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ORIGINAL ARTICLE

BOLD Activity During Correct-Answer Feedback in Cued Recall Predicts Subsequent Retrieval Performance: An fMRI Investigation Using a Partial Trial Design

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Abstract

Receiving correct answer feedback following a retrieval attempt has proven to be a highly effective means of learning new information, yet the mechanisms behind its efficacy remain poorly understood. Here, fMRI was used to examine how BOLD activity measured during a period of feedback could predict subsequent memory (SM) performance on a final test. Twenty-five human subjects studied pairs of associated words, and were then asked to covertly recall target words in response to provided cues. Correct answer feedback was provided immediately after covert retrieval attempts. A partial trial design enabled separate modeling of activity related to retrieval and to feedback processing. During initial study, typical SM effects were observed across the whole brain. During feedback following a failed recall attempt, activity in only a subset of these regions predicted final test performance. These regions fell within the default mode network (DMN) and demonstrated negative SM effects, such that greater deactivation was associated with successful recall. No “task-positive” regions demonstrated SM effects in this contrast. The obtained results are consistent with a growing literature that associates DMN deactivation with successful learning in multiple task contexts, likely reflecting differences in the allocation of attentional resources during encoding.

Key words: Covert cued recall, feedback, fMRI, partial trials, subsequent memory

Introduction

An important feature of neuroimaging is the window it offers into cognitive processes that are difficult to understand based purely on behavioral observation. For instance, mechanisms associated with the successful encoding of information into human memory are difficult to isolate when they must be inferred solely from later retrieval performance. It is perhaps not surprising, then, that when event-related fMRI designs were introduced, one of the first questions asked by researchers was how activity during a study period differed for items that later were remembered successfully as compared to those that were later forgotten (Brewer et al. 1998; Wagner et al. 1998). These "subsequent memory" (SM) effects have proven to be robustly observable (Spaniol et al. 2009; Kim 2011), but are only one example of fMRI helping to guide and constrain hypotheses regarding the underlying causes of behavior. Other, similar questions have been posed regarding retrieval success effects in human memory (i.e., instances in which retrieval attempts are successful as compared with when they are not, Konishi et al. 2000; McDermott et al. 2000), or how the act of practicing retrieval may potentiate the efficacy of a subsequent learning opportunity (Nelson et al. 2013).

Within the context of SM effects, two patterns are typically observed. More commonly discussed and studied are "positive" SM effects, wherein greater activations (typically relative to a resting baseline) are associated with a higher probability of later recall. SM effects of this type were the first to be described in the literature (Brewer et al. 1998; Wagner et al. 1998). However, "negative" SM effects have also been observed, and these refer to situations in which less activity in a given region is associated with better later recall (Otten and Rugg 2001b). These generally manifest as different degrees of deactivation relative to baseline, with greater deactivation associated with a higher probability of later retrieval (e.g., Daselaar et al. 2004). Importantly, the specific regions whose activity can predict SM performance are not fixed, but depend upon the nature of the encoding task or type of retrieval test (Otten and Rugg 2001a; Dolcos et al. 2004; Uncapher et al. 2006; Otten 2007). That is, the conditions existing at both encoding and retrieval dictate which brain regions are predictive of later task performance.

One particularly effective means of encoding that has not adequately been explored using neuroimaging is the use of correct answer feedback following attempted retrieval (e.g, Pashler et al. 2005; Butler et al. 2008; Butler et al. 2013). Here, we use "feedback" to refer to a re-learning opportunity that is meant to aid in explicit retrieval, rather than implying any kind of statistical or other implicit basis for learning from feedback, which is described in a separate literature (e.g., Poldrack et al. 2001; Shohamy et al. 2004). In a typical feedback situation, subjects study a list of materials, take a memory test (usually recall or recognition), and receive the correct answer for each item after it is tested (e.g., Pashler et al. 2005). Discussions of why feedback is effective have included opportunities for error detection (Mory 2004) and have also included the possibility for strong attentional capture that might accompany correct answer feedback (Butterfield and Metcalfe 2006). Despite correct answer feedback being widely regarded as an important tool to encourage successful encoding, its mechanisms remain poorly understood.

The experimental paradigm utilized here allowed us to ask how (and where) neural activity during feedback periods could predict new learning. More specifically, we investigated SM effects during immediate correct answer feedback, focusing on neural activity that differently predicted performance on a final recall test when initial recall was unsuccessful. Subjects studied verbal paired associates and were then cued with the first word of each pair, while being asked to retrieve the second. Recall was covert and its success within the scanner was reported via button press. Feedback followed only a subset of retrieval responses, so that we could leverage the utility of a partial trial design (Shulman et al. 1999; Ollinger et al. 2001a, 2001b). This type of design allows for a separation of different trial components that are otherwise too strongly correlated to effectively estimate separately. Here, the separate trial components were "retrieval" and "feedback" periods during the Initial Recall Test.

When considering situations in which feedback following a failed retrieval attempt produces new learning compared to situations when it does not (i.e., situations in which the feedback is corrective), several possible outcomes can be hypothesized. To the extent that error detection plays a significant role in feedback-related learning, one might expect to see SM effects evident in regions such as the dorsal anterior cingulate cortex (ACC) or anterior insula/frontal operculum (aI/fO) (Nelson et al. 2010b; Neta et al. 2014). It has also been suggested that generating incorrect responses results in a reward prediction error (e.g., Scimeca and Badre 2012), and so feedback-related SM effects may be present within the striatum as well. On the other hand, if error detection *per se* is less critical than is an effective allocation of attentional resources, then one might expect more "classic" SM regions to emerge in an analysis of feedback-related activity, including the left inferior frontal gyrus (IFG) or fusiform gyrus in the case of positive SM effects, or regions within the default mode network (DMN) or parietal memory network in the case of negative SM effects (for reviews, see Kim 2011; Gilmore et al. 2015). To preview the results, typical positive and negative SM effects were observed during the initial study period. However, the only regions that consistently exhibited SM effects during both study and corrective feedback fell within the DMN. These took the form of negative SM effects, displaying different degrees of deactivation. Our findings are consistent with a growing literature that emphasizes the importance of DMN deactivations in the successful encoding of materials into long-term memory, and suggests that they may be particularly sensitive to attentional shifts that are beneficial for learning.

Materials and Methods

fMRI experiment

Participants

Thirty-two participants from Washington University in St. Louis and the surrounding area were recruited to participate in the fMRI portion of this study. Of these, 2 were excluded due to excessive movement within the scanner, 4 for failing to comply with task instructions, and 1 additional participant was excluded after disclosing that they had participated in an earlier pilot version of this experiment. The remaining 25 participants included 17 females with a mean age of 24.2 years (SD = 3.1, range: 18–31). All participants were right-handed, neurologically healthy native English speakers, with normal or corrected-to-normal vision. Informed consent was obtained from all participants in accordance with standard Washington University human research practices. Participants were paid $25/h for their participation.

Stimuli

Stimuli consisted of 180 weakly associated pairs of English words (e.g., disc–laser), selected from the Nelson et al. (2004) norms. The lexical characteristics of the word pairs were selected such that they had a mean forward cue strength of 0.02 (SD = 0.009, range = 0.01–0.07), mean cue frequency of 35.6 per million (SD = 56.8, range = 0–333), mean cue length of 5.9 letters (SD = 1.9, range = 3–12), and mean target length of 5.2 letters (SD = 1.1, range = 3–7). All word pairs were seen by all participants, with the order of presentation varying pseudorandomly across participants. Stimuli were presented as white text on a black background in 48-point Arial type.

fMRI Task Design

After giving consent and reviewing the task instructions, participants entered the fMRI scanner to begin the experiment, which consisted of three phases: Initial Study, Initial Recall Test, and a Final Recall Test (Fig. 1, top). During the Initial Study phase, participants intentionally encoded all 180 word pairs. Words were presented for 3 s, were followed by a variable fixation period of 2–9.5 s, and were presented across a total of 4 functional scan runs (45 words/run). Word pairs were organized such that on average their lexical characteristics did not differ across scan runs.

Immediately following the Initial Study runs, participants were given the Initial Recall Test, which occurred across 6 functional scan runs (30 items/run). During this test, participants were given the first word (the "cue") of each studied pair, and asked to covertly recall the second word (the "target"), which was represented on the screen with a question mark (e.g., DISC -?). Participants reported the success of their retrieval attempt by pressing one of two thumb buttons on a fiber-optic response box ("Yes" or "No"), with response mappings being counterbalanced across participants. The cue was presented for 2.5 s, and participants had until the end of this period to make their button press response.

On 67% of Initial Recall Test trials (20/run; 120 total), the 2.5 s cued recall period was followed by a Feedback period in which the complete pair (cue + target) was presented for 1.5 s, after which a centrally presented crosshair replaced the text on the screen for 1 s. Feedback was provided regardless of whether or not participants reported correctly retrieving the target word. For the remaining 33% of trials (10/run; 60 total), no feedback was provided. All trials, regardless of whether or not feedback was provided, were followed by a period of variable fixation lasting 2.5–10 s in order to improve the efficiency of the experimental design (Miezin et al. 2000). This mixture of trials with and without feedback allowed us to leverage the utility of a partial trial paradigm (Ollinger et al. 2001a, 2001b) to separately estimate BOLD responses related to the covert cued recall and feedback portions of trials. In addition, the trials without feedback also provided a useful means of estimating the accuracy of participant's responses. That is, the trials without feedback did not allow for a restudy opportunity, and so accuracy on the Final Recall Test (which was objectively measured outside the scanner) was expected to be comparable to self-reported accuracy during the (covert) Initial Recall Test taken within the scanner.

