

Imagining is not seeing: lower insight-driven memory reconfiguration when imagining the link between separate events

Anna-Maria Grob ¹, Branka Milivojevic ², Arjen Alink ^{3,4}, Christian F. Doeller ^{5,6,7}, Lars Schwabe ^{1,*}

¹Department of Cognitive Psychology, Institute of Psychology, Universität Hamburg, Hamburg 20146, Germany,

²Donders Institute for Brain, Cognition and Behaviour, Radboud University, Nijmegen 6525AJ, The Netherlands,

³Department of General Psychology, Institute of Psychology, Universität Hamburg, Hamburg 20146, Germany,

⁴Department of Systems Neuroscience, University Medical Center Hamburg-Eppendorf, Hamburg 20246, Germany,

⁵Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig 04103, Germany,

⁶Kavli Institute for Systems Neuroscience, Centre for Neural Computation, The Egil and Pauline Braathen and Fred Kavli Centre for Cortical Microcircuits, Jepsen Centre for Alzheimer's Disease, Norwegian University of Science and Technology, Trondheim 7491, Norway,

⁷Wilhelm Wundt Institute of Psychology, Leipzig University, Leipzig 04109, Germany

*Corresponding author: Department of Cognitive Psychology, Universität Hamburg, Institute of Psychology, Von-Melle-Park 5, Hamburg 20146, Germany.

Email: Lars.Schwabe@uni-hamburg.de

Gaining insight into the relationship between previously separate events allows us to combine these events into coherent episodes. This insight may occur via observation or imagination. Although much of our reasoning occurs in the absence of direct sensory stimuli, how mnemonic integration is accomplished via imagination has remained completely unknown. Here, we combined fMRI with representational similarity analysis and a real-life-like narrative-insight task (NIT) to elucidate the behavioral and neural effects of insight through imagination (vs. observation). Healthy participants performed the NIT in the MRI scanner and underwent memory testing one week later. Crucially, participants in the observation group gained insight through a video, while participants in the imagination group gained insight through an imagination instruction. Although we show that insight via imagination was weaker than insight via direct observation, the imagination group showed better detail memory. Moreover, the imagination group showed no representational change in the anterior hippocampus or increases in frontal and striatal activity for the linked events, as was the case in the observation group. However, the hippocampus and striatum were more activated during linking via imagination, which might indicate that their increased recruitment during imagination impedes concurrent mnemonic integration but may facilitate long-term memory.

Key words: fMRI; imagination; insight; memory integration; hippocampus; striatum; prefrontal cortex.

Our memories are highly dynamic and can be recombined with remarkable flexibility. When we gain insight into how two seemingly separate events are connected, we are able to flexibly integrate these initially discrete events into coherent episodes. These new, overlapping memory representations occur when new learning experiences share a common element with preexisting memory traces, thus prompting the integration of novel information into the existing memory network (Schlichting and Preston 2017). For instance, when we watch a movie, we sometimes experience a “plot twist,” a moment when we realize how earlier, seemingly unrelated scenes are actually connected. This fundamental process of mnemonic integration is thought to underlie a variety of flexible behavior, ranging from decision-making (Wimmer and Shohamy 2012; Shohamy and Daw 2015) or inferring novel relationships (Eichenbaum et al. 1999; Zeithamova and Preston 2010; Zeithamova et al. 2012) to spatial navigation (Gupta et al. 2010; He et al. 2022). In daily life, the relationship of two seemingly unrelated events is often not directly observed but is imagined. For instance, instead of watching a movie, we can also read the book and gain insight into the plot and possible twists through our own imagination. Gaining insight via imagination bears particular importance in educational settings, where existing

discrete units of knowledge are brought together by imagination, triggered by reading or hearing about an event, rather than by direct sensory experience. Imaginative techniques, such as the loci method, have been repeatedly shown to benefit memory in early research (Bower 1970; Yesavage and Rose 1984; Hockley and Christi 1996) and have proven valuable from educational settings to memory championships (Maguire et al. 2003; Richmond et al. 2008). Moreover, previous research demonstrated a memory advantage for deep versus shallow (i.e. perception-based) encoding (Craig and Lockhart 1972; Kapur et al. 1994; Otten et al. 2001; Ritchey et al. 2011). However, despite the importance of imagination for the integration of event knowledge in educational settings and its importance as a mnemonic strategy, previous research on memory integration has focused almost exclusively on integration through direct experience by presenting the unknown connection directly to the observer. Thus, to date, it remains largely unclear exactly how mnemonic integration is accomplished through imagination.

The ability to imagine future or novel scenarios appears to be intimately linked to episodic memory. Studies in patients with medial temporal lobe (in particular, hippocampal) damage revealed that many of these patients lost not only their episodic memory but also their ability to imagine future events

Received: November 24, 2022. Revised: February 1, 2023. Accepted: February 2, 2023

© The Author(s) 2023. Published by Oxford University Press. All rights reserved. For permissions, please e-mail: journals.permission@oup.com

(Tulving 1985; Hassabis et al. 2007; Squire et al. 2010; Race et al. 2011). Likewise, neuroimaging studies showed similar brain activity during recollection and imagination, encompassing brain regions such as the hippocampus (Addis et al. 2009; Benoit and Schacter 2015; Bellana et al. 2017; Benedek et al. 2018). These data led to the “prospective brain” hypothesis, which postulates that the brain uses stored information to imagine, plan, and predict future events (Schacter et al. 2007). The capacity to construct a scene, whether remembered or imagined, depends on the hippocampus, which continuously constructs event representations beyond concrete perception (Gaesser et al. 2013; Maguire and Mullally 2013; Zeidman and Maguire 2016; Barry et al. 2019; Clark et al. 2019).

Beyond imagination, the hippocampus is also critically implicated in mnemonic integration (Collin et al. 2015; Schlichting et al. 2015). To accomplish mnemonic integration, the hippocampus can separate patterns of activity which reduce interference between memory representations, (Marr 1971; McClelland et al. 1995; Norman and O’Reilly 2003; Huffman and Stark 2014; Libby et al. 2019; Brunec et al. 2020) as well as combine related memories into integrated memory representations (Collin et al. 2015; Horner et al. 2015; Milivojevic et al. 2015; Schlichting et al. 2015; Schapiro et al. 2017; Brunec et al. 2020). These opposed processes of pattern separation and completion seem to depend on different parts of the hippocampus, as previous findings suggest a functional division along its longitudinal axis. While the anterior hippocampus has been associated with memory integration, the posterior hippocampus has been more implicated in memory separation (Collin et al. 2015, 2017; Milivojevic et al. 2015; Schlichting et al. 2015; Brunec et al. 2020). Thus, previous research suggests that the hippocampus plays a critical role in both imagination and memory integration, raising the question of whether memory integration can still be fully accomplished when the hippocampus is at least partially occupied by imagination. Until now, however, it remains completely unknown how insight into the relationship between two initially unrelated events comes about through imagination and what neural mechanisms are involved in imagination-based mnemonic integration.

Therefore, the present study aimed to elucidate the neural mechanisms and behavioral consequences of linking initially unrelated events through imagination. To this end, we combined fMRI with multivariate representational similarity analysis (RSA) and a modified life-like narrative-insight task (NIT; Milivojevic et al. 2015; Fig. 1). In this task, participants were first presented a series of unrelated events and then either saw or were asked to imagine how some of these events were linked. One week after encoding, we performed a comprehensive behavioral analysis of the memory for the linked (and nonlinked) events. These delayed memory tests included a free recall and a forced-choice recognition test as well as a multidimensional arena task (MAT) in which participants indicated how related they thought the events were. We hypothesized that insight through imagination is possible but is more difficult to achieve than insight through observation. Because the hippocampus has repeatedly been shown to be relevant to imaginative processes (Maguire and Mullally 2013; Zeidman and Maguire 2016), we predicted greater hippocampal involvement during the imagination relative to the presentation of a linking event. We further assumed that the hippocampal recruitment during imagination might affect its capacity to reconfigure the representation of the now linked events. Finally, we tested how these neural changes associated with imagination-based mnemonic integration would affect subsequent memory for the linked (vs. nonlinked) events.

Materials and methods

Participants

Fifty-six healthy, right-handed individuals (29 males, 27 females, age: $M = 25.68$ years, $SD = 3.97$ years) with normal or corrected-to-normal vision volunteered to participate in this study. Participants were screened using a standardized interview for exclusion criteria that included a history of neurological and psychiatric disease; medication use and substance abuse; cardiovascular, thyroid, or renal disease; body mass index < 19 and > 26 kg/m²; evidence of COVID-19 infection or exposure; and contraindications to MRI examination. It was also ensured that every participant was proficient in the German language. All participants gave informed consent before participation and received a moderate monetary compensation (50€) at the end of the experiment. The procedures were approved by the local ethics committee (Faculty of Psychology and Human Movement Science, Universität Hamburg, Hamburg, Germany, 2017_143 Schwabe) and adhered to the Declaration of Helsinki. The sample size is in line with previous studies on imaginative processes and subsequent memory (Devitt and Schacter 2020) and is further corroborated by an a priori calculation using G*Power, indicating that a sample size of $n = 54$ is sufficient to detect a medium-sized effect ($f = 0.25$) for the crucial group \times link effect with a power of 0.95.

We implemented a mixed-design including the within-subject factors link (linked vs. nonlinked events) and session (pre- vs. post-link) and the between-subjects factor group (imagination vs. observation). Participants were pseudorandomly assigned to one of the two groups to achieve a comparable number of men and women per group and a balanced assignment to the imagination and observation groups. However, this resulted in slightly different group sizes. The imagination group comprised 27 participants (13 females) and the observation group consisted of 29 participants (14 females).

Procedure

The experiment included two days, one week apart. All experiments took place in the afternoon or early evening (between 12 and 6 pm). Before the start of the first experimental day, participants completed questionnaires assessing imagination (FFIS; Zabelina and Condon 2019), trait-anxiety (STAI-T; Laux et al. 1981), depressive symptoms (BDI; Hautzinger et al. 2006), chronic stress (TICS; Schulz and Schlotz 1999), and personality dimensions (BFI-2; Danner et al. 2016). After verification of eligibility for MRI measurements by a radiologist, participants gave informed consent and completed a state-anxiety questionnaire (STAI-S; Laux et al. 1981) and sleep quality questionnaire (PSQI; Buysse et al. 1989). They then performed a training run, which was immediately followed by the measurement of a working memory task (N-back; Kirchner 1958) to control for differences in working memory. Next, they completed a training session of the modified NIT (Milivojevic et al. 2015; Fig. 1), a life-like video-based task that tests the integration of originally separate events into coherent episodes. Participants then completed three runs of the modified NIT in the MRI scanner. One week later, to assess episodic memory integration, participants performed a free recall, a forced-choice recognition test, and a MAT (Kriegeskorte and Mur 2012).

Day 1: working memory control task

To check for possible group differences in working memory, a measurement of working memory performance was performed before participants entered the MRI scanner. Working memory

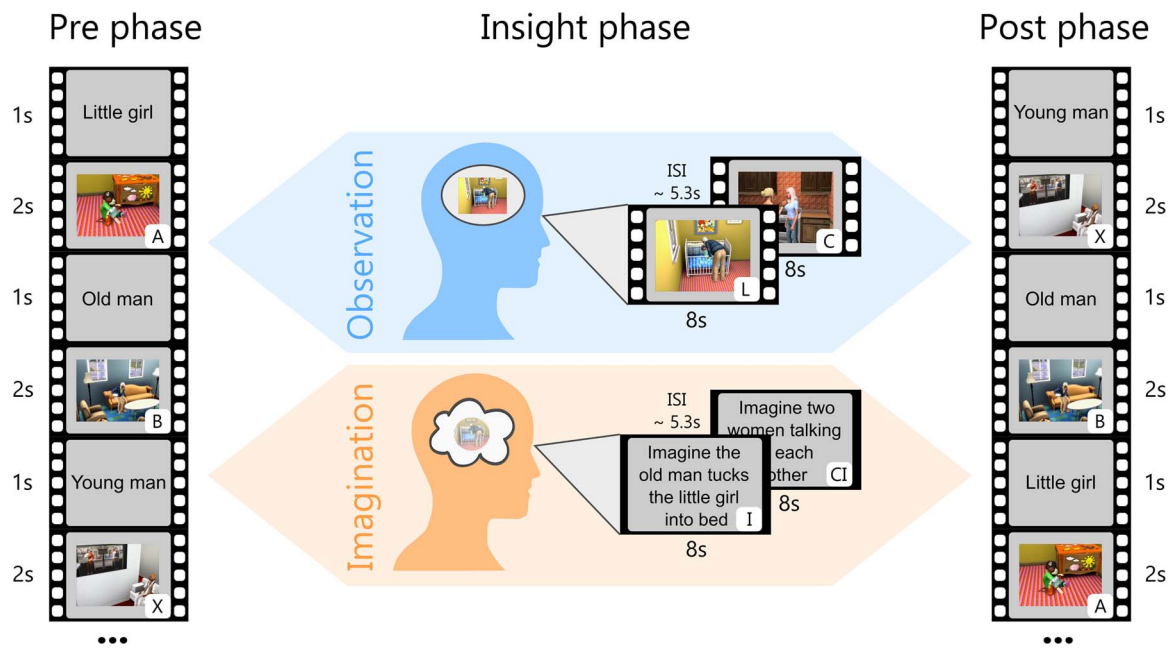


Fig. 1. Modified NIT. In a pre-insight phase, video events (A, B, and X) from each of 6 story lines were each preceded by a title (1 s) and repeated for 6 times. The ISI in the pre phase between an event and the next title was ~ 5.3 s. In a subsequent insight phase, some events could be integrated (events A and B) into narratives. Critically, while some participants saw a linking video (L) intertwined with a control video (C; observation group), others saw a written imagination instruction (I) intertwined with a control imagination instruction (CI; imagination group). The other event (X) was left nonlinked. In a post-insight phase, all video events were presented in exactly the same manner as in the pre-insight phase. Please note that texts were presented in German during the experiment and are translated here.

was measured with an *N*-back task (Kirchner 1958). In this task, participants were presented with single-digit numbers from 0 to 9 and were asked whether the number on the screen (“target”) was the same number as the number presented in *n*-trials before (“cue”). Working memory load was manipulated by using two levels of complexity: 3- and 4-back trials. In addition to these two load levels, participants executed a control task (0-back) in which they had to indicate whether the current number was a 0. Responses were made either by pressing the left button (“no”) or by pressing the right button (“yes”) if the target number was identical to or different from the cue. The selected response was highlighted. In total, participants were shown six pseudorandomized blocks consisting of two blocks from each level (0, 3, and 4 back). All blocks consisted of 20 numbers in random order. The numbers were presented for 500 ms and were separated by a delay of 1.5 s. The blocks were separated by 5 s. Before each block, participants were informed of the type of cognitive task ahead (0-, 3-, or 4-back).

