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«Geometry of Visuospatial Working Memory Information in Miniature Gaze Patterns»

Juan Linde-Domingo & Bernhard Spitzer

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Introduction

Working Memory (WM)

- WM **keeps stimulus information available** for upcoming tasks

- On removal of a stimulus from sight, sensory systems briefly **retain a detailed sensory memory**
- Without active maintenance, these rich ‘photographic’ **memories decay rapidly**
    - Only a **limited amount of information** can be accurately **maintained** in WM
- Despite intense research, the **nature of the information** that WM maintains remains poorly understood

- **Which aspects** of a task-relevant stimulus are retained by WM and in **which format(s)**?

How are WM Representations stored?

- Decoding of WM contents early visual cortices: storage in **sensory format**

- WM tasks are solved using **abstractions** of stimulus parameters (orientation, speed, colour)
  - Reduction of the **amount of information** that has to be maintained
  - Increase in memory **robustness**

Examining WM Representations

- In WM studies, often only a **single stimulus feature** needs to be reported after a delay
  - E.g. Gabor gratings in Lea's master's thesis or CDA

- Research has neglected **temporal dynamics** of WM abstractions neglected (mainly MRI studies)
- Linde-Domingo & Spitzer: **Subtle ocular activity** (e.g. microsaccades) can reflect **attentional orienting** during visuospatial WM tasks
  - Traditionally considered a **confound** to avoid
  - Can reflect certain types of **visuospatial WM information**
  - Even throughout prolonged WM **delays**

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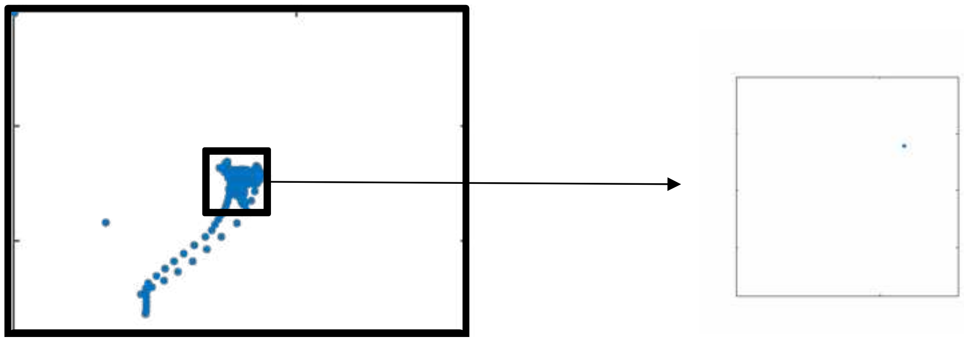
Definition: Microsaccades

Microsaccades

- Saccades: rapid movement of the eye between fixation points

- Microsaccades: small, jerk-like, involuntary eye movements; occuring **during fixation**
  - Controversial definition: What constitutes a microsaccade? Small? Jerk-like? Quick?
  - Definition by Linde-Domingo & Spitzer: **velocity-based**
    - Onsets and endpoints from when the gaze velocity exceeded a **trial-specific threshold** (5 times the median velocity in the trial)
    - Minimum interval of 100 ms between successively detected saccades



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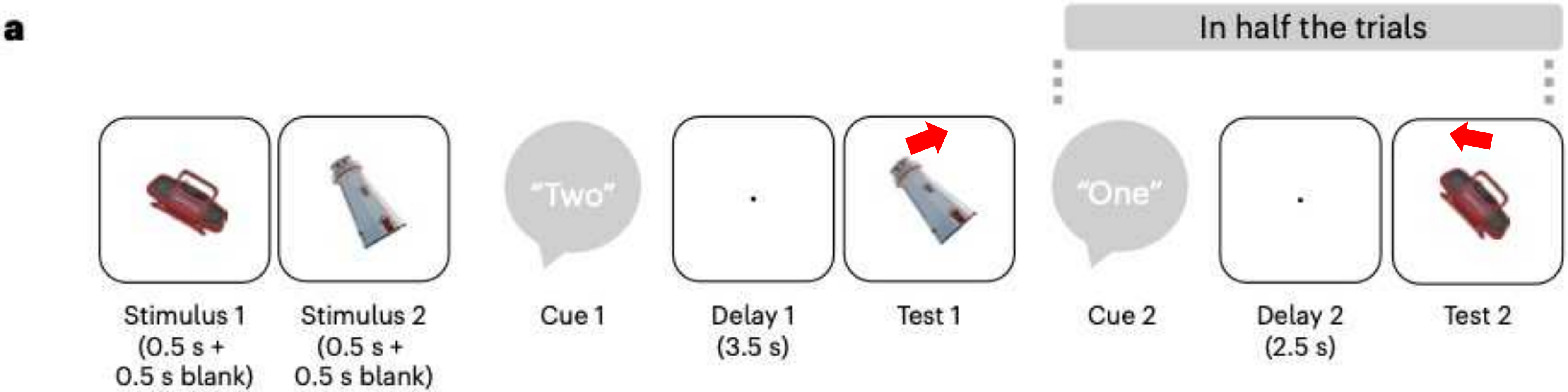
Paradigm

Paradigm

- Nine colour photographs of everyday objects



- Each participant performed 16 blocks of 32 trials, for a total of 512 trials (265 of which included a Test 2)
- **Orientations** of the two objects on each trial were drawn randomly and independently from 16 equidistant values (excluding cardinal axes)

Methods

Participants

- 55 participants (31 female, 24 male, mean age 26.95 $\pm$ 3.98 years)
- 2 exclusions due to eye-tracking problems (glasses)
- 1 exclusion because participant felt unwell
- 9 excluded for failing to perform above chance level in each of the two memory tests
- 2 excluded because more than 15% of the data had to be rejected because of blinks and other artefacts

→ 41 participants for analysis

Stimuli, Task and Procedure

- Nine colour photographs of everyday objects from the BOSS database (mirror symmetry)
  - Grouped pictures into three different sets of three always combining objects with different aspect ratios (width/height)
  - Each participant was assigned one of these sets
- Trial: Each participant performed 16 blocks of 32 trials, for a total of 512 trials (265 of which included a Test 2)
  - fixation dot (8 × 8 px, corresponding to a 0.17 × 0.17° visual angle) displayed at the centre of the screen for 500–1,000 ms (randomly varied)
  - sequential presentation of two objects, each in a random orientation for 500 ms each (display size ~6.5° visual angle, see Fig. 1c) followed by a 500 ms blank screen
  - auditory retro-cue ('one' or 'two', 350 ms) indicated which of the two stimulus orientations was to be reported after a delay (Delay 1, 3,500 ms) in the upcoming memory test (Test 1)
  - Test 1 started with the cued object reappearing on display, but with its previous orientation changed by ±6.43°
  - Participants were asked to indicate by means of key press (2-AFC) whether the object would need to be rotated clockwise or anticlockwise (right or left arrow key) to match its memorized orientation
  - written feedback message ('correct' or 'incorrect') displayed in the upper part of the screen (500 ms)
  - in half the trials, an auditory message ('thanks', 350 ms) signalled the end of the trial
  - in the other half of the trials (randomly varied), a second auditory retro-cue (Cue 2) was presented (for example, 'two', if the first retro-cue was 'one'), indicating that the thus-far-untested stimulus orientation would still need to be reported. In these trials, another delay period ensued (Delay 2, 2,500 ms), and participants' memory for the second-cued stimulus was tested (Test 2), using the same procedure as before for the first-cued stimulus in Test 1

Stimulus Presentation

- Pseudorandom across trials
- each pairing of objects from the participant's object set **occurred equally often**
- each object was **equally often presented** first (as Stimulus 1) and second (as Stimulus 2)
- Stimulus 1 and Stimulus 2 were **equally often cued for Test 1**
- orientations of the two objects on each trial were drawn randomly and independently from 16 equidistant values (11.25° to 348.75° in steps of 22.5°), which **excluded the cardinal axes** (0°, 90°, 180° and 270°)

Behavioural modelling

- Definition of three prototypical geometries:
  - (1) an unbiased ‘circle’ model (Mcircle) corresponding to the memory items’ 16 original orientations
  - (2) a cardinal repulsion model (Mrepulsion) that shifts the 16 orientations to the nearest diagonal orientation
  - (3) a cardinal attraction model (Mattraction) that shifts them to the nearest cardinal orientation
  - The continuum from attraction to repulsion was formalized with a mixture parameter B (ranging from −1 to 1), which blends the circle model with the repulsion model

$$M_{\mathrm{mix}} = -BM_{\mathrm{attraction}} + (1+B)M_{\mathrm{circle}}$$

$$M_{\mathrm{mix}} = BM_{\mathrm{repulsion}} + (1-B)M_{\mathrm{circle}}$$

Behavioural modelling

- To simulate memory reports (clockwise or anticlockwise) for each trial
  - computed the angular difference d between the orientation modelled in Mmix and the probe orientation displayed at test and transformed it into a probability of making a 'clockwise' response using a logistic choice function where s is a noise parameter that relates inversely to memory strength or precision

$$P_{\text{clockwise}} = \frac{1}{1+\exp(-d/s)}$$

  - The model also allowed for greater memory precision near the cardinal axes (a so-called oblique effect)
    - further parameter c, which up- or downregulated noise s for those eight orientations in the stimulus set that were near the cardinal axes relative to the remaining eight orientations that were nearer the diagonal axes

$$s_{\text{near-cardinal}} = \exp(c)s_{\text{near-diagonal}}$$

    - model was fitted to the memory reports of each participant individually using exhaustive gridsearch (B, −1...1; s, 0...1; c, −0.5...0.5; with a step size of 0.01 for each parameter) and least squares to identify the best-fitting parameter values

Eye-Tracking Analysis

- Eye-tracking data were only **minimally preprocessed**
- Zero-centred (using the overall mean over all trials)
- Data points with a Euclidean distance larger than 100 px (correspond- ing to a 2.17° visual angle) from the zero-centre were excluded from analysis
- Analysis in two epochs of interest:
  - time-locked to Stimulus 1 onset (from −500 ms until the onset of Test 1 at 5,850 ms)
  - time-locked to Cue 2 onset (from −500 ms until the onset of Test 2 at 2,850 ms)
- After artefact exclusion, on average 97.87% (s.d. = 1.50%, first epoch) and 95.14% (s.d. = 3.67%, second epoch) of the data remained for analysis

Representational Similarity Analysis: Single-Trial Approach

- Trial average for each of the 16 orientations while leaving out the current trial
- At each time point the 16 Euclidean distances between the gaze position in the current trial and the trial averages formed from the remaining data
- Representational dissimilarity vector (RDV) of the distances between the (single-trial) gaze associated with the orientation in the current trial and the (trial-averaged) gaze associated with each of the 16 orientations (Fig. 2b)
- To examine orientation encoding, we computed at each time point and for each trial the Pearson correlation (ρ) between the empirical RDV and the theoretical RDV predicted under a model of orientation encoding for the orientation on the current trial
- When averaged over trials (and hence also across orientations), the procedure yields a **leave-one-out cross-validated time course of orientation encoding**, similar to more conventional RSA approaches with trial averages
- The single-trial approach additionally retains the trial-by-trial variability in orientation encoding (Fig. 2b, right, and Fig. 2e)

Representational Similarity Analysis: Orientation Encoding within and between Objects

- same approach but obtained the 16 trial averages separately for each of the three different objects in the participant's stimulus set

  → three empirical RDVs per trial (one within and two between objects) that were independently correlated (Pearson's ρ) with the model RDV. The two between-objects correlations were then averaged.

