Neural dynamics of relational memory retrieval across eye movements

Andrey R. Nikolaev, Roger Johansson, Inês Bramão, Mikael Johansson

Lund Memory Lab, Department of Psychology, Lund University, Lund, Sweden

Correspondence: Andrey R. Nikolaev (andrey.nikolaev@psy.lu.se) ORCID: 0000-0001-5126-8566

Abstract

Relational memory retrieval involves a dynamic interplay between eye movements and neural activity, yet the timing of these processes remains unclear. This study investigates how theta and alpha EEG activity align with sequential fixations during relational memory retrieval. Participants performed a two-alternative forced-choice associative memory task while their eye movements and EEG were simultaneously recorded. Results reveal a relational eye-movement effect, with correctly remembered target elements disproportionately viewed during later fixations in the retrieval sequence. Time-frequency EEG analyses across the test interval show that successful retrieval was characterized by an early transient increase in theta power and a sustained decrease in alpha power. Fixation-related analyses linked these effects to specific retrieval processes: the theta increase emerged during the first fixation on the target following the cue, reflecting its role in pattern completion critical for retrieval. In contrast, the alpha decrease extended across subsequent fixations, suggesting a broader involvement in memory reactivation. These findings tie the relational eye-movement effect to distinct neural processes: an early theta increase associated with retrieving cue-target associations and a more gradual alpha decrease linked to memory reactivation across fixations. By uncovering the neural activity underpinning the relational eye-movement effect, this study provides novel insights into the temporal dynamics of relational memory retrieval and highlights the importance of sequential eye movements in shaping memory-guided behavior.

Keywords: EEG, eye movement, free viewing, episodic memory, relational retrieval

Introduction

Eye movements are closely linked to memory for relationships between different elements within an experience (Ryan, Shen, & Liu, 2020; Ryan & Villate, 2009; Smith, Hopkins, & Squire, 2006). Beyond gathering visual information, eye movements actively contribute to relational memory formation by integrating multiple aspects of an experience into a coherent whole (Johansson, Nystrom, Dewhurst, & Johansson, 2022; Kragel & Voss, 2022; Nikolaev, Bramao, Johansson, & Johansson, 2023; Olsen et al., 2015; Wynn, Olsen, Binns, Buchsbaum, & Ryan, 2018). By establishing spatial and temporal relationships, eye movements help construct a unified memory representation that enables effective navigation and interaction with the environment. This process is closely tied to the hippocampus, critical for linking disparate elements into unified event representations (Cohen & Eichenbaum, 1993; Mcclelland, Mcnaughton, & Oreilly, 1995). Eye movements appear to support hippocampal function by guiding the selection and integration of memory elements, ultimately facilitating the creation of cohesive memory traces (Bridge, Cohen, & Voss, 2017; Kragel & Voss, 2022; Ryan et al., 2020; Voss, Bridge, Cohen, & Walker, 2017).

Extending this understanding, research on memory retrieval has demonstrated that gaze patterns provide direct insights into how relational memories are reactivated during remembering. Eye-tracking studies show that, well before explicitly reporting their memory judgment, participants disproportionately direct their gaze toward elements matching a cue from a previously studied event (Chua, Hannula, & Ranganath, 2012; Hannula & Ranganath, 2009; Hannula, Ryan, Tranel, & Cohen, 2007; Smith & Squire, 2018; Urgolites, Smith, & Squire, 2018). This gaze bias emerges specifically when participants are tasked with identifying a matching element from an array of distractors (cf., Hannula et al., 2010). This sensitivity of eye movements to relational memory is known as the *relational eye-movement effect*. At the neural level, this effect is linked to activation of the hippocampus (Hannula & Ranganath, 2009). Notably, these relational memory effects and their associated hippocampal activity have been observed even when participants fail to consciously identify the matching element (Hannula, Baym, Warren, & Cohen, 2012; Hannula & Ranganath, 2009), suggesting that eye movements might reflect relational memories even in the absence of conscious access (Kumaran & Wagner, 2009; Ryals, O'Neil, Mesulam, Weintraub, & Voss, 2019). Together, these findings indicate that memory for relationships between goal-relevant information guides eye movements, a process supported by involvement of the hippocampus.

While these findings offer valuable insights into the relationship between eye movements, memory, and hippocampal activity, they also reveal critical gaps in understanding how relational memory retrieval, eye movements, and neural activity are interconnected during the retrieval process. Addressing these questions requires studying the relational eye-movement effect alongside its neural correlates with high temporal resolution. This enables precise tracking of the dynamic interplay between gaze behavior and neural evidence for memory reactivation.

Building on recent findings that unrestricted eye movements during relational memory formation are linked with EEG activity in the theta (4-8 Hz) and alpha (8-13 Hz) frequency bands when interrelated event elements are sampled across fixations (Nikolaev, Bramao, et al., 2023; Popov & Staudigl, 2023), the present study aims to extend these insights to the retrieval of such relations. In episodic memory research, increases in theta power have been observed to support the retrieval of discrete memories across space and time (Herweg, Solomon, & Kahana, 2020; Staresina & Wimber, 2019). Theta oscillations are a hallmark of hippocampal activity that coordinates sequential inputs of information (Herweg et al., 2020) and supports the successful formation of associative memories (Kota, Rugg, & Lega, 2020). Recent research suggests that theta oscillations guide eye movements during memory formation (Kragel, Schuele, VanHaerents, Rosenow, & Voss, 2021; Kragel et al., 2020) and enable the binding of separate event elements into coherent memory representations

(Nikolaev, Bramao, et al., 2023). An increase in theta power is often accompanied by a decrease in alpha/beta power, associated with spread cortical engagement and the broad reactivation of memory content (Martín-Buro, Wimber, Henson, & Staresina, 2020; Michelmann, Bowman, & Hanslmayr, 2016). The changes in theta and alpha activity are thought to play essential but distinct roles during both memory encoding and retrieval (Hanslmayr, Staresina, & Bowman, 2016).

To investigate the dynamics of gaze behavior and brain activity during retrieval, we simultaneously recorded participants' eye movements and EEG while they performed a two-alternative forced-choice associative memory test. In this task, participants were presented with a cue and asked to select one of two alternatives that had been previously studied alongside it during the study phase, which involved a series of multi-element events. This design allowed us to examine how increases in theta power, presumably involved in retrieving relational memory representations, and decreases in alpha power, likely responsible for reactivating memory content (i.e., event elements), manifest during relational memory retrieval across consecutive fixations. In doing so, we were able to map out the temporal dynamics of the relational eye-movement effect and its underlying neural processes on a fixation-by-fixation basis.

Our approach diverges from prior research on the relational eye-movement effect (Chua et al., 2012; Hannula & Ranganath, 2009; Hannula et al., 2007; Smith & Squire, 2018; Urgolites et al., 2018) in two critical ways. First, most prior studies used paradigms where the cue in the memory test had been studied alongside a single associate, allowing for reactivation of the cue-target association already during cue processing. This makes it difficult to evaluate the specific contributions of target and distractor fixations during retrieval. To address this, we introduced multi-element events during the study phase, reducing the likelihood of retrieving a specific associate solely through cue fixations. Second, previous studies typically presented the target alongside multiple distractors in the memory test to enhance sensitivity to gaze biases favoring the target. In contrast, we adopted a two-alternative forced-choice protocol, presenting only one distractor. This design ensured an equal likelihood of fixating either the target or distractor after the initial cue fixation and provided sufficient fixation-related EEG data for both targets and distractors in subsequent analyses.

We expect the present study protocol to elicit a relational eye-movement effect that reliably differentiates between recalled and forgotten element associations. Specifically, this effect is anticipated to align with an increase in theta power accompanied by a decrease in alpha power. By examining this interplay across successive fixations, we aim to uncover how the neural dynamics of the relational eye-movement effect evolve over time.

Method

Participants

Thirty-six healthy adults participated in the experiment in exchange for a gift card in a shopping mall (approx. €20). Three participants were excluded due to technical problems, three due to below-chance memory performance, and two due to ceiling memory performance (i.e., too few incorrect trials for the planned analyses). Thus, data from 28 participants (20 females; mean age 23.3 years; age range 18-32 years) were included in the analysis. The study was conducted in accordance with the Swedish Act concerning the Ethical Review of Research involving humans (2003:460). All participants gave written informed consent, and the study followed the local ethical guidelines at Lund University.

Stimuli and procedure

Stimuli during study and test encompassed a total of 324 grayscale photos of faces (from the Oslo Face Database, Chelnokova et al., 2014), places (http://www.tarrlab.org), and objects (Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010) in the shape of a square measuring 4.2 degrees of visual angle (dva) (Fig. 1).

The experiment included six blocks with short breaks between them. Each block began with a study phase, comprising nine event screens with six elements from three categories (2 faces, 2 places, 2 objects) presented for 10 s each (Fig. 1A). Participants were to memorize the multiple inter-category associations specific to each event. Image exemplars for the event elements were randomized across events and participants. The test phase began following a distractor task that required participants to count backward in steps of seven from a randomly selected three-digit number for 30 seconds. During the test, participants were prompted to identify which of two event elements had appeared in the same event as the provided cue element.

The test screen consisted of three elements: cue, target, and distractor, and was presented for 2 s (Fig. 1B). While the cue element was always from a different category than the target and distractor elements, the target and distractor elements were always from the same category. The distractor was selected from another event encoded no more than two screens before or after the target event. Because each cue was associated with four potential targets during the study phase, success in the memory test could only occur after the target and/or distractor was fixated. Including a single distractor ensured an equal likelihood of fixating either the target or the distractor following the initial cue fixation. This design also ensured sufficient fixation-related EEG data for both targets and distractors. The position of these three elements was fixed in all test screens: cue element centrally at the top, and target and distractor elements to the right and left at the bottom (Fig. 1B). The spatial configuration of the elements in the test screen was designed to make participants' eye movement patterns stereotypical to the task, involving initial gaze towards the cue at the top and then shifting their gaze towards the target and distractor elements at the bottom (Fig. 1D). After each test screen, participants were to make their memory judgment (Fig. 1C). Their response was registered by pressing the left or right arrow key (corresponding to the locations of where the target and distractor were presented in the preceding test screen). Finally, they also indicated their choice confidence by selecting "Sure", "Maybe", or "Guess" in response to the question "Are you sure?". Choice confidence was registered by the left, down, and right arrow keys, respectively. The relative target and distractor location (right or left) was randomized for each test trial.

