Jointly looking to the past and the future in visual working memory

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ABSTRACT

Working memory enables us to bridge past sensory information to upcoming future behaviour. Accordingly, by its very nature, working memory is concerned with two components: the past and the future. Yet, in conventional laboratory tasks, these two components are often conflated, such as when sensory information in working memory is encoded and tested at the same location. We developed a task in which we dissociated the past (encoded location) and future (to-be-tested location) attributes of visual contents in working memory. This enabled us to independently track the utilisation of past and future memory attributes through gaze, as observed during mnemonic selection. Our results reveal the joint consideration of past and future locations. This was prevalent even at the single-trial level of individual saccades that were jointly biased to the past and future. This uncovers the rich nature of working memory representations, whereby both past and future memory attributes are retained and can be accessed together when memory contents become relevant for behaviour.

INTRODUCTION

Working memory is a fundamental cognitive function that enables us to hold onto past sensory information in service of upcoming future behaviour [1,2]. Accordingly, by its very nature, working memory is concerned with two components: the past and the future.

In conventional laboratory tasks, past and future components are often conflated such as when sensory information in working memory is tested at the same location as where it was encoded. By contrast, in the dynamic situations we face every day, sensory information often disappears at one specific location (where it enters visual working memory) but becomes relevant at another location (as also in [3–5]). Imagine trying to capture a photograph of a precious bird species that you just saw disappear behind a building. Your working memory of the bird is likely to consider not only where you last saw the bird, but also where you expect it to re-appear to capture it on camera. Such situations raise an interesting, underexplored question: when past and future locations of memory contents are not the same, does the brain code internal representations with regard to past, future, or both?

To address this question, we developed a task in which we dissociated the encoding (past) and to-be-tested (future) locations associated with visual representations in working memory. This enabled us to experimentally isolate past and future memory attributes and to track their respective utilisation through spatial biases in gaze behaviour in healthy human volunteers.

RESULTS

Twenty-five human volunteers performed a working-memory task in which visual memory items were encoded and tested at different locations (**Fig. 1a**). Participants memorised two coloured gratings with different orientations presented either vertically or horizontally. The crucial manipulation was that we always tested memory content in the orthogonal axis and at a predictable location (depending on the future rule that we varied across sessions; see **Supplementary Fig. 1** for the four possible rules).

After a delay period, we cued the relevant memory item by changing the colour of the central fixation dot. At this stage, participants were required to select the colour-matching grating from working memory in order to compare it to the upcoming test stimulus (clockwise/counter-clockwise judgement). Crucially, we always presented two stimuli at the test-phase of which only one was relevant, as determined by the future rule. For example, in **Figure 1a**, after the green memory item is cued, the relevant test stimulus will be the right stimulus, given the future rule (top item tested on right) in this session.

Participants were able to perform this dynamic visual working-memory task, with an average accuracy of 70±2 percent correct (mean ± SEM) and an average reaction time of 1218 ± 125 ms.

Gaze reveals the use of both past and future memory attributes that are considered at overlapping time windows

To track the utilisation of past and/or future locations associated with working memory contents, we tracked spatial biases in gaze following the cue to select either memory item. Specifically, we focused on directional biases in saccades, that we have previously shown to be sensitive to selective spatial attention [6–8], even when directed internally [9–11].

As shown in **Figure 1b**, after cue onset, saccades became biased in the direction of the encoded (past) location of the selected memorized target, as demonstrated by significantly more gaze shifts toward vs. away from the encoded location of the target (**Fig. 1b**; cluster $P < 0.001$), starting from around 200 ms after the cue. This is consistent with our prior demonstrations of directional eye-movement biases within the spatial lay-out of working memory [9–11]. In our current task, this uniquely reveals how the retention of items in working memory continues to rely on their past encoded locations, even if items are known to become relevant (tested) at another location.

Having established that past (encoded) memory locations were still utilised by participants in our task (despite us never asking about memory-item locations), an interesting question becomes when the future memory attribute (test location) would be considered after the selection cue. Intuitively, participants may select the relevant item at its past location, before considering the relevant future test location – which would yield a serial pattern of past-before-future. In contrast, as shown in **Figure 1c** and **d**, we found a similar saccade bias to the relevant future location (**Fig. 1c**; cluster $P < 0.001$). Strikingly, this future bias also emerged early after the cue. An overlay of the spatial biases (toward vs. away) in the orthogonally manipulated past and future axes (**Fig. 1d**), revealed consideration of past and future locations at overlapping time windows. Gaze biases in both axes were driven predominantly by microsaccades (**Supplementary Fig. 2**) and occurred similarly in horizontal-to-vertical and vertical-to-horizontal trials (**Supplementary Fig. 3**). These data thus suggest the joint consideration – or "activation" – of past and future memory attributes, at least when analysing past and future memory attributes separately. Below we provide additional single-trial (single-saccade) evidence for this interpretation.