Representational Similarity Analysis: CBPT

- All RSA results were obtained individually for each participant and examined statistically on the group level
- cluster-based permutation testing
    - Indentification **of clusters of consecutive samples** that showed an effect with $P_{sample} < 0.05$ (uncorrected)
    - calculation of the sum of t-values in a cluster as its test statistic
    - Estimation of the probability $P_{cluster}$ that a cluster with a larger test statistic would emerge by chance, on the basis of 20,000 iterations where the individual participant effects were randomly sign-flipped
    - Unless otherwise specified, all reported statistical tests were two-sided

Model Geometries

- Basic orientation model: perfect circle geometry
  - Model RDVs reflected the pairwise Euclidean distances between 16 evenly spaced points on a circle
  - The geometry of this model corresponds to behavioural analysis model with B = 0 (that is, M_{circle}, unbiased)
- To examine bias in the gaze patterns (Fig. 4), we used the Euclidean distance structures associated with our maximally biased models with B = −1 (Mattraction) and B = 1 (Mrepulsion), respectively
  - Comparing these two extreme models yields an **estimate of the extent to which the gaze patterns were repulsively or attractively biased**
  - Distance structures expected under the three different models (B = 0, B = 1 and B = −1) correlate with each other (r = 0.77 and 0.34). We thus did not expect very large differences in their fit of the data and report the results with a more liberal statistical threshold ($P_{cluster} < 0.05$)

Microsaccade Detection

- **velocity-based** detection algorithm (established in previous work[77–79])
  - Gaze-position data were transformed into a **velocity time course** by calculating the Euclidean distances between consecutive samples and smoothing with a 7 ms Gaussian kernel
  - Saccade onsets and endpoints were inferred from when the gaze velocity exceeded a **trial-specific threshold** (5 times the median velocity in the trial) and when it returned to below threshold (minimum interval of 100 ms between successively detected saccades)

Results

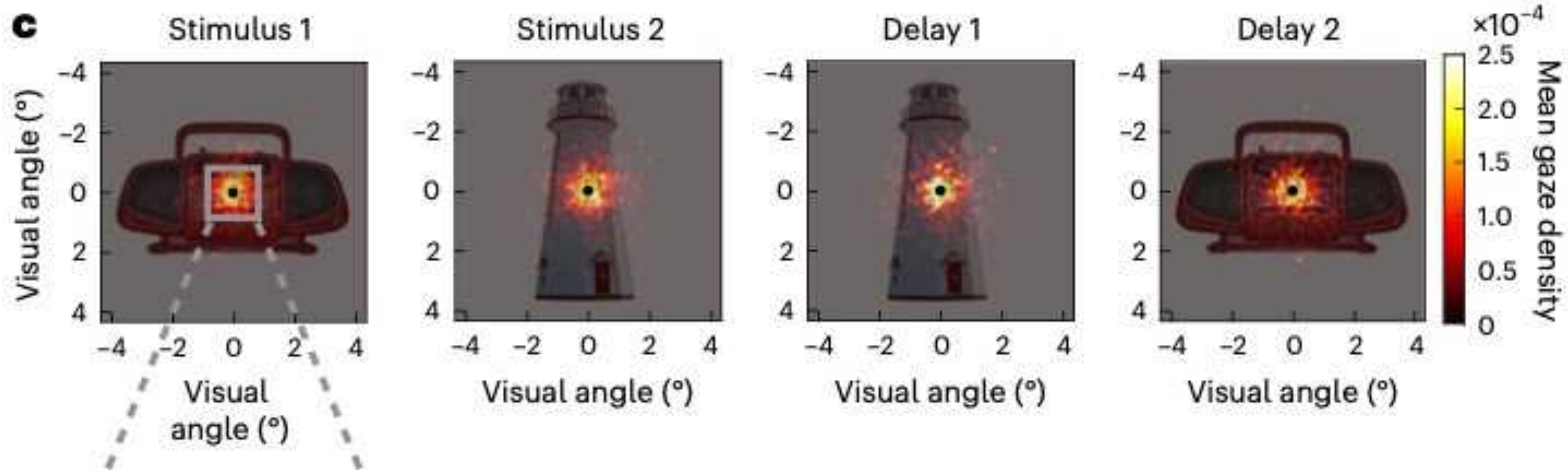
Behavioural

- Percentage of **correct responses was descriptively higher on Test 1** (mean = 73.41%, standard deviation (s.d.) = 6.42%) than on Test 2 (mean = 66.62%, s.d. = 5.78%)
- The **second presented orientation (Stimulus 2) was remembered better** (mean = 70.99%, s.d. = 7.07%) than the first presented orientation (Stimulus 1; mean = 69.04%, s.d. = 6.79%)
  - 2 × 2 repeated-measures analysis of variance (ANOVA) with the factors Test (1/2) and Stimulus (1/2) confirmed that both these effects were significant ($F(1,40) = 95.396$, $P < 0.001$, eta squared ($\eta 2$) = 0.521 and $F(1,40) = 13.319$, $P < 0.001$, $\eta 2 = 0.043$)), whereas there was no significant interaction between the two factors ($F(1,40) = 3.681$, $P = 0.062$, $\eta 2 = 0.008$)
- ‘**mnemonic distance**’ of a stimulus on four levels (from shortest to longest):
  - Stimulus 2 at Test 1
  - Stimulus 1 at Test 1
  - Stimulus 2 at Test 2
  - Stimulus 1 at Test 2)
  - **monotonic decrease across these distance levels** ($t(40) = -9.404$, $P < 0.001$, Cohen’s $d = -1.469$, 95% confidence interval (CI) (−0.038, −0.024); t-test of linear slope against zero)

Gaze Density

- Gaze density heatmaps from aggregated data
- **Gaze density was concentrated narrowly** at centre during both the stimulus and the delay periods

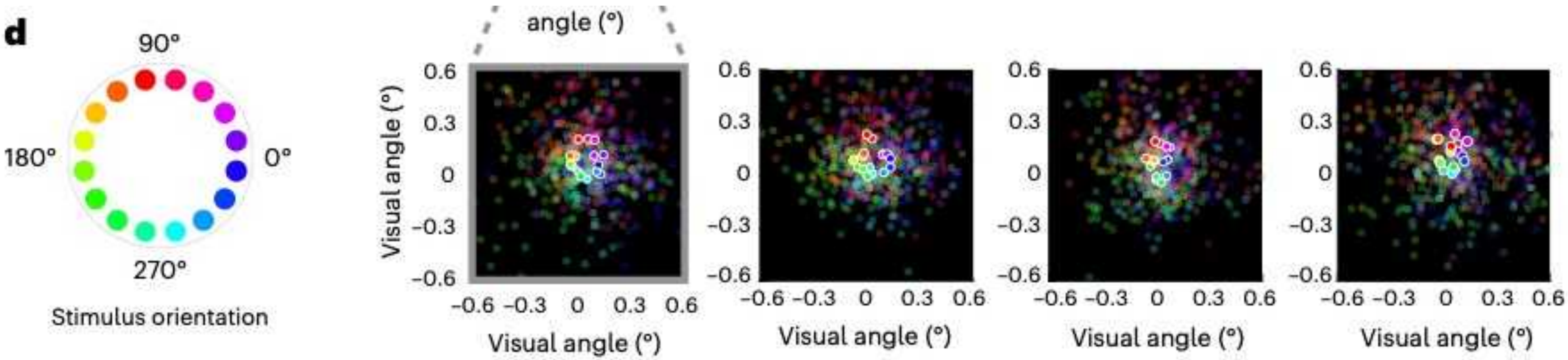
→ Despite the rotational alignment, instructions and online feedback proved effective in preventing participants from averting gaze from fixation dot



Object Orientation was Reflected in Miniature Gaze Patterns

- Mean gaze positions for the 16 different orientations of the currently relevant stimulus
- **Miniature circle-like patterns**

  → Miniscule gaze shifts near fixation might **carry information about the objects' orientation**