After exiting the scanner, participants were given a Final Recall Test. This occurred approximately 10 minutes after completion of the last Initial Recall Test scan. For this test, participants were given each cue word for 5 s, and in this time were instructed to type via keyboard the missing word (rather than indicating success with a button press response), allowing for objective accuracy to be assessed. A fixation cross was presented for 1 s following each final test trial. The presentation order of items in the test-only and feedback conditions was counterbalanced across participants in this final test.

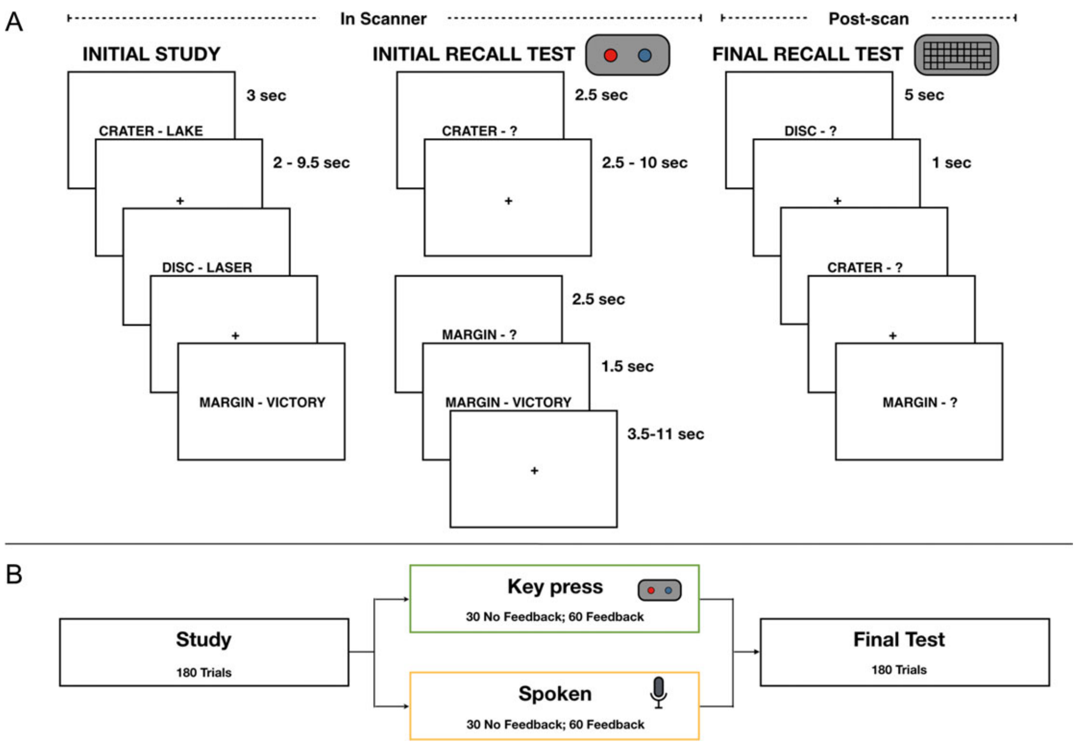

Figure 1. Design of the experiments. (A) fMRI participants encoded 180 word pairs during an Initial Study phase. An Initial Recall Test followed, in which participants covertly recalled the second (target) word when given the first (cue) word, and indicated the success of their retrieval attempt via a button-press response. On 67% of trials (regardless of whether or not recall was successful), feedback was provided by a repeated presentation of the intact word pair. After all 180 pairs had been tested in this manner, a Final Recall Test was given outside the scanner. In this test, participants had to type out the correct target word when prompted with the cue. (B) In a follow-up behavioral experiment, a separate group of participants completed a nearly identical task. Halfway through the Initial Recall Test, the response modality switched between requiring a button-press to requiring the target to be spoken aloud (with the order counterbalanced across participants). This allowed for a direct comparison of covert (button press) and overt (spoken) responses. On the Final Recall Test, participants typed their responses, as in the fMRI experiment.

Behavioral Experiment

Recent work has suggested that overt and covert cued recall similarly affect later recall probability (i.e., the magnitude of the testing effect is similar, suggesting similar processes underlying the 2 types of test, see Putnam and Roediger 2013; Smith et al. 2013). Nevertheless, we conducted a follow-up experiment in a second group of subjects. In this behavioral version of the task, we were able to ensure—within a single group of subjects—that response behaviors did not appreciably differ between overt and covert retrieval conditions.

Participants

Forty-six undergraduate participants were recruited from the Department of Psychological and Brain Sciences participant pool at Washington University. Of these, 3 were excluded due to technical issues affecting data collection, and an additional six were excluded for failing to comply with task instructions. The remaining 37 participants included 29 females, with a mean age of 19.2 years (SD = 1.1, range: 18–21). Informed consent was obtained from all participants, and they were credited for their participation at a rate of 0.5 research credits per 30 min of their participation.

Stimuli

Stimuli used in the behavioral experiment were identical to those used in the fMRI experiment.

Behavioral Task Design

The behavioral experiment consisted of three phases: Initial Study, Initial Recall Test, and a Final Recall Test (Fig. 1, bottom). Participants were instructed on the task prior to beginning the experiment, and a short instruction screen reminded the participants of the task prior to each phase in the experiment. During the Initial Study phase, participants intentionally encoded all 180 word pairs. These were presented for 3 s each, with a fixation cross being presented for 2 s after each pair was presented.

Immediately following the Initial Study phase, participants were given an Initial Recall Test. Consistent with the fMRI experiment's initial test period, participants were given the cue word of each studied pair, and asked to recall the target. Importantly, response modality changed halfway through the test. For half the participants, they began by responding to test trials by overtly speaking the target word (the "Speech" condition), and then switched to using a key press response (the "Key" condition). For the other half, the order was reversed. The output orders were therefore counterbalanced across participants. In the Speech condition, participants were prompted with the instruction "Please speak your responses" at the top of each trial. In the key press condition, participants instead were given the instruction "Please press M for yes and Z for no." The cue was presented for 2.5 s, and participants had until the end of this period to make their response. Voice responses were considered late after 2.6 s, with the additional 100 ms accounting for difficulty in assigning precise onset times of voice responses. For similar reasons, trialwise reaction times (RTs) were not calculated for voice responses. Voice responses which were made within the time limit were compared against the "Yes" button response condition. Non-responses, mumbled/inarticulate responses (for which no specific response could be identified) and late responses were compared against the "No" button press condition. Consistent with the fMRI experiment, 67% of the Initial Recall Test items were followed by Feedback, in which both the cue and the target word were presented. The feedback screen was displayed for 1.5 s. A period of fixation lasting 1–7.5 s followed every trial.

Following a 10-min break that was meant to simulate the delay involved in removing a participant from the scanner and moving them to an experiment room, participants were given a Final Recall Test. As in the fMRI experiment, no feedback was provided on this test, and the order of feedback and no-feedback items was counterbalanced across participants. Test items were presented for 5 s and participants were instructed to type the target word within this time period if they could remember it. Final test trials were separated by a fixation period of 1 s.

Initial and Final Test Performance Analysis

Unless stated otherwise, all statistical tests set $\alpha = 0.05$, and all *t*-tests are paired samples and 2-tailed.

fMRI Data Acquisition

MR images were acquired using a standard lab protocol. To help stabilize head position, participants were given foam pads and thermoplastic masks, which were fastened to the head coil. Noise-isolating headphones dampened scanner noise and enabled in-scanner communication with participants. Images were collected on a Siemens MAGNETOM Tim Trio 3.0 T Scanner (Erlangen, Germany) using a Siemens 12-channel Matrix head coil. High-resolution structural images were obtained for each participant (T1-weighted sagittal MPRAGE; TE = 3.08 ms, TR(partition) = 2400 ms, TI = 1000 ms, flip angle = 8°, 176 slices with 1 mm isotropic voxels) (Mugler and Brookerman 1990). A T2-weighted turbo spin echo sequence (TE = 84 ms, TR = 6.8 s, 32 slices of 4 mm thickness, in-plane resolution 2 × 1 mm) was conducted in the same anatomical plane as the BOLD images to improve atlas registration. Gradient field maps were also collected to estimate inhomogeneities in the magnetic field for each subject. An auto align pulse sequence protocol provided in the Siemens software was used to align the acquisition slices of the functional scans parallel to the anterior commissure–posterior commissure (AC–PC) plane. Slices were therefore collected parallel to the slices in the Talairach atlas (Talairach and Tournoux 1988). Functional imaging was performed using a BOLD contrast sensitive gradient-echo echo-planar sequence (TE = 27 ms, flip angle = 90°, in-plane resolution = 4 × 4 mm, 64 × 64 matrix). Whole-brain echo-planar image volumes (MR frames) of 32 interleaved, 4-mm thick axial slices were obtained every 2.5 s. The first 4 functional images of each scan run were discarded to allow net magnetization to reach a steady state.

