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Overlap between hippocampal pre-encoding and encoding patterns supports episodic memory

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Abstract

It is well-established that whether the information will be remembered or not depends on the extent to which the learning context is reinstated during post-encoding rest and/or at retrieval. It has yet to be determined, however, if the fundamental importance of contextual reinstatement to memory extends to periods of spontaneous neurocognitive activity prior to learning. We thus asked whether memory performance can be predicted by the extent to which spontaneous pre-encoding neural patterns resemble patterns elicited during encoding. Individuals studied and retrieved lists of words while undergoing fMRI-scanning. Multivoxel hippocampal patterns during resting periods prior to encoding resembled hippocampal patterns at encoding most strongly for items that were subsequently remembered. Furthermore, across subjects, the magnitude of similarity correlated with a behavioral measure of episodic recall. The results indicate that the neural context before learning is an important determinant of memory.

KEYWORDS

context, episodic memory, hippocampus, pre-encoding, reinstatement

1 | INTRODUCTION

Why are certain experiences remembered and others forgotten? The literature has established that memory performance is predominantly dependent on the degree to which the neurocognitive context at encoding is reinstated during post-encoding rest and/or at retrieval (Cohen et al., 2015; Morris, Bransford, & Franks, 1977; Sekeres, Moscovitch, & Winocur, 2017; Tulving, 1983; Tulving & Thomson, 1973). For instance, functional magnetic resonance imaging (fMRI) studies in humans have revealed that patterns of brain activity during encoding are similar to patterns elicited during post-encoding rest and during retrieval: the more similar the reinstated pattern to the original one, the better the memory performance (Danker, Tompary, & Davachi, 2016; Gordon, Rissman, Kiani, & Wagner, 2014; Johnson & Rugg, 2007; Mack & Preston, 2016; Manning, Polyn, Baltuch, Litt, & Kahana, 2011;

Ritchey, Wing, LaBar, & Cabeza, 2012; Staresina, Alink, Kriegeskorte, & Henson, 2013; Tompary, Duncan, & Davachi, 2016; Wimber, Alink, Charest, Kriegeskorte, & Anderson, 2015; Wing, Ritchey, & Cabeza, 2015). An open question, however, is whether the fundamental importance of contextual reinstatement to memory is also evident *prior* to encoding. Namely, are neural patterns elicited before learning reinstated during successful encoding, and do they lead to better memory? The current study is aimed at answering this question, with the hypothesis that memory performance should depend on the overlap between pre-encoding and encoding patterns. Thus, the neurocognitive context before learning should be an important determinant of memory.

Our hypothesis stems from the conceptualization of context as the stream of thoughts and associations which continuously evolves and fluctuates over time (Anderson & Bower, 1972; Davelaar, Goshen-Gottstein, Ashkenazi, Haarmann, & Usher, 2005; Estes, 1955; Polyn,

Norman, & Kahana, 2009). This stream of thoughts is partly evoked by the study materials, but is also elicited spontaneously during resting periods prior to study. Thus, encoding should be more successful if the neurocognitive context before learning is similar to that during study. A few pieces of evidence support the idea that processes occurring prior to learning have important effects on learning. Memory performance may be enhanced by providing what has been termed an "episodic specificity induction" task, in which participants are briefly trained on recalling details of an event prior to encoding (e.g., Madore, Addis, & Schacter, 2015; Madore, Szpunar, Addis, & Schacter, 2016). Other studies investigated neural activity immediately prior to presentation of each stimulus and found that brain activity (at times, including the hippocampus), predicted memory performance (Brown et al., 2016; Cohen et al., 2015; Otten, Quayle, Akram, Ditewig, & Rugg, 2006; Sweeney-Reed et al., 2016) and decision-making (Doll, Duncan, Simon, Shohamy, & Daw, 2015). These findings have typically been interpreted to reflect an anticipatory state or heightened attention during the prestimulus periods. Indeed, oftentimes, prestimulus periods were preceded by a cue providing information about the upcoming item.

In contrast to these latter studies, the aim of the current study was not to examine anticipation of an individual experience, or even explicit anticipation at all, but to determine if pre-encoding patterns within ongoing spontaneous neural activity can support memory. We hypothesized that pre-existing neural representations provide the framework for successful encoding of new information. Operationally, this entails that, in humans, spontaneous patterns of neural activity during pre-encoding rest are reinstated to support successful encoding—henceforth referred to as a *pre-encoding effect*. We focused specifically on mnemonic effects in the hippocampus and its related network. We predicted that an item is more likely to be remembered the more similar the neural representation of its memory trace is to a representation spontaneously elicited during pre-encoding rest.

Our hypothesis was inspired by studies on *memory allocation*, a process whereby intrinsically excitable neurons are likely to be included in a memory trace (Josselyn & Frankland, 2018; Rogerson et al., 2014). In memory allocation, the cell assembly that will form a memory trace is not selected at the time of memory formation but is haphazardly activated beforehand. The high excitability of the neurons recruited to encode a certain episode is, furthermore, expected to increase the likelihood that these neurons will also be involved in encoding the subsequent episode. Consequently, these two episodes are more likely to be clustered at retrieval such that recalling the first will lead to subsequently recalling the second (Josselyn & Frankland, 2018; Rogerson et al., 2014).

In humans, such a clustering effect has been well-documented behaviorally (Healey, Long, & Kahana, 2018; Kahana, 1996; Kahana, 2012). Termed the Temporal Contiguity Effect, this phenomenon refers to the increased probability of sequentially recalling two items that were studied in close temporal contiguity. The effect is thought to arise from the largely overlapping temporal contexts shared by neighboring items and is a hallmark of episodic recall (Healey, 2018; Healey & Kahana, 2014; Healey, Long, & Kahana, 2018; Polyn et al., 2009). On the neural level, both memory allocation and the Temporal Context Effect have been shown to be associated with the hippocampus and adjacent structures (Folkerts, Rutishauser, & Howard, 2018;
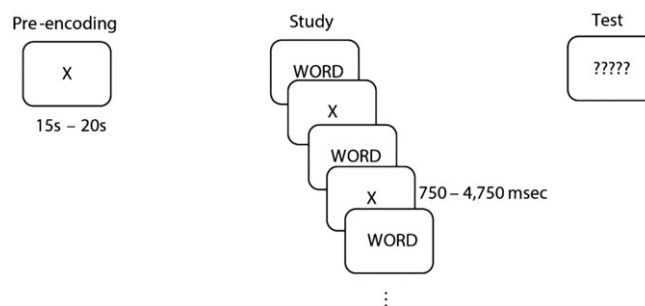

FIGURE 1 Illustration of the design. Illustration of the design for one list. During pre-encoding participants were instructed to rest while fixating on a cross in the middle of the screen. At study 12 words were presented, followed by the recall phase which lasted 22.5 s

Josselyn & Frankland, 2018; Kragel, Morton, & Polyn, 2015; Manning et al., 2011; Rogerson et al., 2014). On the cognitive level, the extent of pre-encoding/encoding overlap reflects the similarity between the neurocognitive context before and during learning, with more similar contexts entailing greater likelihood of relying on contextual cues to drive memory. Taken together, if memory allocation mediates pre-encoding effects and results in temporal clustering, we predict that the extent to which pre-encoding and encoding patterns overlap will be associated with the magnitude of temporal contiguity.

2 | MATERIALS AND METHODS

2.1 | General

Our design included 15–20 s resting periods prior to presentation of the study materials (Figure 1). We used a word-list free recall task, in which participants (*n* = 23) studied and immediately recalled 24 lists of 12 words. During all phases, neural activity was measured using functional magnetic resonance imaging (fMRI).

2.2 | Participants

Participants were 28 neurologically-intact native Hebrew speakers (17 women), right-handed and with normal or corrected-to-normal vision. Data from four participants were excluded due to excessive motion inside the scanner (over 4 mm). Data from an additional participant were excluded due to low performance on the behavioral memory task (mean number of recalled items was over two standard deviations below the group average). All reported analyses thus include data of 23 participants (15 women; ages 21–32 years, mean = 24.5). Participants gave their informed consent prior to the experiment and were compensated for their time monetarily or with course credit. All experimental procedures were approved by the Tel-Aviv Medical Center's Clinical Investigation committee.

2.3 | Materials

The stimuli consisted of 336 Hebrew nouns. All nouns were 5–6 letters long (mean = 5.46). The nouns were divided into 28 lists of 12 words; 24 lists were used for the experiment and four lists for the practice phases (see below).