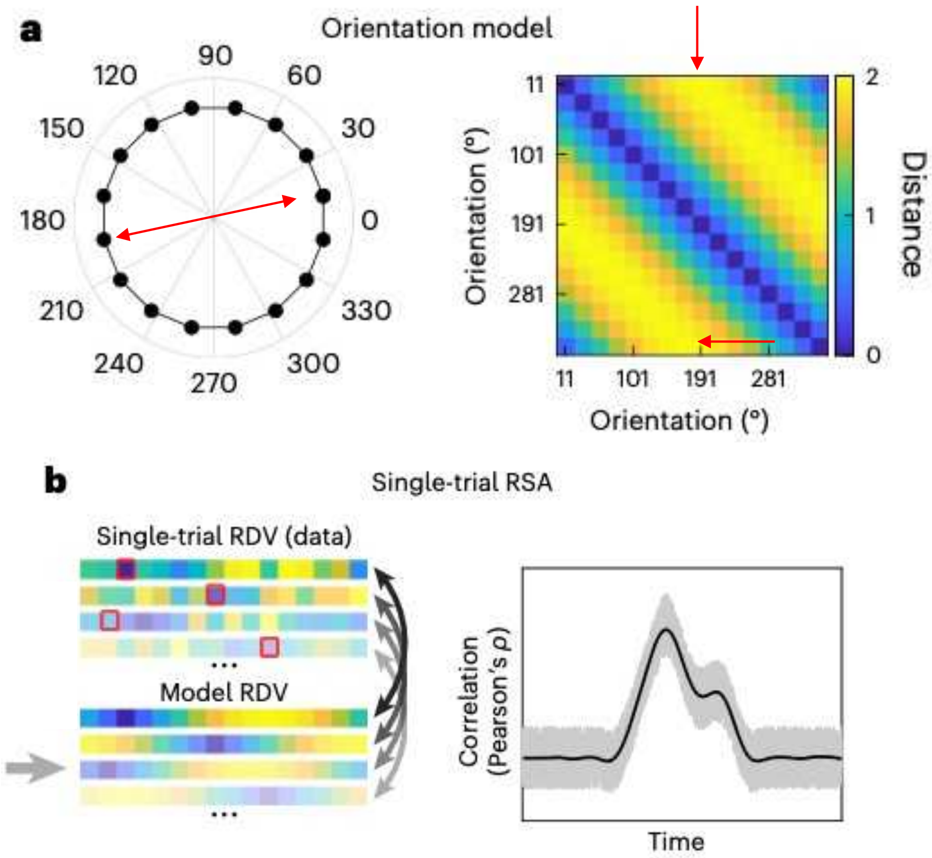


Representational Similarity Analysis

- Representational similarity analysis (RSA)
  - Extent to which the **gaze patterns showed the characteristic Euclidean distance structure** of evenly spaced points on a circle (**a** - left)
  - RSA on the single-trial level (**b**) by correlating for each trial the **model-predicted distances with the vector of gaze distances** between the current trial and the trial average for each stimulus orientation

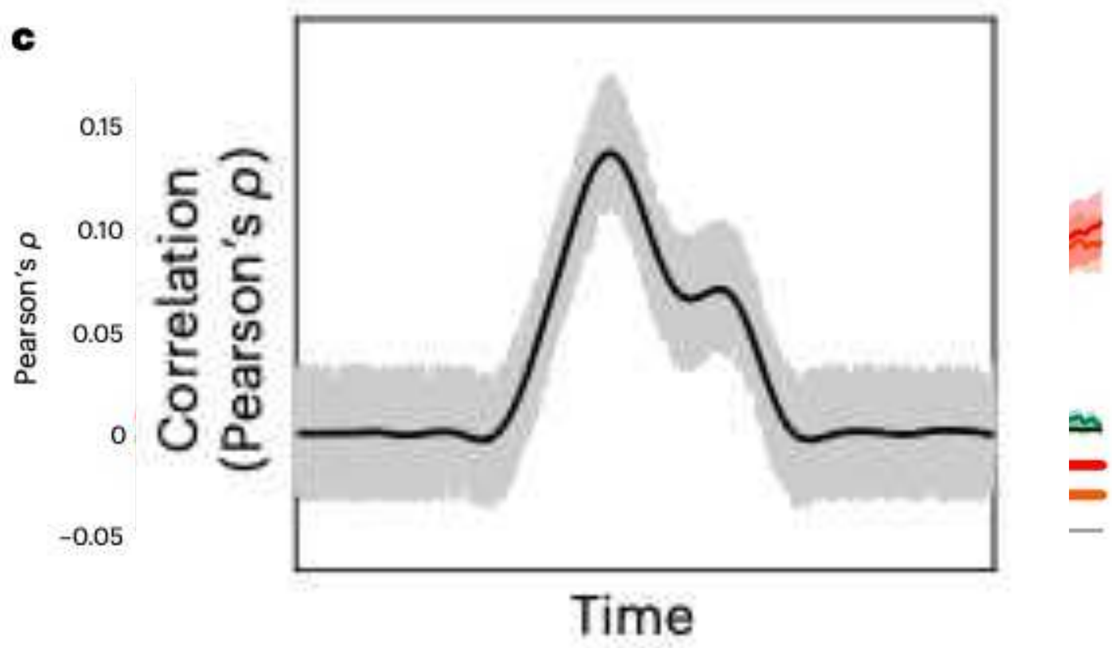
    → **Time course of orientation encoding** (by the gaze pattern) **for each trial**

    → **Cross-validated (LOOCV) estimate of orientation encoding at each time point for every trial**



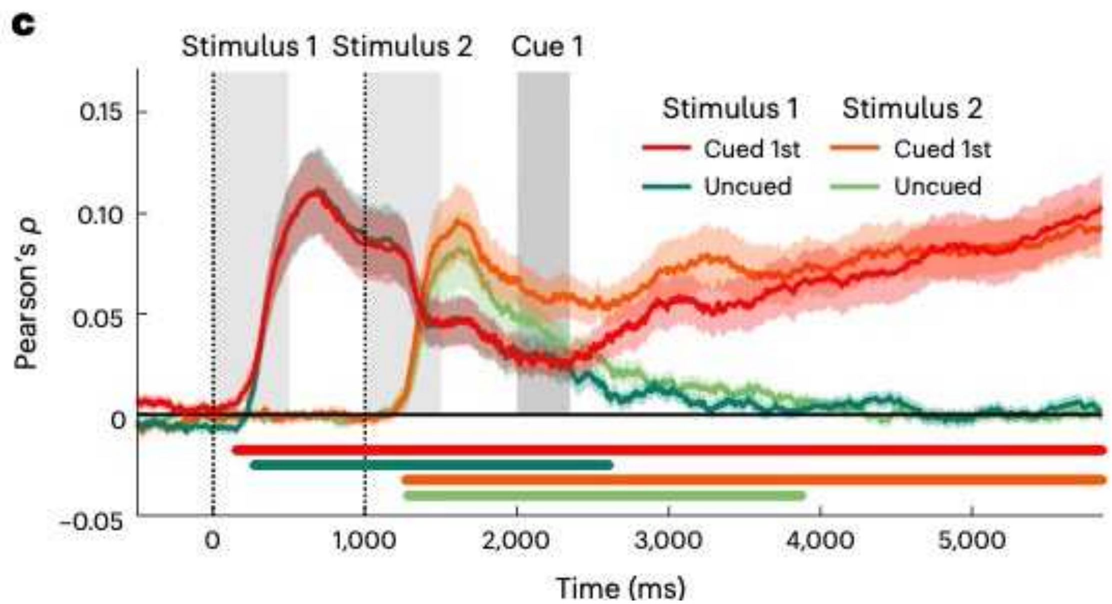
Time Courses of Orientation Encoding

- Mean time courses of orientation encoding (averaged over trials) during stimulus presentation:
  - Robust **encoding of stimulus orientation from about 500 ms after stimulus onset** for both Stimulus 1 and Stimulus 2
  - Encoding of either stimulus orientation peaked at ~650 ms (**after the stimuli's offset**), after which it slowly decayed



Concurrent encoding of Stimulus 1 and Stimulus 2

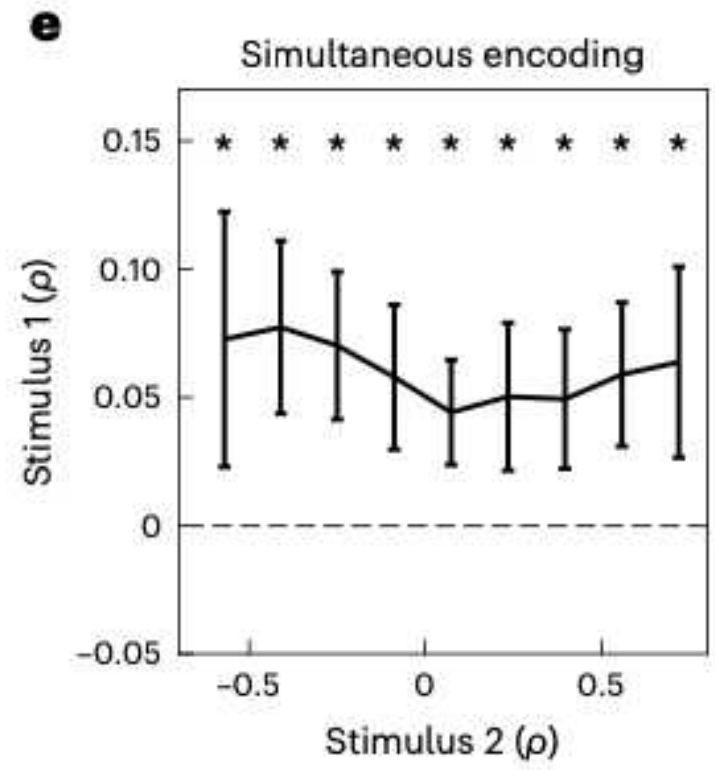
- While encoding the second presented orientation (Stimulus 2), the **gaze pattern also continued to carry information about the first-presented orientation** (Stimulus 1)



Concurrent encoding of Stimulus 1 and Stimulus 2

- Binned each participant's trials according to how strongly the orientation was encoded after Stimulus 2 onset
  - If encoding of the two orientations had alternated between different trials, we would expect a **negative relationship with the encoding of the orientation of Stimulus 1** in the same time window