An Apple iMac computer running PsyScope software (Cohen et al. 1993) was used to display experimental stimuli. An MRI compatible fiber optic key-press device recorded the participants' responses during the initial cued recall test. An LCD projector (Sharp model PG-C20XU) was used to project stimuli onto a MRI-compatible rear-projection screen (CinePlex) at the head of the bore, which the participants viewed through a mirror attached to the coil (screen resolution: 1024 × 768 pixels; field of view = 21° of visual angle).

fMRI Data Preprocessing

Imaging data from each subject were preprocessed to remove noise and artifacts, including (1) temporal re-alignment using sinc interpolation of all slices to the temporal midpoint of the first slice, to account for differences in slice time acquisition, (2) correction for movement within and across scans, using a rigid-body rotation and translation algorithm (Snyder 1996), (3) gradient field map correction to correct for spatial distortion due to local field inhomogeneities using FSL's FUGUE (http://fsl.fMRIb.ox.ac.uk), and (4) mode-1000 intensity normalization, to allow for comparisons across subjects (Ojemann et al. 1997). Functional data were then resampled into 3 mm isotropic voxels and transformed into stereotaxic atlas space. Each subject's T1-weighted image was aligned to a custom atlas-transformed (Lancaster et al. 1995) target template (711–2C) using a series of affine transforms (Michelon et al. 2003).

GLM-Based fMRI Data Analysis

Each of the 4 Initial Study task runs consisted of 134 frames (138 prior to discounting the first 4 frames of each scan), and each of the 6 Initial Recall Test runs were 109 frames (initially 113). For each participant, all runs were concatenated into a single time series (totaling 1190 frames). Data from each participant were analyzed using a general linear model (GLM; Friston et al. 1994; Miezin et al. 2000) in which the data in each voxel are treated as a sum of all effects present at that time point. The time course of activity for effects in each condition was modeled as a set of delta functions following the onset of each coded event (Ollinger et al. 2001a, 2001b). This approach assumes that all events associated with a specific condition evoke the same BOLD response, but makes no assumptions of what the shape of that response might be. Regressors reflect distinct task condition as well as effects of non-interest, the specifics of which are discussed below.

GLM Coding

For each subject, the GLM was coded with 10 separate task regressors. Four of these regressors modeled trial types that occurred during Initial Study, 2 modeled trial types that occurred during the Initial Recall Test, and another 4 modeled activity during Feedback. Those modeling study conditions were based on SM performance, as determined by the Initial and Final Recall Tests. These accounted for Initial Study conditions in which the participant indicated having correctly retrieved the target during the initial test and also produced the target correctly on the final test (CC); indicated having correctly retrieved the target on the initial test but could not produce the target on the final test (CN); indicated that they could not retrieve the target on the initial test but could produce the target on the final test (NC); or indicated that they could not produce the target on the initial test, and also failed to produce the target on the final test (NN). Initial Recall Test regressors coded for whether the target was (TC) or was not (TN) reported as being retrieved. Feedback-related regressors account for activity that occurred during Feedback for CC, CN, NC, and NN trials, based on Initial and Final Test performance. Each of the ten regressors was modeled over eight MR frames. The incorporation of temporal jitter between trials, combined with the inclusion of Initial Recall Test trials that were not followed by a feedback period, provided a sufficient number of independent equations to model the BOLD response for all conditions separately (Ollinger et al. 2001a, 2001b).

In addition to the regressors detailed above, 2 regressors of noninterest were included for each run: a trend term to account for linear changes in signal, and a constant term to model the baseline signal (which was derived from activity occurring during resting fixation periods between trials). Event-related effects are described in terms of percent signal change relative to baseline. Image processing was performed using FIDL fMRI analysis software v2.65 (written in IDL; Research Systems, Inc.). All reported atlas coordinates were converted from the initial target template (711–2C) to MNI152 space using in-house software written by Avi Snyder. For display purposes, statistical maps were projected onto a partially inflated surface representation of the human brain (fs_LR 32k) using Connectome Workbench software (Marcus et al. 2011).

Initial Study Phase SM Analysis

To examine effects related to SM performance, we conducted a voxelwise *t*-test in which activity during Initial Study for items reported as correct on the Initial Recall Test (CC + CN) was compared to activity for items reported as incorrect on the Initial Recall Test (NC + NN). Activity estimates used in this comparison were determined by averaging activity across the third, fourth, and fifth MR frames (5–12.5 s) following the onset of each trial in each set of conditions. This selection was made *a priori* and was intended to capture the main portion of the BOLD response without being influenced by potential noise at the start or end of each modeled time course. The resulting image was smoothed using a spherical Gaussian kernel with a 6 mm FWHM, and corrected for multiple comparisons to achieve a whole-brain FWE of $P < 0.05$. This correction process was based upon prior monte carlo simulations (McAvoy et al. 2001) and required a voxel significance of $z > 2.25$ with a cluster extent of at least 53 voxels.

Local maxima within the resulting statistical image were identified via an automated peak-search algorithm (peak_4dfp). This algorithm searched for peaks that were at least 10 mm apart from one another, and if multiple peaks were identified in a distance under this value, then they were consolidated in a subsequent step via coordinate averaging. Peaks that were located in white matter or CSF were excluded.

Feedback Phase SM Analysis

In addition to examining traditional SM effects, we examined how activity that occurred during Feedback after failed retrieval could differentially predict performance on the final test. That is, for items that were not recalled on the test, how did processing of correct answer feedback differ as a function of whether or not those items were later recalled on the Final Recall Test (i.e., NC and NN items)? To address this question, we conducted a *t*-test between the NC and NN feedback conditions, using test parameters, multiple comparison correction, and peak identification procedures described previously.

Assessment of Overlap Between SM Maps for the Initial Study and Feedback Phases

To assess the consistency of SM effects across different phases of the experiment, the multiple-comparison corrected statistical maps for each direction of each analysis (i.e., positive and negative SM effects for the Initial Study and Feedback phases) were binarized, and then summed. This allowed for identification of voxels that showed positive or negative SM effects throughout the experiment.

The centers of mass for clusters exhibiting overlap were identified using the peak_4dfp algorithm. To identify the centers of binarized overlap clusters, a 2-mm blurring kernel was applied prior to using the peak-finding algorithm. This smoothing step ensured that identified peaks were near the center of mass and were not based on spurious overlap near the edges of regions from binarized maps (see Nelson et al. 2016). The identified peaks were converted into 10-mm diameter regions of interest (ROIs). Within an ROI, BOLD activity in MR frames 3–5 was averaged across all voxels and extracted as a magnitude estimate.

Assessing Differences in Feedback as a Function of Initial Test Correctness

Beyond examining the neural correlates associated with the Feedback NC-NN contrast ("Corrective Feedback" that enabled correct recall after initial failure) we were also able to examine how activity during Feedback differed as a function of correctness on the Initial Recall Test. That is, for items that were ultimately correct on the Final Test, how did Feedback-related activity differ for "Yes" and "No" items on the Initial Recall Test? We conducted a *t*-test between the Feedback NC and Feedback CC conditions (representing a different type of corrective feedback). This contrast in many ways mirrors the initial SM contrast conducted on Initial Study activity, in that it compares a situation in which new learning occurred to one in which learning did not occur (albeit for presumably different reasons in this case). Multiple comparison correction and local maxima identification on statistical maps generated by this contrast were conducted in the manner described previously.

Initial Recall Test Retrieval Success Analysis

In addition to examining SM effects, we also considered retrieval-related effects in this experiment. Retrieval success effects are among those most robustly observed in cognitive neuroscience, and if these appeared unusual it might indicate that the partial trial design was impacting behavior in an unexpected manner. We therefore conducted a voxelwise *t*-test of the TC and TN conditions, comparing activity at MR frames 3–5 as described previously. Multiple comparison correction and local maxima identification were conducted in the manner described previously.

Results

Covert Responses Provided Reliable Estimates of Recall as Determined by a Postscan Final Test

Figure 2A summarizes behavioral response data for the Initial and Final Recall Tests for fMRI participants. While in the scanner, participants reported successfully recalling targets for 41.8% (SEM = 2.5%) of the 180 paired associates. In addition, participants were significantly faster at making "Yes" than "No" button press responses during the Initial Recall Test (M = 1429 ms vs. 1528 ms; $t(24) = 3.11$, $P = 0.005$). If we restrict the analysis only to trials in which participants were correct both during the Initial and Final Recall Test periods, or trials in which participants failed to identify the target at both tests (i.e., CC vs. NN), this pattern remains intact (1404 ms vs. 1511 ms; $t(24) = 3.66$, $P = 0.001$).

Upon exiting the scanner, participants were given a Final Recall Test in which they had to overtly produce (by typing) the target word in response to each cue. This final test allowed us to assess the correspondence between participant responses in the scanner and an objective measure of memory performance. Given that feedback has been shown to improve memory performance (e.g., Gilman 1969; Carrier and Pashler 1992; Pashler et al. 2005) items that were and were not followed by feedback were considered separately.

For items without feedback, participants correctly produced a target on the final test 70.0% of the time if they indicated retrieval in the scanner. Similarly, if a "No" response was given in the scanner, participants were able to recall the correct target only 19.1% of the time. Feedback improved performance on "Yes" responses; word pairs receiving initial feedback were correctly recalled on the final test 87.1% of the time. Unsurprisingly, "No" responses that were followed by feedback were often learned in this feedback period; 63.7% of the "No" responses were later retrieved correctly on the final test.

