Focusing attention in working memory and long-term memory: benefits through dissociable processes

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ABSTRACT

We developed a new experimental approach to compare directly how attentional orienting facilitates retrieval in working memory (WM) and long-term memory (LTM), and how selective attention within these different memory timescales impacts incoming sensory information processing. In two experiments with healthy young adults (*N*s = 30 and 44), retrocues prioritised an item encoded in WM or LTM. Participants then retrieved a memory item or performed a perceptual discrimination task. The retrocue was informative for the retrieval task but not for the perceptual task. Attention orienting improved memory retrieval for both memory types and also enhanced discrimination for visual stimuli at the location matching the prioritised WM or LTM item. Eye-tracking data revealed a striking dissociation in gaze biases related to orienting in WM vs. LTM. The findings suggest potent and at least partly dissociable attention-orienting processes for different memory timescales.

Keywords: visual attention, internal attention, selective retrieval, retrocue, perceptual discrimination, capture, microsaccades, gaze bias

STATEMENT OF RELEVANCE

Attention and memory are cornerstones of human cognition. Despite the pervasiveness and significance of their interactions in everyday life, many fundamental questions remain unsolved, including how attention operates to guide memory retrieval at different timescales and how prioritisation of these different memories impacts subsequent perceptual processing. To address these questions, we developed a brand-new experimental framework that enabled the direct comparison between attentional focusing in working memory and long-term memory. We were thereby able to chart and compare, for the first time, the direct benefits of focusing attention for retrieval of memories with different timescales and the automatic spill-over consequences on sensory visual processing. Strikingly, our results revealed distinctive gaze-bias patterns when attention operates within WM vs. LTM. This discovery not only suggests that different processes are involved when selecting contents in WM and LTM, but also lends insight into the long-debated relationship between WM and LTM themselves.

Selective attention is fundamental to human cognition, delivering information that is relevant to ongoing behaviour among boundless competing signals. Most research has considered how attention operates upon incoming sensory signals, to anticipate, prioritise, and select attributes of goal-relevant stimuli to encode into working memory (WM) and guide action (Desimone & Duncan, 1995; Fawcett et al. 2015; Nobre & Kastner, 2014; Nobre, 2018).

Standard models of attention emphasise the contents of WM as a primary source of control signals guiding attention based on goals (Corbetta & Shulman, 2002; Desimone & Duncan, 1995). Notably, however, the arrow of attention can also point inward to flexibly prioritise and select items within visual WM (Chun et al., 2011; van Ede & Nobre, 2023). Informative cues presented during the WM delay period that retroactively predict goal-relevant items (retrocues) have proved highly useful for investigating the control and modulatory mechanisms of internal selective attention (Griffin & Nobre, 2003; Landmann et al., 2003; Souza & Oberauer, 2016).

Interestingly, like during attentional selection in the external world (Engbert & Kliegl, 2003; Hafed & Clark, 2002; Corneil & Munoz, 2014), orienting attention within visual WM is accompanied by subtle overt orienting behaviours. Small shifts in gaze (Draschkow et al., 2022; van Ede et al., 2019) and head (Thom et al., 2023) position occur, even when these serve no functional purpose, as in the absence of any remaining lateralised external stimulation. The recruitment of spatial sensorimotor processes (see also Nobre et al., 2004) suggests some overlap between mechanisms for orienting attention to sensory stimulation and WM representations (Panichello & Buschman, 2021).

More evidence for a strong overlap between attention in the sensory and WM domains comes from the “spill-over” effects that selecting items in WM has for sensory processing. Selecting an item in WM leads to the capture of attention by items that share matching locations or features (Awh & Jonides, 2001; Downing, 2000; Soto et al., 2007). These capture effects appear obligatory, operating even when they are counter-productive for the perceptual task (Soto & Humphreys, 2014), thus underscoring the strong role of WM in guiding external attention.

While there is a solid appreciation for the strong interrelation between attention and WM, a similar symbiotic relationship has been proposed for attention and long-term memory (LTM). LTM has long been proposed to guide sensory processing, as exemplified by Helmholtz’s view that perception results from unconscious inference based on prior memories (Helmholtz, 1867). Experimental tasks manipulating prior experience with stimulus contexts have since confirmed the role LTM plays in guiding attention (Brockmole et al., 2006; Chun & Jiang, 1998; Fan & Turk-Browne, 2016; Stokes et al., 2012; Summerfield et al., 2006; Theeuwes et al., 2022; Võ et al., 2019).

Reciprocally, researchers have proposed that selective attention can also operate within LTM, guiding retrieval. Suggestive evidence comes from the observation that brain areas controlling external attention orienting are activated in tasks of episodic memory retrieval (Cabeza et al., 2008; Chun & Johnson, 2011; Ciaramelli et al., 2008; Sestieri et al., 2017). Studies showing similar modulation of alpha-band neural activity during visual memory retrieval as during external visual attention have further hinted at a role for attentional selection in guiding LTM retrieval (Sabo & Schneider, 2022; Sutterer et al., 2019).

To build on this promising trail and test whether and how selective attention can modulate LTM retrieval, we need experimental tasks that manipulate the goal relevance of items in LTM. Such tasks should test directly whether orienting attention to a specific item in LTM yields performance benefits relative to retrieving other items associated with the same context.

If positive evidence suggests the ability to orient attention in LTM flexibly and selectively, it would be interesting to probe how similar the processes and consequences are compared to orienting in WM. Would orienting in LTM also be accompanied by gaze biases? Would the selective attention in LTM spill over to modulate sensory processing? A strong correspondence of effects would inform enduring debates regarding the relationship between WM and LTM (Atkinson & Shiffrin, 1968; Cowan, 2008; Fukuda & Woodman, 2017; Hirschstein & Aly, 2022; Logie, 1995), suggesting common neural systems or obligatory gating of LTM retrieval through WM.

Here, we introduce a new experimental framework to test the ability to orient attention selectively among competing LTM contents and to compare directly selective attention in WM and LTM. We borrow from retrocue designs to direct attention to a specific item of a pre-learned array of competing items in LTM or to a specific item of an encoded WM array presented earlier in the trial. In two studies, we measured the consequences of attention orienting in WM vs. LTM for memory retrieval and additionally tested for spill-over effects on sensory processing. At the end of each trial, participants either retrieved a memory item or performed a perceptual discrimination task. The retrocue was informative for the retrieval task but not for the perceptual task. This allowed us to investigate whether attentional selection in WM and LTM enhanced the retrieval of relevant memoranda and biased perceptual processing in an unrelated task in similar ways.

Our first study showed that orienting attention in LTM conferred significant benefits to retrieval and spill-over advantages for discriminating visual stimuli at matching locations, like orienting in WM. The second study replicated and extended the pattern of results by probing for different stimulus dimensions and incorporating eye tracking. Measuring subtle directional biases in gaze allowed us to investigate if overt manifestations of orienting behaviour accompanied attentional selection towards LTM items, as they do for WM contents. The results revealed surprising differences between oculomotor engagement when orienting attention in LTM compared to WM.

Open Practices Statement

All data are publicly available through the Open Science Framework (https://osf.io/n629s/). Code is available from the authors for reasonable purposes.