Day 1: modified NIT

In the MRI scanner, participants underwent a modified version of the NIT (Milivojevic et al. 2015), while functional images were recorded. In this task, participants were presented with videos of life-like events from the computer game *The Sims 3* that belonged to several different storylines. In total, participants saw six different storylines. The videos from each storyline could either be integrated (events A and B) into narratives or not (A and X; see Fig. 1). Unbeknownst to the participant, each narrative had two possible versions to control for nonspecific stimulus effects and visual similarity. The two narrative versions comprised an identical event A, but different events B. Control event X from one version served as event B in the other version. Therefore, all participants saw the same events A, B, and X, but 30 participants

linked events A and X, while 26 participants linked events A and B. In the following, the linked events will always be referred to as events A and B, whereas the nonlinked events will be referred to as A and X. To elucidate the underlying mechanisms of mnemonic integration, two different insight conditions were introduced into the task: imagination and observation.

Each story was presented in three phases: pre-insight phase, insight phase, and post-insight phase (Fig. 1). In the *pre-insight phase*, all participants were presented with events A, B, and X for 2 s each, separated by interstimulus intervals (ISIs) of 1, 4, or 11 s (~ 5.3 s on average). Each video was preceded by a short title (1 s) and was presented 6 times in a pseudorandom order such that each video was shown before the next round of presentations began and the same video was not presented on two consecutive trials. After the pre-insight phase, participants had to indicate on a scale from not at all (1) to very much (4) how much they thought the events belonged together. In the subsequent *insight phase*, the task differed according to whether participants were in the imagination or the observation condition. Participants in the observation condition viewed the linking video event (L) intertwined with a control video event (C), each presented for 8 s and repeated six times (ISIs of 1, 4, or 11 s, ~ 5.3 s on average). Participants in the imagination condition, however, were presented with an instruction (I) to imagine a specific linking scene using the titles from each video to indicate which person was meant, interleaved with a control instruction (CI), each presented for 8 s and repeated six times (ISIs of 1, 4, or 11 s, ~ 5.3 s on average). Participants were instructed to imagine specific scenes only when specifically asked to do so; otherwise, they were told to simply relax and watch the videos or answer the rating questions. In the observation condition, the linking video (L) showed the main characters from videos A and B interacting with each other, while the control video (C) showed only an unknown character engaged in an unrelated activity (e.g. two women talking to each other). In the imagination

condition, the linking instruction (I) instructed them to imagine the main characters from videos A and B interacting with each other, while the control instruction (CI) asked them to imagine an unknown character engaged in an unrelated activity (e.g. two women talking to each other). After the insight phase, participants completed several ratings regarding the understanding of the link and adherence to instructions on a scale ranging from not at all (1) to very much (4). In the final *post-insight phase*, all participants were again presented with events A, B, and X presented for 2 s each, repeated six times, and separated by ISIs of 1, 4, or 11 s (~5.3 s on average). Each video was again preceded by a short title (1 s). Events in the post-insight phase were also presented in a pseudorandom order to reduce potential sequence effects. The main purpose of this phase was to assess the changes in the neural representation of events A and B after they learned that they were linked. After the post phase, participants had to indicate again how much they thought that the events belonged together on a scale from not at all (1) to very much (4). Participants received visual feedback when they entered a rating question by highlighting the selected response. In addition to presenting A, B, and X events in the pre- and post-insight phases, we also presented target events to which participants responded by pressing a button with the index finger of their right hand. These target events accounted for 11% of trials in the pre- and post-insight phases and consisted of a 2 s animated video of a girl on a pink scooter. These target trials were recorded to ensure that participants remained vigilant throughout the experiment.

Day 2: free recall

To assess the detailedness of memory one week after encoding, participants were instructed to recall the events presented on day 1 in as much detail as possible. During free recall, they were voice recorded for a maximum of 15 min. To assess the level of detailedness of the integrated episodes, audio recordings from free recall were scored according to how much detail of the different video events (A, B, and X) were recalled from day 1. The rating scheme was such that it allowed for separate coding of details remembered for the A, B, and X events. The video events (A, B, and X) from the different stories did not differ in how many details could be named (*event*: $F(1.67, 8.37) = 2.93, P = 0.114, \eta_G = 0.296$; mean A = 21.83; *SD* A = 4.62; mean B = 19.17; *SD* B = 3.71; mean X = 25.50; *SD* X = 4.76). The raters were instructed to assign details only to events where it was clear that they belonged exclusively to that event so that there was no confusion of details between different events. Two raters scored the first half of the data and another two raters scored the second half. All raters were blinded to the experimental conditions. To assess the interrater reliability, all raters rated the first five participants, and on average, these ratings were highly correlated with each other (*mean correlation* = 0.83, *SD* = 0.06). To obtain a better estimate of intersubjectivity, these ratings were averaged. The details for the different event types (A, B, and X) were summed across stories to obtain an overall rating of event details. The mean of the linked events (A and B) was then calculated to obtain a measure of linked events. The nonlinked event (X) was left as it was.

Day 2: MAT

To estimate the representational structure of episodic memory, participants were asked to arrange representative images of the video events (A, B, and X) of each story according to their relatedness on a 2D circular arena in a MAT (Kriegeskorte and Mur 2012; Supplementary Fig. S1). They were asked to bring the pictures that had been linked (A and B) one week earlier closer together than

the pictures that had not been linked (A and X) by dragging and dropping them with the computer mouse inside a white circular arena on the computer screen. Thus, participants were instructed to group the events according to the extent to which they were related in the NIT. The images were large enough on the computer screen to be recognized by all participants. All trials were self-paced and could be completed by the participants by pressing "Done". In the first trial, participants had to order all pictures by similarity and were instructed to do so carefully. Subsequent trials consisted of subsets of the first trial selected based on an adaptive procedure aimed at minimizing uncertainty and better approximating the high-dimensional perceptual representational space. This procedure is based on an algorithm optimized to provide optimal evidence for the dissimilarity estimates (Kriegeskorte and Mur 2012). The distances in this MA task were calculated by first computing the squared screen distance (Euclidean distance) between all elements in the first trial to create a roughly estimated representative dissimilarity matrix (RDM) and by iteratively updating this RDM by the weighted average of the scaled trial estimates. This MA task took 10 min to complete.

Day 2: forced-choice recognition test

To also have an estimate of correct recollection for linked versus nonlinked events, participants completed a forced-choice matching task. They were presented with an image of event A at the top of the computer screen and had to indicate whether the image of B or X in the bottom half of the screen belonged to A. Participants were presented with these forced-choice options for each of the stories they had seen a week before. After indicating for a story which event belonged to event A, they had to rate how confident they were in their answer. Confidence was rated on a scale from not at all (1) to very sure (4). This was repeated for each of the six stories. Participants were presented with the forced-choice question and the confidence rating for 5.5 s each, which were separated by ISIs of 1, 4, or 11 s (~5.3 s on average). Participants received visual feedback when they entered a rating question by highlighting the selected response. The forced-choice recognition test lasted for approximately 2–3 min.

Analysis

Behavioral and physiological data analysis

To assess the degree of insight-related mental reorganization, the ratings for the event duplets of interest (AB and AX) from the pre- and post-insight phases were entered into a mixed $2 \times 2 \times 2$ ANOVA with the between-subjects factor group and the within-subject factors time (pre/post) and link (link/nonlink). To evaluate the long-term representation of the integrated events, performance in forced-choice recognition was assessed by calculating the proportion of correct answers. These performance measures (in %) were then entered into a two-sample t-test with the between-subjects factor group. To analyze the representational structure of memory, Euclidean dissimilarity estimates were extracted from the MAT for linked (AB) and nonlinked events (AX), averaged across stories, and then entered into a mixed 2×2 ANOVA with the between-subjects factor group and the within-subject factor link (link/nonlink). Details from free recall were entered into a mixed 2×2 ANOVA with the between-subjects factor group and the within-subject factor item (link/nonlink).

All analyses were performed in R version 4.0.4 (<https://www.r-project.org/>). In case of violation of sphericity, as indicated by the Mauchly test, Greenhouse–Geisser corrected degrees of freedom and P-values are reported. Prior to analysis, data were checked for outliers. Outliers were defined as median ± 3 SD. For the

analysis of the modified NIT, four outliers were identified and excluded (two from the imagination and two from the observation group). For the analysis of the MAT, two outliers were identified and excluded (one from the imagination and one from the observation group). For the free recall analysis, two outliers were identified and excluded (one from the imagination and one from the observation group). For the RSA, one outlier was identified and removed (observation group). These outliers consisted of eight different individuals, as one individual was an outlier in both the NIT and the MAT. Presumably, those identified here as outliers did not understand the tasks as well compared to the other participants.

MRI acquisition and analysis

Imaging data were acquired on a 3T Siemens PRISMA scanner (Siemens, Germany) with a 64-channel head coil. Data were collected on three functional runs, which were separated by short pauses. We used a custom 3D echo-planar imaging (EPI) pulse sequence acquiring interleaved slices with the following parameters: TR=2,000 ms; TE=30 ms; flip angle=60°; volume resolution=2 mm³; slices=62; approx. 530 volumes per run; field of view (FoV)=224 mm; acceleration factor PE=2. Additionally, a structural T1-weighted image was acquired using a MPRAGE-grappa sequence with the following parameters: TR=2,500 ms; TE=2.06 ms; flip angle=9°; voxel resolution=0.8 mm³; slices=256; FoV=244 mm; 3D acceleration factor=1 at the end of the MRI session.

fMRI data preprocessing

Preprocessing and analysis of the fMRI data were performed using functions of the SPM 12 toolbox (Wellcome Trust Centre for Neuroimaging, London, UK) and custom scripts. To allow for magnetic field (T1) equilibration, the first three functional scans were discarded. First, the functional images were spatially realigned and were slice-time corrected. Then, the functional images were coregistered with the structural image by coregistering the structural image to the mean EPI. For multivariate analysis (see below), images were not preprocessed further. For univariate analysis (see below), functional images were normalized to the MNI template and were then smoothed with a 6-mm³ full-width at half maximum Gaussian kernel.

The results of the neural analyses were considered as significant at a family-wise error (FWE)-corrected threshold of $P < 0.050$. To test our hypotheses, we performed, in addition to more explorative whole-brain analyses, region of interest (ROI) analyses with a priori-defined ROIs using small-volume correction (SVC; $P < 0.050$, FWE-corrected) with an initial threshold of $P < 0.001$ as uncorrected. As the hippocampus has been found to be involved in imaginative processes (Addis et al. 2009; Benoit and Schacter 2015; Zeidman and Maguire 2016; Barry et al. 2019), we focused on the hippocampus for our ROI analyses. The hippocampus was split into posterior and anterior subregions, as these have been found to be differentially implicated in mnemonic integration and separation processes (Collin et al. 2015; Robin and Moscovitch 2017; Dandolo and Schwabe 2018). Our hippocampal masks were derived from previous work using the WFU pick-atlas: pHC from $Y = -40$ to -30 , and aHC from $Y = -18$ to -4 (Collin et al. 2015; Dandolo and Schwabe 2018). We corrected for the number of ROIs in the specific analyses by applying Bonferroni correction (P_{corr}).

Univariate fMRI analysis

For univariate fMRI analysis, data from all three runs were concatenated to allow estimation of neural responses using all

acquired data. The concatenated time series were analyzed using a generalized linear model (GLM) as implemented in SPM12. This model included one regressor per event type (A, B, and X) during each phase (pre- and postlink). Each of these six event regressors of interest modeled 36 trials (six trials per each of the six different stories). Each model also included the following nuisance regressors: regressors for the link videos and control videos or the imagination instructions and the CIs in the insight phase, and one regressor for the 24 target events (girl on the pink scooter). All analyses also included six concatenated nuisance regressors to control for head movement as well as three run constants. All task regressors and the nuisance task regressors of no interest were convolved with the canonical hemodynamic response function to obtain a modeled time course of neuronal activity. A high-pass filter of 128 s was used to remove low-frequency drifts, and serial correlations in the time series were accounted for using an autoregressive AR(1)-model. To analyze the neural basis of the change from pre- to post-insight, we computed a contrast comparing postlink events with prelink events ($AB_{post} > AB_{pre}$) and a contrast comparing post nonlink events with pre nonlink events ($X_{post} > X_{pre}$). These contrast images were analyzed at the group level using a two-sample t-test.

Univariate fMRI analysis: insight phase

For the analysis of the insight phase, data from all three runs were concatenated to allow estimation of neural responses using a GLM. This model included individual regressors for all event types (A, B, X, L/I, and C/CI). Critically, to measure the strength of insight during the insight phase, we also included two parametric modulators reflecting the information gained through the link video (or instruction) or the control video (or instruction). To assess the level of insight, the parametric regressor was defined as: decreasing values from the first repetition (6) to the last repetition (1) for both link events (L/I) and control events (C/CI). Critically, this model with its decreasing parametric modulation was set up to focus on the insight gained, which should be greatest at the beginning, as well as to counteract potential repetition effects in the imagination condition (Mulukom et al. 2013). Each model also included the following nuisance variables: one regressor for the 24 target events, six concatenated nuisance regressors to control for head movement as well as three run constants. All task regressors and the nuisance task regressors of no interest were convolved with the canonical hemodynamic response function to obtain a modeled time course of neuronal activity. A high-pass filter of 128 s was used to remove low-frequency drifts, and serial correlations in the time series were accounted for using an autoregressive AR(1)-model. For each participant, contrast images across the six stories were calculated for the insight phase in general, which were then taken to the second-level group analysis. Two-sample t-test analyses were performed at the second level.