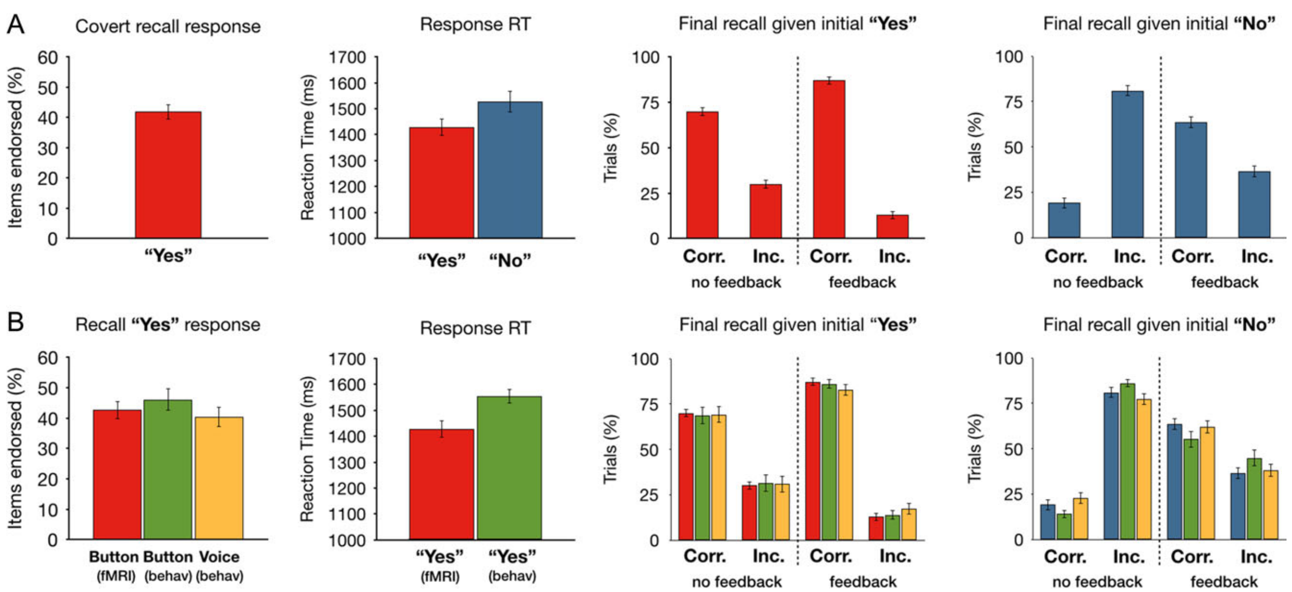

Figure 2. Behavioral results. (*A*) Covert responses appeared to provide reliable estimates of retrieval success as determined by a final (overt) cued recall test. (*B*) A follow-up experiment demonstrated that covert (button press) and overt (spoken) responses lead to very similar response behavior during both Initial and Final Recall tests.

Similar Performance was Obtained using Covert (Button Press) and Overt (Voice) Responses During the Initial Recall Test Period

There is an intuitive objection that covert cued recall conditions may lead to different participant behaviors than do overt cued recall conditions. Recent evidence suggests that this is not the case, and that response overtness does not significantly impact subsequent recall performance (Putnam and Roediger 2013; Smith et al. 2013). Nevertheless, we wished to ensure that performance within the scanner was not being distorted by the covert button press response. In a separate experiment, a new group of participants engaged in the same task as those who participated in the fMRI version, except that participants responded to half of the Initial Recall Test items verbally, while making a button press response for the other half.

Results of this behavioral follow-up are summarized in Figure 2B. Importantly, the proportion of "Yes" responses in the Initial Recall Test did not significantly differ between the covert and overt responses (46.2% vs. 40.4%; $t(36) = 1.94$, $P = 0.059$), despite the fact that in the former condition participants simply pressed a button and in the other condition subjects had to speak responses aloud to an experimenter. Differences in reaction time could not be computed between the response modalities, as no RTs were collected for the voice response condition. However, for the sake of completeness we note that the button press RT was 1555 ms (SEM = 27.5 ms) for "Yes" responses, and 1601 ms (SEM = 29.9 ms) for "No" responses. These values did not significantly differ from one another ($t(36) = 1.16$, $P = 0.252$).

When comparing Final Recall Test performance based on the Initial Recall Test response, as we did with the fMRI data, we once again failed to observe differences between button press and voice response conditions. We analyzed the final test data as a 2 × 2 repeated-measures ANOVA, with factors of Initial Recall Test response modality (button press vs. voice) and feedback condition (with vs. without feedback). For "Yes" items, feedback improved final test performance ($F_{(1,36)} = 31.98$, $P < 0.001$), but no main effect of response modality was observed ($F_{(1,36)} = 0.35$, $P = 0.558$). These factors did not interact ($F_{(1,36)} = 1.27$, $P = 0.268$). A similar pattern was obtained for initial "No" responses, where proportionally better Final Test performance was obtained after receiving feedback than without feedback ($F_{(1,36)} = 207.85$, $P < 0.001$). In this case, we did observe a main effect of Initial Test modality ($F_{(1,36)} = 13.83$, $P = 0.001$), reflecting the slightly greater proportion of correct Final Test responses for items tested under initial button-press, rather than verbal, conditions ($M = .65$ vs. $M = .61$). Importantly, no interaction was observed ($F_{(1,36)} < 0.01$, $P = 0.638$). Taken together, these results indicate that data collected in the fMRI experiment were interpretable in a straightforward manner.

As a brief final note, exploratory post-hoc comparisons indicated that in-scanner response proportions never differed significantly from those obtained in the behavioral follow-up experiment, regardless of whether the button press or voice response outputs were used in comparison. As such, the follow-up not only addressed a potential concern about covert responding within the scanner, but also served as a replication of the behavioral results we obtained in the fMRI experiment (lowest obtained P for fMRI button press vs. behavioral button press response: $t(58.9) = 1.54$, $P = 0.130$; lowest obtained P for fMRI button press vs. behavioral voice response: $t(59.2) = 1.18$, $P = .242$, each corrected for unequal variances but not for multiple comparisons).

Robust Positive and Negative SM Effects were Present During the Initial Study Phase

The design of the current experiment allowed us to separately examine activity during Initial Study, Initial Recall Test, and Feedback portions of the experiment. Consistent with prior research (e.g., Kim 2011), we found that positive SM effects were present across much of left prefrontal cortex (extending from the IFG through the middle frontal gyrus), left dorsal parietal cortex, bilateral fusiform cortex, bilateral visual cortex, ACC, and bilateral pre-SMA (Fig. 3A; Table 1) during the Initial Study phase. In addition, we observed negative SM effects in the right angular gyrus (AG), bilateral posterior cingulate cortex (PCC; extending into the precuneus and parietal-occipital sulcus), and medial prefrontal cortex (mPFC). These are also consistent with the locations of negative SM effects reported in the literature (e.g., Daselaar et al. 2004).

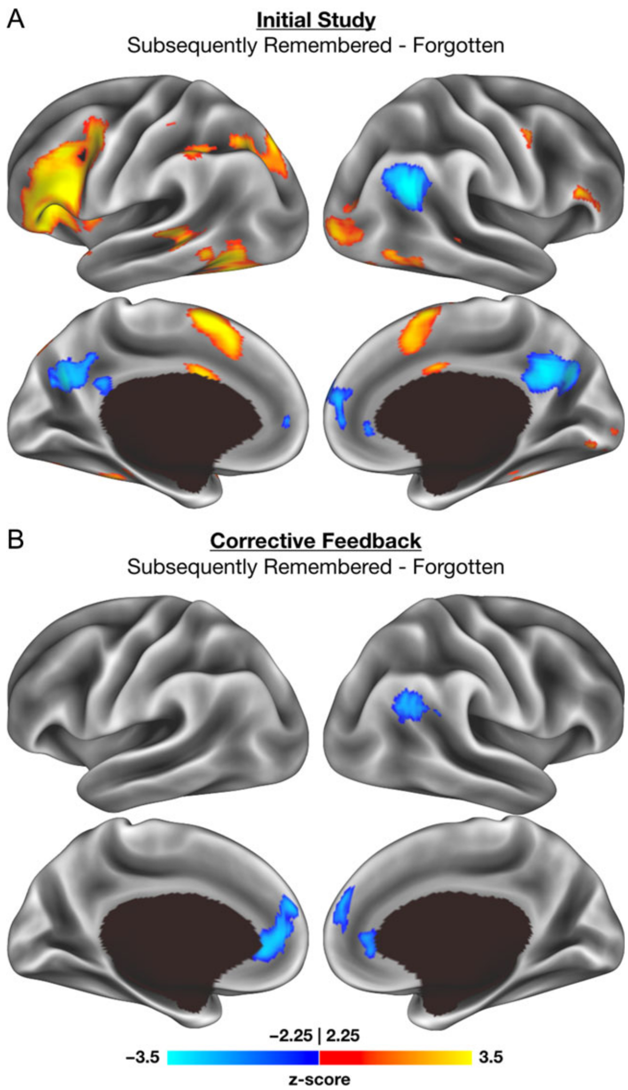

Figure 3. SM effects were observed at multiple phases of the experiment. (A) Typical SM effects (both positive and negative) were observed during the Initial Study phase. (B) During Corrective Feedback, only negative SM effects were observed. These were located in several canonical DMN regions, including mPFC and the right angular gyrus. Voxelwise results are shown on a partially inflated representation of the human cortex using Connectome Workbench software (Marcus et al. 2011).