EXPERIMENT 1

Methods

Participants. Thirty individuals (23 females, 7 males, *M* = 25.13 years, *SD* = 4.15) with reported normal or corrected visual acuity volunteered and received monetary compensation for participation. The experiment was approved by the Central University Research Ethics Committee of the University of Oxford, and all participants provided informed consent before any experimental procedure began.

Apparatus and stimuli. Participants sat in front of a 27″ monitor (1920 × 1080 pixels, 100 Hz) and rested their chin on a chinrest placed 95 cm away from the monitor. The experiment was programmed in MATLAB (MathWorks, Natick, MA, U.S.A.) using the Psychophysics Toolbox

(Brainard, 1997). Stimuli appeared overlaid on a grey background. Throughout the experiment, four squares (2.5° in diameter) were always presented as placeholders at the four quadrants, at 5° horizontally and vertically from the central fixation to the centre of each square. The stimuli consisted of four equiluminant colours (brown [183.5, 113, 19], green [65, 143, 110.5], lilac [138, 117.5, 190], magenta [245.5, 37, 112.5]) drawn from a circle in CIELAB colour space.

Procedure and design. The experiment included a learning session and a testing session, separated by a 5-minute break.

During the learning session, participants were trained to encode two colours and their corresponding locations into LTM (**Fig. 1**). These two colours were randomly selected from the four colours defined above, and they were always located along one of the two pairs of diagonal locations (i.e., top left and bottom right, or top right and bottom left, counterbalanced across participants). We refer to this pair of locations as LTM locations. Each learning trial began with a fixation display lasting randomly between 800 and 1000 ms, after which the LTM display was presented for 150 ms. Following a delay of 850 ms, participants were probed to reproduce either the colour at one location or the location of one colour. On colour reproduction trials, a colour wheel (containing 360 colours) was presented at the centre, and participants responded by rotating the dial and selecting a colour along the wheel. The colour wheel was presented in a random orientation on every colour reproduction trial. On location reproduction trials, one of the two colours was presented at the centre, and participants responded by pressing one of four keys mapped to the four locations. Performance feedback was presented after both colour and location reproduction trials. Each to-be-learned attribute (two colours and two locations) was probed on 20 trials, resulting in a total of 80 learning trials presented in random order.

During the testing session, participants performed either a memory recall task or a perceptual discrimination task on each trial (**Fig. 2A**). Each testing trial began with a fixation display (800-1000 ms). A WM display followed, where the two colours unused in the learning session were presented for 150 ms at the unused pair of diagonal locations. We refer to this pair of locations as WM locations. To make sure the contents in WM were not fixed across trials, each WM colour was randomly assigned to one of the WM locations on every trial. Following a delay of 850 ms, a retrocue that was either neutral or informative was presented for 200 ms. The retrocue was neutral on one-third of the trials; the fixation display changed to white, providing no information about the item to be probed. The retrocue was informative on two-thirds of the trials; the fixation display changed to one of the four colours, matching either a WM or LTM item with equal probability. Informative retrocues indicated the item to be probed in the memory recall task with 100% validity. Following a second delay of 800 ms after the retrocue, the memory recall task and the perceptual discrimination tasks were equally likely to be presented.

In the memory recall task, participants were required to recall the location of the probed item. On trials containing an informative retrocue, participants reported the location of the WM or LTM item indicated by the retrocue. On trials containing a neutral cue, the probed item was indicated by a centrally presented colour, chosen randomly from the WM or LTM colours. Responses were delivered by pressing one of four keys mapped to the four locations (the same keys as used in the location reproduction task during the learning session). Feedback was then presented for 500 ms indicating whether the response was correct or wrong.

In the perceptual discrimination task, four arrows (length: 1.25°, width of the tail: 0.625°, RGB value: [128, 128, 128]) were presented in the placeholders for 100 ms, after which randomly generated Gaussian noise masks were applied to the four locations for 100 ms. Following the mask, one location was probed, and participants pressed one of the arrow keys to report the arrow direction at that location. Each of the four locations had an equal possibility of being probed. The arrow direction at each location was independently drawn from four possible directions (↑, ←, ↓, →), resulting in $4^4 = 256$ possible combinations.

Participants were informed that the memorised items and the retrocue bore no predictive relation concerning the location of the perceptual item to be discriminated. When retrocues were informative, however, participants always needed to maintain the retrocued item in mind for potential future use because of the randomisation of the memory recall and perceptual discrimination trial order, which allowed us to examine any spill-over benefits elicited by the retrocue on the perceptual discrimination task. The relationship between the perceptual discrimination task and the retrocue was totally incidental because all locations were equally likely to be probed no matter which location the retrocue would preferentially bias attention to. As a result, only 25% of informative-retrocue trials in the perceptual discrimination task were “matching” trials on which the probed sensory location coincided with the location of the retrocued item.

The testing session consisted of 480 trials divided into 10 blocks (each including 48 trials). To become familiarised with the task, participants performed an additional 48 practice trials before testing.

Behavioural Analysis. Behavioural data were analysed in MATLAB. For the learning session, we examined the average colour reproduction errors and location reproduction accuracy respectively, by sorting the learning trials of each type into 4 bins (each containing 10 trials). Colour reproduction errors (in units of degrees) were calculated by taking the absolute difference between the angle of the target colour and the reproduced colour on the colour wheel. One-way repeated-measures ANOVAs with linear contrast weights ([-3, -1, 1, 3]) across four bins tested for the efficacy of training.

For the testing session, data from the memory recall and perceptual discrimination tasks were analysed separately. During pre-processing, we excluded trials on which RTs were 3 SD above the individual mean across all conditions in either task. After this exclusion step, an average of 98.35% (SD = 0.44%) trials were retained in the analyses.

To test for benefits of internal selective attention on WM and LTM retrieval, we analysed the average RTs and accuracy for the memory recall task as a function of retrocueing (neutral vs. informative) and the memory timescale of probed items (WM vs. LTM). To examine whether orienting attention to a memory item benefited subsequent perceptual processing at matching locations, we compared perceptual discrimination accuracy on retrocue matching trials vs. neutral trials (matching vs. neutral) when locations associated with WM or LTM items were probed (WM vs. LTM). To gauge the quality of perception, accuracy was the dependent variable of interest, but RTs were also evaluated for completeness. Additional analyses regarding the putative costs of misdirected selective attention in WM and LTM for perceptual discrimination are presented in the **Supplemental Material**.

When comparing behavioural performance between conditions, we applied a repeated-measures ANOVA and reported partial η^2 as a measure of effect size. For post hoc *t*-tests, we reported Bonferroni-corrected *p* values that we denoted as “$p_{\text{Bonferroni}}$”. We reported Cohen's *d* as a measure of effect size for all the *t*-tests. Where relevant, the within-subject standard error of the mean (*SEM*) was calculated from normalised data using the approach from Cousineau (2005). When evaluating potential perceptual benefits elicited by WM and LTM retrocues, we applied one-sample *t*-tests against 0.