The memory test was designed to assess relational memory for event specific inter-category element associations. To this end, inter-category associations were tested for each element in each event on four trials. For example, a face element was tested twice with place elements (once as cue and once as target), and twice with object elements (once as cue and once as target). The cue-target status of the categories was counterbalanced across blocks so that in the odd blocks the cue-target status was faces-places, places-objects, objects-faces, and in the even blocks the cue-target status was places-faces, objects-places, faces-objects. Thus, 12 different associations were tested for each event. In total, 108 associations were tested in each block ($12 \times 9 = 108$ tests for the nine events within a block) with randomized order of presentation. A fixation cross was shown for a random interval from 1 to 1.5 s before each study and test phase.

Two practice sessions with increasing difficulty preceded the main experiment. The first session comprised three event screens in the study phase, and the second session comprised six event screens. The increased difficulty prepared participants for the main experiment, which comprised nine event screens per study phase. In each practice session, participants completed ten memory tests during the test phase, each followed by feedback on the correctness of their response.

The participant's head was stabilized with a chin rest at a distance of 62 cm from the monitor. Stimuli were presented on an EIZO FlexScan EV2451 monitor with a resolution of 1920 x 1080 pixels and a refresh rate 60 Hz. Stimulus presentation and behavioral data collection were controlled using PsychoPy v.2020.2.4 (Peirce et al., 2019).

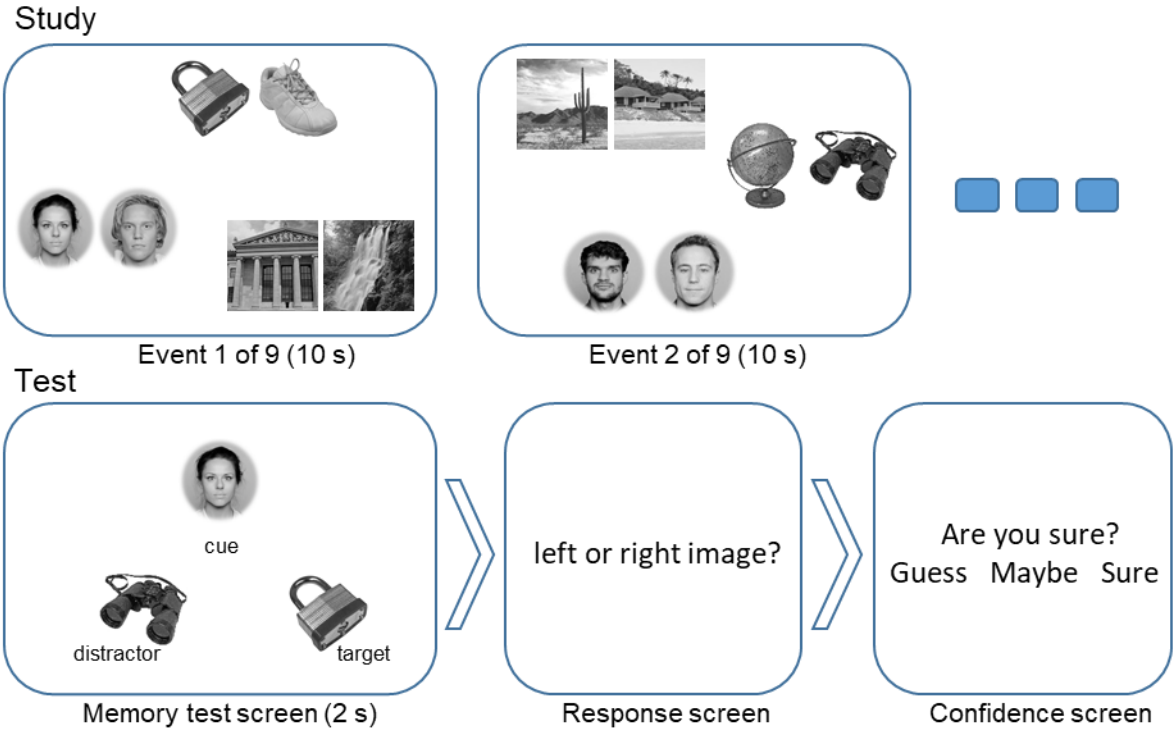

Fig. 1. **Schematics of the study and test phases of the experiment**. During study, nine event screens were presented sequentially for 10 s each. Each event screen comprised six images arranged in three pairs of two exemplars from the same category. The pairs were located along the perimeter of an invisible circle with a radius of 9.2 dva from the screen center. The position of the pairs on the perimeter was random, but equidistant. In the subsequent test phase, test screens were presented for 2 s, comprising three elements: cue, target, distractor. The distance between the cue and the other two elements was 6.5 dva. Participants had to indicate which of the bottom elements (a lock in this example) was from the same event screen as the cue during study. The response was given during the response screen, followed by a confidence question. The response and confidence screens were presented until the answer was given. Note: Faces were obtained from the Oslo Face Database (Chelnokova et al., 2014). All individuals whose faces appear in this figure provided permission for their faces to be published, as documented in the associated user agreement form.

EEG and eye movement recording

EEG and eye movements were recorded concurrently throughout the experiment. EEG was recorded using a Grael 4 K EEG amplifier (Neuroscan, Compumedics Limited, Australia) at a sampling frequency of 2048 Hz using 31 Ag/AgCl electrodes positioned according to the extended 10-20 International system (Easycap GmbH, Germany). Two electrodes placed over the left and right mastoids were used as the recording reference. The ground electrode was AFz. Additional electrodes recorded the vertical and horizontal electrooculograms (VEOG and HEOG): the VEOG electrodes were placed above and below the right eye, the HEOG electrodes were placed at the left and right outer canthi of two eyes. Electrode impedances were kept below 5 kΩ.

The Tobii Pro Spectrum eye tracker (Tobii, Stockholm, Sweden) recorded movements of both eyes with a sampling frequency of 600 Hz. 9-point calibration and validation routines were conducted before each experimental block. An error of 1 dva between calibration and validation was tolerated: if it was larger, the calibration was repeated. The eye tracking was controlled from the PsychoPy experimental program via the open-source toolbox Titta (Niehorster, Andersson, & Nystrom, 2020). The experimental program ran on the same computer that controlled the eye tracker. To synchronize stimulus presentation and EEG recording, a transistor-transistor logic (TTL) signal was sent via a parallel port from the stimulus presentation computer to the EEG system at the beginning and end of each block, encoding event, and memory test. To ensure synchronization between EEG, eye tracking, and stimulus presentation, we used the Black Box ToolKit (The Black Box ToolKit Ltd., UK), including the optodetector, prior to the experiment. We measured the time differences between the image onset on the screen and the TTL signal, as well as between the image onset on the screen and the stimulus onset marker sent to the eye tracker. Constant differences of 23 and 10 ms, respectively, were identified and corrected by shifting the position of the markers offline.

EEG analysis

In the present study, only data from the test phase were analyzed (the results of the study phase were reported in Nikolaev, Bramao, et al., 2023). Analysis was conducted with custom scripts for R (version 4.2.0, 2022) and MATLAB R2024a (The MathWorks Inc., Natick, Massachusetts), using the EEGLAB toolbox (Delorme & Makeig, 2004), the EYE-EEG extension (Dimigen, Sommer, Hohlfeld, Jacobs, & Kliegl, 2011) for EEGLAB, and the Unfold toolbox (Ehinger & Dimigen, 2019). Time-frequency analysis and mapping was performed using the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011).

To analyze EEG in unrestricted viewing, we employed a previously established processing pipeline (Nikolaev, Ehinger, Meghanathan, & van Leeuwen, 2023), comprising four major steps. First, we synchronized the eye-tracking data with EEG using the EYE-EEG extension for EEGLAB (Dimigen et al., 2011). Second, we applied the set of conventional functions to clean EEG from the EEGLAB toolbox (Delorme & Makeig, 2004). Third, we applied the OPTICAT function, which is specifically designed to remove oculomotor artifacts during unrestricted viewing (Dimigen, 2020). Finally, we adjusted for the overlapping effects of subsequent saccades on the EEG and the confounding effects of oculomotor covariates by applying deconvolution modeling using the Unfold toolbox (Ehinger & Dimigen, 2019). See Nikolaev, Ehinger, et al. (2023) for full details of this approach to EEG preprocessing and deconvolution modeling.

EEG preprocessing

The EEG preprocessing aimed to clean the EEG obtained during unrestricted viewing. The key operation of the Unfold toolbox for correcting overlapping effects is time expansion, which requires continuous EEG as input. Therefore, all cleaning was performed on the continuous (i.e., non-segmented) EEG by applying the EEGLAB functions as specified below.

The EEG was downsampled to 256 Hz. Power line noise was removed by using multi-tapering and a Thompson F-statistic implemented in the *pop_cleanline* function. Flat-line channels, low-frequency drifts, noisy channels, and short-time bursts were removed using artifact subspace reconstruction (ASR) with parameter 20, implemented in the *clean_artifacts* function (Mullen et al., 2015). Next, oculomotor artifacts were corrected using the ICA-based *OPTICAT* function (Dimigen, 2020), which removes all types of ocular artifacts (e.g., eyeball rotation, blinking), especially focusing on myogenic saccadic spike activity. This function optimized the ICA decomposition by training it on a copy of the high-pass filtered EEG at 2 Hz, in which sampling points between -20 and +10 ms of saccade onset are overweighted. The obtained ICA weights were applied to the unfiltered version of the same EEG data. This function then computed the ratio between the mean variance of the ocular ICA

components during saccade and fixation; components exceeding the ratio of 1.1 were removed. The obtained ICA components were also checked for other types of artifacts by using the automatic classifier (*pop_iclabel*) (Pion-Tonachini, Kreutz-Delgado, & Makeig, 2019). On average, 15.9 (SD = 3.2) components were removed per participant. The EEG was re-referenced to average reference. The channels removed during ASR (mean = 1.2, SD = 1.03 per participant) were interpolated using spherical spline interpolation.

