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The neurocognitive basis of borrowed context information

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Abstract

Falsely remembered items can be accompanied by episodic context retrieval. This finding is difficult to explain because there is no episode that binds the remembered item to the experimenter-controlled context features. The current study examines the neural correlates of false context retrieval when the context features can be traced to encoding episodes of semantically-similar items. Our neuroimaging results support a “dissociated source” mechanism for context borrowing in false memory. We found that parahippocampal cortex (PHc) activation, thought to indicate context retrieval, was greater during trials that involved context borrowing (an incorrect, but plausible source decision) than during baseline correct context retrieval. In contrast, hippocampal activation, thought to indicate retrieval of an episodic binding, was stronger during correct source retrieval than during context borrowing. Vivid context retrieval during false recollection experiences was also indicated by increased activation in visual perceptual regions for context borrowing as compared to other incorrect source judgments. The pattern of findings suggests that context borrowing can arise when unusually strong activation of a semantically-related item's contextual features drives relatively weak retrieval of the associated episodic binding with failure to confirm the item information within that binding. This dissociated source retrieval mechanism suggests that context-driven episodic retrieval does not necessarily lead to retrieval of specific item details. That is, source information can be retrieved in the absence of item memory.

Keywords

Source memory; Context retrieval; False memory; Recollection; Medial temporal lobe

False memories can be described generally as memories for events that did not occur. Early dual process accounts of recognition assumed false memories must be based on familiarity rather than recollection because recollection requires retrieval of contextual details from the study episode (Gardiner, 1988; Jacoby, 1998; Rajaram, 1993; Yonelinas, 2002). This prediction is inconsistent with the finding that false memories are sometimes distinct and vivid and lead to recollection-based responses via the Remember/Know paradigm (see Yonelinas, 2002 for a review). Source memory paradigms provide additional insight into false recollection judgments because participants are asked to report the specific contextual

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detail that drives each recollection response. Surprisingly, false recollection can be accompanied by spuriously retrieved contextual details in source memory paradigms. Given that the contextual details are retrieved in response to an item that has not been studied, it is not clear how those contextual details are generated. The current study uses the Deese-Roediger-McDermott paradigm (DRM; Deese, 1959; Roediger & McDermott, 1995) to investigate the neural correlates of false source recollection with the goal of identifying potential cognitive and neural mechanisms that may drive the phenomenon. We developed neural predictions by integrating a theory of medial temporal lobe function with cognitive theories of the DRM paradigm.

The DRM paradigm (Deese, 1959; Roediger & McDermott, 1995) uses study words with high semantic similarity to induce false memory for a related, but unstudied, word known as the “critical lure”. Although rates of false recollection in most memory paradigms are low (see Arndt, 2012 for a review), the DRM paradigm gives rise to high rates of false recollection for critical lures (e.g. Anastasi, Rhodes, & Burns, 2000; Gallo & Roediger, 2002; Norman & Schacter, 1997; Roediger & McDermott, 1995). These false recollections cannot be attributed exclusively to errors in phenomenological judgments because they occur, and may even increase, when participants are asked to explicitly report the episodic contextual detail that they have retrieved for the critical lure (Hicks & Hancock, 2002; Hicks & Marsh, 2001; Hicks & Starns, 2006; Roediger, McDermott, Pisoni, & Gallo, 2004).

Previous research examining context retrieval in false memories suggests that context can be “borrowed” from studied items that are related to the unstudied item (Hicks & Marsh, 1999; Lampinen, Meier, Arnal, & Leding, 2005; Mather, Henkel, & Johnson, 1997; Neuschatz, Payne, Lampinen, & Toglia, 2001; Norman & Schacter, 1997; Payne, Elie, Blackwell, & Neuschatz, 1996).¹ For example, when asked to choose the encoding modality (visual or auditory presentation) of an *unstudied* critical lure, participants are more likely to choose the modality of the related DRM list than an alternate modality (Gallo, McDermott, Percer, & Roediger, 2001). Although two prior studies have investigated the neural correlates of context borrowing during encoding, both were focused on demonstrating the phenomenon rather than identifying the mechanism by which it occurs (Gershman, Schapiro, Hupbach, & Norman, 2013; St Jacques, Olm, & Schacter, 2013). For example, Gershman and colleagues (2013) presented scene stimuli as the context of an initial encoding list and showed that neural activity in the parahippocampal place area, involved in scene processing, predicted later context borrowing during a second list that did not include scene stimuli. The processes and representations that give rise to context borrowing have not been determined.