Results

We first tested whether our LTM training in the learning session was effective, by evaluating colour reproduction errors and location reproduction accuracy (**Fig. 1**). Trial bins exerted a significant main effect on colour reproduction errors: a linear contrast analysis showed that participants

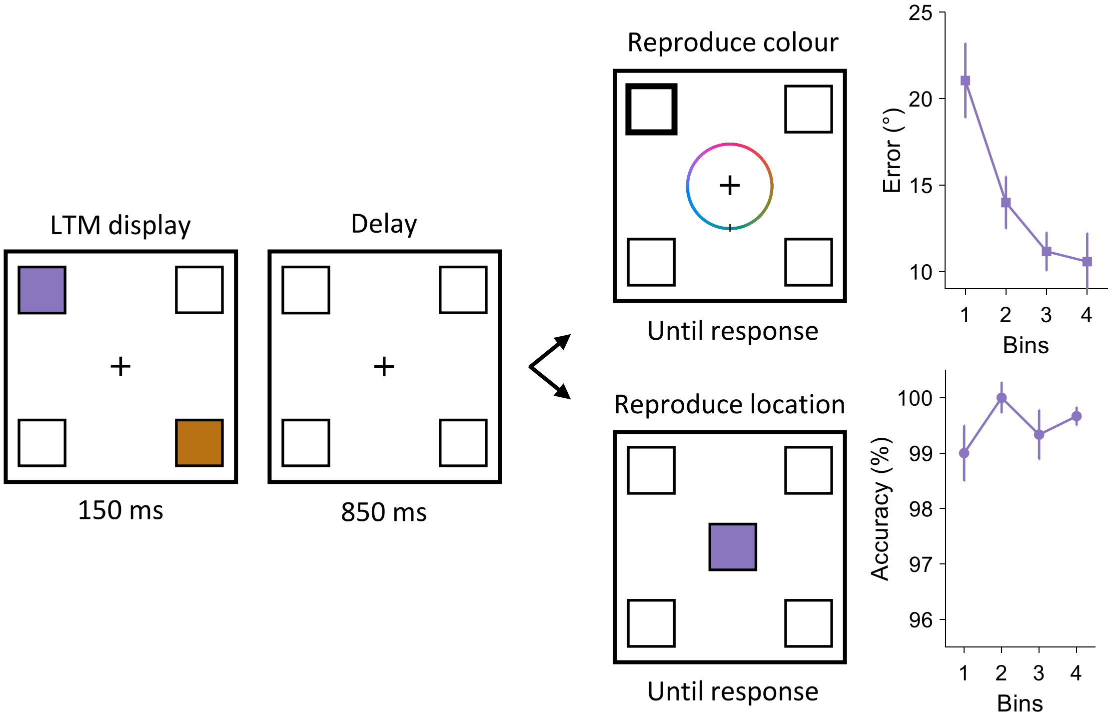

Fig. 1. LTM training in Experiment 1. On every learning trial, participants memorised the same colours and locations of two squares at diagonal locations. When prompted, they reproduced the colour at the probed location or the location of the probed colour. Colour reproduction trials and location reproduction trials were presented in random order. Learning performance was aggregated into 4 bins (of 10 trials each) and shown in the form of errors for colour reproduction and accuracy for location reproduction, respectively. Error bars represent ±1 *SEM* (*n* = 30).

reproduced the LTM colours with smaller errors on late as compared to early trials (F (1, 26) = 16.156, $p < .001$, partial $\eta^2 = 0.157$). For the location reproduction task, participants remained near ceiling-level accuracy across the four bins: first bin: 0.990 ± 0.005 ($M \pm SEM$), last bin: 0.997 ± 0.002, F (1, 26) = 0.480, $p = .490$. Although the location reproduction task was too easy to show the location learning process, the improvement of colour reproduction performance suggests that participants indeed learned the two items and stored them into LTM.

Retrocues improve WM and LTM recall

We then assessed the effects of WM and LTM retrocues on memory recall performance (**Fig. 2B**). Both retrocueing (neutral vs. informative) and the memory timescale of probed items (WM vs. LTM) significantly impacted retrieval speed: RTs in the memory recall task were faster when retrocues were informative (F (1, 29) = 83.205, $p < .001$, partial $\eta^2 = 0.742$) and when WM items were probed (F (1, 29) = 8.239, $p = .008$, partial $\eta^2 = 0.221$). Crucially, retrocueing and memory timescale also interacted (F (1, 29) = 18.627, $p < .001$, partial $\eta^2 = 0.391$). Both WM and LTM retrocues conferred a significant benefit (WM: t (29) = 9.217, $p_{\text{Bonferroni}} < .001$, $d = 1.521$; LTM: t (29) = 6.575, $p_{\text{Bonferroni}} < .001$, $d = 0.833$), but retrocue benefits were stronger for the speed of retrieving WM items (t (29) = 4.316, $p < .001$, $d = 0.748$).

Similar analyses on retrieval quality showed significant main effects of retrocueing (F (1, 29) = 4.340 $p = .046$, partial $\eta^2 = 0.130$) and memory timescale (F (1, 29) = 4.667, $p = .039$, partial $\eta^2 = 0.139$), as well as a significant interaction (F (1, 29) = 12.115, $p = .002$, partial $\eta^2 = 0.295$). Post-hoc comparisons revealed a significant improvement in recall accuracy by retrocues for WM items (t (29) = 2.981, $p_{\text{Bonferroni}} = .012$, $d = 0.465$) but no significant effect of retrocues for LTM items (t (29) = 1.530, $p_{\text{Bonferroni}} = .274$). This could possibly be explained by the overall very high recall accuracy, particularly so for LTM (0.977 ± 0.005), leaving little room for improvement.

Retrocueing WM and LTM items benefits perceptual processing at matching locations

We then examined whether the selective prioritisation of WM and LTM memoranda by retrocues

