Brain areas that control gaze are also recruited for covert shifts of spatial attention. In the external space of perception, there is a natural ecological link between the control of gaze and spatial attention, as information sampled at covertly attended locations can inform where to look next. Attention can also be directed internally to representations held within the spatial layout of visual working memory. In such cases, the incentive for using attention to direct gaze disappears, as there are no external targets to scan. Here we investigate whether the oculomotor system of the brain also participates in attention focusing within the internal space of memory. Paradoxically, we reveal this participation through gaze behaviour itself. We demonstrate that selecting an item from visual working memory biases gaze in the direction of the memorized location of that item, despite there being nothing to look at and location memory never explicitly being probed. This retrospective ‘gaze bias’ occurs only when an item is not already in the internal focus of attention, and it predicts the performance benefit associated with the focusing of internal attention. We conclude that the oculomotor system also participates in focusing attention within memorized space, leaving traces all the way to the eyes.

We report four complementary experiments investigating the recruitment of the oculomotor system of the brain during attentional focusing within the spatial layout of visual working memory. In each experiment, we probed this involvement in the most direct way possible: by investigating gaze behaviour itself. In doing so, we capitalized on the observation that recruitment of the oculomotor system of the brain leaves peripheral traces, even during covert task demands (see ref. 17 for discussion of such peripheral traces).

Each experiment involved memorizing multiple coloured and oriented bars to reproduce the orientation (experiments 1–4) and colour (experiment 4) of one bar after a short memory delay, during which only the central fixation cross remained on the screen. The bar to be reported was always indicated by a change in the colour (experiments 1–4) or shape (experiment 4) of the fixation cross (the memory probe). Response initiation (a key press in experiment 1, or a movement of the computer mouse in experiments 2–4) prompted the appearance of a response dial, which also appeared centrally. In all four experiments, the spatial locations of the memory items were purely incidental and were not strictly required for task performance at any point (colour–orientation bindings were sufficient). Because the probe and response dial always occurred centrally, the anticipation and processing of these stimuli did also not depend on item location.

In experiment 1 (Fig. 1a), each trial contained one left and one right item that were equally likely to be probed for report after a 2–2.5 s memory delay. On average, participants required 758.41 ± 56.69 ms (mean ± s.e.m.) after probe onset to initiate their response, and reproduced the orientation of the probed item with an average absolute error of 14.22° ± 0.91°.

Although item location was never probed, we observed a clear systematic gaze shift in the direction of the original (encoded) location of the probed item. When the probed memory item had previously occupied the left position on the screen, gaze became biased to the left; when the probed memory item had been on the right, gaze became biased to the right (Fig. 1b). To increase sensitivity and interpretability, we combined these time courses in a single metric ‘towardsness’ (Fig. 1c). A cluster-based permutation analysis of this time course (which deals with the multiple comparisons along the time axis) showed that this effect was highly robust (horizontal black line in Fig. 1c; \( \sum T \) (sum of \( T \)-values of the largest cluster) = 3,732.1, 95% of permutations between –864.1 and 826.6, \( n = 23 \) participants, \( P < 0.001 \)). Although the average magnitude of this bias was relatively small (peaking at 2.62% towards the memorized location of the item, corresponding to approximately 0.15 degrees visual angle (dva); Fig. 1e), this gaze bias was positive (towards > away) in every participant (Supplementary Figs. 1 and 2b).

To characterize the temporal window of this gaze bias in relation to our task, we re-aligned the data to response onset (Fig. 1d). This revealed that the bias is particularly prominent just before response onset and dissipates soon after the dial-up of the orientation of the selected item commences. This timing thus coincides with the period of attentional item selection (during which only the fixation cross was present on the screen). Indeed, the onset and time course of the bias is well in line with the time course of the voluntary deployment of attention (as, for example, in refs. 18–21).

To understand how the frequency and magnitude of gaze shifts contributed to the overall bias, we isolated the window in which the bias emerged (300–600 ms post-probe; the window in which putative gaze shifts occurred; Supplementary Fig. 2a) and constructed a density plot for gaze shifts arranged by magnitude (Fig. 1e). This confirmed a higher proportion of gaze shifts towards (versus away from) the memorized location of the probed item. At the same time, this revealed that the bias is composed of gaze shifts of relatively small magnitude. As Fig. 1e makes clear, participants almost never looked all the way to the original location of the probed item (denoted as 100% in Fig. 1e, and corresponding to 5.7 dva; see Supplementary Fig. 3 for the relevant calibration data). The gaze bias reported here therefore differs from earlier reports of gaze revisits to previously occupied locations during long-term memory retrieval or imagery of visual images. Instead, it is in line with the increased propensity for small gaze shifts (microsaccades) to occur in the direction of covertly attended locations, here shown for attended locations within

