

Eye-movement replay supports episodic remembering

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1 **Eye-movement replay supports episodic remembering**

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14

1 **Abstract**

2 When we bring to mind something we have seen before, our eyes spontaneously reproduce a
3 pattern strikingly similar to that made during the original encounter. Eye-movements can then
4 serve the opposite purpose to acquiring new visual information; they can serve as self-generated
5 cues, pointing to memories already stored. By isolating separable properties within the closely
6 bound chain of where and when we look, we demonstrate that specific components of
7 dynamically reinstated eye-movement sequences, facilitate different aspects of episodic
8 remembering. We also show that the fidelity with which a series of connected eye-movements
9 from initial encoding is reproduced during subsequent retrieval, predicts the quality of the
10 recalled memory. Our findings indicate that eye movements are “replayed” to assemble
11 visuospatial relations as we remember. Distinct dimensions of these scanpaths differentially
12 contribute depending on the goal-relevant memory.

13

1 **Eye-movement replay supports episodic remembering**

2 Episodic memory refers to memories of events that we have experienced in a specific time and
3 place, allowing us to relive previous events with a considerable level of detail and specificity¹.
4 The formation of coherent episodic memories critically hinges upon the binding of
5 spatiotemporal relationships into a context, which largely depends on how we visually “sample”
6 the world when we act upon it via eye movements². Although only a limited amount of
7 information is processed at each sample, the sequence of eye movements effectively binds inter-
8 related episodic details together, allowing us to encode a memory representation of the event
9 as a whole^{3,4}. Thus, our visual sampling of the world is highly predictive of the content and
10 quality of episodic memory formation⁵⁻¹¹. Spontaneous eye movements also occur during
11 retrieval of episodic memories, even when there is no longer any relevant information present.
12 These have been demonstrated to largely reproduce the gaze patterns that were established
13 during encoding¹²⁻¹⁸. A prominent view holds that such gaze reinstatements actively support
14 episodic remembering¹⁹⁻²¹, and that eye movements may serve to assemble and organize
15 visuospatial relations across time and space into coherent memories^{12,13,21-25}. This has never
16 been directly demonstrated, however.

17

18 The claim that eye movements have a functional role during episodic remembering receives
19 support from previous research showing that the extent of encoding-retrieval overlaps in
20 fixation locations positively correlates with retrieval performance^{13,26,27}, and with neural
21 reactivation during retrieval^{28,29}. Extending such findings, it has been demonstrated that the
22 likelihood of successful remembering increases when gaze locations during recall are directly
23 manipulated to overlap with those from encoding³⁰⁻³⁴. While these findings clearly show that
24 where you look has important consequences for what you remember, they are all related to mere
25 *gaze positions*, and do not take into account how eye-movements are connected and unfold over

1 time. Also, active manipulations of gaze direction eliminate the spatiotemporal dynamics that
2 are characteristic of free viewing³⁵. To date, there is no evidence for the influential claim that
3 eye-movement reinstatement serves to facilitate episodic reconstruction by binding the
4 constituent parts of the recalled event together into its original spatiotemporal context^{12,16,21-26}.
5 To address this fundamental question, it is necessary to go beyond static gaze positions alone
6 and examine how the replay of whole sequences of connected eye movements – *scanpaths* –
7 may support episodic remembering.

8
9 In the present study, we tackle this issue head on by utilizing state-of-the-art scanpath similarity
10 techniques, capable of decomposing the encoding-retrieval overlap of scanpaths into distinct
11 spatiotemporal properties. It is then possible to examine the degree to which these properties
12 become reinstated during episodic retrieval. Participants encode 36 images with associated
13 verbal labels and subsequently recall each image while looking at a blank screen. In the recall
14 phase, a particular image is cued by its verbal label, and the quality of each episodic
15 reconstruction is rated with respect to overall memory, vividness and spatial accuracy (Fig. 1B).
16 To determine if individual scanpath properties objectively predict the strength and quality of
17 the mnemonic content during recall, our paradigm further combines those subjective ratings of
18 memory quality with a subsequent surprise forced-choice recognition test (Fig. 1B). Finally,
19 we use two types of image stimuli – scenes and object arrangements – to investigate if the
20 individual scanpath properties differentially contribute depending on the nature of the goal-
21 relevant memory. The scenes (N = 18) comprise highly predictable spatial relations between
22 meaningful scene elements, with relatively low demands on relational memory, whereas the
23 object arrangements (N = 18) comprise arbitrary spatial relations between their scene elements
24 (objects), with relatively high demands on relational memory (Fig. 1A). These two types of

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1 stimuli allow us to examine the relative contribution of different scanpath reinstatements as a
2 function of varying demands on relational memory²¹.

A. Stimuli examples

Scenes



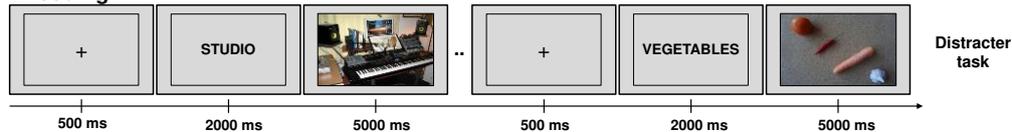
Object arrangements



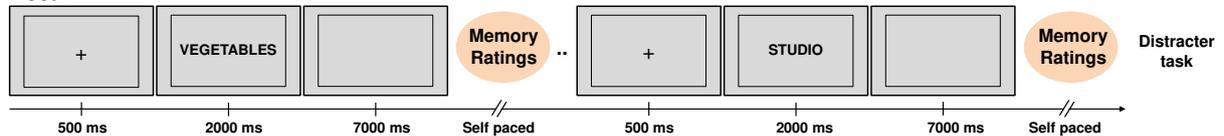
3

B. Experimental design

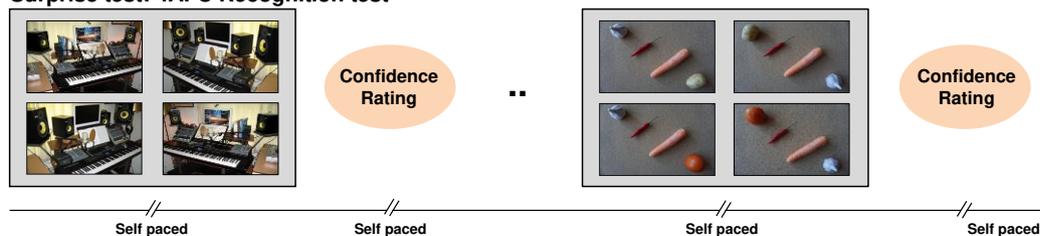
Encoding



Recall



Surprise test: 4AFC Recognition test



4

5 **Fig. 1 Encoding and retrieval of scenes and object arrangements.** (A) Example of stimuli images (Scenes:

6 studio, waterfalls, city street, office; Object arrangements: vegetables, cookies, bathroom things, lego). (B)

7 Experimental design. In an initial encoding phase, participants encode 36 images of the two stimuli types (18

8 scenes, 18 object arrangements), preceded by associated descriptive labels. In a subsequent recall phase, the

9 descriptive labels are presented as cues for memory retrieval, and participants recall each image while looking at

10 a blank screen. After each recollection, they rate the quality (overall memory, vividness, spatial accuracy) of

11 their recollection (0 – 100%). After a full round of encoding and recall, they then reach a surprise test, where

12 each encoded and recalled image is presented in a four-alternative forced-choice (4AFC) recognition task that

13 includes three similar distracters. Participants chose the specific image they believe they had encoded and

14 recalled, and rate their confidence in this selection (0 – 100%).