Functional connectivity analysis

To analyze the crosstalk of the brain areas identified in the previous analyses with other brain areas related to the processes underlying episodic integration during linking, we performed a psychophysiological interaction (PPI) analysis to measure task-dependent connectivity using the bilateral caudate nuclei as seed regions, as the caudate nucleus yielded the highest univariate increases from pre- to post-insight for linked events in the observation group compared to the imagination group. Furthermore, higher connectivity between the caudate and the hippocampus has been linked to better imagination and memory performance

in previous studies (Müller et al. 2018; Faul et al. 2020). Hence, the first eigenvariate of the activity time course of the specific ROI for the link contrast (Link Events > Control Events) was extracted using an anatomical mask and included as a seed in the PPI. A first-level model was set up, including the seed region, a vector coding the contrast of interest and an interaction term, which was computed as an element-by-element product of the first two regressors. The resulting interaction contrasts were brought to the second level to test whether functional connectivity between regions differed between the imagination and observation groups.

We further analyzed the connectivity for the change contrast in the nonlinked event by performing a PPI analysis using the bilateral dorsolateral prefrontal cortex (dlPFC), as this region has been shown to be important in a previous univariate analysis and to be important for relational memory and insight (Murray and Ranganath 2007; Long et al. 2010; Blumenfeld et al. 2011; Tik et al. 2018). Thus, the first eigenvariate of the activity time course of the specific ROI for the nonlink contrast ($X_{\text{post}} > X_{\text{pre}}$) was extracted using an anatomical mask and included as a seed in the PPI. A first-level model was set up, including the seed region, a vector coding the contrast of interest and an interaction term, which was computed as an element-by-element product of the first two regressors. The resulting interaction contrasts were brought to the second level to test whether functional connectivity between regions differed between the imagination and observation groups.

The results of both PPI analyses were corrected by a Bonferroni correction of four ROIs. In addition to the anterior and posterior hippocampus, we also corrected for the seed regions of both PPIs: the caudate nucleus and the dlPFC.

Multivariate analysis

To assess the changes in neural patterns induced by insight into the narrative structure of events and the modulation thereof by the mode of linking, we performed an RSA (Kriegeskorte et al. 2008) using the rsatoolbox (Nili et al. 2014). We focused on the hippocampal long axis since its subregions have been differentially associated with memory integration as well as segregation — two processes that are critical for episodic memory integration (Milivojevic et al. 2015; Schlichting et al. 2015; Collin et al. 2017; Robin and Moscovitch 2017; Brunec et al. 2018; Dandolo and Schwabe 2018). At the first level, functional images from all three runs were concatenated to allow for the estimation of neural responses using a GLM. The analysis was performed in native space and, thus, only nonnormalized and nonsmoothed images were included in the GLM. This model included individual regressors for each event type by phase (A_{pre} , B_{pre} , X_{pre} , L , C , A_{post} , B_{post} , and X_{post}) in each of the six storylines separately. Thus, each event-regressor modeled six trials. Each model also included the following additional nuisance regressors: one regressor for the 24 target events, six concatenated nuisance regressors to control for head movement as well as three run constants. All task regressors and the nuisance task regressors of no interest were convolved with the canonical hemodynamic response function, resulting in a modeled time course of neuronal activity. Voxel-wise beta estimates resulting from the regressors of interest (A_{pre} , B_{pre} , X_{pre} , A_{post} , B_{post} , and X_{post}) were further transformed into t-statistics to account for the unreliability caused by noise (Walther et al. 2016). In a second analysis step, we back-transformed the ROIs from MNI space to subject-space for each participant individually. The computation of representational dissimilarity matrices (RDMs) for each ROI and each subject was, thus, performed in the native space of each participant. The resulting t-images from the regressors of interest were used to create vectors of activity

pattern for each event, separately for each ROI. These activity patterns were used to calculate the dissimilarity between two trials by correlation distances ($1-r$, Pearson's rank order correlation). Dissimilarities for each combination were then entered into a 36×36 RDM. Dissimilarities for linked (AB_{pre} and AB_{post}) and nonlinked events (AX_{pre} and AX_{post}) pre- and post-insight were extracted for each story and were averaged across stories for each participant. These averaged dissimilarities were then entered into a mixed $2 \times 2 \times 2 \times 2$ ANOVA in R version 4.0.4 (<https://www.r-project.org/>) with the between-subjects factor group (imagination vs. observation) and the within-subject factors time (pre- vs. post), link (link vs. nonlink), and hippocampus (anterior vs. posterior). In addition, we performed an exploratory ROI RSA focused on the medial prefrontal cortex, as this region is of interest during mnemonic integration (Milivojevic et al. 2015), using the same approach as for the hippocampal long axis.

To shed light on possible representational changes beyond the hippocampus, we also performed an RSA using a whole-brain searchlight approach with the rsatoolbox (Nili et al. 2014). For this purpose, we used the same GLM as for the ROI RSA, i.e. we performed the searchlight RSA in the native space of each participant. The resulting t-images from the regressors of interest (A_{pre} , B_{pre} , X_{pre} , A_{post} , B_{post} , and X_{post}) were used to create vectors of activity patterns for each event. We then calculated the correlation (Pearson's rank order correlation) between the activity patterns within each searchlight consisting of a minimum of 30 voxels and measuring three voxels in radius and a theoretical model operationalizing the increase in dissimilarity for linked events as found in the ROI RSA for the right anterior hippocampus. The resulting statistics for a single individual were mapped back on the central voxel of each sphere, producing a neural similarity map for a single individual. After normalization and smoothing with a Gaussian kernel of 6 mm^3 , these neural similarity maps were taken to the second-level group analysis. Two-sample t-test analyses were performed at the second level and FWE-corrected P-values are reported.

Correlational analysis

To relate the findings from univariate analyses to the behavioral results, we extracted the peak voxel contrast values of interest in each ROI using the MarsBar toolbox (Brett et al. 2002). Subsequently, the correlation between the extracted neural peak activity of each ROI and behavioral outcomes was estimated by correlating neural activity with behavioral outcomes for the imagination and the observation groups separately and then testing these correlations against each other (Eid et al. 2017).

Results

Imagination results in weaker insight, but stronger memory than observation

To investigate the effects of the mode of insight on mnemonic integration, we used a modified NIT (Fig. 1). In this task, participants first watched three videos showing specific episodes (pre-insight phase). Then, participants were either presented a new (linking) event (L) that linked two of the previously viewed events (A and B) but left the third event unrelated (event X; *observation group*) or received a written instruction (I) to imagine the linking of these events (*imagination group*). Finally, the now linked or nonlinked events were presented again to examine the insight-related changes in representation (post-insight phase). In all these phases, participants were presented with target stimuli to which they were asked to respond, thus controlling

for attention during the task. Participants responded on average to 94.64% ($SD=14.10\%$) of the target presentations without any group differences ($t_{(33,113)}=0.94$, $P=0.352$, $d=-0.26$). The groups adhered well to their instructions as participants in the imagination group indicated that they imagined the linking event very well ($M=3.34$, $SD=0.55$), while participants in the observation group indicated that they understood the presented linking event very well ($M=3.34$, $SD=0.43$). Participants in the imagination group also rated their imagination as rather depictive ($M=3.31$, $SD=0.61$), and participants in the observation group indicated that the link they saw made sense to them ($M=3.37$, $SD=0.43$). Participants in the imagination group engaged significantly more in imagination ($M=3.34$, $SD=0.62$) than did participants in the observation group ($M=2.61$, $SD=0.90$; observation vs. imagination: $t_{(49,788)}=-3.54$, $P<0.001$, $d=0.94$).

In the NIT, participants in the observation group showed better insight into the relationship between the originally separate events than did participants in the imagination group, thus revealing an immediate advantage of gaining insight via observation over gaining insight via imagination (group \times time \times link interaction: $F(1, 50)=5.16$, $P=0.027$, $\eta_G=0.012$; Fig. 2A). A follow-up test indicated that the imagination group had lower link ratings for linked items post-insight compared to participants in the observation group ($t_{(33,104)}=-2.07$, $P=0.046$, $d=0.60$), while the imagination group tended to rate the nonlinked items post-insight as more related than the observation group ($t_{(34,065)}=1.76$, $P=0.088$, $d=-0.50$), pre-insight, there were no group differences (link: $t_{(48,074)}=0.20$, $P=0.844$, $d=0.06$; nonlink: $t_{(48,643)}=0.13$, $P=0.893$, $d=0.04$).

One week later, the performance in the free recall test showed that participants remembered those events that were linked one week before (A and B) in more detail than the event that remained nonlinked (X; item: $F(1, 52)=29.35$, $P<0.001$, $\eta_G=0.150$), suggesting a memory advantage of linked over nonlinked events. Moreover, participants in the imagination group remembered overall more details than those in the observation group in the free recall (group: $F(1, 52)=5.40$, $P=0.024$, $\eta_G=0.067$; group \times item: $F(1, 52)=1.04$, $P=0.314$, $\eta_G=0.006$; Fig. 2B), indicating a memory advantage for all events after linking via imagination compared to linking via observation. Consistent with the memory advantage of the imagination group, those in the imagination group who indicated that they imagined the linking event more strongly, while prompted to do so, also recalled more details about the events (average of A, B, and X) a week later ($r=0.47$, $t_{(22)}=2.52$, $P=0.020$; Fig. 2C). While the imagination group outperformed the observation group in the free recall, there were neither group differences in the forced-choice recognition test ($M=75.89\%$; $SD=24.40\%$; $t_{(53,92)}=0.56$, $P=0.580$, $d=-0.15$; Fig. 2D) nor did the groups differ on the MAT (mean distance for linked events= 0.02 , $SD=0.02$; mean distance for nonlinked events= 0.05 , $SD=0.02$; link: $F(1, 50)=138.63$, $P<0.001$, $\eta_G=0.297$; Fig. 2E). Interestingly, across both groups, those who recalled more details for linked events in the free recall also grouped the linked events in the MAT closer together ($r=-0.49$, $t_{(48)}=-3.92$, $P<0.001$; Fig. 2F). The forced-choice recognition test and the MAT are, compared to the free recall, less demanding and capture memory per se, while the free recall captures detailedness of memory.

Imagination reduces insight-related activity in striatal and frontal regions

In order to assess neural changes associated with insight brought about during the insight phase, we compared BOLD activity changes for events that were linked (A and B) from the pre-

to the post-insight phase ($AB_{\text{post}} > AB_{\text{pre}}$). Our whole-brain analysis revealed that the imagination group showed less activation compared to the observation group in the caudate nucleus (whole-brain cluster-level: $t_{(1, 54)}=-5.07$, $p_{\text{corr}}(\text{FWE})=0.046$, $k=133$, peak: $x=16$, $y=-8$, $z=22$; Fig. 3A), the dlPFC (whole-brain cluster-level: $t_{(1, 54)}=-4.93$, $p_{\text{corr}}(\text{FWE})<0.001$, $k=576$, peak: $x=40$, $y=46$, $z=26$; Fig. 3B), and the orbitofrontal cortex (whole-brain cluster-level: $t_{(1, 54)}=-4.50$, $p_{\text{corr}}(\text{FWE})=0.040$, $k=138$, peak: $x=22$, $y=56$, $z=-6$; Fig. 3C). Interestingly, we found a positive correlation between the change in orbitofrontal activity from pre- to post-insight and the differentiation between linked and nonlinked events in free recall for the imagination but not for the observation group (observation: $r=-0.10$, $t_{(26)}=-0.52$, $P=0.607$; imagination: $r=0.50$, $t_{(24)}=2.87$, $P=0.009$; observation vs. imagination: $z=2.28$, $P=0.011$; Fig. 4). This suggests that a minimal increase in orbitofrontal activity is necessary for differentiation in free recall to occur; smaller increases or even decreases appear to be linked to a reduced differentiation in memory for linked versus nonlinked events. To further shed light on the changes induced by the insight phase, we also compared BOLD activity changes for events that remained nonlinked (X) across the pre- with the post-insight phase ($X_{\text{post}} > X_{\text{pre}}$). Our whole-brain analysis revealed that the imagination group showed a decrease from pre- to post-insight in the anterior cingulate cortex, whereas there was no such change in the observation group (whole-brain cluster-level: $t_{(1, 54)}=-6.15$, $p_{\text{corr}}(\text{FWE})=0.013$, $k=163$, peak: $x=-8$, $y=34$, $z=2$; Fig. 5).

Imagination prevents insight-induced representational change

To further shed light on the neural changes induced by the different types of insight—imagination versus observation—we compared multivariate voxel patterns pre- and post-insight by performing a ROI-based representational similarity analysis (RSA; Fig. 6A). We focused exclusively on the hippocampus in this analysis because the hippocampus has been shown to play a crucial role in the imagination processes (Addis et al. 2007; Mullally and Maguire 2014) and is also of paramount importance for mnemonic integration (Collin et al. 2015; Schlichting et al. 2015). To get more than a coarse picture of what is transpiring in the hippocampus, we divided the hippocampus along its long axis, as anterior regions have been found to be more relevant to mnemonic integration, whereas posterior regions are thought to be more involved in mnemonic segregation (Collin et al. 2015; Milivojevic et al. 2015; Schlichting et al. 2015; Brunec et al. 2018). For this analysis, RDMs were computed for the anterior and the posterior portions of the hippocampal long axis. Next, we extracted the neural dissimilarities averaged across stories for linked and nonlinked events pre- and post-insight from these RDMs for each participant and compared them in a mixed ANOVA (Fig. 6A). We found that while the observation group showed an increase in representational dissimilarity for linked events from pre- to post-insight in the right anterior hippocampus, the imagination group did not show such a reconfiguration (group \times time \times axis \times link interaction: $F(1, 53)=9.28$, $p_{\text{corr}}=0.008$, $\eta_G=0.005$; Fig. 6B). To further follow up on this effect, we performed post hoc tests, showing that this effect was only found for linked events (group \times time \times axis interaction: $F(1, 53)=6.85$, $p_{\text{corr}}=0.024$, $\eta_G=0.012$) but not for nonlinked events (group \times time \times axis interaction: $F(1, 53)=0.81$, $p_{\text{corr}}=0.746$, $\eta_G=0.001$). The increase in representational dissimilarity was only observed in the observation group (time \times axis interaction: $F(1, 27)=5.92$, $p_{\text{corr}}=0.044$, $\eta_G=0.028$) but not for the imagination group (time \times axis interaction: $F(1, 26)=1.56$,