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Fig. 1 | Selection from working memory biases gaze towards the location of memorized visual items. a, Task schematic of experiment 1. Participants memorized two differently coloured and oriented bars to reproduce the orientation of one bar from memory after a 2–2.5 s delay. A colour change of the central fixation cross (the probe) prompted participants to report the orientation of the colour-matching memory item. The central response dial appeared on the screen following response initiation. b, Average gaze position (in the horizontal plane) after the probe, as a function of the memorized location of the probed item. L, left; R, right. c, Gaze bias towards the memorized location of the probed item relative to probe onset. d, Same as in c, but relative to response onset. Horizontal bars in c and d indicate significant temporal clusters; cluster-based permutation tests of the sum of t-values across time points; probe-locked data in c: $\Sigma T = 3.732.1$, 95% of permutations between $-864.1$ and $826.6$, $P<0.001$; decision-locked data in d: $\Sigma T = 8.248.5$, 95% of permutations between $-1.262.1$ and $1.224.4$, $P<0.001$. e, Density of two-dimensional gaze position following probes of left and right items (400–1,000 ms after probe), before and after subtraction of the density values that were shared between left and right item probes. White circles indicate the area occupied by the probed item at encoding. Percentages are defined relative to the centre of item locations at encoding, with 100% corresponding to approximately 5.7 dva. To enhance interpretability, both percentage (in black) and dva (in grey) metrics are depicted on all axes.

The internal space of memory. A complementary quantification of average gaze shift frequency, shift magnitude and duration of ensuing fixations (Supplementary Fig. 2b) confirmed that the identified gaze position bias primarily reflected an increased number of gaze shifts towards (versus away from) the memorized location of the probed item ($\text{Mean}_{\text{towards}} = 0.245$, $\text{Mean}_{\text{away}} = 0.096$ shifts per trial; paired-samples t-test: $t_{19} = 8.058$, $P < 0.001$, $d = 1.68$, 95% confidence interval (95% CI) of Cohen’s $d (d)$ between 1.032 and 2.313), supplemented by a modest increase in their average magnitude ($\text{Mean}_{\text{towards}} = 12.47\%$, 0.711 dva versus $\text{Mean}_{\text{away}} = 10.382\%$, 0.592 dva; $t_{19} = 3.576$, $P = 0.002$, $d = 0.746$, 95% CI of $d$ between 0.275 and 1.203). We did not find evidence for longer fixation durations following gaze shifts towards (versus away from) the memorized location of the probed item ($\text{Mean}_{\text{towards}} = 363.99$ ms versus $\text{Mean}_{\text{away}} = 360.434$ ms; $t_{19} = 0.25$, $P = 0.805$, $d = 0.052$, 95% CI of $d$ between $-0.357$ and 0.461; Supplementary Fig. 2b for a graphical depiction of these data).
As this bias is carried by gaze shifts of relatively small magnitude, it may have often gone unnoticed in previous work, such as in control analyses that only consider larger gaze shifts, or gaze shifts for which the end-location is in the vicinity of the memorized location of the item. This is nicely illustrated by heat maps (two-dimensional density plots) of gaze position in the post-probe window in which the gaze bias is most pronounced (400–1,000 ms; note that this window is different from the 300–600 ms window used for the analysis of the gaze shifts that inevitably precede the position-of-gaze bias that we depict here). When considering only overall fixation within one experimental condition (Fig. 1f, top row), it seems that participants maintain fixation well, even after probes of left and right items. However, subtracting the common part (average) from both heat maps (leaving only the difference in gaze density following left versus right item probes; Fig. 1f, bottom row) reveals that this is not the case: gaze visits clearly prevail in the direction of the memorized location of the probed item.

If the identified gaze bias reflects the attentional selection and focusing of memory items, then this bias should occur whenever an item is selected, even if the selected item has to be held in memory for another delay before a response is prompted. Moreover, it should only occur when the probed item is not already in the focus of attention.

To investigate these predictions, experiment 2 employed a retro-cue task with a four-item array (Fig. 2a). Informative (coloured) retro-cues during the retention period informed participants which item would be probed after a subsequent delay period, with 100% validity. In contrast, neutral (grey) retro-cues also constituted a transient change of the fixation cross, but gave no information regarding which item would most probably be probed after the second delay period.

Retro-cues were highly effective in facilitating behavioural performance (Fig. 2b). Average reproduction errors were vastly reduced in trials with informative versus neutral retro-cues (errors: \( t_{19} = -6.324; P < 0.001, d = -1.414, 95\% \text{ CI} \) of \( d \) between \(-2.031\) and \(-0.779\)), and this facilitation was even clearer in response onset times (\( t_{19} = -9.978; P < 0.001, d = -2.231, 95\% \text{ CI} \) of \( d \) between \(-3.052\) and \(-1.394\)).

Having established the utility of the retro-cues, we turned to the gaze data. For simplicity, we again focused on the aggregate measure of towardness. Informative retro-cues also elicited a robust gaze bias (Fig. 2c; cluster-based permutation test of the sum of \( t \)-values across time points: \( \sum T = 3,986.6, 95\% \text{ CI} \) of \( d \) between \(-1,313.4\) and \(1,427.5, n = 20 \text{ participants, } P < 0.001 \)). Thus, this bias is not strictly linked to responding, but also occurs when items are brought into focus during the retention period. No systematic bias could be observed after neutral retro-cues, because these did not afford selection of any particular item. At the time of the probe, a robust gaze bias was measured in trials with neutral retro-cues, but this was substantially reduced in trials with an informative retro-cue (black horizontal line in Fig. 2c; cluster-based permutation test of the sum of \( t \)-values across time points: \( \sum T = -4,516.7, 95\% \text{ CI} \) of \( d \) between \(-1,593\) and \(1,561.6, n = 20 \text{ participants, } P < 0.001 \)). Having previously focused on the item to be retrieved, in informative retro-cue trials, the probe provided only redundant information for selecting the relevant memorandum. Thus, this gaze bias seems to reflect the process of item selection and focusing that occurs when the item to be selected is not already in the internal focus of attention. This is also in line with the observation that the observed gaze bias is relatively transient, even after informative retro-cues that require the item to be held in the sustained focus of attention throughout the second retention period (Fig. 2c). This gaze bias therefore marks the focusing of attention rather than the focused attentional status of an item per se.