15

16 **Results**

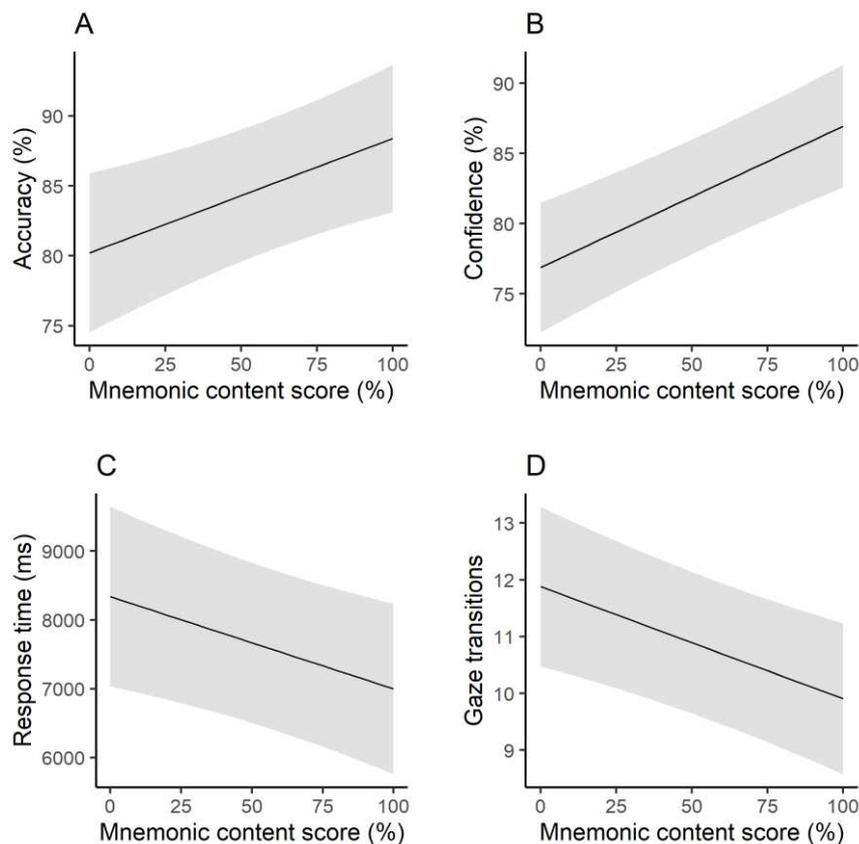
1 Behavioral results

2 We first sought to verify that the object arrangements were more demanding to recall than the
 3 scenes. As expected, mnemonic content was rated higher for scenes than object arrangements
 4 during recall, $\beta = 0.165$, ($SE = 0.0317$), $z = 5.22$, $p < .001$. For the surprise test, results
 5 revealed higher performance for scenes over four different measures of retrieval performance:
 6 response accuracy, $\chi^2(1) = 64.8$, $\beta = 2.17$, ($SE = 0.269$), $z = 8.05$, $p < .001$; confidence, $\chi^2(1) =$
 7 51.0 , $\beta = 0.175$, ($SE = 0.0245$), $z = 7.14$, $p < .001$; response time, $\chi^2(1) = 43.7$, $\beta = 4132$, (SE
 8 $= 625$), $z = 6.61$, $p < .001$; gaze transitions between options (a measure of choice certainty³⁶),
 9 $\chi^2(1) = 53.6$, $\beta = 4.62$, ($SE = 0.631$), $z = 7.32$, $p < .001$. Thus, these results demonstrate that
 10 the object arrangements, placing greater demand on relational memory, were indeed harder to
 11 recall than the scenes (see Table 1).

12 **Table 1 Object arrangements are more demanding to recall than scenes.** Mean values for the performance
 13 data during the recall phase and the surprise test, with standard deviations within brackets. The mnemonic
 14 content score represents the mean of the three subjective ratings (overall memory, vividness, spatial accuracy).
 15 Only correct trials were considered for confidence, response time and gaze transitions between options (a
 16 measure of choice certainty³⁶).

	<i>Total</i>	<i>Scenes</i>	<i>Object arrangements</i>
<i>Performance data</i>			
<i>Recall phase</i>			
Mnemonic Content Score (%)	58 (30)	66 (26)	49 (31)
<i>Surprise test</i>			
Accuracy (%)	85 (36)	95 (22)	75 (43)
Response time (ms)	7699 (6746)	5583 (5672)	9815 (7065)
Confidence (%)	78 (29)	90 (18)	66 (33)
Gaze transitions between options	10.8 (7.4)	8.5 (5.2)	13.2 (8.4)

1 We next tested if the mnemonic content score during recall predicted subsequent retrieval
 2 performance during the surprise test. Results reveal that the mnemonic content score was a
 3 significant predictor of all four measures of retrieval performance: response accuracy, $\chi^2(1) =$
 4 6.17, $\beta = 0.645$, ($SE = 0.260$), $z = 2.48$, $p = .013$; confidence, $\chi^2(1) = 27.4$, $\beta = 0.101$, ($SE =$
 5 0.0192), $z = 5.24$, $p < .001$; response time, $\chi^2(1) = 6.53$, $\beta = -1339$, ($SE = 524$), $z = -2.55$, $p =$
 6 .011; choice certainty, $\chi^2(1) = 11.8$, $\beta = -1.98$, ($SE = 0.575$), $z = -3.44$, $p < .001$. See Fig. 2A-D.
 7 Higher subjective ratings during the recall phase thus predicted more accurate, confident, faster
 8 and certain responses during the subsequent surprise test. We therefore conclude that the
 9 mnemonic content score during recall is a representative index of the memory quality during
 10 episodic remembering.

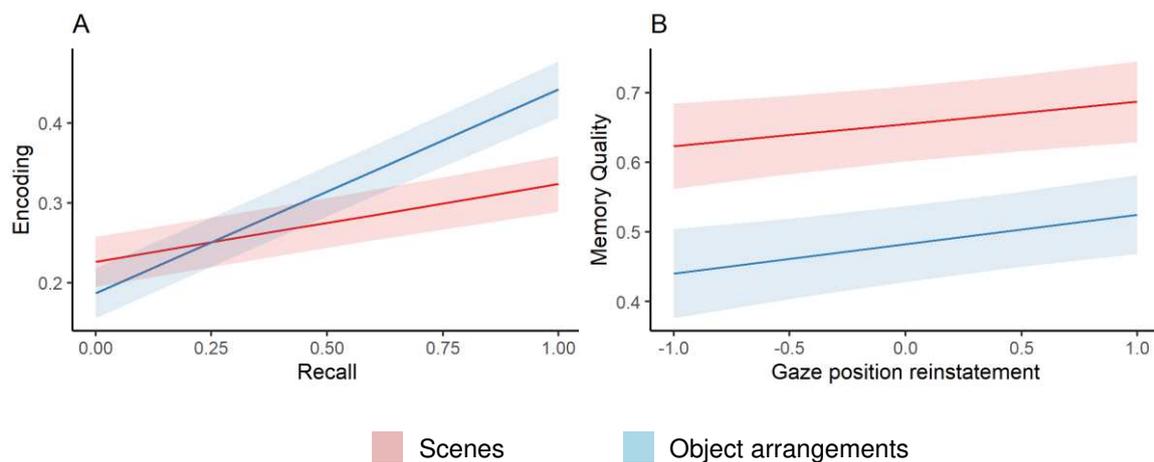


11
 12 **Fig 2 Memory quality during recall predicts subsequent recognition.** How the mnemonic content score from
 13 the recall phase predicted (A) accuracy, (B) confidence, (C) response time, and (D) choice certainty in the
 14 corresponding 4AFC recognition task. Error bars and shaded areas denote 95 % Confidence Intervals.

1

2 **Reinstatement of gaze positions during episodic remembering**

3 In the next step, we examined reinstatement of static position-based gaze, i.e., without
 4 considering the temporal succession of eye movements. Here, we found significant encoding-
 5 retrieval-overlap, and this effect was most pronounced for the more demanding object
 6 arrangements (Fig. 3A). Importantly, we also found that the degree of this reinstatement of
 7 gaze positions predicted the quality of episodic remembering (Fig. 3B). This corroborates
 8 what previous research has found^{13,26,27}, and provide further evidence that the reinstatement of
 9 gaze positions supports episodic remembering. An exhaustive presentation of this analysis is
 10 available as Supplementary material (supplementary details on results).



