Tracking how attentional focusing in working memory benefits long-term memory

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Abstract

Human working memory serves as a key gateway to the formation of lasting memories in long-term memory. While it is well established how attentional focusing during working memory can prioritize internal representation for an imminent task, how such internal focusing affects subsequent long-term memory remains less understood. Here, we developed a two-stage visual working memory/long-term memory task in which we cued attention during working memory and tracked the dynamics of attentional deployment through a recently established gaze marker of internal focusing. Across two experiments, we found that attentional focusing in visual working memory reliably affects subsequent visual long-term memory, driven by a benefit to internally attended objects without a cost to unattended objects. Gaze biases associated with internal focusing revealed how this benefit was mediated by the speed – but not necessarily the degree – of attentional deployment, with faster attentional deployment predicting better subsequent memory. Together, these results highlight how attentional focusing in working memory benefits subsequent long-term memory, and uncover the dynamic processes that instill such lasting benefits – offering new insights into the catalyst function of attention in bridging working memory and long-term memory.

Introduction

Working memory (WM) enables us to maintain relevant sensory information in service of guiding behaviour, and has also been proposed as a crucial gateway to long-term memory (LTM) [1–6]. Given the central significance of both WM and LTM for human cognition, extensive research has focused on elucidating how information held in WM is transferred to LTM, and identifying the factors that influence this transfer. For example, it has become well established that longer maintenance and/or rehearsal of information in WM is associated with better subsequent LTM of this information [7–11]. In similar vein, it has been established that more attentive encoding of sensory information into WM [12–21] or retrieval of information from LTM back into WM [22–25] can positively affect subsequent LTM.

Importantly, the fate of WM content is not only determined by the quality of encoding and the duration/quality of ensuing rehearsal, but also by selective-attention processes that are initiated during WM and that serve to prioritize specific mnemonic contents for guiding imminent behaviour [26–31]. To date, the majority of studies targeting such selective-attention processes during WM following so-called "retro-cues" [32] have focused on whether and how such cues improve performance on the ensuing WM task itself (typically showing robust behavioural benefits; for reviews, see [27,31]). In contrast, whether and how attentional prioritization in WM in service of an upcoming WM task "spills over" into subsequent benefits on LTM remains less well understood.

Regarding 'whether' attentional prioritization in WM affects subsequent LTM, only a handful of retro-cue studies have studied the long-term consequences of selective object prioritization during WM [9,17,33–36] (for complementary studies using "refreshing cues" see e.g., [18,37–40]). These studies have yielded only partially consistent results. While several studies have shown LTM benefits [9,33–36 37–40], others have not [17,18], or have suggested that retrocue effects on LTM may be driven predominantly by a drop in performance for uncued (unattended) objects [33], that may be explained simply by shorter retention in WM.

Even if we take existing behavioural demonstrations as settled that attentional focusing during WM improves subsequent LTM, a key open question remains, pertaining to the 'how': i.e., the mechanisms that mediate the influence of attentional focusing in WM on subsequent LTM. Gaining insight into this pivotal question requires directly tracking the process of attentional focusing during WM, and investigating how this process relates to subsequent LTM. We recently uncovered that attentional focusing in visual WM can be robustly tracked through spatial biases in gaze [41–46]. This opens unique opportunities for directly tracking how the process of spatially selective attentional focusing during visual WM affects subsequent visual LTM. Moreover, owing to its excellent temporal resolution, this gaze marker of internal focusing enables to characterize and disentangle the potential LTM impacts of not only the 'degree' but also the 'timing' of attentional deployment during WM.

To examine whether and how attentional prioritization during visual WM affects LTM, we developed a two-stage visual WM-LTM task, in which we carefully controlled sensory exposure. Across two versions of this task, we investigated behavioural consequences of selective focusing in visual WM, while also tracking such focusing directly through spatial biases in human gaze measurements. To preview our findings, we demonstrate clear benefits to LTM-recognition accuracy for visual objects that are cued during WM for guiding visual search. Comparisons with a neutral-cue condition revealed a selective benefit for the cued (attended) object, with no evidence for a cost incurred to the other uncued (unattended) object. Critically, our continuous gaze marker of attention focusing in WM revealed better LTM in trials in which attention was directed *faster* to the cued object during WM. Together, these results

highlight how attentional focusing in visual WM can have lasting consequences for visual LTM, and provide insight into the dynamic processes that instill such lasting consequences.

Results

Healthy human volunteers performed a combined WM-LTM task in which attention was manipulated (**Fig. 1**). During WM, an attentional cue (retrocue) informed which of two memorized visual objects had to be searched in an upcoming search display – yielding one internally "attended" and another "unattended" memory object. Participants were instructed to report whether the cued memory object was present or absent in the ensuing search display.

Unbeknownst to the participant, the WM task was followed by a surprise LTM task in which participants were repeatedly asked to identify which of two visual objects they had previously encountered during the WM task. This enabled us to assess the influence of attentional focusing in WM on subsequent LTM. Our central interest was in the target-absent-during-search trials in which sensory exposure was balanced between the attended and unattended memory objects (see Methods for details).

We conducted two experiments that were identical except for one aspect. In Experiment 1, each trial contained a 100% informative cue during WM. In Experiment 2, we additionally included neutral cues, whose color did not match either memory object. In these trials, participants were required to keep both objects in mind in order to report whether *either* object was present in the search display.

Attentional focusing in WM leads to better subsequent LTM recognition

In Experiment 1, each trial contained 1 cued (internally attended) and 1 uncued (internally unattended) memory object. One quarter of the search displays contained the memory target (the cued object), while the remaining three quarters of the search displays did not contain the target memory object. The uncued (unattended) object was never in the display. This yielded 4 conditions for investigating the effect of attentional focusing in WM on LTM recognition: cued-and-present, cued-and-absent, uncued-and-absent, and searched-only objects. The critical comparison here involves that between the cued and uncued memory objects in the target-absent-during-search conditions (i.e., cued-and-absent vs. uncued-and-absent). This enabled a direct comparison of the influence of attentional focusing in WM on subsequent LTM, while ensuring the same sensory exposure, given that neither object was repeated in the search display in these critical trials, even though one of them had been cued as the search target.

Figure 1a shows LTM recognition performance for all types of objects presented in the WM task. Our central a-priori-defined comparison of interest revealed better LTM recognition for the cued-and-absent objects than the recognition of the uncued-and-absent objects. This was the case for both accuracy and reaction time (RT) (accuracy: $t(24) = 6.861$, $p < 0.001$; RT: $t(24) = -4.304$, $p < 0.001$; Bonferroni corrected). Given that the cued-and-absent and uncued-and-absent objects had the same sensory exposure (both only seen once during WM encoding) and the only difference between them is the selective attentional focusing to the cued objects during WM delay, these results provide clear evidence that attentional focusing in WM for an upcoming WM task can have lasting consequences for subsequent LTM recognition.

In addition to our central comparison of interest, we also found superior LTM recognition accuracy for the cued-and-present objects (likely owing to both repeated exposure and attentional focusing) compared to all other conditions ($|t|$s ≥ 3.533, ps ≤ 0.005) and worst

recognition for the searched-only objects that only served as fillers in the search display (ts ≥ 11.733, ps ≤ 0.001). For a complete overview of all possible comparisons, see **Table S1**.