Table 1 Regions showing SM effects during the Initial Study phase (Study CC + CN – NC + NN; paired samples t-test, 2-tailed)

Region name	X	Y	Z	z-statistic
Positive SM effects				
L Frontal Pole	−44	57	−6	2.58
L Inferior Frontal Gyrus	−51	43	−7	3.24
L Inferior Frontal Gyrus	−47	37	12	3.48
L Inferior Frontal Gyrus	−52	27	24	3.89
L Inferior Frontal Gyrus	−39	27	14	3.53
L Inferior Frontal Gyrus	−44	26	−5	4.19
L Inferior Frontal Gyrus	−48	14	−10	3.42
L Inferior Frontal Gyrus	−44	14	22	3.97
L Orbitofrontal Cortex	−33	40	−9	2.17
R Inferior Frontal Gyrus	54	39	8	3.23
R Inferior Frontal Gyrus	56	28	23	3.95
L Anterior Insula/Frontal Operculum	−33	29	4	4.37
L Anterior Insula/Frontal Operculum	−44	7	1	3.15
L Temporal Pole	−4	19	68	2.68
R Premotor Cortex	60	15	32	3.06
R Premotor Cortex	13	−6	73	2.30
L Temporal Pole	−65	−4	−12	2.79
R Superior Frontal Gyrus	14	13	68	2.30
L PreSMA	−1	13	59	4.84
R Anterior Cingulate	11	13	46	3.04
R Dorsolateral Prefrontal Cortex	52	6	49	3.40
R PreSMA	3	6	69	3.90
L Superior Temporal Sulcus	−58	5	−14	2.72
L Anterior Cingulate Cortex	−1	3	30	3.64
L Premotor Cortex	−8	3	75	2.58
L Dorsolateral Prefrontal Cortex	−43	2	43	3.63
L Dorsolateral Prefrontal Cortex	−37	−2	31	3.12
L Precentral Gyrus	−44	1	58	2.38
L Putamen	−23	−13	0	2.51
L Parahippocampal Gyrus	−31	−25	−6	3.22
L Parahippocampal Gyrus	−27	−33	−17	2.59
L Superior Temporal Gyrus	−58	−38	5	3.22
L Cerebellum	−16	−39	−19	2.83
L Cerebellum	−4	−73	−15	3.09
L Cerebellum	−26	−78	−19	2.77
R Superior Temporal Sulcus	47	−39	−1	2.67
R Fusiform Gyrus	34	−41	−19	3.36
R Fusiform Gyrus	51	−53	−9	3.20
R Fusiform Gyrus	40	−54	−25	3.91
L Anterior Intraparietal Sulcus	−46	−42	55	3.04
L Anterior Intraparietal Sulcus	−42	−44	40	3.38
L Anterior Intraparietal Sulcus	−31	−45	40	2.19
L Fusiform/Parahippocampal Gyrus	−31	−42	−22	3.74
L Fusiform Gyrus	−41	−47	−16	3.12
L Fusiform Gyrus (VWFA)	−48	−55	−4	4.18
L Fusiform Gyrus (VWFA)	−43	−63	−16	4.45
L Fusiform Gyrus (VWFA)	−49	−72	−18	3.69
R Occipital Cortex	57	−63	−10	3.35
R Occipital Cortex	41	−73	−7	3.02
R Occipital Cortex	28	−91	2	2.80
L Intraparietal Sulcus	−27	−69	37	3.89
L Intraparietal Sulcus	−22	−77	47	3.44
R Cerebellum	44	−69	−24	3.77
R Cerebellum	35	−75	−22	3.40
R Cerebellum	13	−77	−20	3.53
R Cerebellum	18	−80	−39	3.99
R Cerebellum	20	−83	−24	3.30
R Lingual Gyrus	9	−78	−9	2.65
R Lingual Gyrus	16	−86	−5	2.65
L Dorsal Precuneus	−12	−79	53	2.87

(Continued)

Table 1 (Continued)

Region name	X	Y	Z	z-statistic
R Occipital Cortex	35	−80	19	2.85
R Occipital Cortex	37	−80	4	2.72
L Posterior Intraparietal Sulcus	−24	−82	32	3.12
L Occipital Cortex	−23	−91	25	2.37
Negative SM effects				
R Superior Frontal Gyrus	13	60	21	−2.67
R Medial Prefrontal Cortex	5	53	7	−3.29
R Medial Prefrontal Cortex	6	52	17	−2.85
R Medial Prefrontal Cortex	2	43	0	−3.31
L Medial Prefrontal Cortex	−12	50	6	−2.66
L Posterior Cingulate Cortex	−11	−54	37	−2.81
R Posterior Cingulate Cortex	12	−58	31	−3.55
R Angular Gyrus	51	−58	29	−3.85
R Angular Gyrus	49	−71	42	−2.56
L Precuneus	−9	−69	28	−3.70

Negative, but not Positive, SM Effects were Observed During Corrective Feedback Following Failed Recall

The primary contribution of the current experimental design was its ability to examine brain activity during Feedback following an initial retrieval episode. Here, we primarily focus on regions involved in the "successful incorporation" of feedback ("Corrective Feedback"), such that items transition from retrieval failures on the Initial Recall Test to being correctly recalled on a Final Recall Test. To examine this question, we examined Feedback-related activity for items that were not retrieved on the Initial Recall Test, contrasting activity for those items that later went on to be successfully or unsuccessfully retrieved on the Final Recall Test (i.e., Feedback NC vs. NN items). Results of this contrast are shown in Figure 3B and reported in Table 2. No significant positive SM effects were observed. Negative SM effects were present, and were located in the right AG, ACC and portions of mPFC.

Negative SM Effects were Observed in Consistent Regions During Initial Study and Corrective Feedback Following Failed Recall

To better characterize the overlap between SM effects during Initial Study and for Corrective Feedback, conjunction images were separately made for positive SM and negative SM maps for each contrast. As no positive SM effects were observed in the Corrective Feedback contrast, no overlap was observed across the two comparisons (Fig. 4A). For negative SM effects, overlap was present in several regions of mPFC (center of mass coordinates in MNI space: 0, 46, 4; 4, 54, 18; −12, 48, 5) and in the right AG (50, −58, 30) (Fig. 4B). These regions are canonical members of the DMN (Shulman et al. 1997; Buckner et al. 2008), and deactivations in these and similar regions have been linked with successful learning in other contexts as well (e.g., Nelson et al. 2016). BOLD activity magnitudes underlying effects in several example regions showing (study-only) positive and (consistent) negative SM effects are presented in Figure 4C and D.

Feedback-Related Activity Differed for Correctly and Incorrectly Retrieved Items on the Initial Recall Test

In addition to our primary Corrective Feedback contrast, we were also able to examine how differences in "initial" recall success impacted activity during the Feedback period for items that would ultimately be recalled correctly. This addressed the question of how activity differed for items that were correctly retrieved on the Initial Recall test and for items that were not correctly recalled, in cases where both were ultimately recalled on the Final Recall test (NC-CC). This comparison can be considered complementary to the Initial Study conditions contrasted presented in Figure 3A and Table 3, but in this case attentional differences might more intuitively follow unsuccessful retrieval attempts (which required a restudy opportunity) than successful retrieval attempts (which presumably did not require significant processing). Results of this contrast are shown in Figure 5, and were generally consistent with the original SM based on activity observed during Initial Study. Greater activity for new learning (NC > CC) was present across much of left prefrontal cortex (extending from the IFG through the middle frontal gyrus), left dorsal parietal cortex, bilateral fusiform cortex, bilateral visual cortex, ACC, bilateral somatomotor cortex, and bilateral pre-SMA. Effects in the opposite direct (CC > NC) were present in the right AG, bilateral PCC (extending into the precuneus), right temporal cortex, right superior and middle frontal gyri, and mPFC.

Table 2. Regions exhibiting SM effects during Corrective Feedback (Feedback NC - NN; paired samples *t*-test, 2-tailed).

Region name	X	Y	Z	z-statistic
Positive SM Effects				
None				
Negative SM effects				
R Medial Prefrontal Cortex	4	55	28	−3.15
R Medial Prefrontal Cortex	6	47	9	−2.84
R Dorsomedial Prefrontal Cortex	8	46	37	−2.12
L Medial Prefrontal Cortex	−5	41	1	−3.21
L Anterior Cingulate Cortex	−12	45	16	−2.50
R Angular Gyrus	52	−49	28	−2.53
R Angular Gyrus	49	−60	29	−2.64

Retrieval Success Effects were Consistent with those Observed Previously in the Literature

The design of the fMRI experiment allowed us to examine BOLD activity during the Initial Recall Test in addition to activity during Initial Study and Feedback periods. To examine activity related to subjectively correct retrieval (i.e., "Yes" responses) compared to incorrect retrieval ("No" responses), we compared activity during trials in which participants reported being able to recall the target word (TC), and trials in which they could not recall the target word (TN). Results of the contrast of these conditions are shown at the top of Figure 6 and in Table 4. These resembled typical recognition memory retrieval success maps as