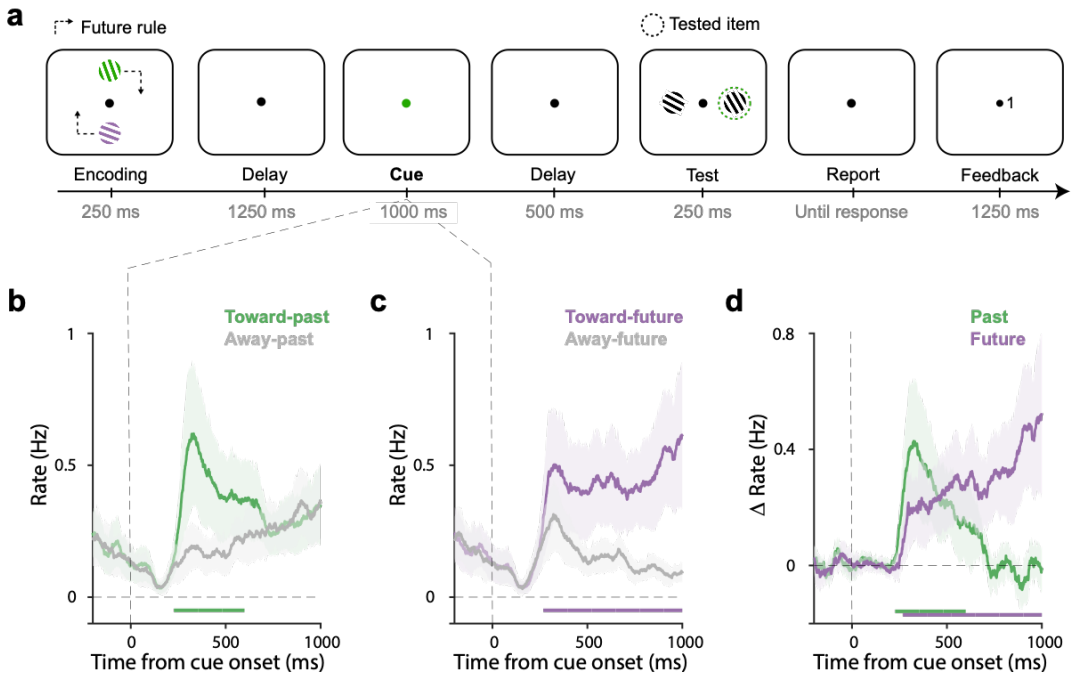

Figure 1. Directional gaze biases by past and future locations during mnemonic selection overlap in time. a) Task schematic. Participants memorised two oriented gratings with different colours presented either vertically or horizontally. Following a delay, a colour change of the central fixation dot prompted participants to select the colour-matching item from working memory to report its orientation later. After another delay, two test gratings appeared transiently and participants compared the cued memory grating to the relevant test grating (clockwise/counter-clockwise judgment) that was determined by the 'future rule' that was stable within each block. Dash lines serve to explain the association between the encoding and test locations and were never presented in the actual experiment. **b-c)** Time courses of gaze shift rates (number of saccades per second) for shifts toward and away from the encoded (panel b) and to-be-tested (panel c) locations. **d)** Overlays and comparisons of the difference in gaze-shift rates (toward minus away) for the past (encoded) location and the future (to-be-tested) location. Horizontal lines indicate significant temporal cluster (cluster-based permutation test, $P < 0.001$). Data are presented as mean values with shading reflecting 95% confidence intervals, calculated across participants ($n = 25$).

Individual saccades reveal truly joint consideration of past and future memory attributes

In principle, the observed joint activation of the past and future locations associated with the cued memory content in the trial-averaged and participant-averaged data could result from two alternative scenarios with different interpretations. First, either the past or the future alone may be considered in different trials and/or participants, without past and future memory attributes ever being considered together. Alternatively, participants may truly consider both past and future memory attributes jointly at the single-trial, single-saccade level.