Several well-specified accounts have been proposed to explain false memories in the DRM paradigm and provide insight into potential mechanisms for context borrowing. Spreading activation theories of false memory (Howe, Wimmer, Gagnon, & Plumpton, 2009; Roediger, Balota, & Watson, 2001; Roediger, Watson, McDermott, & Gallo, 2001) propose that the semantically-related items in the DRM paradigm induce spreading of activation along their

¹The Lampinen et al. (2005) study uses the term “content borrowing” to indicate retrieval of context information for related items in response to an unstudied item. We prefer the term “context borrowing” which is specific to the type of content that is involved and will use this term instead.

associative links and thereby activate the critical lure. Semantic overlap accounts of the DRM effect rely more heavily on retrieval processing as a mechanism for false memory than do spreading activation accounts. According to these theories, the appearance of the critical lure as a test item provokes activation of features that the critical lure holds in common with the list items that were studied.

In order to interpret the predictions of cognitive theories for the neural correlates of false recollection, we will apply a theory of neural processing in the medial temporal lobe (MTL): the Binding of Item and Context (BIC) theory. BIC proposes a framework for understanding the involvement of MTL subregions in episodic memory encoding and retrieval (Diana, Yonelinas, & Ranganath, 2007; Eichenbaum, Yonelinas, & Ranganath, 2007). The theory postulates that the contextual information for an episode is processed within parahippocampal cortex (PHc), while item information, the focus of attention during encoding, is processed within perirhinal cortex (PRc). These two types of information are then associated through specialized hippocampal processing, which creates a unified, holistic, representation of the event. The BIC theory is supported by a number of findings from the source memory literature which have demonstrated that item memory is associated with PRc activation whereas context retrieval is associated with PHc and hippocampal activation (e.g. Davachi, Mitchell, & Wagner, 2003; Ranganath et al., 2004). Based on these and other findings (see Diana et al., 2007), we will interpret cognitive predictions about the strength or activation of episodic bindings as predicted changes in hippocampal activation. Predictions of degraded or strengthened context representations will be interpreted as predicted directional changes in PHc activation. We will also assume that context representations in PHc give rise to perceptual reinstatement in the appropriate modality via activation of modality-specific brain regions (Okado & Stark, 2003; Slotnick & Schacter, 2004; C. E. L. Stark, Okado, & Loftus, 2010).

The activation-monitoring account is a spreading activation theory developed to explain DRM findings (Gallo & Roediger, 2003; Roediger, Balota, et al., 2001; Roediger & McDermott, 1995; Roediger et al., 2004; Roediger, Watson, et al., 2001). If the convergence of spreading activation from related list items onto a single critical lure is sufficient to drive that critical lure into consciousness, the item is self-generated within the encoding context. Although a failure of source monitoring could lead that item to be falsely recollected during retrieval, it is not clear how contextual details that are specific to experimenter-presented items (such as a font or voice) would be incorporated into the internally-generated critical lure representation. Source retrieval for the critical lure should lead to identification of the item as self-generated in this scenario, as indicated by Gallo and Roediger (2003, p. 1037): “[I]nternally generated thoughts of nonpresented associates, on their own, should not be accompanied with the detailed recollections of actual presentation that are typically observed (e.g., perceptual characteristics).”

Although Gallo and Roediger argue that specific source retrieval *should not* occur, we might propose that it *can* occur when contextual encoding processes fail. If context representations linked to a self-generated critical lure are insufficiently specified during encoding, the activation-monitoring theory can explain false context retrieval in the DRM paradigm. In this case, perceptual information that belongs to a list item may be encoded as a feature of

the self-generated item. Therefore the modified activation monitoring account predicts that content borrowing in the DRM paradigm relies on successful retrieval of a holistic episodic representation, via hippocampal activation, which then triggers activation of an underspecified context representation, via PHc activation. Because the critical lure was not actually viewed or heard with the perceptual details suggested by the retrieved source information, perceptual reinstatement of those details (via primary visual cortex, V1, activation in the current experiment) should be weak or absent. As indicated in Table 1, when contrasted with accurate source recollection, the activation monitoring account predicts similar levels of hippocampal activation, reduced PHc activation, and reduced V1 activation.

