Selective memory retrieval revealed by electroencephalographic (EEG) neural pattern reinstatement

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Keywords: Episodic memory, Recollection, EEG, Neural Pattern Reinstatement, Pre-retrieval Control

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1. Abstract

For past experiences to guide our actions we need to retrieve the relevant memories. Here, we used electroencephalography (EEG) to investigate how memories are selected for retrieval from a large store of mnemonic traces, and to test how current goals and external retrieval cues drive selection during the retrieval cascade. We analysed data from two studies in which people studied objects in picture or auditory word formats, and later recalled them using either written words (Experiment 1, N=28) or line drawings (Experiment 2, N=28) as retrieval cues. We used multivariate decoding to quantify the reinstatement of study phase neural patterns when people successfully identified items that had been studied in the format currently designated as targets, versus non-targeted items. Neural reinstatement emerged at around 500 ms post-stimulus, as did the established left parietal event-related potential (ERP) signature of recollection. Reinstatement was also target-selective (greater for targets than non-targets) when test cues overlapped more with targets, a pattern previously shown for the left parietal ERP (Moccia & Morcom, 2021). In contrast, when cues overlapped more with non-targets, neural reinstatement was reversed – greater for non-targets – unlike the left parietal ERP. We also tested for goal-directed mental reinstatement proposed to guide selection prior to retrieval cues. When words were cues there was strong evidence of this proactive reinstatement, but it was not detected when pictures were cues. Together, the data suggest that selection can act at multiple stages of memory retrieval and depends on both external cues and goal-directed control.

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2. Introduction

Our brains store memories of a vast number of past experiences. To use these experiences to guide behaviour, we must somehow select the relevant memories for retrieval. Electrophysiological studies in humans have provided compelling evidence that this selection can act proactively, before memories are retrieved (Herron & Rugg, 2003; Mecklinger, 2010; Rosburg & Mecklinger, 2017). However, little is known about when selection operates in the retrieval processing cascade, or how it is achieved. Here, we used time-resolved multivariate decoding of scalp-recorded electroencephalographic (EEG) patterns to investigate the neural dynamics of selective recollection and the goal representations proposed to enable it.

Current evidence for pre-retrieval selection comes mainly from event-related potential (ERP) studies measuring the left parietal 'old/new' effect, an established index of successful episodic retrieval. This ERP occurs about 500-800 ms after a retrieval test cue and is typically larger when items are recollected than when they are only familiar (see Friedman & Johnson, 2000; Kwon et al., 2023; Rugg & Curran, 2007). It is also larger when more detail is recollected (Vilberg & Rugg, 2007), and when recollection is more precise (Murray et al., 2015). Selective retrieval is shown when the left parietal ERP is larger for currently targeted than non-targeted items (Herron & Rugg, 2003; Rosburg & Mecklinger, 2017). A strength of this electrophysiological approach is its high temporal precision. We know that the left parietal ERP onsets at around the same time as intracranial recollection signals (Staresina & Wimber, 2019), so any modulation of this ERP must be due to processing taking place before or during retrieval. However, the left parietal ERP may not index the initial stages of recollection, but likely reflects activity in lateral and/or medial parietal cortex supporting integrative processing downstream in the retrieval cascade (Bergström et al., 2013; Rugg & Vilberg, 2013).

Recollection is thought to occur when a cue partially reinstates neural patterns associated with a stored memory trace (Alvarez & Squire, 1994; Norman & O'Reilly, 2003; Treves & Rolls, 1994). This partial cue then triggers pattern completion by the hippocampus, leading to the reinstatement of distributed neural patterns that represented the original experience (Buckner & Wheeler, 2001; Damasio, 1989; Kosslyn, 1994). Human functional magnetic resonance imaging (fMRI) studies have provided strong support for a role of cortical reinstatement in successful recollection (Johnson & Rugg, 2007; Polyn, 2005; Staresina, Henson, et al., 2012; see Buckner & Wheeler, 2001 and Danker & Anderson, 2010 for reviews). Preliminary evidence suggests that this reinstatement can be modified by goals, meaning that it is stronger for 'targeted' events or event features of current interest (Elward & Rugg, 2015; Favila et al., 2018; Kuhl et al., 2013; McDuff et al., 2009; Wimber et al., 2015). However, due to the poor time resolution of fMRI it is difficult to separate selective recollection from later goal-dependent processes that operate on the products of recollection. Initial studies applying multivariate decoding approaches to electrophysiological data have begun to reveal the representational dynamics of recollection (Jafarpour et al., 2014; Johnson et al., 2015a; Wimber et al., 2012), but have not yet clarified the point at which selection modifies reinstatement.

Reinstated cortical representations have been hypothesized to support the vivid and multi-dimensional experience referred to as 'reliving the past' (Danker & Anderson, 2010; Tulving, 1983; Wheeler et al., 2000). Alternatively, neural reinstatement may be necessary but not sufficient for recollection, in line with findings that it can be just as strong when people fail to recollect as when they succeed (Thakral et al., 2015, 2017). Initial reinstatement may be an automatic consequence of pattern completion (Moscovitch, 2008) and subject to further, constructive processing (Damasio, 1989; Favila et al., 2018; Linde-Domingo et al., 2019). We assumed a simple model of the retrieval cascade in which selection may operate at two non-exclusive stages, yielding two alternative predictions. Cue-driven retrieval selection implies that target memories are selected at the point of

pattern completion, ensuring that non-target memories are not reinstated. If goal-driven processing contributes nothing further to selection, reinstatement will follow the same pattern of selectivity as the left parietal ERP. In contrast, goal-driven retrieval selection assumes that where both target and non-target information is initially reinstated, goal-dependent processing amplifies target information. If this goal-driven mechanism operates alone, reinstatement will show a non-selective pattern while the left parietal ERP is selective for target memories.

The ability to control what we recollect means we do not need to rely on external cues to trigger retrieval. There is good evidence for such internal, goal-driven control from EEG studies that have revealed goal-related ERP modulations before and during retrieval attempts (see Evans & Herron, 2019; Herron & Rugg, 2003; Mecklinger, 2010; Morcom & Rugg, 2002). Goal-related EEG activity occurring before retrieval cues are presented can also predict recollection success (Herron & Evans, 2018; Kerrén et al., 2021). The longstanding encoding specificity and transfer-appropriate processing principles (Morris et al., 1977; Tulving & Thomson, 1973) suggest a mechanism for this pre-retrieval control: internal goal-directed reinstatement of contextual information stored in sought-for memory traces. This proposal has long been supported by indirect behavioural evidence (Smith & Vela, 2001). More direct neural evidence for internal reinstatement can be obtained from both fMRI and EEG studies assessing reactivation of neural patterns from targeted studied events. Several studies have shown that neural activity prior to cued retrieval attempts differed according to retrieval goals (Bramão et al., 2022; Bramão & Johansson, 2018; Manning et al., 2011), and McDuff et al. (2009) found fMRI evidence of internally reinstated neural patterns from the study phase during retrieval attempts. This evidence is complemented by findings that study phase neural patterns reappear in the first second or so of memory search in free recall tasks, although such patterns are difficult to distinguish from those accompanying initial recollection (Kragel et al., 2021; Polyn, 2005; Polyn et al., 2012; see also Bramão et al., 2022; Bramão & Johansson, 2018). Thus, no study has yet demonstrated proactive reinstatement of study neural patterns before retrieval unfolds.

Here, we examined two existing datasets for which the pattern of left parietal ERP target selectivity was known. In the previous report, the left parietal ERP was larger for targets than non-targets when the retrieval cues had a high degree of overlap with the targeted material (auditory words in Experiment 1, and pictures in Experiment 2; Moccia & Morcom, 2021). To assess the locus of selection and the contributions of cue-driven and goal-driven selection, we investigated whether neural reinstatement is target-selective in the same task conditions in which the left parietal ERP is selective. We also tested the prediction that internal reinstatement occurs prior to retrieval.

3. Materials and Methods

3.1 Participants

Data from 56 right-handed participants were analyzed, $N = 28$ in Experiment 1 (20 female, 8 male, age $M = 22.79$ years, $SD = 4.14$) and $N = 28$ in Experiment 2 (20 female, 8 male, age $M = 24.57$ years, $SD = 3.71$). Data from one further participant in Experiment 2 were excluded due to an insufficient number of artefact-free trials. All reported having normal or corrected to normal vision and hearing, being in good health, not taking medication that might affect cognition, and being very fluent in English. Sample sizes were determined *a priori* for comparisons of left parietal ERPs (see Moccia & Morcom, 2021). The Psychology Research Ethics Committee at the University of Edinburgh approved the experiments, ref.: 135-1819/1 and 300-1819/1. Participants were students who were compensated with university credits or cash.

3.2 Materials

The same 262 pictures and names of common objects were used as stimuli in both experiments (Figure 1). Of these, 240 served as critical items and 12 were used as fillers at the beginning of each study and test list, and 12 in practice lists. At study, objects appeared as either coloured pictures or as auditory words spoken by an English native male voice. At test, memory was probed with visual words in Experiment 1, or grey-scale line drawings in Experiment 2 (for further detail see Moccia & Morcom, 2021). The critical items were divided into 6 sets of 40 objects. For each of the two study-test cycles, one set of pictures and one of auditory words were combined to create a study list of 80 items. The corresponding visual words (Experiment 1) or line drawings (Experiment 2) were then combined with a third set of new items to create the test list of 120 items. For each study-test cycle, half the items studied as pictures, half those studied as auditory words, and half the new items were allocated to the first test block, and the remainder to the second test block. In total, there were 80 critical targets, 80 critical non-targets, and 80 critical new items. Item presentation order was determined randomly within each study and test list.

3.3 Procedure

The EEG was recorded in two experiments where participants performed a recognition exclusion task in which retrieval goals are manipulated (Jacoby, 1991). Selective recollection is quantified by comparing neural signatures of successful retrieval elicited by target versus non-target items (Herron & Rugg, 2003). The task involved two study-test cycles (Figure 1).