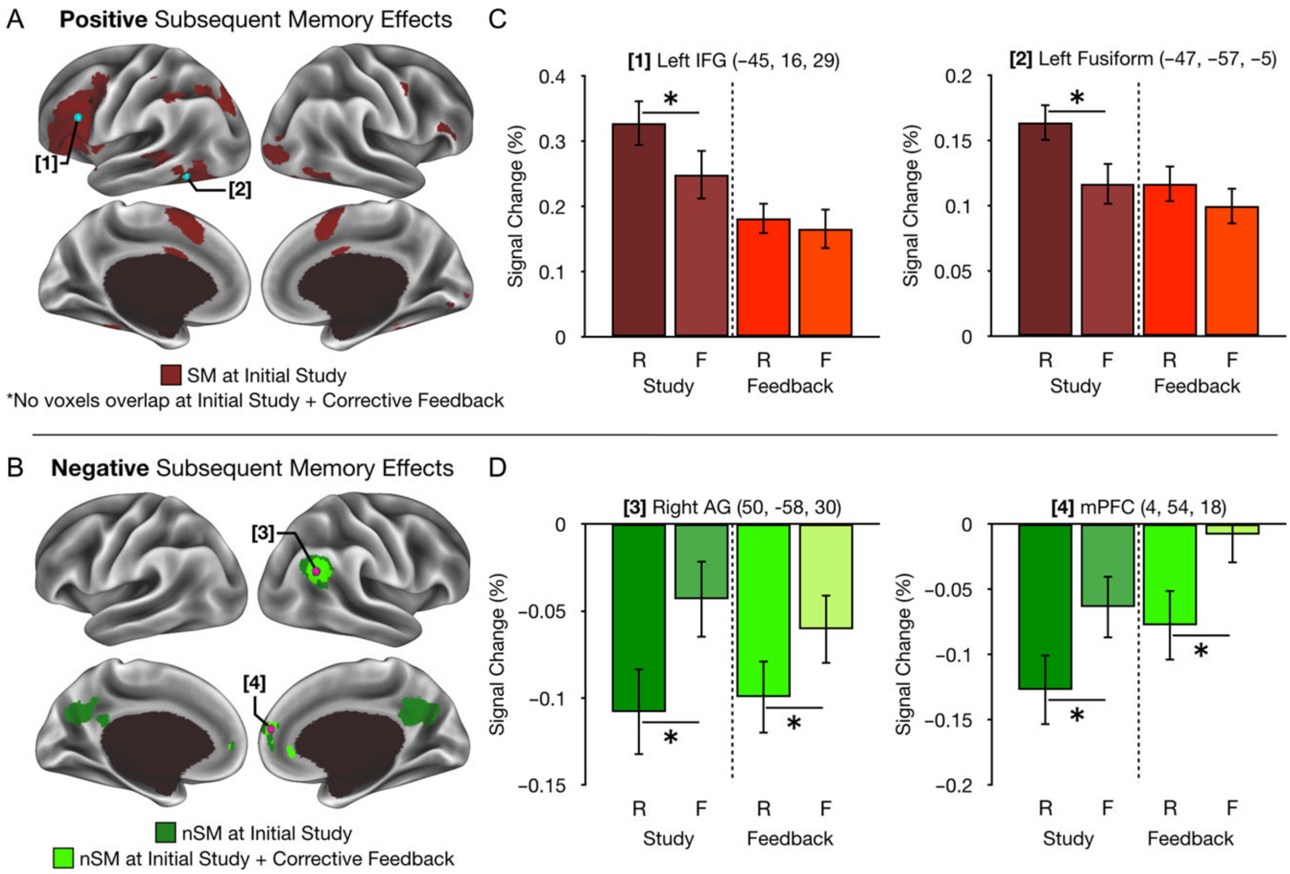

Figure 4. Overlap between positive and negative SM effects observed during Initial Study and Feedback. (*A*) No regions showed positive SM effects during both phases. Response magnitudes from several positive SM regions defined within the current dataset are shown for demonstration purposes. (*B*) Negative SM effects were observed during both Initial Study and Feedback periods, and with the Feedback effects overlapping with those observed during Initial Study. These fell within mPFC and the right angular gyrus. (*C*) Example response magnitudes during Initial Study and Feedback for positive SM regions. (*D*) Example response magnitudes during Initial Study and Feedback for negative SM regions.

Table 3. Regions exhibiting SM effects during Feedback, for items which were correctly retrieved on the Final Recall Test but differed on Initial Recall Test performance (Feedback NC - CC; paired samples *t*-test, 2-tailed).

Region name	X	Y	Z	z-statistic
Positive SM effects				
L Inferior Frontal Gyrus	−44	35	7	3.88
L Inferior Frontal Gyrus	−46	26	24	4.88
L Inferior Frontal Gyrus	−40	11	31	6.05
R Dorsal Anterior Cingulate Cortex	14	27	28	3.25
R Dorsal Anterior Cingulate Cortex	13	20	37	2.95
L Frontal Operculum	−30	25	12	4.49
L Anterior Insula	−29	24	1	4.79
L Pre−SMA	−5	14	55	5.15
R SMA	10	6	51	3.39
L Putamen	−20	4	12	3.47
R Motor Cortex	60	0	38	2.68
L Inferior Temporal Cortex	−46	−5	39	4.03
R Ventral Somatomotor Cortex	66	−10	25	3.35
L Postcentral Gyrus	−23	−36	51	3.63
L Superior Parietal Lobule	−21	−51	55	3.23
L Superior Parietal Lobule	−28	−62	42	3.99
L Fusiform Gyrus (VWFA)	−46	−56	−2	3.63
R Cerebellum	13	−77	−20	2.97
R Cerebellum	15	−79	−36	2.88
R Cerebellum	19	−80	−48	2.60
Negative SM effects				
Medial Prefrontal Cortex	0	69	2	−2.94
Medial Prefrontal Cortex	0	39	−4	−2.78
R Medial Prefrontal Cortex	2	62	20	−3.29
R Medial Prefrontal Cortex	5	52	12	−3.88
R Superior Frontal Gyrus	16	66	20	−2.57
R Superior Frontal Gyrus	16	59	28	−4.36
R Superior Frontal Gyrus	19	36	49	−3.89
R Superior Frontal Gyrus	20	22	59	−4.62
R Dorsomedial Prefrontal Cortex	3	48	31	−3.60
R Dorsomedial Prefrontal Cortex	11	44	47	−4.58
L Medial Prefrontal Cortex	−13	45	19	−3.31
R Anterior Cingulate Cortex	4	25	−3	−3.62
R Anterior Insula	26	20	−13	−3.78
R Middle Frontal Gyrus	39	20	45	−4.68
R Nucleus Accumbens	10	17	−9	−2.44
L Nucleus Accumbens	−5	15	−2	−2.67
R Putamen	18	6	−9	−3.00
R Mid-cingulate Cortex	2	−20	38	−3.22
R Middle Temporal Gyrus	62	−20	−12	−3.94
R Middle Temporal Gyrus	62	−34	−4	−4.14
R Posterior Cingulate Cortex	7	−40	36	−3.59
R Posterior Cingulate Cortex	7	−56	35	−3.82
R Anterior Inferior Parietal Lobule	52	−53	38	−4.66

derived from several recent meta-analyses (McDermott et al. 2009; Nelson et al. 2010a) (Fig. 6, middle rows), and a conjunction of all three images reveals a strong overlap (Fig. 6, bottom row). Thus, results from the specific retrieval task implemented in this experiment (i.e., covert responses in a cued recall test and partial trials) did not dramatically depart from retrieval success BOLD responses derived from other methods (see also Kim 2013).

Discussion

In this study, we employed a covert cued recall paradigm and incorporated partial trials to examine activity related to correct answer feedback during learning using fMRI. During the Initial Study phase,

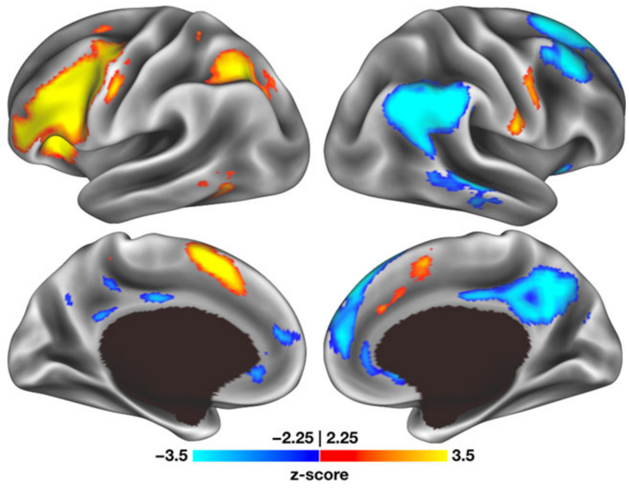

Figure 5. A contrast of Feedback-related activity for items that were recalled correctly during the Final Recall Test, but differed in their reported success on the Initial Recall Test. The contrast reflects a situation in which new learning occurred as compared to one in which it did not need to occur. These results largely recapitulate those shown in Figure 3A.

we found typical positive and negative SM effects. However, across multiple task phases, only negative SM effects were consistently observed. These were located within canonical DMN regions, and always demonstrated a pattern whereby increased levels of deactivation accompanied successful learning. We now discuss these findings in the context of the broader literature.

A Partial Trial Design Separated Retrieval and Feedback

Partial trial designs have been employed in studies of attention to separate activity related to preparatory cues from those related to a "probe" or "target" period (e.g., Shulman et al. 1999; Shulman et al. 2002), but in principle can be applied whenever successive trial components can be temporally separated (Ollinger et al. 2001a, 2001b; Ruge et al. 2009). Implementing partial trials throughout the experiment meant that we could statistically decouple activity related to retrieval from that related to the processing of feedback, which in turn enabled us to investigate each component of the trial separately. In a more traditional event-related fMRI design, our results would have been much less interpretable due to the difficulties involved in partitioning variance between the different trial components. The results—which will be discussed in more detail presently—emphasize a general utility of the partial trial design whenever separate components of a trial may be of interest, and provide a demonstration that this technique is useful well beyond the realm of attention.

