, 22(3), 477–483. doi:10.1038/s41593-018-0335-6 [PubMed: 30718904]

van Loon AM, Olmos-Solis K, Fahrenfort JJ, & Olivers CN (2018). Current and future goals are represented in opposite patterns in object-selective cortex. Elife, 7. doi:10.7554/eLife.38677

van Moorselaar D, Theeuwes J, & Olivers CN (2014). In competition for the attentional template: can multiple items within visual working memory guide attention? J Exp Psychol Hum Percept Perform, 40(4), 1450–1464. doi:10.1037/a0036229 [PubMed: 24730738]

Verbruggen F, McLaren R, Pereg M, & Meiran N (2018). Structure and Implementation of Novel Task Rules: A Cross-Sectional Developmental Study. Psychol Sci, 29(7), 1113–1125. [PubMed: 29746205]

Wallis G, Stokes M, Cousijn H, Woolrich M, & Nobre AC (2015). Frontoparietal and Cingulo-opercular Networks Play Dissociable Roles in Control of Working Memory. J Cogn Neurosci, 27(10), 2019–2034. doi:10.1162/jocn_a_00838 [PubMed: 26042457]

Wolff MJ, Ding J, Myers NE, & Stokes M (2015). Revealing hidden states in visual working memory using electroencephalography. Frontiers in Systems Neuroscience, 9.

Wolff MJ, Jochim J, Akyurek EG, & Stokes MG (2017). Dynamic hidden states underlying working-memory-guided behavior. Nat Neurosci. doi:10.1038/nn.4546

Zokaei N, Board AG, Manohar SG, & Nobre AC (2019). Modulation of the pupillary response by the content of visual working memory. Proc Natl Acad Sci U S A, 116(45), 22802–22810. doi:10.1073/pnas.1909959116 [PubMed: 31636213]

Zokaei N, Manohar S, Husain M, & Feredoes E (2014). Causal evidence for a privileged working memory state in early visual cortex. J Neurosci, 34(1), 158–162. doi:10.1523/JNEUROSCI.2899-13.2014 [PubMed: 24381277]

Public Significance Statement

Working memory allows us to keep information actively in mind, so that we can use that information to achieve our moment-to-moment goals. However, this working memory maintenance process may unintentionally impact our interactions with the environment, and can occasionally interfere with our immediate external goals. This study formalizes the everyday “action slips” that humans commit when we type out or say the wrong word aloud in conversation because it was held in mind for a different goal. The results show that internally maintained content can influence the direction and speed of hand movements that are executed during working memory maintenance. However, the extent of this action interference varies with the relevance of the maintained content to either immediate or temporally-extended task goals. That is, working memory can bias our actions, but we can control the behavioral state of working memory content to reduce the likelihood of these everyday errors.