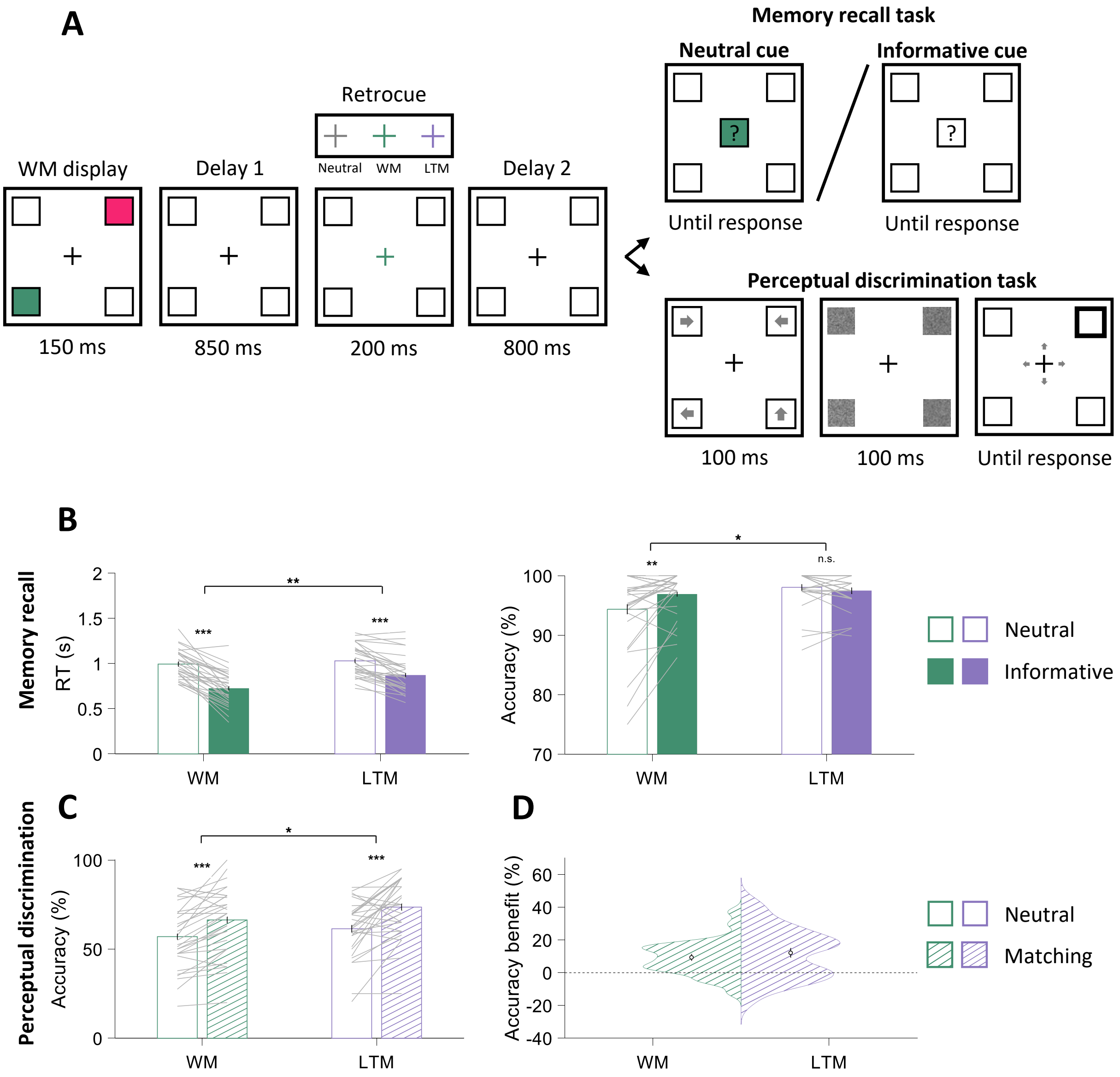

Fig. 2. Prioritising WM and LTM representations guides recall and perception in Experiment 1. A, task schematic of the testing trials in Experiment 1. Participants first encoded two items into WM, with different colours and locations from those in LTM. After the first delay, neutral retrocues were uninformative, whereas informative retrocues (WM or LTM) indicated which location would be relevant in the memory recall task. After a second delay, the memory recall task and the perceptual discrimination task were equally likely to be presented. In the recall task, participants recalled the location of a randomly chosen colour on neutral-retrocue trials and the location of the retrocued colour on informative-retrocue trials. In the perceptual task, participants discriminated the direction of one of the four arrows that briefly appeared at the four quadrants before being masked. The location of the probed arrow was indicated by a post-cue. **B**, memory recall mean RTs and accuracy for WM and LTM items, grouped by neutral-retrocue and informative-retrocue trials. **C**, perceptual discrimination accuracy at WM and LTM locations, grouped by retrocue neutral and matching trials. **D**, means and distributions of perceptual accuracy benefits for WM and LTM locations matching retrocues. Error bars in **B-D** represent ±1 *SEM* (n = 30).

also incidentally impacted perceptual discrimination of items occurring at the matching location (see **Fig. 2C**).

Perceptual discrimination accuracy showed a main effect of retrocue matching (F (1, 29) = 31.541, $p < .001$, partial $\eta^2 = 0.521$). Accuracy was superior for discriminating the arrow direction at the retrocue matching location (0.699 ± 0.029) than for items on neutral-retrocue trials (0.592 ± 0.027). Surprisingly, we also found a main effect of the memory timescale associated with probed locations (F (1, 29) = 4.887, $p = .035$, partial $\eta^2 = 0.144$). Accuracy was higher when LTM locations were probed (0.655 ± 0.026) compared to WM locations (0.601 ± 0.032). There was no interaction between retrocue matching and memory timescale of the probed location, F (1, 29) = 0.926, $p = .344$. **Fig. 2D** shows that incidental retrocue benefits on perceptual discrimination were significantly larger than zero for both memory timescales (WM: 0.094 ± 0.020, t (29) = 4.804, $p < .001$, $d = 0.877$; LTM: 0.121 ± 0.028, t (29) = 4.362, $p < .001$, $d = 0.797$) but did not differ in size (t (29) = 0.962, $p = .344$).

For completeness, analysis of RT revealed a main effect of retrocue matching on perceptual discrimination RTs: participants were faster for items at matching vs. neutral locations (F (1, 29) = 5.469, $p = .027$, partial $\eta^2 = 0.159$). There was no main effect of the memory timescale (F (1, 29) = 0.194, $p = .663$) or interaction between the factors (F (1, 29) = 0.541, $p = .468$).

EXPERIMENT 2

Experiment 2 was designed to replicate and extend the general pattern of findings from Experiment 1 using more complex stimuli and a recall task that did not emphasize associations with the spatial location of items.

In Experiment 1, items were defined by colour and location, with the memory recall task requiring participants to reproduce the location of an item based on its colour. The recall task thus naturally encouraged the prioritisation of the retrocued item's location in anticipation of the recall probe.

This follow-up experiment tested whether the location of the memoranda would be prioritised automatically and incidentally benefit perceptual discrimination, even when the recall task did not require retrieval of the item's location. Improvements in discriminating spatially matching visual stimuli under such conditions would add to the growing evidence that visual memories preserve a spatial layout based on the sensory layout at encoding (e.g., Dell'Acqua et al., 2010; Groen et al., 2022; Kuo et al., 2009) and that spatial locations can play a special role in scaffolding memory contents (e.g., Pertzov & Husain, 2014; Schneegans & Bays, 2017; Treisman & Zhang, 2006). To test for incidental spatial prioritisation in non-spatial WM and LTM recall tasks, Experiment 2 used more complex stimuli defined by unique shapes in addition to colours and required reporting of non-spatial features (shapes) on memory recall trials.

Previous research demonstrated that systematic small shifts in gaze position (gaze biases) accompany shifts in the internal focus of attention within working memory (Draschkow et al., 2022; van Ede et al., 2019, 2020). Experiment 2 employed eye tracking to compare directly whether and how the involvement of the oculomotor system might differ when WM and LTM representations are prioritised for potential use in the memory recall task.

Methods

Participants. A total of 44 volunteers (27 females, 17 males, *M* = 25.93 years, *SD* = 4.51) with reported normal or corrected-to-normal visual acuity were recruited. The sample size was chosen to achieve 90% power for the one-sample *t*-tests (Faul et al., 2007) performed to test the significance of perceptual benefits following WM and LTM retrocues. The effect sizes for these comparisons in Experiment 1 were 0.877 and 0.797. We assumed a conservative approach and aimed to power for the detection of a medium effect size (0.5) because we expected that the manipulation in Experiment 2 would lead to a smaller effect due to the incidental nature of the spatial attributes in the task.

Most of the experimental setup was identical to Experiment 1, with the following modifications.