While it is notoriously hard to disentangle the single-trial interpretation of averaged data [12], we were here able to do so by interrogating the individual saccade characteristics for which the two alternative scenarios make different predictions. In the first scenario, saccades should be biased to either the past or the future location, but there should be no dependency between them (i.e. a saccade may be biased to the past location regardless of the future location, and vice versa). In contrast, in the second scenario, with truly joint consideration of the past and future, there should be a clear dependency: it should be those saccades that are biased to the past that are also biased to the future. In other words, the future-biased saccades should predominantly be driven by the past-biased saccades, and vice versa.

To disentangle these alternatives at the single-trial level of individual saccades, we focused on the first saccades after the cue, in the 200-600 ms window. We previously identified this windows as the relevant window for microsaccade biases by internal selective attention [9], and this is also where we observed the overlapping past and future biases in the average here (see **Figure 1d**). To facilitate visualisation and quantification, we rotated all detected saccades to match a consistent coordinate

frame, in which the past location is represented horizontally (right=towards, left=away), and the future location vertically (top=toward, bottom=away; see **Fig. 2a**).

As shown in **Figure 2a**, the majority of first-detected microsaccades in our window of interest were made toward the past (right > left) and toward the future (top > bottom), replicating our prior analyses. Critically, this visualisation and quantification enabled us to disentangle the two alterative sketched above in which past and future saccades at the single-trial (individual-saccade) level were either independent (past bias regardless of future and future bias regardless of past) or dependent (joint past and future bias). Our data supported the latter.

Figure 2b shows the bias toward the past as a function of saccade direction with regard to the future. Likewise, **Figure 2c**, shows the future bias as a function of whether saccades were also biased to the past. In both cases, we see a clear dependency: the past bias is particularly pronounced for saccades that also have a future bias (**Fig. 2b**) and, vice versa, the future bias is most pronounced for saccades that also have a past bias (**Fig 2c**). This is perhaps best appreciated by the binarised quantification of these same data in **Figure 2d**: showing the percentage of identified first saccades toward or away from the future location, as a function of whether the same saccades were also biased toward or away from the past location. We found a clear interaction ($F(1, 24) = 18.1$, $P < 0.001$, partial $\eta^2 = 0.43$), whereby the bias toward the future location was exclusively observed for those saccades that were also biased toward the past location. Indeed, follow-up t-tests revealed no difference future bias for saccades that were away from the past ($t(24) = 1.13$, $P_{Bonferroni} = 1$, $d=0.23$), but a clear future effect for saccades that were toward the past ($t(24) = 4.65$, $P_{Bonferroni} < 0.001$, $d=0.93$). This would not be expected if single saccades cared exclusively about either the past or the future location. Instead, this provides single-trial-level support with the truly joint consideration of past and future memory attributes.