For the analysis of the event-related and fixation-related potentials, the continuous EEG was filtered between 0.1 and 30 Hz using the *pop_eegfiltnew* function with default settings. For analysis of the theta and alpha power, we first evaluated the time-frequency difference between memory conditions at the level of the entire test interval. Specifically, we calculated the power spectrum of 2-s EEG segments for frequencies between 1 and 30 Hz with the multi-taper method with a Hanning taper and a fixed 0.5-second time window for each frequency, using the *ft_freqanalysis* function of the FieldTrip toolbox. The resulting power values were log-transformed, grand averaged, and subtracted (recalled minus forgotten condition). The areas of maximum difference were used to select the frequency ranges for fixation-related EEG power analyses: 3-5 Hz for the theta band and 8-13 Hz for the alpha band, as explained in Results. To analyze theta and alpha activity at the fixation level, which had to be submitted to deconvolution, we used the procedure proposed by (Ossandón, König, & Heed, 2020). First, the continuous EEG was filtered in the theta and alpha bands found as described above. Next, the instantaneous power was obtained with the Hilbert transform. Finally, the power at each sampling point was normalized (in dB) to its ratio to the mean power: for the test-level analysis, in the interval from -200 to 0 ms before the test screen onset, and for the fixation-level analysis, in the interval from -200 to -100 ms before the fixation onset (to avoid the saccade execution interval). Power values were log-transformed.

Deconvolution

Correcting for overlapping effects of sequential saccades on the EEG and controlling for the effects of continuous covariates on the EEG, such as oculomotor characteristics (e.g., saccade size, fixation duration) or temporal positions of a fixation (e.g., fixation rank), is an important step in the analysis of EEG co-registered with eye movements in unrestricted viewing (Dimigen & Ehinger, 2021; Dimigen et al., 2011; Nikolaev, Meghanathan, & van Leeuwen, 2016). To do this, we used the regression-based deconvolution modeling implemented in the Unfold toolbox (Ehinger & Dimigen, 2019). The output of the toolbox was time series of regression coefficients (betas) representing the partial effects of the predictors, adjusted for the covariates included in the model. The time series corresponded to subject-level averaged waveforms in traditional EEG analysis.

The deconvolution model included predictors at the level of entire trials and at the level of fixations. To account for the EEG activity evoked by the memory test screen presentation we included in the model only its onsets (the intercept term). Similarly, the fixation onsets were included. The categorical predictors were defined by the combination of the memory outcome (recalled vs. forgotten) and the fixated element (cue or target and distractor). Specifically, separate deconvolution models were run for fixations of rank 1 on the cue, fixations of rank 2 on the target and distractor, and fixations of rank 3-4 on the target and distractor. To ensure that the overlapping effect of each fixation of a trial was corrected, fixations not of interest to the current model were accounted for by assigning them to the “other” level of the categorical predictor. We also included fixation rank in the model because it affects fixation-related EEG (Fischer, Graupner, Velichkovsky, & Pannasch, 2013; Guérin-Dugué et al., 2018; Kamienkowski, Varatharajah, Sigman, & Ison, 2018; Nikolaev, Meghanathan, & van Leeuwen, 2018). The order of memory tests over the course of an experiment (as trial numbers from 1 to 648) was also included, since increasing fatigue and decreasing vigilance during an experiment may affect EEG (Makeig & Jung, 1996; Tran, Craig, Craig, Chai, & Nguyen, 2020). As eye movement covariates, we included fixation duration, saccade size and

angle. These eye movement characteristics are known to affect fixation-related EEG (Cornelissen, Sassenhagen, & Vo, 2019; Dimigen et al., 2011; Nikolaev et al., 2016) and so they were included in the model. Because their effects on the EEG are nonlinear (Dimigen & Ehinger, 2021; Nikolaev et al., 2016), they were modeled with spline predictors. In general, the model formula was as follows:

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Screen onset: EEG ~ 1
Fixation: EEG ~ 1 + categorical predictor + fixation rank + trial N +
spl(fixation duration,5) + spl(sac_amplitude,5) + circspl(sac_angle,5,-180,180)
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Statistical analysis

For EEG analyses over the entire-test interval, EEG power (after removing artifacts) was segmented from -200 to 2000 ms relative to the test screen onset, averaged across trials, and baseline corrected to the interval from -200 to 0 ms. For the fixation-related EEG analyses, the deconvolution output provided by the Unfold toolbox is an analog of the averaged EEG power in the -200 to 400 s interval relative to fixation onset. For statistical analysis of fixation-related EEG power, we used mean power values in the 0-200 ms window after fixation onset. This window encompassed the first peak of the cycle of the theta and alpha activity around fixation onset. Because EEG power was normalized to the -200-100 ms interval in the continuous power time series prior to deconvolution, and the deconvolution output was not baseline corrected, this window captured a combination of EEG response evoked by the current fixation as well as ongoing oscillations. The starting time of the window was chosen to be at the fixation onset, because EEG filtering in the narrow frequency band used (theta, alpha) leads to temporal smoothing of the EEG signal due to longer impulse responses, which reduces the accuracy of time-locking the filtered EEG signal to the onset of fixation (see Discussion for further rationale and challenges in selecting analytical windows in free viewing).

We used a priori selected groups of three electrodes around the landmark electrodes of the International 10-20 System of Electrode Placement: F3, F4, C3, C4, P3, P4, O1, O2. They comprised eight regions of interest (ROIs) over frontal, central, parietal and occipital brain regions of the left and right hemispheres (FL, FR, CL, CR, PL, PR, OL, OR) (the inset in Fig. S1). EEG was averaged across the three electrodes in each ROI.

Statistical analyses were conducted using repeated-measures ANOVA with the factors of Memory (forgotten vs. recalled), ROI (frontal, central, parietal, occipital), and Hemisphere (left vs. right) on the power values averaged over the time windows. In the analysis of the fixation-related EEG for target and distractor, the factor Element was added to this ANOVA (see below). When presenting EEG results below, we report statistical effects and interactions only when they involve the Memory factor. We used the Huynh-Feldt correction for p-values associated with two or more degrees of freedom to control for sphericity violation and the Tukey test for post-hoc analyses. Statistical analyses were performed using STATISTICA 10 (TIBCO Software Inc., Palo Alto, CA, USA) and R (version 4.2.0, 2022).

Results

Recalled and forgotten trials

Test performance was assessed by considering both retrieval correctness (‘correct’, ‘incorrect’) and confidence (‘guess’, ‘maybe’, ‘sure’). These response outcomes thus provide six possible combinations that in theory could be used to disambiguate between different levels of successful relational memory.

The average of correct memory retrieval across participants was 68.6 ± 8.3 % (mean ± SD). The percentage of correct and incorrect responses depending on response confidence is shown in Table 1.

Table 1. Percentage of correct and incorrect responses by confidence levels (mean (SD) % across 28 participants)

	guess	maybe	sure
correct	13 (8.6)	28 (9.3)	27 (14.9)
incorrect	11 (6.6)	16 (8.6)	4 (3.2)

To increase the contrast between retrieval outcomes and to maximize the number of trials for the fixation-related EEG analysis, we considered two memory retrieval trials: recalled and forgotten relations. In the recalled trials, we considered test trials that resulted in correct responses with confidence ratings of 'maybe' and 'sure'. In the forgotten trials, we included test trials that resulted in incorrect responses, as well as any trials with a confidence rating of 'guess'.

The relational eye-movement effect

Each fixation within the 2-s memory test trial was given a sequential number, i.e., *fixation rank*, which indicated the visiting order of each element in the screen. The typical eye movement pattern involved first fixating on the cue (fixation rank 1) and then shifting gaze to the elements below, with an equal number of fixations on the target and distractor (fixation ranks 2 and subsequent fixations). The number of fixations gradually decreased over the course of a trial (Fig. 2A), so that fixation ranks later than 4 did not provide sufficient data for reliable eye movement and EEG analyses.

We then verified the presence of the expected relational eye movement effect and examined how it evolved along the fixations rank 1 to 4 with respect to recalled and forgotten relations. To do this, we compared the time spent looking at the target versus the distractor during the 2-s test interval. We computed the duration of fixations on the target and distractor of each rank relative to the mean duration of fixations on all 3 elements within the test interval (similar to Hannula et al., 2007). After we calculated the ratio of these normalized fixation durations between the target and the distractor. A ratio greater than 1 indicates disproportionate viewing of the target compared to the distractor (Fig. 2B).

To examine the time course of disproportionate target viewing, we compared the target-to-distractor viewing ratios against 1 across fixation ranks using a one-tailed t-test with FDR-corrected p-values. In the recalled, the proportion of viewing time directed to the target was significantly greater than to the distractor for fixation ranks 2-4 (all p:s < .02). This effect is further illustrated in Fig. 2B, where the 0.95 confidence intervals for these fixation ranks do not include 1. These findings indicate that the relational eye-movement effect was present for recalled but not for forgotten relations.