11

12 **Fig 3 Spatial gaze reinstatement.** (A) Reinstatement of gaze positions over the two image types (scenes,
 13 objects). The x- and y-axis corresponds to proportion gaze within the areas of interest on the presentation frame
 14 (see supplementary details on results). (B) The relationship between the degree of gaze position reinstatement
 15 and memory quality during recall. Shaded areas denote 95 % Confidence Intervals.

16

17

18 **Scanpath reinstatement during episodic remembering**

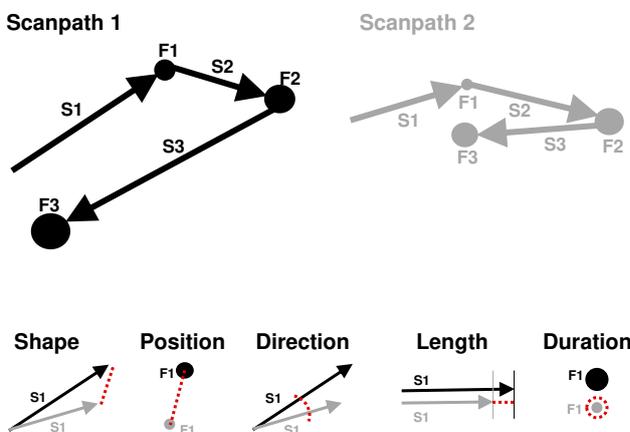
1 To achieve the central goals of the present study, we next investigated encoding-retrieval
 2 overlap in scanpaths, and how the reinstatement of dynamically unfolding eye movements
 3 may support episodic remembering.

4

5 To measure scanpath similarity between encoding and recall, we used MultiMatch (MM),
 6 which was introduced as a method for comparing scanpaths over different spatiotemporal
 7 dimensions³⁷, and has subsequently been validated, applied, and evaluated against other
 8 scanpath comparison tools^{35,38-41}. The basic principle is that the MM algorithm simplifies the
 9 two scanpaths under comparison (in this case, one from encoding and the other from recall)
 10 into virtualized sequences of saccadic vectors and then temporally aligns them with each
 11 other. Similarity between the temporally aligned scanpaths can then be separately determined
 12 for the MM-dimensions: (1) position, (2) shape, (3) direction, (4) length, and (5) duration. See
 13 Fig. 4A. The five MM-dimensions of scanpath similarity thus reflect different embodied
 14 connections between eye movements and memory, allowing us to not only investigate *if* a
 15 replay of connected eye movements supports episodic remembering, but also to scrutinize
 16 *how* qualitatively distinct aspects of such scanpaths influence this interplay.

17

A. Scanpath Similarity analysis (MultiMatch)



B. Examples of varying Encoding-Retrieval similarity

	Encoding	Recall	
i.			High Position High Shape High Direction High Length High Duration
ii.			Low Position High Shape Low Direction Low Length Low Duration
iii.			Low Position Low Shape High Direction Low Length Low Duration
iv.			Low Position Low Shape Low Direction Low Length Low Duration

18

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1 **Fig 4 Scanpath similarity.** (A) Overview of the MultiMatch scanpath similarity analysis. The top panel shows
2 two relatively similar scanpaths under comparison, where fixations are represented as dots (F1-F3) and saccades
3 as arrows between the fixations (S1-S3). Larger dots represent longer fixation duration. The bottom panel
4 illustrates differences over the five dimensions of shape, position, direction, length and duration for the first pairs
5 of aligned saccades (S1) and fixations (F1). The numeric difference between each dimension is illustrated with a
6 red dotted line for each dimension separately. The Position dimension relies on spatial coordinates in absolute
7 space and quantifies how similar aligned fixations are in respect to Euclidean distances. In contrast, the Shape,
8 Direction and Length dimensions rely on differences in relative space. The Shape dimension quantifies how
9 similar aligned saccadic vectors are in overall geometric shape, whereas the Direction dimension quantifies how
10 similar aligned saccadic vectors are in geometric angle. The Length dimension quantifies how similar aligned
11 saccades are in their absolute amplitude. The Duration dimension does not rely on any spatial coordinates and
12 quantifies how similar aligned fixations are in their duration. (B) Examples of varying encoding-retrieval
13 similarity: (i) complete encoding-retrieval overlap in respect to all five MM-dimensions; (ii) relatively high
14 encoding-retrieval similarity in Shape, but relatively low similarity in Position (due to dislocation in absolute
15 space during recall), Direction (due to large differences in saccadic angles during recall) , Length (due to overall
16 shorter saccades during recall), and Duration (due to overall longer fixation durations during recall); (iii) high
17 encoding-retrieval similarity in Direction, but low similarity in Shape (due to local differences in saccadic
18 lengths during recall), Position (due to dislocation in absolute space during recall), Length (due to
19 disproportional saccadic lengths during recall), and Duration (due to overall longer fixation durations during
20 recall); (iv) low similarity over all five MM-dimensions.

21
22 To determine if and how scanpaths from encoding become reinstated during recall, we first
23 calculated encoding-retrieval-similarity scores over all five MM-dimensions (Position, Shape,
24 Direction, Length, and Duration) by comparing the scanpaths produced by a participant
25 during the encoding of an image, with those produced during recall of the same image. See
26 Fig. 4B for examples of varying encoding-retrieval similarity over the five MM-dimensions.
27 Second, by comparing the scanpaths produced by a participant during the encoding of an
28 image with those produced during recall of all the other images from the same type (Scenes,

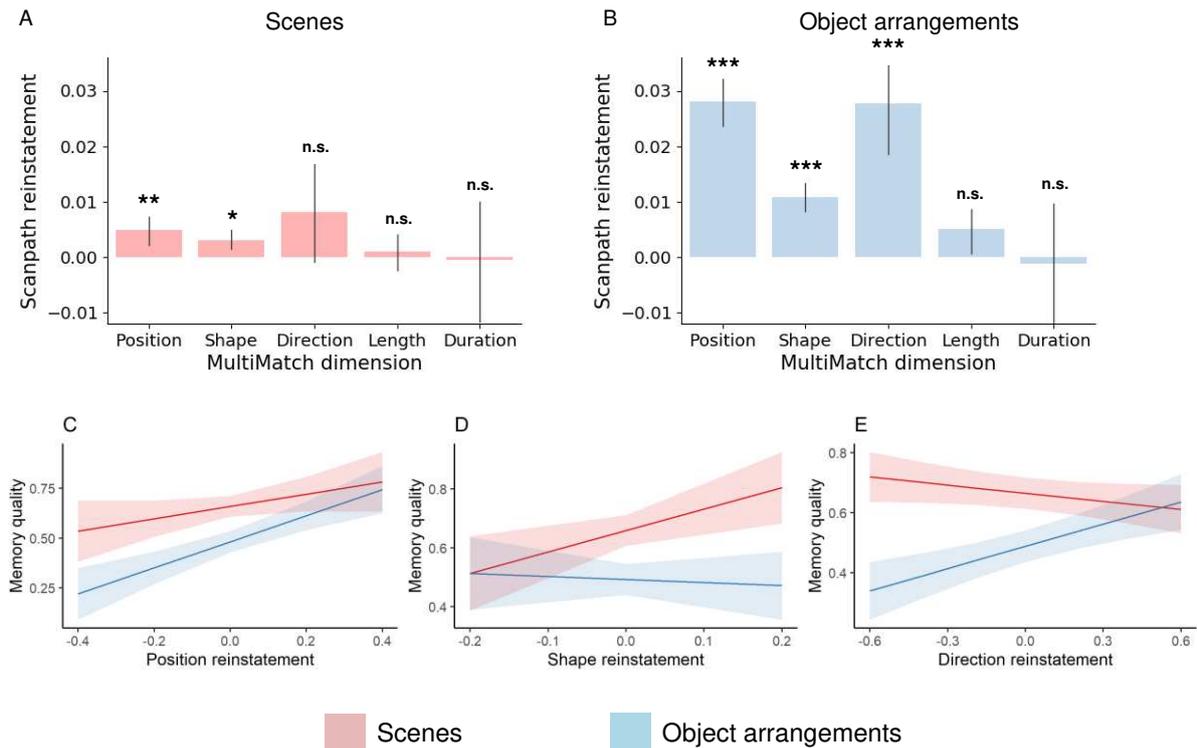
1 Object arrangements), and then averaging across the scores calculated for all images, we
2 acquired a Baseline Similarity score. This represents the average encoding-retrieval similarity
3 in scanpaths for each participant across images.