2.4 | Behavioral procedure

Prior to entering the scanner, participants were given detailed instructions and two practice lists of the free-recall task, which included overt pronunciation of the encoded words. A primary goal of this practice session was to ensure that participants verbalized the words clearly yet softly enough to avoid head motion.[1] Two additional practice lists were presented within the scanner.

The experiment consisted of four identical free-recall runs, each lasting 7:25 min. The set of words was randomly divided into four, with a quarter of the words (i.e., 72 words, divided into six lists of 12 words each) assigned to each run. The order of the runs was counterbalanced across participants. In addition, three runs of a semantic fluency task were interleaved in between the free-recall runs. The purpose of the semantic fluency task was extraneous to the current endeavor, and therefore we do not discuss it further.

In each of the four runs, six lists of 12 words each were presented for study followed by a free-recall test. The order in which the words were presented was random. Presentation of three of the six lists (randomly selected) was preceded by a fixation block, which we term the "Pre-encoding Phase." During this phase, participants were instructed to rest while fixating on a cross in the middle of the screen. The durations of the pre-encoding phases were 15, 17.5, and 20 s and their order was counterbalanced across runs. Only lists which included a pre-encoding phase were included in the current analyses.

Presentation of each of the study lists was preceded by a 2.5 s display in which the word PREPARE appeared at the center of the screen, signaling participants to prepare for the upcoming list. The study phase then began, with each of the 12 words in the list presented sequentially for 1,750 ms in the center of the screen followed by a 750–4,750 ms fixation cross. For four of the six lists (whose order was randomly assigned and counterbalanced across sessions), a fixation trial of 0.5–8.25 s was presented at the offset of the study phase. The aim of these trials was to jitter the beginning of the recall phase with regard to the TR. The recall phase then began, with presentation of five question marks at the center of the screen signaling participants to start recalling. Recall was executed by overtly pronouncing as many words as possible from the last list presented, in any order, until the cue preparing them for the next list appeared on the screen. The recall phase lasted 22.5 s. Verbal responses were digitally recorded using Audacity software (http://audacity.sourceforge.net). As an incentive to enhance performance, participants were told that they would be awarded monetary prizes (comparable to $200) if they reached the highest scores in the experiment. Figure 1 illustrates the experimental design for a single list which is preceded by a pre-encoding phase.

2.5 | Imaging procedure

Participants were scanned on a GE 3T Signa Horizon LX 9.1 echo speed scanner (Milwaukee, WI). During each of the runs, whole-brain T2*-weighted EPI functional images were acquired (TR = 2,500 ms, 20 cm FOV, 64 × 64 matrix, Flip Angle = 85°, TE = 35, 44 coronal slices perpendicular to the hippocampal axis, 3 mm thickness with 0.7

gap, sequential acquisition). In each run, 174 volumes were acquired. Four additional volumes were acquired at the beginning of each run to allow for T1 equilibration (and were excluded from the analysis).

2.6 | Data analysis

2.6.1 | Behavioral analysis

The behavioral recall data were transcribed manually by research assistants. Based on the transcription, the study items were classified into the following categories: (a) Words subsequently recalled at the first three output positions. These may reflect retrieval from a short term memory store (but see Howard, Kahana, & Sederberg, 2008), whose span is 3–4 items (Jonides et al., 2008; Luck & Vogel, 1997), which was not the focus of the current study. Crucially, these items were not included in any of the analyses, including those examining Temporal Context Effects. (b) Words subsequently recalled correctly, from all output positions but the first three ("Remembered"); (c) Words which were not subsequently recalled ("Forgotten").

The Temporal Context Effect was examined using scripts from http://memory.psych.upenn.edu/Software. To reiterate, the Temporal Context Effect refers to the phenomenon whereby the smaller the absolute temporal lag between two items at study, the higher the probability that these two items will be recalled consecutively. We examined conditional-response probabilities (CRPs): the probability of making transitions at a certain lag conditional on this lag being available (Howard & Kahana, 1999). For the analysis examining across-subject correlation with pre-encoding magnitude, temporal-factor scores were calculated for each participant (Polyn et al., 2009). The temporal factor score is a measure of the tendency of a participant to successively retrieve items with short temporal lags (namely, which appeared close to each other at encoding), with a score of 0.5 indicating no effect of temporal contiguity.

2.6.2 | Preprocessing

Imaging data were preprocessed and analyzed using SPM8 (Wellcome Department of Cognitive Neurology, London). A slice-timing correction to the first slice was performed followed by realignment of the images to correct for subject movement. Next, data were spatially normalized to an EPI template based upon the MNI305 stereotactic space (Cocosco, Kollokian, Kwan, & Evans, 1997). The images were resampled into 2 mm cubic voxels and spatially smoothed with an 8 mm FWHM isotropic Gaussian kernel. Finally, images were resliced to be aligned to the anatomical ROIs.

Our choice to spatially smooth the data was driven by our focus on relatively coarse spatial patterns within our regions of interest (Bilateral hippocampi and Hippocampal Network; see section 3), rather than on small regions with fine-grained spatial patterns. Furthermore, we followed evidence which showed that smoothing does not decrease decoding sensitivity[2] and, most importantly, that an

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[1] We were able to record overt responses during the fMRI scanning sessions by using adaptive noise cancelling microphone and headphones (FOMRI-III; Optoacoustics, Israel; see also Sadeh et al., 2012).

[2] Previous studies have shown that smoothing generally reduces the decoding accuracy (Gardumi et al., 2016; Kriegeskorte, Cusack, & Bandettini, 2010). The conflicting results were suggested to be due to the normalization of the data to an MNI template in Op de Beeck (2010)'s study—with normalization making the data less sensitive to different smoothing kernels (Gardumi et al., 2016). In our study too, normalization was applied and, therefore, our data should be less sensitive to the negative effects of smoothing.

8 mm FWHM smoothing kernel yields more reliable results (higher correlations) in correlational multivariate analyses (CMA), in which the spatial activity pattern between two subsets of the same data are correlated (Op de Beeck, 2010).

2.6.3 | Pattern similarity analysis

Effects of pre-encoding were investigated using a method introduced by Staresina et al. (2013) to study reactivation of individual items. The pre-encoding phases were broken down to pre-encoding timepoints, each corresponding to a single TR. Likewise, the study phase was broken down by TRs. Since study trials were not temporally aligned with the TRs, the onset of each study trial was defined as that of the closest TR. TRs corresponding to trials whose onsets overlapped those of another trial were excluded from the analyses. As suggested in a recent methodological analysis (Mumford, Turner, Ashby, & Poldrack, 2012), all trials were shifted forward in time by two TRs (5 s; parallel to the "Add4-6" method), since the peak BOLD response is ~5 s after the onset of each trial. For each trial/timepoint, a multi-voxel pattern of activity within regions of interest was extracted from the BOLD data. The time-course of each voxel was z-scored and data were detrended to remove linear drifts. A similarity score, indexed by Pearson correlation, was then calculated between the pattern of each pre-encoding timepoint and of each study trial (Figure 2). A Fisher transformation was applied to the correlation coefficients, aiming to make their sampling distribution approach that of the normal distribution, and the results were divided by the coefficients' standard deviations ($SD = 1/\sqrt{n-3}$; Rissman, Gazzaley, & D'Esposito, 2004).