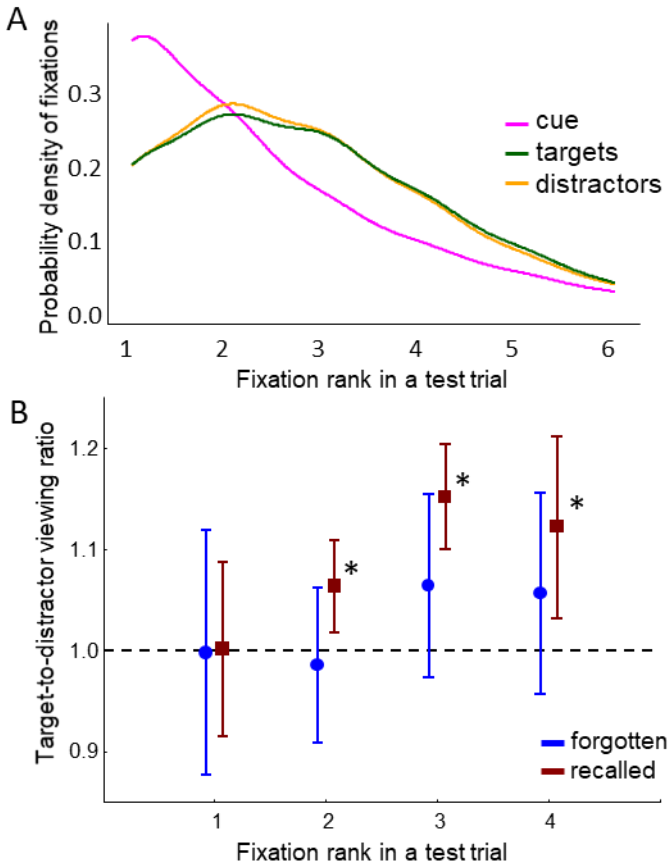

Fig. 2. **Time course of relational eye movements**. (A) Probability density of fixations on cue, target, and distractor during test as a function of fixation rank, i.e., the order of the fixations in a test trial. Thus, in most cases, the test trials started with a fixation on the cue (fixation of rank 1) and continued with fixations on the target or distractor with equal probability (fixations of ranks 2, 3, 4 and so on). (B) Relational eye-movement effect. The target-to-distractor viewing ratio over all participants (N=28) as a function of fixation rank. Values above 1 indicate disproportionate viewing of the target compared to the distractor. Error bars denote 0.95 confidence intervals across participants. Asterisks mark significant differences from 1.

Neural activity during the entire-test interval

Figure 3 illustrates the correspondence between successive eye movements and retrieval-related changes in theta and alpha activity over the entire 2-s test interval. The time course of eye movements is shown by the latencies of fixation onsets of the first six ranks, which vary increasingly over time along the retrieval time window (Fig. 3A). The time-frequency plot contrasting recalled and forgotten trials shows that retrieval is associated with a theta increase peaking between 500 and 1000 ms and a gradual alpha decrease starting at 500 ms and lasting until the end of the trial (Fig. 3B). The first fixation, which predominantly occurred on the cue, was not associated with any EEG differences between the two memory conditions. The following fixations, which mainly occurred on target and distractor, at ranks 2 to 4 corresponded to the interval of the higher theta power. In comparison, the fixations at ranks 3 to 6 corresponded to the interval of lower alpha power.

The maximum power differences between recalled and forgotten trials in Fig. 3B and S1B are observed at 3-5 Hz in the 500-1000 ms interval and at 8-13 Hz in the 1000-2000 ms interval. Accordingly, we extracted the instantaneous power using the Hilbert transform at 3-5 Hz for the

theta band and at 8-13 Hz for the alpha band and averaged the power values within these early and late time windows for statistical analysis.

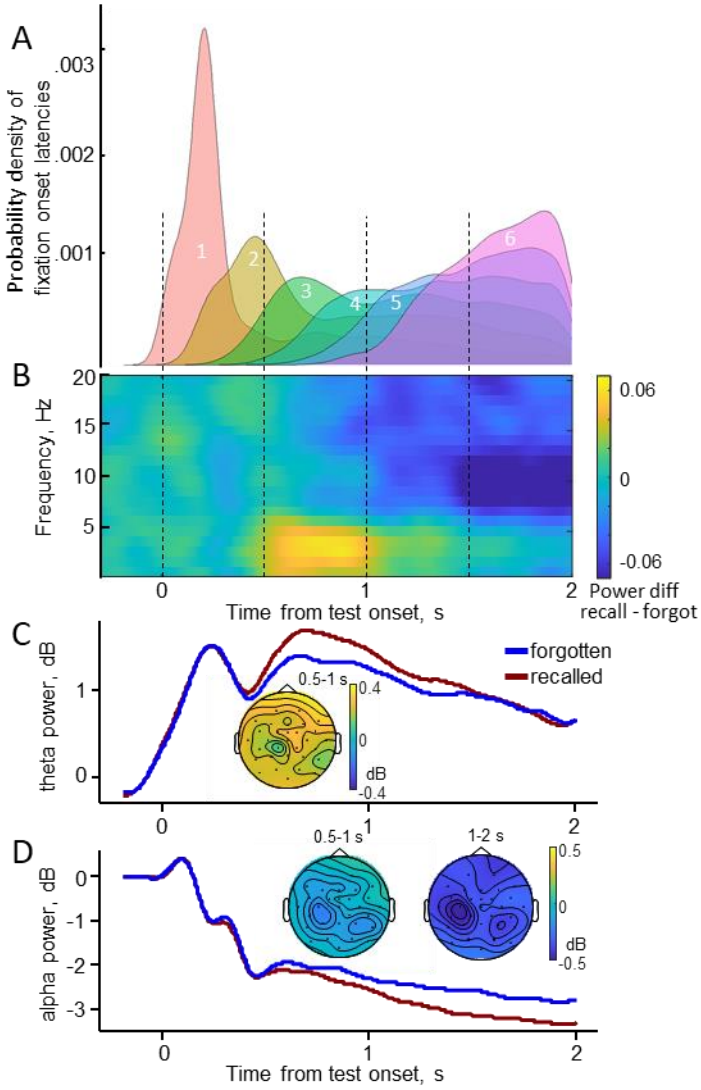

Fig. 3. **Evolution of eye movements and EEG over the entire 2-s test interval**. (A) Probability density of fixation onset latencies for fixations of the first 6 ranks in the memory test trial, pooled across 28 participants. (B) Grand averaged time-frequency difference plot (recalled minus forgotten trials) averaged over all electrodes for the entire 2-s memory test trial duration. (C) theta and (D) alpha power time-locked to the test display onset for the recalled vs. forgotten trials. EEG power was baseline corrected to the -200-0 ms interval before the test screen onset, grand averaged across 28 participants and averaged over all electrodes. The insets show the topography of the memory effects as difference maps in the windows with significant differences for theta (C) and alpha (D) power.

In the theta band, we found higher power for recalled compared with forgotten trials in the early time window ($F(1, 27) = 22.4$, $p < .001$), but no difference in the late window (Fig. 3C, S1A). In the alpha band, we found lower power in the recalled than in the forgotten trials in both the early ($F(1, 27) = 11.5$, $p = .002$) and late time windows ($F(1, 27) = 43.1$, $p < .001$) (Fig. 3D, S1A).

In sum, on the time scale of the entire-test interval, successful recall was predicted by higher theta power in the 500-1000 ms interval after the test screen onset and by lower alpha power over the

extended 500-2000 ms interval. The higher theta combined with lower alpha power is a well-documented neural signature of successful recall in previous research where stimuli were presented at fixation (e.g., Hanslmayr et al. 2016).

Neural activity across eye movements

To uncover the neural correlates of correct recall reflected in the relational eye-movement effect, we compared the neural correlates of recalled and forgotten trials in the EEG time-locked to the onset of fixations of first four ranks (Fig. 2B). Given that rank 1 fixations were predominantly located on the cue and fixations of subsequent ranks (2-4) were primarily located on the target and distractor (see Fig. 2A), we considered rank 1 fixations as cue-related and fixations of ranks 2 through 4 as target and distractor related. Accordingly, we performed separate deconvolutions for rank 1 fixations on the cue, for rank 2 fixations on the target and distractor, and rank 3-4 fixations on the target and distractor. A single deconvolution model included the factorial combinations of fixation elements and memory outcome (recalled vs. forgotten). The minimum number of fixations per condition per rank was set to 30. We pooled fixations from ranks 3 and 4 to reach this number. For the analysis of cue fixations of rank 1, the minimum number was reached in 23 participants, and for the analysis of target and distractor fixations of ranks 2 and 3-4, in 20 participants. The number of fixation-related EEG epochs in each condition and fixation rank is reported in the Supplementary Table 1. To analyze EEG at rank 1 cue fixations, we used a three-factor (Memory, ROI, Hemisphere) ANOVA, as described in Methods. To analyze EEG at ranks 2 and 3-4 for target and distractor fixations, we used four-factor (Memory, ROI, Hemisphere, and Element (target vs. distractor)) ANOVAs. Deconvolution and ANOVA were performed separately for theta and alpha power and for ranks 2 and 3-4 fixations.

Fixation-related theta power

For rank 1 fixations on the cue, no significant memory effect on the fixation-related theta activity was observed (Fig. S2A). For rank 2 fixations, a main effect of Memory ($F(1, 19) = 13.1$, $p = .002$) indicated higher theta power for the recalled than for the forgotten trials (Fig. 4, S2B). The figures suggested a larger theta memory effect for the target than for the distractor, which was corroborated by a weak tendency for an interaction between Memory and Element involving Hemisphere ($F(1, 19) = 2.7$, $p = .12$). Post-hoc test indicated that for the target, theta power was significantly higher in recalled compared to forgotten trials over the left hemisphere ($p = .007$). To further test this result, we conducted the planned contrast analysis by setting the target or distractor level to zero. When the distractor level was zeroed out, we found a significant Memory effect ($p = .016$) and an interaction between Memory and Hemisphere ($p = .049$), but not when the target level was zeroed out: ($p = .1$) and ($p = .48$), respectively.

For rank 3-4 fixations, there was an interaction between Memory, Element and Hemisphere ($F(1, 19) = 5.2$, $p = .03$) (Fig. 4A, S2C, E). However, post-hoc tests showed no significant differences (all $p > .23$). Furthermore, the planned contrast analysis as for rank 2 fixations showed no differences when either target or distractor levels were zeroed out (all $p > .11$).