Multiple Forms of SM Effect were Observed Across Initial Study and Feedback Phases

Both positive and negative SM effects were observed during the Initial Study phase, in which participants encoded verbal paired associates (Fig. 3A, Table 1). The regions showing effects in each direction were consistent with those reported previously in the literature (cf. Kim 2011). The location of SM effects observed during the Feedback phase varied depending upon the specific contrast conducted. SM effects related to Corrective Feedback (Feedback NC-NN conditions) manifested as negative SM effects that were restricted to DMN regions (Fig. 3B, Table 2). This pattern differed substantially from that obtained when

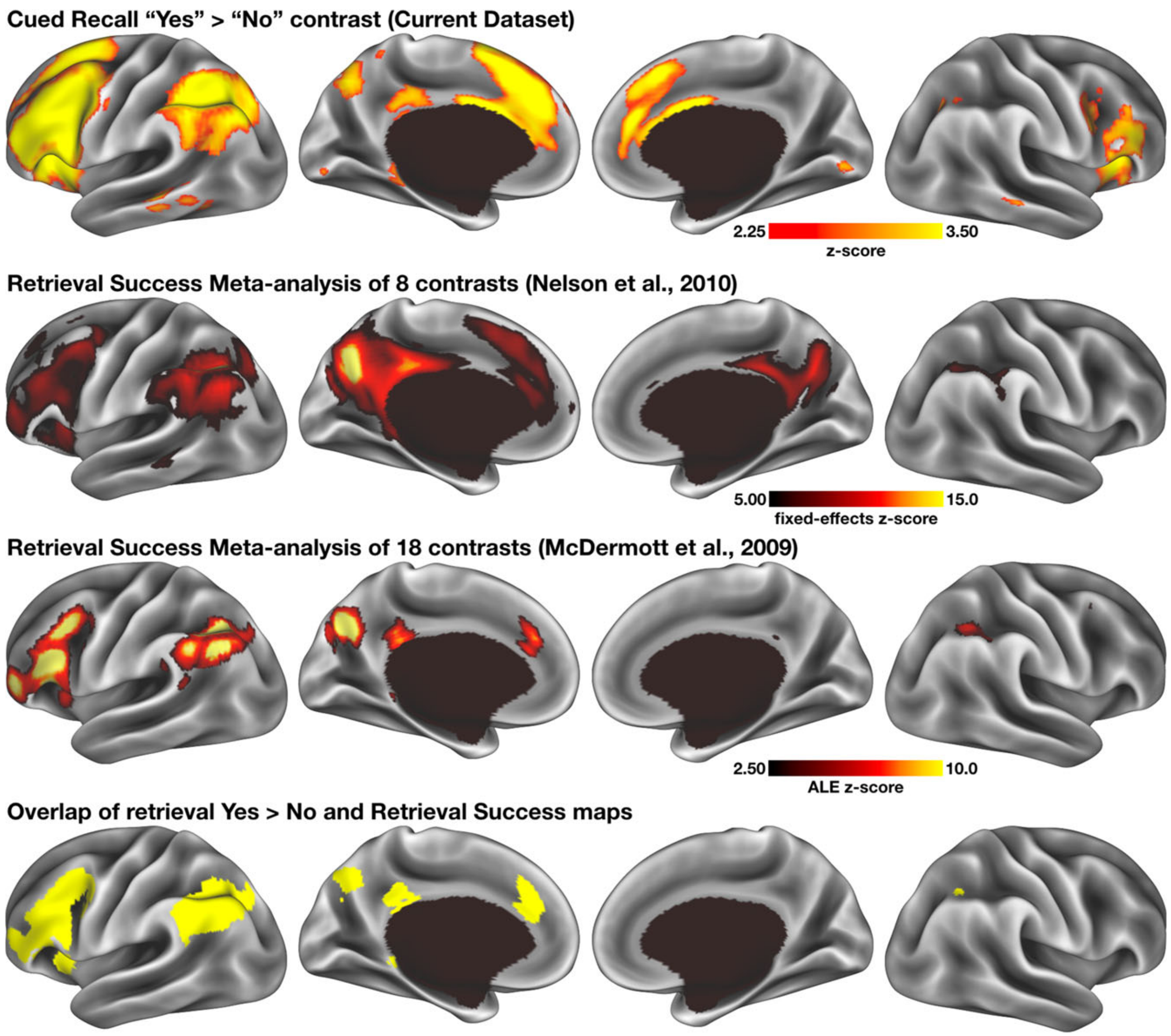

Figure 6. Retrieval success effects ("Yes" > "No") observed during the Initial Recall Test (Top Row) are similar to those observed previously in two separate meta-analyses of retrieval success effects (Middle Rows). A conjunction analysis revealed significant overlap among the three statistical maps (bottom row).

comparing activity related to items which were equated for final performance, but differed in correctness on the Initial Recall Test (i.e., Feedback NC-CC conditions; Fig. 5), suggesting that different conclusions might be usefully drawn from each contrast. We begin by considering results related to Initial Study and Corrective Feedback.

The lack of consistency observed in positive SM effects across Initial Study and Corrective Feedback contrasts echoes a broader finding in the literature, in that the location of such effects appears to depend upon the nature of the experimental task demands (e.g., Otten and Rugg 2001a; Dolcos et al. 2004; see also Kim 2011). In the case of Corrective Feedback, we did not observe any positive SM effects (Fig. 3B). This was an unexpected result, and we can speculate several possible reasons for obtaining it. Our results may, for instance, reflect a type II error—we may simply have failed to detect a "true" difference. An examination of several positive SM regions defined from the Initial Study period reveals that small, non-significant numeric differences in activity were present in the expected direction between subsequently remembered and forgotten items when examining activity during Corrective Feedback (Fig. 4C, D). These differences may be small as a consequence of sampling error, or it may be possible that the recent prior exposure to experimental stimuli caused a reduction in the overall magnitude of the BOLD response (i.e., resulted in repetition suppression) which rendered the effects undetectable given our current sample size. Although we do not wish to summarily dismiss this aspect of our results, it is certainly the case that regions exhibiting positive SM effects in the present experiment frequently show repetition suppression in the literature (Henson 2003; Schacter et al. 2007; Kim 2017). Why repetition may have impaired detection only of positive and not negative SM effects is unclear, but cannot be ruled out at present. Future examinations of feedback-related activity will be required to clarify (and indeed, simply replicate) the current result, but for now it appears that "typical" SM regions such as left IFG or the fusiform gyrus are similarly engaged regardless of whether or not new learning occurs in response to correct answer feedback.

Table 4 Regions displaying retrieval success effects during the Initial Recall Test (TC – TN; paired samples t-test, 2-tailed)

Region name	X	Y	Z	z-statistic
"Yes" > "No" response				
L Frontal Pole	−35	61	6	2.86
L Dorsomedial Prefrontal Cortex	−8	59	32	2.79
L Dorsomedial Prefrontal Cortex	−7	34	39	4.28
L Superior Frontal Gyrus	−19	56	22	3.15
L Superior Frontal Gyrus	−18	42	27	3.88
L Medial Prefrontal Cortex	−9	42	10	3.31
L Inferior Frontal Gyrus	−45	41	6	6.25
L Inferior Frontal Gyrus	−42	35	−14	2.69
L Inferior Frontal Gyrus	−54	33	−3	3.94
L Inferior Frontal Gyrus	−36	33	8	4.87
L Inferior Frontal Gyrus	43	32	−12	3.13
L Inferior Frontal Gyrus	47	28	16	3.50
L Inferior Frontal Gyrus	−39	25	−18	2.59
L Inferior Frontal Gyrus	−49	23	−11	2.99
L Inferior Frontal Gyrus	−50	15	10	3.80
L Inferior Frontal Gyrus	−41	2	31	5.63
R Anterior Cingulate Cortex	11	37	12	3.96
R Anterior Cingulate Cortex	14	35	23	4.54
R Anterior Cingulate Cortex	9	28	18	3.65
R Anterior Cingulate Cortex	14	27	36	2.96
L Middle Frontal Gyrus	−43	36	19	5.64
L Middle Frontal Gyrus	−30	35	45	2.46
L Middle Frontal Gyrus	−43	27	28	5.02
L Middle Frontal Gyrus	−32	16	40	4.51
L Middle Frontal Gyrus	−43	14	38	4.85
L Middle Frontal Gyrus	−40	3	55	3.04
L Middle Frontal Gyrus	−49	2	43	3.64
L Anterior Cingulate Cortex	−7	32	16	3.32
R SMA	7	24	49	4.37
R SMA	11	12	50	3.40
L Anterior Insula	−27	23	3	4.82
L Anterior Insula	−31	17	15	3.57
L Anterior Insula	−33	16	−9	3.91
R Anterior Insula	33	23	2	3.71
R Anterior Insula	37	17	−11	2.97
R Anterior Insula/Frontal Operculum	41	15	10	3.01
L Superior Frontal Sulcus	−19	22	47	3.75
L Superior Frontal Sulcus	−26	15	56	3.60
L Frontal Operculum	−42	21	−1	4.14
L Pre-SMA	−4	20	51	4.34
R Middle Frontal Gyrus	52	16	34	3.49
R Inferior Frontal Gyrus	57	16	6	2.94
L Caudate	−13	10	10	4.36
L SMA	−8	10	65	3.68
R Caudate	13	9	5	4.59
R Caudate	16	−2	18	3.80
R Premotor Cortex	54	7	47	3.18
R Premotor Cortex	34	1	32	3.51
L Frontal Eye Fields	−21	5	52	3.29
Mid-cingulate Cortex	0	4	30	4.91
L Putamen	−19	0	−2	3.91
L Putamen	−27	−7	−4	2.80
L Nucleus Accumbens	−4	−6	12	4.24
R Thalamus	15	−15	1	3.87
R Thalamus	11	−19	16	3.45
R Thalamus	11	−30	5	2.87
L Thalamus	−9	−16	1	3.10
L Thalamus	−26	−19	−1	3.06
L Thalamus	−4	−25	17	3.46
R Midbrain	2	−29	−5	3.91