2.6.4 | Regions of interest definition

Masks of 90 cortical and subcortical regions spanning the brain (excluding the cerebellum) were obtained using the Automated Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002).
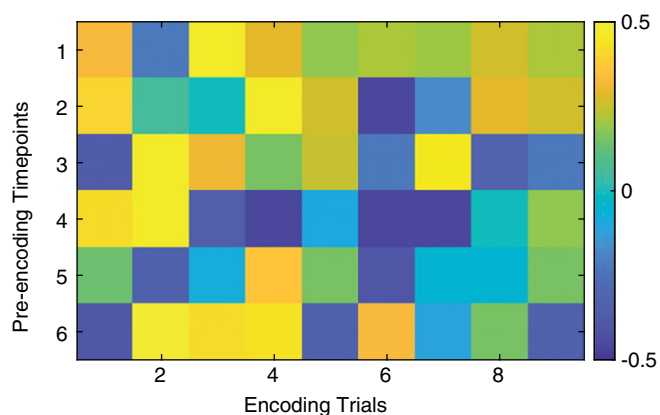

FIGURE 2 Illustration of the analysis. Analysis of the pattern of similarity between a single pre-encoding session and a single list for a hypothetical data set. The pre-encoding phases were broken down to pre-encoding timepoints, each corresponding to a single TR. Likewise, the study phase was broken down by TRs. A similarity score, indexed by Pearson correlation, was then calculated between the pattern of each pre-encoding timepoint and of each study trial [Color figure can be viewed at wileyonlinelibrary.com]

3 | RESULTS

3.1 | Behavioral results

Unless mentioned otherwise, all reported statistical *t*-tests are two-tailed. Participants correctly recalled a mean of 6.34 words per list (*SEM* = 0.36). Of the total number of words recalled 4% were extra-list intrusions and 2.5% were prior-list intrusions, namely words from lists presented previously in the experiment. The prior-list intrusions showed a typical effect of higher probability of intrusions from temporally proximal lists, as compared to more distant lists (e.g., more likely to be a word from the preceding list than from lists presented earlier on in the experiment; Zaromb et al., 2006). To test the significance of this pattern, we correlated, for each participant, the percentage of intrusions from each of the preceding lists with the distance between the current list and the list from which the intrusion occurred. The average Pearson correlation coefficient was −0.39 and was significantly smaller than zero, as revealed by a one-sample *t* test ($t[22] = -12.2$, $p < 0.001$). Recall probability as a function of serial position (serial position curve) is presented in Figure 3. The results show a typical serial position curve with pronounced primacy and recency effects (this analysis did not exclude the first three recalls).

As illustrated in Figure 4, a typical Temporal Context Effect (Howard & Kahana, 1999) was observed, demonstrating that the closer two items had been presented at study, the higher their probability of being recalled consecutively. Because we excluded the first three words recalled from each list to eliminate possible effects of short term memory store, whose span is 3–4 items (Cowan, 2001; D'esposito & Postle, 2015; Jonides et al., 2008; Luck & Vogel, 1997), the magnitude of the Temporal Context Effect is comparable to that of delayed free-recall paradigms (Howard & Kahana, 1999; Sadeh, Moran, & Goshen-Gottstein, 2015).

3.2 | Pre-encoding effects in the hippocampus

Fisher-transformed Pearson correlation coefficients (Rissman et al., 2004) indexing similarity scores were calculated between the multi-
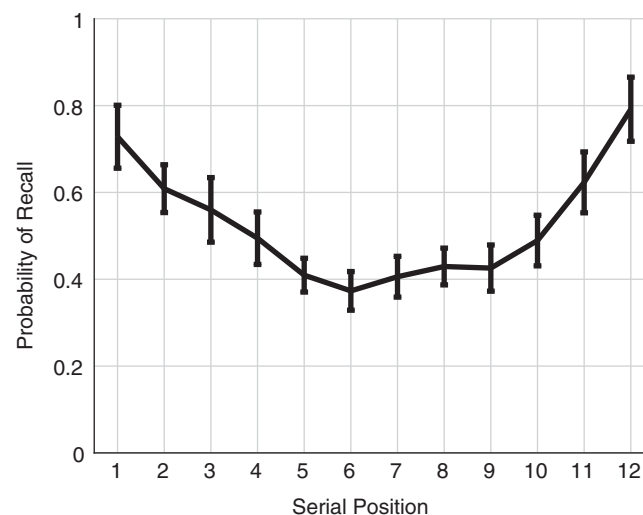

FIGURE 3 The serial position curve. Probability of recall as a function of study serial position. Error bars reflect 95% confidence intervals for within-subject designs (Loftus & Masson, 1994)
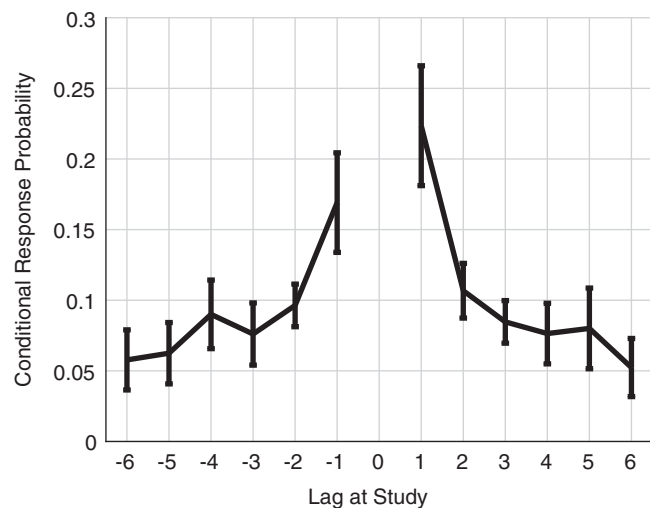
FIGURE 4 The temporal context effect. The temporal context effect for all but the first three words recalled (which may reflect reliance on short-term memory store rather than on episodic memory; see Section 2). Conditional response probability (CRP) measures the probability that a transition between two successively recalled items would be made across a certain lag (Howard & Kahana, 1999). The probabilities are conditional on the event that a transition of a certain lag would yield a studied item that has not already been retrieved. Lag refers to the distance, at study, between the serial-position of two successively recalled words. Error bars reflect 95% confidence intervals for within-subject designs (Loftus & Masson, 1994)

voxel pattern of each pre-encoding TR and of each study trial (see section 2 for further details). For each participant, similarity scores were then averaged across trials for each of the two conditions (Remembered and Forgotten). As predicted, the mean similarity scores in the Remembered condition (Mean Fisher's Z = 0.43) were greater than in the Forgotten condition (Mean Fisher's Z = 0.27; paired-sample t test: $t[22]$ = 2.94, p = 0.008, Cohen's d = 0.61). Thus, a significant pre-encoding effect was demonstrated.

3.3 | Controlling for distance from pre-encoding between Remembered and Forgotten items

Our analysis of pre-encoding effects was aimed at demonstrating that, as compared to Forgotten items, the neural patterns elicited by Remembered items exhibit enhanced similarity with spontaneous patterns elicited during the pre-encoding phase. It was essential to rule out the possibility that pre-encoding effects are driven by differential distances from pre-encoding between Remembered and Forgotten items: if Remembered items are closer to the pre-encoding phase than Forgotten items, differences between the two conditions could be due to trivial effects of temporal autocorrelation, rather than pre-encoding effects.

For each encoded item, we calculated its distance in TRs from the pre-encoding phase. As might be expected considering the primacy effect, Remembered items were closer to the pre-encoding phase than Forgotten items (Mean Remembered = 7.4 TRs, Mean Forgotten = 8.4 TRs; paired-sample t test: $t[22]$ = 3.63, p = 0.001). To control for the effects of distance from encoding, for participants whose Remembered items were, on average, closer to the pre-encoding phase than the Forgotten items (n = 16), we randomly excluded ~25%

of the closest Remembered items and ~25% of the farthest Forgotten items. With this exclusion, the distances from pre-encoding were greater (though not significantly; $t[22]$ < 1, p = 0.9) for Remembered than Forgotten trials (Mean Remembered = 7.64 TRs, Mean Forgotten = 7.62 TRs; for further details see Supporting Information).

All subsequently reported analyses were conducted on the data controlling for the differences in distances between Remembered and Forgotten items as described above (Mean number of Remembered trials per block = 2.43, SD = 0.82; Mean number of Forgotten trials per block = 3.3, SD = 1.25). As a further control for the distance from pre-encoding, we ran the analysis of pre-encoding effects in the hippocampus excluding the first item in each list.

The analysis controlling for distances in Remembered and Forgotten trials revealed a significant pre-encoding effect. Thus, the mean similarity scores in the Remembered condition (Mean Fisher's Z = 0.42) were greater than in the Forgotten condition (Mean Fisher's Z = 0.3; paired-sample t test: $t[22]$ = 2.59, p = 0.017, Cohen's d = 0.54). Figure 5 depicts the results of this analysis for our a priori region of interest (ROI): the bilateral hippocampi. This result confirms that the pre-encoding effect is not fully driven by temporal autocorrelation.

The additional control analysis excluding the first item from each list (which was the closest to the pre-encoding stage) revealed the same pattern, with greater similarity in the Remembered condition (Mean Fisher's Z = 0.4) than in the Forgotten condition (Mean Fisher's Z = 0.26; paired-sample t test: $t[22]$ = 2.56, p = 0.018, Cohen's d = 0.53).