Thus, although the expected interaction between Memory and Element did not reach significance for rank 2 fixations, the following analyses revealed a stronger memory effect for the target than for the distractor. In contrast, although the interaction between Memory and Element and Hemisphere reached significance for rank 3-4 fixations, the following analyses did not reveal the difference in theta power between target and distractor. These findings indicate that higher theta power over the left hemisphere specifically predicts successful retrieval during rank 2 fixations on the target. This suggests that at this stage, theta activity during target fixation specifically supports the connection between the cue and the target.

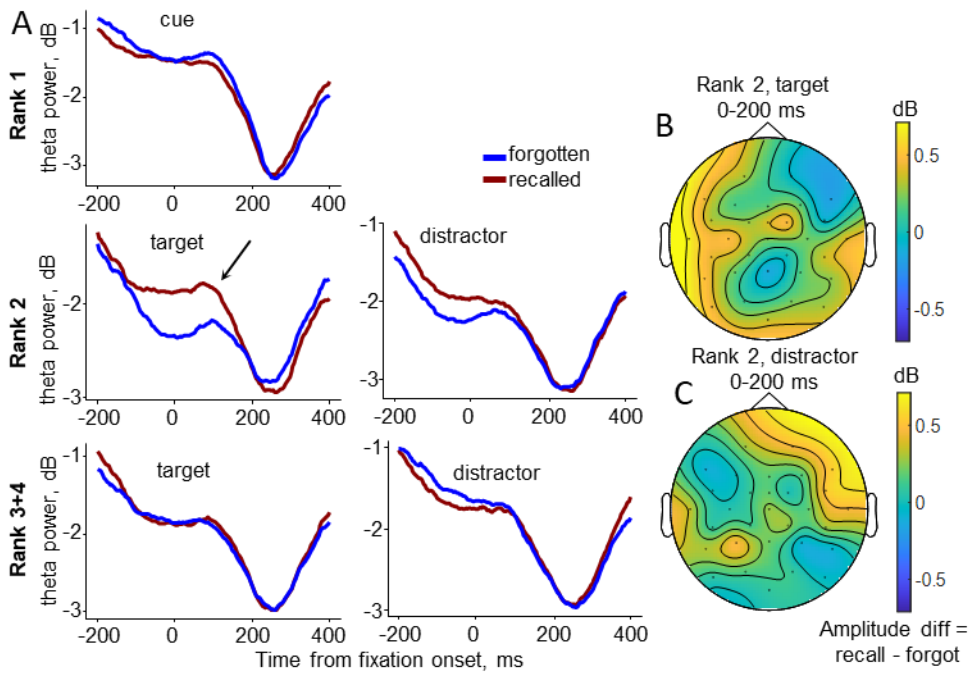

Fig. 4. **Fixation-related theta power as a function of fixation rank**. (A) Grand-averaged theta power averaged across the left hemisphere for cue, target, and distractor elements, comparing recalled and forgotten trials. A significant difference between recalled and forgotten trials is indicated by an arrow. Difference maps for the 0-200 ms window for fixations of rank 2 on the target (B) and on the distractor (C).

Fixation-related alpha power

For rank 1 fixations on the cue, no significant effect of Memory on the fixation-related alpha activity was observed (Fig. S3A). For rank 2 fixations, a main effect of Memory ($F(1, 19) = 7.5$, $p = .01$) indicated lower alpha power for the recalled than for the forgotten trials (Fig. 5, S3B). There was an interaction between Memory, Element, ROI, and Hemisphere ($F(3, 57) = 7.6$, $p = .002$, $\varepsilon = .61$). Post hoc tests indicated that alpha power was significantly lower in recalled compared to forgotten trials over the left parietal ($p = .02$) and right frontal ($p = .008$) areas only for the target (Fig. 5A-C, S3B, F). For rank 3-4 fixations, there was a main effect of Memory ($F(1, 19) = 18.7$, $p < .001$) and an interaction between Memory and Element ($F(1, 19) = 4.7$, $p = .04$) (Fig. 5A, D, E, S3C). Post hoc tests revealed that the lower alpha power for recalled trials compared to forgotten trials was evident for the target ($p < .001$) and not for the distractor ($p = .17$). Thus, lower alpha power predicted successful retrieval during target fixations of both ranks 2 and 3-4, suggesting that relevant memory content is activated at these time points.

For both theta and alpha power, the observed interactions between Memory, Element, and Hemisphere could potentially be due to participants being more correct when targets are presented on the right side of the screen compared to the left side. To rule out this possibility, we repeated the same ANOVAs for rank 2 and 3-4 fixations as described above on the dataset with an equalized number of left and right-side epochs. In equalization, the same number of epochs on the side with more epochs as on the side with fewer epochs was randomly selected. The equalization removed 26% (SD=7.5%) of the epochs. As expected, this reduced the significance of the interactions, but qualitatively the pattern of results remained the same (see Supplementary for detailed results). These control analyses ensured that the observed hemispheric differences in memory effects for the

target were not driven by an imbalance in the number of "correct" epochs across the left/right side of the screen.

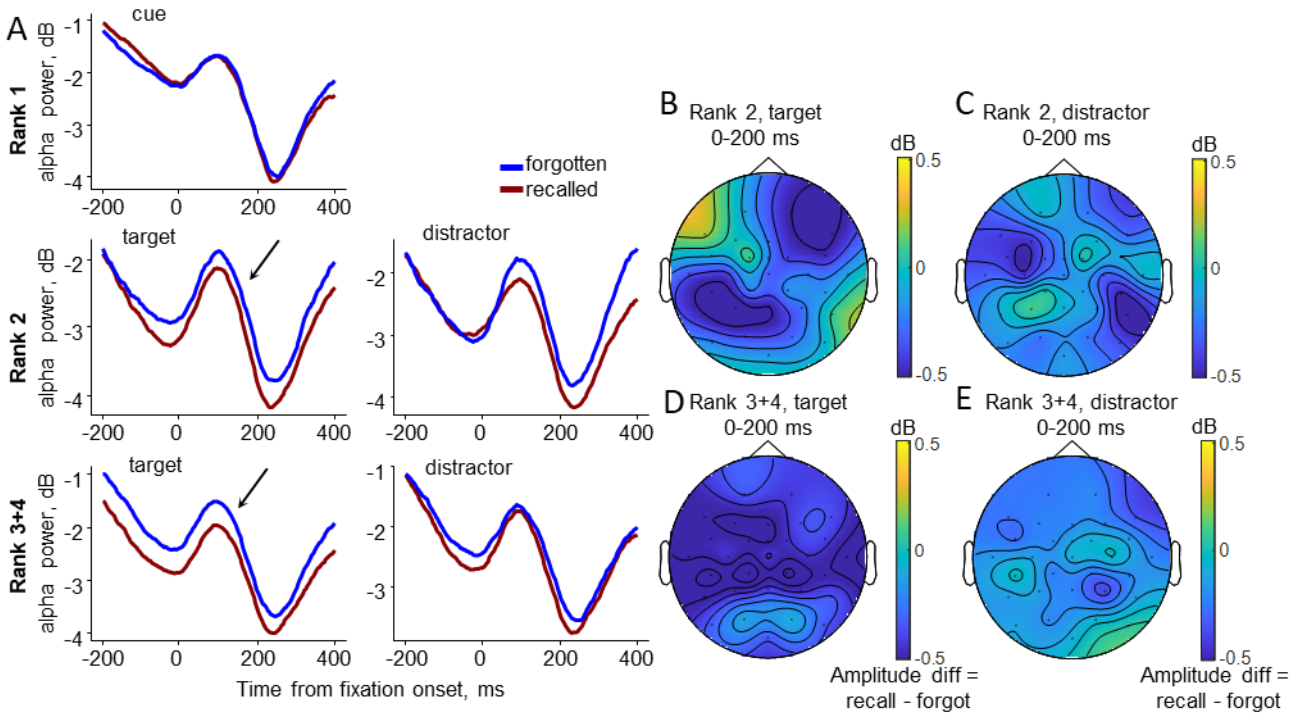

Fig. 5. **Fixation-related alpha power as a function of fixation rank**. (A) Grand-averaged alpha power averaged across all ROIs for cue, target, and distractor elements, comparing recalled and forgotten trials. Significant differences between recalled and forgotten trials are indicated by arrows. Difference maps for the 0-200 ms window for rank 2 fixations on the target (B) and distractor (C) and for ranks 3 and 4 fixations on the target (D) and distractor (E).

Comparison of entire-test interval and fixation-related activity

To elucidate the relationship between theta and alpha memory effects measured over the entire-test interval and those observed during individual fixations (Fig. 3), we compared their topographical distributions. Memory effects were quantified as the difference in theta or alpha power between recalled and forgotten trials for eight regions of interest (ROIs). We then conducted a repeated-measures ANOVA on these differences with the factors Interval (entire-test vs. fixation), ROI (frontal, central, parietal, occipital), and Hemisphere (left vs. right). Significant interactions between Interval and either ROI or Hemisphere would suggest that the two intervals capture distinct neural mechanisms. We performed this analysis for theta power between the 500-1000 ms entire-test window vs. rank 2 and 3-4 fixations, and for alpha power between the 500-1000 ms and 1000-2000 ms entire-test windows vs. rank 2 and 3-4 fixations, for target and distractor separately.

For theta activity, there was an interaction between Interval and Hemisphere for rank 2 target fixations ($F(1, 19) = 5.1$, $p = .04$) (Fig. 3C vs. Fig. 4B). Post hoc tests indicated that the memory effect was more pronounced in the entire-test than in the fixation intervals over the right ($p = .02$) but not the left ($p = 1$) hemisphere. This topographic difference resulted from comparable memory effects over the left hemisphere in the fixation interval and over both hemispheres in the entire-test intervals, in contrast to a significantly lower memory effect over the right hemisphere in the fixation interval. There were no interactions of interest for rank 2 distractor fixations and rank 3-4 target and distractor fixations.