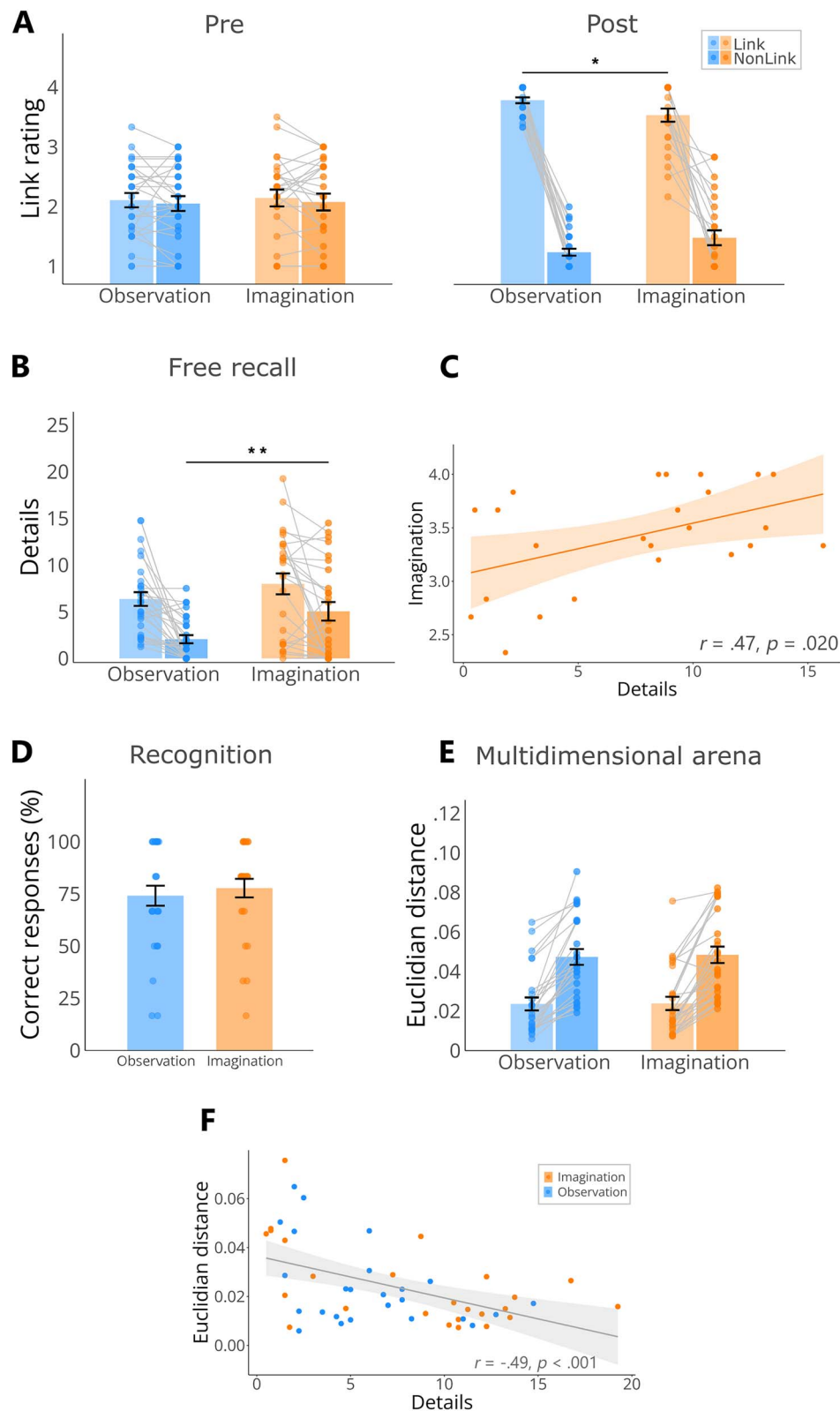


Fig. 2. Behavioral measures of insight and memory performance. A) No differences between the imagination and the observation group pre-insight for linked and nonlinked events, but lower ratings for linked events for the imagination group compared with the observation group post-insight, whereas there were no differences for nonlinked events. B) No difference in free recall between the groups for linked (A and B) events, but more details remembered in the imagination group for nonlinked events compared to the observation group. C) Significant positive correlation between the average strength of imagination during the insight phase and the remembered details on average (A, B, and X) one week later. D) High performance (correct responses (%)) in the forced-choice recognition test for both groups. E) Significant differences between linked and nonlinked events in the MAT (Euclidian distance) for the imagination and observation group. F) Significant negative correlation between the Euclidian distance between linked events in the MAT and the recalled details for linked events in the free recall. Data represent mean (+/-SE); * $P < 0.05$, ** $P < 0.01$.

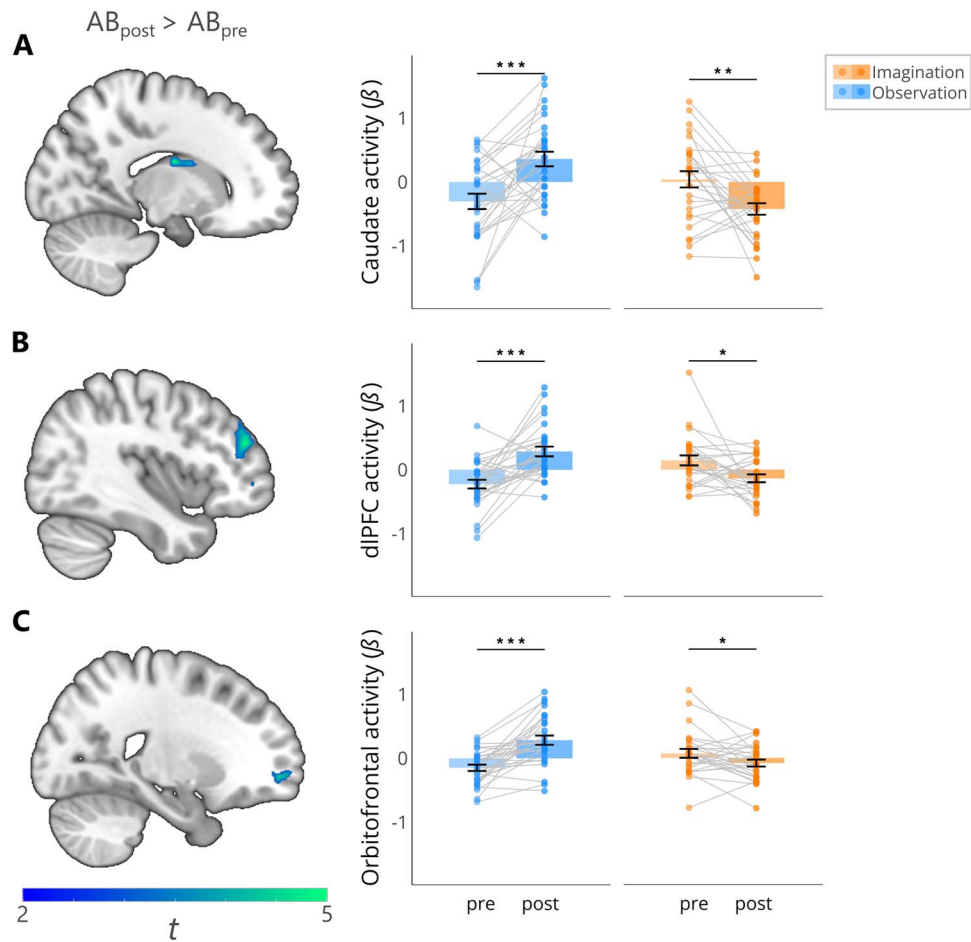


Fig. 3. Neural change for linked events. A) Masked caudate nucleus cluster on sagittal T1 image. Extracted beta values from caudate nucleus cluster for pre- and post-insight linked events, separately for the observation and the imagination group. B) Masked dlPFC cluster on sagittal T1 image. Extracted beta values from dlPFC cluster for pre- and post-insight linked events, separately for the observation and the imagination group. C) Masked orbitofrontal cortex cluster on sagittal T1 image. Extracted beta values from orbitofrontal cortex cluster for pre- and post-insight linked events, separately for the observation and the imagination group. Data represent mean (\pm SE); * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

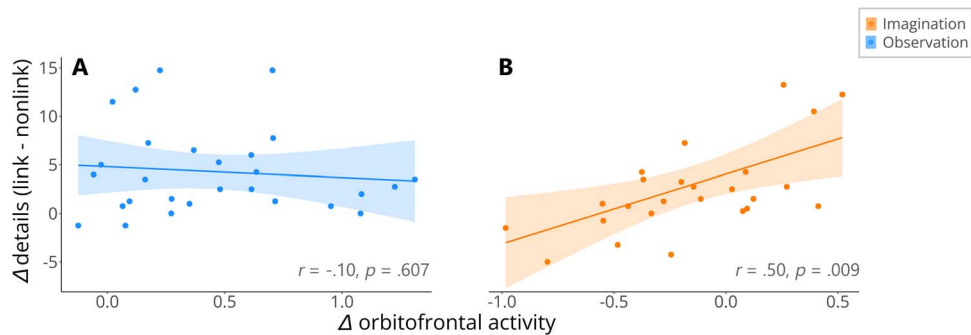


Fig. 4. Association between change in orbitofrontal activity and memory performance. A) Nonsignificant positive correlation between change in orbitofrontal activity from pre- to post-insight and the difference in free recall between linked and nonlinked events (linked events – nonlinked events) in the observation group. B) Significant correlation between change in orbitofrontal activity from pre- to post-insight and the difference in free recall between linked and nonlinked events (linked events – nonlinked events) in the imagination group.

$p_{\text{corr}} = 0.446$, $\eta_G = 0.004$). Follow-up tests showed a strong trend for a change in representational pattern dissimilarity from pre- to post-insight in the right anterior hippocampus ($t_{(27)} = -2.30$, $p_{\text{corr}} = 0.060$, $d_{\text{repeated measures}} = -0.43$) but not in the right posterior hippocampus ($t_{(27)} = 0.25$, $p_{\text{corr}} = 1$, $d_{\text{repeated measures}} = -0.05$) of the observation group. Interestingly, over both groups, those with higher dissimilarity in the right anterior hippocampus post-insight also differentiated better between linked and nonlinked

events in the MAT by arranging those events that were linked much closer together than those that were nonlinked ($r = -0.31$, $t_{(49)} = -2.32$, $P = 0.025$; Fig. 6F). Moreover, over both groups, those with more representational change from pre- to post-insight also recalled less details for the nonlinked event ($r = -0.27$, $t_{(51)} = -2.01$, $P = 0.049$; Fig. 6F), suggesting that they focused less on the nonlinked event. Furthermore, we performed an exploratory ROI-based RSA focusing on the medial prefrontal cortex, as

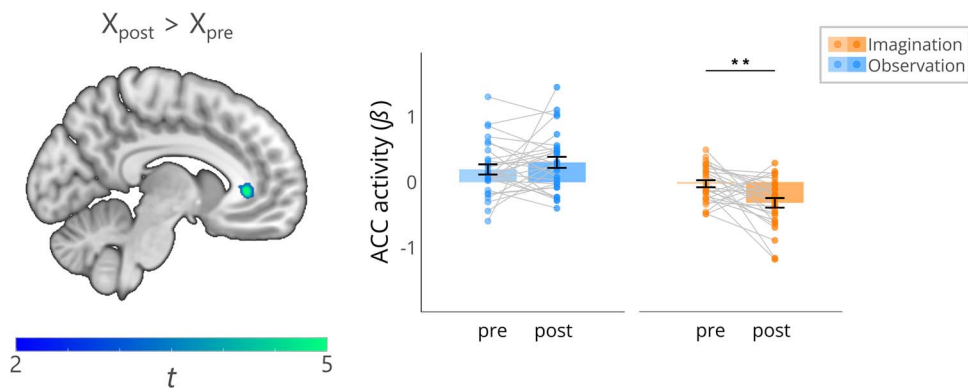


Fig. 5. Neural change for the nonlinked event. Masked anterior cingulate cluster on sagittal T1 image. Extracted beta values from anterior cingulate cluster for pre- and post-insight linked events, separately for the observation and the imagination group. Data represent mean (+/-SE); ** $P < 0.01$.

previous research has highlighted its importance for episodic memory integration (Milivojevic et al. 2015). We found a trend for an increase in neural dissimilarity from pre- to post-insight for linked events, which is similar to the representational change in the right anterior hippocampus, which was not the case for nonlinked events (time \times link interaction: $F(1, 54) = 3.92$, $P = 0.053$, $\eta_G = 0.013$; Supplementary Fig. S2). Follow-up t -tests, however, yielded no significant effects (all P s > 0.139). In addition, we performed a whole-brain searchlight RSA with a theoretical model operationalizing the increase in dissimilarity from pre- to post-insight to explore possible representational changes beyond the hippocampus. This searchlight analysis, however, yielded no significant representational patterns (whole-brain cluster-level: all $p_{\text{corr}}(\text{FWE}) > 0.719$; whole-brain peak-level: all $p_{\text{corr}}(\text{FWE}) > 0.572$).