3.3.1 Study phase. Participants saw pictures or heard auditory words and were instructed to learn the items for a subsequent memory test, while rating their pleasantness on a 4-point scale from "very pleasant" to "not pleasant". On each trial, a preparatory cue (pre-cue) presented for 1,000 ms signalled the format of the upcoming item, either a yellow asterisk '*' or a blue lowercase 'o' (allocation to pictures and auditory words was counterbalanced). This was followed by a blank screen for 100 ms, then the stimulus for 1,000 ms. Afterwards, a 1,500 ms red fixation cross preceded the word "RESPOND", shown at the centre for up to 3,000 ms and during which participants responded via keyboard presses. A 100 ms blank screen separated each trial.

3.3.2 Test phase. Each study phase was followed by a brief pen-and-paper distractor task, then two memory test blocks with different target designations: in each, studied objects previously presented in one format were designated as targets (Target-Audio or Target-Pictures). For example, in the Target-Audio block, participants were instructed to answer 'yes' to an item if they remembered hearing the object name in the preceding study phase and 'no' to all other items. Target designation was also signaled on each trial using the same preparatory symbols as at study. In Experiment 1, retrieval cues were visual words, and in Experiment 2, they were grey-scale line drawings, in both cases shown at the center of the screen. Timing of test trials were as follows: stimuli were preceded by pre-cues for 500 ms and a black fixation for 1,800 ms. Then, the retrieval cues were shown for 3,000 ms followed by a red fixation for 500 ms in Experiment 1, and 500 ms followed by a 3,000 ms fixation in Experiment 2. Participants' responses were recorded during stimulus presentation in Experiment 1 and during fixation in Experiment 2. We changed the time-point where participants' responses were collected in Experiment 2 to avoid excessive ocular movements during presentation of pictorial cues. The order of the Target-Picture and Target-Audio blocks and the mapping of the keypress responses to left and right hands were counterbalanced across participants.

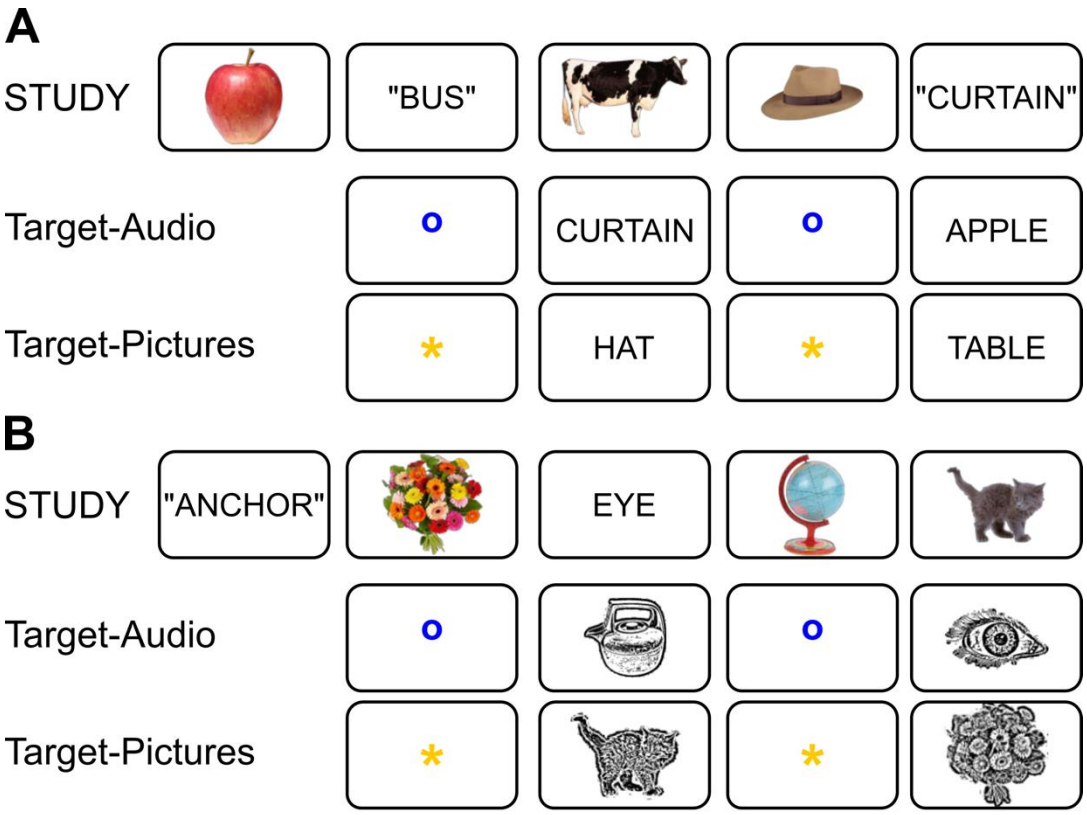

Figure 1. Experimental paradigm. A) Experiment 1 (visual word test cues); B) Experiment 2 (line drawing test cues). In both experiments, participants studied a single block of pictures intermixed with auditory words. In each of the test blocks, either items studied as pictures or auditory words were targets (see Materials and Procedure).

3.4 EEG recording and preprocessing

EEG data were recorded with a BioSemi Active Two AD-box with 24-bit signal digitization from 64 active silver/silver chloride electrodes in an elastic cap using the extended International 10-20 system configuration. Vertical and horizontal eye movements (electrooculogram; EOG) were recorded with bipolar electrodes above and below the right eye and on the outer canthi. EEG and EOG signals were acquired continuously at a 1024-Hz with amplifier bandwidth of 0±208 Hz (3 dB), referenced to a CMS electrode. EEG data were preprocessed using EEGLAB and MATLAB R2018a. A 0.1-40 Hz Hamming windowed-sinc FIR and a 50 Hz notch filter for line noise were applied after re-referencing the raw signal to linked mastoid electrodes. Following automatic rejection of gross artefacts, the data were partitioned into epochs including pre-cue and stimulus, time-locked to the stimulus onset (4,500 ms epochs for study and 6,700 ms for test). Vertical and horizontal EOG artefacts were corrected using Independent Component Analysis (ICA) with manual removal of components. Further details of recording and initial preprocessing are reported in Moccia and Morcom (2021). To increase signal-to-noise for multivariate decoding, we also smoothed the ERP data using a 20 ms full-width half-maximum Gaussian kernel.

3.5 Multivariate decoding analyses

To identify neural reinstatement, we used multivariate decoding analysis to assess the similarity between EEG neural patterns at study and at test. We focused on neural patterns that

differentiated memories of hearing auditory words versus seeing pictures at study. To decode these patterns we used linear discriminant analysis (LDA) in three main steps: i) We initially decoded study phase data to determine the time windows that would capture the most salient differences between hearing auditory words and seeing pictures; ii) Next, we trained LDA classifiers on study phase data and applied the trained classifiers to memory test phase data so that classifier performance at test indexed reinstatement of these study phase neural patterns during memory retrieval; iii) We also applied LDA classifiers trained on study phase data to preparatory cue test phase data to assess reinstatement during goal-directed processing prior to memory retrieval.

MATLAB code (version 2019b) was custom-written using LDA functions adapted from Linde-Domingo et al. (2019, https://osf.io/ywt4g/). In all cases data were downsampled before decoding, to approximately 8 ms time bins (i-ii) or 15 ms time bins (iii). Multivariate noise normalization with shrinkage regularisation was then applied per participant to single trial data using the method of (Guggenmos et al., 2018; Linde-Domingo et al., 2019). Trials were subsampled within training (encoding) conditions to ensure equal numbers per class and the outcomes averaged over 12 iterations.

In all LDA analyses, classifier features were the EEG ERPs from the 64 scalp electrodes at a given time-point. We extracted a decision (*d*) value for each trial and time-point that indicates the distance to the decision boundary dividing the two classes in a feature space. The sign of *d* indicates the category the data-point was classified as (+ for pictures and – for auditory words). The resulting value - when the sign is correct - indexes classifier fidelity: how confidently the classifier assigned that trial's neural pattern to its class.

3.5.1 Study phase decoding. The methods for the initial decoding of auditory word versus picture trials are detailed in the Supplementary Methods. This analysis revealed significant decoding of study format throughout the stimulus presentation time-window with an initial peak from around 150 ms to 1,000 ms and a main peak at around 250 ms in both experiments (Figure S1). In order to capture the main period during which audio and picture trials were differentially processed during encoding we therefore selected study phase data from 150 to 1,000 ms to train the study-test classifiers used to assess reinstatement.

3.5.2 Study-test reinstatement during memory retrieval. This second, principal analysis allowed us to quantify study-test neural pattern reinstatement while participants retrieved target and non-target memories using the same retrieval cues (visual words in Experiment 1 or line drawings in Experiment 2). To do this, we cross-classified study and test data, pairing each training (study phase) time point with each test (test phase) time point to yield a confusion matrix of values. Each LDA classifier was trained to discriminate between ERPs observed from pictures and auditory words at study. Subsequently, these classifiers were evaluated on ERPs observed in response to test cues. The test cues were coded according to whether they had been studied in picture or auditory format, or were previously unstudied (new items). The procedures followed were identical to those for the study phase decoding, except that all test phase trials were used after training on subsampled study trials, and training data were restricted to the 8 ms time bins from the selected 150-1,000 ms study phase time window. To correct for pre-stimulus activity unrelated to successful retrieval, ERPs were first baseline-corrected using a 200 ms pre-stimulus period.