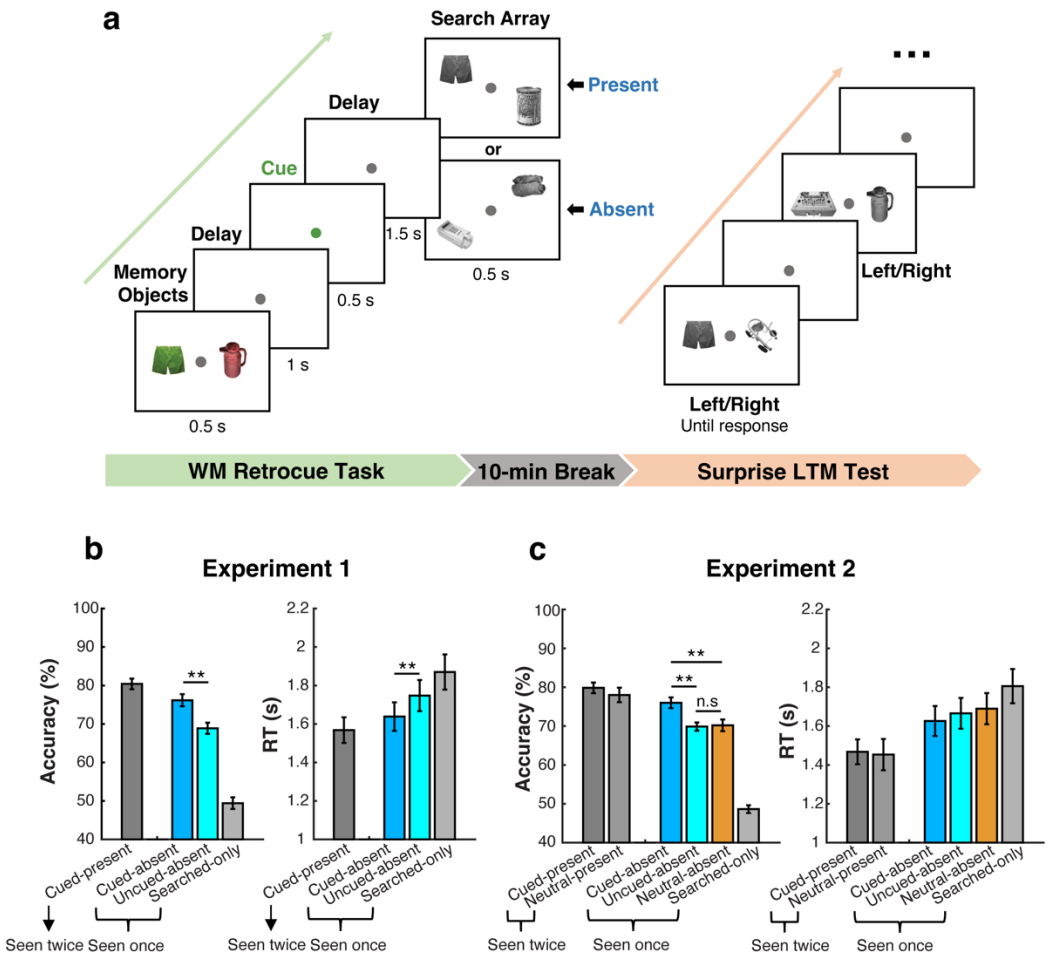

Figure 1. Experimental procedure and LTM recognition performance across experiments. a) The two-stage WM-LTM task procedure. In the visual WM task stage (left panel), participants memorized two visual objects, of which one could be cued (through its color) for an upcoming WM-guided search task. Upon the search display, participants were instructed to indicate the presence or absence of the cued object (or of both objects, in case of a neutral-cue trial that we included only in Experiment 2). Following a 10-minute break, they completed a surprise LTM test (right panel) where they needed to repeatedly indicate which one of the two objects they recognized from the preceding WM task. **b**) Performance on the surprise LTM recognition test as a function of attentional status of the objects during WM in Experiment 1 (containing exclusively informative cues). **c**) Performance on the surprise LTM recognition test as a function of attentional status of the objects during WM in Experiment 2 (containing both informative and neutral cues). Blue, cyan, and orange bars represent our key conditions from target-absent-during-search trials, consisting of objects that were cued-and-absent, uncued-and-absent, and neutrally cued-and-absent, respectively. Left and right panels show comparisons between recognition accuracy and response time (RT). Error bars represent ±1SEM. *, **, n.s represent significance levels $p < 0.05$, $p < 0.01$, and non-significant after Bonferroni correction. Note: only statistics of our main interest are highlighted in this figure. For a full overview of pairwise comparisons, see **Table S1**.

The LTM benefit is driven by a facilitation of the attended memory object, not a cost of the unattended memory object

In Experiment 1, we observed a robust effect of attentional cueing during WM on subsequent LTM. However, because we only included 100% informative cues, we could not ascertain whether the effect on LTM was driven by a relative benefit for the cued (attended) object or a relative cost for the uncued (unattended) object. For example, it is possible that the uncued

object showed reduced subsequent LTM performance because it could be dropped from WM midway the trial (i.e. after the retrocue), and was thus retained in WM for a shorter duration.

To address this possibility, we designed Experiment 2 in which we included neutral cues whose color did not match either object in WM. In these trials, participants were required to retain both objects until the search display, and report whether *either* object was present (or, alternatively, whether both objects were absent). By comparing the LTM performance for cued and uncued objects with the objects in trials with a neutral cue, we could resolve whether the cueing benefit on LTM was predominantly driven by a facilitation of the cued (attended) object or a cost to the uncued (unattended) object. Again, we focused on target-absent-during-search trials, where sensory exposure was equated.

First, results from Experiment 2 confirmed that participants used the informative cues during the WM task, as evidenced by superior search performance on the WM task in trials with informative vs. neutral cues (**Fig. S1**). This was the case for both accuracy and RT (Main effect of Cue Type: accuracy: $F(1,49) = 29.668$, $p < 0.001$, $\eta^2 = 0.377$; RT: $F(1,49) = 21.606$, $p < 0.001$, $\eta^2 = 0.306$,).

Having confirmed the use of the cue during WM, we turned to our critical LTM results. As in Experiment 1, we observed reliable benefits on LTM recognition accuracy when comparing cued vs. uncued memory objects that were matched for sensory exposure (**Fig. 1b**, target-absent-during-search trials, $t(49) = 7.375$, $p < 0.001$). Critically, these cueing effects were driven exclusively by a benefit of the cued (attended) object, as we found a clear LTM benefit for cued objects compared to neutral objects (**Fig. 1b** $t(49) = 4.992$, $p < 0.001$), while no difference between uncued (unattended) and neutral objects ($t(49) = -0.281$, $p = 0.778$).

These data rule out that the cueing benefit on LTM is driven by a shorter retention duration of uncued (unattended) objects, and instead show how attentional focusing of the cued memory object brings about a benefit to subsequent LTM, compared to a control condition with the same retention duration but without attentional focusing during WM.

Attentional deployment in WM can be tracked by directional biasing of gaze

Having established that attentional focusing in visual WM instills a lasting benefits on visual LTM, we aimed to track the attentional deployment process in WM directly, to understand the mechanisms that mediate the influence of WM focusing on subsequent LTM.

Recently, we have uncovered and reported how attentional shifts to visual objects in WM can be tracked by reliable spatial biases in eye-movements [41–52]. In our current data, we could also track attentional deployment through reliable spatial biases in saccade direction following the attentional retrocue (**Fig. 2**), despite there being nothing to look at on the screen apart from the central fixation marker. Specifically, consistent with our prior studies, we observed more saccades in the direction toward the memorized location of the cued object than in the opposite, away, direction – a finding that replicated across both experiments (**Fig. 2a**). A direct comparison of toward vs. away saccades (**Fig. 2b**) confirmed that these biases were highly reliable (permutation test $p = 0.002$ for Experiment 1; $p < 0.001$ for Experiment 2). Moreover, by visualizing these toward vs. away biases as a function of saccade size (**Fig. 2c**), we observed that the spatial saccade biases included, to a considerable extent, saccades below 1 degree (within a range of microsaccades [53–56]), which was particularly clear in Experiment 2 for which we also had more data.