Apparatus and stimuli. Eye movements were recorded with the EyeLink 1000 Desktop Mount (SR Research, Ottawa, ON, Canada) at 1000 Hz. Eye-tracker calibration used the built-in calibration and validation protocols from the EyeLink software. When possible, horizontal and vertical gaze positions were continuously recorded for both eyes. For some participants (*N* = 13), only one eye was tracked due to a lack of good-quality binocular tracking (mostly because of wearing glasses).

Stimuli appeared on a white background. Four shapes were equidistantly sampled from the Validated Circular Shape (VCS) space (Li et al., 2020), and then randomly assigned to each WM and LTM item, adding a new feature dimension to the existing configurations in Experiment 1. These same four shapes were used across all participants, but the shapes assigned to WM and LTM items were randomised across participants.

Procedure and design. During the learning session, participants were trained to memorise the colours and shapes of the two LTM items (**Fig. 3**). On every trial, they were probed to reproduce either the colour or the shape of one item. At the response stage, either a colour wheel or a shape wheel was presented at the centre, indicating the feature dimension to be reproduced in this trial. Both the colour and shape wheels were presented in a random orientation each time. The shape wheel consisted of 360 shapes from the VCS space. To avoid clustering, eight shapes sampled from equidistant positions on the wheel were displayed along the cardinal axes (i.e., every 45 degrees). These eight shapes served as visual anchors, which were also randomly chosen every time in accordance with the orientation of the shape wheel. Participants responded using a computer mouse that controlled the dial on the wheel. Participants had unlimited time to retrieve the item from memory and to decide what to reproduce. However, once they started moving the dial, they had only 2500 ms to complete their reproduction. This was intended to encourage participants to recall the exact colour or shape before moving the dial. The position of the dial when participants clicked the left mouse button or when the time limit was reached was taken as the response. Immediately after their response, participants received feedback for 500 ms. Each colour and shape were probed on 20 trials, resulting in a total of 80 learning trials presented in random order.

During the testing session, each WM shape was randomly combined with one of the WM colours on every trial (**Fig. 4A**). As in Experiment 1, participants performed either a memory recall task or a perceptual discrimination task on each trial equiprobably. In the memory recall task, participants reproduced the shape of the item matching the retrocued colour or a randomly probed colour when the retrocue was neutral. The shape wheel was identical to that used during the learning session and was randomly rotated across trials. Uninformative, grey neutral retrocues appeared on one-fifth of the trials. The remaining trials contained informative coloured retrocues matching each of the LTM or WM colours with equal probability. The perceptual discrimination task was the same as that in Experiment 1.

The testing session consisted of 600 trials divided into 10 blocks (each including 60 trials). To become familiarised with the task, participants performed an additional 30 practice trials before testing.

Behavioural Analysis. The analyses of interest were basically the same as in Experiment 1, with location reproduction in the learning and testing sessions replaced by shape reproduction. Shape reproduction errors (in units of degrees) were calculated by taking the absolute difference between the angle of the target shape and the reproduced shape on the shape wheel. The RTs in the memory recall task were calculated as the time from probe onset to when the response was recorded, either when participants clicked the left mouse button or when the time limit was reached. After excluding memory recall and perceptual discrimination trials on which RTs were 3 SD above the individual mean across all conditions, an average of 98.66% (SD = 0.47%) trials were retained in the analyses.

Eye-tracking Analysis. Data were first converted from edf to asc format and subsequently read into RStudio. For binocularly tracked participants, data from the left and right eyes were averaged to obtain a single horizontal and a single vertical gaze position channel. Blinks were marked by detecting NaN clusters in the eye-tracking data and then interpolated using a linear interpolation procedure. Data were epoched from 250 ms before to 1000 ms after cue onset. To make our analyses more robust to drift of the eyes during fixation, we obtained the average gaze position within the 250 ms window before cue onset for every trial and participant, and subtracted it from every corresponding time course. We performed analyses on horizontal and vertical channels separately. For both channels, we only included trials on which gaze position remained within ± 50% from fixation (with 100% denoting the centres of the original item locations at a ± 5° visual angle) throughout the course of the trial, as previous work showed that the gaze bias phenomenon is constituted by a bias in gaze around fixation (Draschkow et al., 2022; van Ede et al., 2019, 2020). For the horizontal channel, data for all 44 participants were used, with an average of 9.6% ± 1.7% (*M* ± *SEM*) trials excluded per participant. For the vertical channel, six participants had to be removed due to a high number of excluded trials (> 50%). For the 38 participants retained, an average of 14.6% ± 2.1% trials were excluded. Gaze time courses were smoothed using a 25-ms average moving window.

For the horizontal channel, we compared trial-averaged gaze-position time courses between conditions in which the retrocued item occupied the left side (top/bottom left location) or the right side (top/bottom right location) during encoding, separately for trials with WM retrocues and trials with LTM retrocues. For the vertical channel, we did the same between conditions in which the retrocued item occupied the bottom side (bottom left/right location) or the top side (top left/right location) during encoding, also separately for trials with WM and LTM retrocues. For both channels, trial-averaged gaze-position time courses were also obtained for trials with neutral retrocues. To increase sensitivity, we also constructed a measure of towardness separately for trials with WM and LTM retrocues, which expressed the gaze bias toward the side of the retrocued item in a single value (Draschkow et al., 2022; van Ede et al., 2019, 2020). We did this for both horizontal and vertical channels to obtain towardness in horizontal and vertical directions, respectively.

Statistical evaluation of the towardness time courses used a cluster-based permutation approach (Maris & Oostenveld, 2007) implemented in the *permuco* package (Frossard & Renaud, 2021), which is ideally suited to evaluate physiological effects across multiple time points while retaining high sensitivity.

Results

As in Experiment 1, we first confirmed that participants learned the colours and shapes of LTM items over training (**Fig. 3**). For the colour reproduction task, although the result of the linear contrast analysis on colour reproduction errors was not significant (F (1, 40) = 2.304, p = .132), the errors remained relatively low with a numerically decreasing trend across bins (first bin: 23.107°

± 2.295, last bin:19.182° ± 1.612). Learning performance improved significantly for the shape reproduction task, with errors decreasing across bins (F (1, 40) = 17.939, $p < .001$, partial η^2 = 0.122).