To quantify memory-related reinstatement for targets and non-targets in each test block we needed to control for non-memory-related processes that could contribute to classifier performance for test cues. For example, in Experiment 1 in the Target-Audio block, targets were items studied as audios and non-targets were items studied as pictures. Here, the neural patterns for the visual word test cues might be closer to patterns for pictures at study because the former two types of stimuli elicited shared, non-mnemonic, visual information. To adjust for this kind of effect before running the statistical analysis of target and non-target decoding, we therefore adjusted the classifier's decision

boundary according to its performance (*d* value) for new unstudied items within the same block. This was accomplished by calculating the classifier fidelity of new items, which necessarily do not bear memory-related information. As LDA is a linear classifier, this correction can be achieved by shifting the classification boundary along the vector orthogonal to the boundary. This is implemented by subtracting the mean classifier fidelity for new items from the mean target and non-target classifier fidelities per participant and test block (see Figure S2 for illustration and supplementary information). Performance of these adjusted classifiers can be interpreted in terms of evidence for audio and picture information during test and thus neural reinstatement *relative* to new items, which could not elicit memory retrieval.

Our main hypotheses concerned the degree to which study-test pattern reinstatement was target-selective, i.e., greater for test cues associated with target than non-target memories. We wanted to examine how target-selectivity depended on the retrieval goals and test cues, so we quantified target-selectivity as the difference in reinstatement for targets versus non-targets within each test block and experiment. We assessed reinstatement in two *a priori* test phase time windows. The early window focused on pre-recollection memory processing from 200-500 ms. The late time window focused on recollection processing from 500-800 ms. The late window corresponds to the typical timing of the left parietal ERP and the earlier window to earlier mnemonic or pre-retrieval processes (Rugg & Curran, 2007; Staresina & Wimber, 2019; Tsivilis et al., 2001). We indexed test phase reinstatement using a directional reactivation index constructed by thresholding classifier fidelity to include only positive values ($d > 0$) , which indicated correct classification of the studied class of stimuli (see Fuentemilla et al., 2010; Johnson et al., 2015b for similar approaches). We then quantified overall reinstatement per participant in each time window by collapsing over the outputs of classifiers trained in all study phase bins. Thus for each test window we computed the mean classifier fidelity across all study bins that showed positive classification at test. Lastly, we computed the mean reactivation over test bins. In calculating this mean, we first removed any test time bin that did not show evidence of reactivation in any study time bin. One participant in Experiment 1 did not show reactivation across any of the test time-bins during the late (500-800 ms) test window and thus was removed from the analyses in this time-window.

3.5.3 Pre-retrieval study-test reinstatement. The third and final analysis step tested for goal-related preparatory reinstatement before memory retrieval could occur. We examined reinstatement of the study phase neural patterns during the pre-cue phase of the test trials. An LDA classifier was again trained on study phase data, then tested on test phase ERPs time-locked to the pre-stimulus preparatory cues. We summed the d values over trials in each class (condition) per participant to obtain overall preparatory reinstatement. Study and test phase data for the pre-cue analysis were downsampled to approx. 15 ms time bins to accommodate the longer test data epoch during pre-cue presentation. To enable detection of state-related activity these data were not baseline-corrected. The study phase time-window was the same as for the retrieval cue analysis and the test phase window encompassed 200-2,300 ms after the preparatory cue.

3.6 Statistical analysis

We conducted statistical analysis in R (version 3.5.4, https://www.r-project.org). Alpha was set at .05, with Benjamini and Hochberg (1995) False Discovery Rate corrections for multiple *post hoc* analyses when relevant, which provides a reasonable balance between detecting significant effects meaningfully while controlling for multiple comparisons. Given the non-normality of our reactivation index, which had a lower bound at zero and long positive tail (see Multivariate decoding analyses), we analysed these data with Generalized Linear Mixed effects models (GLMM) assuming a gamma distribution with log-link function using the glmer function in the lme4 package (Bates et al., 2015). GLMMs for each time-window and experiment had factors of Target Designation (target-picture/

target-audio) and Item Type (target/ non-target) as fixed effects, and participants as random intercept. All GLMMs were fit with the BOBYQA optimiser. Model parameters were tested using the joint_tests function in the emmeans package (Lenth, 2023). Pairwise comparisons arising from significant interaction terms were analysed using Wald's z-tests using the emmeans function, testing pairwise differences between conditions and within each test block. We also examined study x test confusion matrices for each experiment, Target Designation block and Item Type. To detect significant clusters in these maps we used a cluster permutation multiple comparisons family-wise error correction (Maris & Oostenveld, 2007). After identifying clusters with 1-tailed paired-sample *t* tests comparing fidelity values to 0 at uncorrected alpha = .05, we computed cluster mass as the sum of *t*-values per cluster. Statistical significance (at 1-tailed alpha = .05) was then calculated by comparing the cluster mass against its permutation distribution, based on 1,000 LDA iterations of fitting models with randomly shuffled training trial class labels.

4. Results

4.1 Behavioural results

In both Experiment 1, when test cues were words, and in Experiment 2, when test cues were line drawings, memory tended to be better for items studied as pictures, whether tested as targets or non-targets. Response times (RTs) were also faster for targets studied as pictures than audios in Experiment 1, and for all trial types in Experiment 2 (see supplementary Table S1; for statistical analyses Moccia and Morcom, 2021).

4.2 Decoding reinstated neural patterns

To quantify neural reinstatement in each retrieval condition we tested the trained LDA classifiers on trial data for studied retrieval test cues (targets and/or non-targets). Decoding was run within test blocks, classifying studied items according to their study format: 1) targets studied as pictures (in the Target-Picture block); 2) targets studied as auditory words (in the Target-Audio block); 3) non-targets studied as auditory words (in the Target-Picture block); 4) non-targets studied as pictures (in the Target-Audio block). In each case, we corrected the classifier for LDA performance for the new items in each test block – for which no information should be retrieved – by adjusting the classifier decision boundary. This was done by subtracting the mean classification for the new (unstudied) items within each block. For example, for 1), picture targets had been studied as pictures so we tested performance of the trained LDA classifier coded as pictures adjusting for classifier performance for new items in the same block, Target-Pictures, also coded as pictures. Then for 2), picture block non-targets had been studied as audio so we tested LDA performance on coded as audio items, again adjusting for new items in the same block, coded as pictures (see Materials and Methods: Multivariate decoding analyses and Figure S2 for details).

4.2.1 Decoding neural patterns during successful retrieval.

In initial exploratory analyses, we examined reinstatement for each combination of study phase (training) and test phase (test) time bins, per participant and experiment, Target Designation and Item Type within test blocks. This revealed significant neural reinstatement of studied information at test in both experiments (Figures 2A and 2B). Reinstatement was maximal at approximately the same time post-retrieval cue as the left parietal event-related potential (ERP), i.e., in the late test window, after around 500 ms. However, in Experiment 2 the clusters extended from around 300 ms after the retrieval cue, i.e., into the early test window. Qualitatively, the information carried in reinstated neural

patterns at retrieval differed according to whether the object was studied in a picture or audio format, as expected if reinstatement involves format-specific cortical networks (Danker & Anderson, 2010). In both experiments, recollecting objects that had been studied as auditory words reinstated information carried early in the study epochs after stimulus presentation (from 150 to 400 ms in Experiment 1 and from 150 to 350 ms in Experiment 2). In contrast, when people recollected objects that had been studied as pictures, they reinstated neural patterns from later in the study epochs (from ~340 to the end of study window, 1,000 ms, for targets in Experiment 1, and from ~400 and ~430 until the end for targets and non-targets in Experiment 2, respectively).

These confusion matrices of study-test decoding also revealed prominent non-target as well as target reinstatement in the two conditions in which the left parietal ERP had showed a non-selective pattern that did not differ in magnitude between targets and non-targets in Moccia and Morcom (2021). These were the two conditions in which retrieval cues had low overlap with the currently targeted information. In the Target-Picture block in Experiment 1 (verbal test cues), we found significant clusters for both targets and non-targets (cluster-corrected p = .004 and p = .030, respectively), and the same in the Target-Audio block of Experiment 2 (pictorial test cues; p = .049 and p = .001, respectively). In contrast, the picture was more one of target-selectivity in the other two conditions that had shown target-selective left parietal ERPs, although in the Target-Audio block of Experiment 1 neither target nor non-target reinstatement was separately significant (p = .200 and p = .307). In the Target-Picture block of Experiment 2, reinstatement was only significant for targets (p = .001; p = .332 for non-targets). However, the separate decoding of target and non-target patterns did not allow us to test whether reinstatement was significantly target-selective – i.e., whether it differed between targets and non-targets – in any of these test blocks. The next analysis step allowed us to make this direct comparison.