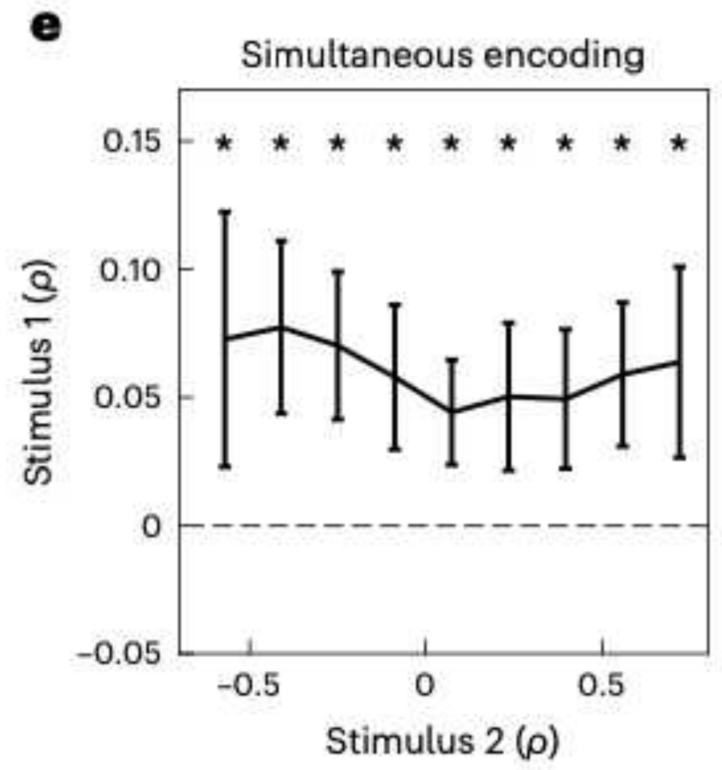
    → No significant relationship



Concurrent encoding of Stimulus 1 and Stimulus 2

- Encoding of Stimulus 1's orientation was significantly above chance even on those trials on which the encoding of Stimulus 2's orientation was maximally strong

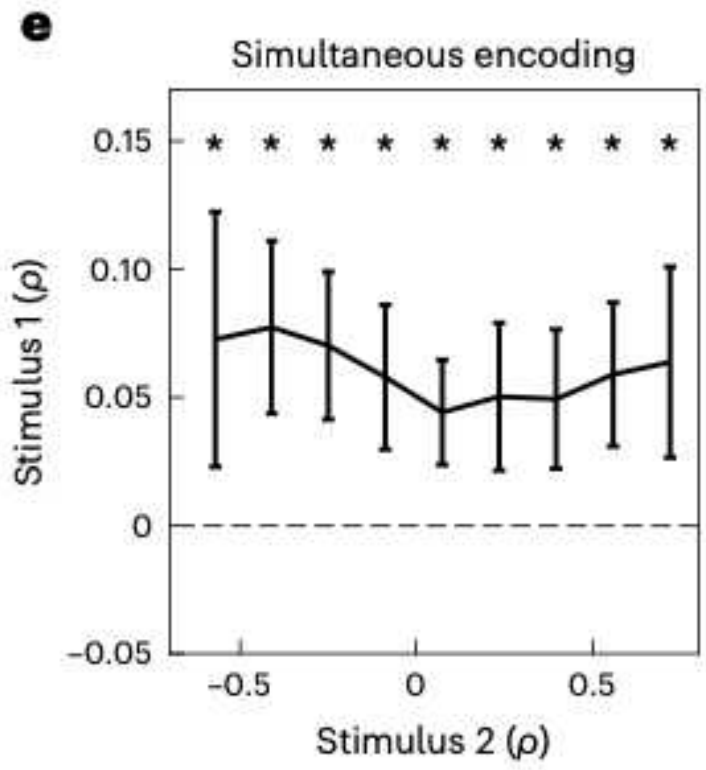
→ Small shifts in 2D gaze space **carried information about the two stimulus orientations simultaneously**, on the same trials



Concurrent encoding of Stimulus 1 and Stimulus 2

- Single-trial approach and binned each participant's trials according to how strongly the orientation of Stimulus 2 was encoded between 250 and 1,000 ms after Stimulus 2 onset
- If encoding of the two orientations had alternated between different trials, we would expect a negative relationship with the encoding of the orientation of Stimulus 1 in the same time window.
  - no significant relationship ($t(40) = -1.368$, $P = 0.18$, $d = -0.214$, 95% CI (−0.006, 0.001); linear trend analysis)
  - Encoding of Stimulus 1's orientation was significantly above chance even on those trials on which the encoding of Stimulus 2's orientation was maximally strong ($t(40) = 3.656$, $P = 0.01$, $d = 0.571$, 95% CI (0.029, 0.099); t-test against 0)

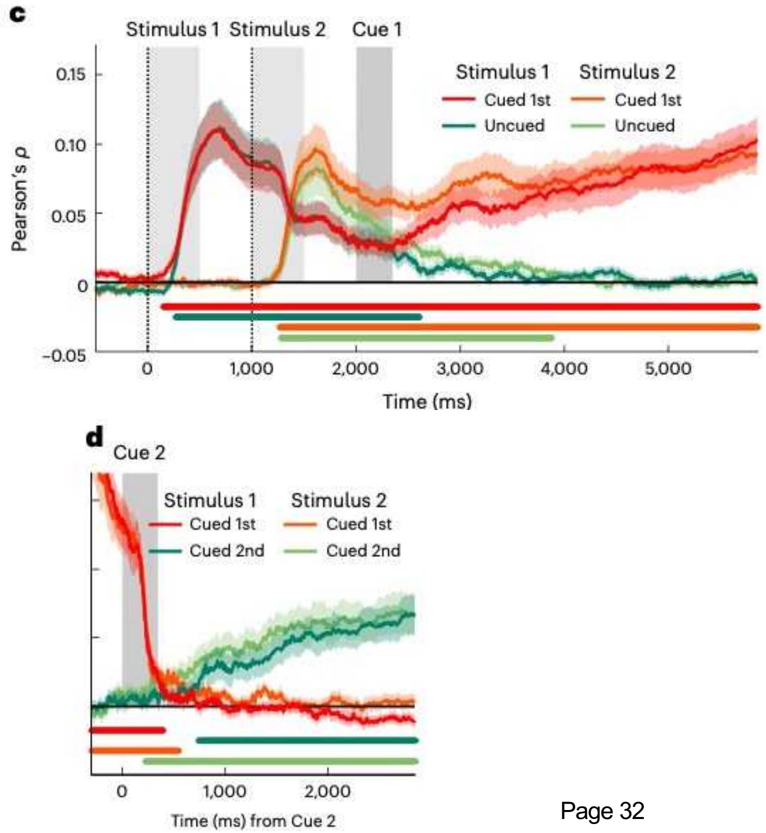
→ small shifts in 2D gaze space **carried information about the two stimulus orientations simultaneously**, on the same trials



Encoding of the cued Orientations throughout the Delay Periods

- **How did the gaze patterns reflect information storage** during the delays?
  - Delay 1: encoding of the cued orientation ramped up and continuously increased in strength until the time of Test 1, whereas the encoding of the uncued orientation slowly returned to baseline (**c**)
  - Delay 2: similar ramping-up pattern for the second-cued orientation (**d**)

  → miniature gaze deflections robustly encoded the currently cued (or ‘attended’) memory information during the two delay periods in a ramp-up fashion that **resembled the encoding of WM information in neural recordings**

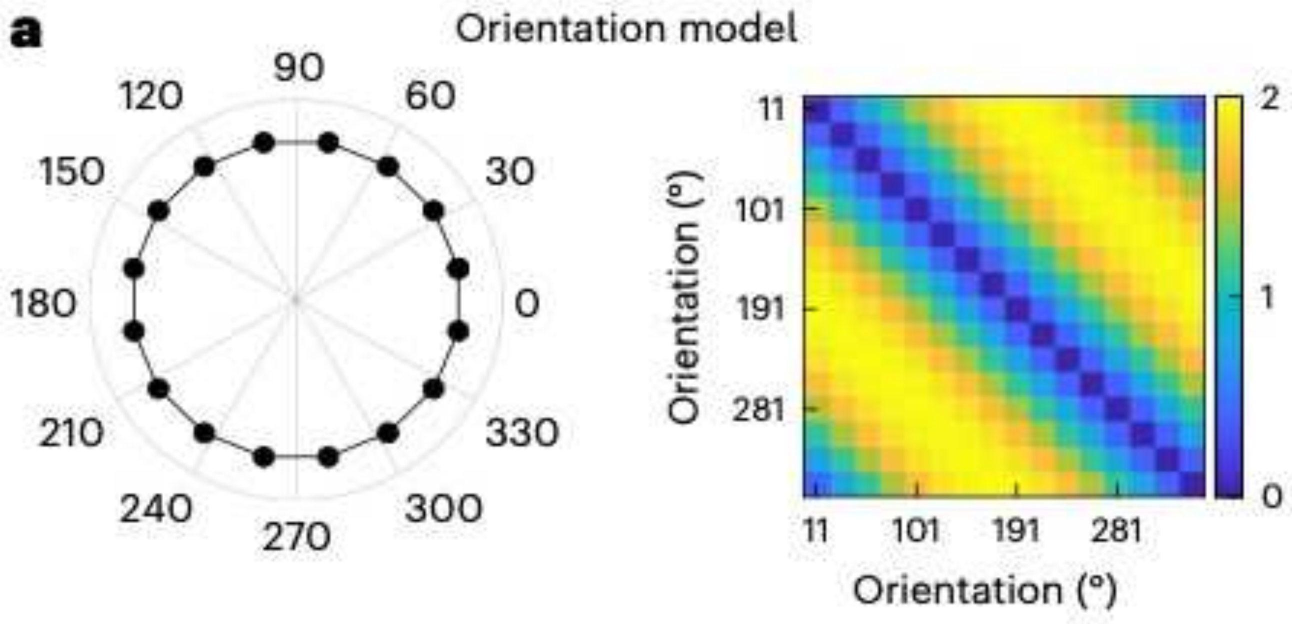


Orientation Encoding: Object-specific versus Object-independent

- Two formats in which the gaze patterns may reflect the WM information:
  - Concrete visual memory of the presented stimulus
    - **Object-specific** (gaze patterns not transferable)
  - On the basis of a mental abstraction of orientation (e.g. directional spatial coordinates)
    - **Object-independent** (gaze patterns transferable)

