Study-Phase Reinstatement: Encoding Spontaneous Thoughts as Memories

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Abstract

Can the brain improve the retrievability of an experience after it has occurred? Systems consolidation theory proposes that cortical reactivation during extended post-encoding rest periods facilitates the formation of stable memory representations, a prediction supported by neural evidence in humans [1, 2] and animals [3, 4]. Such reactivation may also occur on short time scales as spontaneous thoughts come to mind during encoding, offering a potential account of classic list memory phenomena [5–9] but lacking in support from neural data. Leveraging the high-temporal specificity of intracranial electroencephalography (iEEG), we investigate spontaneous reactivation of previously experienced items during brief sub-second intervals between individual encoding events. Across two large-scale free recall experiments, we show that reactivation, as measured by spectral iEEG similarity, during these periods predicts subsequent recall. In a third experiment, we show that the same methodology can identify post-encoding reactivation that correlates with subsequent memory, consistent with previous results. Thus, spontaneous study-phase reinstatement reliably predicts memory behavior, linking

psychological accounts to neural mechanisms and providing the first such evidence for rapid consolidation processes during encoding.

Keywords: Memory, Reinstatement, intracranial EEG, Psychology, Neuroscience

1 Introduction

Recent evidence from functional magnetic resonance imaging (fMRI) and intracranial electroencephalography (iEEG) suggests that spontaneous neural reactivation of specific previously encoded content during sleep or awake rest predicts subsequent recognition [10], cued recall [1, 2] and reconstruction [11] of that content. Theoretically, neuroscientific two-stage models of memory [12, 13] propose that reactivation during post-encoding rest periods improves memory via a consolidation mechanism that turns fragile hippocampal memories into stable cortical representations. Consolidation can be a spontaneous process, happening even or especially without cues from the external environment. Psychological theories of memory encoding [e.g. 5–7, 14] and data on overt rehearsal [15–25] suggest that reactivation during or between encoding other experiences also determines subsequent recall probability and organization.

If the psychological construct of rehearsal, covert repetition of previously encoded items, is a type of consolidation, this implies that consolidation-like processes may actually be happening during a broader range of time periods and shorter time scales than previously studied. Indeed, the possibility of more frequent or opportunistic consolidation periods has been recognized by some theorists [26, 27] but the consensus in the field appears to be that sleep or rest remain special times for consolidation [12, 13, 28, 29] and thus the existing neural evidence for reactivation involves these time periods. Recent work suggests that the brain can transition rapidly between "online" externally-driven states and "offline" consolidation-promoting states on the time-scale of seconds [30, 31] but no study to date has been able to link this to reinstatement of content. It therefore remains unknown whether such rapid, spontaneous item-specific neural reinstatement during a study phase predicts subsequent recall much as reinstatement during post-encoding periods does. Furthermore, it is unclear whether neural measurements of reinstatement play the same role in memory that the psychological construct of rehearsal does. In addition to the overall amount of rehearsal correlating with recall probability, work on overt rehearsal demonstrates that rehearsal predicts output order (more rehearsal predicts earlier recall [15]) and organization (items rehearsed together are also recalled together [24]). The present work leverages the high temporal precision of intracranial EEG and three large-scale free recall experiments to address these gaps in our knowledge.

Some neuroscientific studies have investigated reactivation correlates of instructed rehearsal. Fellner and colleagues [32], using a directed forgetting paradigm, showed that activity after the forgetting cue showed greater reinstatement on to-be-remembered trials that were later remembered relative to to-be-forgotten trials. The authors therefore interpreted this reinstatement as corresponding to deliberate rehearsal. In addition, Bird et al. [33] instructed participants to rehearse previously

seen videos when cued with the video title while in an fMRI scanner. They showed that the degree of reinstatement during these rehearsal periods correlated with subsequent memory for video details. However, neither of these directed rehearsal experiments investigated reinstatement signatures of *spontaneous* rehearsal.

Additionally, a number of recent studies have shown that neural pattern similarity of two repeated item presentations predicts subsequent memory for those items [34–37] and have argued that this is an index of covert study-phase retrieval of previous presentations. The spacing effect [38–40], the finding that repetition is more effective for memory when repetitions are spaced out, has been a key source of behavioral evidence for study-phase retrieval [6, 8]. Feng and colleagues [41] show that the degree of reinstatement depends on whether the repetitions are massed or spaced. However, reinstatement in these studies is not spontaneous as it is cued by the presentation of a repeated item.

In what may be the most direct evidence for spontaneous study-phase reinstatement, Wu and colleagues [42, 43] investigated how reactivation during a delay period immediately following the presentation of a sequence of images affected subsequent memory for details of the sequence. In one experiment with semantically coherent sequences, they found that the degree of reinstatement of images in the sequence differed between sequences where subjects recalled an above average or below average number of details in a subsequent cued recall test. In contrast, there was no similar effect when sequences were not coherent, leading Wu et al. to conclude that people reinstate sequences during a study phase to extract higher-level semantic information. Unlike the current study, Wu and colleagues did not investigate whether reinstatement of specific images led to improved memory for that specific image. Thus the reinstatement they found could represent a reinstatement of the entire list context leaving open the question of whether item-specific study-phase reinstatement predicts future memory.