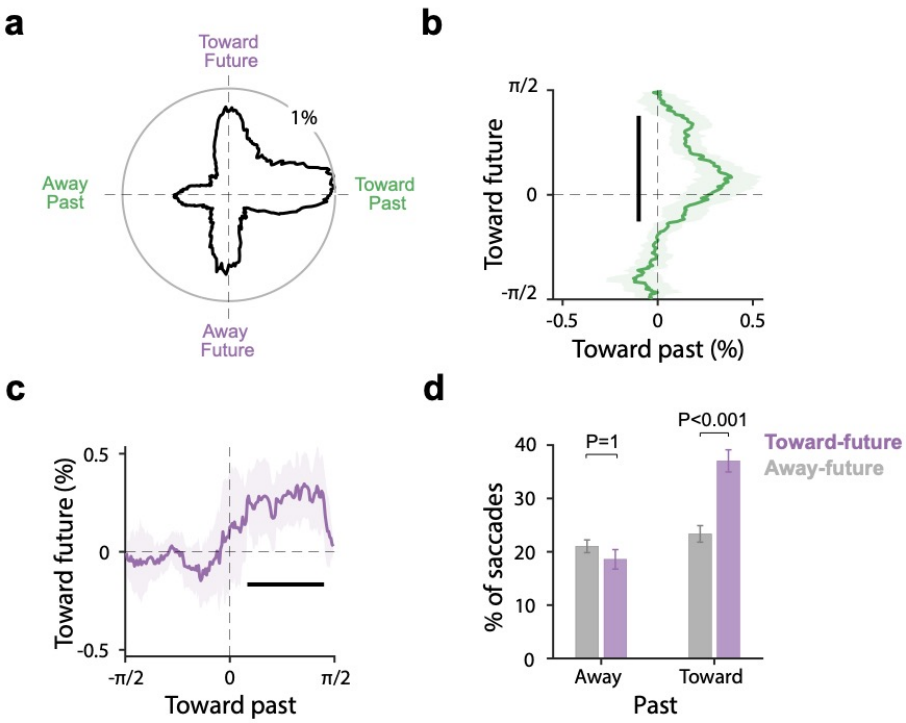

Figure 2. Individual saccades are jointly biased to past and future memory attributes. a) The distribution of the direction of the first saccades we detected after cue onset relative to past (horizontal) and future (vertical) locations. Data from the different sessions were rotated to match a common coordinate frame. **b)** The bias toward the past (x-axis) as a function of saccade direction with regard to the future (y-axis). **c)** The bias toward the future (y-axis) as a function of saccade direction with regard to the past (x-axis). In **b-c**, The bold black line indicates the significant temporal cluster (cluster-based permutation test, $P < 0.001$). Data are presented as mean values with shading indicating 95% confidence intervals, calculated across participants (n = 25). **d)** The percentage of identified first saccades toward or away from the future location as a function of whether the same saccades were also biased toward or away from the past location. Error bars in panel d indicate ±1 SEM calculated across participants (n = 25).

DISCUSSION

Here, we brought the study of visual working memory into a dynamic context by experimentally dissociating (orthogonalising) the past (last-seen location) and future (to-be-tested location) attributes of visual memory contents, and independently tracking the utilisation of these two attributes through gaze. Doing so, we unveil a novel, fundamental property of working memory – the joint availability and utilisation of past and future memory attributes. As such, our data provide key support for the proposal that memory is fundamentally future-oriented [2,13,14], while also reminding us that past memory attributes are not forgotten, even when these do not become relevant again.

Our finding of joint utilisation of past and future memory attributes emerged from at least two alternative scenarios of how the brain may deal with dynamic everyday working memory demands in which memory content is encoded at one location but needed at another. First, memory contents could have directly been remapped (cf. [3,15–17]) to their future-relevant location (in which case we should have only found a future gaze bias). Second, when dealing with multiple memory contents, contents could be stored at the past location at first and the future location could be considered only after relevant memory content has been selected (in which case the past bias should have *preceded* the future bias). In contrast, our data suggest that the brain simultaneously retains the copy of both past and future-relevant locations in working memory, and (re)activates each during mnemonic selection.

By capitalising on the discrete nature of saccades, we were able to demonstrate the truly joint consideration of past and future attributes, at the single-trial level. As such we were able to bypass a fundamental challenge of disentangling multiple potential single-trial interpretations when only having trial-average data available (for related discussions, see [12,18,19]). For example, when only considering the temporally overlapping past and future signals at the trial-average level, it was impossible to tell whether these joint effects resulted from a mix of trials and/or participants that relied on either the past *or* the future. By considering the discrete events – the individual saccades at the single-trial level – we could demonstrate how biases to the past and the future co-existed at the single-saccade level, supporting a truly joint consideration of past and future.

In current study, we tracked spatial attention using microsaccades. Compared to the commonly used online indicator of spatial attention, such as electrophysiological measures, microsaccades have important features that make them a promising complementary tool for uncovering the mechanisms of spatial attention [8,20], including when directed internally as we have shown here. First, as we have discussed above, microsaccades are discrete events, allowing to track spatial attention at the single-trial level. Second, microsaccades are not limited to tracking spatial attention toward the left or right visual field, as electrophysiology indicators often are. These two aspects were paramount to our demonstration of joint single-trial consideration of past and future memory attributes, and are likely to open additional doors for future investigations.

While the past gaze bias that we report here replicates our own prior studies [9–11], here we for the first time demonstrate a similar bias to the future-relevant memory location that is similarly driven by microsaccades. This signal may reflect either of two situations: the selection of a future-copy of the cued memory content or anticipatory attention to its the anticipated location of its associated test-stimulus. Either way, by the nature of our experimental design, this future signal is memory-content specific, as the two memory contents were always associated with opposite testing locations. Accordingly, our data reveal how this future feature can be accessed from memory together with the specific content that it is associated with, implying joint storage and utilisation of past and future memory attributes.