Object-specific versus Object-independent Orientation Encoding

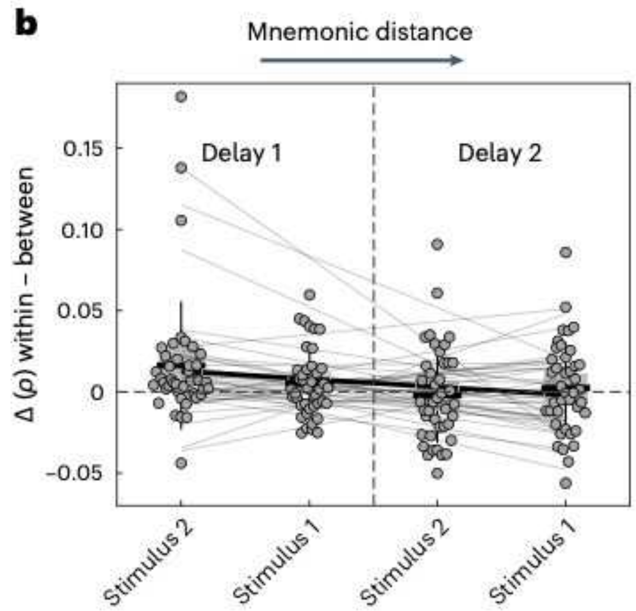
- Examination by comparing the orientation encoding in gaze distances **within objects** with that in gaze distances **between objects**
- The **degree of object specificity** is inferred from the extent to which within-objects encoding is stronger than between-objects encoding



Differences in Object Specificity with Mnemonic Distance

- Difference in orientation encoding within objects compared to between objects for the cued stimulus during each delay period
  - conditions are sorted by '**mnemonic distance**'

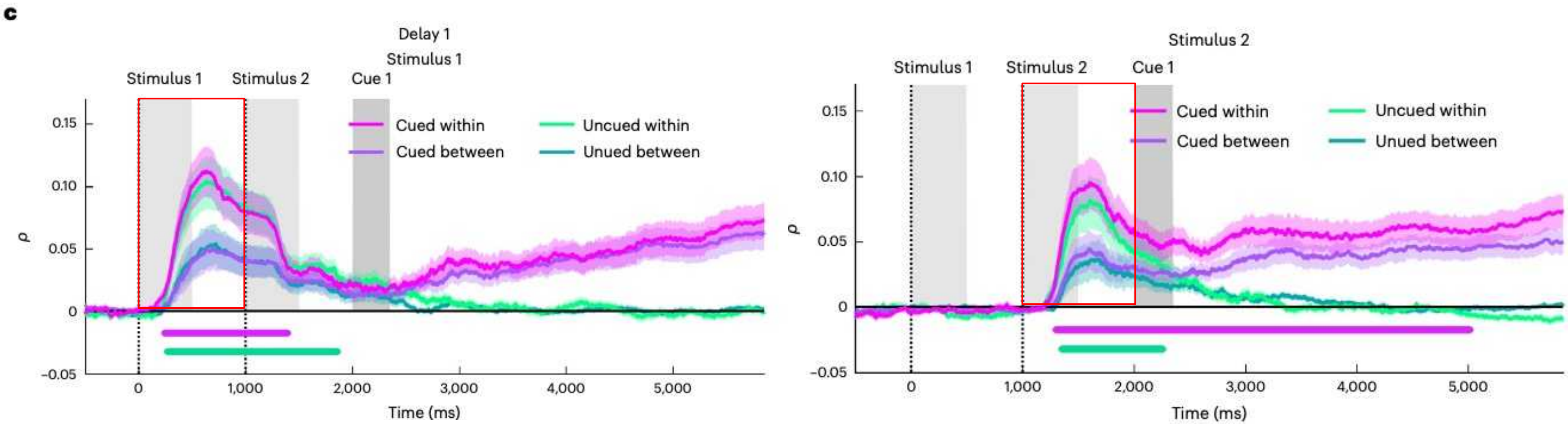
- Main effect of delay period
  - **Greater object specificity during Delay 1**
  - No effect of presentation order
- Moderate interaction between the two factors
  - Difference between the two delays was stronger for Stimulus 2



→ **Decrease in object specificity** (i.e. abstraction) **with increasing mnemonic distance**

Object-Specificity on Stimulus Presentation

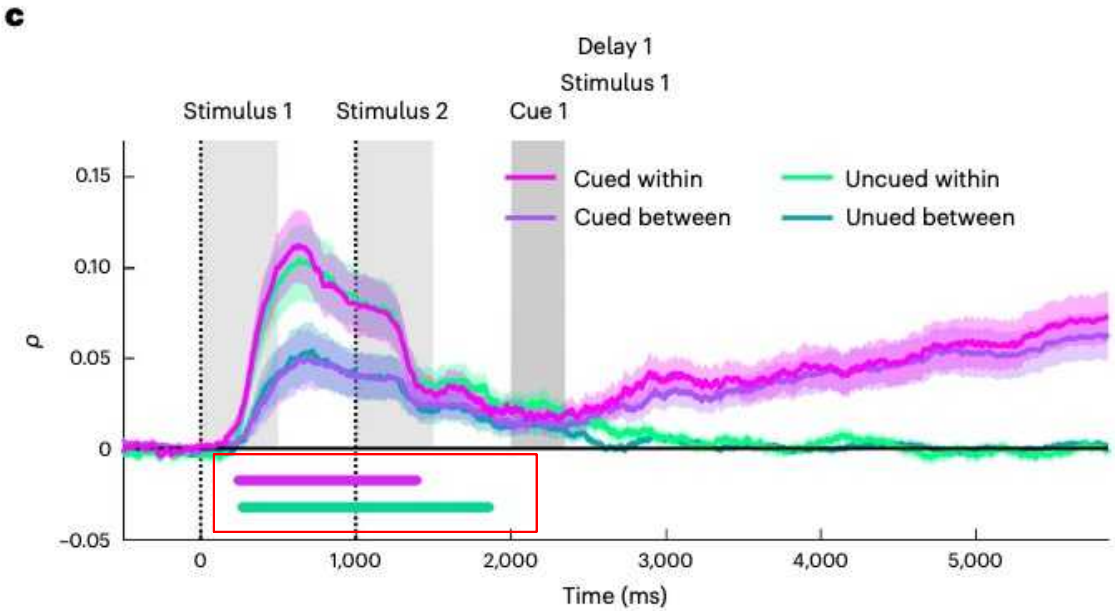
- **Orientation encoding time courses** within and between objects during Delay 1
  - Shown separately for when the stimulus was cued (pink and purple) or uncued (light and dark green)



→ **within-objects encoding clearly exceeded between-objects encoding**

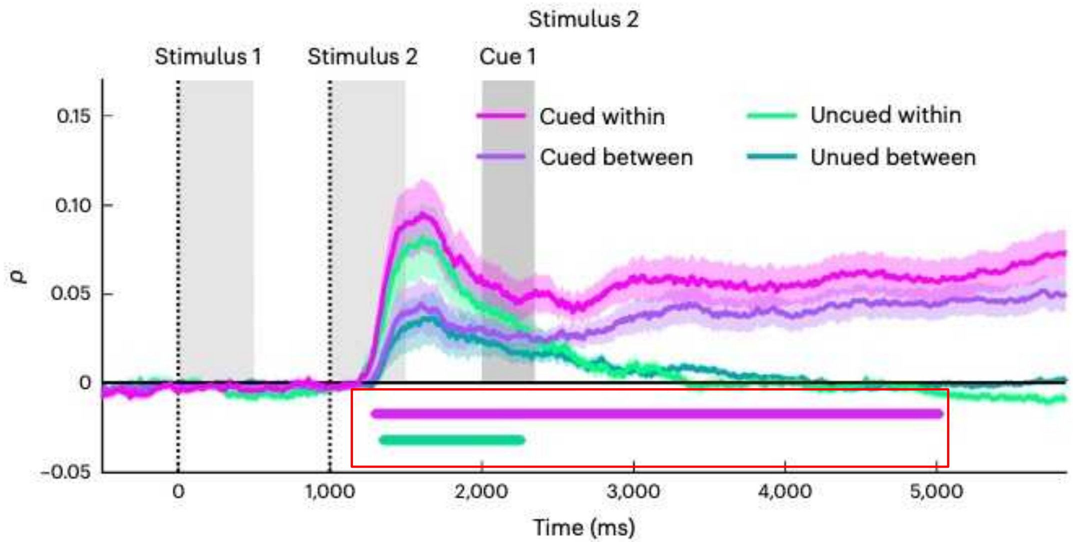
Orientation Encoding: Stimulus 1

- For Stimulus 1, the **object specificity diminished abruptly** after ~1,300 ms
  - When the gaze patterns began to also encode Stimulus 2
  - Changed to a more **object-independent format** for the remainder of the trial epoch



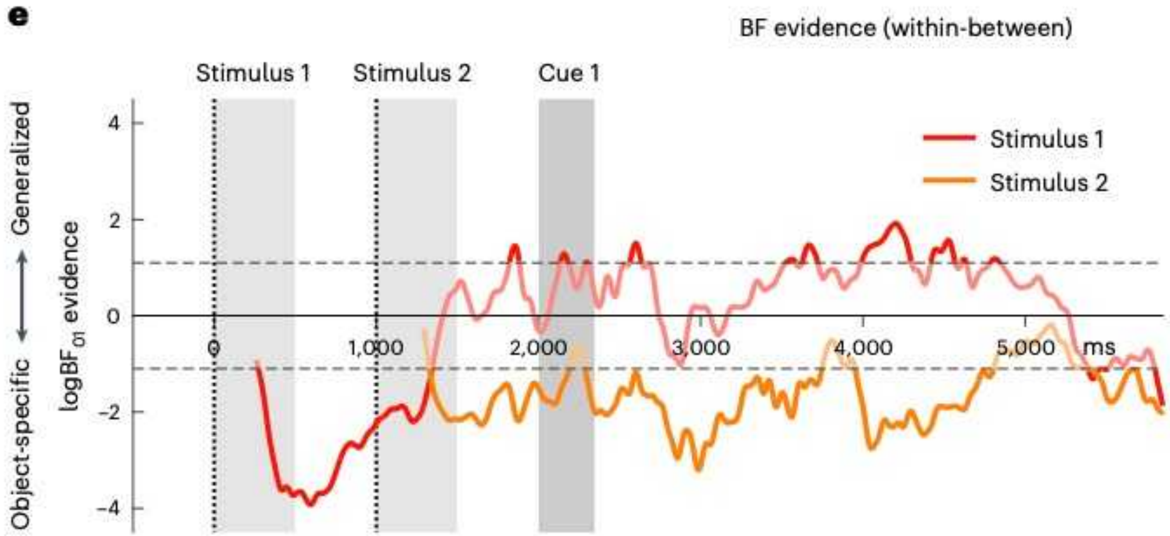
Orientation Encoding: Stimulus 2

- Stimulus 2, in contrast, when cued for Test 1, the **object specificity decayed less and was sustained throughout most of Delay 1**