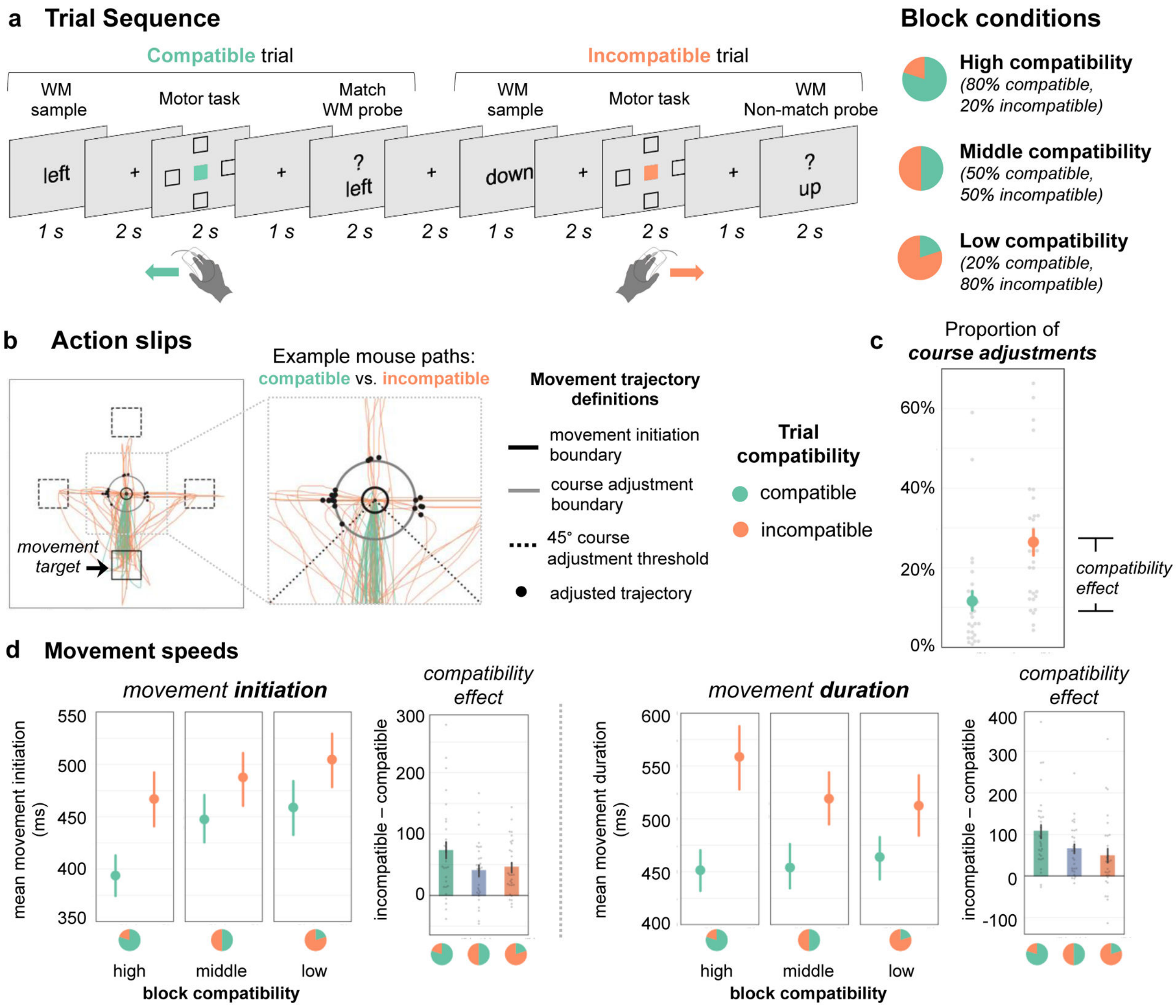

Fig 1. Experiment 1 task design and results.

(a) Example *compatible* and *incompatible* trial sequences (left), which were delivered in 3 block conditions (right). **(b)** Movement trajectories for *compatible* (green) and *incompatible* trials (orange) from an example subject on middle compatibility blocks. Detail illustrates criteria for categorizing trials as “course adjustments.” **(c)** The proportion of course adjustments on *compatible* (green) and *incompatible* (orange) trials, collapsed across block condition. **(d)** Point plots show mean movement speeds for all trial and block conditions, while barplots show the difference between *compatible* (green) and *incompatible* (orange) for each block condition. Left: *Movement initiation*, or ‘reaction time’. Right: *Movement duration*, or ‘movement time’. Error bars represent SEM. Gray dots are data points from individual participants.