Our data complement other recent studies investigating visual working memory in more dynamic contexts [3,10,21–24], and showcase the rich nature of working memory representations. For example, akin to our finding of joint consideration of past and future locations in working memory, recent studies have uncovered the joint consideration of allocentric and egocentric spatial frames [23,25]. While storing memory content at a single location (or with reference to a single frame) would appear more intuitive and efficient, our data reveal an intriguing alternative. We speculate that the joint retention of multiple spatial attributes may make memories more robust, as well as more flexible for serving continuously evolving demands during everyday behaviour.

METHODS

Ethics. Experimental procedures were reviewed and approved by the local Ethics Committee at the Vrije Universiteit Amsterdam. Each participant provided written consent before participation and was reimbursed €10/hour.

Participants. Twenty-five healthy human volunteers participated in the study (age range: 20-27; 10 male and 15 female; 23 right-handed; 10 corrected-to-normal vision: 5 glasses and 5 lenses). Sample size of 25 was determined a-priori based on previous publications from the lab with similar experimental designs and that relied on the same outcome measure [9,10,26]). To achieve the intended sample size, three participants were replaced due to chance-level performance.

Stimuli and procedure. Participants performed a visual working memory task in which we orthogonalised the encoding and to-be-tested location in order to track the utilisation of past and future working-memory attributes.

Participants were required to encode and maintain two visual items (tilted coloured gratings) in working memory to later report one of their orientations (**Fig. 1a**). Each trial began with a brief (250 ms) encoding display in which two to-be-memorised gratings with different colours and orientations appeared vertically or horizontally on either side of the fixation dot, at 4 degrees visual angle. After a retention delay of 1250 ms, the fixation dot changed colour for 1000 ms. This colour change served as a 100% valid retro-cue, prompting participants to select the colour-matching target memory item. The retro-cue was followed by another retention delay of 500 ms, before the test display. The test display always contained two black gratings with different orientations that were presented vertically or horizontally on either side of the fixation dot (again at 4 visual degrees to each side). Based on a rule that described in the following paragraph, one of the black gratings was relevant to the task (the test grating), while the other merely served as a filler. After seeing the test display, participants were required to compare the cued memory grating to the relevant test grating and report whether the memory grating should be turned clockwise or counterclockwise rotated to match the relevant test grating in the test display.

In the encoding display, the gratings were randomly assigned two distinct colours: green (RGB: 133, 194, 18) and purple (RGB: 197, 21, 234) and two distinct orientations ranging from 0° to 180° with a minimum difference of 20° between each other. During the test display, the gratings are always black (RGB: 64, 64, 64). The relevant grating was always rotated 20 degrees in either a clockwise or counter-clockwise direction compared to the to-be-tested memory grating. The orientation of the irrelevant grating in the test display was chosen randomly.

The unique element of our task was that we dissociated the encoding and testing location by presenting the gratings in the test display on the orthogonal axis as where the items were presented on the encoding display. Relevant examples can be found in **Figure 1a** and **Supplementary Figure 1**. For example, if the two memory items appeared vertically at the top and bottom at encoding, the test gratings would appear horizontally to the left and right in the test display (see **Fig. 1a**).

To to-be-tested location was always linked to the encoded location by virtue of a future rule. For counterbalancing reasons, we used four unique rules that were presented across four sessions (**Supplementary Fig. 1**) and that always remained stable within a session. In rule 1: the two memory items were encoded vertically on the top and bottom. If the top memory item was cued, the relevant test grating would be on the right, while if the bottom item would be cued, the relevant test grating would be on the left in the test display. In rule 2, the mapping was reversed: the two memory items would again be encoded vertically, but this time if the top memory item would be cued the relevant test grating is on the left, while if the bottom item is cued the relevant test grating is on the right. Rules

3 and 4 follow the same logic, except that now the memory items are presented horizontally, and the test gratings vertically. Before every session, participants were notified of the future rule that applied to the upcoming session.

To ensure the use of the future rule, we made it task relevant by always presenting two test gratings in the test display of which only one was relevant: the one that matched the future rule (i.e., without applying the future rule, one would not know which test grating was to be used). It is for this reason that we consider the future location an attribute of the memory items, as each memory item was associated with its own unique test location.

In total, the study consisted of 4 sessions, that each contained 5 blocks of 32 trials each. At the start of each session, participants were notified of the session-specific future rule and then practiced the task with the current rule for 16 trials before starting the formal session. We did not include practice trials in our analyses. The study lasted approximately 70 minutes per participant.