For alpha activity, for the 500-1000 ms window, there was an interaction between Interval, ROI and Hemisphere for rank 2 target fixations ($F(3, 57) = 6.2$, $p = .007$, $\varepsilon = .6$) (Fig. 3D vs. Fig. 5B), but post hoc tests showed no significant differences. There were no interactions of interest for rank 2 distractor fixations and rank 3-4 target and distractor fixations. For the 1000-2000 ms test window, there was an interaction between Interval, ROI and Hemisphere for rank 2 target fixations ($F(3, 57) = 4.0$, $p = .04$, $\varepsilon = .54$) (Fig. 3D vs. Fig. 5D). Post hoc tests indicated that the memory effect was more pronounced in the entire-test than in the fixation intervals over the left frontal area ($p = .001$). This topographic difference resulted from comparable memory effects over the right frontal area in the fixation interval and all areas in the entire-test intervals, in contrast to a significantly lower memory effect over the left frontal area in the fixation interval. There were no interactions of interest for rank 2 distractor fixations and rank 3-4 target and distractor fixations.

Thus, the topographical distributions of both theta and alpha activity differed significantly between the entire-test interval and rank 2 fixations for target stimuli. These findings underscore the critical importance of the initial fixation on the target for relational memory retrieval – a process not captured when analyzing the entire-test interval.

Discussion

This study investigated the neural dynamics underlying the relational eye-movement effect on a fixation-by-fixation basis during a two-alternative forced-choice associative memory test (Fig. 1). Eye-tracking results revealed a pronounced relational eye-movement effect, characterized by disproportionate viewing of targets during fixations of ranks 2-4. Next, we examined how this behavioral effect aligned with theta and alpha EEG activity, both across the entire-test interval and at the level of individual fixations.

Across the entire-test interval (2000 ms), successful recall of element associations was predicted by an increase in theta power between 500-1000 ms after test screen onset and a decrease in alpha power from 500 until the end of the interval. The timing of the theta increase aligns with previous research linking theta activity to the retrieval of episodic associations (Hanslmayr & Staudigl, 2014; Herweg et al., 2020; Hsieh & Ranganath, 2014). Similarly, the timing of the alpha decrease corresponds with prior findings on its onset and evolution during episodic memory retrieval (Griffiths, Martín-Buro, Staresina, Hanslmayr, & Staudigl, 2021; Karlsson, Wehrspaun, & Sander, 2020; Martín-Buro et al., 2020; Michelmann et al., 2016).

Fixation-related EEG analysis revealed that the theta increase was primarily associated with the initial fixation (fixation rank 2) on the target element, following the gaze transition from the cue fixation. In contrast, the alpha decrease at the target fixations was more gradual, extending from the second to fourth fixations. These findings suggest that theta activity during first fixations on the target is specifically linked to relational memory retrieval, whereas alpha activity may support the reactivation of memory contents, such as individual event elements, across more extended ranges of fixation ranks.

Prior eye-tracking research has demonstrated that the relational eye-movement effect emerges quite early – well before explicit responses and sometimes even without conscious awareness (Hannula & Ranganath, 2009; Hannula et al., 2007; Nagy & Király, 2018). In line with these findings, our results suggest that processes at the first target fixation are aligned with this early, potentially implicit stage of retrieval (cf., Kumaran & Wagner, 2009). This target fixation – specifically, the second fixation of a trial following the initial cue fixation – appears to play a pivotal role in retrieval within our task. Our two-alternative forced-choice design required participants to retrieve a single

association from multiple potential cue-target associations, necessitating a gaze transition from the cue to the target to enable correct recall. Given the tight link between eye movements and attentional direction, and the role of attentional shifts toward a target location in signaling the timing of memory retrieval (Kragel & Voss, 2022), the second target fixation likely marks the initiation of the neural processes that support retrieval of the correct association.

This interpretation is further corroborated by the observed left-hemispheric lateralization of the theta memory effect, consistent with previous findings demonstrating left-lateralized theta activity during accurate episodic retrieval (Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011; Jacobs, Hwang, Curran, & Kahana, 2006; Klimesch, Doppelmayr, Schimke, & Ripper, 1997; Rajan, Cuevas, & Bell, 2021). Such retrieval-related activation of the left hemisphere has also been observed in ERP research on recognition memory (Rugg & Curran, 2007), as well as retrieval of both verbal and nonverbal materials in various episodic memory tasks (Spaniol et al., 2009). This left-lateralized retrieval effect has been linked specifically with activity in the left posterior parietal cortex, which may contribute to deploying selective attention to facilitate strategic orienting of memory (Wagner, Shannon, Kahn, & Buckner, 2005). Within our study context, this may involve gaze target selection that launches theta-driven pattern completion of information associated with a cue, which is essential for successful relational retrieval (Staresina & Wimber, 2019).

The fronto-parietal alpha effect at rank 2 target fixation may reflect top-down control of visual attention mediated by a dorsal attentional network that includes the right frontal eye field (FEF) in prefrontal cortex and posterior cortical regions around the intraparietal sulcus (IPS) (Corbetta & Shulman, 2002). Specifically, a virtual lesion in the right prefrontal cortex during spatial attention tasks impairs target identification and reduces lateralized attention-related alpha amplitude. This finding supports a causal role for fronto-parietal alpha activity in the top-down guidance of visuospatial attention (Capotosto, Babiloni, Romani, & Corbetta, 2009; Sauseng, Feldheim, Freunberger, & Hummel, 2011). Considering the known involvement of right prefrontal cortical regions in episodic memory retrieval (Lepage, Ghaffar, Nyberg, & Tulving, 2000), the right-frontal alpha effect at rank 2 target fixation, which differed from the alpha effect in the entire-test interval, likely reflects top-down control processes that facilitate selective gaze-related reactivation of target representations leading to successful recall. However, in contrast to the transient theta effect at the second fixation, the prolonged alpha reduction persisted during both rank 2 and rank 3-4 target fixations. This sustained alpha decrease may indicate the ongoing extraction of target-related information and its gradual embedding into explicit awareness (e.g., recognition of event elements) (Babiloni, Vecchio, Bultrini, Romani, & Rossini, 2006; Kumaran & Wagner, 2009; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009). Specifically, during retrieval tasks, decreases in alpha power have been linked to the amount of information recovered from episodic memory (Griffiths et al., 2021; Hanslmayr et al., 2016; Karlsson et al., 2020; Martín-Buro et al., 2020). Specifically, the reduction in alpha power observed at target fixations suggests that fixating on the target retrieves more information than does fixating on the distractor. Together, these findings imply that theta and alpha activity reflect distinct neural mechanisms underlying target processing.

The primary advantage of fixation-related EEG analysis is its ability to provide a detailed, time-resolved view of the neural activity underlying the processes identified across the entire-test interval analysis. For example, the onset of the alpha effect in the entire-test interval aligns with the alpha effect at rank 2 (Fig. 3). This alpha effect becomes progressively stronger as the task progresses, reflected in a more pronounced alpha decrease from early to later time windows in the entire-test analysis (Fig. 3D), as well as across fixations from rank 2 to ranks 3-4 (the main effect F-values = 7.5 and 18.7, respectively, Fig. 5).

In contrast, the relationship between the fixation-related and entire-test-interval theta effects needs further consideration. While the target-specific theta effect at fixation rank 2 aligns with the onset of the theta effect observed in the entire-test interval (Fig. 3C), later fixations (ranks 3-4) do not show this theta effect (Fig. 4), even though their onset falls within the theta effect interval identified in the test-level analysis (Fig. 3A). This discrepancy is unlikely to be related to differences in the underlying retrieval-related processes because the topographies of the theta memory effects at target rank 3-4 fixations and in the 500-1000 ms entire-test window were comparable. However, it may arise from other factors. First, the entire-test interval EEG analysis benefits from greater statistical power due to the higher number of trials included. Second, variations in preceding gaze sequences may obscure later fixation-related effects. For instance, rank 3 target fixations could be preceded by different types of fixation sequences (e.g., cue-distractor or cue-target). For rank 4 target fixations, the number of possible preceding sequences increases further (e.g., cue-distractor-distractor or cue-target-distractor). In some cases, retrieval-related theta activity may occur before fixation ranks 3-4, rendering the effect undetectable at those fixations. Our study was unable not isolate and analyze these variations in gaze sequences across the cue, target, and distractor elements. Future research should utilize paradigms specifically designed to track EEG activity across a variety of fixation sequences to capture these nuances and facilitate more generalizable conclusions.

Comparing the topographical distribution of memory effects between entire-test and fixation-related intervals provides deeper insights into fixation-level processes critical for relational retrieval. The distinct theta and alpha power topographies observed in entire-test intervals versus rank 2 target fixations underscore the vital role of the initial target fixation in relational memory retrieval. These topographical differences suggest that the two analytical approaches capture distinct neural mechanisms at this stage. Specifically, fixation-related analysis may isolate the key process of cue-target association occurring during the initial target fixation, whereas entire-test analysis likely reflects the engagement of a broader set of memory-related processes, including extended cognitive control (Badre & Wagner, 2007; Klimesch, Freunberger, & Sauseng, 2010; Nyhus & Curran, 2010).

Although eye movements in our paradigm followed a stereotyped pattern, they were not restricted. Analyzing EEG data coregistered with unrestricted eye movements poses specific challenges, including overlapping effects of successive saccades and condition-specific influences of eye movements (Dimigen et al., 2011; Nikolaev et al., 2016). These effects may distort, mask, or confound the effects of experimental conditions on the EEG. This issue is particularly relevant for studies of the relational eye-movement effect, as disproportionate target viewing prolongs fixation duration, making eye movements and corresponding fixation-related EEG incompatible across conditions. Addressing these challenges is critical for free-viewing EEG research. In this study, we used deconvolution modeling (Dimigen & Ehinger, 2021) to isolate the neural correlates of memory retrieval during unrestricted eye movements, providing a robust approach to mitigate these confounds.