Higher striato-hippocampal coupling during linking via imagination

To finally assess the underlying neural processes while gaining insight through imagination versus presentation, we measured BOLD activity using fMRI while participants learned that two initially unrelated events were actually linked (A and B) through a linking video (L) or a linking instruction (I) interleaved with a control video (C) or control instruction (CI). Our initial whole-brain analysis revealed that, during the insight phase, participants in the imagination group exhibited higher activity in the supplementary motor area (whole-brain cluster-level: $t_{(1, 54)} = -5.20$, $p_{\text{corr}}(\text{FWE}) = 0.002$, $k = 260$, peak: $x = -4$, $y = 0$, $z = 60$) and in the lingual gyrus (whole-brain cluster-level: $t_{(1, 54)} = 4.43$, $p_{\text{corr}}(\text{FWE}) < 0.001$, $k = 1097$, peak: $x = 8$, $y = -76$, $z = 0$). Interestingly, we found that those in the imagination group with higher activation of the lingual gyrus during the insight phase also rated linked events post-insight as belonging more together and nonlinked events as belonging less together ($r = 0.42$, $t_{(23)} = 2.22$, $P = 0.036$). Activation in these two areas provides a further validation of the condition participants were in: both the supplementary motor area and the lingual gyrus have been found to be active during reading (Mechelli et al. 2000; Cummine et al. 2017), which was required while the imagination instructions were shown. In addition, the lingual gyrus was found to be implicated in visuospatial working memory (Ragland et al. 2002; Schmidt et al. 2007; Gutiérrez-Garralda et al. 2014), suggesting that participants might have manipulated internal visuospatial layouts. The observation group further showed, compared to the imagination group, increased activity in the lateral occipital

cortex (whole-brain cluster-level: $t_{(1, 54)} = -7.68$, $p_{\text{corr}}(\text{FWE}) < 0.001$, $k = 4138$, peak: $x = 50$, $y = -72$, $z = 0$), the occipital pole (whole-brain cluster-level: $t_{(1, 54)} = -7.16$, $p_{\text{corr}}(\text{FWE}) < 0.001$, $k = 1777$, peak: $x = -16$, $y = -102$, $z = 10$) as well as the parietal operculum (whole-brain cluster-level: $t_{(1, 54)} = -4.71$, $p_{\text{corr}}(\text{FWE}) = 0.042$, $k = 144$, peak: $x = 62$, $y = -38$, $z = 20$). These findings are in line with other studies reporting stronger activation in these lower visual, occipital regions during perception compared to imagination (Kosslyn et al. 1997; Ganis et al. 2004; Stokes et al. 2009). Beyond these whole-brain differences that are directly linked to sensory aspects of the presentation form, we found increased activity in the imagination group compared to the observation group in the bilateral anterior hippocampi (left anterior HC: SVC peak level: $x = -18$, $y = -4$, $z = -22$; $t_{(1, 54)} = 3.93$, $p_{\text{corr}}(\text{FWE}) = 0.024$; right anterior HC: SVC peak level: $x = 22$, $y = -2$, $z = -20$; $t_{(1, 54)} = 3.76$, $p_{\text{corr}}(\text{FWE}) = 0.040$). Interestingly, those in the observation group with more activity in the right anterior hippocampus during linking also showed a greater increase from pre- to post-insight in representational dissimilarity for linked events in the right anterior hippocampus; however, this appeared to be less the case for the imagination group (observation: $r = 0.43$, $t_{(26)} = -2.47$, $P = 0.021$; imagination: $r = 0.20$, $t_{(25)} = 1.00$, $P = 0.326$; observation vs. imagination: $z = -0.94$, $P = 0.175$; Supplementary Fig. S3).

In a next step, we assessed changes in the functional connectivity of the areas identified in the previous analyses during the linking of initially unrelated events using a PPI analysis (Fig. 7). We focused on the caudate nuclei as seed regions, as these yielded the highest univariate increase from pre- to post-insight for linked events in the observation group compared to the imagination group. Moreover, higher connectivity between the caudate and the hippocampus has been linked to better imagination and memory performance in previous studies (Müller et al. 2018; Faul et al. 2020). When comparing the link event with the control event (Link $>$ Control), we found that participants in the imagination group showed, at the whole-brain level, higher functional connectivity than the observation group between the left caudate (seed) and the intracalcarine cortex (whole-brain cluster-level: $t_{(1, 54)} = 4.78$; $p_{\text{corr}}(\text{FWE}) < 0.001$, $k = 941$, peak: $x = -2$, $y = -86$, $z = 2$). We further found higher functional connectivity between the right caudate (seed) and the occipital pole in the imagination relative to the observation group (whole-brain cluster-level: $t_{(1, 54)} = 4.92$; $p_{\text{corr}}(\text{FWE}) = 0.003$, $k = 232$, peak: $x = 16$, $y = -98$, $z = 6$). Interestingly, when focusing on our ROIs, we also found higher coupling between the left caudate and the left hippocampus in the imagination compared to the observation group (SVC peak level: $x = -30$, $y = -30$, $z = -8$; $t_{(1, 54)} = 4.40$; $p_{\text{corr}}(\text{FWE}) = 0.016$, $k = 22$;

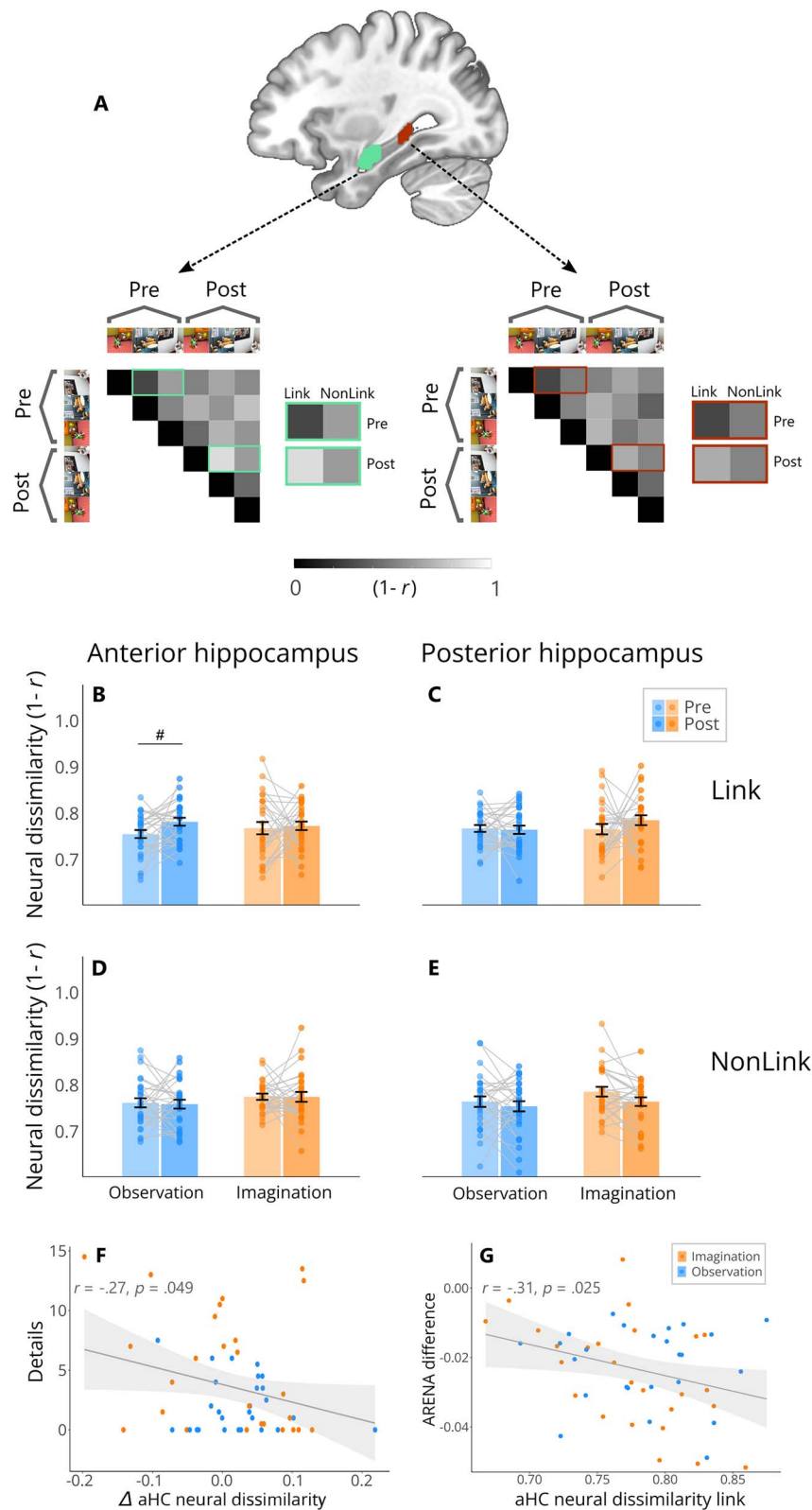


Fig. 6. Conceptual RSA and results for RSA. A) Masked right anterior and posterior hippocampus with conceptual RDMs for each region. Dissimilarities pre- and post-insight were extracted per region and averaged over six stories per participants before they were entered into an ANOVA. B) Trending difference between pre- and post-insight for linked events in the right anterior hippocampus in the observation and nonsignificant difference in the imagination group. C) Nonsignificant pre- and post-insight neural dissimilarities for linked events in the right posterior hippocampus for the observation and the imagination group. D) Nonsignificant pre- and post-insight neural dissimilarities for nonlinked events in the right anterior hippocampus for the observation and the imagination group. E) Nonsignificant pre- and post-insight neural dissimilarities for nonlinked events in the right posterior hippocampus for the observation and the imagination group. F) Significant negative correlation between representational change in the right anterior hippocampus (aHC; post – pre) and recalled details for the nonlinked event in free recall. G) Significant negative correlation between the neural dissimilarity for linked events in the right anterior hippocampus (aHC) and the difference in the MAT between linked and nonlinked events (link – nonlink). Data represent mean (+/–SE); # $P_{corr} = 0.06$.

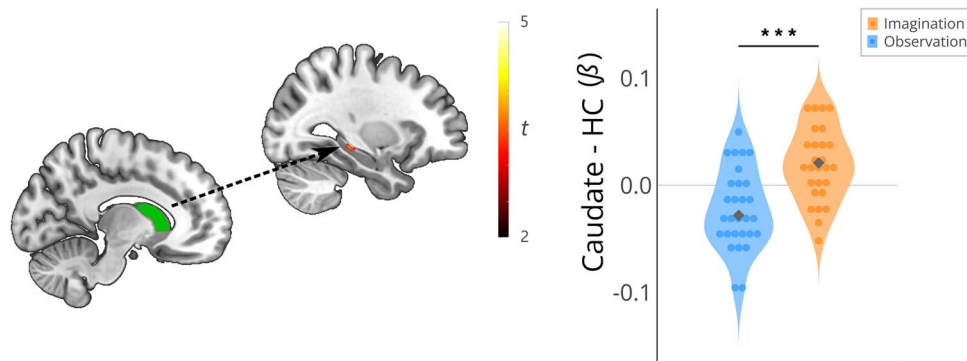


Fig. 7. PPI results with seed from caudate nucleus. Masked left caudate nucleus seed on sagittal T1 image and masked left hippocampal connectivity. Violin distribution of extracted connectivity beta values from left hippocampus ($x = -30$, $y = -30$, $z = -8$) for the observation and imagination groups separately. Within-group mean: gray rectangle. *** $P < 0.001$.

Table 1. Control variables.

Measure	Imagination		Observation		P
	M	SD	M	SD	
FFIS-C	23.59	3.92	22.24	5.60	.298
FFIS-D	18.74	4.91	16.69	4.51	.110
FFIS-E	14.30	6.58	14.90	5.74	.718
FFIS-F	26.26	8.56	25.03	10.27	.629
STAI-T	37.19	6.27	35.90	8.87	.531
STAI-S	34.13	6.22	35.72	7.35	.395
PSQI	5.17	2.88	4.41	1.31	.245
TICS	27.48	7.91	25.21	9.05	.320
BDI	6.30	5.91	4.79	4.44	.290
BFI-2 E	39.81	8.29	40.76	6.69	.643
BFI-2 N	28.96	6.15	28.62	9.23	.870
BFI-2 O	44.93	7.88	43.17	9.00	.441
BFI-2 C	40.93	7.09	43.31	7.95	.241
BFI-2 A	47.07	5.76	47.07	6.28	.997

Note. The questionnaires FFIS with its dimensions: FFIS-C (complexity of imagination), FFIS-D (directedness of imagination), FFIS-E (emotional valence of imagination), and FFIS-F (frequency of imagination); STAI-T; BDI; BFI-2 with its dimensions: BFI-2 E (extraversion), BFI-2 N (neuroticism), BFI-2 O (openness to experience), BFI-2 C (conscientiousness), and BFI-2 A (agreeableness), and TICS (Trier Inventory of Chronic Stress) were completed via an online link before participants came in for day 1, and STAI-S and PSQI were completed at the beginning of the experiment. No significant differences between the groups were observed on these measures. Data represent means (\pm SD).

Fig. 7). Accordingly, those in both groups, who had higher functional connectivity between the left caudate and the left hippocampus, also recalled more details on average one week later ($r = 0.27$, $t_{(52)} = 2.02$, $P = 0.048$).

We further performed a PPI for the change from pre to post for the nonlinked event with the bilateral dlPFC as seed regions since these regions have also been found to be implicated in a change from pre to post in a previous analysis. When comparing the increase from pre to post for the nonlinked event ($X_{\text{post}} > X_{\text{pre}}$), we found that participants in the imagination group tended to show a lower functional connectivity increase between the left dlPFC and the right anterior hippocampus than participants in the observation group (SVC peak level: $x = 30$, $y = -4$, $z = -26$; $t_{(1, 54)} = 3.89$, p_{corr} (FWE) = 0.068; $k = 5$). Furthermore, participants in the imagination group tended to show a lower functional connectivity increase between the right dlPFC and the right anterior hippocampus (SVC peak level: $x = 30$, $y = -4$, $z = -26$; $t_{(1, 54)} = 3.92$, p_{corr} (FWE) = 0.060; $k = 3$).

Control variables

To rule out the possibility that the imagination and observation groups differed in terms of trait imagination capacity (FFIS), trait-anxiety (STAI-T), state-anxiety (STAI-S), sleep quality (PSQI),

chronic stress (TICS), depressive symptoms (BDI), and personality dimensions (BFI-2), participants completed corresponding questionnaires before the experiment. There were no differences between the groups on any of these measures (all P s > 0.110 ; see Table 1).

Furthermore, there was no difference between groups in their working memory capacity, as measured by an N -back task at baseline (all P s > 0.180 ; see Table 2). Thus, it is unlikely that differences during the NIT (or in the retention test one week later) were influenced by mere group differences in working memory.

Discussion

Gaining insight into the relationship of initially separate events often comes with an insight-induced memory reconfiguration (Collin et al. 2015; Milivojevic et al. 2015), enabling the integration of memories. This process of memory integration is fundamental to many cognitive processes, such as decision-making (Gupta et al. 2010; Zeithamova et al. 2012; Shohamy and Daw 2015). Gaining insight into the relationship of events is a fundamental memory process and is also highly important for educational settings. Notably, in educational contexts, the integration of knowledge is often achieved by reading. To this point, however, mnemonic

Table 2. N-back task.