In the following work, we ask whether spontaneous reinstatement during a study phase can impact future memory behavior, as suggested by psychological explanations of memory behavior. These theories suggest that, in addition to externally-driven perceptual experiences being encoded in memory, internally-driven thoughts, reminders, retrieved memories and imagined scenarios can themselves become encoded in memory, greatly expanding the role of neural reactivation beyond that examined in previous studies. We use two two large, independent data sets with intracranial EEG to relate the degree of spontaneous item-specific reinstatement while encoding other experiences (study-phase reinstatement) to subsequent recall probability and organization for that item. In a separate third dataset using the same methodological approach, we ask whether we observe similar reinstatement during an unfilled delay interval between the initial encoding period and later recall, as in previous studies of reactivation. Overall, these analyses aim to answer the question of whether study-phase reinstatement performs a similar role in memory behavior as past studies of post-encoding reinstatement.

2 Results

All three data sets we analyzed involved intracranial EEG recorded during variations on free recall tasks (see Figures 1 and 4). Subjects studied twelve words and, following a brief delay, attempted to recall as many as they could remember. In Experiments 1 and 2, subjects performed a math distractor task during the delay interval; in Experiment 3, the interval remained unfilled. In experiment three, some words repeated two or three times in the same list, resulting in 27 word presentations in total during the encoding interval. In experiment one, words on the list were drawn from three semantic categories while in the other two experiments, words were drawn at random from a wordpool. In all other respects, the three experiments did not differ, providing the opportunity to replicate our key results several times. Neurosurgical patients performed all three experiments while intracranial EEG was being recorded. These neural recordings provide the basis for identifying latent spontaneous reinstatement

We used a spectral representational similarity analysis (RSA) [44–48] approach to studying reinstatement. This method compares a representation of the neural signals at two time points and allows us to asses the degree of similarity tbetween the neural representations. We first decomposed the neural signals from each bipolar pair of electrodes into power in eight log-spaced frequency bands. We then compute the z-transformed [49] Pearson correlation between the signals at the two time points across all electrodes and frequencies. This correlation measure is our dependent metric of reinstatement in the following analyses.

2.1 Semantic pattern similarity

We first validate our RSA-based [44–46] approach by examining the degree to which time and semantic content determined spectral power similarity during the encoding periods in Experiment 1. Our future analyses, aimed at detecting item reactivation during inter-stimulus intervals, rely on the neural patterns representing the semantic content of the items. This experiment provides an ideal setting to investigate this because lists comprised items from three different categories. By comparing the similarity of items from the same category to items from different categories, we can determine whether semantic content drives spectral pattern similarity. Figure 2 shows the correlation between the spectral power representations at two encoding time points on the same list as a function of their absolute serial position difference and whether or not the words come from the same semantic category. The dominant effect on pattern similarity is distance in time (as represented by an item's serial position). However, semantics additionally determines a component of similarity as items from the same category are more similar than items from different categories across all serial position distances. These analyses conceptually replicate effects demonstrated in [47] and [48], using a different data set and method. In addition, [50] demonstrated an ability to predict serial position and semantic category using the same spectral power components using a subset of 69 subjects from the current dataset. However, neither of those papers demonstrates these two effects simultaneously in the same neural signals, as shown here. Finally, a key difference between our analyses and past work using intracranial EEG (including the papers previously mentioned as well as [10]) is