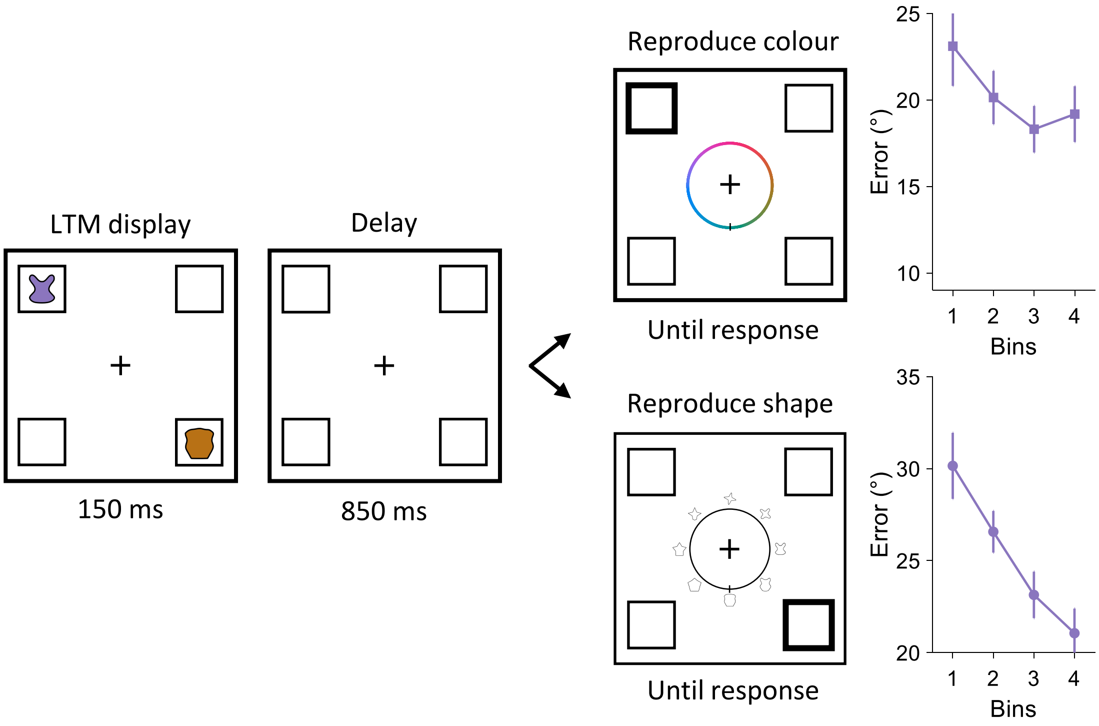

Fig. 3. LTM training in Experiment 2. On every learning trial, participants memorised two consistent items at diagonal locations defined by unique colours and shapes. When prompted, they reproduced the colour or shape at one location. Colour reproduction trials and shape reproduction trials appeared in random order. Learning performance was sorted into 4 bins (with 10 trials each) and shown in the form of errors for both colour and shape reproduction. Error bars represent ±1 *SEM* ($n = 44$).

Retrocues improve WM and LTM recall

We examined the effects of WM and LTM retrocues on memory recall performance (**Fig. 4B**). Retrocueing significantly shortened RTs (F (1, 43) = 179.198, $p < .001$, partial η^2 = 0.807). Although RTs were equivalent for both memory timescales (F (1, 43) = 0.436, $p = .513$), there was a significant interaction between the two factors (F (1, 43) = 24.568, $p < .001$, partial η^2 = 0.364). RT benefits were present for both WM (t (43) = 11.657, $p_{\text{Bonferroni}} < .001$, $d = 0.594$) and LTM (t (43) = 9.016, $p_{\text{Bonferroni}} < .001$, $d = 0.273$) but were stronger for WM (t (43) = 4.957, $p < .001$, $d =$

0.929).

For recall accuracy, both retrocueing (F (1, 43) = 8.971, p = .005, partial η^2 = 0.173) and memory timescale (F (1, 43) = 32.995, p < .001, partial η^2 = 0.434) exerted significant main effects. The two factors also interacted (F (1, 43) = 7.441, p = .006, partial η^2 = 0.163). Post-hoc comparisons revealed that WM retrocues significantly reduced shape reproduction errors (t (43) = 4.322, $p_{\text{Bonferroni}}$ < .001, d = 0.429) but LTM retrocues did not (t (43) = 1.250, $p_{\text{Bonferroni}}$ = .436). Shape reproduction was very accurate and errors were smaller when LTM shapes were reproduced (16.610° ± 1.519) as compared to WM shapes (27.603° ± 2.417), possibly reflecting ceiling effects.

Retrocueing WM and LTM items benefits perceptual processing at matching locations

We then examined whether retrocueing memory items incidentally benefitted items at matching locations in the perceptual discrimination task, even though retrieving spatial locations was never required for either task (**Fig. 4C**).

Perceptual discrimination accuracy was sensitive to both experimental factors. Discrimination was more accurate for arrows at retrocue matching locations than items on neutral-retrocue trials (F (1, 43) = 9.504, p = .004, partial η^2 = 0.181) and for arrows appearing at LTM locations (F (1, 43) = 55.213, p < .001, partial η^2 = 0.562). Retrocue matching and memory timescale did not interact (F (1, 43) = 0.067, p = .797). **Fig. 4D** shows that perceptual benefits for items matching WM and LTM retrocue locations were both significantly larger than zero (WM: 0.037 ± 0.003, t (43) = 2.191, p = .034, d = 0.330; LTM: 0.032 ± 0.002, t (43) = 2.176, p = .035, d = 0.328) and did not differ in size (t (43) = 0.259, p = .797).

RTs during perceptual discrimination were faster for arrows appearing at LTM locations (main effect of memory timescale: F (1, 43) = 14.297, p < .001, partial η^2 = 0.250). Retrocue matching had no significant effect (F (1, 43) = 0.638, p = .429) and the factors did not interact (F (1, 43) = 3.353, p = .074).

When comparing the size of perceptual benefits in Experiments 1 and 2, we found a main effect of Experiment (1 vs. 2), F (1, 72) = 13.357, p < .001, partial η^2 = 0.157, indicating a significantly