4
5 For the scenes, results revealed that the encoding-retrieval similarity score was significantly
6 higher than the baseline similarity score for position, $\chi^2(1) = 6.83$, $\beta = 0.0048$, ($SE = 0.0018$),
7 $z = 2.61$, $p = .009$, and shape, $\chi^2(1) = 5.70$, $\beta = 0.0030$, ($SE = 0.0013$), $z = 2.39$, $p = .017$. For
8 the object arrangements, results revealed that the encoding-retrieval similarity score was
9 significantly higher than the baseline similarity score for position, $\chi^2(1) = 148$, $\beta = 0.0278$,
10 ($SE = 0.0023$), $z = 12.2$, $p < .001$, shape, $\chi^2(1) = 55.8$, $\beta = 0.0106$, ($SE = 0.0014$), $z = 7.47$, $p <$
11 $.001$, and direction, $\chi^2(1) = 33.0$, $\beta = 0.0269$, ($SE = 0.0047$), $z = 5.74$, $p < .001$. Length and
12 duration were not significant predictors for either scenes or object arrangements ($\chi^2(1) < 2.30$,
13 $ps > .13$). See Fig. 5A-B. These results thus show that position, shape and direction are
14 scanpath properties that were reinstated during recall. However, direction reinstatement was
15 only observed for the object arrangements. Length and duration were not reinstated for either
16 case of image type. As the length and duration dimensions typically depend on visual
17 properties from the image^{40,42}, which are absent during recall, there is no particular reason to
18 expect encoding-retrieval similarity for either of those. Moreover, it is well known that
19 fixation durations become longer when there are no external features to look at¹².

20

21

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1
2

3 **Fig 5 Encoding-retrieval similarity over different scanpath dimensions.** Scanpath reinstatement over the five
4 dimensions for the (A) scenes and (B) object arrangements. The measure of scanpath reinstatement represents
5 the difference between encoding-retrieval similarity and baseline similarity (a value greater than zero indicates
6 scanpath reinstatement). (C) The relationship between encoding-retrieval similarity in position and memory
7 quality. (D) The relationship between encoding-retrieval similarity in shape and memory quality. (E) The
8 relationship between encoding-retrieval similarity in direction and memory quality. Error bars and shaded areas
9 denote 95 % Confidence Intervals, * $p < .05$, ** $p < .01$, *** $p < .001$.

10

11 **Functional relevance for episodic remembering**

12 In the final step, we then tested whether the degree of scanpath reinstatement for the significant
13 MM-dimensions (position, shape and direction) predicted the quality of episodic remembering
14 during the recall phase. To quantify the degree of scanpath reinstatement, we used a similar
15 rationale as Wynn, Ryan and Buchsbaum⁴³, and subtracted the Baseline Similarity score from
16 the Encoding-Retrieval-Similarity score for each MM-dimension over each participant and
17 image. The best model fit of memory quality revealed significant effects of image type, position

1 reinstatement, and significant interaction effects between image type and shape reinstatement,
 2 and between image type and direction reinstatement (Table 2). Greater position reinstatement
 3 predicted better memory quality independent of image type (Fig. 5C), whereas greater shape
 4 reinstatement only predicted better memory quality for the scenes (Fig. 5D), and greater
 5 direction reinstatement only predicted better memory quality for the object arrangements (Fig.
 6 5E).

7
 8 **Table 2 Scanpath reinstatement predicts memory quality.** Results of the best fit model of Memory Quality,
 9 with Image Type (Scenes, Object arrangements), and the significant MultiMatch dimensions (Shape, Position,
 10 Direction) as the independent variables. Participants and Images were modelled as random effects (intercepts).
 11 R-squared conditional = 0.37.

<i>Effects</i>	<i>B</i>	<i>SE</i>	<i>95% CI</i>	<i>t</i>	<i>p</i>
(Intercept)	0.578	0.022	0.533, 0.621	25.91	< .001 ***
Image Type	0.172	0.030	0.114, 0.229	5.83	< .001 ***
Shape Reinstatement	0.312	0.197	-0.075, 0.699	1.58	0.114
Position Reinstatement	0.480	0.116	0.254, 0.707	4.16	< .001 ***
Direction Reinstatement	0.079	0.043	-0.005, 0.162	1.84	0.066
Image Type × Shape Reinstatement	0.831	0.395	0.056, 1.606	2.10	0.036 *
Image Type × Position Reinstatement	-0.345	0.231	-0.798, 0.109	-1.49	0.136
Image Type × Direction Reinstatement	-0.336	0.085	-0.504, -0.169	-3.94	< .001 ***
		Variance	SD		
Random effects for Participant (Intercept)		0.0168	0.130		
Random effects for Image (Intercept)		0.007	0.082		
Model equation: Memory Quality ~ 1 + Image Type + Shape Reinstatement+ Position Reinstatement + Direction Reinstatement + Image Type × Shape Reinstatement + Image Type × Position Reinstatement + Image Type × Direction Reinstatement + (1 FP) + (1 Image)					
Total observations: 2017					

12
 13 The results thus show that independent of the mnemonic content, looking at locations (i.e.
 14 position reinstatement) in a similar order during retrieval as during the original encoding

1 predicts the quality of episodic remembering. The interaction effects demonstrate that shape
2 and direction reinstatement contributed differently depending on the mnemonic content.
3 General spatial structure (i.e. shape reinstatement) appears to be more important when
4 reconstructing the more predictable spatial relations in the scene images. Conversely, the
5 particular heading of eye movements (i.e. direction reinstatement) appears to be more important
6 when reconstructing the arbitrary spatial relations in the object arrangements.

7

8 **Facilitating remembering or a consequence of the memory representation?**

9 While the results indicate a functional role of scanpath reinstatements in episodic
10 reconstruction, an alternative explanation is that greater reinstatement is a consequence of
11 having a strong memory representation. To disambiguate between those two explanations, we
12 sought to determine whether scanpath reinstatements depends on how well the images are
13 initially encoded into memory. Previous research has established that the cumulative number
14 of fixations during encoding is a reliable index of how well a visual stimulus is encoded into
15 memory⁵⁻¹¹. Thus, to account for effects of encoding strength, we added the cumulative
16 number of study fixations on each image into our model. The model was significantly
17 improved, $\chi^2(1) = 24.90, p < .001$. All previous effects and interaction effects were significant
18 also in this model, and as expected, the cumulative number of study fixations significantly
19 predicted memory quality during recall, $\beta = 0.008, (SE = 0.002), z = 4.99, p < .001$, which
20 confirms the validity of this measure as an index of encoding strength. Interactions of number
21 of study fixations and the other predictors (position reinstatement, shape reinstatement,
22 direction reinstatement, image type), were then stepwise added to the model. Importantly,
23 none of those interactions significantly improved the model (p -values $> .19$). Thus, the
24 reported effects of scanpath reinstatements upon memory quality do not reduce to how well
25 the images were originally encoded into memory. Instead, our results substantiate the idea that

1 the replay of eye movements supports the reconstruction of inter-related and task-relevant
2 mnemonic features into a spatiotemporal context.