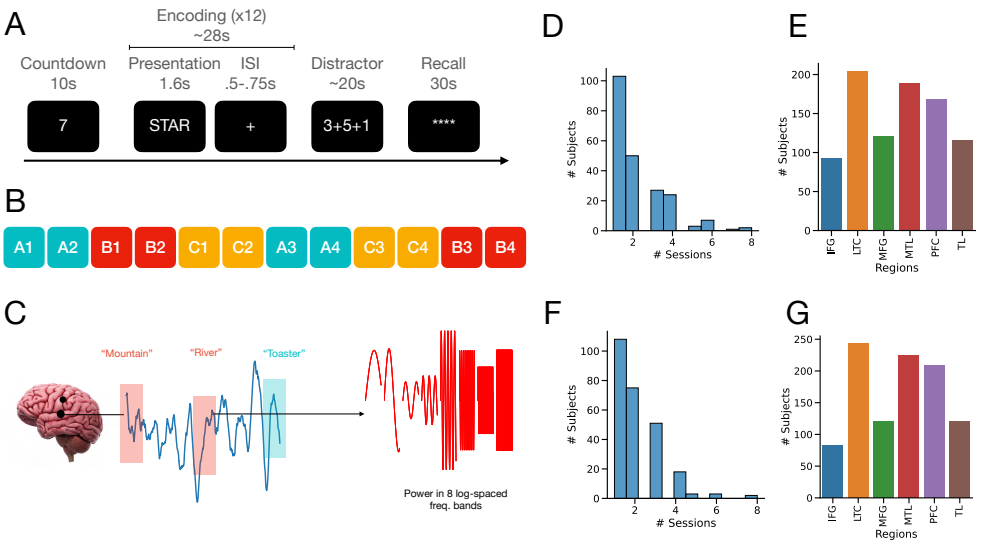

Fig. 1 Experimental tasks and methods for experiments 1 and 2. A. Timeline for a single trial of free recall. Following a ten second countdown, twelve words appear sequentially on screen for 1.6 seconds each with .5 to .75 second inter-stimulus intervals. Following this encoding period, subjects perform twenty second math distractor task in order to prevent rehearsal. Finally, during the recall period, subjects have 30 seconds to recall as many words as possible. B. Category structure of experiment 1 on a given twelve word list. Four words are drawn from three categories and presented in a block structure as shown. C. Methods used for constructing spectral features. EEG signals are taken each electrode from specific time period, e.g., while a word is on the screen and then decomposed into power in 8 log-spaced frequency bands. They are then compared to this spectral representation at other time points, e.g., during the inter-stimulus interval. D. Number of sessions collected per subject in experiment 1. E. Number of subjects with electrodes in each region for experiment 1. F. Number of sessions collected per subject in experiment 2. G. Number of subjects with electrodes in each region for experiment 2.

that we did not perform any selection of electrodes or time points prior to analyzing pattern similarity.

To test these differences statistically, we fit a mixed effect model predicting the pattern similarity between signals associated with two items as a function of whether the items were from the same category and the temporal distance between the items in terms of serial position. In this model and all other models we fit, we also included varying intercepts and slopes as a function of subject, session, list and the serial positions of the two items as well as their interactions. Because the large number of random effects could lead to overfitting, we reduced the model iteratively to account for the structure present in the data using the procedure from [51]. The full model is described in detail in the *Methods* section. We found significant main effects of serial position distance ($F(1, 88.62) = 151.65, p \leq 0.001$) and the two items being from the same category (($F(1, 3.03) = 20.93, p = 0.02$). We did not find a significant interaction between the two ($F(1, 22.31) = 1.72, p = .2$). Examining the point estimates, we found

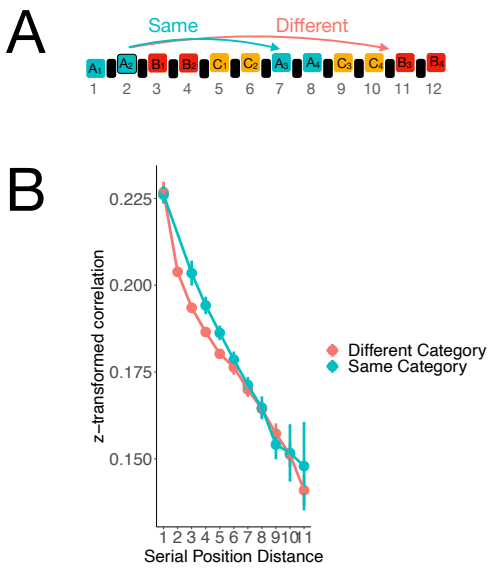

Fig. 2 Similarity of two time points during encoding word presentations on the same list as a function of the absolute serial position distance and whether the two words came from the same category or not. Because of the constraints on list order in the experimental design, it was impossible for words from the same category to appear at a distance of two serial positions away. A. Schematic of comparison, indicating which items are from the same category and which are not. B. Similarity computed from experiment 1. Error bars reflect variation within list using an approach similar to [52]

that, as expected, similarity decreases as a function of temporal distance and increases if the items are from the same category.

2.2 Study-phase reinstatement

Having (1) validated the pattern similarity measure during encoding and (2) replicated prior context reinstatement results, we now use the same measure to examine study-phase reinstatement. For this analysis, we investigate whether neural patterns associated with a particular encoded item reactivate during the inter-stimulus intervals following future items on the list. We compared patterns of spectral power between item presentations (during the 500-750ms ISI period, the *ISI*) with power while a word was presented on the screen (the *initial encoding presentation*). Figure 3 shows similarity as a function of whether the initially presented word was itself subsequently recalled (**Recalled**), whether the word prior to the ISI was recalled and whether the two words were from the same category. We include these variables in the analysis because we would expect that both of these variables would increase similarity between the initial encoding presentation and the ISI even without spontaneous reinstatement. Qualitatively, we find that similarity increases when the encoded item was subsequently recalled, regardless of the values of the other two variables. We additionally examined whether reinstatement differed as a function of recall organization in two ways, based on results from the overt rehearsal literature [15, 24]. First, we would expect a greater degree of reinstatement for the first recalled item than items recalled

later. Second, we would expect that the degree of reinstatement during a particular ISI would predict the strength of associations between the item before the ISI and the reinstated item and therefore the likelihood that items will later be recalled sequentially. To test these differences statistically in experiment 1, we used a mixed effects model in `lme4` [53] with the following specification for the fixed effects:

$$\texttt{similarity} \sim (\texttt{item_recalled} + \texttt{item_first}) * \texttt{item_before_isi_recalled} * \texttt{same_category} \\ + \texttt{recall_neighbor} + \texttt{recall_neighbor} : \texttt{same_category}$$