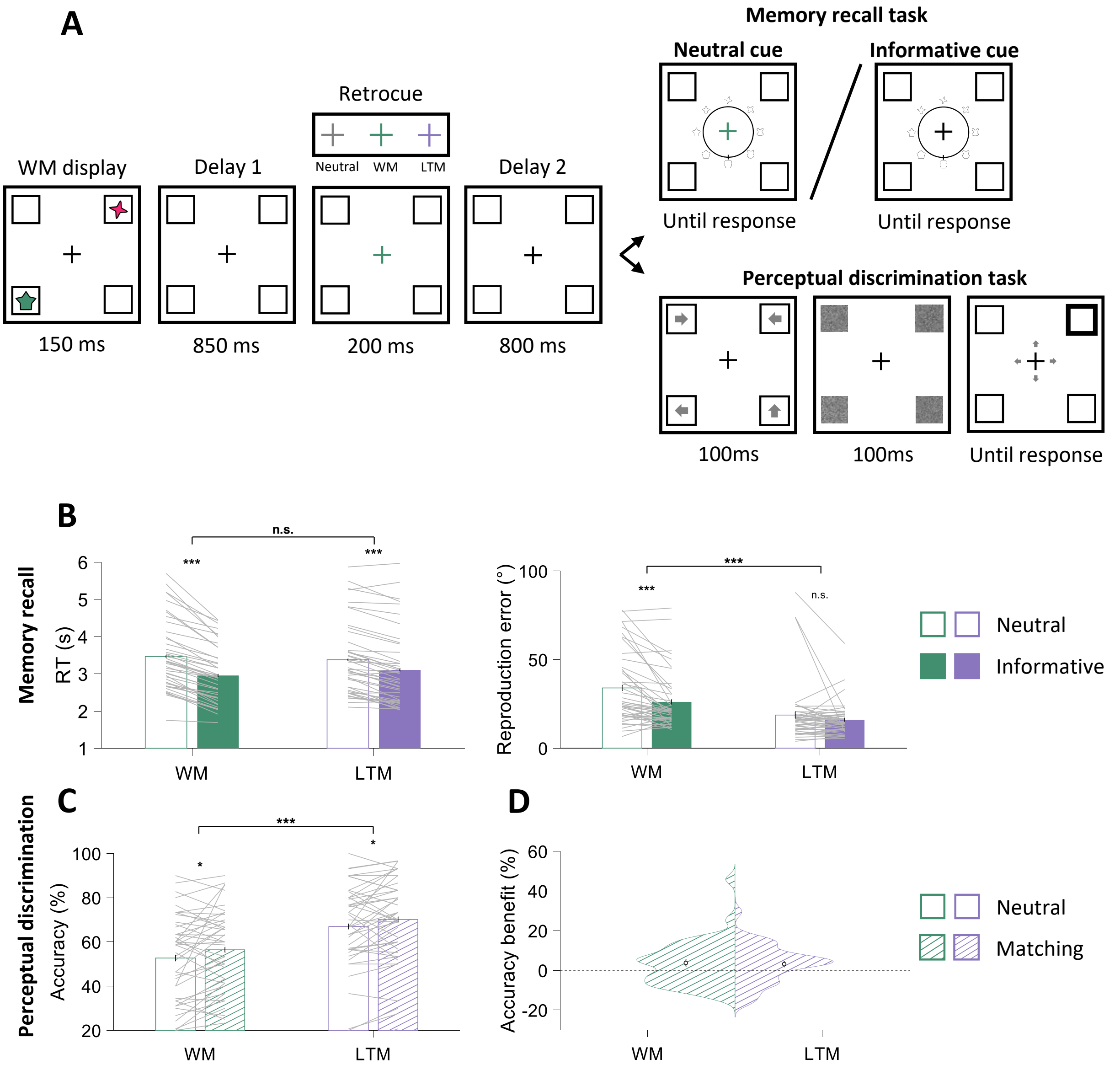

Fig. 4. Prioritising WM and LTM representations guides recall and perception in Experiment 2. A, task schematic of the testing trials in Experiment 2. Participants first encoded two items in WM. Their colours, shapes, and locations differed from those in LTM. After the first delay, neutral retrocues were uninformative, whereas informative retrocues (WM or LTM) indicated which item shape would be relevant in the memory recall task. After a second delay, the memory recall task and the perceptual discrimination task were equally likely to be presented. In the recall task, participants recalled the shape of the item matching a randomly chosen colour on neutral-retrocue trials and the shape of the item matching the retrocued colour on informative-retrocue trials. In the perceptual task, participants discriminated the direction of one of the four arrows that briefly appeared at the four quadrants before being masked. The location of the probed arrow was indicated by a post-cue. **B**, memory recall mean RTs and accuracy for WM and LTM items, grouped by neutral-retrocue and informative-retrocue trials. **C**, perceptual discrimination accuracy at WM and LTM locations, grouped by retrocue neutral and matching trials. **D**, means and distributions of perceptual accuracy benefits for WM and LTM locations matching retrocues. Error bars in **B-D** represent ±1 *SEM* ($n = 44$).

larger benefit size in Experiment 1 compared to Experiment 2. No main effect of memory timescale (WM vs. LTM, F (1, 72) = 0.560, p = .457) or interaction between Experiment and memory timescale (F (1, 72) = 1.151, p = .287) was found.

WM but not LTM retrocues elicit directional gaze biases

Eye gaze measurements revealed a striking dissociation between orienting attention in WM and LTM. Replicating previous findings (Draschkow et al., 2022; van Ede et al., 2019, 2020), WM retrocues elicited significant gaze biases in the direction of attention orienting. In contrast, no evidence of similar gaze biases occurred when orienting attention in LTM. **Fig. 5A** and **5C** show the horizontal and vertical gaze biases, respectively, following neutral, WM, and LTM retrocues. Eye traces after neutral cues showed a characteristic pattern of leftward and downward shifts in eye position. Compared to this baseline pattern of gaze shifts, systematic changes were observed for trials with WM retrocues depending on the direction of the retrocued item, both horizontally and vertically. No significant changes occurred for trials with LTM retrocues, on which the baseline pattern of gaze shifts was observed regardless of the retrocued item direction.

These differences between gaze biases following WM and LTM retrocues were evident in the associated towardness time courses (**Fig. 5B** and **5D**). There were significant clusters in both horizontal and vertical towardness time courses following WM retrocues (cluster-based permutation tests, horizontal: ps < .045; vertical: ps < .047). Critically, there were significant differences between the towardness time courses following WM and LTM retrocues along both horizontal and vertical directions (cluster-based permutation tests, horizontal: approximately 450-1000 ms after cue onset, p = .002; vertical: approximately 420-870 ms after cue onset, p = .003; Maris & Oostenveld, 2007; Sassenhagen & Draschkow, 2019). There were no significant clusters in either time course following LTM retrocues.