Eye-tracking acquisition and pre-processing. Gaze was tracked from a single eye (right eye in all participants except 1 for which the left eye provided a better signal) using an EyeLink 1000 (SR Research) at a sampling rate of 1000 Hz. The eye tracker camara was positioned on the table ∼5 cm in front of the monitor and ∼65 cm away from the eyes. Gaze position was tracked continuously along the horizontal and vertical axes. Before recording, the built-in calibration and validation protocols from the EyeLink software were used to calibrate the eye tracker.

After recording, the eye-tracking data were converted from the original .edf to the .asc format and analysed in Matlab using the Fieldtrip analysis toolbox [27] in combination with custom code. Blinks were marked by detecting NaN clusters in the eye-tracking data. All data from 100 ms before to 100 ms after the detected NaN clusters were also set to NaN to eliminate residual blink artefacts. Finally, data were epoched from -1000 to +2000 ms relative to after the onset of the retro-cue.

Gaze-shift detection. We focused our analysis on spatial biases in gaze shifts (saccades/microsaccades). To identify gaze shifts, we employed a velocity-based method that we established in our prior studies [9,28], that builds on other velocity-based detection methods (e.g. [6]). First, gaze velocity was calculated by taking the Euclidean distance between temporally successive gaze-position values in the 2-dimensional plane (horizontal and vertical gaze position). Velocity was smoothed with a Gaussian-weighted moving average filter with a 7-ms sliding window (using the built-in function "smoothdata" in MATLAB). When the velocity exceeded a trial-based threshold of 5 times the median velocity, we marked the first sample after the threshold crossing as the onset of a saccade. To avoid counting the same saccade multiple times, a minimum delay of 100 ms between successive saccades was imposed. Saccade magnitude and direction were calculated by estimating the difference between pre-saccade gaze position (-50 to 0 ms before saccade onset) vs. the post-saccade gaze position (50 to 100 ms after saccade onset).

To focus our analysis on (micro)saccades that were driven by attention, we here focused on the "start microsaccade" defined as the saccade that moves gaze away from the fixation dot (as opposed to saccades that bring gaze back to fixation). We extracted start saccades using a method that we recently validated in another study [28]. For each detected saccade, we estimated the pre- and post-saccade distance from the central fixation dot. If the post-saccade distance was larger than the pre-saccade distance, we defined the saccade as a start microsaccade. To minimise the contribution of gaze drift, we defined gaze positions associated with looking at the central fixation dot using the median gaze position in the fixation period from [-0.8 to -0.2 ms] relative to cue onset.

Time courses of gaze-shift rates (in Hz) were quantified using a sliding time window of 50 ms, advanced in steps of 1 ms. We additionally decomposed shift-rates into a time-magnitude representation (as in

[9]), showing the time-resolved rate of attention-driven shifts (toward vs. away) per second, as a function of the saccade size (see **Supplementary Fig. 2)**. For magnitude sorting, we used successive magnitude bins of 0.2 visual degree in steps of 0.04 visual degree.

Individual shift level analysis. For our analysis at the single-trial, single-saccade level, we focused on the first start saccade observed during the 200-600 ms post-cue period that we have previously identified as the relevant time window for the effect of interest [9]. For all 'first saccades', we then looked at the spatial distribution of saccade directions relative to the relevant past (encoding) and future (to-be-tested) locations associated with the cued memory item. To facilitate visualisation and quantification, we rotated all detected saccades to a common coordinate system, in which the past location was represented horizontally (left=away, right=toward), and the future location vertically (top=toward, bottom=away).

To obtain the proportional distribution of saccades in this coordinate system (see **Fig. 2A**), we used successive angular bins of 20 degrees in steps of 1 angle degree and simply calculated the proportion of saccades in each angular bin (with angles being defined with reference to past and future locations).

To quantify whether saccades were jointly biased to the past and future (as opposed to either alone), we decomposed these distributions into the bias toward the past (toward vs. away from past) as a function of saccade direction with regard to the future (**Fig. 2b**) and the bias toward the future (toward vs. away from future) as a function of saccade direction with regard to the past (**Fig. 2c**). Finally, we binarised saccades as either going toward or away from the past and toward or away from the future (**Fig. 2d**). This enabled us to test whether saccades were jointly biased to the past and the future (which would predict an interaction whereby those same saccades that were biased to the past were also biased to the future).