`item_recalled` and `item_first` reflect whether the specific item was recalled and whether it was recalled first. `item_before_isi_recalled` indicates whether the item before the ISI was recalled and `same_category` indicates that the initial encoding item and the item before the ISI are drawn from the same category. Finally, `recall_neighbor` indicates whether the encoding item and the item before the ISI were recalled next to each other during the recall period, given that both items were recalled. The model has varying intercepts and slopes for each term as a function of nested grouping variables subject, session, list and the serial positions of both the encoded item and the item before the ISI. In addition, the model included random effects for across-subject effects of list ID, serial positions of the encoded item and the ISI and the interaction between the pair of serial positions. For experiment 2, we used the same model but without the terms involving `same_category` because items in this experiment were randomly sampled from a common wordpool.

Given the results from our first analysis, it is likely that the effects of recency and categorical similarity drive much of pattern similarity. To focus on spontaneous reinstatement, we therefore limit the analyses to pattern similarity comparisons involving initial encoding presentations from the first half of the list (the first six serial positions) and ISIs from the latter half (the five intervals between the last six serial positions). In the case of Experiment 1, we also ensured that there was at least one category pair between the initial encoded item and the comparison ISI. This ensures that any observed reactivation is unlikely to be due to recency and similarity alone.

In Experiment 1, we found a main effect of `item_recalled` such that items that were subsequently recalled were more similar to activity during subsequent ISIs during encoding than items that were not subsequently recalled (Fig. 3, $F(1, 15.5) = 13.66, p = .002$). Post-hoc comparisons revealed significant effects of recall status, regardless of whether the item before the ISI was from the same category or was itself recalled. However, we could not reliably identify whether the items recalled first had consistently different levels of reactivation than other recalled items ($F(1, 52.2) = 1.43, p = .24$). we also did not see consistent differences between items that were sequentially recalled and pairs of items that were both recalled but not sequentially ($F(1, 16.4) = 0.01, p = .94$). Additionally, we find that the recall status of the item before the ISI is a consistently positive predictor of similarity ($F(1, 11.2) = 5.43, p = .04$), indicating that some component of the similarity may be due to cognitive processes that occur when viewing items that subjects subsequently

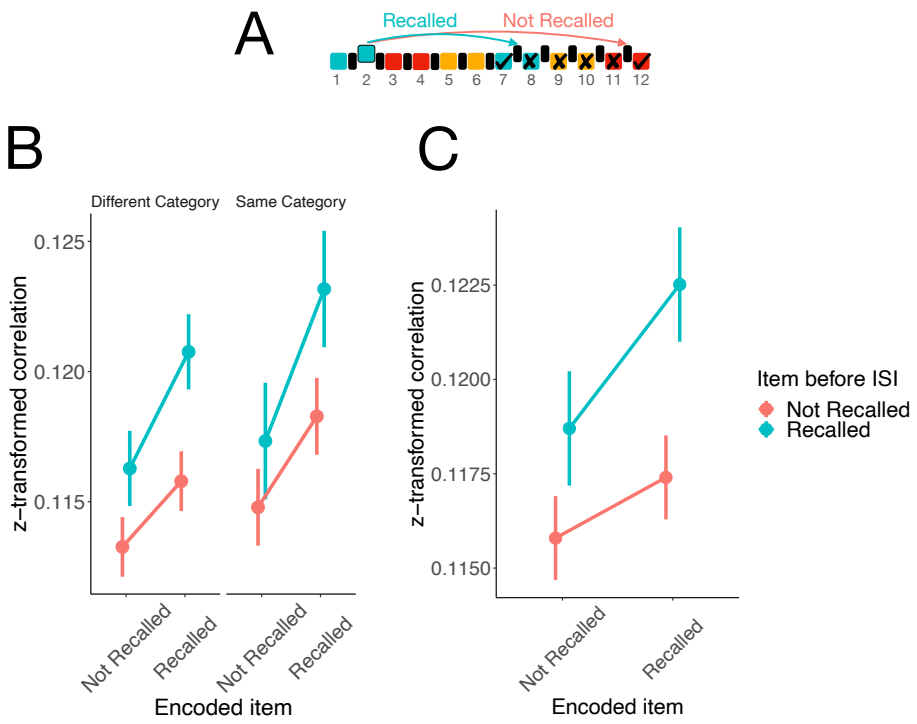

Fig. 3 Similarity of time points during encoding word presentations and time points during inter-item intervals as a function of whether the word was itself subsequently recalled (**Recalled**) Estimates are derived from the mixed effect model described in the main text. Error bars reflect 95% confidence intervals on the difference between remembered and forgotten, using an algorithm implemented by the R package `emmeans` and described in [54] that is a generalization of Loftus-Masson intervals [55, 56]. A. Schematic showing time points being compared when computing RSA, encoding time point from first half of list and inter-stimulus interval from second half. Checks and crosses indicate whether the item was subsequently recalled and colors indicate category, indicating the relevant control variables. B. results from experiment 1. C. results from experiment 2.

recall. However, two items being from the same category is not a significant predictor ($F(1, 25.5) = 1.12, p = .3$), although, as can be seen in figure 3, the estimates of the difference between recalled and not recalled are positive, the direction we would predict.