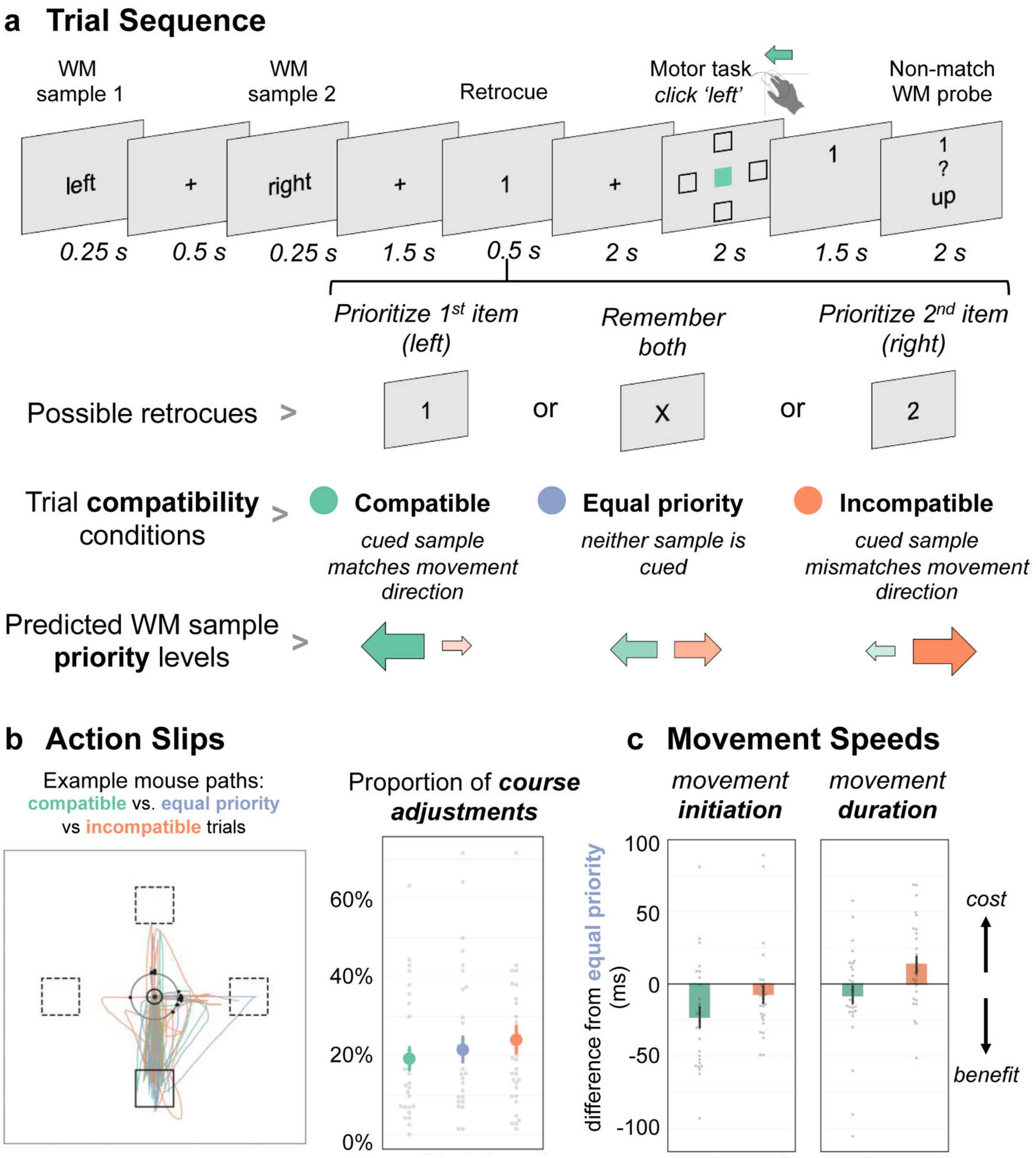

Fig 2. Experiment 2 task design and results.

(a) An example trial sequence with possible retrocue and compatibility conditions. Green and orange arrows illustrate the hypothetical priority levels of the WM samples in this example trial. **(b)** Movement trajectories for *compatible* (green), *equal priority* (blue), and *incompatible* (orange) trials from an example subject on 3 blocks (left). Proportion of course adjustments on *compatible, equal priority, and incompatible* trials (right). **(c)** Benefits (green) and costs (orange) of compatible and incompatible cueing (compared to equal priority) on movement initiation (left) and duration (right) times. Error bars represent SEM. Gray dots are data points from individual participants.