3

4 **Discussion**

5 Corroborating previous research^{13,26 27,30,31} we found that encoding-retrieval similarity in gaze
6 locations predicts the fidelity of episodic remembering. State-of-the-art scanpath-similarity
7 techniques (MultiMatch³⁵) allowed us to move beyond this to examine reinstatement of
8 qualitatively different scanpath properties during episodic reconstructions. Of central
9 importance, we provide evidence that the replay of eye movement behavior, over-and-above
10 static position-based gaze, supports episodic remembering and that different spatiotemporal
11 properties of the unfolding scanpaths differentially contribute depending on the nature of the
12 goal-relevant memory. Specifically, we found that encoding-retrieval overlaps in scanpath
13 shape contribute more to reconstructing the memory of a global scene structure; whereas
14 encoding-retrieval overlaps in scanpath direction contribute more to reconstructing particular
15 object arrangements. Finally, we provide evidence that these scanpath reinstatement effects on
16 episodic remembering are not simply a consequence of how well the event was originally
17 encoded.

18

19 The claim that gaze behavior actively supports episodic recollection dates back to (at least)
20 Ulric Neisser and Donald Hebb. Neisser argued that eye movements – or the processes that
21 drives them – are actively associated with the construction of a visual memory²³, and Hebb
22 claimed that eye movements are necessary to assemble and organize “part images” into a whole
23 visualized image²². Such ideas were further developed in Noton and Stark’s Scanpath Theory,
24 which states that memories are stored in a “feature ring”, comprising visual features and the
25 sequence of eye movements (scanpaths) linking them together^{24,25}. Scanpath Theory holds that

1 (1) eye movements during recall play out in the same sequential order as during encoding, and
2 (2) such scanpath replay serves a functional role in episodic remembering. While a strong
3 interpretation of Scanpath Theory, where memory is accompanied by an exact and full scanpath
4 recapitulation, has been refuted in more recent research^{16,21,44}, there is extensive evidence that
5 episodic remembering involves eye movements that largely reproduce gaze patterns at
6 encoding^{12-16,26,28}. Thus, the first tenet of Scanpath Theory, that episodic remembering is
7 accompanied by scanpath replay, is well established in the literature, and gains further support
8 from the present study. However, there is to date virtually no evidence for the second tenet, that
9 scanpath reinstatements play a functional role in episodic memory retrieval. Recent work has
10 demonstrated that gaze reinstatements promote cortical reconstruction^{28,29} and successful
11 remembering^{13,26,27,30-34}. However, these findings are all related to static position-based gaze
12 and shed no light upon the proposition that unfolding sequences of connected eye movements
13 reconstruct and bind spatiotemporal information into a coherent memory. Interesting recent
14 research on recognition memory shows that a temporal replay of gaze patterns can support
15 recognition performance^{45,46}. Still, recognition tasks involve situations where all encoded
16 information is available as a “copy cue”, and where visual information accumulates until
17 sufficient evidence is available to solve the old/new-discrimination task. The purpose of visual
18 exploration under such conditions is thus considerably different from a recall task, where the
19 rememberer needs to mentally reconstruct the complete spatiotemporal properties of a prior
20 event without supporting visual input⁵. Here, we present direct evidence that a temporal replay
21 of eye movements plays an active role in episodic reconstruction in a pure recall task.

22

23 Recently, Wynn and colleagues proposed that eye movements support active memory retrieval
24 by broadly reinstating the spatiotemporal context based on current task demands and available
25 cognitive resources²¹. The idea that the facilitatory role of gaze reinstatements increases with

1 task demands has been supported by their studies on older adults²⁷ and task difficulty⁴³. Further
2 support comes from the present findings where more extensive scanpath reinstatements were
3 seen during the reconstruction of the object arrangements as compared to the scenes. The scenes
4 comprised predictable spatial relations between meaningful elements due to schematic and
5 situational knowledge for the common scenarios, and memory for such information poses
6 relatively low demands on relational memory. Reconstruction of such an event should involve
7 a rather coarse arrangement of key elements within the overall context, which was also
8 supported by the finding that the general spatial structure of the scanpath (position and shape)
9 contributed to successful remembering. The object arrangements, on the other hand, comprised
10 arbitrary spatial relations among scene elements (objects), which puts relatively high demands
11 on relational memory. The ensuing reconstruction should require a more precise arranging of
12 the objects into an ordered context, which was supported by the finding that the scanpath
13 properties of position and direction contributed to successful remembering.

14

15 A vast amount of research has demonstrated that the hippocampus plays a critical role in
16 binding information in space and time during memory formation, and it is assumed that the
17 hippocampus stores an event index, pointing to the cortical representations of each aspect of
18 the whole event (for a review see ref. ⁴⁷). Remembering depends on a retrieval cue matching
19 the hippocampal index, which in turn triggers pattern completion and the reactivation of the
20 cortical traces (and thus the experience of remembering the original event). Based on this
21 cortical-hippocampal interplay, a prominent view holds that the reconstruction of past events
22 fundamentally relies on mental simulations that reinstate approximations of the sensorimotor
23 processes that characterized the original event^{48,49}. Successful episodic remembering is
24 considered to depend on the overlap between available retrieval cues and stored memory
25 traces⁵⁰. Compatibility between the processes triggered by a retrieval cue and those engaged

1 during encoding increases the likelihood of successful retrieval^{50,51}. As previous research has
2 demonstrated that gaze behavior during encoding and retrieval are linked to activity in the
3 hippocampus⁵²⁻⁵⁵, and that gaze reinstatement correlates with neural reactivation^{28,29}, it is
4 conceivable that the scanpath replay reported here is responsible for promoting cortical-
5 hippocampal reactivation of visuospatial relations during episodic memory reconstruction. The
6 successive reinstatement of eye movements may act as internally generated retrieval cues that
7 continuously updates in an iterative fashion as the rememberer moves his/her eyes during the
8 pattern completion process. In situations with high demands on relational memory, as for the
9 recollection of the object arrangements, more specified retrieval cues would be required during
10 the pattern completion process, as compared to the less demanding scenes, where the pattern
11 completion process would be supported by more predictable scene semantics.

12

13 **Conclusion**

14 Reinstatement of gaze positions has proven important for episodic remembering. The present
15 study extends this finding and provides direct evidence that the actual replay of eye movements
16 unfolding over time facilitates episodic remembering, and that specific spatiotemporal scanpath
17 properties differentially contribute depending on the nature of the goal-relevant memory.

18

19 **Methods**

20 **Participants**

21 Sixty-two healthy adults participated in the experiment. Two were removed owing to
22 extensive data loss and technical problems, leaving sixty participants (34 females; mean age
23 25.2, SD 6.4). Power analyses⁵⁶ for bivariate measures of association indicated that our
24 sample size should be sufficient to detect a large correlation ($r = 0.5$) and difference between
25 means ($d = .6$) with 90% power ($\alpha = 0.05$), which is in line with prior work on gaze

1 reinstatement^{16,26} and scanpath similarity³⁹. All participants were fluent in Swedish and had
2 normal or corrected-to-normal vision. Participants gave written informed consents and were
3 compensated with a cinema voucher. All methods were conducted in accordance with the
4 Swedish Act concerning the Ethical Review of Research involving Humans (2003:460).

5

6 **Data Acquisition and Materials**

7 Gaze data was recorded from both eyes individually, using a Sensory Motoric Instruments
8 (SMI RED-M) eye tracker, running iView X 2.7 software and sampling at 120 Hz. A Dell
9 Optiplex 755 PC presented stimuli using PsychoPy⁵⁷ on a 22'' monitor with a resolution of
10 1680 × 1050 pixels. Participants were seated with their heads in a chin and forehead rest, 65
11 cm away from the monitor. Calibration and validation of gaze data was conducted prior to
12 each participant's experimental session. Spatial accuracy during validation across all
13 participants was 0.53 ± 0.22 degrees (x offset), and 0.48 ± 0.22 (y offset) (M±SD). Spatial
14 precision was computed for each participant as the root-median-square (RMS) of inter-sample
15 distances for all recorded samples. The average RMS value across all participants was $0.10 \pm$
16 0.19 degrees (x offset), and 0.08 ± 0.15 degrees (y offset) (M±SD). Proportion data loss was
17 defined as all lost samples divided by the total number of samples. Proportion data lost across
18 all participants was 0.05 ± 0.14 (M±SD). Fixations were detected with the I2MC algorithm⁵⁸.
19 Stimuli comprised 18 scenes and 18 object arrangements that were presented in a frame that
20 covered 80% of the monitor (see Fig. 1B). The scenes were taken from the MIT test set
21 Cat2000 <http://saliency.mit.edu/datasets.html>⁵⁹ and the object arrangements were photographs
22 shot for this particular study (available here: <https://osf.io/d9zng/>).