3.4 | Pre-encoding effects in the hippocampal network

Our a priori assumption was that pre-encoding effects reflect the similarity between the neurocognitive context at pre-encoding and the context associated with the memory traces of the subsequently presented items. On the neural level, the memory trace consists of an entire hippocampal–neocortical ensemble, in which the hippocampus acts as a pointer to a cortical network representing the perceptual and semantic details of the episode (Nadel & Moscovitch, 1997; Teyler &
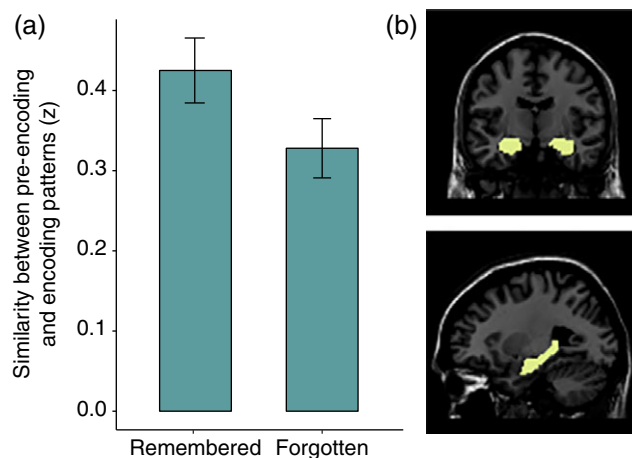

FIGURE 5 Pre-encoding effect in the bilateral hippocampi. Difference between remembered and forgotten words with regard to similarity between pre-encoding and encoding patterns ($t[22]$ = 2.59, p = 0.017, Cohen's d = 0.54). Error bars denote standard error of the mean [Color figure can be viewed at wileyonlinelibrary.com]
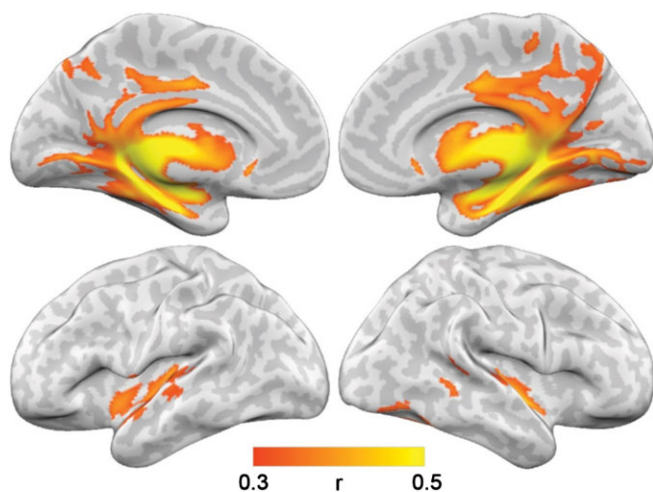
FIGURE 6 Group hippocampal network ROI. Regions co-fluctuating (functionally connected) with the hippocampus during the experiment (voxels for which the mean correlation coefficient surpassed a threshold of 0.3, averaged across participants) [Color figure can be viewed at wileyonlinelibrary.com]

DiScenna, 1986). We, therefore, hypothesized that the pre-encoding effect extends to the network of regions which, together with the hippocampus, constitutes the memory trace.

To examine this possibility, we next turned to investigate pre-encoding effects within the network of regions that co-fluctuated with the hippocampus throughout the experiment. To this end, the time-courses for all voxels within the bilateral hippocampi ROI were averaged and used as the seed in a functional connectivity analysis. Because each of the experimental phases is relatively short for examining functional connectivity (e.g., Honey et al., 2009), we included the data of all phases to investigate connectivity throughout the experiment—that is, during all experimental phases (pre-encoding, encoding, and recall). This analysis aimed to identify voxels whose activity correlates with the hippocampus. The correlations were calculated separately for each run, then averaged across runs. For each participant, a Hippocampal Network ROI was defined that included all voxels for which the correlation coefficient surpassed a threshold of 0.3.[3] Using the same threshold, a group Hippocampal Network ROI was created by averaging together all of the individual-subjects' Hippocampal Network ROIs (see Figure 6 for the Group Hippocampal Network ROI). The group-level functional-connectivity analysis revealed a set of regions associated with memory for perceptually rich experiences (McCormick, Moscovitch, Valiante, Cohn, & McAndrews, 2017; St-Laurent, Moscovitch, & McAndrews, 2016). These included the parahippocampal gyrus, occipital–temporal regions, the posterior cingulate cortex, lingual gyrus, and precuneus. In addition, large clusters were detected in the thalamus, the striatum, and regions in the cerebellum.

The analysis comparing pre-encoding effects between the Remembered and Forgotten conditions was repeated for these ROIs. As in the analysis of the hippocampus, here, too, the mean similarity score in the

Remembered condition (Mean Fisher's Z = 0.19) was significantly greater than in the Forgotten condition (Mean Fisher's Z = 0.096), as revealed in a paired-sample t test ($t[22]$ = 3.32, p = 0.003, Cohen's d = 0.69). In the Group Hippocampal Network ROI, the effect was also significant (Mean Fisher's Z for Remembered = 0.14; Mean Fisher's Z for Forgotten = 0.038; $t[22]$ = 2.97, p = 0.007, Cohen's d = 0.62).

Importantly, though these analyses reveal that the pre-encoding effect extends to brain regions which are functionally coupled with the hippocampus, it is unlikely to be a whole-brain effect, as revealed by a follow-up analysis. This analysis explored 90 individual AAL ROIs spanning the entire brain and found that only a subset of 26 regions—20 of which overlapped with the Hippocampal Network ROI—showed a significant effect at p < 0.05 (for the full list see Supporting Information Table S1). Furthermore, none of these regions passed correction for multiple comparisons (q[FDR] < 0.05; Benjamini & Hochberg, 1995).

3.5 | The pre-encoding effect as a function of distance from study

The memory allocation hypothesis suggests that neurons with high excitability immediately before learning are more likely to be allocated to a memory trace. Thus, it is possible that patterns toward the end of the pre-encoding phase would exhibit more similarity to encoding patterns than pre-encoding patterns at the beginning of the pre-encoding phase. To examine this hypothesis, we conducted the pre-encoding analyses again, this time separately for the first and second halves of the pre-encoding phases. An ANOVA with pre-encoding section (First, Second) and subsequent memory (Remembered, Forgotten) as within-subject factors was conducted. As hypothesized, a main effect for section was found, with pre-encoding/encoding overlap being larger for the second half of the pre-encoding phase (for bilateral hippocampi: $F[1,22]$ = 5.97, p = 0.023, η^2_p = 0.21; for Hippocampal Network ROI: $F[1,22]$ = 26.23, p < 0.001, η^2_p = 0.54). A main effect for subsequent memory was also found: greater overlap for subsequently-remembered than subsequently-forgotten items (for bilateral hippocampi: $F[1,22]$ = 6.75, p = 0.016, η^2_p = 0.24; for Hippocampal Network ROI: $F[1,22]$ = 10.18, p = 0.004, η^2_p = 0.32). However, the interaction between section and subsequent-memory was not significant (for bilateral hippocampi: $F[1,22]$ = 0.43, p = 0.52, η^2_p = 0.019; for Hippocampal Network ROI: $F[1,22]$ = 1.53, p = 0.23, η^2_p = 0.065). Thus, the pre-encoding effect was not stronger for the later, as compared to the earlier, section of the pre-encoding phase.