N-back	Imagination		Observation		P
	M	SD	M	SD	
3-back Acc	75.09%	12.74%	79.40%	10.93%	.182
3-back RT	789.91 ms	169.03 ms	729.20 ms	164.91 ms	.180
4-back Acc	75.37%	10.18%	77.24%	11.52%	.522
4-back RT	768.43 ms	145.96 ms	722.75 ms	206.18 ms	.341

Note. Participants completed the N-back task before they went into the scanner. Groups did not differ on these N-back measures. Data represent means (+/–SD).

integration has been investigated exclusively by presenting participants a linking event as a direct experience, while it has remained understudied how insight can come about through imagining that link. Therefore, in the present study, we aimed to elucidate the behavioral and neural consequences of linking previously unrelated events via imagination and contrasted these with the mechanisms and effects of linking through direct observation. Our results show that it is possible to gain insight through imagination, although this insight is weaker than the insight gained via presentation of videos of the linking event. Dovetailing these behavioral findings, we also found lower insight-related increases in the frontal and striatal activities as well as an absence of representational change in the anterior hippocampus when gaining insight via imagination. Interestingly, very similar regions were more strongly recruited while linking via imagination: The anterior hippocampus showed increased activity, and we also found increased coupling between the striatum and the hippocampus when participants imagined the link between initially unrelated events. These findings suggest that these regions may have been more occupied by the process of imagination and may, thus, not have been able to accomplish these insight-induced changes, as was the case when linking via observation. Although immediate insight was weaker in the imagination group, we found an overall memory enhancement one week later.

All participants gained insight into which events were linked and which were left nonlinked, demonstrating that gaining insight is possible through both imagination and observation. However, insight was stronger with observation than with imagination of the linking event, which may be explained by the fact that imagination is a more demanding process, given its neural overlap with working memory and association with visual working memory performance (Baddeley and Andrade 2000; Keogh and Pearson 2011; Albers et al. 2013; Christophel et al. 2015). Imagination could further be viewed as a weak form of perception with a reversed information flow compared to perception (Grossman and Blake 2001; Naselaris et al. 2009; Breedlove et al. 2020; Dijkstra et al. 2020), which could also explain why actual perception (i.e. observation) led to stronger insight. One might also argue that the imagination group showed lower insight because they first had to read the instruction, recall the video events (A and B), and then imagine the linking event, whereas the observation group gained insight immediately while only watching the video. Although this alternative explanation can hardly be ruled out, we consider this alternative rather unlikely because the linking event presentation was long and repeated for six times, which may have also led to recognition of the event descriptions and hence speeded up the reading process. In line with this view, participants indicated that they could imagine the linking events well. Another factor that may have contributed to the lower insight in the imagination group is the higher activity of the anterior hippocampus during linking. Compared to the posterior hippocampus, the anterior

hippocampus has not only been shown to be a hub for imaginative scene construction in previous research (Mullally and Maguire 2014; Zeidman and Maguire 2016) but to be also of pivotal importance for mnemonic integration (Collin et al. 2015; Schlichting et al. 2015). Thus, imagining the link may have interfered with gaining insight in the imagination group.

Beyond the differential insight into the links between initially unrelated events, we obtained also significant differences between the imagination and observation groups in the insight-driven neural reconfiguration of memory representations. Specifically, we observed a representational change from pre- to post-insight in the right anterior hippocampus for linked events in the observation group. The anterior hippocampus is known to be involved not only in mnemonic integration (Collin et al. 2015; Schlichting et al. 2015) but also in processing of spatial context (Fritch et al. 2020) and novelty detection (Bunzeck and Düzel 2006), which are both features that may have been at play here: Spatial layouts were processed while viewing the events (A, B, and X), and novelty processing may have been required when discovering that the events A and B belong together. We found an increase in dissimilarity in the right anterior hippocampus but no increase in similarity as reported in some previous studies (Collin et al. 2015; Schlichting et al. 2015; Dimsdale-Zucker et al. 2018). This change in neural dissimilarity appeared to be rather specific to the anterior hippocampus, as we observed only a trend for a similar pattern in the medial prefrontal cortex but no similar representational changes elsewhere in the brain. It has been presumed that hippocampal similarity may increase when events share item as well as context associations but not when events share either context (scene) or item (people) information (Libby et al. 2019), which may have been the case in the present study. However, this was equally the case in a previous study using the same paradigm which found increased similarity for linked events in the anterior hippocampus (Collin et al. 2015). However, the present study also deviated from previous work in that titles were shown prior to the presentation of each video (A, B, and X), which may have elicited a different strategy than that found in previous work with this task (Collin et al. 2015; Miliwojevic et al. 2015). Further evidence suggests that memory representations that have been moderately coactivated, result in increased dissimilarity (Wammes et al. 2022). Increases in dissimilarity between related memories might be interpreted as a pattern separation mechanism allowing inferences across events (Molitor et al. 2021). Indeed, increased dissimilarity has been associated with better memory performance in several previous studies (Hulbert and Norman 2015; Favila et al. 2016; Chanales et al. 2017; Dandolo and Schwabe 2018; Koolschijn et al. 2019). In line with these findings, we also found a positive association between neural dissimilarity post-insight in the right anterior hippocampus and memory performance across groups. Therefore, it seems likely that the remapping of neural codes

we observed was actually hippocampal pattern separation—a process that is necessary to distinguish memories from one another (Muller and Kubie 1987; Leutgeb et al. 2007; Yassa and Stark 2011). Importantly, the change in anterior hippocampal representational dissimilarity from pre- to post-insight was only observed in the observation group but not in participants who imagined the link between events, which dovetails the weaker immediate insight in the imagination group on a behavioral level.

Beyond the hippocampus, the observation group also showed an increased activity from pre- to post-insight in the caudate nucleus and the dorsolateral prefrontal and orbitofrontal cortices for linked events. Previous studies have shown that dorsal striatal regions were involved in the processing of integrated episodes, prediction-error based learning, and associative learning (Ben-Yakov and Dudai 2011; Mattfeld and Stark 2015; Pine et al. 2018), which may all be processes directly underlying mnemonic integration. Furthermore, dorsolateral prefrontal regions have been found to be important for relational memory (Murray and Ranganath 2007; Long et al. 2010; Blumenfeld et al. 2011) and insight per se (Tik et al. 2018). Whereas, orbitofrontal regions have been found to be involved in the processing of reward experiences in general (Kringelbach 2005; Salimpoor et al. 2011; Kringelbach et al. 2012) and in an insight-related reward signal in particular (Oh et al. 2020). All of these processes are important for mnemonic integration, as relational memory of events must be updated via the insight gained, which in turn can be rewarding.

However, the imagination group showed smaller increases or even decreases in activity for linked events in these regions, which is again consistent with weaker immediate insight in the imagination group. Interestingly, those in the imagination group with less increase or a decrease in orbitofrontal activity for linked events from pre- to post-insight also recalled less details for linked events and more details for nonlinked events, indicating that the increase in orbitofrontal activity at encoding plays a specific role in discriminating between memories for linked and nonlinked events one week later. We further found an increased connectivity between the bilateral dorsolateral prefrontal regions and the right anterior hippocampus in the observation group. The connectivity between the dlPFC and the hippocampus has been previously found to be linked to spatial working memory (Böhner et al. 2015), and successful updating of already existing memories (Kluen et al. 2019), which may have especially been the case here.

In addition to these increases for linked events in the observation group, we found decreased activity in the anterior cingulate from pre- to post-insight for nonlinked events in the imagination group. The anterior cingulate has been found to be important during conflict monitoring (Botvinick et al. 2001, 2004) and is part of a salience network, which appears to be tasked with detecting salient events and thus contributes to behavioral control (Uddin 2015; Seeley 2019; Becker et al. 2020). The decrease in anterior cingulate activity observed in the imagination group from pre- to post-insight for nonlinked events might, therefore, suggest that the nonlinked event was less monitored as an event that provoked conflict and became less salient compared to the observation group. This, however, remains speculative as our design did not allow a distinction of different levels of saliency.

How may the imagination of the linking event have reduced the insight into the link between initially unrelated events and the neural mechanisms associated herewith? To address this question, we focused on the insight phase. We hypothesized that the hippocampus would be more involved in linking via imagination than in linking via presentation because the hippocampus has been shown to play an important role in imagination

(Addis et al. 2009; Mullally and Maguire 2014; Zeidman and Maguire 2016). We further assumed that this hippocampal recruitment during imagination could hinder mnemonic integration, as this process is also highly hippocampus-dependent (Collin et al. 2015; Schlichting et al. 2015). Indeed, we found stronger activation of the anterior hippocampus during the insight phase in the imagination group compared to the observation group, i.e. in the same area that appeared to be implicated in the mnemonic reconfiguration in the observation group. In addition to our univariate analyses, we also analyzed connectivity during linking and found higher coupling between the left caudate and the left hippocampus in the imagination group specifically for the link event compared to a control event during the insight phase. Higher connectivity between the hippocampus and the caudate nucleus has been associated with better imagination as well as better memory performance (Müller et al. 2018; Faul et al. 2020). Indeed, those with higher connectivity between the hippocampus and the caudate nucleus recalled more details one week later. Notably, the imagination group also showed a reduced increase in the caudate nucleus from pre- to post-insight for linked events compared to the observation group. This could suggest that resources required for linking were occupied by the imagination, which might have prevented the insight-induced increase in caudate activity, as observed in the observation group.

Beyond the immediate insight gained during the insight phase, insight also manifested in memory. Although participants showed near-ceiling performance in the forced-choice recognition test and were able to arrange events according to whether they were linked or nonlinked in the MAT, both groups also showed a memory advantage for details of linked versus nonlinked events, suggesting that narrative coherence promotes prioritization in memory. This finding dovetails with the assumption that the brain stores episodic memories as coherent narratives (Tulving 1983) and with more recent findings that integrated episodes can be recalled more easily (Wang et al. 2015; Cohn et al. 2021). The greater accessibility of these integrated episodes may be attributed to the fact that any element of the episode can be used as a cue for the entire episode (Nakazawa et al. 2002; Horner et al. 2015).

However, there was also an overall memory advantage for the imagination group in the number of details recalled, suggesting that memory in general, rather than specifically the effect of insight on memory, was enhanced by imagining the link. Consistent with this memory enhancement through imagination, there was even a positive relationship between the strength of imagination and the number of details remembered by the imagination group for linked events. This result is also consistent with studies that used imagination as a mnemonic technique and showed that it led to better memory performance (Bower 1970; Hockley and Christi 1996) and also with other results that showed that learning via imagination has a lasting effect on behavioral and neural outcomes (Reddan et al. 2018; Greening et al. 2022). As a result of the increased engagement of the imagination group during the linking phase, the results could also be due to a deeper processing effect (Craik and Lockhart 1972). It is well known that active engagement with the encoding material, as was the case in the imagination group, improves memory compared to passive viewing (Slamecka and Graf 1978; Johns and Swanson 1988; Bertsch et al. 2007). Interestingly, however, we observed here a memory boost both for linked events and for nonlinked events, i.e. the memory boost was not limited to the actually imagined event but occurred for all events that were presented on day 1. Thus, if there was an effect of active engagement, it was a more general

and no specific effect. With the current design, it was not possible to distinguish whether the general memory boost observed in the imagination group was due to active engagement with the task or to imagining the linking instruction. Future studies might investigate this aspect further using a more active control group to disentangle imagination and active engagement effects. Overall, it seems that, although direct insight decreased in the imagination group, memory performance increased and that insight through imagination appears to result in a trade-off: lower direct insight, but better memory performance.

In line with many everyday examples, our data show that gaining insight into the relationship between events is possible not only through direct experience but also through imagining the link between those events. Gaining insight via imagination, however, came at the cost of a diminished immediate insight and an impeded representational change in the anterior hippocampus. Linking via imagination resulted in higher hippocampal activity and connectivity with the striatum during linking, which may have impeded the neural changes required for mnemonic integration on the one hand but may have facilitated long-term memory formation on the other hand. Together, our data shed light on how initially unrelated events can be integrated when the link between them is either directly observed or mentally constructed, and could lead to an emphasis on the benefits of hands-on experiences for gaining knowledge in educational settings, while using imaginative techniques to promote long-term memory.

Acknowledgments

We gratefully acknowledge the assistance of Carlo Hiller with programming the task; Hamed Nili for his support during data analysis; and Anica Koslowski, Dania Al Darwich, Merve Tural, Carlotta Reinhardt, Sophie Lutter, Mihriban Sahin, and Dewi Soetjipto for their assistance during data collection.

Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

Data availability statement

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

Funding

This project was funded by the German Research Foundation (DFG; grant SCHW1357/22 to LS and CFD). CFD's research is supported by the Max Planck Society, the European Research Council (ERC-CoG GEOCOG 724836), the Kavli Foundation, the Jebsen Foundation, Helse Midt Norge, and the Research Council of Norway (223262/F50 and 197467/F50).

Conflict of interest statement: None declared.