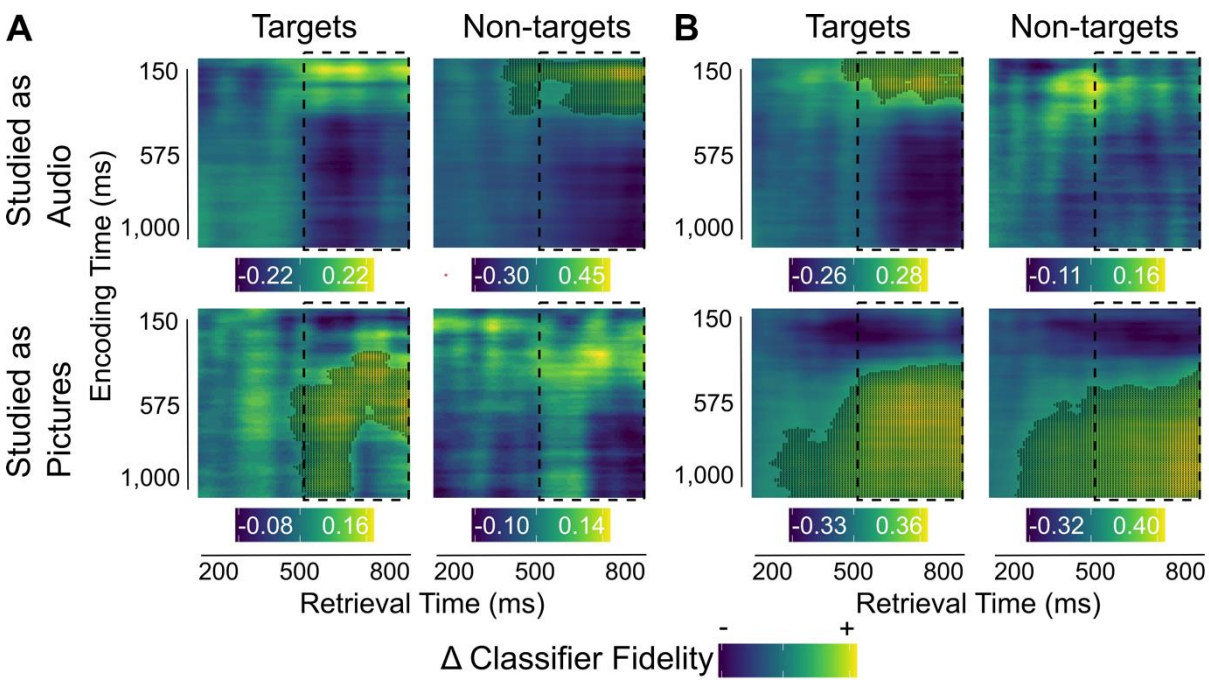

Figure 2. Decoding neural patterns during successful retrieval. Images illustrate study x test confusion matrices of reinstatement strength according to study phase timepoints (y axis) and test phase timepoints post-retrieval cue (x axis) in A) Experiment 1 and B) Experiment 2. The dashed areas indicate the late test time-window (200-800 ms). Reinstatement is indicated by above-zero classifier fidelity, shown in yellow. Timepoints belonging to significant clusters (1-tailed tests) are

highlighted with superimposed black circles. Each decoding analysis compared targets or non-targets after subtracting a baseline of new, unstudied items from the same test block (see Multivariate decoding analyses).

4.2.2 Target-selective reinstatement tracks cue overlap

To test our main experimental hypotheses, we then asked whether neural reinstatement was target-selective in the experimental conditions in which the left parietal ERP had shown a target-selective pattern. Figure 3 shows the results of this analysis and Figure 4 contrasts these with the pattern of ERP selectivity previously reported by Moccia and Morcom (2021). To assess the amount of reinstatement of study phase neural patterns for targets versus non-targets, we quantified the reactivation index for each condition during the early (200-500 ms) and late (500-800 ms) test windows (see Methods, Multivariate decoding analysis for details). Target and non-target reinstatement was compared within test blocks to quantify selectivity when the retrieval goal was held constant.

In Experiment 1 (with verbal cues; Figure 3A), GLMMs on mean reactivation showed that target and non-target reinstatement differed significantly during the late test window only (see Table S2 for results for the early test window). The main effects of Target Designation and Item Type were not significant, $\chi^2(1) = 2.05$, $p = .152$ and $\chi^2(1) = 0.14$, $p = .711$, but the interaction was significant, $\chi^2(1) = 10.03$, $p = .002$. *Post hoc* tests showed that memory pattern reinstatement was numerically but not significantly greater for targets than non-targets in the Target-Audio block (when targets were studied as auditory words), demonstrating a trend towards target-selective reinstatement, $z = 1.94$, $p = .052$. There was also a reversed pattern in the Target-Picture block (when targets were studied as pictures) revealing significantly stronger reinstatement for *non-targets* than targets, $z = -2.50$, $p = .013$.

In Experiment 2 (with pictorial cues; Figure 3B) a similar but stronger pattern of target-selectivity emerged, showing a similar reversal, and once again significant in the late test window only (see Table S5 for results for the early test window). The GLMM run on the reactivation score showed non-significant main effects of Target Designation, $\chi^2(1) = 1.88$, $p = .170$, and of Item Type, $\chi^2(1) = 3.49$, $p = .062$, but a significant interaction, $\chi^2(1) = 18.67$, $p < .001$. Pairwise *post hoc* comparisons on memory pattern reactivation confirmed that there was significant target-selective neural reinstatement in the Target-Picture block, $z = 4.41$, $p < .001$. This time, in the Target-Audio block, reinstatement did not significantly differ between targets and non-targets, although it was numerically greater for non-targets, $z = -1.74$, $p = .082$.

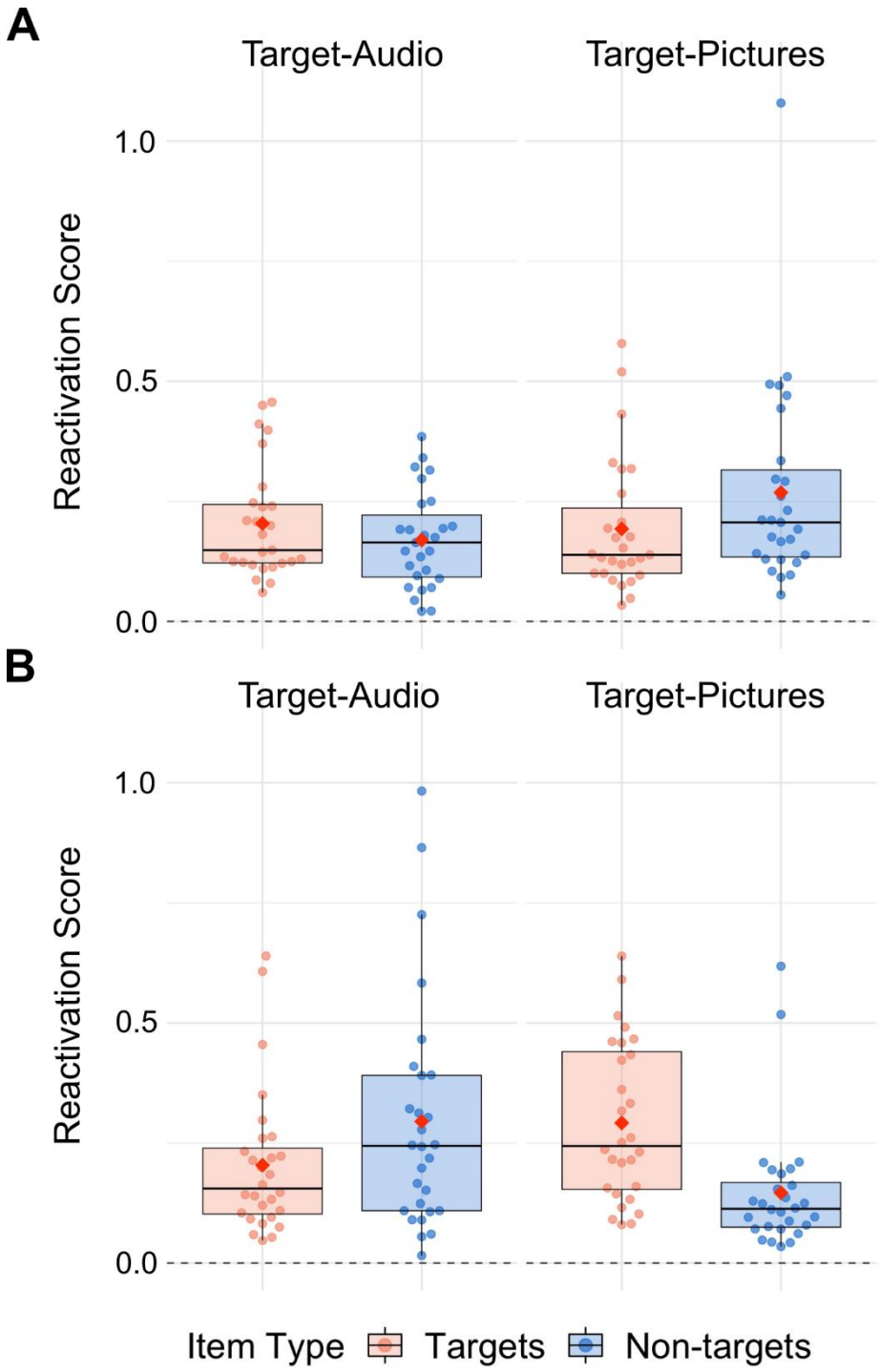

Figure 3. Target-selectivity for memory pattern reinstatement. Plots show effects of target designation – whether targets are items studied as audios or pictures – on reinstatement (LDA fidelity *d*) for targets and non-targets in A) Experiment 1 (verbal retrieval cues) and B) Experiment 2 (pictorial retrieval cues). Data points represent participants, red points are means, and boxplots show the medians and interquartile ranges.

From the above findings, it appeared that reinstatement during the late test-window (500-800 ms) could either be target- or non-target-selective depending on which source was targeted. We therefore wanted to know whether, across experiments, this pattern followed the previously reported

pattern for the left parietal ERP, in which target-selectivity depended on the degree of overlap between the retrieval cues and the currently targeted source (Moccia & Morcom, 2021). By combining data across experiments we were able to code the trials according to cue-target overlap so that both pictures and audios were included as targets and non-targets in each condition: when cues were words in Experiment 1, trials in the Target-Audio block were the high overlap condition, and when cues were pictures in Experiment 2, those in the Target-Picture block were the high overlap condition. A further GLMM with a gamma link function on the reactivation data from the late test window had fixed effects of Experiment (experiment 1/ experiment 2), Overlap (high/ low), and Item Type (target/ non-target) and participants as random effect. The model revealed a main effect of overlap, $\chi^2(1) = 3.89$, $p = .049$, and a significant interaction between Overlap and Item Type, $\chi^2(1) = 28.29$, $p < .001$ (but no other significant effects, see Table S8 for all model results). These results showed that memory pattern reinstatement from 500-800 ms was more target-selective when cue-target overlap was high than when it was low (Figure 4). Pairwise comparisons comparing target versus non-target reactivation in each overlap condition confirmed that targeted neural patterns were reinstated more strongly than non-targeted patterns in the high overlap condition, $z = 4.57$, $p < .001$, while non-targeted neural patterns were reinstated more strongly than targeted patterns in the low overlap condition, $z = -2.93$, $p = .003$. To obtain an estimate of the effect size of the target- and non-target selectivity in the two overlap conditions, we calculated Cohen's *d* based on estimated degrees of freedom (see supplementary results Table S9 for details). These effects showed a small-to-medium and a small effect size of $d = 0.36$ and $d = 0.23$, respectively. Thus, across experiments, reinstatement was target-selective when external cues overlapped strongly with the targeted information, and reversed, i.e. *non-target*-selective, when external cues did not overlap strongly with the targeted information. In these 'low overlap' conditions, the test cues instead overlapped strongly with the non-targeted information.