These findings replicate gaze biases during internal orienting of attention that we have reported previously, and show that such gaze biases also occur when directing attention to

memorized images of real-world objects (as opposed to the simpler stimuli that were used in prior studies of this bias).

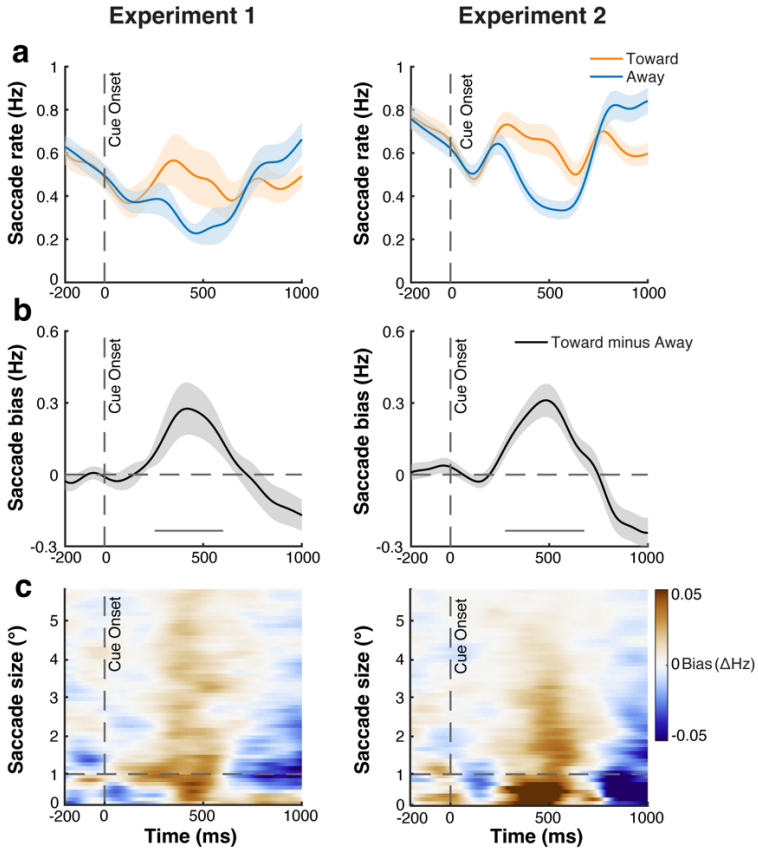

Figure 2. Spatial biasing of eye-movements tracks internal attentional focusing during WM in both experiments. a) Saccade rates toward (orange line) and away (blue line) from the memorized location of the cued object relative to cue onset in the WM task. **b**) The difference between toward and away saccades (i.e. the spatial bias). Horizontal grey lines above the x-axis represent significant clusters. **c**) Saccade rate effects (toward vs. away) as a function of saccade size, in degrees visual angle.

Faster attentional deployment in WM is associated with better subsequent LTM

Having established the gaze marker of internal attention shifts in our WM task, we finally turn to our central question regarding the mechanisms by which internal attention shifts during WM confer LTM benefits. To this end, we adopted the logic of the 'subsequent memory effect' (SME; see e.g., [13–18]) by splitting the WM trials according to whether the cued objects were later correctly recognized (i.e., later-remembered) vs. incorrectly recognized (i.e., later-forgotten) in the LTM recognition test. While we found clear gaze biases following the attentional cue during WM, both for objects that were later-remembered or later-forgotten, we also observed faster gaze biases in trials in which cued objects were later-remembered (**Fig. 3**), consistent with an earlier – putatively more effective – attentional deployment.

To quantify these differences, we directly compared attentional deployment – as tracked in our spatial gaze bias – for later-remembered and later-forgotten trials in two ways. First, we compared the time courses between these trial types directly using a cluster-based permutation analysis [57]. Second, we quantified gaze-bias latency as the first sample that reached 50% of the peak and quantified latency differences using a jackknife analysis (as in: [58,59]).

As shown in **Figure 3a,b**, the pattern of delayed attentional deployment for later-forgotten memory objects was qualitatively similar in both experiments. For statistical quantification, when only considering the data from Experiment 1, we found an early difference in the saccade bias for objects that were later-remembered vs. later-forgotten (permutation test p = 0.042), while the jackknife analysis on onset latency almost reached significance (p = 0.075). Conversely, when only considering the data from Experiment 2, now the cluster permutation analysis did not yield a significant difference cluster, but the jackknife analysis did yield a reliable difference with faster gaze bias associated with later-remembered objects (p = 0.032). To achieve maximum sensitivity, we also combined the data from Experiment 1 and Experiment 2 (**Fig. 3c**). We could do so because the condition of interest here – the condition with an informative retrocue – was identical in the two experiments. When interrogating these differences with maximum sensitivity (**Fig. 3c**), the observed delay was confirmed both by a reliable difference cluster in the permutation analysis (p = 0.038), and a significant latency difference in the jackknife analysis (p = 0.001). This latency difference was 108.2 ± 32.1 [M±SE] ms.

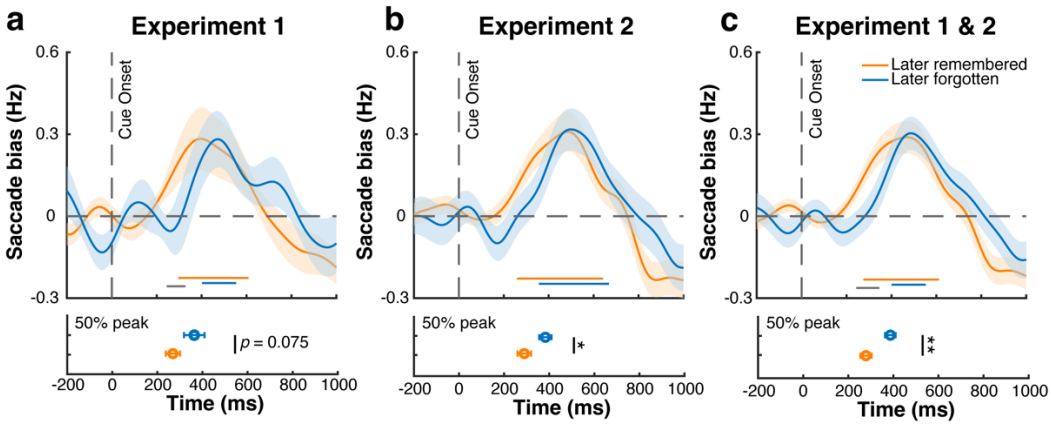

Figure 3. Faster attentional deployment in WM is associated with better subsequent LTM recognition. a) Top panel: spatial saccade bias (toward minus away) after the retrocue during the WM task, for later-remembered and later-forgotten objects in Experiment 1. Bottom panel: latency of the saccade bias, defined as the 50% of the peak value The error bars represent standard errors obtained using a jackknife approach. **b**,**c**) Same as in panel **a**, but for Experiment 2 (panel b) and Experiment 1 and 2 combined (panel c). Orange and blue horizontal lines above the x-axis in top panels indicate significant clusters; grey horizontal lines represent significant difference clusters. Shading and error bars represent ±1SEM. *, ** represent significance level $p < 0.05$ and $p < 0.01$ after Bonferroni correction.