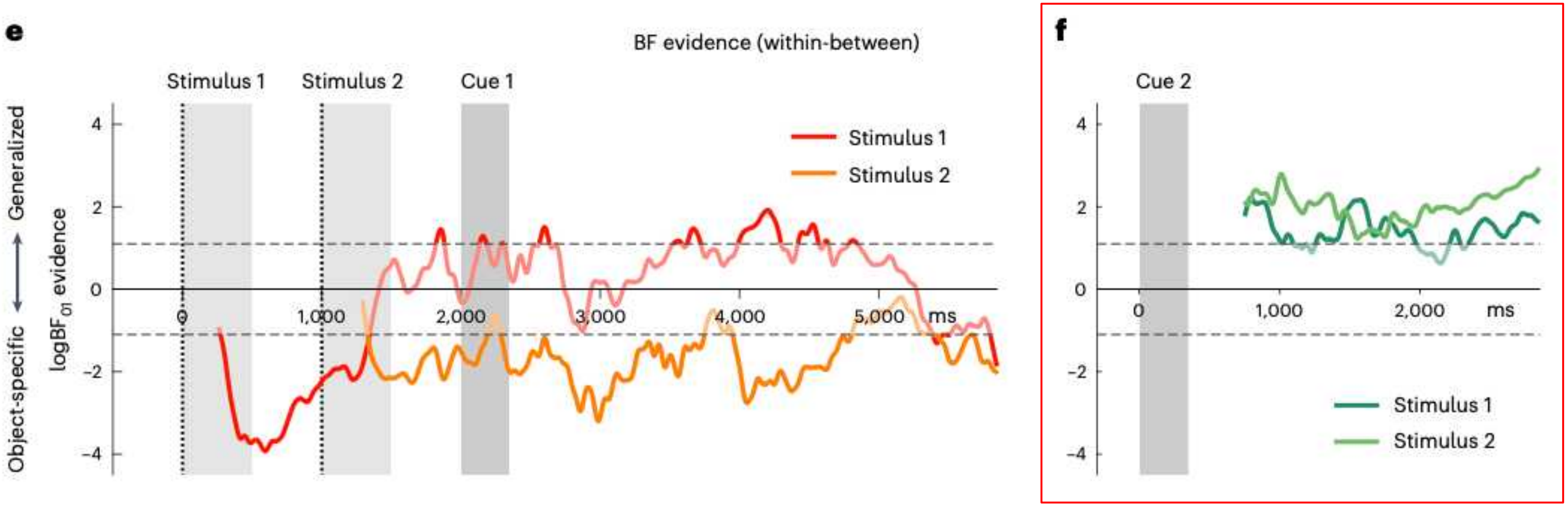


Temporal Evolution of Object Independence

- Bayes Factor analysis of the **difference between within- and between-objects encoding**
  - Negative values indicate stronger evidence for object-specific encoding (within > between) than for object-independent encoding (within ≤ between)
- **Swift change** of **Stimulus 1** encoding from object-specific **towards object-independent** at the time of Stimulus 2 encoding
- Encoding of **Stimulus 2** **retained object specificity** during Delay 1



Delay 2: Object-Independence for both Stimuli



Differences in object specificity between delay periods

- object specificity of cued orientation encoding differed between the two delay periods (Delay 1 or 2) and/or between the first and second pre- sented stimulus (Stimulus 1 or 2)
  - 2 × 2 repeated-measures ANOVA on the difference in encoding strength (within- minus between-objects, averaged across the respective delay periods) showed a **main effect of delay period** (Delay 1/2; $F(1,40) = 6.204$, $P = 0.017$, $\eta 2 = 0.064$) indicating **greater object specificity during Delay 1** but no effect of presentation order (Stimulus 1/2; $F(1,40) = 0.985$, $P = 0.327$)
  - **moderate interaction between the two factors** ($F(1,40) = 4.466$, $P = 0.041$, $\eta 2 = 0.027$), reflecting that the **difference between the two delays was stronger for Stimulus 2**.
  - **decrease in object specificity with increasing mnemonic distance** ($t(40) = -2.473$, $P = 0.018$, $d = -0.386$, 95% CI (−0.010, −0.001); ttest of linear slope against zero).

Object Specificity (Abstraction) over Time

Unlike during perceptual processing, **gaze patterns during the delay periods reflected WM information in more generalized (or abstract) coordinates**

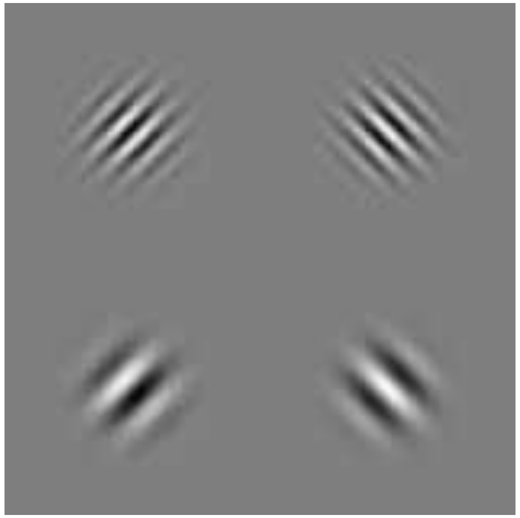
and

the level of this abstraction increased after periods of temporary (or partial) inattention

Cardinal Repulsion Bias in Gaze Patterns and Behaviour

- In studies of WM for stimulus orientation (e.g. Gabor gratings) it is commonly observed that behavioural reports are **biased away from the cardinal axes**

- Investigation:
  - Is there repulsive cardinal bias also with **rotated object stimuli**?
  - Is the strength of bias modulated by **periods of inattention**?
  - To which extent is the bias already expressed in the **geometry of the miniature gaze patterns** during the delays?



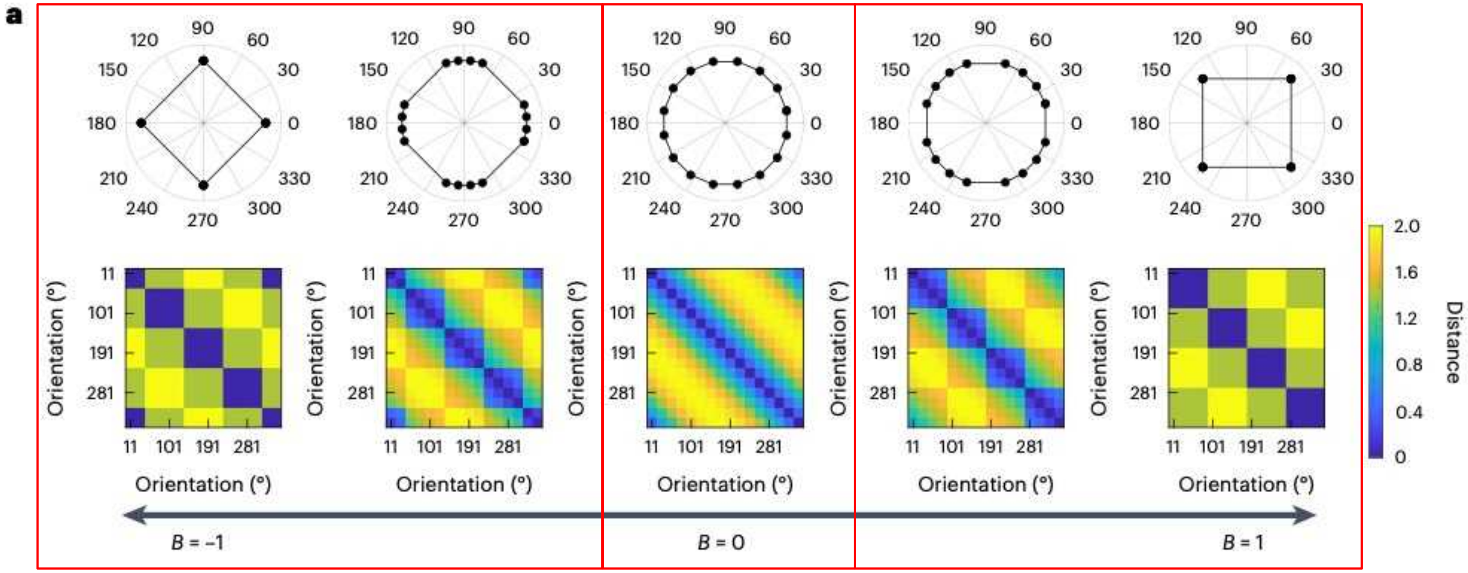
Geometrical Approach for Bias Quantification

- Quantification of bias as a mixture of a perfect (unbiased) circle and perfect (fully biased) square geometries
- Mixture parameter B quantifies the extent to which the reported orientations were **repulsed away from the cardinal axes**

Repulsion: B > 0

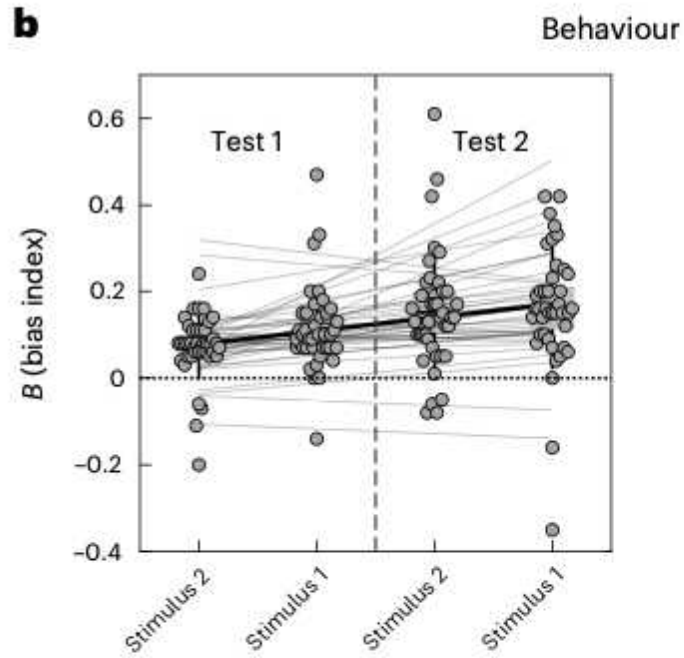
No bias: B = 0

Attraction: B < 0



Fitting the Geometric Model to Participants' Behavioural Responses

- Results from the model fitted to the behavioural memory reports
- Main effect of test indicating a **stronger bias on Test 2** and a **main effect of presentation order**
  - **Increase in cardinal bias with increasing mnemonic distance** from stimulus presentation
- Bias for both stimuli in both memory tests
  - Overall **repulsive cardinal bias** (B > 0)