To formally compare the above pattern to the selectivity of the left parietal ERP, a final analysis tested the left parietal amplitude elicited by targets versus non-targets between 500 to 800 ms across experiments, coding trials by overlap as above. To account for the effects of goal-related states as done in 'old/new' ERP analyses (c.f., Rugg & Curran, 2007) and to parallel the neural pattern reactivation index (Methods, Multivariate decoding analyses), we subtracted the mean ERP amplitude for new items in each test block from the mean amplitudes for targets and non-targets before statistical analysis. Because ERP data were normally distributed, we ran a Linear Mixed Effect Model on the left parietal ERPs with Experiment (experiment 1/ experiment 2), Overlap (high/ low) and Item Type (target/ non-target) as fixed effects and participants as random intercepts. Reported degrees of freedom are adjusted based on the Kenward-Roger approximation, as default. This revealed a significant main effect of Experiment, $F(1, 54) = 4.58$, $p = .037$, a significant main effect of Item Type $F(1, 162) = 14.40$, $p < .001$, and a significant Overlap x Item Type interaction, $F(1, 162) = 21.19$, $p < .001$ (no other significant terms were found, see Table S10 for complete model results). Pairwise *t*-tests comparing the left parietal ERP elicited by targets and non-targets revealed that in the high overlap condition, the left parietal ERP showed a strongly target-selective pattern, $t(162) = 5.94$, $p < .001$, $d = 0.47$. In contrast, the left parietal ERP did not show a significant difference between targets and non-targets in the low overlap condition, $t(162) = -0.57$, $p = .569$, $d = 0.04$. So, in the late test window, the two indices of selective retrieval diverged.

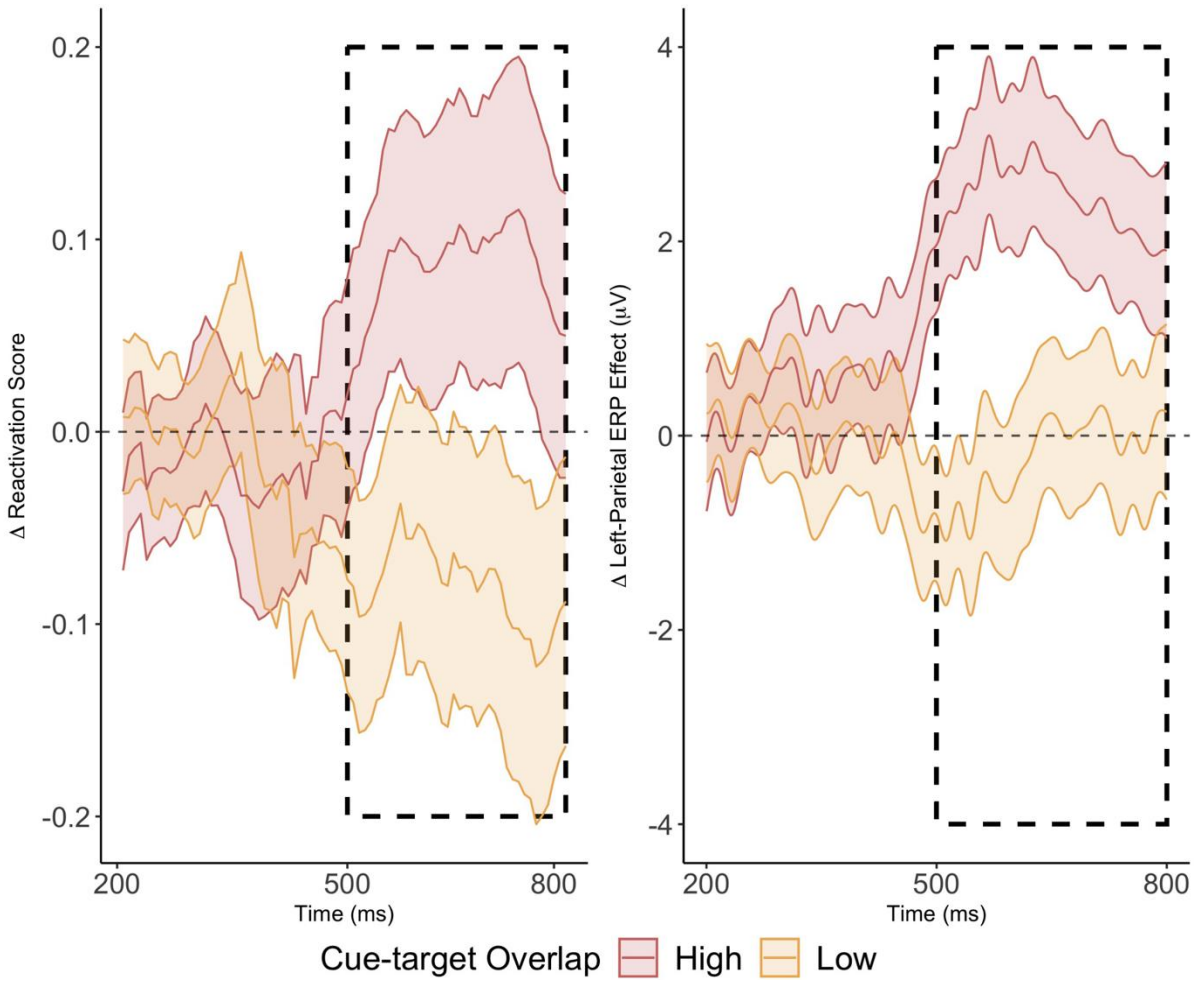

Figure 4. Target-selectivity for study-test reinstatement compared to the left parietal ERP. Plots show effects of cue-target overlap – whether items had high or low overlap with targeted source – on reinstatement (LDA fidelity *d,* left panel) and the left parietal ERPs (right panel) collapsed across experiments. Left panel shows the difference in the reactivation index for targets and non-targets for conditions with high versus low retrieval cue-target overlap and plotted per 8 ms retrieval time bin. Right panel shows the corresponding univariate left parietal ERP data from Moccia & Morcom (2021). The shaded areas in the line plots are the 95% within-subject confidence intervals for each time-point adjusted using the Cosineau-Morey method (Morey, 2008; cf. Craddock, 2016). The dashed rectangle indicates the analysed time-window. For details of measures see main text.

4.3 Decoding retrieval goals from preparatory cue EEG

The foregoing analyses showed the effects of strategic control on selective retrieval by revealing selection prior to or during the recollection time window around 500 ms after the retrieval cue. In the final set of analyses, we tested for mental reinstatement of study phase neural patterns by decoding the retrieval goal *before* any specific retrieval cue was presented. To do this, we assessed neural pattern similarity between the study phase and the preparatory cue interval at test (for the task timing see Figure 1; for analysis details see *Pre-retrieval study-test reinstatement*). The results are shown in Figure 5. In Experiment 1, the LDA classifier trained to differentiate picture and audio trials at study was able to distinguish at test between preparation to retrieve picture targets and preparation to retrieve audio targets: the classifier fidelity measure revealed three significant clusters of

reinstatement from approx. 900-1,800 ms after the preparatory cue (cluster p = .006, .006), and a further cluster just before retrieval cue onset (p = .023). This shows sustained proactive reinstatement of the currently relevant study context while participants prepared to target items studied in one of the two formats. However, in Experiment 2, the classifier did not significantly decode the retrieval goal (cluster p = .498).