Having established an association between faster internal attentional deployment (as reflected in our gaze-bias marker) and better subsequent LTM performance, one may expect this effect to be particularly clear in those individuals for whom attentional cueing in WM had a relatively large impact on LTM. To verify this, we split participants into two groups using a median split, based on their LTM benefit of attentional cueing during WM (i.e., the difference in LTM recognition accuracy between cued-and-absent objects and uncued-and-absent objects). Consistent with our reasoning, and consistent across experiments (**Fig. S2**), faster attentional deployment for later-remembered vs. later-forgotten objects was particularly pronounced in those participants who showed the larger LTM benefit of WM cueing (**Fig. 4**). This pattern was verified by a two-way mixed repeated-measures ANOVA with between-subject factor of Group (small-LTM-benefit participants vs. large-LTM-benefit participants) and a within-subject factor of the Subsequent Memory Effect (i.e. SME: later-remembered vs. later-forgotten) on jackknife-adjusted onset latencies [58]. The ANOVA revealed a significant main effect of SME ($F(1,73) = 18.163$, $p < 0.001$, $\eta^2 = 0.199$) and an interaction of Group x SME ($F(1,73) = 4.825$, $p = 0.031$, $\eta^2 = 0.062$). Post-hoc t-tests revealed that the interaction was driven by a clear SME effect in the large-LTM-benefit participants ($t(36) = -4.242$, $p < 0.001$) that was

significantly less pronounced (and insignificant) in the small-LTM-benefit group ($t(37) = -1.585$, $p = 0.146$), even if the trend was in the same direction in this group of participants.

Together, these results provide evidence (from both the across-trial and the across-participant level) that the speed of attentional deployment within WM mediates the influence of mnemonic focusing on subsequent LTM performance. Faster attentional deployment during WM is associated with better subsequent LTM recognition, and this effect is particularly pronounced in those individuals who show the strongest influence of WM focusing on subsequent LTM.

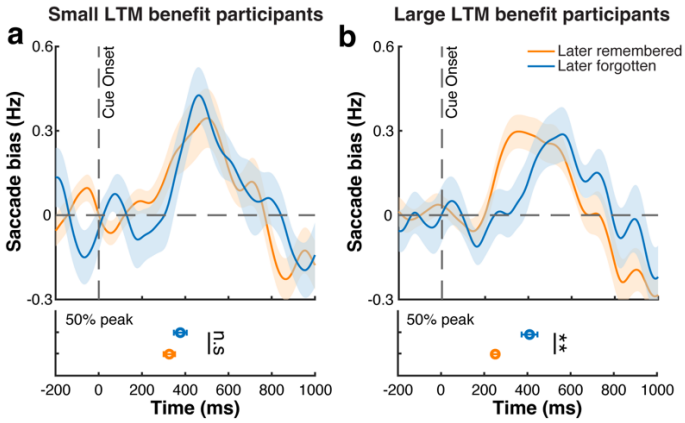

Figure 4. The latency of attentional deployment in WM predicts subsequent LTM particularly for individuals with larger LTM benefit. a) Gaze bias for later-remembered and later-forgotten trials in the subset of participants with relatively little benefit of cueing during WM on subsequent LTM. Conventions as in Figure 3. **b**) Gaze bias for later-remembered and later-forgotten trials in the subset of participants with relatively large benefit of cueing during WM on subsequent LTM. Shading and error bars represent ±1SEM. *, **, n.s represent significance levels $p < 0.05$, $p < 0.01$, and non-significant after Bonferroni correction. Note: to maximum the statistical power of this group analysis, the plots illustrate the merged dataset of Experiment 1 & 2. We found similar patterns across both experiments, as shown in **Supplemental Fig. S2**.

The observed relation between the timing of attentional deployment and subsequent LTM is not mediated by object memorability nor by time-on-task

We reported how the speed of attentional deployment in WM – as reflected in the reported gaze bias after the retrocue – predicted subsequent LTM performance. This suggests that the speed (or, tentatively, the efficacy) of attentional deployment can have lasting consequences on memory. However, besides variability in the attentional process itself, may there be other, more trivial, generic explanations that can account for these key results? Below we consider, and rule out, two such viable alternative accounts.

Object memorability

First, it could be that some of our objects are simply more memorable, and that these more memorable objects are somehow also associated with a faster gaze bias when cued for selection during WM. To assess this first possibility, we estimated the memorability of all objects by sorting them by the overall correct identification rate during the LTM test (collapsed across our full sample of participants and combining both experiments for maximum sensitivity). To assess whether this measure of overall object memorability could account for latency differences in the gaze bias, we split the objects into high and low memorability (based on a median split) and assessed the time courses of the reported gaze bias as a function of memorability condition (**Fig. 5a & Fig. S3a**). This revealed no evidence for a difference in the latency of the gaze bias when attention was directed to objects with generic low or high memorability.

In addition to our above approach, where we defined object memorability empirically based on our own LTM performance data, we also quantified object memorability using a state-of-the-art machine-learning model for predicting the intrinsic memorability of an image – ResMem [60]. We again found no evidence for a difference in the latency of the gaze bias between objects with low or high memorability, after having quantified memorability this way (**Fig. 5b & Fig. S3b**).

Together, these results suggest that the observed influence of the latency of attentional deployment during WM on subsequent LTM is unlikely driven by a difference in the memorability of the visual objects themselves.

Time-on-task

Second, we considered time-on-task during the WM task as another potential mediator for the observed link between gaze bias latency and subsequent LTM performance. For example, gaze bias may become progressively faster during the WM task, and later trials in the WM may also have better LTM performance because they are more recent. To assess this second possibility, we also split our trials into the first-half vs. the second-half of trials in the WM task (**Fig. 5c & Fig. S3c**). Again, we found no evidence that time-on-task could account for the observed difference in latency of the gaze bias during the WM task.

These additional analyses suggest that the reported effect of the speed of attentional deployment – as tracked in the gaze bias – in WM are not simply mediated by the objects themselves, nor by time on the WM task. Instead, this central result likely reflects variability in the process of directing attention to internal WM contents, with consequences for LTM.

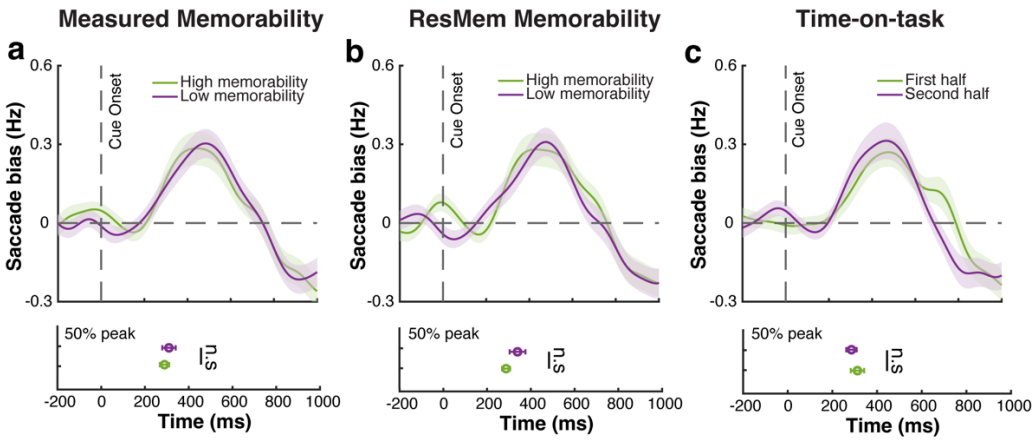

Figure 5. The observed relation between the timing of attentional deployment and subsequent LTM is not mediated by object memorability nor by time-on-task. a) Spatial saccade bias after the informative cue during the WM task for cued objects with high (green) and low (purple) general memorability. Memorability was estimated from LTM performance from the current experiments, and objects were sorted using a median split. **b**) As panel a, but quantifying object memorability using ResMem [60]. **c**) Spatial saccade bias for objects presented in the first-half (green lines) vs. objects presented in the second-half (purple lines) of the WM session. Bottom panels and all other conventions as in preceding figures. n.s represents non-significant after Bonferroni correction. Note: to increase the statistical power, the plots illustrate the merged dataset from Experiments 1 & 2. Similar patterns were observed across both experiments, as shown in **Supplemental Fig. S3**.