Statistical analysis. To evaluate the reliability of patterns in our gaze data, we used a cluster-based permutation approach [29]. This method is ideal for evaluating patterns at multiple neighbouring points while circumventing the problem of multiple comparisons. We used this approach for all evaluations involving a series of data, such as along a time axis (**Fig. 1b-d**; **Fig. 2b-c**).

To create a permutation distribution, we randomly permuted the trial-average data at the participant level 10000 times and identified the largest clusters found at each time. The p-values of the clusters in the original data were calculated as the proportion of permutations for which the size of the largest cluster after permutation was larger than the size of the observed cluster in the original, non-permuted data. We created the permutation distribution using Fieldtrip with default cluster settings (grouping adjacent same-signed data points that were significant in a mass univariate t-test at a two-sided alpha level of 0.05 and defining cluster size as the sum of all t-values in a cluster).

In addition, statistical evaluation for the single-trial, single-saccade analysis was performed on the binarised quantification of saccade proportions using a two-way repeated-measures ANOVA with the factors past (toward/away) and future (toward/away). ANOVA results were complemented with Bonferroni-corrected post-hoc t-tests. For measures of effect size we used Partial eta squared (for our ANOVA) and Cohen's d (for follow-up t-tests). P-values of follow-up t-tests were Bonferroni corrected.

Data availability. All data will be made publicly available before publication.

Code availability. Relevant code associated with the here-presented analyses will be made available through GitHub before publication.

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ACKNOWLEDGEMENTS

This research was supported by an ERC Starting Grant from the European Research Council (MEMTICIPATION, 850636) and an NWO Vidi grant by the Dutch Research Council (grant number 14721) to F.v.E.

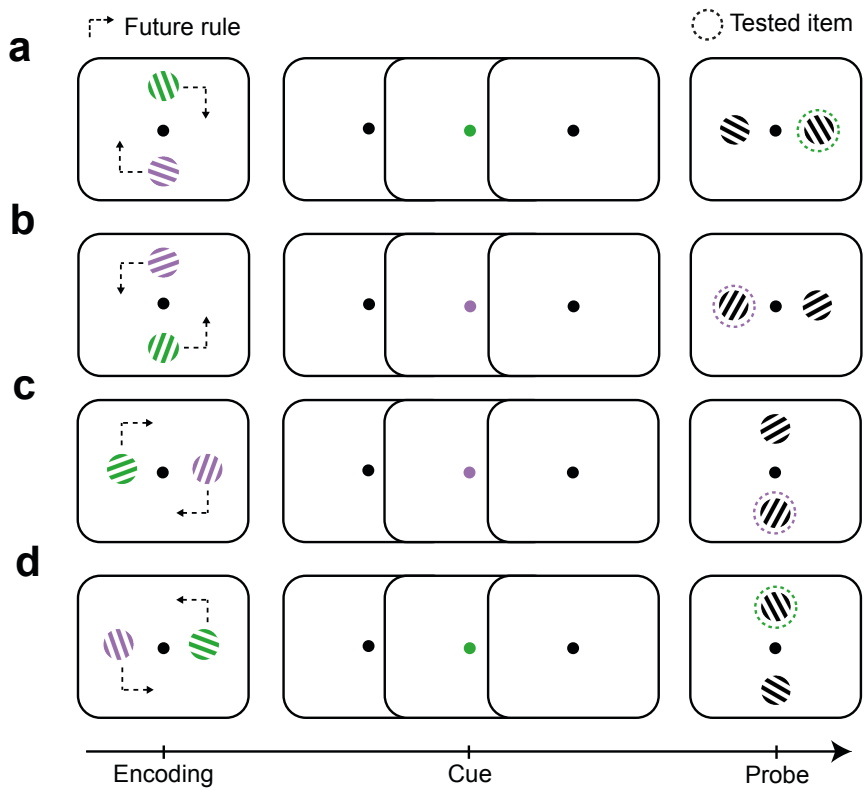
AUTHOR CONTRIBUTIONS

B.L and F.v.E designed and programmed the experiments, B.L. and S.A acquired the data. B.L, S.A, and F.v.E analysed and interpreted the data. B.L and F.v.E drafted and revised the manuscript.