Under this focusing account, the observation of residual gaze bias after the probe (in informative retro-cue trials) may reflect the occasional failure to use the retro-cue effectively to place the retro-cued item in the focus of attention. To investigate this possibility, we sorted informative retro-cue trials into quartiles according to cue benefit, as indexed by response-onset times, given that the largest effect of informative retro-cues was observed on response times (Fig. 2b). Figure 2d shows that slower trials indeed showed a reduced average gaze bias (peak bias of 1.585% for the slowest trials, compared to 4.12% for the fastest trials) following the informative retro-cues (cluster-based permutation test of the sum of \( t \)-values of the parametric effect across time points: \( \sum T = -3,067.3, 95\% \text{ CI} \) of \( d \) between \(-1,091.1\) and \(1,129.3, n = 20 \text{ participants, } P = 0.002 \); light blue horizontal line in Fig. 2d). The gaze bias that follows the retro-cue thus marks the success of this cue to facilitate subsequent performance by reducing the need to (re-)focus on the to-be-reported item after the probe.

Heat maps of the retro-cue-induced gaze bias in the 400–1,000 ms window after the informative retro-cue (Fig. 2e) confirmed the same nature of this bias as in experiment 1. The heat maps further demonstrate that this bias occurs along both the horizontal and vertical planes, thus adhering to a two-dimensional spatial layout of visual working memories. As in Fig. 1f, this only became clear after subtracting the common part from all four heat maps (see Supplementary Fig. 4 for a comparison of heat maps before and after common-part subtraction).

Experiments 1 and 2 show that attentional selection from working memory leads to involuntary gaze shifts. In experiment 3, we asked whether the reverse can also be demonstrated: whether involuntary (by which we mean not deliberate or goal-directed) gaze shifts can also trigger the attentional selection of an item in visual working memory. To this end, we introduced a task manipulation to induce a small gaze shift during the retention period. We did this by temporarily displacing the fixation cross for 500 ms slightly towards (congruent) or away from (incongruent) the memorized location of the item that would subsequently be probed, before repositioning it in the centre (Fig. 3a). Fixation displacements were never predictive of which item would be probed. We chose the magnitude of this fixation displacement (0.5 dva; 7.5% towards the centre of either bar) to render gaze shifts comparable to those observed during attentional selection of items from working memory (see Fig. 1c and Supplementary Fig. 2). If gaze shifts of this order were sufficient to trigger attentional selection of the side-congruent item, then we predicted that congruent fixation displacements should act similarly to informative retro-cues: facilitating performance (compared to incongruent trials) and reducing the subsequent gaze bias after the probe (as following informative retro-cues in experiment 2).

Figure 3c shows that the fixation displacement manipulation yielded a reliable gaze shift towards (congruent) or away from (incongruent) the item that would subsequently be probed (for example, comparing the average towardness in the period between fixation displacement and probe onset yielded a highly reliable difference: \( t_{19} = 11.197; P < 0.001, d = 2.504, 95\% \text{ CI} \) of \( d \) between \(1.593\) and \(3.39\)). This was the case even though participants were instructed to ignore this displacement. Despite the successful implementation of the manipulation, we did not observe either of the predicted effects. Performance was virtually indistinguishable between congruent and incongruent trials (Fig. 3b; errors: \( t_{19} = -0.564, P = 0.579, d = -0.126, 95\% \text{ CI} \) of \( d \) between \(-0.565\) and \(0.316\)) and response times were slightly (although not significantly) longer for congruent trials (\( t_{19} = 1.553, P = 0.137, d = 0.347, 95\% \text{ CI} \) of \( d \) between \(-0.109\) and \(0.158\)).
Complementing this absence of the predicted performance effect, we also found no evidence for the predicted reduction of gaze bias following the congruent probe (Fig. 3c).

These data suggest that involuntary gaze shifts of comparable magnitude to those observed during attentional item selection may be insufficient to cause the type of attentional shifts that bring an
Involuntary gaze shifts are insufficient to trigger attentional facilitation in visual working memory. a. Task schematic of experiment 3. Experiment 3 involved the same orientation reproduction working memory task as experiments 1 and 2, but with a fixation displacement manipulation during the delay period. Fixation displacements were equally often in the same (congruent) or opposite (incongruent) directions as the memorized location of the to-be-probed item and were therefore uninformative. b. Average reproduction errors and response onset times for trials with congruent and incongruent fixation displacements. Paired-samples t-tests; errors: $t_{9} = -0.564$, $P = 0.579$, $d = -0.126$, 95% CI of $d$ between $-0.565$ and $0.316$; response onset times $t_{9} = 1.553$, $P = 0.137$, $d = 0.347$, 95% CI of $d$ between $-0.109$ and $0.795$. c. Gaze bias towards the memorized location of the probed item for trials with congruent and incongruent fixation displacements. Horizontal bars indicate significant temporal clusters; cluster-based permutation tests of the sum of t-values across time points; congruent: $\sum t = 11,700$, 95% of permutations between $-1,506.8$ and $1,549.3$, $P < 0.001$; incongruent: $\sum t$ left cluster $= -7,360.3$, $\sum t$ right cluster $= 3,037.8$, 95% of permutations between $-1,629.8$ and $15,75.3$, $P$ left cluster $< 0.001$, $P$ right cluster $= 0.002$. Conventions as in Fig. 1. Error bars and shaded areas in b and c represent ±1 s.e.m. ($n = 20$).