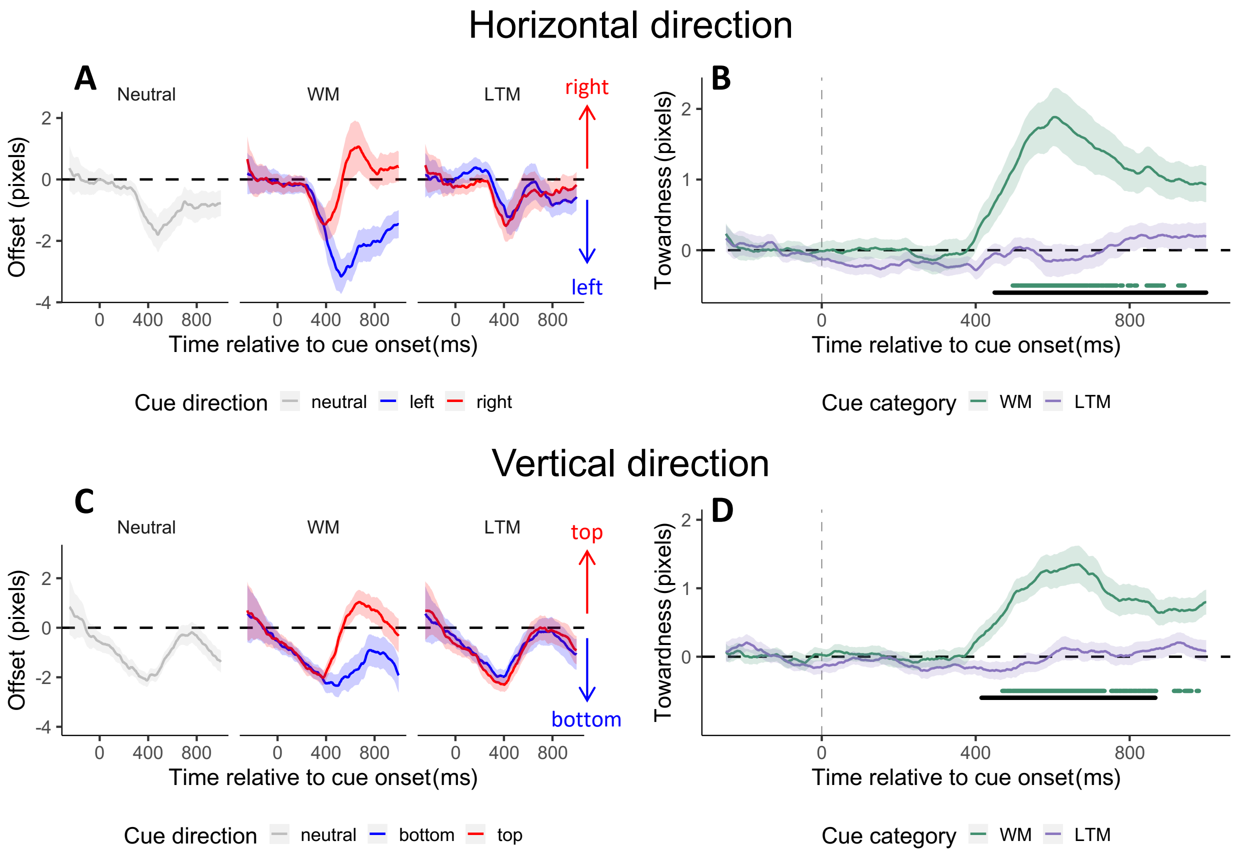

Fig. 5. Attention-related gaze biases following WM but not LTM retrocues in Experiment 2. A, time courses of horizontal gaze biases following neutral, WM, and LTM retrocues. For WM and LTM retrocues, time courses are shown separately for conditions in which the retrocued item occupied the left side (top/bottom left location) or the right side (top/bottom right location) during encoding. **B**, time courses of horizontal gaze bias towardness on trials with WM and LTM retrocues, corresponding to the data in **A**. **C**, time courses of vertical gaze biases following neutral, WM, and LTM retrocues. For WM and LTM retrocues, time courses were shown separately for conditions in which the retrocued item occupied the top side (top left/right location) or the bottom side (bottom left/right location) during encoding. **D**, time courses of vertical gaze bias towardness on trials with WM and LTM retrocues, corresponding to the data in **C**. Horizontal lines below the time courses in **B** and **D** indicate significant temporal clusters (green: WM compared to zero; black: WM-LTM difference). No significant clusters were detected on trials with LTM retrocues in either horizontal or vertical directions.

DISCUSSION

We demonstrated that internal attention-directing cues benefit both WM and LTM recall and that selective prioritisation of WM and LTM items also brought significant, spill-over advantages for discriminating visual stimuli at the location matching the selected memory item. Eye tracking revealed a striking difference in the mechanisms for internal shifts of attention in WM vs. LTM. Our findings reinforce the increasing recognition of the strong and multidirectional relationship between attention and memories of different timescales (Nobre & Stokes, 2019, 2020) as well as the plurality of mechanisms supporting their interactions (van Ede & Nobre, 2023).

Our data demonstrate the capacity to orient attention flexibly to a specific item in LTM, highlighting similarities with orienting in WM. In our tasks, orienting attention to contents in LTM significantly improved retrieval speed in a similar, though less pronounced way as for WM. No benefits were found for the accuracy of LTM, in contrast to WM, which could be related to the very high retrieval accuracy in our tasks, especially for LTM. It will be important, therefore, to explore possible consequences to retrieval accuracy in more challenging memory tasks. The current pattern of results suggests that attention can, at least, enhance the accessibility or "readiness" to act on LTM memory representations. The modulations observed for WM compared to LTM retrieval were stronger, shortening response times to a greater degree and affecting retrieval accuracy. The findings could point to differences in the types of mechanisms of internal attention within these different memory domains or could, instead, reflect variations in the strength of the memory representations themselves and the resulting retrieval demands. Future studies can examine these interesting emerging possibilities systematically.

Across the two experiments, we also revealed spill-over effects that orienting in WM and LTM has for sensory processing. In the perceptual discrimination task, prioritising items within the spatial layout of either WM or LTM boosted the discrimination accuracy of location-matching stimuli. While previous reports of this phenomenon focused on the influence of WM (Olivers et al., 2011; Soto et al., 2008), our results showed a comparable effect from prioritised LTM representations. There was no strategic benefit for using the retrocue information in the perceptual task since the location of the retrocued item only matched the probed location on 25% of the trials. Consequences of memory selection for sensory processing were therefore likely incidental.

Moreover, when locations were never probed for reproduction in Experiment 2 (colour-shape bindings were sufficient to perform well in the memory recall task), we still observed discrimination accuracy benefits following WM and LTM retrocues. This suggests memory retrieval involves prioritization of location information even when this is not required, thereby supporting prior research indicating the privileged role of spatial locations in binding features held in memory (Pertzov & Husain, 2014; Schneegans & Bays, 2017; Treisman & Zhang, 2006). Furthermore, shape reporting on a randomly oriented wheel in Experiment 2 also controlled for the possible effects of motor preparation in Experiment 1 related to the consistent response mappings of location reports. Thus, retrocues necessarily enhanced recall performance by improving the accessibility to and/or quality of sensory information. Future research should address in detail the various possible targets and modulatory mechanisms underlying internal attention in WM and LTM (Nobre & Stokes, 2019; van Ede & Nobre, 2023).

Our eye-tracking data yielded the most suggestive evidence for a functional dissociation between the mechanisms for orienting attention in WM and LTM. We found a striking difference in oculomotor involvement on trials with WM and LTM retrocues by capitalising on subtle directional biases in human gaze behaviour (Corneil & Munoz, 2014; Engbert & Kliegl, 2003; Hafed & Clark, 2002). Consistent with previous work (Draschkow et al., 2022; van Ede et al., 2019, 2020), we observed that gaze was biased toward retrocued WM items. Critically, this bias was more pronounced in WM compared to LTM. No significant gaze biases were detected following LTM retrocues. The findings thus reveal differential involvement of oculomotor mechanisms when orienting in WM vs LTM.

An unexpected finding in our experiments was the better perceptual discrimination performance when LTM locations were probed compared to WM locations in both experiments (higher accuracy for LTM locations in Experiment 1, and both higher accuracy and faster RTs for LTM locations in Experiment 2). It will be fascinating to explore whether this finding points to a primacy of LTM to guide perception (see Helmholtz, 1867) or rather reflects a peculiarity of our experimental conditions. For example, the greater consistency of feature mappings to LTM locations than WM locations in our tasks may have decreased competition among memories and lead to stronger sensory biases. Or, instead, the results may be tapping into something more fundamental, such as relevant LTM representations exerting stronger and more automatic biases, akin to sensory salience effects (see Theeuwes, 2019; Wolfe, 2021).

In summary, we compared the effects of focusing attention within WM vs. LTM and discovered that both bring significant benefits to retrieval and subsequent sensory processing, most likely through dissociable mechanisms. The strikingly distinct oculomotor signatures of covert spatial attention in WM and LTM corroborate a plurality of functional properties when memories of different timescales guide adaptive behaviour and open novel opportunities for furthering our understanding of the relationship between WM and LTM.

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Author Contribution Statement

Dongyu Gong: Conceptualization; Methodology; Software; Investigation; Data curation; Formal analysis; Visualization; Writing – original draft

Dejan Draschkow: Conceptualization; Methodology; Software; Data curation; Writing – Review & Editing; Supervision.

Anna C. Nobre: Conceptualization; Methodology; Resources; Data curation; Writing – Review & Editing; Supervision; Project administration.

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