Another key consideration in EEG-eye movement coregistration during unrestricted viewing is the selection of baseline and time windows for analysis. In traditional stimulus-response paradigms, where most information arrives at stimulus onset, EEG baselines are typically taken before the stimulus and time windows several hundred milliseconds after stimulus onset. However, in free-viewing tasks, information unfolds sequentially across fixations, and processing builds cumulatively rather than restarting with each fixation (Kragel & Voss, 2022). Consequently, fixation-related EEG may reflect not only the brain's response to new information but also its modulation by previous representations. This sequential input poses challenges for baseline selection and time window determination (Nikolaev et al., 2016). In this study, we normalized EEG power to the pre-fixation interval in the continuous EEG (before deconvolution) and used time windows starting from fixation onset without traditional baseline correction. This allowed us to capture the dynamics of EEG activity

across fixations. However, this approach does not account for the phase of ongoing oscillations, which is reset with each saccade (Hoffman et al., 2013; Ito, Maldonado, Singer, & Grün, 2011; Nikolaev et al., 2016). Moreover, the distinct phases of hippocampal theta oscillations precede retrieval-guided and novelty-driven eye movements, possibly coordinating switches between encoding and retrieval during free viewing (Kragel et al., 2020). In relational memory retrieval, the cycle of ongoing theta oscillations organizes sequential inputs by simultaneously representing current and previously visited items or locations (Herweg et al., 2020). Future fixation-related EEG studies of relational memory should investigate how specific phases of theta influence retrieval success to elucidate the underlying neural mechanisms further.

The specific temporal dynamics of fixations and neural activity reported in the present study should be interpreted within the context of existing research on the relational eye-movement effect. Unlike previous studies that typically employed single cue-target associations and included several distractors in their retrieval tasks (Chua et al., 2012; Hannula & Ranganath, 2009; Hannula et al., 2007; Smith & Squire, 2018; Urgolites et al., 2018), our study was designed to evaluate fixations on both target and distractor elements within scenarios featuring multiple potential cue-target associations. This methodological variation might affect the specific roles of fixations following the initial cue fixation across different paradigms. However, the general pattern of interplay between gaze behavior and neural activity in the theta and alpha bands observed in our study is likely consistent across different memory retrieval scenarios, regardless of specific paradigm parameters.

In summary, our findings underscore the active role of eye movements in relational memory retrieval. The observed increase in theta power at the initial target fixation following the cue highlights the importance of gaze transitions in initiating relational memory. In contrast, the sustained decrease in alpha power across subsequent fixations reflects the extended retrieval demands involved in navigating associative memory tasks. Together, these findings emphasize the dynamic relationship between neural activity and gaze behavior in reconstructing episodic memories. Future research should expand on these findings by investigating the neural and behavioral mechanisms of relational memory retrieval in more ecologically valid settings, such as tasks set in naturalistic environments and involving complex contextual associations. Such investigations will enhance our understanding of how memory processes are integrated with active exploration to guide goal-relevant behavior.

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Ethics statement
Data collection was conducted in accordance with the Swedish Act Concerning the Ethical Review of Research Involving Humans (2003:460), the Code of Ethics of the World Medical Association (Declaration of Helsinki), and the local ethical guidelines at Lund University. As established by Swedish authorities and specified in the Swedish Act concerning the Ethical Review of Research involving Humans (2003:460), the present study does not require specific ethical review by the Swedish Ethical Review Authority due to the following reasons: (1) it does not deal with sensitive personal data, (2) it does not use methods that involve a physical intervention, (3) it does not use methods that pose a risk of mental or physical harm, (4) it does not study biological material taken from a living or dead human that can be traced back to that person

(https://etikprovningsmyndigheten.se/wp-content/uploads/2024/05/Guide-to-the-ethical-review_webb.pdf). The data collection was anonymous and did not involve recording any potentially identifying demographic information.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Addante, R. J., Watrous, A. J., Yonelinas, A. P., Ekstrom, A. D., & Ranganath, C. (2011). Prestimulus theta activity predicts correct source memory retrieval. *Proceedings of the National Academy of Sciences of the United States of America, 108*(26), 10702-10707.

Babiloni, C., Vecchio, F., Bultrini, A., Romani, G. L., & Rossini, P. M. (2006). Pre- and poststimulus alpha rhythms are related to conscious visual perception: A high-resolution EEG study. *Cerebral Cortex, 16*(12), 1690-1700.

Badre, D., & Wagner, A. D. (2007). Left ventrolateral prefrontal cortex and the cognitive control of memory. *Neuropsychologia, 45*(13), 2883-2901.

Bridge, D. J., Cohen, N. J., & Voss, J. L. (2017). Distinct Hippocampal versus Frontoparietal Network Contributions to Retrieval and Memory-guided Exploration. *Journal of Cognitive Neuroscience, 29*(8), 1324-1338.

Brodeur, M. B., Dionne-Dostie, E., Montreuil, T., & Lepage, M. (2010). The Bank of Standardized Stimuli (BOSS), a New Set of 480 Normative Photos of Objects to Be Used as Visual Stimuli in Cognitive Research. *Plos One, 5*(5).

Capotosto, P., Babiloni, C., Romani, G. L., & Corbetta, M. (2009). Frontoparietal Cortex Controls Spatial Attention through Modulation of Anticipatory Alpha Rhythms. *Journal of Neuroscience, 29*(18), 5863-5872.

Chelnokova, O., Laeng, B., Eikemo, M., Riegels, J., Loseth, G., Maurud, H., . . . Leknes, S. (2014). Rewards of beauty: the opioid system mediates social motivation in humans. *Molecular Psychiatry, 19*(7), 746-747.

Chua, E. F., Hannula, D. E., & Ranganath, C. (2012). Distinguishing highly confident accurate and inaccurate memory: Insights about relevant and irrelevant influences on memory confidence. *Memory, 20*(1), 48-62.

Cohen, N. J., & Eichenbaum, H. (1993). *Memory, Amnesia, and The Hippocampal System*. Cambridge, MA: MIT Press.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3*(3), 201-215.

Cornelissen, T., Sassenhagen, J., & Vo, M. L. H. (2019). Improving free-viewing fixation-related EEG potentials with continuous-time regression. *Journal of Neuroscience Methods, 313*, 77-94.

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods, 134*(1), 9-21.

Dimigen, O. (2020). Optimizing the ICA-based removal of ocular EEG artifacts from free viewing experiments. *Neuroimage, 207*, 116117.

Dimigen, O., & Ehinger, B. V. (2021). Regression-based analysis of combined EEG and eye-tracking data: Theory and applications. *Journal of vision, 21*(1).

Dimigen, O., Sommer, W., Hohlfeld, A., Jacobs, A. M., & Kliegl, R. (2011). Coregistration of eye movements and EEG in natural reading: analyses and review. *Journal of experimental psychology: General, 140*(4), 552-572.

Ehinger, B. V., & Dimigen, O. (2019). Unfold: an integrated toolbox for overlap correction, non-linear modeling, and regression-based EEG analysis. *PeerJ, 7*, e7838.

Fischer, T., Graupner, S. T., Velichkovsky, B. M., & Pannasch, S. (2013). Attentional dynamics during free picture viewing: evidence from oculomotor behavior and electrocortical activity. *Frontiers in systems neuroscience, 7*, 17.

Griffiths, B. J., Martín-Buro, M. C., Staresina, B. P., Hanslmayr, S., & Staudigl, T. (2021). Alpha/beta power decreases during episodic memory formation predict the magnitude of alpha/beta power decreases during subsequent retrieval. *Neuropsychologia, 153*.

Guérin-Dugué, A., Roy, R. N., Kristensen, E., Rivet, B., Vercueil, L., & Tcherkassof, A. (2018). Temporal Dynamics of Natural Static Emotional Facial Expressions Decoding: A Study Using Event- and Eye Fixation-Related Potentials. *Frontiers in Psychology, 9*.

Hannula, D. E., Althoff, R. R., Warren, D. E., Riggs, L., Cohen, N. J., & Ryan, J. D. (2010). Worth a glance: using eye movements to investigate the cognitive neuroscience of memory. *Frontiers in Human Neuroscience, 4*.

Hannula, D. E., Baym, C. L., Warren, D. E., & Cohen, N. J. (2012). The Eyes Know: Eye Movements as a Veridical Index of Memory. *Psychological Science, 23*(3), 278-287.

Hannula, D. E., & Ranganath, C. (2009). The Eyes Have It: Hippocampal Activity Predicts Expression of Memory in Eye Movements. *Neuron, 63*(5), 592-599.

Hannula, D. E., Ryan, J. D., Tranel, D., & Cohen, N. J. (2007). Rapid onset relational memory effects are evident in eye movement behavior, but not in hippocampal amnesia. *Journal of Cognitive Neuroscience, 19*(10), 1690-1705.

Hanslmayr, S., Staresina, B. P., & Bowman, H. (2016). Oscillations and episodic memory: addressing the synchronization/desynchronization conundrum. *Trends in Neurosciences, 39*(1), 16-25.

Hanslmayr, S., & Staudigl, T. (2014). How brain oscillations form memories--a processing based perspective on oscillatory subsequent memory effects. *Neuroimage, 85 Pt 2*, 648-655.

Herweg, N. A., Solomon, E. A., & Kahana, M. J. (2020). Theta oscillations in human memory. *Trends in Cognitive Sciences, 24*(3), 208-227.

Hoffman, K. L., Dragan, M. C., Leonard, T. K., Micheli, C., Montefusco-Siegmund, R., & Valiante, T. A. (2013). Saccades during visual exploration align hippocampal 3-8 Hz rhythms in human and non-human primates. *Frontiers in systems neuroscience, 7*, 43.

Hsieh, L. T., & Ranganath, C. (2014). Frontal midline theta oscillations during working memory maintenance and episodic encoding and retrieval. *Neuroimage, 85 Pt 2*, 721-729.