These data nevertheless help convey our main contribution, which is the demonstration of a directional gaze bias during the attentional focusing of items in visual working memory. Namely, the data re-confirm that this bias is highly replicable and show that it occurs even when the eyes have only just returned from a previous gaze shift.

In experiments 1–3, participants received a colour probe that indexed the relevant memory item, and were asked to retrieve and report its memorized orientation. Although item orientation was independent of item location (the latter being the key variable in our gaze analyses), it may be that the gaze bias effect is specific to cases in which individuals are asked to retrieve and report orientation. For example, orientation could be particularly strongly coupled to information about spatial location, provided orientation is itself also a spatial feature. Alternatively, the gaze bias may reflect a general phenomenon that occurs whenever individuals retrieve and report features of items in visual working memory, even when these features are intrinsically non-spatial, such as colour.

To test the generality of the gaze bias effect, in experiment 4 (Fig. 4a), we added a condition that reversed the roles of item colour and orientation as features used for cueing and reporting. In the new ‘colour blocks’, participants viewed two bars of distinct orientations and reproduced the colour of the item that was probed through its orientation. We compared this with the ‘orientation blocks’, in which participants reported the orientation of the item probed through its colour (as in experiments 1–3). For comparability, items in orientation blocks (Fig. 4a, top) had 2 unique colours (green and purple) and were drawn from 180 unique colours, whereas items in colour blocks (Fig. 4a, bottom) had 2 unique orientations (vertical and horizontal) and were drawn from 180 unique colours. We found no statistically significant difference in reproduction errors between orientation and colour reports (Fig. 4b; $t_{9} = 0.579$, $P = 0.567$, $d = 0.126$, 95% CI of $d$ between $-0.565$ and $0.315$), although response onset times for colour reports were slower than for orientation reports (Fig. 4b; $t_{9} = 6.935$, $P < 0.001$, $d = 1.551$, 95% CI of $d$ between $-0.885$ and $2.198$).
Fig. 4 | Gaze bias generalizes across visual features. a, Task schematic of experiment 4. Experiment 4 consisted of two types of blocks. Orientation blocks involved the same orientation-reproduction working-memory task as experiments 1–3. In colour blocks, the roles played by item colour and orientation were reversed; orientation (vertical or horizontal) was used to probe the to-be-selected memory item, of which participants were required to report the colour. b, Average reproduction errors and response onset times for blocks with orientation and colour reports. Paired-samples t-tests; errors: t_8 = −0.565, P = 0.579, d = −0.126, 95% CI of d between −0.565 and 0.315; response onset times: t_8 = 6.935, P < 0.001, d = 1.551, 95% CI of d between −0.885 and 2.198. c, Gaze bias towards the memorized location of the probed item for blocks with orientation and colour reports. Horizontal bars indicate significant -values across time: orientation reports: \( \sum T = 3,522.5 \), 95% of permutations between −1,000.6 and 1,053.8, \( P < 0.001 \); colour reports: \( \sum T = 4,065.3 \), 95% of permutations between −988.6 and 978.1, \( P < 0.001 \). Conventions as in Fig. 1. Error bars and shaded areas in b and c represent ± s.e.m. (n = 20).

The main result in experiment 4 is that the identified gaze bias was similarly observed when participants reported memorized colour (orange time course in Fig. 4c; cluster-based permutation test of the sum of -values across time: \( \sum T = 4,065.3 \), 95% of permutations between −988.6 and 978.1, \( n = 20 \) participants, \( P < 0.001 \)). Moreover, this gaze bias was at least as prominent and robust for colour as it was for orientation (Fig. 4c), with no significant differences between block types (no clusters found). The identified gaze bias—which depends on the memorized location of the probed item—thus generalizes across the retrieval of orientation or colour of the memory item at that location.

Our results show that focusing attention on an item within the spatial layout of working memory involves the oculomotor system of the brain, with consequences that can be traced all the way to the eyes and be used to predict subsequent performance benefits. These findings expand the attentional role of the oculomotor system to the internal space of memory and carry relevant implications for the study, as well as our understanding, of the neural mechanisms by which our brains flexibly prioritize information in memory to serve adaptive behaviour.