Discussion

Our data reveal how focusing attention on visual objects held in WM for an upcoming WM task instills a lasting benefit on visual LTM recognition. We show that this is driven by a benefit to internally attended objects without a cost to unattended objects. In addition, we here uniquely

tracked the process that mediates this LTM benefit, capitalizing on spatial biases in eye-movements that track focusing in visual working memory with high temporal resolution. This revealed that faster attentional deployment during WM is associated with better subsequent LTM for the attended WM object. These findings advance our understanding of the foundational mechanisms that mediate the influence of attentional focusing in WM on subsequent LTM.

Our behavioural performance data complement and reinforce several prior studies investigating the impact of attentional focusing during WM maintenance on subsequent LTM following either *retrocues* [9,17,33–36] or *refreshing cues* [18,37–40]. Like other prior work using retrocues, our attentional manipulation involved focusing of specific memory objects in service of an upcoming WM task. Despite the fact that participants did not yet know they would later be tested for their LTM recognition of the objects, we found clear consequences of this type of WM focusing on subsequent LTM. By adding neutral cues, we could further show that this focusing operation engaged a benefit for the focused memory object, without incurring a cost to the other object in WM that could be dropped after the cue (cf. [32,61–68]). This is important because a cost to the uncued/unattended object (as reported in [33]) could be explained by shorter maintenance duration in WM [7–9], while a boost to the cued/attended object (compared to our neutral control) cannot.

It is important to note that our observed LTM benefits cannot be attributed to differential sensory processing, nor to differential sensory exposure. First, during encoding, participants could not yet know which of the two objects would become cued (or, in Experiment 2, whether the cue would be informative or neutral). Hence, sensory encoding was always equated between our attentional-cueing conditions. Further note how this also separates our findings from ample prior work focusing on attentional influences on LTM encoding [12–21]. Second, we made sure to include WM trials in which the cued memory objects were never repeated in the search display (requiring an 'absent' report). In these critical target-absent-from-search trials – that were randomly interleaved with target-present trials – participants used the retrocue to prepare the search for the cued object, but the attended memory object never re-appeared during search. Thus, not only was sensory processing at encoding equated between cued/uncued/neutral trials, but so was total sensory exposure (all objects seen once) when considering these critical target-absent-during-search trials.

A central novelty of our study is our focus on tracking the mechanisms by which attentional focusing during WM influences subsequent LTM. To provide new insight into this key underexplored question, we here took advantage of a recently established index of attentional deployment within the spatial layout of visual WM – spatial biases in eye-movements [41–46] (for complementary findings, see also [47–52]). We first established that this gaze marker also tracked attentional focusing in WM in our case with images of real-world object (complementing our prior studies where we used more simple visual stimuli). Having established this, we adopted the logic of the subsequent memory effect (SME, [13–18,21]) to address whether and how this marker of attentional deployment following the retrocue predicted whether participants subsequently remembered vs. forgotten the cued objects. This revealed our key insight that the speed of attentional deployment during WM – and not the strength/degree of attentional deployment per se – predicts subsequent LTM.

A major limitation of the subsequent-memory effect approach we adopted here is its correlational nature. While we observed that the speed of attentional deployment following the cue predicted subsequent LTM, we cannot be sure that the speed of attentional deployment *causes* better subsequent LTM. Even so, we made sure to address and rule-out variable alternative explanations for this observed effect, ruling out object memorability and time-on-

task as viable mediating variables. Having ruled out these variables, we tentatively posit that our findings may reflect genuine temporal variability in the process of directing attention to internal WM contents, with consequences for LTM. Our findings from a secondary analysis in which we split participants by the size of their LTM benefit (**Fig. 4**) further corroborated this interpretation. This showed that the latency of the gaze bias following the cue is particularly predictive of subsequent LTM in those participants whose LTM also benefitted most from the cue during WM. If the gaze-bias latency predicted LTM for more generic reasons (other than attentional variability), then one may have predicted a generic influence across all participants, and not just in those participants that also showed the largest LTM benefit from the cue.

Our study focused on visual LTM [69–74] tested via a forced-choice task, and imposed only a short delay between our WM and LTM tasks (in the same range as at least several prior complementary studies: e.g., [9,17,33–36]). In future work, it will be interesting to extend our findings to other forms of LTM, to other forms of LTM testing, and to consider longer delays before testing LTM, to see how generic and long-lasting the here reported effects are. It will further be interesting to delineate the neural basis of the here reported effects, such as the potential role of the Posterior Parietal Cortex that has been implicated in attention, eye-movements, and memory [75–83].

At face value, our data may appear reminiscent of other established findings from the LTM literature, such as the 'testing effect', whereby elements that are retrieved from LTM as part of a test show better subsequent LTM (in comparison to elements that are merely studied for longer) (e.g., [22–25]). While one can of course conceive our findings after the retrocue as a form of 'retrieval', there are key differences with the aforementioned LTM literature. First, our retrocue prompted the selection of an object from WM, not from LTM. Moreover, it prompted a selection between one out of two possible objects, rather than one out of an almost infinite number of objects in LTM. For this reason, we have described our results from the perspective of attentional focusing in WM, consistent with a large body of research from the WM literature [26–32]. By studying such selective focusing in the context of a WM task with visual objects, we were also in a position to directly track such focusing through spatial-attentional biases in gaze, yielding key novel insight into the ways by which such attentional focusing in WM affects LTM.

To conclude, our data make clear how attentional focusing during visual WM can instill a lasting effect on visual LTM that is driven by a benefit for the focused memorandum. We have shown how this benefit is mediated by faster – and not necessarily more – attentional deployment during WM. Our data open the door to future studies in which it will be interesting to extend our findings to other forms of memory, to test LTM after longer periods of time, and to causally manipulate the speed of attentional focusing during WM. Our findings may further prove of interest to future studies on patients with memory and/or attentional problems or in educational settings in which the transfer of information from WM to LTM is a key goal.

Methods

Participants

Twenty-five healthy human volunteers participated in Experiment 1, with ages ranging from 18 to 26 (16 female and 9 male; all right-handed). Sample size was set a-priori based on prior publications from our lab with comparable eye-tracking outcome variables [41–46]. Experiment 2 extended Experiment 1 by adding an important additional condition with neutral cues, resulting in less trials per condition. To counteract having less trial per condition, we decided to double the sample size for Experiment 2. For Experiment 2, we recruited 50 participants, with ages ranging from 18 to 33 (34 female, 12 male, 4 non-binary; 46 right-handed, 1 left-handed, and 3 ambidextrous). Participant recruitment was performed independently for the two Experiments. Participants that had participated in Experiment 1 could not enrol in Experiment 2. The experimental procedures received approval from the Research Ethics Committee of the Faculty of Behavioral and Movement Sciences at the Vrije Universiteit Amsterdam. All participants provided written informed consent prior to participation, and received compensation of 10 Euros per hour, or course credits as reimbursement for their time.