References

- Addis DR, Wong AT, Schacter DL. Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. *Neuropsychologia*. 2007;45(7):1363–1377. <https://doi.org/10.1016/j.neuropsychologia.2006.10.016>.
- Addis DR, Pan L, Vu M-A, Laiser N, Schacter DL. Constructive episodic simulation of the future and the past: distinct subsystems of a core brain network mediate imagining and remembering. *Neuropsychologia*. 2009;47(11):2222–2238. <https://doi.org/10.1016/j.neuropsychologia.2008.10.026>.
- Albers AM, Kok P, Toni I, Dijkerman HC, de Lange FP. Shared representations for working memory and mental imagery in early visual cortex. *Curr Biol*. 2013;23(15):1427–1431. <https://doi.org/10.1016/j.cub.2013.05.065>.
- Baddeley AD, Andrade J. Working memory and the vividness of imagery. *J Exp Psychol Gen*. 2000;129(1):126–145. [Scopus 10.1037/0096-3445.129.1.126](https://doi.org/10.1037/0096-3445.129.1.126).
- Bähler F, Demanuele C, Schweiger J, Gerchen MF, Zamoscik V, Ueltzhöffer K, Hahn T, Meyer P, Flor H, Durstewitz D, et al. Hippocampal–dorsolateral prefrontal coupling as a species-conserved cognitive mechanism: a human translational imaging study. *Neuropsychopharmacology*. 2015;40(7):Article 7. <https://doi.org/10.1038/npp.2015.13>.
- Barry DN, Barnes GR, Clark IA, Maguire EA. The neural dynamics of novel scene imagery. *J Neurosci*. 2019;39(22):4375–4386. <https://doi.org/10.1523/JNEUROSCI.2497-18.2019>.
- Becker M, Sommer T, Kühn S. Verbal insight revisited: fMRI evidence for early processing in bilateral insulae for solutions with AHA! Experience shortly after trial onset. *Hum Brain Mapp*. 2020;41(1):30–45. <https://doi.org/10.1002/hbm.24785>.
- Bellana B, Liu Z-X, Diamond NB, Grady CL, Moscovitch M. Similarities and differences in the default mode network across rest, retrieval, and future imagining. *Hum Brain Mapp*. 2017;38(3):1155–1171. <https://doi.org/10.1002/hbm.23445>.
- Benedek M, Schües T, Beaty RE, Jauk E, Koschutnig K, Fink A, Neubauer AC. To create or to recall original ideas: brain processes associated with the imagination of novel object uses. *Cortex*. 2018;99:93–102. <https://doi.org/10.1016/j.cortex.2017.10.024>.
- Benoit RG, Schacter DL. Specifying the core network supporting episodic simulation and episodic memory by activation likelihood estimation. *Neuropsychologia*. 2015;75:450–457. <https://doi.org/10.1016/j.neuropsychologia.2015.06.034>.
- Ben-Yakov A, Dudai Y. Constructing realistic engrams: poststimulus activity of hippocampus and dorsal striatum predicts subsequent episodic memory. *J Neurosci*. 2011;31(24):9032–9042. <https://doi.org/10.1523/JNEUROSCI.0702-11.2011>.
- Bertsch S, Pesta BJ, Wiscott R, McDaniel MA. The generation effect: a meta-analytic review. *Mem Cogn*. 2007;35(2):201–210. <https://doi.org/10.3758/BF03193441>.
- Blumenfeld RS, Parks CM, Yonelinas AP, Ranganath C. Putting the pieces together: the role of dorsolateral prefrontal cortex in relational memory encoding. *J Cogn Neurosci*. 2011;23(1):257–265. <https://doi.org/10.1162/jocn.2010.21459>.
- Botvinick MM, Braver TS, Barch DM, Carter CS, Cohen JD. Conflict monitoring and cognitive control. *Psychol Rev*. 2001;108:624–652. <https://doi.org/10.1037/0033-295X.108.3.624>.
- Botvinick MM, Cohen JD, Carter CS. Conflict monitoring and anterior cingulate cortex: an update. *Trends Cogn Sci*. 2004;8(12):539–546. <https://doi.org/10.1016/j.tics.2004.10.003>.
- Bower GH. Imagery as a relational organizer in associative learning. *J Verbal Learn Verbal Behav*. 1970;9(5):529–533. [https://doi.org/10.1016/S0022-5371\(70\)80096-2](https://doi.org/10.1016/S0022-5371(70)80096-2).
- Breedlove JL, St-Yves G, Olman CA, Naselaris T. Generative feedback explains distinct brain activity codes for seen and mental images. *Curr Biol*. 2020;30(12):2211–2224.e6. <https://doi.org/10.1016/j.cub.2020.04.014>.

- Brett, M., Anton, J.-L., Valabregue, R., & Poline, J.-B. (2002, June 2-6). Region of interest analysis using an SPM toolbox [abstract]. Presented at the 8th International Conference on Functional Mapping of the Human Brain, Sendai, Japan. Available on CD-ROM in *NeuroImage*, 2002;16:(2), abstract 497.
- Brunec IK, Bellana B, Ozubko JD, Man V, Robin J, Liu Z-X, Grady C, Rosenbaum RS, Winocur G, Barense MD, et al. Multiple scales of representation along the hippocampal anteroposterior axis in humans. *Curr Biol*. 2018;28(13):2129–2135.e6. <https://doi.org/10.1016/j.cub.2018.05.016>.
- Brunec IK, Robin J, Olsen RK, Moscovitch M, Barense MD. Integration and differentiation of hippocampal memory traces. *Neurosci Biobehav Rev*. 2020;118:196–208. <https://doi.org/10.1016/j.neubiorev.2020.07.024>.
- Bunzeck N, Düzcel E. Absolute coding of stimulus novelty in the human substantia nigra/VTA. *Neuron*. 2006;51(3):369–379. <https://doi.org/10.1016/j.neuron.2006.06.021>.
- Buysse D, Reynolds C, Monk T, Berman S, Kupfer D. The Pittsburgh sleep quality index—a new instrument for psychiatric practice and research. *Psychiatry Res*. 1989;28(2):193–213. [https://doi.org/10.1016/0165-1781\(89\)90047-4](https://doi.org/10.1016/0165-1781(89)90047-4).
- Chanales AJH, Oza A, Favila SE, Kuhl BA. Overlap among spatial memories triggers repulsion of hippocampal representations. *Curr Biol*. 2017;27(15):2307–2317.e5. <https://doi.org/10.1016/j.cub.2017.06.057>.
- Christophel TB, Cichy RM, Hebart MN, Haynes J-D. Parietal and early visual cortices encode working memory content across mental transformations. *NeuroImage*. 2015;106:198–206. <https://doi.org/10.1016/j.neuroimage.2014.11.018>.
- Clark IA, Hotchin V, Monk A, Pizzamiglio G, Liefgreen A, Maguire EA. Identifying the cognitive processes underpinning hippocampal-dependent tasks. *J Exp Psychol Gen*. 2019;148:1861–1881. <https://doi.org/10.1037/xge0000582>.
- Cohn-Sheehy BI, Delarazan AI, Crivelli-Decker JE, Reagh ZM, Mundada NS, Yonelinas AP, Zacks JM, Ranganath C. Narratives bridge the divide between distant events in episodic memory. *Mem Cogn*. 2021;50:478–494. <https://doi.org/10.3758/s13421-021-01178-x>.
- Collin SHP, Milivojevic B, Doeller CF. Memory hierarchies map onto the hippocampal long axis in humans. *Nat Neurosci*. 2015;18(11):1562–1564. <https://doi.org/10.1038/nn.4138>.
- Collin SHP, Milivojevic B, Doeller CF. Hippocampal hierarchical networks for space, time, and memory. *Curr Opin Behav Sci*. 2017;17:71–76. <https://doi.org/10.1016/j.cobeha.2017.06.007>.
- Craik FIM, Lockhart RS. Levels of processing: a framework for memory research. *J Verbal Learn Verbal Behav*. 1972;11(6):671–684. [https://doi.org/10.1016/S0022-5371\(72\)80001-X](https://doi.org/10.1016/S0022-5371(72)80001-X).
- Cummine J, Hanif W, Dymouriak-Tymashov I, Anchuri K, Chiu S, Boliek CA. The role of the supplementary motor region in overt reading: evidence for differential processing in SMA-proper and pre-SMA as a function of task demands. *Brain Topogr*. 2017;30(5):579–591. <https://doi.org/10.1007/s10548-017-0553-3>.
- Dandolo LC, Schwabe L. Time-dependent memory transformation along the hippocampal anterior-posterior axis. *Nat Commun*. 2018;9(1):1205. <https://doi.org/10.1038/s41467-018-03661-7>.
- Danner D, Rammstedt B, Bluemke M, Treiber L, Berres S, Soto CJ, John OP. (2016). Die deutsche Version des Big Five Inventory 2 (BFI-2). Mannheim: GESIS - Leibniz-Institut für Sozialwissenschaften. <https://doi.org/10.6102/zis247>.
- Devitt AL, Schacter DL. Looking on the bright side: aging and the impact of emotional future simulation on subsequent memory. *J Gerontol B*. 2020;75(9):1831–1840. <https://doi.org/10.1093/geronb/gbz041>.
- Dijkstra N, Ambrogioni L, Vidaurre D, van Gerven M. Neural dynamics of perceptual inference and its reversal during imagery. *elife*. 2020;9:1–19.
- Dimsdale-Zucker HR, Ritchey M, Ekstrom AD, Yonelinas AP, Ranganath C. CA1 and CA3 differentially support spontaneous retrieval of episodic contexts within human hippocampal subfields. *Nat Commun*. 2018;9(1):1–8.
- Eichenbaum H, Dudchenko P, Wood E, Shapiro M, Tanila H. The hippocampus, memory, and place cells: Is it spatial memory or a memory space? *Neuron*. 1999;23(2):209–226. [https://doi.org/10.1016/S0896-6273\(00\)80773-4](https://doi.org/10.1016/S0896-6273(00)80773-4).
- Eid M, Gollwitzer M, Schmitt M. (2017). *Statistik und Forschungsmethoden* (5th ed). Weinheim, Germany: Beltz Verlag. https://www.beltz.de/produkt_detailansicht/8413-statistik-und-forschungsmethoden.html.
- Faul L, St. Jacques PL, DeRosa JT, Parikh N, De Brigard F. Differential contribution of anterior and posterior midline regions during mental simulation of counterfactual and perspective shifts in autobiographical memories. *NeuroImage*. 2020;215:116843. <https://doi.org/10.1016/j.neuroimage.2020.116843>.
- Favila SE, Chanales AJH, Kuhl BA. Experience-dependent hippocampal pattern differentiation prevents interference during subsequent learning. *Nat Commun*. 2016;7(1):Article 1. <https://doi.org/10.1038/ncomms11066>.
- Fritch HA, MacEvoy SP, Thakral PP, Jeye BM, Ross RS, Slotnick SD. The anterior hippocampus is associated with spatial memory encoding. *Brain Res*. 2020;1732:146696. <https://doi.org/10.1016/j.brainres.2020.146696>.
- Gaesser B, Spreng RN, McLelland VC, Addis DR, Schacter DL. Imagining the future: evidence for a hippocampal contribution to constructive processing. *Hippocampus*. 2013;23(12):1150–1161. <https://doi.org/10.1002/hipo.22152>.
- Ganis G, Thompson WL, Kosslyn SM. Brain areas underlying visual mental imagery and visual perception: an fMRI study. *Cogn Brain Res*. 2004;20(2):226–241. <https://doi.org/10.1016/j.cogbrainres.2004.02.012>.
- Greening SG, Lee T-H, Burleigh L, Grégoire L, Robinson T, Jiang X, Mather M, Kaplan J. Mental imagery can generate and regulate acquired differential fear conditioned reactivity. *Sci Rep*. 2022;12(1):Article 1. <https://doi.org/10.1038/s41598-022-05019-y>.
- Grossman ED, Blake R. Brain activity evoked by inverted and imagined biological motion. *Vis Res*. 2001;41(10):1475–1482. [https://doi.org/10.1016/S0042-6989\(00\)00317-5](https://doi.org/10.1016/S0042-6989(00)00317-5).
- Gupta AS, van der Meer MAA, Touretzky DS, Redish AD. Hippocampal replay is not a simple function of experience. *Neuron*. 2010;65(5):695–705. <https://doi.org/10.1016/j.neuron.2010.01.034>.
- Gutiérrez-Garralda JM, Hernandez-Castillo CR, Barrios FA, Pasaye EH, Fernandez-Ruiz J. Neural correlates of spatial working memory manipulation in a sequential Vernier discrimination task. *Neuroreport*. 2014;25(18):1418–1423. <https://doi.org/10.1097/WNR.000000000000280>.
- Hassabis D, Kumaran D, Vann SD, Maguire EA. Patients with hippocampal amnesia cannot imagine new experiences. *Proc Natl Acad Sci*. 2007;104(5):1726–1731. <https://doi.org/10.1073/pnas.0610561104>.
- Hautzinger M, Keller F, Kühner C. *BDI-II. Beck depressions inventar revision—manual*. Frankfurt, Germany: Harcourt Test Services; 2006.
- He Q, Liu JL, Beveridge EH, Eschapsse L, Vargas V, Brown TI. Episodic memory integration shapes value-based decision-making in spatial navigation. *J Exp Psychol Learn Mem Cogn*. 2022;48(8):1098–1109. <https://doi.org/10.1037/xlm0001133>.