In the domain of perception, the deployment of spatial attention has previously been shown to increase the propensity of small fixational gaze shifts (microsaccades) in the direction of covertly attended locations outside of current fixation\(^{28,29}\); this may be critical for attentional facilitation to occur\(^{29}\). This has been interpreted as an inadvertent spillover effect\(^{17,27}\) from activating oculomotor brain areas (such as the frontal eye field and superior colliculus) that are recruited for both spatial attention and gaze. In the context of perception, however, it remains possible that such gaze behaviour reflects the sub-threshold consequence of the urge to look at the attended (or expected) item when explicitly instructed not to do so. Here, we demonstrate a similar gaze bias within the context of visual working memory, where there was nothing to look at (or expected) in the direction of the bias. These data therefore not only imply a role for the oculomotor system in focusing attention within the internal space of memory, but also show that such oculomotor engagement leaves peripheral traces even when there is no incentive for the traces (see ref. \(^{17}\) for discussion of such peripheral traces).

Memory-based ‘looking at nothing’ (see ref. \(^{17}\) for review) has previously been reported in the contexts of long-term memory retrieval\(^{28}\), visual imagery\(^{22,24,25}\) and semantic comprehension\(^{21,24}\). Our data provide a clear example of memory-based gaze behaviour in the context of visual working memory. In contrast to earlier work, however, gaze behaviour in our task did not involve revisiting
previously occupied locations, but was constituted by gaze shifts of much smaller magnitudes (thus being more in line with the microsaccade propensity biases discussed; although we do not rule out the possibility that ocular drifts, previously may contribute to the observed gaze position bias as well). In this sense, our observations reflect a looking-towards-nothing, rather than a looking-at-nothing, phenomenon. Moreover, unlike previous accounts, our data revealed that the identified gaze bias was not the consequence of the automatic co-activation of the ‘spatial tag’ of an item that occurs whenever an item is retrieved (probed) from memory. Instead, our bias depended on the need to bring the item into the internal focal region of attention. Whether internal focusing may also account for previous demonstrations of looking-at-nothing remains an interesting possibility to be investigated.

We observed the spatial gaze bias even though participants were not questioned on item location. Participants were asked to reproduce the orientation of the item that was probed through its colour, or the colour of the item that was probed through its orientation. In principle, colour-orientation bindings were thus sufficient to perform well on our working memory tasks. The fact that gaze became biased as the direction of incidental memory locations implies that the locations were nevertheless retained in memory and were used to select and focus attention on the appropriate item. This therefore provides compelling evidence for a grounding role of spatial location in organizing, as well as accessing and prioritizing, visual working memories (see also refs. 16–36 for further evidence supporting such a grounding role). It also shows that the oculomotor system is utilized for visual working memory (as also demonstrated in refs. 16–36), even when spatial location is not the target memory attribute.

In addition to these conceptual advances, these data also carry relevant practical implications. They show that gaze behaviour can provide a reliable and real-time proxy for attentional focusing in visual working memory, and can even predict the degree to which one benefits from such focusing for guiding subsequent behaviour. The real-time nature of this measure—capturing attentional focusing while it occurs—complements traditional measures of accuracy and reaction time that only provide a single value at the end of each trial. This provides a new, non-invasive way to investigate the involvement of the human oculomotor system in visual working memory, as well as the associated spatial grounding of this fundamental memory system.

Methods
Experimental procedures were reviewed and approved by the Central University Research Ethics Committee of the University of Oxford.

Participants. We present eye-tracking data from four complementary experiments. Data from experiment 1 are from an electroencephalography (EEG) study that investigated electrophysiological brain activity associated with working-memory-guided action1. Here, we report complementary eye-tracking data from this experiment that were not part of the original article. Twenty-five human volunteers participated in experiment 1 (age range 19–36 years, 11 male, 2 left-handed). Sample size for experiment 1 was set based on our planned EEG analysis. No statistical methods were used to pre-determine sample size, but our sample size was chosen to be similar to those reported in previous publications from the lab that focused on similar neural signatures (for example, ref. 14). For the current eye-tracking analysis, data from two participants were excluded due to poor eye-tracking quality. Experiments 2–4 were specifically designed to follow-up the eye-tracking results of experiment 1. Because the identified gaze bias in experiment 1 was so robust, we set the sample size to 20 in experiments 2–4 (experiment 2: age range 22–40 years, 9 male, 0 left-handed; experiment 3: age range 19–32 years, 8 male, 2 left-handed; experiment 4: age range 18–37 years, 6 male, 0 left-handed). In experiment 3, one participant was excluded and replaced due to repeated eye closure during the experiment. Participant sampling was performed separately for each task. All participants had normal or corrected-to-normal vision. Participants provided written consent before participation and were reimbursed £15 per hour for experiment 1 (which included EEG) and £10 per hour for experiments 2–4.