23

24 The content of the scene images comprised an equal amount of indoor and outdoor global
25 scenes, where the spatial relations among scene elements were highly congruent in respect to

1 the image's semantic structure. The content of the object arrangement images comprised four
2 separate objects from the same category, where the spatial relations between the objects were
3 completely arbitrary in respect to the image's semantic structure. The 18 object arrangements
4 all comprised unique spatial configurations (see Fig. 1A; complete set of images available
5 here: <https://osf.io/d9zng/>). In contrast to the scene images, we thus had full experimental
6 control over the spatial relations among individual scene elements (objects) in the object
7 arrangement images.

8

9 **Design and procedure**

10 The experiment was divided into three phases: encoding, recall, and surprise test (see Fig.
11 1B). To conceal the true objective of the study, participants were told that the experiment
12 concerned pupil dilation in relation to mental workload, and it was explained that their eyes
13 were filmed for this matter.

14

15 **Encoding phase.** Participants encoded 36 images accompanied by a verbal label that
16 preceded each image. The verbal label described the semantic content of the succeeding
17 image (e.g., “studio”, “vegetables”). The images comprised two different types: scenes (n =
18 18) and object arrangements (n = 18) and were each presented for 5 s in randomized order.
19 Participants were instructed to memorize each image as thoroughly as possible (see Fig. 1A).
20 When the encoding phase finished, participants engaged in a distracter task, where they were
21 to count backwards in steps of 3 from a randomly generated three-digit number for 12 s.

22

23 **Recall phase.** Participants recalled all 36 encoded images while looking at a blank screen.
24 Participants were cued by the associated verbal label (preceding the blank screen) in a
25 randomized order and were then instructed to recall and visualize the corresponding image in

1 as much detail as possible while looking at the blank screen. The blank screen remained for 7
2 s. After each recollection, participants were to rate the quality of their recollection based on
3 overall memory, vividness and spatial accuracy. Overall memory was rated on a scale 0-100%
4 in relation to the statement “It was easy for me to remember the image”. Vividness was rated
5 on a scale 0-100% in relation to the statement “My mental image was clear, vivid and detailed
6 – almost as if I could see the image in front of me”. Spatial accuracy was rated on a scale 0-
7 100% in relation to the statement “I could indicate, with high spatial accuracy, where different
8 objects/scene elements were located in the image”. See Table 1. Based on a mean of those
9 three ratings, a Mnemonic Content Score was calculated for each image and participant.

10

11 **Surprise test.** Participants completed four-alternative forced-choice (4AFC) recognition tests
12 that covered all 36 images presented during encoding. Participants were not aware that they
13 would engage in this test beforehand. The target image and three different distracter images
14 were presented in the four quadrants of the screen, and participants were instructed to select
15 the image they had encoded and recalled as accurately and quickly as possible. After each
16 selection, participants rated how confident (0-100%) they were in their choice. For the scenes,
17 the distracter images comprised: (1) a horizontal flip of the target image; (2) a similar lure
18 image; and (3) a horizontal flip of the lure image. For the object arrangements, the distracter
19 images comprised: (1) a lure image, where two of the original objects had switched locations;
20 (2) a lure image, where one of the objects had been exchanged with another semantically
21 congruent object; and (3) a lure image, where one of the objects had been exchanged with the
22 other semantically congruent object, and also the location of this new object had been
23 switched with one of the other objects.

24

1 The present experimental design allowed us to collect *spontaneous eye movements* during
2 recall, and to use the surprise test to evaluate the validity of the subjective ratings as a
3 measure of recall success.

4

5 **Statistical analyses**

6 All data were analyzed using generalized linear mixed-effects models (GLMM; glmer of
7 package lme4⁶⁰) and linear mixed-effects models (LMEM), where participants and images
8 were modelled as random effects (intercepts). In order to describe the model-fit of an
9 independent variable, the deviance of the proposed model was contrasted against an
10 unconditional null model, including only the intercept and the random factors. When building
11 models with several independent variables, we used a backward selection approach, starting
12 with a maximal model, which included all variables and their interactions. We then used
13 likelihood-ratio tests to compare models and then step-by-step removed non-significant
14 effects until no further model changes resulted in a significant likelihood-ratio test.

15

16 **Author contributions**

17 R.J. and M.J. conceived the study. R.J. designed the study. R.J., M.N., and R.D. implemented
18 and conducted the experiment. R.J. and M.N. analyzed the data. R.J. and M.J. wrote the
19 manuscript, with comments and edits by R.D. and M.N.

20

21

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1

2 **Additional information**

3 **Supplementary information** includes supplementary details on results

4 **Correspondence and requests for materials** should be addressed to R.J.

5 **Competing interests**

6 The authors declare no competing interests

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Figures

A. Stimuli examples

Scenes

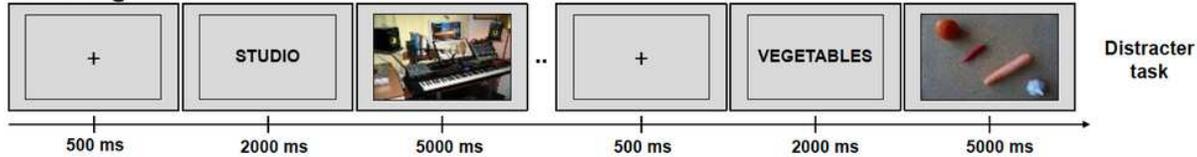


Object arrangements

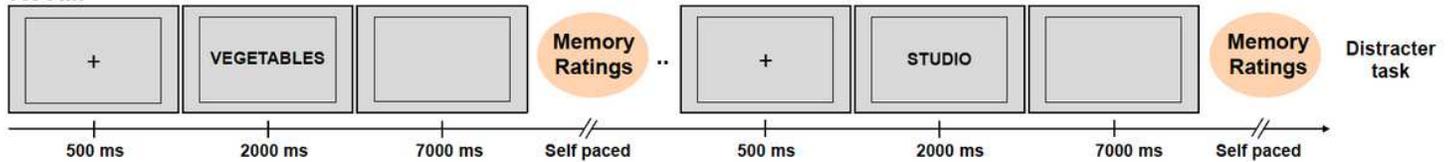


B. Experimental design

Encoding



Recall



Surprise test: 4AFC Recognition test

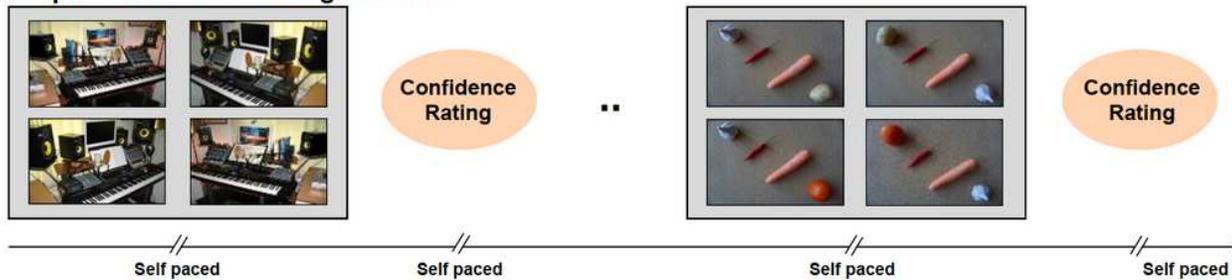


Figure 1

Encoding and retrieval of scenes and object arrangements. (A) Example of stimuli images (Scenes: studio, waterfalls, city street, office; Object arrangements: vegetables, cookies, bathroom things, lego). (B) Experimental design. In an initial encoding phase, participants encode 36 images of the two stimuli types (18 scenes, 18 object arrangements), preceded by associated descriptive labels. In a subsequent recall phase, the descriptive labels are presented as cues for memory retrieval, and participants recall each image while looking at a blank screen. After each recollection, they rate the quality (overall memory, vividness, spatial accuracy) of their recollection (0 – 100%). After a full round of encoding and recall, they then reach a surprise test, where each encoded and recalled image is presented in a four-alternative forced-choice (4AFC) recognition task that includes three similar distracters. Participants chose the specific image they believe they had encoded and recalled, and rate their confidence in this selection (0 – 100%).