Task and Procedure

In both experiments, participants completed a two-stage WM-LTM task, with an attentional manipulation in the WM task. Our focus was on the influence of attentional prioritisation during WM on subsequent LTM. In Experiment 1, all trials contained an informative retrocue (presented during WM retention) that instructed which of two WM objects would be needed for the ensuing WM search task. In Experiment 2, we additionally included trials with a neutral retrocue that enabled us to disentangle retrocue benefits for cued (attended) WM objects from costs for uncued (unattended) WM objects. In both experiments, the WM task was followed by a surprise LTM test that enabled us to test the influence of prioritisation during WM on subsequent visual LTM.

WM Task

The WM task is depicted in **Figure 1a**. Each trial started with an encoding display containing two images of real-world objects, each with a different color, presented for 500 ms. Memory objects were taken from the databased in Brady et al 2013 [71] (for full details about the stimuli, see the “Stimuli” section below). The encoding display was followed by an initial delay period during which a central fixation dot remained on the screen for 1000 ms. Subsequently, the color of the central fixation dot changed to match one of the memorized objects for 500 ms, serving as the attentional retrocue that indicated which memory object needed to be searched for after another delay of 1500 ms. Following this second delay, participants were presented with two greyscale objects on both sides of the screen. In trials with an informative retrocue (all trials in Experiment 1), participants were always instructed to search exclusively for the previously cued memory object (i.e., the memorized object with the same color at encoding as the preceding cue) within the search array, and to indicate whether it was present or absent. In Experiment 2, we additionally included neutral trials. In these trials, the retrocue color did not match either object in WM and participants were instead instructed to search for the presence of *either* memorized object during search.

The search array was displayed on the screen for 500 ms (matching the duration of the memory array). Participants used their fingers to press the “F” or “J” key on the keyboard, to indicate the presence or absence of the cued memory object, with the assignment of keys for "present" and "absent" fully counterbalanced across all participants. Following each response, feedback was provided on the fixation dot, with "1" denoting a correct response and "x" indicating an incorrect response. As mentioned above, the procedure for neutral-cue trials mirrored that of informative retrocue trials, except that during the WM delay, the central fixation dot changed to a third color that did not match the color of either of the two memorized objects.

In these trials, participants were instructed to indicate whether either memory object was present in the search array (or, alternatively, whether both were absent).

We carefully chose a search task for testing WM contents after the retrocue. The search task with its critical target-absent trials enabled a vital control for equating sensory exposure between cued and uncued memory objects. Unlike in target-present trials, in target-absent trials, the cued/attended memory object never re-appeared at test. Accordingly, in these trials, any influence of retrocueing on subsequent LTM cannot be attributed to differential sensory exposure between cued and uncued objects. Our main interest was thus in the target-absent trials where sensory exposure was equated between our conditions of interest. Considering this, the majority of trials (3 out of 4) were target-absent trials. The remaining trials with a target present in the search array were merely included to keep participants engaged in the WM task. Target-present and target-absent trials were randomly intermixed.

In both experiments, trials featuring different types of cues (retrocue or neutral cue) and various testing conditions (present or absent) were intermixed within block for the WM task. Participants completed one WM block consisting of 192 and 216 trials for Experiment 1 and Experiment 2, respectively. In Experiment 1, all trials contained an informative retrocue, while in Experiment 2, one third of the trials contained a neutral cue (72 trials) and the remaining 144 trials contained an informative cue. Because the ratio of the number of target-absent-at-search vs. arget-present-at-search trials is 3:1, this resulted in 144 test-absent and 48 test-present trials in Experiment 1, and 162 test-absent and 54 test-present trials in Experiment 2.

LTM Task

Following completion of the WM task, participants were given a 10-minute break. This delay was set mainly for pragmatic reasons, and was in the same range as the delay used in complementary studies considering the relation between WM and LTM [9,17,33–36]. Only after the break, participants were instructed about the surprise LTM test. They were informed that although they could not have known that these objects would be tested later, they might still retain some memories of them.

The LTM test is depicted in **Figure 1b**. During the LTM test, each test array consisted of two greyscale real-world objects positioned on the left and right sides of the screen, that required a 2 alternative-forced choice (2AFC) response. One of the two objects had always been presented during the WM stage (either as one of the encoded objects or as a filler in the search display). Another object during each 2AFC LTM test was always a completely novel object. Participants used their fingers to indicate whether the object presented on the left or right side of the screen was the one they had encountered in the preceding WM task (pressing "F" with the left finger if the old object was on the left, or "J" with the right finger if the old object was on the right). The locations of the old and new objects were fully counterbalanced across trials. After each response, feedback was provided on the fixation dot, with "1" indicating a correct response and "x" indicating an incorrect response.

In both experiments, participants completed one LTM test block consisting of 438 and 486 trials for Experiment 1 and Experiment 2, respectively. Within the LTM test, one out of seven trials (48 and 54 trials for E1 and E2, respectively) were images of fillers that only presented during WM search stage. The remaining trials were images of all objects presented during WM encoding stage (384 and 432 trials for E1 and E2, respectively). The order in which the objects would occur in the LTM test was independent of the order they would appear in the WM test.

Stimuli

The stimuli were presented using MATLAB (R2020a; MathWorks) and the Psychophysics Toolbox (version 3.0.16, [84]) on a LED monitor. The monitor was a 23-inch (58.42-cm) screen operating at 240 Hz with a resolution of 1920 by 1080 pixels. Participants were seated 70 cm from the screen with their head resting on a chin rest to ensure stable eye-tracking.

Throughout the experiment, a white background (RGB = 255 255 255) was maintained, along with a grey fixation dot (0.8° visual angle, RGB = 192 192 192) presented in the center of the screen. The memory and search objects were real-world object pictures (obtained and modified from [71]) measuring 4° in size, presented at 6° eccentricity to central fixation. During WM encoding, the memory objects were displayed in two colors randomly chosen from a color pool comprising red (RGB = 158 73 76), green (RGB = 51 129 42), and purple (RGB = 82 88 172). The third color was used as the color of the neutral cue in Experiment 2. The two colors for the memory objects were consistent within each participant but randomized between participants to prevent any systematic sensory preference for a particular color. The memory objects were horizontally aligned to the fixation dot, with their colors and locations fully counterbalanced across trials. The objects in the search display were greyscale pictures (RGB = 128 128 128), presented at two out of four possible locations (top-left, top-right, bottom-right, bottom-right, 6° eccentricity to central fixation), with always one object on each side of the screen to balance visual inputs. The LTM test arrays comprised two greyscale objects (RGB = 128 128 128, size of 4°) presented on the left and right sides of the screen, horizontally aligned to the fixation dot (6° eccentricity to central fixation).

Color was exclusively used so that we could use a color change in the central fixation dot as a non-spatial cue to direct attention to either memory object during the WM task. The non-spatial nature of the cue was important to avoid sensory confounds when comparing our gaze data between cues directing attention to the left or right memory object. Color was thus used to cue the relevant object, but color itself was never tested; not during WM, nor during LTM.

All images came from the same database [71]. In Experiment 1, the WM task featured 384 real-world object images used as memory objects (colored), while the search array included 336 separate filler objects (greyscale) randomly selected from the remaining images. The LTM recognition test contained 432 objects from the WM test (old objects, all in greyscale) and 432 novel objects. The 432 old objects comprised all 384 objects presented in the memory array (in greyscale during the LTM test), along with 48 fillers, with fillers randomly chosen from the total number of fillers used in the search array during the WM task. Novel objects were taken from a left-out subset of the images from the same object database. For convenience, we used the same subset of images as memory objects, filler objects, and novel objects for all participants. Within the pool of memory objects, the designation into the different attentional conditions (cued/uncued/neutral) was randomized, and was thus different for each participant. Experiment 2 utilized 432 colored images for the memory array, 378 fillers for the search array during WM task, and 486 old and 486 novel objects for the LTM recognition test. The 486 old objects included all 432 objects presented in the memory array in greyscale, along with 54 (1/7 of all fillers) randomly chosen objects from the fillers used in the search array during the WM task.