- Hockley WE, Christi C. Tests of the differential encoding of item and associative information. *Mem Cogn*. 1996;24:202–216.
- Horner AJ, Bisby JA, Bush D, Lin W-J, Burgess N. Evidence for holistic episodic recollection via hippocampal pattern completion. *Nat Commun*. 2015;6(1):1–11. <https://doi.org/10.1038/ncomms8462>.
- Huffman DJ, Stark CEL. Multivariate pattern analysis of the human medial temporal lobe revealed representationally categorical cortex and representationally agnostic hippocampus. *Hippocampus*. 2014;24(11):1394–1403. <https://doi.org/10.1002/hipo.22321>.
- Hulbert JC, Norman KA. Neural differentiation tracks improved recall of competing memories following interleaved study and retrieval practice. *Cereb Cortex*. 2015;25(10):3994–4008.
- Johns EE, Swanson LG. The generation effect with nonwords. *J Exp Psychol Learn Mem Cogn*. 1988;14:180–190. <https://doi.org/10.1037/0278-7393.14.1.180>.
- Kapur S, Craik FI, Tulving E, Wilson AA, Houle S, Brown GM. Neuroanatomical correlates of encoding in episodic memory: levels of processing effect. *Proc Natl Acad Sci*. 1994;91(6):2008–2011. <https://doi.org/10.1073/pnas.91.6.2008>.
- Keogh R, Pearson J. Mental imagery and visual working memory. *PLoS One*. 2011;6(12):e29221. <https://doi.org/10.1371/journal.pone.0029221>.
- Kirchner WK. Age differences in short-term retention of rapidly changing information. *J Exp Psychol*. 1958;55(4):352–358. <https://doi.org/10.1037/h0043688>.
- Klunen LM, Dandolo LC, Jocham G, Schwabe L. Dorsolateral prefrontal cortex enables updating of established memories. *Cereb Cortex*. 2019;29(10):4154–4168. <https://doi.org/10.1093/cercor/bhy298>.
- Koolschijn RS, Emir UE, Pantelides AC, Nili H, Behrens TEJ, Barron HC. The hippocampus and neocortical inhibitory engrams protect against memory interference. *Neuron*. 2019;101(3):528–541.e6. <https://doi.org/10.1016/j.neuron.2018.11.042>.
- Kosslyn SM, Thompson WL, Alpert NM. Neural systems shared by visual imagery and visual perception: a positron emission tomography study. *NeuroImage*. 1997;6(4):320–334. <https://doi.org/10.1006/nimg.1997.0295>.
- Kriegeskorte N, Mur M. Inverse MDS: inferring dissimilarity structure from multiple item arrangements. *Front Psychol*. 2012;3(245). <https://doi.org/10.3389/fpsyg.2012.00245>.
- Kriegeskorte N, Mur M, Bandettini PA. Representational similarity analysis—connecting the branches of systems neuroscience. *Front Syst Neurosci*. 2008;2. <https://doi.org/10.3389/neuro.06.004.2008>.
- Kringelbach ML. The human orbitofrontal cortex: linking reward to hedonic experience. *Nat Rev Neurosci*. 2005;6(9):Article 9. <https://doi.org/10.1038/nrn1747>.
- Kringelbach ML, Stein A, van Hartevelt TJ. The functional human neuroanatomy of food pleasure cycles. *Physiol Behav*. 2012;106(3):307–316. <https://doi.org/10.1016/j.physbeh.2012.03.023>.
- Laux L, Glanzmann P, Schaffner P, Spielberger CD. *State-trait anxiety inventory—manual of the German version*. Beltz: Weinheim, Germany; 1981
- Leutgeb JK, Leutgeb S, Moser M-B, Moser EI. Pattern separation in the dentate gyrus and CA3 of the hippocampus. *Science*. 2007;315(5814):961–966. <https://doi.org/10.1126/science.1135801>.
- Libby LA, Reagh ZM, Bouffard NR, Ragland JD, Ranganath C. The hippocampus generalizes across memories that share item and context information. *J Cogn Neurosci*. 2019;31(1):24–35. https://doi.org/10.1162/jocn_a_01345.
- Long NM, Öztekin I, Badre D. Separable prefrontal cortex contributions to free recall. *J Neurosci*. 2010;30(33):10967–10976. <https://doi.org/10.1523/JNEUROSCI.2611-10.2010>.
- Maguire EA, Mullally SL. The hippocampus: a manifesto for change. *J Exp Psychol Gen*. 2013;142(4):1180. <https://doi.org/10.1037/a0033650>.
- Maguire EA, Valentine ER, Wilding JM, Kapur N. Routes to remembering: the brains behind superior memory. *Nat Neurosci*. 2003;6(1):Article 1. <https://doi.org/10.1038/nn988>.
- Marr D. A theory of archicortical function. *Proc R Soc Lond B Biol Sci*. 1971;262:23–81.
- Mattfeld AT, Stark CEL. Functional contributions and interactions between the human hippocampus and subregions of the striatum during arbitrary associative learning and memory. *Hippocampus*. 2015;25(8):900–911. <https://doi.org/10.1002/hipo.22411>.
- McClelland JL, McNaughton BL, O'Reilly RC. Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connectionist models of learning and memory. *Psychol Rev*. 1995;102(3):419–457. <https://doi.org/10.1037/0033-295X.102.3.419>.
- Mechelli A, Humphreys GW, Mayall K, Olson A, Price CJ. Differential effects of word length and visual contrast in the fusiform and lingual gyri during. *Proc R Soc Lond Ser B Biol Sci*. 2000;267(1455):1909–1913. <https://doi.org/10.1098/rspb.2000.1229>.
- Milivojevic B, Vicente-Grabovetsky A, Doeller CF. Insight reconfigures hippocampal-prefrontal memories. *Curr Biol*. 2015;25(7):821–830. <https://doi.org/10.1016/j.cub.2015.01.033>.
- Molitor RJ, Sherrill KR, Morton NW, Miller AA, Preston AR. Memory reactivation during learning simultaneously promotes dentate gyrus/CA_{2,3} pattern differentiation and CA₁ memory integration. *J Neurosci*. 2021;41(4):726–738. <https://doi.org/10.1523/JNEUROSCI.0394-20.2020>.
- Mullally SL, Maguire EA. Memory, imagination, and predicting the future: a common brain mechanism? *Neuroscientist*. 2014;20(3):220–234. <https://doi.org/10.1177/1073858413495091>.
- Muller RU, Kubie JL. The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells. *J Neurosci*. 1987;7(7):1951–1968. <https://doi.org/10.1523/JNEUROSCI.07-07-01951.1987>.
- Müller NCJ, Konrad BN, Kohn N, Muñoz-López M, Czisch M, Fernández G, Dresler M. Hippocampal-caudate nucleus interactions support exceptional memory performance. *Brain Struct Funct*. 2018;223(3):1379–1389. <https://doi.org/10.1007/s00429-017-1556-2>.
- Murray LJ, Ranganath C. The dorsolateral prefrontal cortex contributes to successful relational memory encoding. *J Neurosci*. 2007;27(20):5515–5522. <https://doi.org/10.1523/JNEUROSCI.0406-07.2007>.
- Nakazawa K, Quirk MC, Chitwood RA, Watanabe M, Yeckel MF, Sun LD, Kato A, Carr CA, Johnston D, Wilson MA, et al. Requirement for hippocampal CA3 NMDA receptors in associative memory recall. *Science*. 2002;297(5579):211–218. <https://doi.org/10.1126/science.1071795>.
- Naseleris T, Prenger RJ, Kay KN, Oliver M, Gallant JL. Bayesian reconstruction of natural images from human brain activity. *Neuron*. 2009;63(6):902–915. <https://doi.org/10.1016/j.neuron.2009.09.006>.
- Nili H, Wingfield C, Walther A, Su L, Marslen-Wilson W, Kriegeskorte N. A toolbox for representational similarity analysis. *PLoS Comput Biol*. 2014;10(4):e1003553. <https://doi.org/10.1371/journal.pcbi.1003553>.

- Norman KA, O'Reilly RC. Modeling hippocampal and neocortical contributions to recognition memory: a complementary-learning-systems approach. *Psychol Rev*. 2003;110(4):611–646. <https://doi.org/10.1037/0033-295X.110.4.611>.
- Oh Y, Chesebrough C, Erickson B, Zhang F, Kounios J. An insight-related neural reward signal. *NeuroImage*. 2020;214:116757. <https://doi.org/10.1016/j.neuroimage.2020.116757>.
- Otten LJ, Henson RNA, Rugg MD. Depth of processing effects on neural correlates of memory encoding: relationship between findings from across- and within-task comparisons. *Brain*. 2001;124(2):399–412. <https://doi.org/10.1093/brain/124.2.399>.
- Pine A, Sadeh N, Ben-Yakov A, Dudai Y, Mendelsohn A. Knowledge acquisition is governed by striatal prediction errors. *Nat Commun*. 2018;9:1673. <https://doi.org/10.1038/s41467-018-03992-5>.
- Race E, Keane MM, Verfaellie M. Medial temporal lobe damage causes deficits in episodic memory and episodic future thinking not attributable to deficits in narrative construction. *J Neurosci*. 2011;31(28):10262–10269. <https://doi.org/10.1523/JNEUROSCI.1145-11.2011>.
- Ragland JD, Turetsky BI, Gur RC, Gunning-Dixon F, Turner T, Schroeder L, Chan R, Gur RE. Working memory for complex figures: an fMRI comparison of letter and fractal n-back tasks. *Neuropsychology*. 2002;16:370–379. <https://doi.org/10.1037/0894-4105.16.3.370>.
- Reddan MC, Wager TD, Schiller D. Attenuating neural threat expression with imagination. *Neuron*. 2018;100(4):994–1005.e4. <https://doi.org/10.1016/j.neuron.2018.10.047>.
- Richmond AS, Cummings R, Klapp M. Transfer of the method of loci, pegword, and keyword mnemonics in the eighth grade classroom. *Researcher*. 2008;21(2):1–13.
- Ritchey M, LaBar KS, Cabeza R. Level of processing modulates the neural correlates of emotional memory formation. *J Cogn Neurosci*. 2011;23(4):757–771. <https://doi.org/10.1162/jocn.2010.21487>.
- Robin J, Moscovitch M. Details, gist and schema: hippocampal-neocortical interactions underlying recent and remote episodic and spatial memory. *Curr Opin Behav Sci*. 2017;17:114–123. <https://doi.org/10.1016/j.cobeha.2017.07.016>.
- Salimpoor VN, Benovoy M, Larcher K, Dagher A, Zatorre RJ. Anatomically distinct dopamine release during anticipation and experience of peak emotion to music. *Nat Neurosci*. 2011;14(2):257–262.
- Schacter DL, Addis DR, Buckner RL. Remembering the past to imagine the future: the prospective brain. *Nat Rev Neurosci*. 2007;8(9):Article 9. <https://doi.org/10.1038/nrn2213>.
- Vv M, Schacter DL, Corballis MC, Addis DR. Re-imagining the future: repetition decreases hippocampal involvement in future simulation. *PLoS One*. 2013;8(7):e69596. <https://doi.org/10.1371/journal.pone.0069596>.
- Schapiro AC, Turk-Browne NB, Botvinick MM, Norman KA. Complementary learning systems within the hippocampus: a neural network modelling approach to reconciling episodic memory with statistical learning. *Philos Trans R Soc B Biol Sci*. 2017;372(1711):20160049. <https://doi.org/10.1098/rstb.2016.0049>.
- Schlichting ML, Preston AR. The hippocampus and memory integration: building knowledge to navigate future decisions. In: Hannula DE, Duff MC, editors. *The hippocampus from cells to systems: structure, connectivity, and functional contributions to memory and flexible cognition*. Basel, Switzerland: Springer International Publishing; 2017. p. 405–437. https://doi.org/10.1007/978-3-319-50406-3_13.
- Schlichting ML, Mumford JA, Preston AR. Learning-related representational changes reveal dissociable integration and separation signatures in the hippocampus and prefrontal cortex. *Nat Commun*. 2015;6(1):1–10. <https://doi.org/10.1038/ncomms9151>.
- Schmidt D, Krause BJ, Weiss PH, Fink GR, Shah NJ, Amorim MA, Müller H-W, Berthoz A. Visuospatial working memory and changes of the point of view in 3D space. *NeuroImage*. 2007;36(3):955–968. <https://doi.org/10.1016/j.neuroimage.2007.03.050>.
- Schulz P, Schlotz W. Trierer Inventar zur Erfassung von chronischem Sre (TICS): Skalenkonstruktion, teststatistische Überprüfung und Validierung der Skala Arbeitsüberlastung. [The Trier Inventory for the Assessment of Chronic Stress (TICS). Scale construction, statistical testing, and validation of the scale work overload.]. *Diagnostica*. 1999;45(1):8–19. <https://doi.org/10.1026/0012-1924.45.1.8>.
- Seeley WW. The salience network: a neural system for perceiving and responding to homeostatic demands. *J Neurosci*. 2019;39(50):9878–9882. <https://doi.org/10.1523/JNEUROSCI.1138-17.2019>.
- Shohamy D, Daw ND. Integrating memories to guide decisions. *Curr Opin Behav Sci*. 2015;5:85–90. <https://doi.org/10.1016/j.cobeha.2015.08.010>.
- Slamecka NJ, Graf P. The generation effect: delineation of a phenomenon. *J Exp Psychol Hum Learn Mem*. 1978;4:592–604. <https://doi.org/10.1037/0278-7393.4.6.592>.
- Squire LR, van der Horst AS, McDuff, SG, Frascino, JC, Hopkins, RO, & Mauldin, KN. Role of the hippocampus in remembering the past and imagining the future. *Proc Natl Acad Sci*. 2010;107(44):19044–19048. <https://doi.org/10.1073/pnas.1014391107>.
- Stokes M, Thompson R, Cusack R, Duncan J. Top-down activation of shape-specific population codes in visual cortex during mental imagery. *J Neurosci*. 2009;29(5):1565–1572. <https://doi.org/10.1523/JNEUROSCI.4657-08.2009>.
- Tik M, Sladky R, Luft CDB, Willinger D, Hoffmann A, Banissy MJ, Bhattacharya J, Windischberger C. Ultra-high-field fMRI insights on insight: neural correlates of the Aha!-moment. *Hum Brain Mapp*. 2018;39(8):3241–3252.
- Tulving E. *Elements of episodic memory*. Oxford, United Kingdom: Oxford University Press; 1983
- Tulving E. Memory and consciousness. *Can Psychol/Psychologie Canadienne*. 1985;26(1):1–12. <https://doi.org/10.1037/h0080017>.
- Uddin LQ. Salience processing and insular cortical function and dysfunction. *Nat Rev Neurosci*. 2015;16:55–61. <https://doi.org/10.1038/nrn3857>.
- Walther A, Nili H, Ejaz N, Alink A, Kriegeskorte N, Diedrichsen J. Reliability of dissimilarity measures for multi-voxel pattern analysis. *NeuroImage*. 2016;137:188–200. <https://doi.org/10.1016/j.neuroimage.2015.12.012>.
- Wammes J, Norman KA, Turk-Browne N. Increasing stimulus similarity drives nonmonotonic representational change in hippocampus. *elife*. 2022;11:e68344. <https://doi.org/10.7554/eLife.68344>.
- Wang Q, Bui V-K, Song Q. Narrative organisation at encoding facilitated children's long-term episodic memory. *Memory*. 2015;23(4):602–611. <https://doi.org/10.1080/09658211.2014.914229>.
- Wimmer GE, Shohamy D. Preference by association: how memory mechanisms in the hippocampus bias decisions. *Science*. 2012;338(6104):270–273.
- Yassa MA, Stark CEL. Pattern separation in the hippocampus. *Trends Neurosci*. 2011;34(10):515–525. <https://doi.org/10.1016/j.tins.2011.06.006>.
- Yesavage JA, Rose TL. Semantic elaboration and the method of loci: a new trip for older learners. *Exp Aging Res*. 1984;10(3):155–159. <https://doi.org/10.1080/036107738408258560>.

- Zabelina DL, Condon DM. The four-factor imagination scale (FFIS): a measure for assessing frequency, complexity, emotional valence, and directedness of imagination. *Psychol Res*. 2020;84:2287-2299. <https://doi.org/10.1007/s00426-019-01227-w>.
- Zeidman P, Maguire EA. Anterior hippocampus: the anatomy of perception, imagination and episodic memory. *Nat Rev Neurosci*. 2016;17(3):173-182. <https://doi.org/10.1038/nrn.2015.24>.
- Zeithamova D, Preston AR. Flexible memories: differential roles for medial temporal lobe and prefrontal cortex in cross-episode binding. *J Neurosci*. 2010;30(44):14676-14684. <https://doi.org/10.1523/JNEUROSCI.3250-10.2010>.
- Zeithamova D, Dominick AL, Preston AR. Hippocampal and ventral medial prefrontal activation during retrieval-mediated learning supports novel inference. *Neuron*. 2012;75(1):168-179. <https://doi.org/10.1016/j.neuron.2012.05.010>.