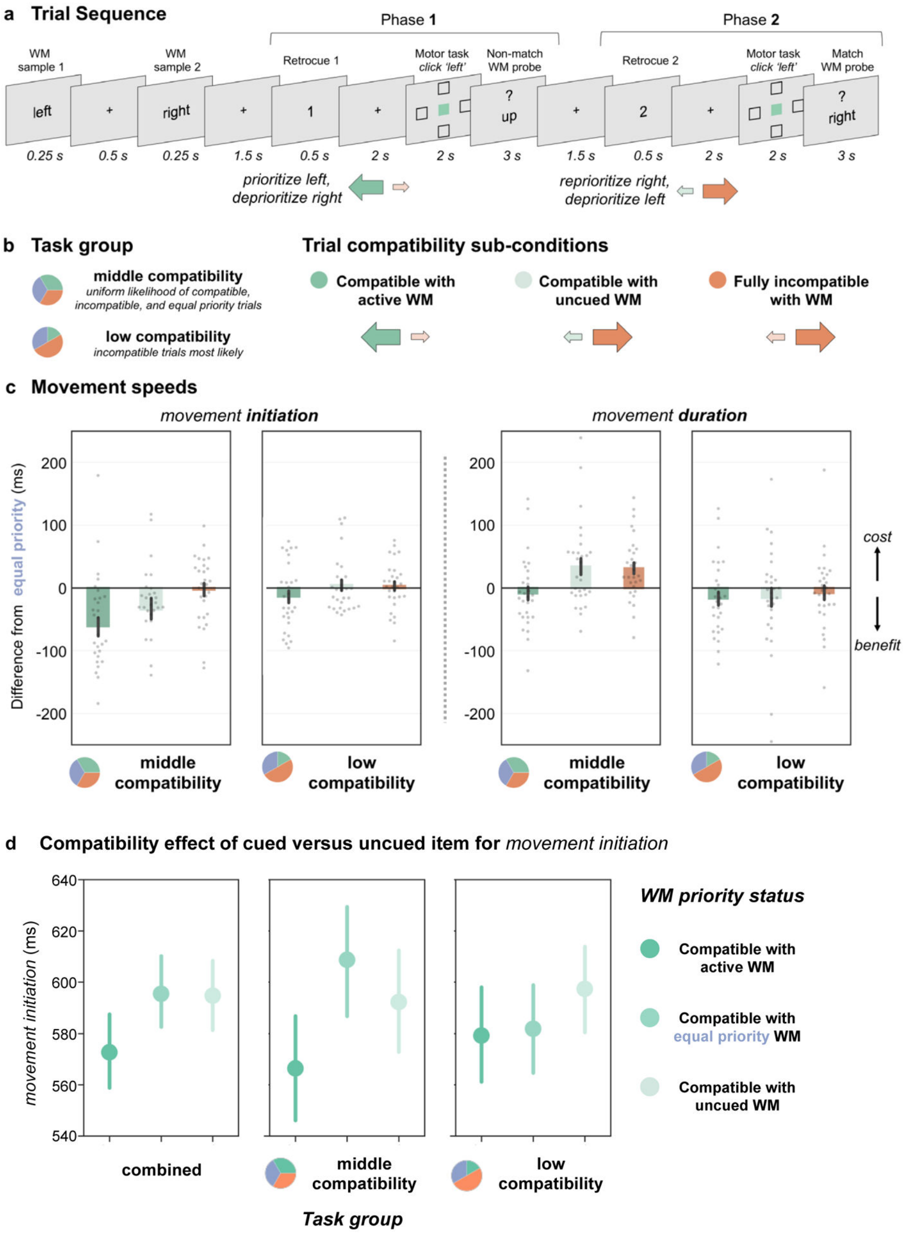

Fig. 3. Experiment 3 task design and results.

(a) Example trial sequence. For each task phase, the cued WM sample could be either *compatible, uninformative (equal priority), or incompatible* with the movement direction. **(b)** Green and orange arrows illustrate the hypothetical priority levels of the WM samples in this example trial (left). Task predictability conditions differed across two task groups (right). (c) Cost and benefits relative to *equal priority* trials, split by 3 compatibility subtypes (*compatible with active WM / compatible with uncued WM / incompatible with WM*) for each movement measure (*initiation / duration*) and task phase (*Phase 1 / Phase 2*). **(d)** Phase 1 *movement initiation* times split by experiment task group (columns) and WM priority status (*compatible with active WM* / *compatible with equal priority WM* / *compatible with uncued WM*). Error bars represent SEM. Gray dots are data points from individual participants. In (c), one data point was excluded for visualization, but was included in all statistics.