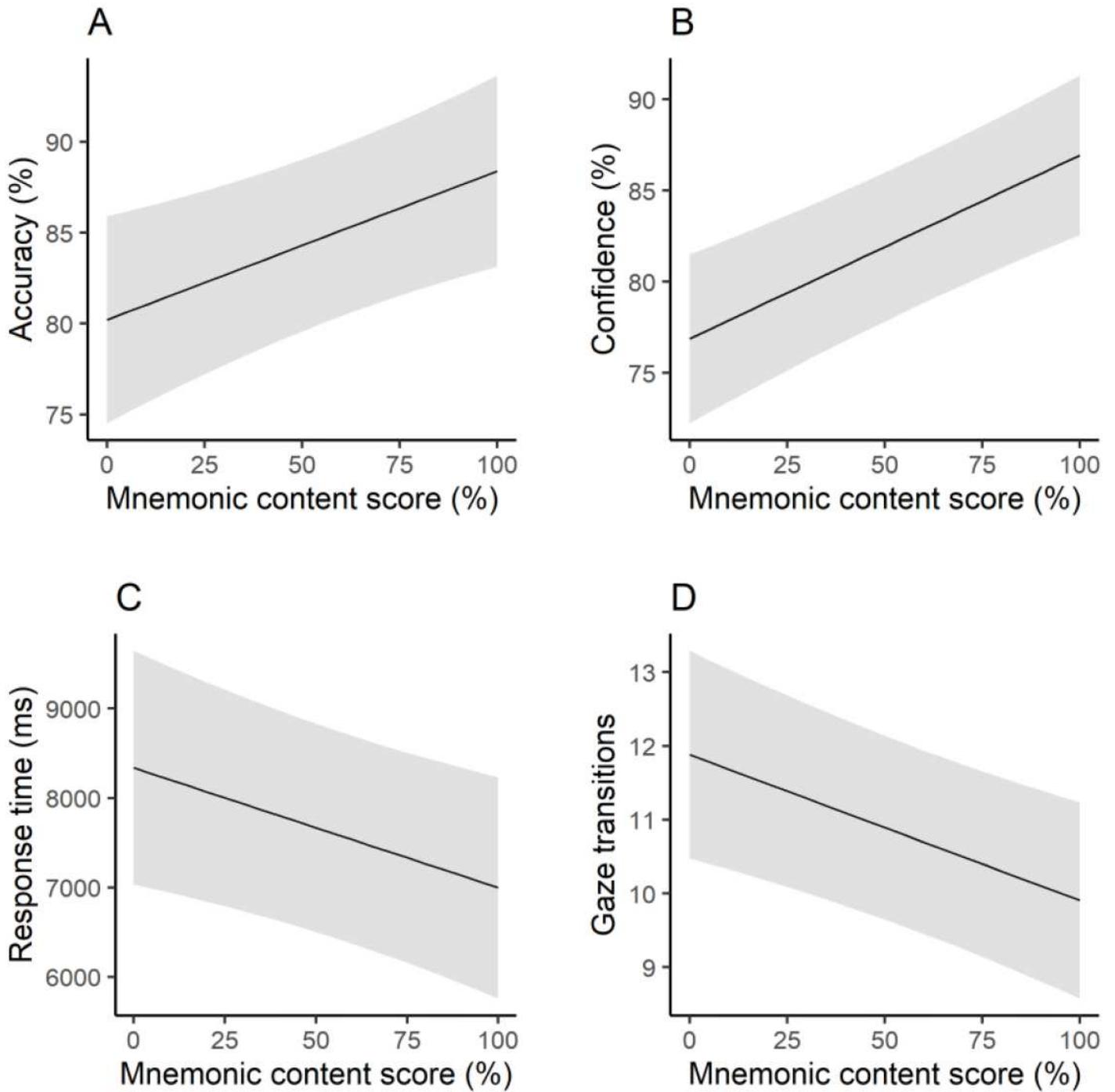


Figure 2

Memory quality during recall predicts subsequent recognition. How the mnemonic content score from the recall phase predicted (A) accuracy, (B) confidence, (C) response time, and (D) choice certainty in the corresponding 4AFC recognition task. Error bars and shaded areas denote 95 % Confidence Intervals.

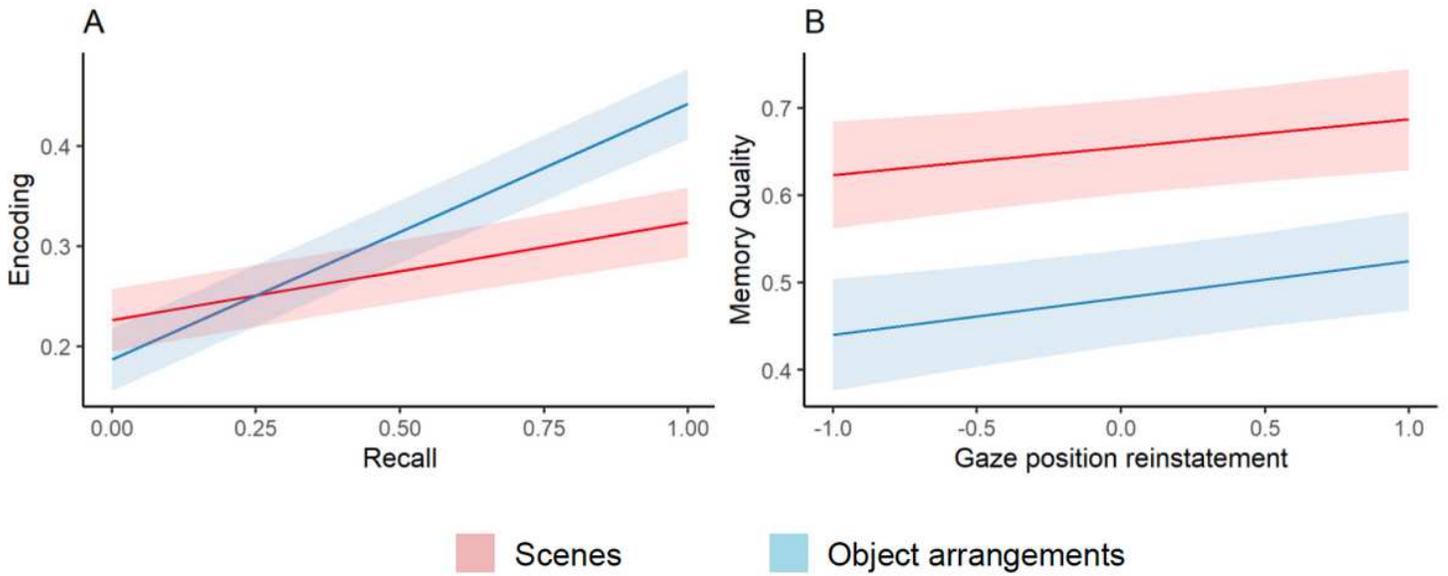
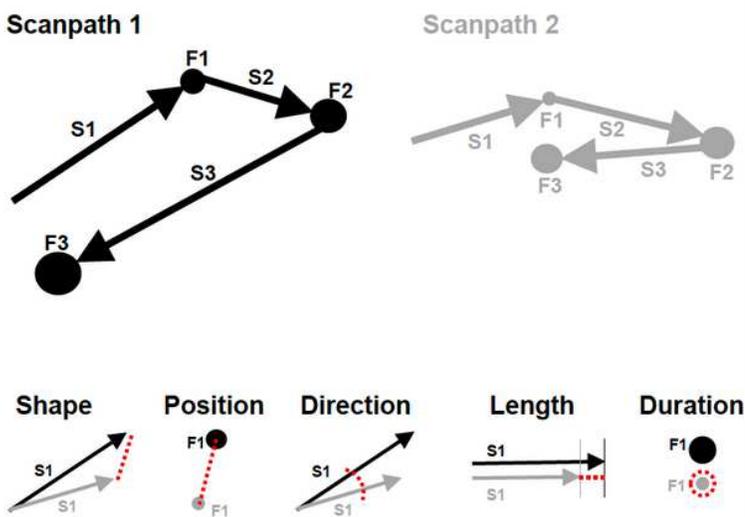