Analysis of behavioral data

We analysed both response accuracy and response time (RT), for both the WM and the LTM task. Our focus was on performance in the LTM 2AFC recognition task, as a function of objects' attentional status during WM (cued and uncued in Experiment 1; cued, uncued and neutral in Experiment 2). We separately considered objects from target-present and target-absent WM-search trials, with our focus on target-absent-during-search trials in which sensory exposure was equated between attention conditions (as detailed above). For completeness,

we also included 'search-only' objects (i.e., objects that served as fillers in the search arrays) when considering LTM recognition of objects encountered in the WM task.

Eye-tracking acquisition and pre-processing

The eye tracker (EyeLink 1000, SR Research SR) was positioned approximately 5 cm in front of the monitor on a table, approximately 65 cm away from the participants' eyes. Horizontal and vertical gaze positions were continuously recorded for a single eye at a sampling rate of 1000 Hz. Prior to recording, the eye tracker underwent calibration using the built-in calibration and validation protocols provided by the Eye-Link software. Participants were instructed to keep their chin stable on the chin rest for the entire block following calibration.

For the offline analyses, eye-tracking data were converted from the .edf to the .asc format and imported into MATLAB using Fieldtrip [85]. Blinks were identified by detecting clusters of zeros in the eye-tracking data. Subsequently, data from 100 ms before to 100 ms after the detected blink clusters were marked as Not-a-Number (NaN) to be excluded from further analysis. Following blink rejection, data were epoched relative to the onset of the cue in the WM task.

Saccade detection

We utilized a velocity-based approach for saccade detection (as in: [41,42,86]) that was developed building on closely-related velocity-based methods for saccade detection (e.g., [48]). Because the memory objects in our experiment were always presented horizontally at center-left and center-right positions, our saccade detection targeted the horizontal channel of the eye data. This approach has previously demonstrated to be effective for capturing directional biases in saccades during internal attention shifts, as expanded on in [42].

We computed gaze velocity by measuring the distance between gaze position in consecutive samples. To improve accuracy and reduce noise, we applied temporal smoothing to the velocity using a Gaussian-weighted moving average filter with a 7-ms sliding window, utilizing the "smoothdata" function in MATLAB. Subsequently, we identified the onset of a saccade as the first sample where the velocity exceeded a trial-based threshold set at 5 times the median velocity. To prevent multiple classifications of the same saccade, we imposed a minimum delay of 100 ms between successive saccades. Saccade magnitude and direction were determined by evaluating the difference between pre-saccade gaze position (from -50 to 0 ms before threshold crossing) and post-saccade gaze position (from 50 to 100 ms after threshold crossing). Each identified saccade was then classified as "toward" or "away" based on its direction (left/right) and the side of the cued memory object (left/right). "Toward" denoted a saccade in the direction of the memorized location of the cued object, while "away" indicated a saccade in the opposite direction.

Following saccade identification and categorization, we analyzed the time courses of saccade rates (in Hz) using a sliding time window of 50 ms, progressing in 1 ms increments. For our primary analyses, we focused directly on the spatial bias in saccades, calculated as the differences (in Hz) between toward and away saccades.

Finally, to further characterize the the saccade bias, we computed the saccadic bias as a function of saccade size (as in: [41,42,86]). For this, we quantified the saccade bias (toward vs. away) iteratively for saccades falling within specific saccade-size bins. We used size bins of 0.5 degrees, that were advanced in steps of 0.1 degrees.

Subsequent memory effect

Our primary interest was to link attentional deployment during WM to subsequent changes in LTM performance. To this end, capitalised on the classic subsequent-memory effect (SME:

[13–18]), and applied it to our gaze signature of attentional allocation during WM. We focused on cued memory objects and split the WM trials depending on whether these cued objects were later remembered or later forgotten during the LTM test.

Having established a subsequent memory effect in our data, we wished to rule out obvious "third factors" that could have mediated our effect. First, we considered object memorability itself. Some objects may be more memorable and these objects may render different attentional allocation during WM. To rule this out, we also sorted our WM gaze data based on object memorability, using a median split. We did this twice, following two different ways to quantify object memorability. First, we estimated the memorability of all objects by sorting them by the overall correct identification rate during the LTM test, collapsed across our full sample of participants and combining both experiments for maximum sensitivity. In addition to our first approach, where we defined object memorability empirically based on our own LTM performance data, we also quantified object memorability using a state-of-the-art machine learning model for predicting the intrinsic memorability of an image – ResMem [60].Next to object memorability, we also considered time-on-task as another factor that may have mediated our observed subsequent memory effect. For this, we simply split our WM data into 'early' and 'late' trials (i.e., first half vs. second half of WM trials), to compare our gaze data of interest as a function of time on task.

Saccade bias latency analysis

To evaluate condition differences in the timing of the spatial saccade bias following the cue, we utilized a simplified jackknife method (as described in [58]). Specifically, we compared the onset latencies of the spatial saccade bias after the cue in the WM task between later-remembered and later-forgotten objects, as derived from responses on the LTM task. The onset latency was determined by the time at which the amplitude reached 50% of the peak value.

Statistical analysis

For the performance data, our main focus was on accuracy and RT in the LTM task, as a function of attentional status of the objects during the preceding WM task. We first applied one-way repeated measures ANOVAs with within-subject factor of Object Type (Experiment 1: cued-and-present vs. cued-and-absent vs. uncued-and-absent vs. searched-only; Experiment 2: cued-and-present vs. cued-and-absent vs. uncued-and-absent vs. neutral-and-present vs. neutral-and-absent vs. searched-only). We applied this once to participants' response accuracy and once to their RT during the LTM recognition test. After that, we conducted pre-planned paired-sample t-tests between conditions with different cueing and probing types during the WM task on the LTM task. Our focus was on WM objects in trials in which the cued object was absent in the search array (in which sensory exposure was equated between cued, uncued, and neutral objects). For completeness, we also considered objects in target-present-during-search trials, and objects that only appeared at test as fillers in the search display. To account for multiple comparisons, all reported p-values were Bonferroni corrected. In addition, in Experiment 2 we also compared performance on the WM task between trials with informative vs. neutral cues (in Experiment 1 all trials contained an informative retrocue, so this comparison could not be made).

To analyze the temporal patterns of spatial modulations in eye movements (saccade bias), we utilized a cluster-based permutation approach [57] implemented with the 'ft_timelockstatistics' function from the Fieldtrip toolbox, employing the 'montecarlo' method. This methodology is particularly well-suited for assessing the consistency of data patterns across multiple adjacent data points (effectively circumventing the issue of multiple comparisons by evaluating the full time-course under a single permutation distribution of the

largest cluster). We conducted 10,000 permutations to generate the permutation distribution of the largest cluster that could occur by chance. Clusters were identified using Fieldtrip's default settings, which involve grouping temporally adjacent data points with the same sign that were statistically significant in a mass univariate t-test at a two-sided alpha level of 0.05. The size of each cluster was defined as the sum of all t values within that cluster. This approach was applied to evaluate the time-series of the spatial saccade bias following the cue against 0 (effectively testing toward vs. away), as well as to directly compare spatial biases after the cue between later-remembered and later-forgotten objects.