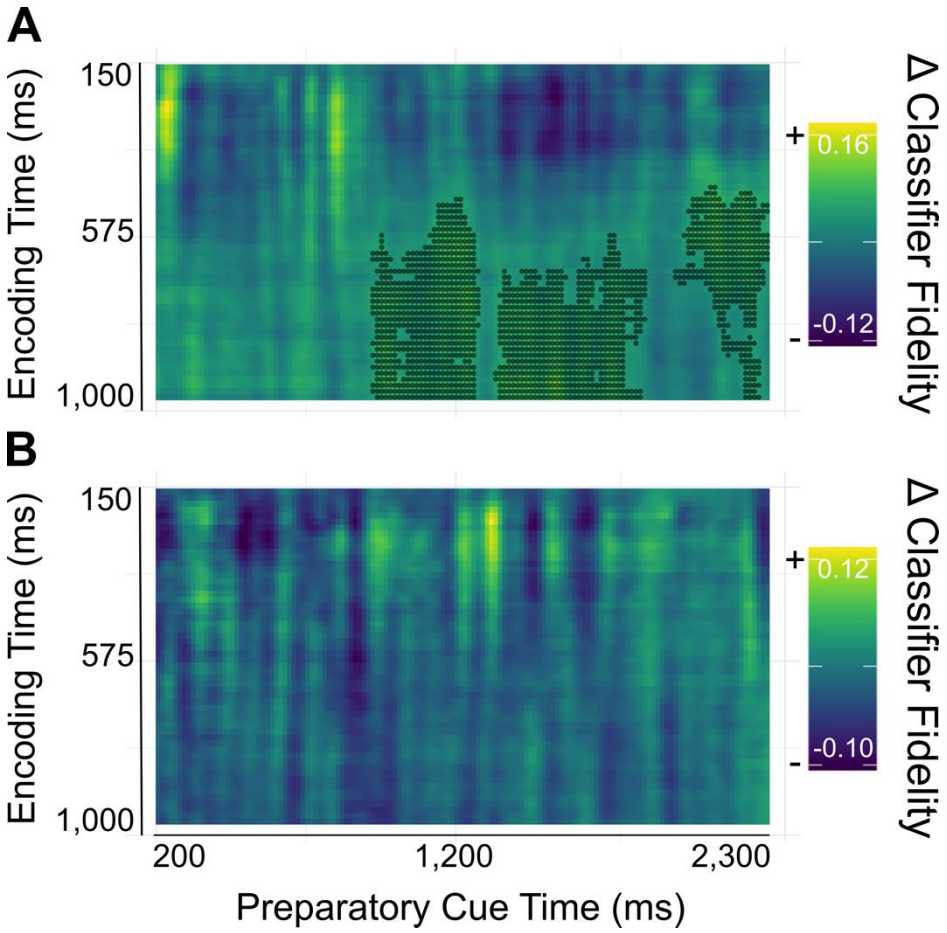

Figure 5. Goal-driven reinstatement prior to the retrieval cue. The images show the strength of reinstatement during the preparatory cue periods in A) Experiment 1 and B) Experiment 2, according to study phase timepoints (y axis) and test phase timepoints (x axis). Reinstatement is indicated by above-zero classifier fidelity, shown in yellow. Timepoints belonging to the max significant cluster are highlighted with superimposed black circles. No significant clusters were found in Experiment 2.

5. Discussion

A central function of memory is to recall past experiences that are relevant to current goals. Here, we used multivariate EEG decoding to investigate how and when relevant memories are selected during the brain's retrieval cascade. We measured reinstatement of study phase neural patterns before and during recollection in a task where goals and external cues were manipulated (Moccia & Morcom, 2021). During recollection, people reinstated distinct neural patterns from the time that the auditory words or pictures had been studied that reflected the categories that were remembered. We showed that these reinstated neural patterns were selective for targeted over non-targeted information when retrieval cues had high overlap with targets – i.e., when targets were

auditory words and test cues were written words (Experiment 1) or targets were pictures and test cues were line drawings (Experiment 2). This pattern was similar to the one found for the left parietal ERP signature of recollection, which was also previously shown to be target-selective in these experimental conditions (Moccia & Morcom, 2021). In contrast, when retrieval cues had higher overlap with non-targets than targets, we observed a reversed pattern with greater reinstatement of non-target information. Since the left parietal ERP had been shown to be non-selective in these conditions, the two measures now diverged. These distinct patterns of selectivity revealed by the two electrophysiological measures of retrieval success support the notion that selection takes place at multiple stages before and during recollection.

Neural models of recollection specify that cortical reinstatement is triggered by hippocampal pattern completion (Alvarez & Squire, 1994; Norman & O'Reilly, 2003; Treves & Rolls, 1994). Pattern completion itself is assumed to be an automatic autoassociative process, but memory theories so far say little about the information flow during subsequent cortical memory reconstruction. For instance, it is unclear if initial pattern-completed representations are sufficient for recollective experience, as has been proposed (Damasio, 1989). Alternatively, reinstated information may require further, integrative and constructive processing for conscious recollection to occur, perhaps involving the posterior parietal cortex (Bergström et al., 2013; Humphreys et al., 2021; Hutchinson et al., 2009; Linde-Domingo et al., 2019; Vilberg & Rugg, 2009). On this basis, our simple model assumed that goal-directed selection might act at one or both of these two retrieval stages. If cue-driven selection acts at the point of hippocampal pattern completion, then all subsequent activity in the retrieval cascade should be target-selective, including both reinstatement and the left parietal ERP. We observed this pattern to some degree, in two experimental conditions, where the left parietal ERP and reinstatement were both target-selective. Strikingly, in the other two conditions, non-targeted mnemonic information was reinstated more strongly than targeted information, while the left parietal ERP was merely non-selective, with no significant difference between targets and non-targets. The data point to goal-driven amplification of target relative to non-target signals, excluding reinstated non-target information from the further stages of processing reflected in the left parietal ERP.

What drives these two stages of retrieval selection? External retrieval cues appear to be critical. In the current study we found that neural reinstatement was highly cue-dependent, prioritising memories with high overlap with the external cues regardless of whether these were currently targeted. This supports the assumption that the overlap between external partial cues and stored memory traces influences selection of which memories will be retrieved by modifying pattern completion, or, perhaps, initial reinstatement (Norman & O'Reilly, 2003). Our detection of neural pattern reinstatement associated with non-targeted memories is also consistent with previous findings from tasks in which retrieval cues are associated with multiple competing memories (e.g., Bramão et al., 2022; Khader et al., 2005; Kuhl et al., 2011). Our data provide converging evidence that unintended memory reinstatement can occur even when memories do not compete for the same retrieval cue.

The mechanisms of goal-driven amplification of relevant mnemonic information are less clear. Our data suggest that amplification cannot enable selective retrieval on its own, since the left parietal ERP was non-selective rather than target-selective in the low cue-target overlap conditions which showed stronger non-target reinstatement. However, the current experiments only compared two extreme conditions in which *either* targets or non-targets strongly overlapped with external cues, and it may be possible for amplification to transform initially non-selective reinstatement into target-selective later processing. Goal-driven selection in the low cue-target overlap conditions may also have been underestimated to the degree that some participants used recall-to-reject strategies that prioritised non-target retrieval (see Moccia & Morcom, 2021). Further data are needed to clarify the degree to which goal-driven amplification can generate selective retrieval signals when neither target nor non-target recall is strongly cued externally, or when non-target recall is more strongly cued.

Our findings go further than fMRI studies that have so far suggested that retrieval can be selective for targeted over non-targeted information. Both univariate activation (Elward & Rugg, 2015; Morcom & Rugg, 2012) and multivariate reinstatement (Favila et al., 2018; Kuhl et al., 2013; McDuff et al., 2009) have been shown to be stronger for experimental events or event features designated as task-relevant. Kuhl and colleagues (2013) showed that goal-relevant information was reinstated more strongly than irrelevant information in lateral parietal cortex, unlike in sensory cortical regions (Kuhl et al., 2013; see also Favila et al. 2018). This is compatible with our proposal that amplification involves higher-order regions like the parietal cortex. However, Kuhl and colleagues (2013) interpreted their selective reinstatement in lateral parietal cortex in terms of post-retrieval processes that enhance recovered mnemonic representations in line with goals. This may be correct, but fMRI does not have sufficient time resolution to establish whether selection operates on the output of retrieval or before retrieval is completed (c.f., Rugg & Wilding, 2000). Here, the temporal advantage of EEG allowed us to address this theoretical question. The timing of most of the reinstatement we observed was consistent with intracranial studies showing that cortical reinstatement follows hippocampal pattern completion from about 500 ms after the retrieval cue (Ludowig et al., 2008; Merkow et al., 2015; Mormann et al., 2005; Staresina, Fell, et al., 2012; see Staresina & Wimber, 2019 for review). The fact that reinstatement and the left parietal ERP were both target-selective between 500-800 ms points clearly to pre-retrieval selection. Moreover, at least in Experiment 2, reinstatement began prior to the left parietal ERP, consistent with our assumption that cue-driven processes initiate the retrieval cascade (Wimber et al., 2012). The data fit with intracranial recording evidence that reinstatement takes place at different times in different brain regions (see Staresina & Wimber, 2019). However, any conclusions regarding the relative timings of selective reinstatement and amplification must be tentative, as both selective neural signals co-occurred within a broad time window. We also did not examine post-retrieval reinstatement here, but it is likely that this also occurs as people evaluate the products of retrieval relative to their goals, as proposed by Kuhl and colleagues (2013). Disentangling the spatiotemporal dynamics of selective reinstatement and amplification will also require methods like EEG-fMRI fusion or intracranial EEG that can measure time-resolved brain activity from specific locations.

Reinstated neural patterns in the current study differed qualitatively according to whether remembered items had been studied in an auditory or picture format. The patterns that were reinstated at test corresponded to earlier or later study phase activity, respectively (Figure 2). Thus scalp EEG patterns depended on memory contents, converging with fMRI studies showing auditory and visual reactivation in format-consistent brain regions during retrieval (Wheeler et al., 2000; Danker & Anderson, 2010 for review). Our data suggest that there is also temporal specificity, since information from distinct temporal stages during study trial processing was reinstated when participants retrieved memories involving auditory versus pictorial material. It has previously been proposed that participants might focus on semantic information when remembering pictures but emphasize phonological information when recalling auditory words (see Hornberger et al., 2004, 2006). The relatively early study phase processing reinstated for audio items, around 150-400 ms after stimulus onset, was consistent with this possibility, although the later study phase processing reinstated for picture items, around 350-1000 ms, was later than is typical for semantic (or visual) processing of object images (e.g. Linde-Domingo et al., 2019).