3.6 | Across-subject correlation between pre-encoding/encoding overlap and context reinstatement

We next examined the across-subject Pearson correlation between (a) the magnitude of overlap between pre-encoding and encoding representations and (b) the Temporal Context Effect per participant. The magnitude of pre-encoding/encoding overlap per participant was indexed by the mean correlation coefficients between pre-encoding timepoints and subsequent encoding trials. With regard to the behavioral measure, for each participant, a temporal factor score was

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[3]The connectivity analysis is not redundant with the finding of a Pre-encoding effect in the hippocampus. While the hippocampal Pre-encoding effect concerns spatial correlation and is calculated on an item-by-item basis, the connectivity analysis concerns temporal correlation and is calculated across the whole session.
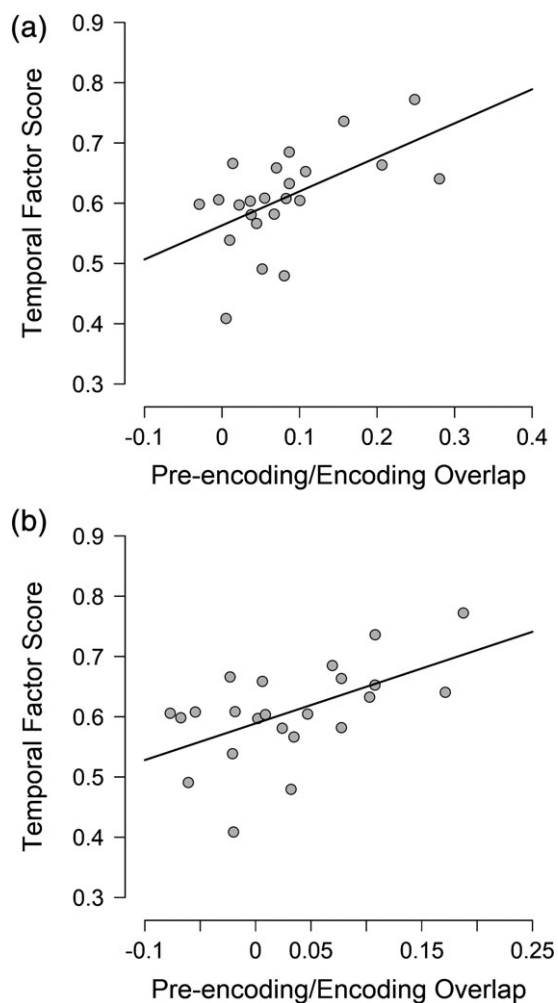
FIGURE 7 Correlation between pre-encoding/encoding overlap and the temporal context effect. Pre-encoding/encoding overlap refers to similarity between pre-encoding and encoding trials, indexed by Pearson's correlation. For both ROIs, the correlation between pre-encoding/encoding overlap and the temporal context effect is significant (r = 0.56, p = 0.006). a, bilateral hippocampi; b, hippocampal network ROI

calculated. This score represents the tendency of a participant to successively retrieve items in short temporal lags, or to rely on temporal context at recall (see "Behavioral analysis"). Because Pearson correlation values are sensitive to extreme values, we estimated the bias-corrected 95% confidence intervals for correlation coefficients. To this end, we applied nonparametric bootstrapping with 10,000 permutations using the "BCa" option in "boot.ci" in the R package "boot" (https://cran.r-project.org/web/packages/boot/index.html). The 95% confidence intervals are presented in square brackets following the p values.

A significant positive correlation was found both for the bilateral hippocampi and for the Hippocampal Network ROI: the greater the pre-encoding/encoding overlap, the stronger the reliance on temporal context (for bilateral hippocampi: r = 0.56, p = 0.006, [0.269, 0.787]; for the Hippocampal Network ROI: r = 0.56, p = 0.006, [0.270, 0.786]). Results for the bilateral hippocampi and the Hippocampal Network are illustrated in Figure 7.

3.7 | Waxing and waning of a general encoding state?

We maintain that the pre-encoding effects demonstrated here reflect correspondence between specific pre-encoding neural patterns and neural patterns of subsequently experienced events which form memory traces. However, an alternative interpretation of our findings is that the pre-encoding effects are a result of a general encoding state (or even an attentional state; see section 4) that waxes and wanes over time. According to this interpretation, the pre-encoding effects reflect a general similarity between pre-encoding and encoding neural states that is not item-specific.

To examine this possibility, we ran a sham analysis in which we aggregated across pre-encoding sections of all lists, and, in addition, across encoding sections of all lists. We next created two correlation matrices per subject: one including correlation coefficients between all pre-encoding timepoints (across all lists) and all subsequently remembered encoding trials, and one between all pre-encoding timepoints and all subsequently forgotten trials. An average correlation coefficient was then calculated (and Fisher-transformed) for each of these two matrices. A sham pre-encoding effect was defined as the difference between these two averages—namely, between the subsequently remembered average Fisher-transformed correlation coefficient and the subsequently forgotten average Fisher-transformed correlation coefficient. If the alternative, "encoding state", interpretation is true, it is expected that the sham pre-encoding effects would be of a similar magnitude as the original pre-encoding effects. Results of the sham analysis argue against this interpretation. For both the hippocampus and the Hippocampal Network ROI, the original pre-encoding effects were significantly greater than the sham pre-encoding effects (for the hippocampus: t[22] = 2.33, p = 0.029,
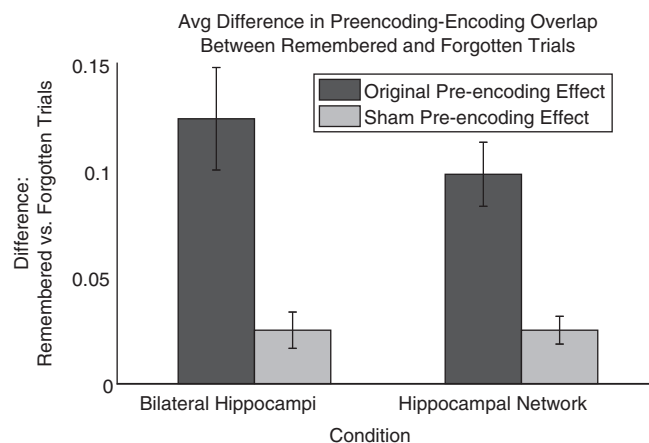

FIGURE 8 Comparison of original and sham pre-encoding effects. Pre-encoding effects are the difference between remembered and forgotten trials with regard to similarity between pre-encoding and encoding patterns. The original pre-encoding effect refers to similarity between the pre-encoding trials preceding a certain list and the encoding trials of that specific list. The sham pre-encoding effect refers to similarity between all pre-encoding trials (across all lists) and all encoding trials. The left panel depicts pre-encoding effects in the bilateral hippocampi and the right panel depicts pre-encoding effects in the hippocampal network ROI. Error bars denote standard error of the mean

Cohen's d = 0.49; for the Hippocampal Network ROI: $t[22]$ = 2.72, p = 0.012, Cohen's d = 0.57; Figure 8). This indicates that the patterns of remembered items are more similar to the pre-encoding phase which immediately preceded them as compared to the pre-encoding phases of the other lists.

3.8 | Changes in pre-encoding/encoding overlap over the course of the experiment?

Our final analysis examined the possibility that pre-encoding/encoding overlap increases with time and/or experience—namely, is stronger for later lists, as compared to earlier ones. The rationale underlying this idea is that as participants become more experienced in the free recall task (and perhaps more attentive to the specific task demands; Healey et al., 2018), it might result in greater similarity between pre-encoding and encoding patterns. To this end, we examined the pre-encoding/encoding overlap per participant twice: once for the first two runs—the first half of the experiment—and once for the last two runs—the second half of the experiment. As before, the pre-encoding/encoding overlap was indexed by the mean Fisher-transformed Pearson correlation coefficients between pre-encoding timepoints and subsequent encoding trials. For the bilateral hippocampi ROI, the mean pre-encoding/encoding similarity was, indeed, greater for the second half of the experiment (mean Fisher transformed coefficient = 0.39) than for the first half of the experiment (mean Fisher transformed coefficient = 0.34). However, this difference did not reach statistical significance ($t[22]$ = 0.46, p = 0.65, Cohen's d = 0.096). For the Hippocampal Network ROI, the mean pre-encoding/encoding similarity was greater for the first half of the experiment (mean Fisher transformed coefficient = 0.17) than for the second half of the experiment (mean Fisher transformed coefficient = 0.11). This difference did not reach statistical significance ($t[22]$ = 0.79, p = 0.44, Cohen's d = 0.16). These findings suggest that the pre-encoding effect is immune at least to some consequences of learning.

4 | DISCUSSION

Our results demonstrate that spontaneous neural patterns elicited during an ongoing pre-encoding resting period are reinstated during successful encoding of individual items. The pre-encoding effects we found are not fully accounted for by temporal autocorrelation, as revealed by our controls for temporal distance. As predicted, these effects were found in spatial activity patterns of the hippocampus, as well as in its functionally coupled network.

Furthermore, we found that individual differences in the magnitude of pre-encoding/encoding overlap correlated with reinstatement of context at retrieval, as indexed by the Temporal Context Effect. The Temporal Context Effect refers to the increased probability of sequentially recalling two items that were studied in close temporal contiguity (Polyn & Kahana, 2008; Sederberg, Howard, & Kahana, 2008). This effect is supported by the hippocampus and its adjacent structures (Folkerts et al., 2018; Kragel et al., 2015; Manning et al., 2011) and is thought to arise from the largely overlapping temporal (and neural) contexts shared by neighboring items. That the magnitude of the Temporal Context Effect is predicted by pre-encoding/

encoding overlap further establishes the importance of the neurocognitive context prior to learning to successful encoding. To the best of our knowledge, this is the first demonstration that this seminal effect can be predicted by pre-encoding neural activity.