For the saccade bias latency comparison between later-remembered vs. later-forgotten objects, we used standard paired-samples t-tests to compare the latency estimates that we obtained from the employed jackknife methods [58].

Data and code availability

All data and analysis scripts are publicly available in OSF: https://osf.io/szp5n/.

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Conflicts of Interest

There are no commercial interests or conflicts related to this study.

Supplemental Materials

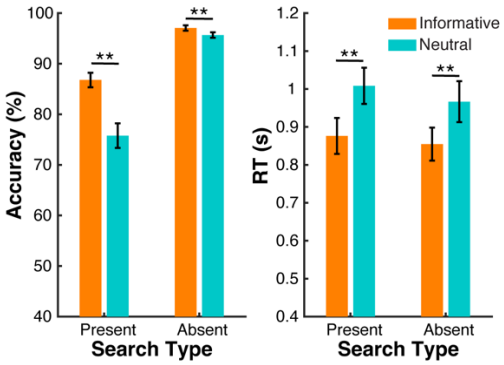

Figure S1. Attentional cueing effects on WM performance in Experiment 2. The WM search performance for objects with different cue types in Experiment 2, where we included both informative and neutral cues. In both target-present-during-search and target-absent-during-search trials, the search performance (accuracy-left panel and RT-right panel) for the informatively cued objects outperformed trials with neutral cues. Orange and blue bars represent informative and neutral cue trials, respectively. Error bars represent ±1SEM. *, ** represent significance level $p < 0.05$ and $p < 0.01$ after Bonferroni correction.

Table S1. Statistics for LTM recognition performance

Experiment 1				Experiment 2			
LTM recognition accuracy				LTM recognition accuracy			
		$t_{(24)}$	p			$t_{(49)}$	p
Cued-present	Cued-absent	3.533*	.010	Cued-present	Cued-absent	4.365**	.001
	Uncued-absent	9.564**	.000		Uncued-absent	10.100**	.000
	Searched-only	16.036**	.000		Neutral-present	1.234	1.000
					Neutral-absent	7.827**	.000
					Searched-only	18.726**	.000
Cued-absent	**Uncued-absent**	**6.861****	**.000**	**Cued-absent**	**Uncued-absent**	**7.375****	**.000**
	Searched-only	13.656**	.000		Neutral-present	-1.311	1.000
					Neutral-absent	**4.992****	**.000**
					Searched-only	15.368**	.000
Uncued-absent	Searched-only	11.733**	.000	**Uncued-absent**	Neutral-present	-5.589**	.000
					Neutral-absent	**-.281**	**1.000**
					Searched-only	14.171**	.000
				Neutral-present	Neutral-absent	5.360**	.000
					Searched-only	13.996**	.000
				Neutral-absent	Searched-only	12.450**	.000

*, ** represent significance level $p < 0.05$ and $p < 0.01$ after Bonferroni correction. Conditions with bold font represent our key comparisons.

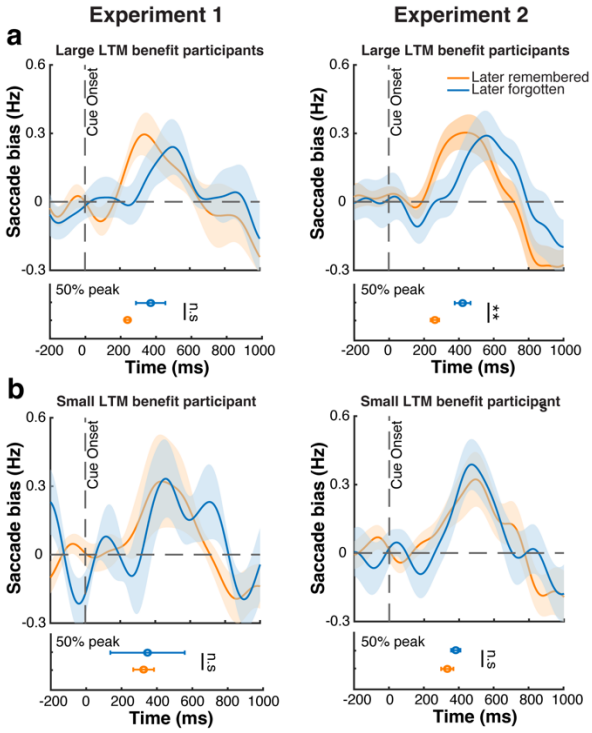

Figure S2. The latency of attentional deployment in WM predicts subsequent LTM particularly for individuals with larger LTM benefit across both experiments. a) Gaze bias for later-remembered and later-forgotten trials in the subset of participants with relatively little benefit of cueing during WM on subsequent LTM across both experiments (left panel – Experiment 1, right panel – Experiment 2). **b**) Gaze bias for later-remembered and later-forgotten trials in the subset of participants with relatively large benefit of cueing during WM on subsequent LTM across both experiments (left panel – Experiment 1, right panel – Experiment 2). Shading and error bars represent ±1SEM. *, ** represent significance level $p < 0.05$ and $p < 0.01$ after Bonferroni correction.

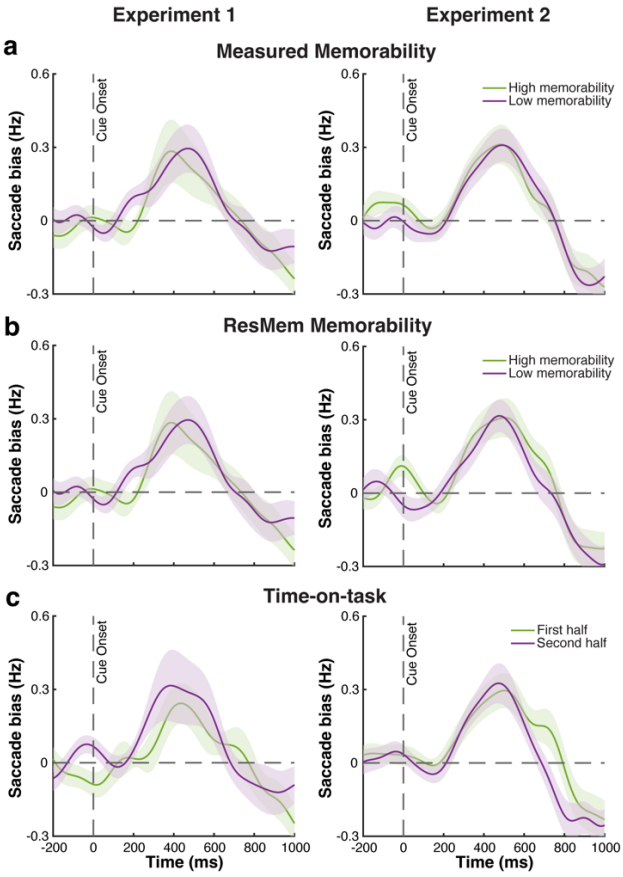

Figure S3. The observed relation between the timing of attentional deployment and subsequent LTM is not mediated by object memorability nor by time-on-task across both experiments. a) Spatial saccade bias after the informative cue during the WM task for cued objects with high (green) and low (purple) general memorability across both experiments (left panel – Experiment 1, right panel – Experiment 2). Memorability was estimated from LTM performance from the current experiments, and objects were sorted using a median split. **b**) As panel a, but quantifying object memorability using ResMem [60]. **c**) Spatial saccade bias for objects presented in the first-half (green lines) vs. objects presented in the second-half (purple lines) of the WM session across both experiments (left panel – Experiment 1, right panel – Experiment 2). Bottom panels and all other conventions as in preceding figures. Shading areas represent ±1SEM.