Ito, J., Maldonado, P., Singer, W., & Grün, S. (2011). Saccade-related modulations of neuronal excitability support synchrony of visually elicited spikes. *Cerebral Cortex, 21*(11), 2482-2497.

Jacobs, J., Hwang, G., Curran, T., & Kahana, M. J. (2006). EEG oscillations and recognition memory: Theta correlates of memory retrieval and decision making. *Neuroimage, 32*(2), 978-987.

Johansson, R., Nystrom, M., Dewhurst, R., & Johansson, M. (2022). Eye-movement replay supports episodic remembering. *Proceedings of the Royal Society B: Biological Sciences, 289*(1976), 20220964.

Kamienkowski, J. E., Varatharajah, A., Sigman, M., & Ison, M. J. (2018). Parsing a mental program: Fixation-related brain signatures of unitary operations and routines in natural visual search. *Neuroimage, 183*, 73-86.

Karlsson, A. E., Wehrspaun, C. C., & Sander, M. C. (2020). Item recognition and lure discrimination in younger and older adults are supported by alpha/beta desynchronization. *Neuropsychologia, 148*.

Klimesch, W., Doppelmayr, M., Schimke, H., & Ripper, B. (1997). Theta synchronization and alpha desynchronization in a memory task. *Psychophysiology, 34*(2), 169-176.

Klimesch, W., Freunberger, R., & Sauseng, P. (2010). Oscillatory mechanisms of process binding in memory. *Neuroscience and Biobehavioral Reviews, 34*(7), 1002-1014.

Kota, S., Rugg, M. D., & Lega, B. C. (2020). Hippocampal Theta Oscillations Support Successful Associative Memory Formation. *Journal of Neuroscience, 40*(49), 9507-9518.

Kragel, J. E., Schuele, S., VanHaerents, S., Rosenow, J. M., & Voss, J. L. (2021). Rapid coordination of effective learning by the human hippocampus. *Science Advances, 7*(25).

Kragel, J. E., VanHaerents, S., Templer, J. W., Schuele, S., Rosenow, J. M., Nilakantan, A. S., & Bridge, D. J. (2020). Hippocampal theta coordinates memory processing during visual exploration. *Elife, 9*.

Kragel, J. E., & Voss, J. L. (2022). Looking for the neural basis of memory. *Trends in Cognitive Sciences, 26*(1), 53-65.

Kumaran, D., & Wagner, A. D. (2009). It's In My Eyes, but It Doesn't Look that Way to Me. *Neuron, 63*(5), 561-563.

Lepage, M., Ghaffar, O., Nyberg, L., & Tulving, E. (2000). Prefrontal cortex and episodic memory retrieval mode. *Proceedings of the National Academy of Sciences of the United States of America, 97*(1), 506-511.

Makeig, S., & Jung, T. P. (1996). Tonic, phasic, and transient EEG correlates of auditory awareness in drowsiness. *Cognitive Brain Research, 4*(1), 15-25.

Martín-Buro, M. C., Wimber, M., Henson, R. N., & Staresina, B. P. (2020). Alpha Rhythms Reveal When and Where Item and Associative Memories Are Retrieved. *Journal of Neuroscience, 40*(12), 2510-2518.

Mathewson, K. E., Gratton, G., Fabiani, M., Beck, D. M., & Ro, T. (2009). To see or not to see: prestimulus alpha phase predicts visual awareness. *Journal of Neuroscience, 29*(9), 2725-2732.

Mcclelland, J. L., Mcnaughton, B. L., & Oreilly, R. C. (1995). Why There Are Complementary Learning-Systems in the Hippocampus and Neocortex - Insights from the Successes and Failures of Connectionist Models of Learning and Memory. *Psychological Review, 102*(3), 419-457.

Michelmann, S., Bowman, H., & Hanslmayr, S. (2016). The Temporal Signature of Memories: Identification of a General Mechanism for Dynamic Memory Replay in Humans. *Plos Biology, 14*(8).

Mullen, T. R., Kothe, C. A., Chi, Y. M., Ojeda, A., Kerth, T., Makeig, S., . . . Cauwenberghs, G. (2015). Real-Time Neuroimaging and Cognitive Monitoring Using Wearable Dry EEG. *Ieee Transactions on Biomedical Engineering, 62*(11), 2553-2567.

Nagy, M., & Király, I. (2018). Evidence of relational retrieval, even in the absence of the relational eye movement effect (REME). *Consciousness and Cognition, 66*, 40-53.

Niehorster, D. C., Andersson, R., & Nystrom, M. (2020). Titta: A toolbox for creating PsychToolbox and Psychopy experiments with Tobii eye trackers. *Behavior Research Methods, 52*(5), 1970-1979.

Nikolaev, A. R., Bramao, I., Johansson, R., & Johansson, M. (2023). Episodic memory formation in unrestricted viewing. *Neuroimage, 266*.

Nikolaev, A. R., Ehinger, B. V., Meghanathan, R. N., & van Leeuwen, C. (2023). Planning to revisit: Neural activity in refixation precursors. *Journal of vision, 23*(7).

Nikolaev, A. R., Meghanathan, R. N., & van Leeuwen, C. (2016). Combining EEG and eye movement recording in free viewing: pitfalls and possibilities. *Brain and Cognition, 107*, 55-83.

Nikolaev, A. R., Meghanathan, R. N., & van Leeuwen, C. (2018). Refixation control in free viewing: a specialized mechanism divulged by eye-movement related brain activity. *Journal of Neurophysiology, 120*(5), 2311-2324.

Nyhus, E., & Curran, T. (2010). Functional role of gamma and theta oscillations in episodic memory. *Neuroscience and Biobehavioral Reviews, 34*(7), 1023-1035.

Olsen, R. K., Lee, Y., Kube, J., Rosenbaum, R. S., Grady, C. L., Moscovitch, M., & Ryan, J. D. (2015). The Role of Relational Binding in Item Memory: Evidence from Face Recognition in a Case of Developmental Amnesia. *Journal of Neuroscience, 35*(13), 5342-5350.

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Computational Intelligence and Neuroscience, 2011*.

Ossandón, J. P., König, P., & Heed, T. (2020). No Evidence for a Role of Spatially Modulated alpha-Band Activity in Tactile Remapping and Short-Latency, Overt Orienting Behavior. *Journal of Neuroscience, 40*(47), 9088-9102.

Peirce, J., Gray, J. R., Simpson, S., MacAskill, M., Hochenberger, R., Sogo, H., . . . Lindelov, J. K. (2019). PsychoPy2: Experiments in behavior made easy. *Behavior Research Methods, 51*(1), 195-203.

Pion-Tonachini, L., Kreutz-Delgado, K., & Makeig, S. (2019). ICLabel: An automated electroencephalographic independent component classifier, dataset, and website. *Neuroimage, 198*, 181-197.

Popov, T., & Staudigl, T. (2023). Cortico-ocular coupling in the service of episodic memory formation. *Progress in Neurobiology, 227*.

Rajan, V., Cuevas, K., & Bell, M. A. (2021). Memory binding and theta EEG during middle childhood. *Developmental Psychobiology, 63*(6).

Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Sciences, 11*(6), 251-257.

Ryals, A. J., O'Neil, J. T., Mesulam, M. M., Weintraub, S., & Voss, J. L. (2019). Memory awareness disruptions in amnestic mild cognitive impairment: comparison of multiple awareness types for verbal and visuospatial material. *Aging Neuropsychology and Cognition, 26*(4), 577-598.

Ryan, J. D., Shen, K., & Liu, Z. X. (2020). The intersection between the oculomotor and hippocampal memory systems: empirical developments and clinical implications. *Annals of the New York Academy of Sciences, 1464*(1), 115-141.

Ryan, J. D., & Villate, C. (2009). Building visual representations: The binding of relative spatial relations across time. *Visual Cognition, 17*(1-2), 254-272.

Sauseng, P., Feldheim, J. F., Freunberger, R., & Hummel, F. C. (2011). Right prefrontal TMS disrupts interregional anticipatory EEG alpha activity during shifting of visuospatial attention. *Frontiers in Psychology, 2*.

Smith, C. N., Hopkins, R. O., & Squire, L. R. (2006). Experience-dependent eye movements, awareness, and hippocampus-dependent memory. *Journal of Neuroscience, 26*(44), 11304-11312.

Smith, C. N., & Squire, L. R. (2018). Awareness of what is learned as a characteristic of hippocampus-dependent memory. *Proceedings of the National Academy of Sciences of the United States of America, 115*(47), 11947-11952.

Spaniol, J., Davidson, P. S. R., Kim, A. S. N., Han, H., Moscovitch, M., & Grady, C. L. (2009). Event-related fMRI studies of episodic encoding and retrieval: Meta-analyses using activation likelihood estimation. *Neuropsychologia, 47*(8-9), 1765-1779.

Staresina, B. P., & Wimber, M. (2019). A Neural Chronometry of Memory Recall. *Trends in Cognitive Sciences, 23*(12), 1071-1085.

Tran, Y., Craig, A., Craig, R., Chai, R. F., & Nguyen, H. (2020). The influence of mental fatigue on brain activity: Evidence from a systematic review with meta-analyses. *Psychophysiology, 57*(5).

Urgolites, Z. J., Smith, C. N., & Squire, L. R. (2018). Eye movements support the link between conscious memory and medial temporal lobe function. *Proceedings of the National Academy of Sciences of the United States of America, 115*(29), 7599-7604.

Voss, J. L., Bridge, D. J., Cohen, N. J., & Walker, J. A. (2017). A closer look at the hippocampus and memory. *Trends in Cognitive Sciences, 21*(8), 577-588.

Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences, 9*(9), 445-453.

Wynn, J. S., Olsen, R. K., Binns, M. A., Buchsbaum, B. R., & Ryan, J. D. (2018). Fixation Reinstatement Supports Visuospatial Memory in Older Adults. *Journal of Experimental Psychology-Human Perception and Performance, 44*(7), 1119-1127.