Figure 3

Spatial gaze reinstatement. (A) Reinstatement of gaze positions over the two image types (scenes, objects). The x- and y-axis corresponds to proportion gaze within the areas of interest on the presentation frame (see supplementary details on results). (B) The relationship between the degree of gaze position reinstatement and memory quality during recall. Shaded areas denote 95 % Confidence Intervals.

A. Scanpath Similarity analysis (MultiMatch)



B. Examples of varying Encoding-Retrieval similarity

	Encoding	Recall	
i.			High Position High Shape High Direction High Length High Duration
ii.			Low Position High Shape Low Direction Low Length Low Duration
iii.			Low Position Low Shape High Direction Low Length Low Duration
iv.			Low Position Low Shape Low Direction Low Length Low Duration

Figure 4

Scanpath similarity. (A) Overview of the MultiMatch scanpath similarity analysis. The top panel shows two relatively similar scanpaths under comparison, where fixations are represented as dots (F1-F3) and

saccades as arrows between the fixations (S1-S3). Larger dots represent longer fixation duration. The bottom panel illustrates differences over the five dimensions of shape, position, direction, length and duration for the first pairs of aligned saccades (S1) and fixations (F1). The numeric difference between each dimension is illustrated with a red dotted line for each dimension separately. The Position dimension relies on spatial coordinates in absolute space and quantifies how similar aligned fixations are in respect to Euclidean distances. In contrast, the Shape, Direction and Length dimensions rely on differences in relative space. The Shape dimension quantifies how similar aligned saccadic vectors are in overall geometric shape, whereas the Direction dimension quantifies how similar aligned saccadic vectors are in geometric angle. The Length dimension quantifies how similar aligned saccades are in their absolute amplitude. The Duration dimension does not rely on any spatial coordinates and quantifies how similar aligned fixations are in their duration. (B) Examples of varying encoding-retrieval similarity: (i) complete encoding-retrieval overlap in respect to all five MM-dimensions; (ii) relatively high encoding-retrieval similarity in Shape, but relatively low similarity in Position (due to dislocation in absolute space during recall), Direction (due to large differences in saccadic angles during recall), Length (due to overall shorter saccades during recall), and Duration (due to overall longer fixation durations during recall); (iii) high encoding-retrieval similarity in Direction, but low similarity in Shape (due to local differences in saccadic lengths during recall), Position (due to dislocation in absolute space during recall), Length (due to disproportional saccadic lengths during recall), and Duration (due to overall longer fixation durations during recall); (iv) low similarity over all five MM-dimensions.

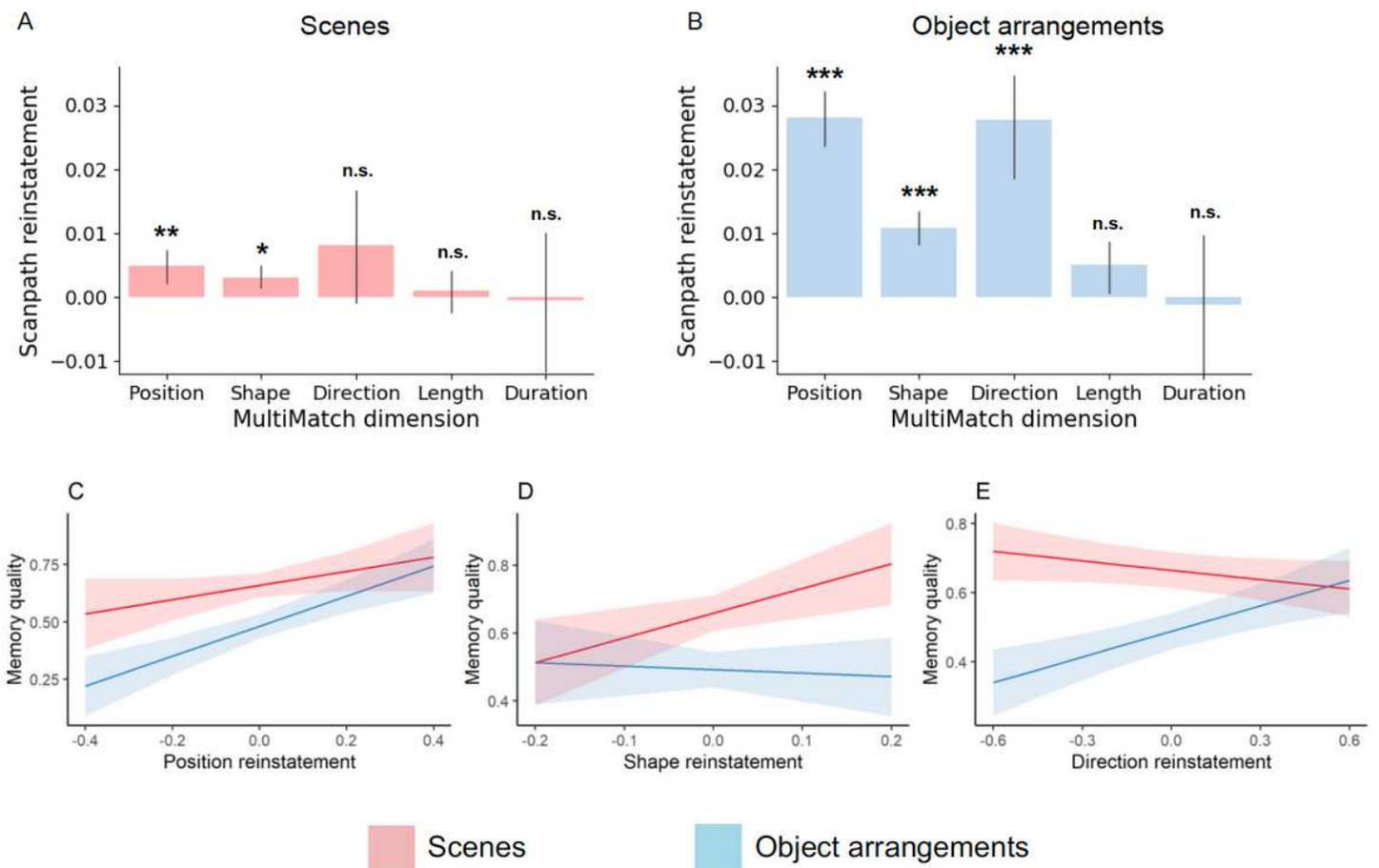


Figure 5

Encoding-retrieval similarity over different scanpath dimensions. Scanpath reinstatement over the five dimensions for the (A) scenes and (B) object arrangements. The measure of scanpath reinstatement represents the difference between encoding-retrieval similarity and baseline similarity (a value greater than zero indicates scanpath reinstatement). (C) The relationship between encoding-retrieval similarity in position and memory quality. (D) The relationship between encoding-retrieval similarity in shape and memory quality. (E) The relationship between encoding-retrieval similarity in direction and memory quality. Error bars and shaded areas denote 95 % Confidence Intervals, * $p < .05$, ** $p < .01$, *** $p < .001$.

Supplementary Files

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- [NatBehavSupplMatJohanssonetal2010VRSCanpaths20210222.docx](#)