We fit the same model to Experiment 2, dropping the terms involving `same_category`. We replicated the main effect of subsequent recall on study-phase spectral pattern similarity, i.e. items with more similar activity during subsequent ISIs during encoding than items that were not subsequently recalled (Fig. 3, $F(1, 12.74) = 6.39, p = .02$). In a post-hoc comparison, we could not establish a reliable difference when the item before the ISI was itself recalled ($\beta = .01, t(10) = 1.6, p = .14$). However, the estimates were positive qualitatively, replicating the results from Experiment 1. In addition, the interaction between recall status of the encoding item and the item before the ISI was only marginally significant, ($F(1, 11.43) = 3.29, p = .1$),

suggesting that we cannot reliably determine whether the specific pairwise comparison is different from the overall main effect. Again, we could not establish the direction of effects of first recall ($F(1, 52.2) = 1.43, p = .24$) or being a recall neighbor ($F(1, 13.36) = .67, p = .43$) on pattern similarity. Replicating results from Experiment 1, we find a main effect of the recall status of the item before the ISI ($F(1, 45.4) = 8.0, p = .007$).

2.3 Post-encoding reinstatement

Having identified study-phase reinstatement in two experiments, we sought to confirm that similar methods could identify the previously found post-encoding reinstatement. Therefore, in a third experiment, we investigated pattern similarity between initial encoding presentations and a subsequent unfilled 7s delay interval prior to recall. To test differences statistically, we fit the following statistical model:

$$\texttt{similarity} \sim (\texttt{item_recalled} + \texttt{item_first}) * \texttt{serial_position}$$

In addition to predicting reinstatement as a function of recall status, this model allowed for interactions with serial position in order to test the possibility that earlier serial positions showed greater effects of reinstatement, as suggested by the literature on overt rehearsal [25]. This analysis conceptually replicates past work on reinstatement (such as [2] and [42]) but applied to individual lists in a free recall task. As in the analyses of the inter-stimulus intervals, we find a main effect of recall status such that remembered items are more similar to the delay interval than forgotten items ($F(1, 28.43) = 30.12, p \leq .001$. We additionally find a main effect of serial position ($F(1, 53.12) = 110.75, p \leq .001$) but do not find any interactions between the recall effect and serial position ($F(1, 2603) = 1.12, p = .29$). As before, we do not find any reliable differences between first recalls and other recalls ($F(1, 18.36) = 1.57, p = .23$) or any interaction with serial position ($F(1, 17.65) = .11, p = .74$).

3 Discussion

Three separate experiments involving intracranial EEG recordings from large samples reveal that subsequently recalled items reinstate during unfilled intervals to a greater degree than forgotten items. In the first two experiments, these intervals occurred between study opportunities, a time period not investigated in past work on reinstatement and yet one that figures prominently in psychological theorizing and data on rehearsal processes. In addition, reinstatement effects were item-specific and relevant for recall of a specific list, even in an experimental context where there were several lists.

Overt rehearsal studies show that when subjects rehearse items together they also recall them together [24]. Similarly, subjects tend to recall items they rehearsed more earlier in their output [15]. Here, we consider the possibility that study-phase reinstatement and rehearsal measure similar processes. The above results make two key predictions. First, finding greater study-phase reinstatement of an item from an earlier