Are the pre-encoding patterns merely random variations in neural firing that are fortuitously co-opted by neural events at encoding, as the allocation hypothesis suggests? If so, does the pre-encoding effect arise from a general encoding or attentional state (Aly & Turk-Browne, 2016) that waxes and wanes during pre-encoding and encoding? If this interpretation is true, the overlapping pre-encoding and encoding patterns reflect points in time in which the mnemonic system is in a preferred, or good, encoding and/or attentional state. Hence, we would expect encoding patterns to overlap not only with patterns elicited during the preceding pre-encoding block but with patterns elicited during all resting blocks in the experiment. Our sham analysis reveals that this is not the case—namely, that our results cannot be fully accounted for by the notion of a general encoding or attentional state. Rather, our results are at least partially (if not fully) driven by spontaneous 'preinstatement' of item-specific contextual associations.

While the particular states or thoughts represented by the pre-encoding neural patterns are not amenable to direct investigation, it is possible that they reflect, at least in part, episodic thoughts which are idiosyncratically associated with the to-be-studied items. This idea does not, of course, entail any form of precognition (Bendor & Spiers, 2016). Namely, we do not claim that during pre-encoding rest participants spontaneously thought of the exact same words that subsequently appeared during the study phase. Rather, it is possible that spontaneous idiosyncratic thoughts during pre-encoding became associated with (at least some of) the study words and constituted part of their memory traces, perhaps due to shared contextual features between the spontaneous thoughts and the memory traces of the study words. Such spontaneous thoughts and associations are constantly evoked during rest—a finding well-established in the literature regarding the brain's default mode at rest (Buckner & Carroll, 2007; Gusnard, Akbudak, Shulman, & Raichle, 2001; Spreng, Mar, & Kim, 2009). These thoughts and associations are the cognitive correlate of the presumed pre-existing neural representations which support encoding of new information and give rise to the pre-encoding effects. Although it would be interesting, and informative, if there were such cognitive correlates, their presence is not crucial for our results to be valid.

Recent studies in rodents may further support the idea that pre-encoding processes affect subsequent learning. It has been shown that hippocampal place-cells firing in a particular temporal sequence while an animal is navigating a route also fire spontaneously in the same sequence during a resting period prior to the experience—a finding referred to as "preplay" (Buhry, Azizi, & Cheng, 2011; Diba & Buzsaki, 2007; Dragoi & Tonegawa, 2011; Dragoi & Tonegawa, 2013; Eichenbaum, 2015; Grosmark & Buzsáki, 2016; Johnson & Redish, 2007; Pfeiffer & Foster, 2013; Silva, Feng, & Foster, 2015).[4] In the absence of this pre-encoding pattern, new patterns must be formed from less

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[4]It has recently been suggested that this finding may only be obtained if the animal is already familiar with the spatial environment or the goal, but the path to the goal is novel (Eichenbaum, 2013).

activated neurons, thereby reducing their chances of survival in a memory trace (Josselyn & Frankland, 2018; Rogerson et al., 2014).

Based on these and other preplay findings and (e.g., McNaughton et al., 1996), Eichenbaum (2013) concluded that "neural ensembles in the hippocampus create contextual representations based on pre-existing population connectivity, which then integrates across experiences to create a temporal organization for memories". Crucially, these contextual representations are largely comprised of internal, temporal context as described by temporal context models (e.g., Howard et al., 2014; Howard & Eichenbaum, 2013)—that is, the stream of thoughts and associations which continuously evolves and fluctuates over time. Similar ideas concerning the effects of temporal context have been raised with regard to replay of memories (Eichenbaum, 2014)—that is, offline reactivation of temporally-sequenced cell firings. Indeed, the phenomena of preplay are considered by some as an extension of the well-established replay phenomena (Pfeiffer & Foster, 2013).

Our result regarding the correlation of pre-encoding with the magnitude of the Temporal Context Effect also has a parallel in animal research. As mentioned, what can be conceptualized as a neural manifestation of the Temporal Context Effect has been proposed in the rodent literature in the theoretical framework of Memory Allocation (Josselyn & Frankland, 2018; Rogerson et al., 2014). According to the notion of Memory Allocation, neurons with intrinsically high excitability are more likely to be allocated to a memory trace of an item than neurons with lower excitability. These more excitable neurons are also more likely to be included in the memory traces of items studied adjacently to the given item. Consequently, neighboring items at study are also more likely to cue each other during test and thus be clustered together at retrieval. This clustering phenomenon is exactly that which the Temporal Context Effect refers to, and which was found to be associated with the magnitude of the pre-encoding effect. Furthermore, with regard to the allocation hypothesis, we examined the idea that neurons with high excitability immediately before learning are more likely to be allocated to a memory trace. We found that patterns toward the end of the pre-encoding phase were more similar to encoding patterns than pre-encoding patterns at the beginning of the pre-encoding phase. Though this finding is consistent with the allocation hypothesis, it could also be the result of temporal autocorrelation. We, therefore, examined the interaction between pre-encoding section and memory fate (Remembered, Forgotten), which, unfortunately, did not reach significance. Thus, we cannot conclude that the pre-encoding effect was stronger for the end of the pre-encoding section as compared to the beginning of it.

In our paradigm, pre-encoding resting periods most frequently followed periods of recall of words from the previous lists. This relation raises the possibility that the pre-encoding patterns were influenced by words from the previous lists. Thus, the pre-encoding patterns may have reflected reinstatement of the contextual associations evoked by items from previous lists. Consistent with the current findings within the hippocampus, effects of replay of individual items within the medial temporal lobe have been recently reported (Staresina et al., 2013). The "bleeding" of contextual representations from previous lists to encoding of a given list has also been previously shown on the behavioral level, and is accounted for by temporal context models (e.g., Craik, Gardiner, & Watkins, 1970; Darley & Murdock, 1971;

Sirotin, Kimball, & Kahana, 2005; Zaromb et al., 2006). According to these models, because lists of items presented in close temporal proximity most likely share similar temporal contexts, prior-list intrusions are more likely to be from temporally proximal lists than from temporally distant lists. Indeed, the influence of contextual representations from previous lists was also evident in the current study, where prior-list intrusions were more likely to be from temporally proximal lists, as compared to more distant lists. In further support of the effects of prior learning on memory, it has been found that prior list recall is the best predictor of current-list recall (Kahana, Aggarwal, & Phan, 2018).

An additional hypothesis we examined was that with time and practice participants' performance will improve and so would the magnitude of pre-encoding/encoding overlap. In line with this idea is the finding that the Temporal Contiguity effect increases with experience (Healey et al., 2018). However, we found an increase in the magnitude of pre-encoding/encoding overlap only on the descriptive level and only for the Hippocampus. This lack of finding could be due to the opposing effects of experience, on the one hand, and fatigue on the other. Another possibility, however, is that the pre-encoding effect is immune to such strategic influences which are unlikely to increase the excitability of pre-encoding neurons which may be mediating the effect. Increased arousal or attention, however, may have the desired effect, a possibility we plan to test in subsequent studies.

All pre-encoding effects reported so far were found both for the a priori bilateral hippocampal ROI and for the network of regions functionally coupled with the hippocampus, (referred to in the Results sections as "Hippocampal Network ROIs"). This latter result held both when the functional network was defined per subject and when defined at the group level. An additional analysis (see Supporting Information) sought to identify whether the network results reflect only patterns within individual ROIs (or subsets of the network) or also a global pattern of amplitudes across the different ROIs in the network—namely, a network effect. The analysis, which we term the "Global-pattern ROI", also revealed a significant pre-encoding effect. This finding suggests that the current pre-encoding effects may be driven in part by a global pattern of amplitudes (namely, by network-wide effects).