We also examined the control processes proposed to enable selective retrieval. In a process known as mental reinstatement, people are thought to generate internal cue representations that overlap sought-for memories (Anderson & Bjork, 1994; Burgess & Shallice, 1996; Rugg & Wilding, 2000; Smith & Vela, 2001). In Experiment 1, the classifier trained to differentiate between audio and picture study formats was able to decode when people were preparing to target items from these two different formats (Figure 5). This preparatory reinstatement was present for a sustained period prior to the retrieval cue, implicating proactive goal-related reinstatement of study context in preparation for retrieval (mental reinstatement). These results converge with earlier evidence that people engaged

visual and auditory sensory cortical areas when attempting to remember studied pictures and auditory words (Hornberger et al., 2006; see also Hornberger et al, 2004; McDuff et al., 2009). They also converge with previous studies that have shown study context reinstatement during memory search at the start of free recall (Kragel et al., 2021; Manning et al., 2011; Polyn, 2005), or have successfully decoded differing retrieval goals prior to retrieval (Kerrén et al., 2021). In contrast, we did not detect preparatory reinstatement in Experiment 2. Although this null finding does not rule out such processing, it is possible that proactive control processing differed in the two experiments. In Experiment 2, mental reinstatement may have been attenuated because the line-drawing external cues overlapped even more completely with targeted pictures than the verbal cues in Experiment 1 did with targeted auditory words. Hence, participants may have relied more on these external cues. This possibility fits with the smaller goal-related ERPs during retrieval attempts we previously found in Experiment 2 (see Moccia & Morcom, 2021). Indirect converging evidence from scene context cueing tasks also suggests that people engage less internal control when study context is strongly externally cued at test (Smith & Vela, 2001). However, this proposal requires further, direct evaluation. Future studies with a greater number of trials will also be needed to test the additional prediction of the encoding specificity and transfer-appropriate processing principles, that preparatory reinstatement will predict successful performance on the upcoming trials. Nonetheless, the current data provide the first demonstration that preparation to retrieve elicits reinstatement of goal-relevant information, prior to a retrieval attempt.

Together, the data from this study provide several novel insights into how goals shape the way that recollection unfolds. We show for the first time that cue-driven processes acting before or during retrieval can lead to selective reinstatement of study phase neural patterns at the time of recollection. Our data also support the proposal that selection acts at multiple stages during the retrieval processing cascade. They suggest that external cues can modulate initial neural reinstatement while internal goals amplify processing of prioritised relative to other memories in a process of goal-driven selection. The finding of proactive, goal-directed reinstatement of study context while participants were preparing to retrieve targets also revealed the mental reinstatement that has been hypothesised to contribute to selective recollection, although its link to better memory is yet to be established. These results have implications for populations such as older adults who can remember less selectively, and may benefit from environmental support (Dywan et al., 1998; Keating et al., 2017; Morcom, 2016).

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7. Conflict of interest

The authors have no financial or non-financial interests to disclose.

8. Author contributions

A. Moccia and A.M. Morcom developed the study concept and design. Testing and data collection for pre-existing dataset were performed by A. Moccia. M. Plummer, A. Moccia, A. M. Morcom, and I. Simpson designed the analysis strategy. A. Moccia, A. M. Morcom and M. Plummer performed data analyses. A. Moccia drafted the manuscript with M. Plummer's input to the Methods. A.M. Morcom, A. Moccia, and I. Simpson provided critical revisions. All authors approved the final version of the manuscript for submission.

9. Data availability statement

Data and analysis scripts are uploaded to the Open Science Foundation repository (see https://osf.io/ywt4g/) and will be made publicly available upon publication in a scientific journal. Raw data, task materials and scripts are publicly available and can be accessed here: https://osf.io/erjdu/ and https://osf.io/dnz9e/ (for Experiment 1 and Experiment 2, respectively).

10. Ethics approval.

All procedures performed in these studies were approved by the Psychology Research Ethics Committee at the University of Edinburgh, ref.: 135-1819/1 (Experiment 1) and 300-1819/1 (Experiment 2).

11. Abbreviations

1. ERP = Event-Related Potential
2. Left parietal ERP = Left parietal ‘old/new’ Event-Related Potential
3. fMRI = Functional Magnetic Resonance Imaging
4. EOG = Electrooculogram
5. CMS electrode = Common Mode Sense active electrode
6. Hamming windowed-sinc FIR filter = Hamming windowed-sinc Finite Impulse Response filter
7. ICA = Independent Component Analysis
8. LDA = Linear Discriminant Analysis
9. GLMM = Generalised Linear Mixed effects Models
10. FDR = False Discovery Rate

12. Reference

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13. Supplementary Materials

13.1 Supplementary behavioural results

13.1.1 Exclusion task performance. Participants' recognition performance in the exclusion task was assessed by coding items according to their target designation. These were targets (items studied as pictures in the Target-Pictures condition or as auditory words in the Target-Audio condition), non-targets and new items. Full performance is reported in Table S1 (see Moccia & Morcom, 2021 for statistical analyses).

	Verbal test cues (Experiment 1)			Pictorial test cues (Experiment 2)		
	Target	Non-target	New	Target	Non-target	New
Target-Audio block						
Accuracy	.78	.90	.87	.71	.94	.81
	[.74, .81]	[.88, .93]	[.84, .91]	[.67, .76]	[.92, .96]	[0.76, .86]
RTs	1200	1257	1264	1315	1188	1529
	[1139, 1261]	[1222, 1293]	[1199, 1,330]	[1263, 1367]	[1136, 1240]	[1467, 1592]
Target-Picture block						
Accuracy	.81	.86	.92	.89	.88	.91
	[.78, .85]	[.83, .90]	[.89, .94]	[.86, .91]	[.85, .91]	[.89, .93]
RTs	1097	1308	1294	1062	1297	1310
	[1028, 1165]	[1249, 1367]	[1224, 1363]	[1008, 1116]	[1259, 1335]	[1234, 1385]

Table S1. Memory Task Performance. Table displays means and [95% confidence intervals] for accuracy proportions and median response times (RTs in ms) for correctly identified items per condition and experiment. The Cousineau-Morey method for within-participant variables was used to adjust the confidence intervals (Morey, 2008).

13.2 Study phase decoding

In an initial step we used linear discriminant analysis (LDA) to decode study phase neural patterns when participants saw object pictures versus heard object names. The goal of this analysis was to inform selection of time windows for the study-test decoding between 0 and 1,000 ms post stimulus. We trained the LDA classifier to discriminate between picture and audio trials by iteratively training on all trials but one and testing on the left-out trial (a leave-one-out procedure; Linde-Domingo et al., 2019). Classifier features were ERP amplitudes from the 64 scalp electrodes, after subtraction of a 200 ms pre-stimulus baseline. Downsampling was applied to create approximately 8 ms time bins by averaging across time-points, temporal smoothing and multivariate noise normalization were applied as in the main study-test analysis. Trials were sub-sampled and mean classifier fidelity value determined over 12 iterations (see Methods, Multivariate decoding analyses in main manuscript for details).

We found that the LDA classifier could confidently assign study phase neural patterns to picture and auditory trials throughout almost the entire study phase time window in both experiments (Figure S1). One-sample *t*-tests on the classifier fidelity values in each encoding time-bin showed significant and reliable above zero decoding from ~ 50 ms until ~ 1,000 ms after stimulus onset in Experiment 1 (all $p \leq .001$, with exception of time-bin four: 24-32 ms, $p \leq .05$, and time-bin seven: 48-56 ms, $p \leq .01$, corrected with the Benjamini-Hochberg method; Benjamini & Hochberg, 1995) and from ~ 30 until ~ 1,000 ms in Experiment 2, after correcting for multiple comparisons (all *p*-values $\leq .001$, with exception of time-bins 4 to 8: 24-64 ms, $p \leq .05$, and time-bin 9: 64-72 ms, $p \leq .01$, adjusted with the Benjiamini-Hochberg correction). As these tests were run on all encoding time-bins, used the Benjiamini-Hochberg False Discovery Rate (FDR) correction to maximise sensitivity, while minimising the chance of incurring in Type I errors when running multiple comparisons. We therefore used the study phase data from ~ 150 to 1,000 as training for the classifiers testing test phase reinstatement.

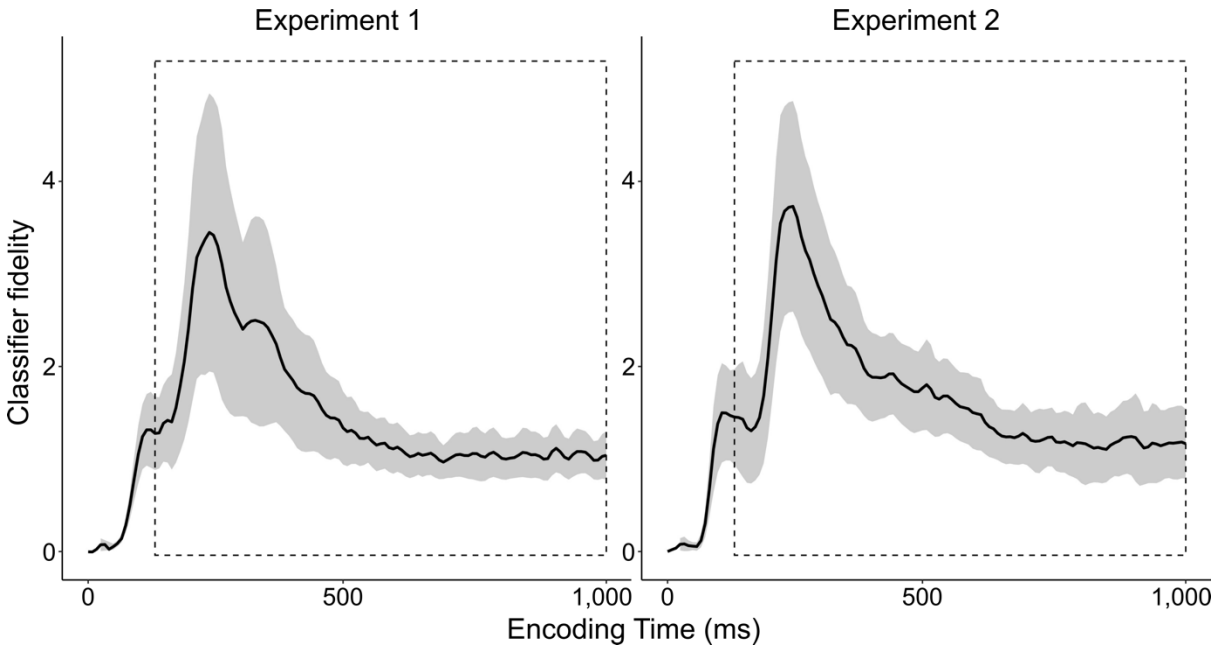

Figure S1. Mean classifier fidelity of study phase neural patterns in Experiment 1 and Experiment 2. The shaded area represents the 95% confidence intervals around the encoding time-bins showing significant above-zero decoding fidelity (see text for details). Dashed lines are the study time window (~150-1,000 ms) used as training for the test phase decoding analyses.