Task essentials. All four experiments involved the same basic visual working memory task in which participants memorized the orientation and colour of multiple visual bars to reproduce the orientation (experiments 1–4) and colour (experiment 4) of one bar after a working memory delay. Bars were centred at a viewing distance of 5.7 dva and were 5.7° in length and 0.8° in width. The to-be-reported bar was indicated by a change in colour (experiments 1–4) or shape (experiment 4) of the central fixation cross (the memory probe). In experiments 1–3, bars had unique colours that were drawn from a set of four (green, purple, orange and blue), whereas in experiment 4 bars were drawn either from a set of two colours (green and purple; report orientation blocks) or from a set of 180 colours (report colour blocks, detailed below). Each bar in a display was equally likely to be probed (either retro-cued before the probe, as in experiment 2, independent of its colour, orientation or location. Participants had unlimited time after the memory probe before response initiation. The response dial consisted of a circle (5.7 dva in diameter) with two small circular handles that could be re-aligned to match the memorized orientation (experiments 1–4) and colour (experiment 4) of the probed bar. Dial-up was performed with either the keyboard (experiment 1) or the mouse (experiments 2–4), as further detailed below. The response dial angle was recorded on the screen only at response initiation and was always positioned around the fixation cross. Bar colour and orientation were always independent of bar location, and participants were never explicitly questioned about bar location. Participants received feedback immediately after response termination by changing the colour of the fixation cross to green for 200 ms for reproduction errors less than 20°, and to red otherwise. A custom gaze calibration module was inserted after every task block. Participants were instructed to look at a small white calibration point that was re-positioned every 1–1.5 s to 1 of 7 positions that were visited in a randomized order. Distance-positions used were left-top, left-middle, left-bottom, right-top, right-middle and right-bottom, as well as the centre of the screen (see also Supplementary Fig. 3). Calibration positions were set to 5.7 dva in the horizontal and the vertical axes, corresponding to the centres of the bars used in the memory tasks.

Task variations. Experiment 1 (Fig. 1a) involved the most basic task with no additional manipulations, whereas experiment 2 incorporated a retro-cue manipulation (Fig. 2a), experiment 3 incorporated a fixation displacement manipulation (Fig. 3a), and experiment 4 included blocks in which participants reported the colour of the probed item as opposed to its orientation (Fig. 4a).

The retro-cue manipulation in experiment 2 involved a transient (200 ms) colour change of the fixation cross that occurred in the middle of the retention interval (see Fig. 2a for exact intervals). The fixation cross either changed from black to a colour (corresponding to one of the four bars: red, blue, green or purple) or remained black (neutral retro-cue). Informative retro-cues informed with 100% validity that the colour-matching bar would be probed after the second delay. Neutral cues were uninformative. Informative and neutral retro-cues were equally likely and were randomly intermixed across trials. The fixation displacement manipulation in experiment 3 also occurred in the middle of the retention interval (Fig. 3a) and involved a temporary (500 ms) displacement (0.5 dva) of the fixation cross to either the left or the right. After displacement, the fixation cross was repositioned in the centre. Fixation displacements were not predictive of which bar would subsequently be probed as they were equally likely to be in the same (congruent) or opposite (incongruent) direction as the memorized location of the to-be-probed bar. Congruent and incongruent trials were randomly intermixed. Finally, experiment 4 consisted of two types of blocks, which were randomly intermixed. In orientation blocks, participants were asked to report memorized bar orientation following a colour change of the fixation cross (as per experiments 1–3). One bar was always green and the other purple, and bar orientations were randomly determined in colour blocks, detailed below. Each bar was located in the central fixation cross (the memory probe). In experiments 1–3, bars were drawn from a circular (CIELAB-based) colour space with 180 distinct colour values. In these blocks, the probe consisted of a shape change (turning the fixation cross to a ‘□’ or ‘—’), and participants reported the colour of the shape-matching item on a mirror-symmetrical colour wheel (Fig. 4b). We used horizontal and vertical bar and probe orientations as these are neutral with respect to left–right gaze biases, and a mirror-symmetrical colour wheel to increase comparability with the orientation report.

There were also some subtle differences in settings between experiments. However, because we observed the same qualitative gaze bias across the four experiments, these variations do not seem to be essential for this bias to be manifest, and we therefore mention them only briefly. In experiment 1, bars were oriented between ±20° to ±70° (avoiding 20° from horizontal and vertical), whereas in experiments 2–4 they spanned from 0° to ±90° (full circle). In experiment 1, one bar was always oriented to the left and the other oriented to the right (although bar orientation and location remained orthogonal across trials), whereas in experiments 2–4, bar orientations were drawn independently from each other. Experiment 1, bars faced 1, 3 and 4 always in the same order. In experiment 2, bars were always positioned to the left and right of the fixation cross (at 5.7 dva), whereas experiment 2 contained 4 bars positioned in the 4 quadrants of the screen (at 5.7 dva in the horizontal and vertical axes). Bars were presented at encoding for 250 ms in experiments 1, 3 and 4, but for 500 ms in experiment 2. In experiment 1, orientation dial-up was performed by holding down 1 of 2 keys on the keyboard (the ‘/’ key to rotate the dial leftward and the ‘?’ key to rotate the dial rightward) and the response was terminated at key release. In experiments 2–4, the mouse (operated with the dominant hand) was used for dial-up, and the response was terminated when the left mouse button was...
pressed (or after the maximum dial-up time of 2,500 ms after response initiation). The dial always started from the vertical (upright) orientation in experiment 1, and from a random orientation in experiments 2–4. Exact intervals differed between experiments (see task schematics in Figs. 1–3). Experiment 1 contained two consecutive sessions of 1 h (with a 15 min break), whereas experiments 2–4 each involved one session that lasted 1–1.5 h. In experiments 1–3, sessions always contained 10 blocks, whereas experiment 4 contained 14 blocks (7 orientation blocks and 7 colour blocks). Blocks contained 60 trials each (0.67 s per trial, and 50% of trials total), we collected 1,200 trials in experiment 1, 500 trials in experiment 2, 600 trials in experiment 3, and 840 trials in experiment 4 (per participant).