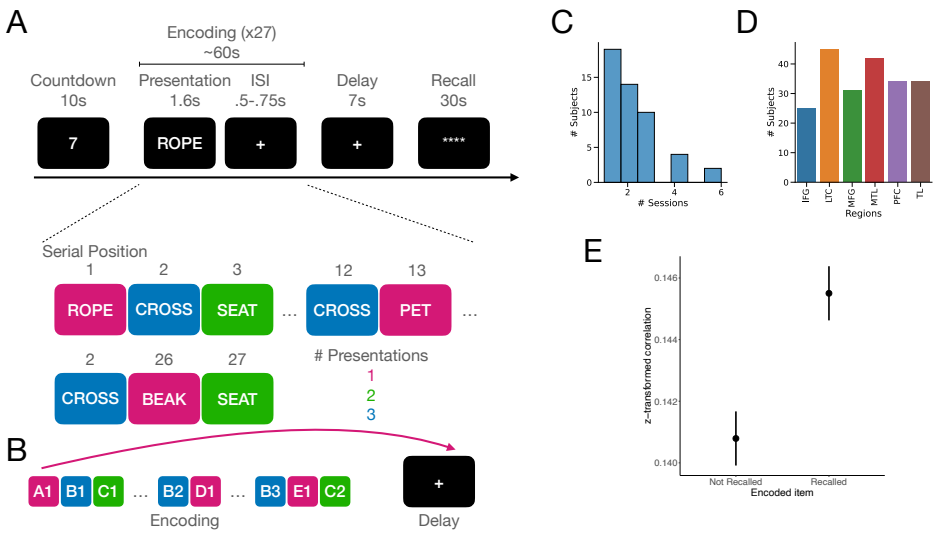

Fig. 4 A. Task design for Experiment 3. Task is similar to Experiments 1 and 2 except that lists include repeated items (some of which are presented twice and some presented three times) and the distractor task is replaced with an unfilled seven second delay interval. B. Schematic of comparisons used in analysis in panel E. C. Distribution of sessions across subjects. D. Number of subjects with electrodes in each memory-related region. E. Similarity of time points during encoding word presentations and time points during a delay period as a function of whether the word was itself subsequently recalled (**Recalled**). Estimates are derived from the mixed effect model described in the main text. Error bars reflect error bars of the difference between remembered and forgotten, using an algorithm implemented by the R package `emmeans` and described in [54] that is a generalization of Loftus-Masson intervals [55, 56].

list position in the inter-stimulus interval immediately following a later item should increase the likelihood of those two items being successively recalled (as compared with being recalled in non-sequential output positions). Second, items with greater reinstatement should be more likely to be recalled first. However, we failed to find reliable evidence for either of these effect. One possibility is that this indicates a difference between overt rehearsal and the covert rehearsal processes signaled by our measures of neural reinstatement. However, another possibility is that detecting such effects requires a high degree of precision relative to reinstatement effects on overall recall probability. This is due to the organization effects making predictions about specific inter-stimulus intervals rather than integrated over all ISIs throughout the learning period.

In seeking theoretical models of behavioral memory data, psychologists have frequently turned to study-phase retrieval as an explanatory construct [5–7, 9, 14, 57]. This has been used to explain why reliable false memory effects exist [58] as well as why rehearsal, repetitions, repeated testing or even presentations of similar items can improve memory for a past experience. While theoretically compelling, it remains challenging to obtain direct evidence for study-phase retrieval because of the lack of corresponding overt behavioral correlates. Here, we provide evidence of a potential

neural foundation for such retrieval processes, both bolstering such claims and also allowing for future work to investigate specific predictions in more detail. This work also broadens the scope of previous work on neural reactivation and its effects on subsequent memory to include time periods during encoding events, rather than only potential consolidation periods.

How can we be confident that the reinstatement effects we uncovered reflect true spontaneous reactivation? In the analyses of study-phase reinstatement, one potential issue is that activity driven by the item prior to the inter-stimulus interval could carry over into the delay period. This activity could be similar to prior items for two reasons unrelated to spontaneous reactivation. One reason is that semantically similar items will have more similar neural representations than different ones [59]. Semantic similarity effects [60] imply that the probability of recalling an item increases when semantically similar items are also recalled. Thus, strong semantic representations of the item prior to the ISI could predict greater recall probabilities. A second reason is that similar cognitive processes are involved in processing the item. Subsequent memory effects [61–64] show that neural activity when viewing stimuli that will be recalled consistently differ from neural activity during forgotten stimuli. Thus, the similarity of neural responses to an item and other recalled items on a list should predict the item's probability of recall. To handle both of these potential confounds, we include terms in the model for whether the item before the ISI was itself recalled and, in the case of Experiment 1, whether it is from the same category as the earlier item. We show that the difference in reactivation exists even in the case where the item before the ISI was not recalled and from a different category in the case of Experiment 1. In Experiment 2, the pairwise comparison when the item before the ISI is not recalled is marginally significant and in the same direction as all of the other pairwise comparisons. In addition, the interaction between the recall status of the encoded item and the item before the ISI is not significant in an analysis of variance, suggesting that there is not reliable evidence for a difference in effects depending on whether the item before the ISI is recalled. Thus, we conclude that our findings likely reflect spontaneous reactivation.

Our results provide consistent evidence across multiple large studies for a relation between spontaneous, sub-second, study-phase reinstatement and subsequent recall. Whereas intracranial EEG recordings provide high spatial and temporal precision, there is frequently little overlap in electrode locations across patients. To maximize the inclusion of electrodes and measure the similarity of neural activity across as wide of a span of cortex as possible, we include all available electrodes in our representational similarity analyses. However, this makes it difficult to investigate in great detail the anatomical substrates of such reactivation and their consistency across people. We therefore leave this investigation to future work, either with more regionally specific data sets or using recording methodologies that allow for broad coverage and alignment across subjects (e.g. fMRI). As shown in Figures 1E and G and 4D, many subjects have at least one electrode in regions thought to be relevant for memory. In this work, we focused on a single memory task with relatively short study-test delays. While this allowed us to easily test generalization across variants of this task (with surprisingly close quantitative estimates in figures 3B and C), one may ask whether the effects

here generalize to the longer time scales studied in studies involving sleep [1, 11]. Although we demonstrate covert reactivation within the short interstimulus intervals and we measure recall following a 30 second filled distractor period, the effects of study-phase reactivation may be different after hours or days. Future research examining the relation between sub-second covert reactivation and longer term retrieval will be required a more complete understanding of the relation between rapid consolidation and consolidation over longer periods.