Demonstrating the existence of a mechanism of pre-encoding provides a crucial contribution to our understanding of why certain experiences are remembered and others are forgotten. The mnemonic fate of studied-items greatly depends on the extent to which spontaneous neural representations, within an ongoing pre-encoding period, are reinstated during encoding. Because the individual's neural state at the resting time preceding encoding likely differs from one occasion to the next—and correspondingly so do the idiosyncratic thoughts/autobiographical associations which are prominent during rest (Gusnard et al., 2001; Spreng et al., 2009)—so will the mnemonic outcome of studied items be different, even if all external stimuli and conditions are kept the same in all occasions. This idea closely resonates with the notion of intra-individual variability in memory performance (Kahana et al., 2018), namely, that a certain individual might remember certain items from an event in some circumstances and other items in other circumstances. Though such intra-individual variability in memory performance has been demonstrated empirically (Kahana et al., 2018),

current Temporal Context models are not fully able to account for it. We suggest that incorporating the effects of pre-encoding/encoding similarity as an extension of these models can go a long way in explaining intra-individual variability.

Whatever the specific nature of pre-encoding patterns might be, our findings illustrate that they play a crucial role in memory for subsequently presented information. We thus provide a novel demonstration in humans that the determinants for the mnemonic fate of an experience can be traced back to spontaneously elicited neural patterns prior to the experience. Thereby, we establish that pre-encoding constitutes a fundamental aspect of the neurocognitive basis of human memory. These findings have important implications for memory-interventions in healthy and in memory-impaired people from early development to aging, by extending the focus of such interventions to processes occurring prior to presentation of memoranda. Future research should extend these results to examine finer-grained item-specific preinstatement (see Staresina et al., 2013). In addition, such studies may seek to better characterize the pre-encoding process by applying pre-encoding manipulations that may enhance or disrupt it.

AUTHOR CONTRIBUTION

T.S., Y.G.G., and M.M. conceived the study; T.S. managed performance of the experiments; J.C. and T.S. devised the analysis strategy; T.S. performed the analyses of the data; T.S., J.C., and M.M. took part in interpretation of the results; T.S. wrote the main manuscript text with comments and corrections from all the other authors; Y.G.G., M.M., and T.S. obtained funding; M.M. supervised the study; All authors reviewed the manuscript.

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REFERENCES

Aly, M., & Turk-Browne, N. B. (2016). Attention promotes episodic encoding by stabilizing hippocampal representations. *Proceedings of the National Academy of Sciences of the United States of America*, 113(4), E420–E429.

Anderson, J. R., & Bower, G. H. (1972). Recognition and retrieval processes in free recall. *Psychological Review*, 79(2), 97–123.

Bendor, D., & Spiers, H. J. (2016). Does the hippocampus map out the future? *Trends in Cognitive Sciences*, 20(3), 167–169.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B: Methodological*, 57, 289–300.

Brown, T. I., Carr, V. A., LaRocque, K. F., Favila, S. E., Gordon, A. M., Bowles, B., ... Wagner, A. D. (2016). Prospective representation of navigational goals in the human hippocampus. *Science*, 352(6291), 1323–1326.

Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences*, 11(2), 49–57.

Buhry, L., Azizi, A. H., & Cheng, S. (2011). Reactivation, replay, and preplay: How it might all fit together. *Neural Plasticity*, 2011, 1–11.

Cocosco, C. A., Kollokian, V., Kwan, R. K.-S., & Evans, A. C. (1997). Brain-Web: Online Interface to a 3DMRI Simulated. *NeuroImage*, 5, S425.

Cohen, N., Pell, L., Edelson, M. G., Ben-Yakov, A., Pine, A., & Dudai, Y. (2015). Peri-encoding predictors of memory encoding and consolidation. *Neuroscience & Biobehavioral Reviews*, 50, 128–142.

Cowan, N. (2001). Metatheory of storage capacity limits. *Behavioral and Brain Sciences*, 24(1), 154–176.

Craik, F. I., Gardiner, J. M., & Watkins, M. J. (1970). Further evidence for a negative recency effect in free recall. *Journal of Verbal Learning and Verbal Behavior*, 9(5), 554–560.

Danker, J. F., Tompary, A., & Davachi, L. (2016). Trial-by-trial hippocampal encoding activation predicts the fidelity of cortical reinstatement during subsequent retrieval. *Cerebral Cortex*, 27(7), 3515–3524.

Darley, C. F., & Murdock, B. B. (1971). Effects of prior free recall testing on final recall and recognition. *Journal of Experimental Psychology*, 91(1), 66–73.

Davelaar, E. J., Goshen-Gottstein, Y., Ashkenazi, A., Haarmann, H. J., & Usher, M. (2005). The demise of short-term memory revisited: Empirical and computational investigations of Recency effects. *Psychological Review*, 112(1), 3–42.

D'esposito, M., & Postle, B. R. (2015). The cognitive neuroscience of working memory. *Annual Review of Psychology*, 66, 115–142.

Diba, K., & Buzsaki, G. (2007). Forward and reverse hippocampal place-cell sequences during ripples. *Nature Neuroscience*, 10(10), 1241–1242.

Doll, B. B., Duncan, K. D., Simon, D. A., Shohamy, D., & Daw, N. D. (2015). Model-based choices involve prospective neural activity. *Nature Neuroscience*, 18(5), 767–772.

Dragoi, G., & Tonegawa, S. (2011). Preplay of future place cell sequences by hippocampal cellular assemblies. *Nature*, 469(7330), 397–401.

Dragoi, G., & Tonegawa, S. (2013). Distinct preplay of multiple novel spatial experiences in the rat. *Proceedings of the National Academy of Sciences of the United States of America*, 110(22), 9100–9105.

Eichenbaum, H. (2013). Memory on time. *Trends in Cognitive Sciences*, 17(2), 81–88.

Eichenbaum, H. (2014). Time cells in the hippocampus: A new dimension for mapping memories. *Nature Reviews. Neuroscience*, 15(11), 732–744.

Eichenbaum, H. (2015). Does the hippocampus preplay memories? *Nature Neuroscience*, 18(12), 1701–1702.

Estes, W. K. (1955). Statistical theory of spontaneous recovery and regression. *Psychological Review*, 62(3), 145–154.

Folkerts, S., Rutishauser, U., & Howard, M. W. (2018). Human episodic memory retrieval is accompanied by a neural contiguity effect. *The Journal of Neuroscience*, 38, 4200–4211.

Gardumi, A., Ivanov, D., Hausfeld, L., Valente, G., Formisano, E., & Uludağ, K. (2016). The effect of spatial resolution on decoding accuracy in fMRI multivariate pattern analysis. *NeuroImage*, 132, 32–42.

Gordon, A. M., Rissman, J., Kiani, R., & Wagner, A. D. (2014). Cortical reinstatement mediates the relationship between content-specific encoding activity and subsequent recollection decisions. *Cerebral Cortex*, 24(12), 3350–3364.

Grosmark, A. D., & Buzsáki, G. (2016). Diversity in neural firing dynamics supports both rigid and learned hippocampal sequences. *Science*, 351(6280), 1440–1443.

Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, 98(7), 4259–4264.

Healey, M. K. (2018). Temporal contiguity in incidentally encoded memories. *Journal of Memory and Language*, 102, 28–40.

Healey, M. K., & Kahana, M. J. (2014). Is memory search governed by universal principles or idiosyncratic strategies? *Journal of Experimental Psychology: General*, *143*(2), 575–596.

Healey, M. K., Long, N. M., & Kahana, M. J. (2018). Contiguity in episodic memory. *Psychonomic Bulletin & Review*. https://doi.org/10.3758/s13423-018-1537-3.

Honey, C. J., Sporns, O., Cammoun, L., Gigandet, X., Thiran, J. P., Meuli, R., & Hagmann, P. (2009). Predicting human resting-state functional connectivity from structural connectivity. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(6), 2035–2040.

Howard, M., & Kahana, M. J. (1999). Contextual variability and serial position effects in free recall. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *25*(4), 923–941.

Howard, M. W., & Eichenbaum, H. (2013). The hippocampus, time, and memory across scales. *Journal of Experimental Psychology: General*, *142*(4), 1211–1230.

Howard, M. W., Kahana, M. J., & Sederberg, P. B. (2008). Postscript: Distinguishing between temporal context and short-term store. *Psychological Review*, *115*(4), 1125–1126.

Howard, M. W., MacDonald, C. J., Tiganj, Z., Shankar, K. H., Du, Q., Hasselmo, M. E., & Eichenbaum, H. (2014). A unified mathematical framework for coding time, space, and sequences in the hippocampal region. *Journal of Neuroscience*, *34*(13), 4692–4707.

Johnson, A., & Redish, A. D. (2007). Neural ensembles in CA3 transiently encode paths forward of the animal at a decision point. *The Journal of Neuroscience*, *27*(45), 12176–12189.