13.3 Test phase decoding

13.3.1 Decoding study-test reinstatement during memory retrieval.

We controlled for perceptual similarity with test cues when quantifying memory-related study-test reinstatement for targeted and non-targeted items in each test block. We did this by subtracting the mean of the unstudied new item classifier fidelity scores from the mean target and non-target classifier fidelities per participant and test block, therefore shifting the classifier boundary orthogonal to the decision hyperplane for each test block (Figure S2). This adjusted classifier fidelity can be interpreted in terms of neural reinstatement for studied items *relative* to new (unstudied) items, which in turn do not elicit memory retrieval.

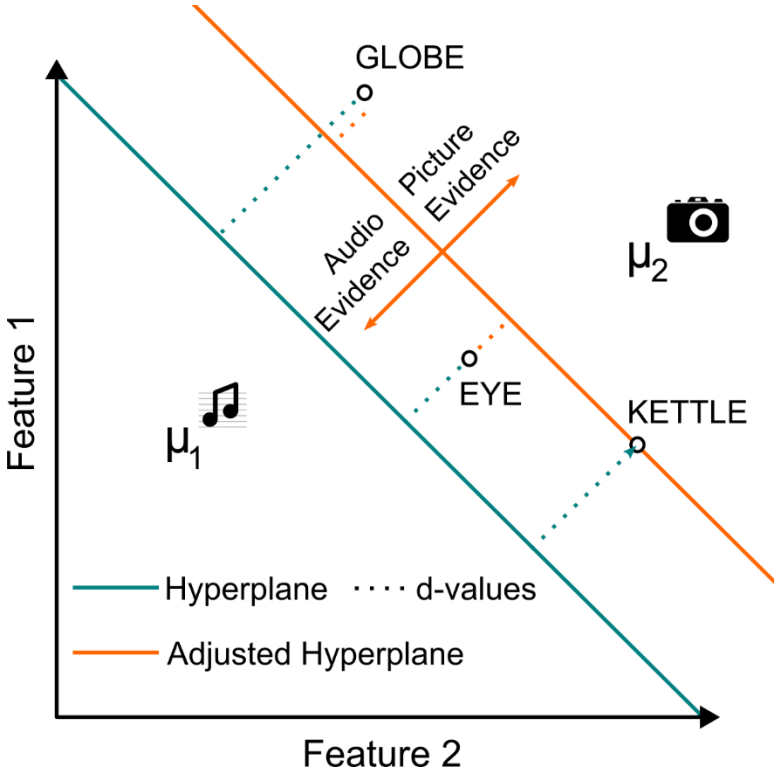

Figure S2. Linear discriminant classification analyses. Images illustrate the multivariate classification approach used on test trials after training LDA classifiers to classify neural patterns associated with hearing words and seeing pictures during encoding, and the adjustment for new (unstudied) items. The position of items in relation to the *x*- and *y*-axes illustrate (for a 2D feature space) the position of trained LDA classification boundaries (*hyperplanes*) and test items within the multivariate coordinate spaces for the test data. The music icons denote the position of the auditory word study conditions relative to the LDA hyperplane after training (with means μ1) and the camera icons the position of the picture study conditions (with means μ2). The teal lines show the hyperplanes determined by LDA on the training (study phase) data. The orange lines show the adjusted hyperplane after *d*-values for unstudied items were taken into account for each block (see text for further details). The dotted lines show the distance to the hyperplane (*d*-values). Teal dotted lines are the original *d*-values before new items adjustment, whereas the orange dotted lines are the

adjusted *d*-values and therefore represent the classifier evidence for audio (negative values) and picture (positive value) mnemonic information, respectively.

13.3.2 Decoding goal-related neural patterns during retrieval attempts.

To assess goal-related reinstatement during the recollection time-window, we applied LDA classifiers trained on the study phase (pictures/ auditory words) to the test phase data from new item trials. Since no information should be retrieved on new trials, any difference in reinstated neural patterns can be assumed to index differences in retrieval goals (Rugg & Wilding, 2000). Here, retrieval goals had been manipulated in the Target-Picture block versus the Target-Audio block.

However, in both experiments the LDA classifier was unable to reliably distinguish at test between attempting to retrieve picture targets and attempting to retrieve audio targets. In Experiment 1, the classifier fidelity measure revealed two non-significant clusters of reinstatement from approx. 400 to 800 ms after the retrieval cue (cluster p = .202, .422). In Experiment 2, a slightly later-onsetting cluster was found between approximately 600 to 800 ms that was not statistically significant (cluster p = .080).

13.4 Supplementary results: GLMMs on Reactivation Scores

The following tables show the results of the generalised linear mixed effect models (GLMMs) run on the reactivation scores. All models assume a gamma distribution with log-link function (see Statistical analysis in the main manuscript for details).

Table S2.

GLMM on the Reactivation Scores with Target Designation and Item Type (Fixed Effects) and Subjects (Random Intercept) during the Early Test Window (T1).

Experiment 1			
Model terms	*df*	χ^2	*p*
Target Designation	1	0.17	.676
Item Type	1	0.60	.440
Target Designation x Item Type	1	0.02	.889

Table S3.

GLMM on the Reactivation Scores with Target Designation and Item Type (Fixed Effects) and Subjects (Random Intercept) during the Late Test Window (T2).

Experiment 1			
Model terms	*df*	χ^2	*p*
Target Designation	1	2.05	.152
Item Type	1	0.14	.711
Target Designation x Item Type	1	10.03	.002

Table S4.

Post-hoc z-tests: Selective Reinstatement Effects in T2.

Experiment 1			
Target Designation	Contrast	*z*	*p*
Target Audio Block	Targets vs Non-targets	1.94	.052
Target Picture Block	Targets vs Non-targets	- 2.50	.013

Table S5.

GLMM on the Reactivation Scores with Target Designation and Item Type (Fixed Effects) and Subjects (Random Intercept) during the Early Test Window (T1).

Experiment 2			
Model terms	*df*	χ^2	*p*
Target Designation	1	2.01	.157
Item Type	1	0.57	.450
Target Designation x Item Type	1	0.05	.824

Table S6.

GLMM on the Reactivation Scores with Target Designation and Item Type (Fixed Effects) and Subjects (Random Intercept) during the Late Test Window (T2).

Experiment 2			
Model terms	*df*	χ^2	*p*
Target Designation	1	1.88	.170
Item Type	1	3.49	.062
Target Designation x Item Type	1	18.67	<.001

Table S7.

Post-hoc z-tests: Selective Reinstatement Effects in T2.

Experiment 2			
Target Designation	Contrast	*z*	*p*
Target Audio Block	Targets vs Non-targets	- 1.74	.082
Target Picture Block	Targets vs Non-targets	4.41	< .001

13.5 Supplementary results: GLMM on Reactivation Scores by Cue-Target Overlap

The following tables show the results of the GLMM run on the reactivation scores across the two Experiments (N = 55, one participant was excluded). The model assumes a gamma distribution with log-link function (see Statistical analysis in the main manuscript for details).

Table S8.

GLMM on the Reactivation Scores with Experiment, Overlap, and Item Type as (Fixed Effects) and Subjects (Random Intercept) during the Late Test Window (T2).

Experiment 1 & 2 (N = 55)			
Model terms	*df*	χ^2	*p*
Experiment	1	0.32	0.571
Overlap	1	3.89	.049
Item Type	1	1.34	.247
Experiment x Overlap	1	0.003	.954
Experiment x Item Type	1	2.78	.095
Overlap x Item Type	1	28.29	<.001
Experiment x Overlap x Item Type	1	1.53	0.217

Table S9.

Post-hoc z-tests: Selective Reinstatement Effects by Cue-Target Overlap in T2.

Experiment 1 & 2 (N = 55)					
Overlap	Contrast	*z*	*df*	*p*	Cohen's d
High	Targets vs Non-targets	4.57	159	<.001	0.36
Low	Targets vs Non-targets	- 2.93	159	.003	- 0.23

Note: Degrees of freedom (*df*) are estimated by running an equivalent linear mixed effect model on the reactivation scores assuming a normal distribution. Estimated *df*s are then used to calculate Cohen's *d*.

13.6 Supplementary results: LMM on the Left Parietal ERPs by Cue-Target Overlap

The following tables show the results of the linear mixed effect model run on left parietal ERPs across the two Experiments (N = 56; see Statistical analysis in the main manuscript for details).

Table S10.

LMM on the Left Parietal ERPs with Experiment, Overlap, and Item Type as (Fixed Effects) and Subjects (Random Intercept) during the Late Test Window (T2).

Experiment 1 & 2 (N = 56)			
Model terms	*df*	*F*	*p*
Experiment	54	4.58	.037
Overlap	162	2.10	.150
Item Type	162	14.40	<.001
Experiment x Overlap	162	0.03	.861
Experiment x Item Type	162	0.06	.804
Overlap x Item Type	162	21.19	<.001
Experiment x Overlap x Item Type	162	2.70	.134

Table S11.

Post-hoc t-tests: Selective Reinstatement Effects by Cue-Target Overlap in T2.

Experiment 1 & 2 (N = 56)					
Overlap	Contrast	*t*	*df*	*p*	Cohen's d
High	Targets vs Non-targets	5.94	162	<.001	0.47
Low	Targets vs Non-targets	-0.57	162	.569	-0.04

14. Reference

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