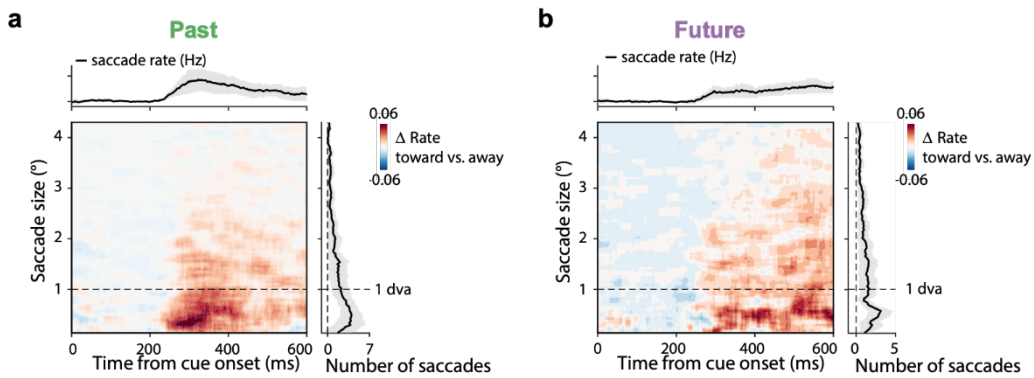
COMPETING INTERESTS STATEMENT

The authors declare no competing interests.

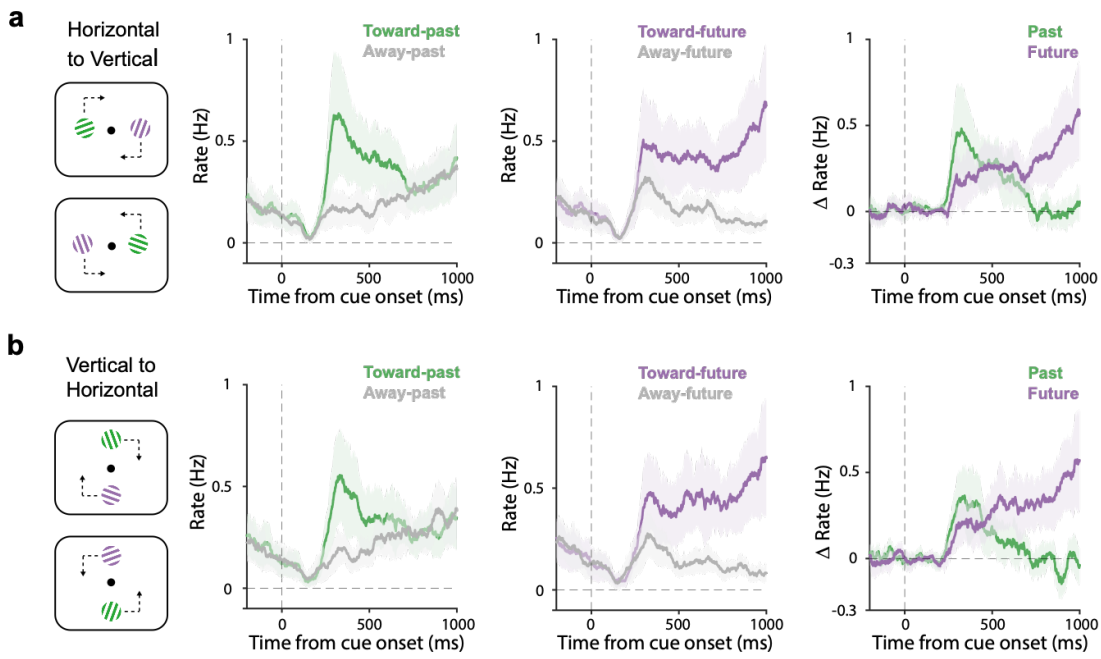
Supplementary Information – Figures S1-S3



Supplementary Figure 1. Four possible associations between encoding and test locations.



Supplementary Figure 2. Early saccade biases by past and future memory attributes are predominantly driven by microsaccades. Difference in gaze-shift rates toward minus away relative to past location (panel **a**) or future location (panel **b**), as a function of saccade size (y axes). For reference, dashed horizontal lines indicate 1° visual angle. Additionally, for each panel, we separately show the difference in gaze-shift rates (toward minus away) in time course at the top (collapsed over all depicted saccade sizes) and the difference in number of gaze-shift as a function of gaze-shift magnitude to the right (collapsed over all depicted times).



Supplementary Figure 3. Trials with vertical or horizontal configurations show similar joint consideration of past and future memory attributes. Conventions as in Main Figure 1b-d, separately for trials that encoded items horizontally and tested items vertically (panel **a**) and trials that encoded items vertically and tested items horizontally (panel **b**).