The present findings show that covertly and spontaneously reactivated neural traces while encoding other experiences predict future memory. This provides direct electrophysiological evidence for cognitive theories which posit such latent retrieval as a fundamental mechanism of human (and animal) learning. That we can observe the memorial consequences of study-phase reactivation suggests that the process of memory consolidation, hypothesized to underlie the formation of long-term memory representations, is a much more general phenomenon than many previously thought. Indeed, it likely occurs throughout awake experience with rapid switches between externally- and internally-focused cognitive states. While several theorists have previously suggested this opportunistic view on consolidation and reinstatement [26, 27, 31], this work provides the first direct neural evidence. Many open questions remain about the psychological and neural mechanisms. If the measured reinstatement corresponds to rehearsal processes, to what extent is it under cognitive control? Can rehearsal and reinstatement be targeted in a way to optimize for goal-directed behavior [11, 65]? And if this is the same process as consolidation during longer rest and sleep periods, are the physiological mechanisms are the same? Although there are several possibilities that may operate on different time scales [26], future work will have to determine whether the behavioral consequences of consolidation depend on the neural process or whether they are functionally equivalent. With this ability to directly measure these processes with neural data, we can now begin to answer these questions and many others. Overall, identifying the connection between neural consolidation processes and psychological constructs developed to explain behavioral data will allow for a tighter link in theory development across cognitive and neural levels of analysis, a central goal of the cognitive neuroscience of memory.

4 Methods

4.1 Task and participants

In Experiment 1, we recorded intracranial EEG from 217 neurosurgical patients while they performed a categorized free-recall task [66]. Lists consisted of 12 items, presented in same-category pairs, from three distinct categories with categories drawn from total set of 25. Presentation of words during encoding was followed by a 20s post-encoding delay, during which subjects performed an arithmetic task in order to disrupt memory for end-of-list items (Fig. 2). Finally, subjects attempted to freely recall as many words as possible during a 30 second interval.

In experiment 2, we collected EEG from 260 neurosurgical patients while they performed a standard free-recall task. Lists consisted of 12 items selected so that the average pairwise semantic similarity based on latent semantic analysis [67, 68] was

.2. Presentation of words during encoding was followed by a 20s post-encoding delay, during which subjects performed an arithmetic task in order to disrupt memory for end-of-list items (Fig. 2). As in Experiment 1, subjects then attempted to freely recall as many words as possible during a 30 second interval.

In Experiment 3, we collected EEG from 49 neurosurgical patients while they performed a free-recall task with repeated items. Lists consisted of 12 unique items and used the same wordpool as Experiment 2. However, 3 items were repeated twice and six items were repeated three times resulting in twenty-seven total encoding presentations per list. Presentation of words during encoding was followed by a 7s unfilled post-encoding delay. As the previous experiments, subjects then attempted to freely recall as many words as possible during a 30 second interval.

4.2 Intracranial EEG

As described in [66], we recorded from subdural grids and strips (space between adjacent contacts: 10 mm) and from depth electrodes (space between adjacent contacts: 5–10 mm) on a variety of recording systems across clinical sites with sampling rates varying between 500 and 2000 Hz to accommodate the local recording environment. We rereferenced all recordings using a bipolar referencing scheme [69] and applied a 4th order Butterworth filter with a 58-62 Hz stop-band to remove line noise. We then Fourier resampled the data to 1000 Hz and convolved the resulting signals with Morlet wavelets (wave number 5; 8 center frequencies, log-spaced between 3 and 180 Hz) to obtain a representation of spectral power in each bipolar pair. For the analysis of encoding data, we averaged power over the entire 1600 (15-1575) ms stimulus presentation interval. For analysis of the intra-stimulus intervals, we use the same approach but for the 500ms interval immediately preceding the presentation of the subsequent stimulus. For the analysis of the delay interval data in Experiment 3, we first preprocess all 7 seconds using the same approach as above. We then divide it into 7 one second bins and average over the 1 second, using a resampling technique (cite PTSA). For analyses presented here, we then average over the 1 second bins. In order to compare activity across periods and subjects, we normalize all data relative to spectral signals collected during the 10 second countdown period prior to each list. We first preprocess the 10 seconds using the same approach as above. We then divide it into 10 one second bins and average over the 1 second, using a resampling technique (cite PTSA). We then compute the mean and standard deviation across lists for each session. All spectral power estimates in subsequent periods are then normalized by subtracting the countdown mean and dividing by the countdown standard deviation.