Randomization. All four experiments used within-subjects designs. We did not compare results across experiments. Within each experiment, probed item location was always fixed across trials, whereas one cue variable (normative versus neutral) in experiment 2 and the congruency of fixation displacement in experiment 3. The colour task and the orientation task in experiment 4 were randomized across blocks. Before randomization, all conditions of interest were set to have equal trial numbers. Data collection and analysis were not performed blinded to the conditions of the experiments.

Eye-tracking acquisition. Participants sat in front of a monitor (with a 100 Hz refresh rate) at a viewing distance of approximately 95 cm with their head resting on a chin rest. An eye tracker (EyeLink 1000, SR Research) was positioned on the table approximately 15 cm in front of the monitor. During the task, gaze was continuously tracked for both eyes simultaneously, at a sampling rate of 1,000 Hz. Before acquisition, we calibrated the eye tracker using the built-in calibration and validation protocols from the EyeLink software.

Eye-tracking analysis. Eye-tracking data were first converted from edf to asc format, and subsequently read into MATLAB using the FieldTrip analysis toolbox6. Eye blinks were detected and interpolated (±100 ms around identified blinks) using a spline interpolation procedure, using custom code. While blink correction increased signal quality, we observed the identified gaze bias even before any such correction. After blink correction, data from the left and the right eye were averaged, yielding two channels per trial: one containing the time course of horizontal gaze position (x channel) and the other of vertical gaze position (y channel). We epoched data around probe onset, response onset and calibration point onset.

Our main analysis focused on gaze position. Position data were normalized using the data from the custom calibration modules. We obtained the median gaze position values (in both x and y channels) that were associated with each of our 7 gaze calibration positions (Supplementary Fig. 3), considering gaze position values from 500–1,000 ms after each calibration point displacement. These empirical gaze values corresponded to the values that would be obtained if participants looked at the centre of the memory items. Accordingly, we defined these values as ±100% (corresponding to ±5.7 dva). Calibration values were found separately for each participant and were used to normalize the single-trial gaze position data during the task. To enhance interpretability, we report both percentage and dva values in all relevant graphs.

Task modulations of gaze position were first identified (in experiment 1) by comparing trial-averaged normalized gaze position time courses between conditions in which the probed memory item occupied the left or the right position during encoding. To increase sensitivity and interpretability, we also constructed a measure of towardness that expressed the gaze bias towards the memorized location of the probed bar in a single value. In experiments 1, 3 and 4 (with 1 left and 1 right item), towardness was defined as the average gaze position in the x channel following probes of right memory items minus left memory items, divided by 2. For experiment 2 (with 1 item in each quadrant), this also involved the complementary quantification in the y channel (for top and bottom item positioning), and the averaging of the x and y channels towardness values. Before averaging across participants, gaze time courses were smoothed by a Gaussian kernel with a 10 ms s.d.

For visualization purposes, we also constructed heat maps of gaze density. Within a desired time window of interest, we created two-dimensional histograms of gaze position, aggregating gaze position values within this time window from all trials (not averaging over time points or trials). To express this as a density, gaze position counts were divided by the total number of gaze position samples that entered the analysis. Two-dimensional histograms were obtained at a 1% x 1% spacing, ranging from −150% to +150% (in normalized space). Before averaging across participants, maps were warped using a 10% x 10% rectangular box car. To zoom in on the gaze biases of interest that depended on memorized item location, we also subtracted gaze density values that were shared between conditions in which the probed memory item had different locations. This removed values associated with the average gaze density following probing of left and right items in experiment 1 and following probing of all quadrant items in experiment 2 to some extent (though not on the difference between them).

In addition to gaze position, we also quantified gaze shifts, focusing on shifts along the horizontal axis (x channel) in experiment 1. To identify shifts, we took the absolute value of the temporal derivative of gaze position and defined samples that exceeded 10 times the median value as a shift. To avoid the same shift being counted multiple times, we imposed a minimum delay of 200 ms between successive gaze shifts. Shift magnitude was defined as the difference in normalized gaze position between the 50 ms period preceding the identified shift sample and the 50–100 ms period after this sample (after minus before). Because gaze shifts were directional, we could label them as towards or away from the memorized location of the probed memory item. Identified gaze shifts with an estimated magnitude smaller than 1% (that is smaller than 0.057 dva) were considered noise and therefore not considered further (although these may still have contributed to the average gaze position bias quantified in our main analyses). We calculated gaze shift density (quantified as number of shifts per trial, at a given magnitude) as a function of shift magnitude by including all gaze shifts identified within the desired time window for analysis. For magnitude sorting, we used successive magnitude bins (that were defined in our normalized space), ranging from 1–120% in steps of 1%. Similarly, we quantified gaze shift density as a function of time (Supplementary Fig. 2a), for which we used a sliding time window of 100 ms that we advanced in steps of 20 ms. Although we are aware that many of these parameters are relatively arbitrary, we note that highly similar patterns were obtained when using different settings for gaze shift identification, gaze magnitude estimation and gaze density quantification.