Johnson, J. D., & Rugg, M. D. (2007). Recollection and the reinstatement of encoding-related cortical activity. *Cerebral Cortex*, *17*(11), 2507–2515.

Jonides, J., Lewis, R. L., Nee, D. E., Lustig, C. A., Berman, M. G., & Moore, K. S. (2008). The mind and brain of short-term memory. *Annual Review of Psychology*, *59*, 193–224.

Josselyn, S. A., & Frankland, P. W. (2018). Memory allocation: Mechanisms and function. *Annual Review of Neuroscience*, *41*, 389–413.

Kahana, M., Aggarwal, E., & Phan, T. (2018). The variability puzzle in human memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *44*(12), 1857–1863.

Kahana, M. J. (1996). Associative retrieval processes in free recall. *Memory & Cognition*, *24*(1), 103–109.

Kahana, M. J. (2012). *Foundations of human memory*. New York, NY: Oxford University Press.

Kragel, J. E., Morton, N. W., & Polyn, S. M. (2015). Neural activity in the medial temporal lobe reveals the Fidelity of mental time travel. *The Journal of Neuroscience*, *35*(7), 2914–2926.

Kriegeskorte, N., Cusack, R., & Bandettini, P. (2010). How does an fMRI voxel sample the neuronal activity pattern: compact-kernel or complex spatiotemporal filter? *Neuroimage*, *49*(3), 1965–1976.

Loftus, G., & Masson, M. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review*, *1*(4), 476–490.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, *390*(6657), 279–281.

Mack, M. L., & Preston, A. R. (2016). Decisions about the past are guided by reinstatement of specific memories in the hippocampus and perirhinal cortex. *NeuroImage*, *127*, 144–157.

Madore, K. P., Addis, D. R., & Schacter, D. L. (2015). Creativity and memory: Effects of an episodic-specificity induction on divergent thinking. *Psychological Science*, *26*(9), 1461–1468.

Madore, K. P., Szpunar, K. K., Addis, D. R., & Schacter, D. L. (2016). Episodic specificity induction impacts activity in a core brain network during construction of imagined future experiences. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(38), 10696–10701.

Manning, J. R., Polyn, S. M., Baltuch, G. H., Litt, B., & Kahana, M. J. (2011). Oscillatory patterns in temporal lobe reveal context reinstatement during memory search. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(31), 12893–12897.

McCormick, C., Moscovitch, M., Valiante, T. A., Cohn, M., & McAndrews, M. P. (2017). Different neural routes to autobiographical memory recall in healthy people and individuals with left medial temporal lobe epilepsy. *Neuropsychologia*, *110*, 26–36.

McNaughton, B. L., Barnes, C. A., Gerrard, J. L., Gothard, K., Jung, M. W., Knierim, J. J., ... Suster, M. (1996). Deciphering the hippocampal polyglot: The hippocampus as a path integration system. *Journal of Experimental Biology*, *199*(1), 173–185.

Morris, C. D., Bransford, J. D., & Franks, J. J. (1977). Levels of processing versus transfer appropriate processing. *Journal of Verbal Learning and Verbal Behavior*, *16*(5), 519–533.

Mumford, J. A., Turner, B. O., Ashby, F. G., & Poldrack, R. A. (2012). Deconvolving BOLD activation in event-related designs for multivoxel pattern classification analyses. *NeuroImage*, *59*(3), 2636–2643.

Nadel, L., & Moscovitch, M. (1997). Memory consolidation, retrograde amnesia and the hippocampal complex. *Current Opinion in Neurobiology*, *7*(2), 217–227.

Op de Beeck, H. P. (2010). Against hyperacuity in brain reading: Spatial smoothing does not hurt multivariate fMRI analyses? *NeuroImage*, *49*(3), 1943–1948.

Otten, L. J., Quayle, A. H., Akram, S., Ditewig, T. A., & Rugg, M. D. (2006). Brain activity before an event predicts later recollection. *Nature Neuroscience*, *9*(4), 489–491.

Pfeiffer, B. E., & Foster, D. J. (2013). Hippocampal place-cell sequences depict future paths to remembered goals. *Nature*, *497*(7447), 74–79.

Polyn, S. M., & Kahana, M. J. (2008). Memory search and the neural representation of context. *Trends in Cognitive Sciences*, *12*(1), 24–30.

Polyn, S. M., Norman, K. A., & Kahana, M. J. (2009). A context maintenance and retrieval model of organizational processes in free recall. *Psychological Review*, *116*(1), 129–156.

Rissman, J., Gazzaley, A., & D'Esposito, M. (2004). Measuring functional connectivity during distinct stages of a cognitive task. *NeuroImage*, *23*(2), 752–763.

Ritchey, M., Wing, E. A., LaBar, K. S., & Cabeza, R. (2012). Neural similarity between encoding and retrieval is related to memory via hippocampal interactions. *Cerebral Cortex*, *23*(12), 2818–2828.

Rogerson, T., Cai, D. J., Frank, A., Sano, Y., Shobe, J., Lopez-Aranda, M. F., & Silva, A. J. (2014). Synaptic tagging during memory allocation. *Nature Reviews Neuroscience*, *15*(3), 157–169.

Sadeh, T., Maril, A., Bitan, T., & Goshen-Gottstein, Y. (2012). Putting Humpty together and pulling him apart: Accessing and unbinding the hippocampal item-context engram. *Neuroimage*, *60*(1), 808–817.

Sadeh, T., Moran, R., & Goshen-Gottstein, Y. (2015). When items 'pop into mind': variability in temporal-context reinstatement in free-recall. *Psychonomic bulletin & review*, *22*(3), 779–790.

Sederberg, P. B., Howard, M. W., & Kahana, M. J. (2008). A context-based theory of recency and contiguity in free recall. *Psychological Review*, *115*(4), 893–912.

Sekeres, M. J., Moscovitch, M., & Winocur, G. (2017). Mechanisms of memory consolidation and transformation. In N. Axmacher & B. Rasch (Eds.), *Cognitive neuroscience of memory consolidation* (pp. 17–44). New York: Springer.

Silva, D., Feng, T., & Foster, D. J. (2015). Trajectory events across hippocampal place cells require previous experience. *Nature Neuroscience*, *18*(12), 1772–1779.

Sirotin, Y., Kimball, D., & Kahana, M. (2005). Going beyond a single list: Modeling the effects of prior experience on episodic free recall. *Psychonomic Bulletin & Review*, *12*(5), 787–805.

Spreng, R. N., Mar, R. A., & Kim, A. S. (2009). The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: A quantitative meta-analysis. *Journal of Cognitive Neuroscience*, *21*(3), 489–510.

Staresina, B. P., Alink, A., Kriegeskorte, N., & Henson, R. N. (2013). Awake reactivation predicts memory in humans. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(52), 21159–21164.

St-Laurent, M., Moscovitch, M., & McAndrews, M. P. (2016). The retrieval of perceptual memory details depends on right hippocampal integrity and activation. *Cortex*, *84*, 15–33.

Sweeney-Reed, C. M., Zaehle, T., Voges, J., Schmitt, F. C., Buentjen, L., Kopitzki, K., ... Knight, R. T. (2016). Pre-stimulus thalamic theta power predicts human memory formation. *NeuroImage*, *138*, 100–108.

Teyler, T. J., & DiScenna, P. (1986). The hippocampal memory indexing theory. *Behavioral Neuroscience*, *100*(2), 147–154.

Tompary, A., Duncan, K., & Davachi, L. (2016). High-resolution investigation of memory-specific reinstatement in the hippocampus and perirhinal cortex. *Hippocampus*, *26*, 995–1007.

Tulving, E. (1983). *Elements of episodic memory*. New York: Oxford University Press.

Tulving, E., & Thomson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review*, *80* (5), 352–373.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., … Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *NeuroImage*, *15*, 273–289.

Wimber, M., Alink, A., Charest, I., Kriegeskorte, N., & Anderson, M. C. (2015). Retrieval induces adaptive forgetting of competing memories via cortical pattern suppression. *Nature Neuroscience*, *18*(4), 582–589.

Wing, E. A., Ritchey, M., & Cabeza, R. (2015). Reinstatement of individual past events revealed by the similarity of distributed activation patterns during encoding and retrieval. *Journal of cognitive neuroscience*, *27*(4), 679–691.

Zaromb, F. M., Howard, M. W., Dolan, E. D., Sirotin, Y. B., Tully, M., Wingfield, A., & Kahana, M. J. (2006). Temporal associations and prior-list intrusions in free recall. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *32*(4), 792.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.