Cardinal repulsion bias in gaze patterns and behaviour

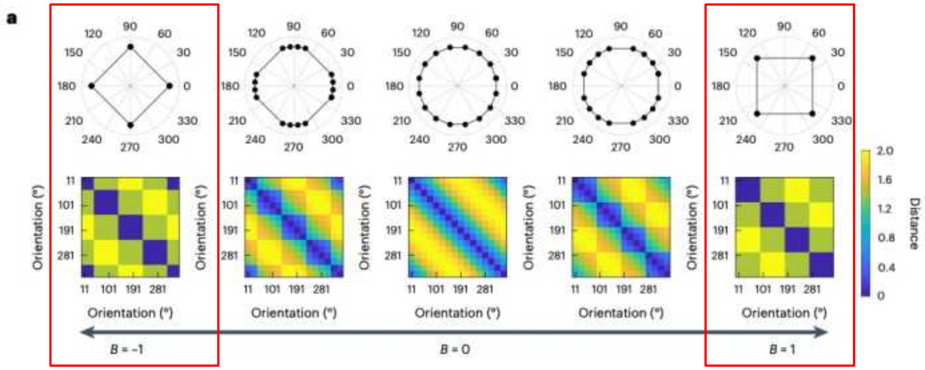
- Fitting the model to participants' behavioural responses:
  - values of B > 0 (grand mean, 0.124, s.d. = 0.092) in both memory tests (Test 1 and 2) and for both orientations (Stimulus 1 and 2; all B > 0.071; all t(40) > 4, all $P < 0.001$; t-tests against 0)

    → participants overall showed a **repulsive cardinal bias**, which replicates and extends previous work with simpler stimuli (such as gratings)
  - A 2 × 2 repeated-measures ANOVA showed a **main effect of test** (Test 1/2; $F(1,40) = 19.743$, $P < 0.001$, $\eta 2 = 0.144$) indicating a **stronger bias on Test 2** and a **main effect of presentation order** (Stimulus 1/2; $F(1,40) = 4.669$, $P = 0.037$, $\eta 2 = 0.024$) with **no interaction between the two factors** ($F(1,40) = 1.083$, $P = 0.304$)
  - Overall pattern**: increase in cardinal bias with increasing mnemonic distance from stimulus presentation** ($t(40) = 5.315$, $P < 0.001$, $d = 0.830$, 95% CI (0.019, 0.043); t-test of linear slope against zero; Fig. 4b, left).

→ **robust cardinal repulsion in participants' overt memory reports, and this bias increased with periods of unattended storage**

Reflection of Cardinal Bias in Gaze Patterns

- Geometric model: distance structures for extreme cardinal repulsion (B = 1) and attraction (B = −1)



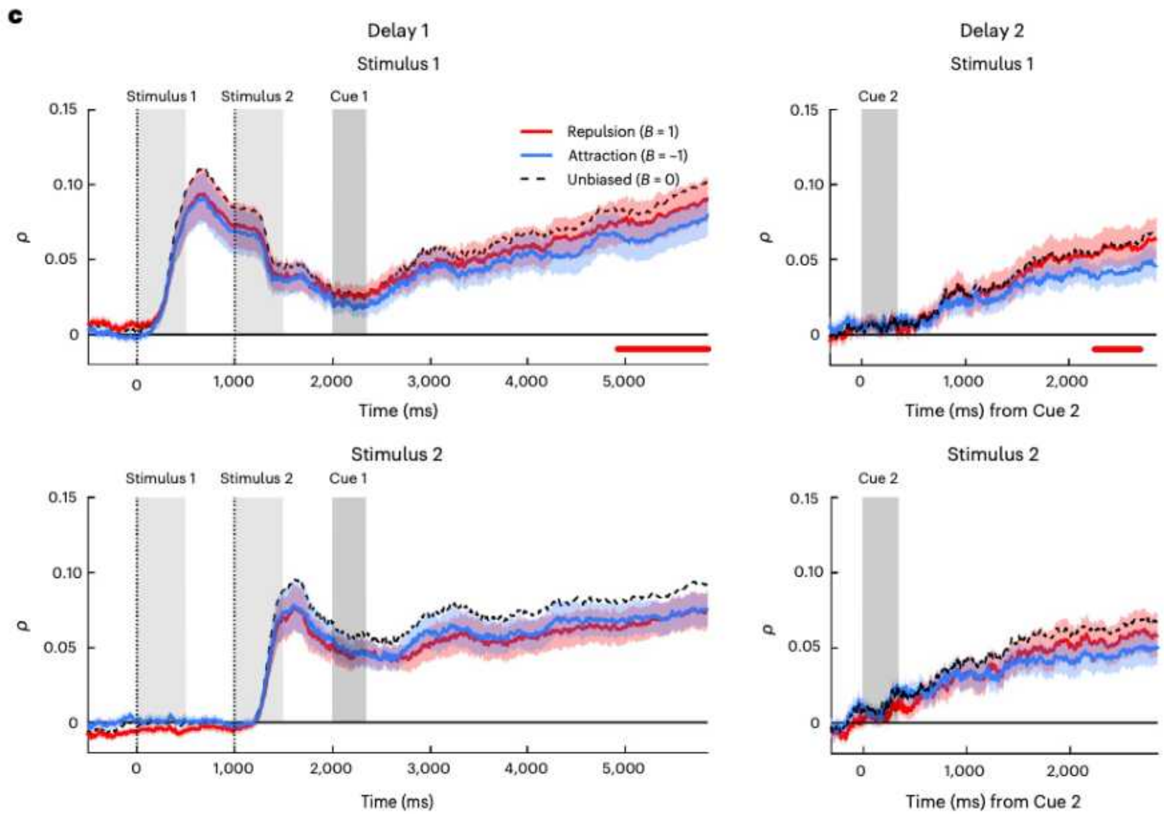
- If the gaze patterns were unbiased, we would expect both these ‘square’ models to correlate less well with the data than the unbiased (‘circle’) model (B = 0)
- If gaze patterns were repulsively biased, we would expect the repulsion model to outperform the attraction model, nearing or even exceeding the circle model (B = 0)

Reflection of Cardinal Bias in Gaze Patterns

- Time course of correlations with the repulsion and attraction models during the delay periods

→ **Gaze patterns may have carried a repulsive cardinal bias**

  - Most evidently during the **later portions of the WM delays**
  - And after temporary and/or partial **inattention** to the WM information



Reflection of Cardinal Bias in Gaze Patterns

- 3 Models (repulsion, unbiased, attraction) showed only small differences in correlation with the data
  - statistical power to detect bias in the gaze data was relatively low
- 2 small clusters indicating a repulsive bias near the end of the delay periods for Stimulus 1
- Main effect of presentation order indicating a stronger repulsive bias for the first presented orientation
- Complementary analysis in terms of mnemonic distance (Fig. 4b, right) showed a positive trend similar to that for behaviour

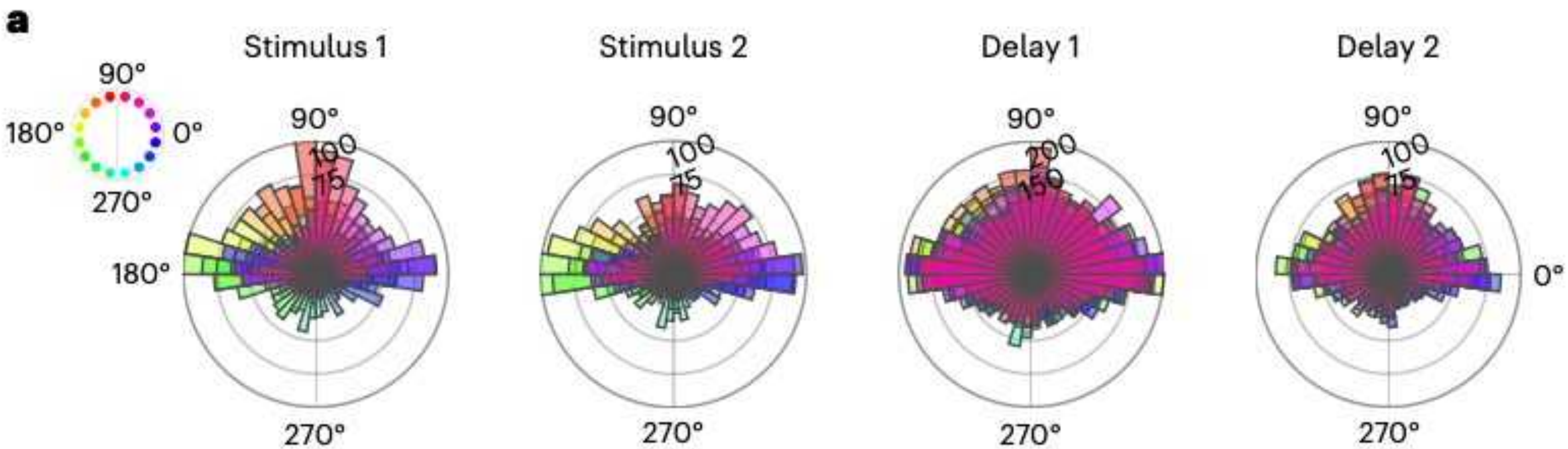
→ Although the differentiation of models (repulsive, unbiased, attractive) in the gaze data was not as clear-cut as in behaviour the **gaze patterns may have carried a repulsive cardinal bias**, most evidently during the **later portions of the WM delays** and after temporary and/or partial **inattention** to the WM information