Statistical evaluation. Reproduction errors and response times were compared between conditions using paired samples t-tests. Reproduction errors were defined as the absolute difference (in degrees) between the orientation of the probed item and the reported orientation. Response onset times (in milliseconds) were defined as the time from probe onset to response initiation. Trials with response times with a z-score larger than four were removed before statistical evaluation.

Statistical evaluation of the gaze time courses was done using a cluster-based permutation approach . This approach is ideally suited for evaluating physiological effects across multiple data points (in our case, gaze position data across time). This approach effectively circumvents the multiple-comparisons problem by evaluating clusters in the observed group-level data against a single permutation distribution of the largest clusters that are found after random permutations (or sign-flipping) of the condition-specific trial-averaged data at the participant level. We used 10,000 permutations and used the default cluster settings of the FieldTrip analysis toolbox. Specifically, we clustered adjacent time points whose univariate (uncorrected) t-statistic of interest was significant (two-sided, alpha level of 0.05), and calculated our cluster statistic as the sum of all t-values in each cluster. After each permutation, the largest cluster was defined as the cluster with the largest summed t-value. When the data before permutation contained more than one cluster, each observed cluster was evaluated under the same permutation distribution of the largest cluster.

Inferential statistical evaluations of gaze were all based on the towardness time courses of gaze position. We also quantified densities of gaze position and gaze shifts in selected time windows that were identified in the towardness analysis. These follow-up analyses served only to characterize (in a descriptive sense) the nature of the identified gaze position bias.

All reported measures of spread involved ±1 s.e.m. calculated across participants. All inferences were two-sided at an alpha level of 0.05 (0.025 per side). Confidence intervals of effect sizes (Cohen’s d) were calculated using the toolbox described in ref. 3. Data distributions were assumed to be normal, but this was not formally tested.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Code availability
Code is available from the authors on reasonable request.

Data availability
All data are publicly available through the Dryad Digital Repository at: https://doi.org/10.5061/dryad.m99r286.

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Author contributions

F.v.E. and A.C.N. conceived and designed the experiments. F.v.E. programmed the experiment 4. F.v.E. also wish to thank A. Board and R. Silva Zunino for their help with the data collection of experiment 4.

Competing interests

The authors declare no competing interests.

Additional information

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- Neurobs Presentation version 18.3 07.18.16
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Study description
Quantitative Eyetracking study

Research sample
Data from experiment 1 came from an electroencephalography (EEG) study with the original purpose to study electrophysiological brain activity associated with working memory guided action (van Ede et al., under review). Here, we report the complementary eye-tracking data from this experiment that were not part of the original article. Twenty-five human volunteers participated in experiment 1 (11 male, age range 19-36, 2 left handed). No statistical methods were used to pre-determine sample size, but our sample size was chosen to be similar to those reported in previous publications from the lab that focused on similar neural signatures. For the current eye-tracker analysis, data from two participants had to be excluded due to too poor eye-tracking quality. Experiments 2-4 were specifically designed to follow-up the eye tracking results of experiment 1. Because the identified gaze bias in experiment 1 was so robust, we set the sample size to 20 in experiments 2-4 (experiment 2: 5 male, age range 22-40, 0 left handed; experiment 3: 8 male, age range 19-32, 2 left handed; experiment 4: 6 male, age range 18-37, 0 left handed). One participant kept closing the eyes during experiment 3 and was replaced. Participant sampling was performed separately for each task. All participants had normal or corrected-to-normal vision. Nearly all participants were undergraduate students at the University of Oxford or at Brookes University.

Sampling strategy
In each experiment, we used a within-subjects design with random participant sampling. Sample sizes were set as described above.

Data collection
Eyetracking data were collected using an Eyelink 1000 Eyetracker, and stored by a computer. Behavioural task-responses were collected and stored by another computer. The experimenter was aware of the experimental aims during experiment 2-4, but not during experiment 1. The main aims in experiment 1 regarded the neural dynamics of memory guided action (as tracked using EEG) and the observations regarding gaze behavior, that we report on here, involved an incidental discovery at that stage.

Timing
April 2017 to June 2018

Data exclusions
Two participants were excluded from experiment 1 due to too poor eye tracking quality (eyetracking not being the main aim of the study). 1 participant was replaced in experiment 3, as this participant kept closing the eyes during the experiment.

Non-participation
No participants dropped out or declined participation.

Randomization
The study did not contain experimental groups as each task involved a within-subjects design. Probed item location was always randomised across trials. All other within subject variables (retro-cue presence in experiment 2, congruency of fixation displacement in experiment 3, and colour/orientation task in experiment 4) were randomised across trials (experiments 2 and 3) or blocks (experiment 4). Before randomisation, all conditions of interest were set to have equal trial numbers.

Reporting for specific materials, systems and methods
Materials & experimental systems

| n/a | Involved in the study |
|-----|-----------------------|
| ✔️  | Unique biological materials |
| ✔️  | Antibodies |
| ✔️  | Eukaryotic cell lines |
| ✔️  | Palaeontology |
| ✔️  | Animals and other organisms |
| ✔️  | Human research participants |

Methods

| n/a | Involved in the study |
|-----|-----------------------|
| ✔️  | ChiP-seq |
| ✔️  | Flow cytometry |
| ✔️  | MRI-based neuroimaging |

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Population characteristics See research sample above.

Recruitment Participants were recruited through flyers and an online participant database (SONA) at the University of Oxford.