4.3 Analysis

Our main analysis approach relies on analyzing the similarity of spectral power patterns [44–46] in the eight frequency bands across all bipolar pairs, regardless of location in the brain. As is common in the literature, similarity was determined as the Fisher's z-transformed Pearson correlation [49] between power at two time points.

4.4 Modeling

For all models, we use mixed effect models to account for systematic variation unrelated to our effects of interest, as well as variability in these effects across the population and task structure.

In our first model, we test whether pattern similarity between two word presentations at encoding is driven by both semantic and temporal distance. We allow these effects to vary by subject, session, list and serial position. The full model that we fit, as specified in `lme4`, is:

$$\begin{aligned}\texttt{similarity} \sim & \texttt{same_category} * \texttt{absolute_serial_position_distance} + \\ & (\cdot|\texttt{subject}) + \\ & (\cdot|\texttt{subject} : \texttt{session}) + \\ & (\cdot|\texttt{subject} : \texttt{session} : \texttt{list}) + \\ & (\cdot|\texttt{subject} : \texttt{session} : \texttt{list} : \texttt{serial_position_1}) + \\ & (\cdot|\texttt{subject} : \texttt{session} : \texttt{list} : \texttt{serial_position_2}) + \\ & (\cdot|\texttt{list}) + \\ & (\texttt{same_category}|\texttt{serial_position_1}) + \\ & (\texttt{same_category}|\texttt{serial_position_2}) + \\ & (\texttt{same_category}|\texttt{serial_position_1} : \texttt{serial_position_2})\end{aligned} \tag{1}$$

where `same_category` indicates that the two items are from the same category and `absolute_serial_position_distance` indicates the distance in terms of serial positions between the two items as a linear effect. The dot $(\cdot)$ indicates that all terms vary as a function of that random effect grouping variable. `list` indicates the list position within the session (from 1 to 25) and `serial_position_1` indicates the earlier serial position in the pair while `serial_position_2` indicates the later one.

In the second set of models, we test whether pattern similarity between a word presentation and a later inter-stimulus interval at encoding is driven by whether the initial word was recalled, whether it was recalled first and whether it was recalled next to the item before the ISI. We also adjust for potential effects and interactions with semantic similarity and whether the item before the ISI was itself recalled. We again allow these effects to vary by subject, session, list and serial position. The full model that we fit, as specified in `lme4`, is:

$$\begin{aligned}\texttt{similarity} \sim & (\texttt{item_recalled} + \texttt{item_first}) * \texttt{item_before_isi_recalled} * \texttt{same_category} \\ & + \texttt{recall_neighbor} + \texttt{recall_neighbor} : \texttt{same_category} + \\ & (\cdot|\texttt{subject}) + \\ & (\cdot|\texttt{subject} : \texttt{session}) + \\ & (\cdot|\texttt{subject} : \texttt{session} : \texttt{list}) +\end{aligned} \tag{2}$$

$$
\begin{aligned}
&(\cdot|\texttt{subject}:\texttt{session}:\texttt{list}:\texttt{serial_position})+\\
&(\cdot|\texttt{subject}:\texttt{session}:\texttt{list}:\texttt{serial_position_isi})+\\
&(\cdot|\texttt{list})+\\
&(\cdot|\texttt{serial_position})+\\
&(\cdot|\texttt{serial_position_isi})+\\
&(\cdot|\texttt{serial_position}:\texttt{serial_position_isi})
\end{aligned}
$$

`item_recalled` and `item_first` reflect whether the specific item was recalled and whether it was recalled first. `item_before_isi_recalled` indicates whether the item before the isi was recalled and `same_category` indicates that the initial encoding item and the item before the ISI are from the same category. Finally, `recall_neighbor` indicates that, if both items were recalled, whether they were recalled next to each other during the recall period. The dot $(\cdot)$ indicates that all terms vary as a function of that random effect grouping variable. `serial_position` indicates the serial position of the initial presentation while `serial_position_isi` indicates serial position preceding the ISI.

In the final set of models, we examine the degree to which items that are subsequently recalled are reinstated during a delay interval between the encoding phase and the test phase. To test this, allowing for potential interactions with serial position, we use the following specification:

$$
\begin{aligned}
\texttt{similarity} \sim &(\texttt{item_recalled}+\texttt{item_first})*\texttt{serial_position}+ \qquad (3)\\
&(\cdot|\texttt{subject})+\\
&(\cdot|\texttt{subject}:\texttt{session})+\\
&(\cdot|\texttt{subject}:\texttt{session}:\texttt{list})+\\
&(\texttt{item_recalled}+\texttt{item_first}|\texttt{subject}:\texttt{session}:\texttt{serial_position})+\\
&(\cdot|\texttt{list})+\\
&(\texttt{item_recalled}+\texttt{item_first}|\texttt{serial_position})
\end{aligned}
$$

This model captures serial position effects with a continuous fixed effect as well as random effects for each serial position that allow for deviations from linear effects.

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