(Continued)

Table 4 (Continued)

Region name	X	Y	Z	z-statistic
R Midbrain	6	−30	−16	3.55
L Mid-cingulate Cortex	−5	−32	38	3.43
L Parahippocampal Gyrus	−16	−38	−7	3.25
L Posterior Cingulate Cortex	−5	−39	30	2.98
L Supramarginal Gyrus	−49	−39	49	4.23
L Middle Temporal Gyrus	−60	−39	−8	2.70
L Intraparietal Sulcus	−37	−47	41	4.59
R Cerebellum	3	−49	−18	3.14
R Cerebellum	40	−62	−27	3.33
R Cerebellum	30	−67	−29	3.64
R Cerebellum	39	−69	−47	3.88
R Cerebellum	17	−77	−26	2.97
R Cerebellum	19	−82	−50	−0.49
L Dorsal Precuneus	−4	−50	63	2.97
L Supramarginal Gyrus	−53	−53	32	3.23
L Middle Temporal Gyrus	−55	−54	2	3.31
L Intraparietal Sulcus	−38	−55	53	4.67
R Intraparietal Sulcus	33	−58	39	2.80
L Occipito-temporal Cortex	−46	−59	−5	3.50
R Fusiform Gyrus	48	−62	−17	2.33
L Angular Gyrus	−40	−63	27	3.16
L Posterior Intraparietal Sulcus	−30	−64	44	5.30
R Posterior Intraparietal Sulcus	35	−69	34	3.18
L Dorsal Precuneus	−8	−70	52	2.95
L Superior Parietal Lobule	−25	−74	55	3.35
L Cerebellum	−4	−80	−18	3.07
R Lingual Gyrus	3	−85	−6	2.64
"No" > "Yes" response				
L Occipital Cortex	−51	−79	4	−2.42
L Occipital Cortex	−46	−86	12	−2.89
L Occipital Cortex	−40	−86	1	−3.03
L Occipital Cortex	−38	−93	18	−2.63

Unlike positive SM effects, negative effects were observed consistently across Initial Study and Corrective Feedback (Fig. 3). Several previous findings speak to what the effects may represent in this dataset. One growing area of literature has associated the degree of DMN deactivation with effective learning and task execution in a number of domains (Lustig et al. 2003; Daselaar et al. 2004; Huijbers et al. 2012; Vannini et al. 2013; de Chastelaine and Rugg 2014; Lee et al. 2016; Nelson et al. 2016). In this literature, greater deactivation is thought to be reflective of more effective resource allocation in stimulus processing regions, and is typically attributed to a suppression of irrelevant or competing information processing that might occur within DMN regions (Vannini et al. 2011; de Chastelaine and Rugg 2014; Nelson et al. 2016). In addition to univariate analyses suggesting this possibility, multivariate pattern classification techniques have led to a similar conclusion. More specifically, Lee et al. (2016) examined parietal deactivations associated with the successful encoding of faces and scenes, and found that the voxels "least" tuned to the processing of a particular stimulus type were "most" deactivated during encoding. As such, negative SM effects within the current dataset likely reflect proper allocation of resources in other processing regions.

A separate but related literature has focused on DMN activity as it relates to the shift of attention between internal and external orientations. Within this literature, failures to deactivate DMN regions during tasks requiring external attention are associated with mind wandering (Christoff et al. 2009), longer RTs (Weissman et al. 2006), and attentional lapses in general (for reviews, see Buckner et al. 2008; Anticevic et al. 2012). The literature would thus suggest that in the present case negative SM effects reflect not only proper allocation of neural resources, but also the timely engagement of those resources in a manner that supports successful encoding. Indeed, in the case of SM effects related to corrective feedback—in which only deactivations were observed—the shift of attention away from operations associated with retrieval and toward the re-presented word pair was likely of primary importance, as proper stimulus processing requires an effective shift away from internal representations and to what was presented on the screen.

To briefly revisit the hypotheses outlined in the introduction that were based on behavioral work, we did not see any activity in dorsal ACC, aI/fO, or other task control regions during Feedback that was predictive of performance on the Final Recall Test. This does not mean that the regions were uninvolved in error processing in the current experiment, but it does suggest that processing differences did not correlate with later memory test performance. This interpretation relies on the use of reverse inference, and should be investigated more directly in future work before firm conclusions are drawn (and other possible processes dismissed). On the other hand, as can be surmised from the preceding discussion of DMN deactivations, there does appear to be evidence that immediate Corrective Feedback is beneficial, at least in part, due to the way in which it encourages attention to be allocated to-be-learned materials.

Comparing Useful and Redundant Feedback Provides Potential Insights into Basic SM Effects

As a supplementary analysis, we also examined SM effects during feedback as determined by a comparison of items that were all correctly produced on the final test, but differed in correctness on the Initial Recall Test (i.e., NC–CC items). One can think of this (at a surface level) as being a comparison between situations in which the feedback can usefully result in learning (NC) and situations in which the feedback is redundant (CC). Further supporting this conceptual similarity, the effects revealed by the NC–CC comparison are strikingly similar to those observed during the Initial Study SM contrast (Figs 3A and 5).

Why might these maps overlap so extensively? One hypothesis is anticipated by prior explanations of SM effects, and asserts that attentional processing differs between the 2 conditions. For NC items, Feedback was important to attend to and process in order to accomplish the basic goal of learning a given word pair. CC items, on the other hand, had "already" been successfully retrieved prior to the Feedback period, and so they did not require the same amount of processing. Stated briefly, one might assume that the same general cause (differences in attentional capture or stimulus processing) underlies the effects observed here as during the Initial Study phase, with the underlying cause differing between the two cases. Importantly, this explanation is not at odds with our previous discussion related to Corrective Feedback —in the present case, the main differences are determined prior to Feedback and are a consequence of correctness on the Initial Recall Test, whereas in the case of corrective feedback all items have the same history and thus the differences are driven by the degree to which feedback can be successfully utilized.

Covert Cued Recall Represents a Useful Alternative to Recognition Memory Testing in the Scanner

The current experiment used a covert cued recall procedure, in which participants initially indicated via a button-press response whether or not their initial retrieval attempt was successful. A cued recall approach was selected because it fit naturally with a partial trial design, in that cue and probe portions of a word pair could be presented separately and sequentially. This procedure is rarely reported in the literature (but is used on occasion, e.g., Wing et al. 2013), and retrieval performance within the scanner is overwhelmingly assessed using variations of recognition testing. Although its implementation is straightforward, concerns have been raised for a long time regarding the degree to which recognition-related retrieval may be reflective of retrieval processes as a whole (for further discussion, see Rugg and Henson 2002; McDermott et al. 2009; Roediger and McDermott 2013; Chen et al. 2017). Spoken word recall is another alternative to recognition, but is accompanied by motion-related concerns that must be carefully considered and addressed (see e.g., Kragel and Polyn 2016). On the other hand, covert cued recall requires no movement beyond a simple button press, gives experimental control over the recall target without requiring a complete copy cue (as is the case with recognition memory), and does not appear to appreciably change response behavior compared to overt recall (Fig. 2B).

An important observation from the current dataset is the similarity the retrieval success effects bear to those obtained in standard old/new recognition memory contrasts (Fig. 6). This is not always the case for overt cued recall paradigms, wherein retrieval success maps tend to recapitulate aspects of the DMN (e.g., Hayama et al. 2012). At the same time, the current retrieval success image also includes activations in right anterior prefrontal cortex that have been associated with recall that are not typically observed in recognition contrasts (cf. Fig. 6, top vs. middle rows). In other words, the retrieval success map derived from the current experimental design appears to include elements associated both with recognition and recall. We cannot conclusively state what drove this result, but one possibility is that the covert nature of the task created a situation in which a "recognition-like" decision was encouraged in addition to covert recall. This may have resulted from the conversion of a retrieval operation into a binary button press, or the nature of the retrieval may have encouraged decision-making or monitoring strategies that are more typically associated with recognition memory (and familiarity-based judgments) than with recall (or recollection-based judgments) (Dobbins et al. 2002, 2003; Miller and Dobbins 2014).

With these considerations in mind, we suggest that covert cued recall as implemented in this experiment may represent a useful alternative to either recognition memory or overt recall: it provides experimenters with a means of assessing memory without providing a direct copy cue and without concerns related to vocal responses in a scanner. In exchange, one likely loses a degree of process purity, but future work may be targeted in a way that can speak to this final concern more directly. When comparing covert and overt retrieval conditions, however, one must be cautious as motion will necessarily be correlated differently with overt and covert responses.

Conclusions

Partial trials and covert cued recall were used to examine feedback-related processes with fMRI. Consistent effects were observed only for negative SM effects, in which greater deactivations were associated with successful retrieval both during an initial study period, as well as during a feedback period. This work contributes to a growing literature on the importance of task-induced deactivations leading to successful learning, and highlights the general utility offered by implementing a partial-trial design to examine separable—but typically overlapping—processes related to learning and memory.

Supplementary Material

Supplementary data are available at *Cerebral Cortex* online.

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Notes

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