Reflection of Cardinal Bias in Gaze Patterns

- Three models (repulsion, unbiased, attraction) showed only small differences in correlation with the data
  - The statistical power to detect bias in the gaze data was relatively low
  - Nevertheless, contrasting the repulsion model with the attraction model showed two small clusters (Pcluster = 0.02 and Pcluster = 0.035), indicating a **repulsive bias**, near the end of the delay periods for Stimulus 1
  - A similar tendency for Stimulus 2 failed to reach significance in Delay 2 (Pcluster = 0.085, below display threshold) and was absent in Delay 1 (no cluster-forming time points)
  - A 2 × 2 repeated-measures ANOVA on the difference between repulsion and attraction models (averaged across the last second of the delay periods) showed a **main effect of presentation order** (Stimulus 1/2; $F(1,40) = 4.561$, $P = 0.039$ $\eta 2 = 0.026$; main effect of Delay 1/2: $F(1,40) = 1.650$, $P = 0.206$; interaction: $F(1,40) < 1$) indicating a **stronger repulsive bias for the first presented orientation** (Stimulus 1)
  - Complementary analysis in terms of mnemonic distance showed a positive trend similar to that for behaviour, albeit only at the significance level of a one-tailed test ($t(40) = 1.772$, $P = 0.042$, $d = 0.278$, 95% CI lower bound −0.001; t-test of linear slope against zero; one-tailed, hypothesis derived from behavioural result)

Orientation-dependent Microsaccades

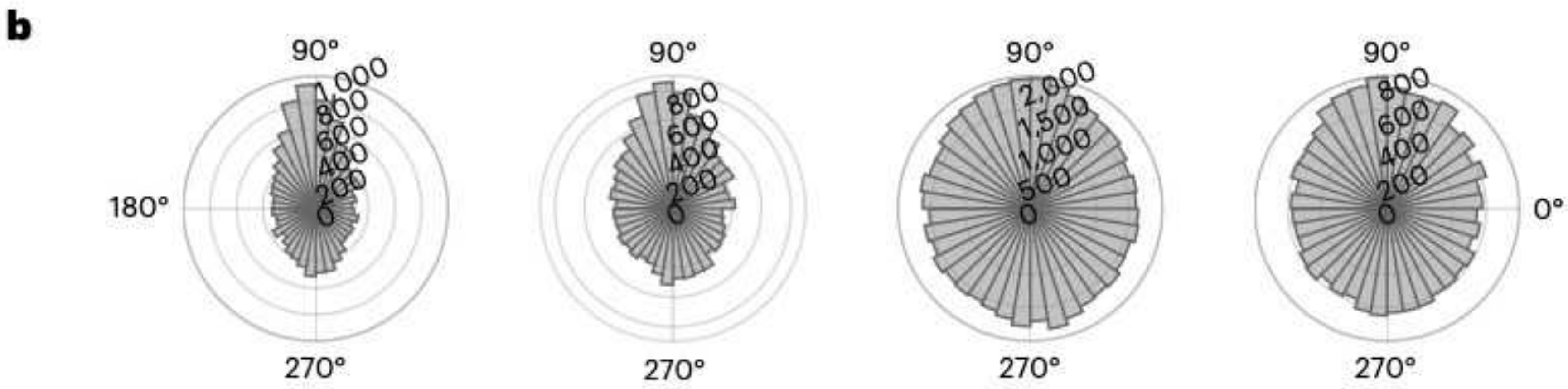
- Microsaccade detection with a velocity-based threshold



- Saccade directions in the poststimulus periods correlated positively with **stimulus orientation**
- Weakly positive correlations were also evident during the delay periods

Orientation-dependent Microsaccades

- Rotated trial data to illustrate the saccade directions relative to the objects' real-world (upright) orientation



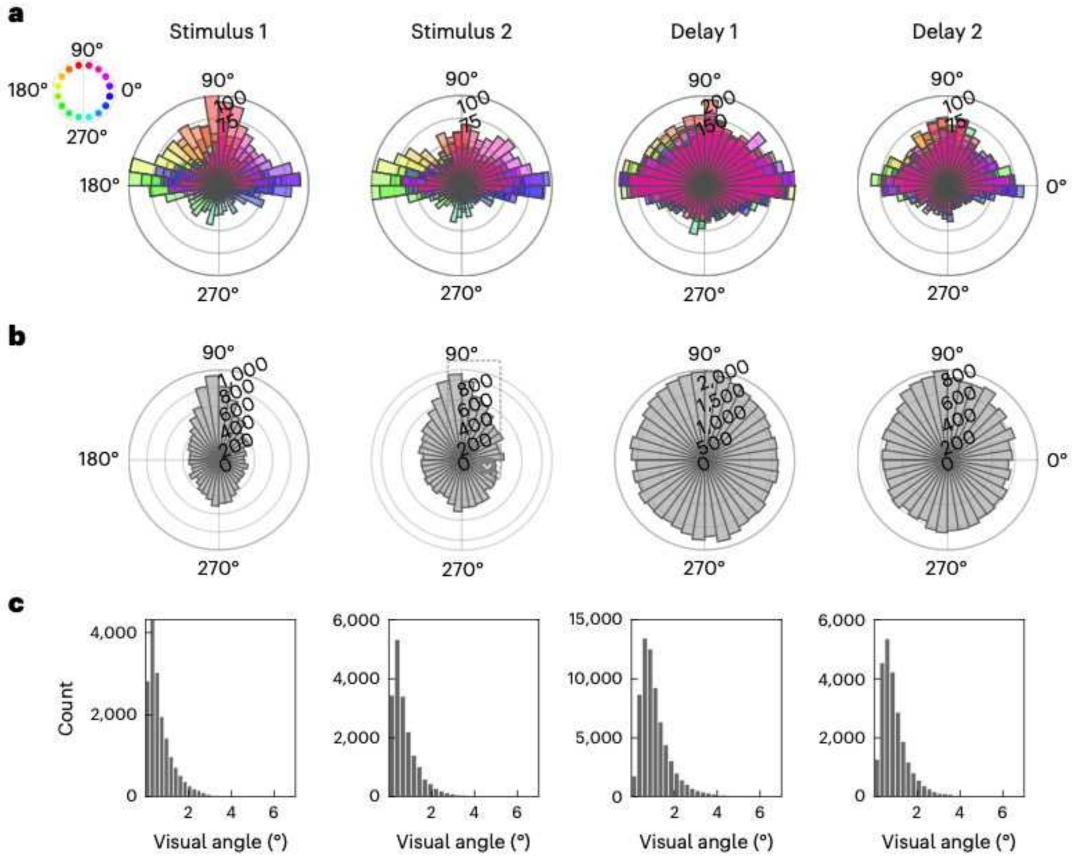
→ Effects observed in main analyses may have been related to **microsaccadic activity during attempted fixation**

Orientation-dependent microsaccades

- Saccade directions in the poststimulus periods correlated positively with stimulus orientation (circular correlation coefficients (R): Stimulus 1, $R = 0.089$; Stimulus 2, $R = 0.077$; both, $P < 0.001$). Weakly positive correlations were also evident during the delay periods (Delay 1, $R = 0.01$; Delay 2, $R = 0.03$; both, $P < 0.001$)
- For further inspection, we again rotated the trial data (analogous to Fig. 1b,c) to illustrate the saccade directions relative to the objects' real-world (upright) orientation
- As expected, if microsaccades reflected stimulus orientation, in all time windows, the aligned distributions were not uniform (Rayleigh tests for uniformity: all $z > 34.36$, all $P < 0.001$) but appeared egg-shaped, with a main peak near the object's real-world top (at 90°) and another, smaller peak near the opposite angle (270° , which may reflect 'return' microsaccades to fixation)

→ Together, these complementary results support the idea that the effects observed in our main analyses may have been related to microsaccadic activity during attempted fixation.

Orientation-dependent microsaccades



Discussion

WM Object Specificity

- Gaze patterns during perceptual processing were clearly object-specific
  - Indicating a **focus on concrete visual details**
- When the last-seen stimulus was immediately cued, some of this object specificity was sustained throughout the ensuing WM delay
- In contrast, for the first-presented stimulus, the object specificity dropped abruptly as soon as Stimulus 2 processing commenced
- Stimulus 1 encoding did continue throughout Stimulus 2 processing
  - However, its **format changed to object-independent** during the object-specific encoding of Stimulus 2

→ **Temporary (or partial) inattention may render the task-relevant WM information increasingly less ‘concrete’ and more generalized (or ‘abstract’)**

→ **Adaptive format changes in WM potentially provide fast protection from interference** beyond the overall reallocation of attention between different stimuli and/or tasks

Cardinal Repulsion Bias

- **Repulsive cardinal reporting bias increased** with the time a given stimulus had been temporarily unattended
  - More explicit semantic categorization (e.g. 'left'/'right' and 'up'/'down')
  - Increased reliance on semantics and/or (pre)verbal labels when restoring information from unattended storage → **higher level of abstraction**

Information Content of Microsaccades

- Miniature gaze deflections can disclose WM-associated phenomena (in addition to neural recordings)
  - Unlikely that results are attributable to reflexive saccades to the location of peripheral stimulus features
  - More likely reflect **microsaccadic activity during attempted fixation**
- Systematic microsaccade patterns have previously been linked to covert spatial attention
  - Reflection of **mental orienting** towards a spatial coordinate or direction

→ Participants generally **oriented attention towards the objects' real-life 'top',** but with varying degrees of bias **towards specific object features** (resulting in object-specific orientation patterns) and/or **away from cardinal axes** (resulting in cardinal repulsion)

Summary

- The **orientation of visual objects is robustly reflected in miniature gaze patterns** during cued WM maintenance
- The geometry of the gaze patterns undergoes **systematic changes**, indicating that **temporary inattention increased the level of abstraction** (and categorical bias) of the information in WM
- Stimulus-dependent eye movements may not only pose a potential confound but also be a **valuable source of information** in studying visuospatial WM

Questions