Global-matching models, a type of semantic overlap account, propose that a mental “memory probe” is created upon presentation of a test stimulus. Retrieval responses are determined by the similarity of that memory probe to the available encoded events. A sufficiently strong match between the memory probe and encoded events, which need not be identical, leads to recognition of the test item. In the case of DRM lists, the semantic features common to the list items and critical lure drive partial activation of multiple encoded memory traces during retrieval and thereby drive false memory for the critical lure (Arndt & Hirshman, 1998; Hicks & Starns, 2006; Hintzman, 1988; Hunt & McDaniel, 1993). False recollection is explained in global matching models by specifying that the memory probe formed during retrieval includes both item and contextual information, as do the encoded memory traces (Hicks & Starns, 2006). That is, participants create imagined representations of the critical lure as though it were studied in each of the available contexts and thereby probe the encoded traces with various options. The memory probe that matches the context information encoded with the similar DRM list items will provide a stronger match than probes created from context alternatives and therefore the list-context-associated memory probe will be selected.

Thus, global matching models propose that any source information retrieved with a critical lure is derived from correct retrieval of the episodic information (including both item and context) that belongs to the related DRM list items. In this account, because memory responses are based on the matching strength of a constructed representation of the critical lure, the details of false recollection are derived from the imagined memory probe itself rather than the original memory trace. The context detail representation and any associated perceptual reinstatement during false recollection should be functionally equivalent to those occurring during correct recollection. Therefore global matching models predict, as shown in Table 1, that neural activation in response to false recollection will be similar to correct recollection in hippocampal, PHc, and V1 areas.

The Source of Activation Confusion (SAC) model (Diana, Reder, Arndt, & Park, 2006; Reder & Anderson, 1980; Reder & Ross, 1983) proposes a third mechanism for source retrieval associated with critical lures (Arndt & Reder, 2003; Oates, Reder, Cook, & Faunce, 2015). According to SAC, encoding of DRM list items involves creating a link between a concept (i.e. the word) and an experimental context via a newly created “episode node”. Grouped exposure to multiple related items leads to creation of an additional “theme node” which is also linked to the experimental context and concept nodes but not directly to the

episode node. Retrieval depends on activation of the concept node alone (via familiarity processes) or activation of the episode node and the experimental context (via recollection processes). False recollection of critical lures is based on a partial match between the features of the critical lure and feature representations associated with episode nodes for the DRM list items, including context features. This creates an atypical type of recollection in which the episode node becomes active *without* prior activation of its associated concept node (Oates et al., 2015). According to SAC, false recollection in the DRM paradigm arises from retrieval of contextual information that is sufficiently strong to drive retrieval of the associated episodic binding in the absence of item activation. Thus, context representations must be exceptionally strong in order for false recollection to proceed. Therefore, SAC predicts stronger context activation (via PHc) and stronger perceptual reinstatement as a result (via V1) for false memories than true memories. SAC predicts similar retrieval of the holistic episode representation, or hippocampal activation, in true and false source memory although it is supported by different mnemonic links.

Fuzzy trace theory provides an account of false recollection in the DRM paradigm (termed “phantom recollection” in this theory) that is based on two types of representations being formed during encoding: verbatim and gist-based traces (Brainerd, Wright, Reyna, & Mojardin, 2001; Reyna & Brainerd, 1995; Reyna, Corbin, Weldon, & Brainerd, 2016). The general meaning of the studied event is known as a gist trace, while the representation of details of the studied item, including perceptual information such as that manipulated in source memory studies, is known as a verbatim trace. These traces can be retrieved separately. Gist traces formed by the study of DRM list items match the critical lure and thereby drive false memory. False recollection is explained as spurious generation of a subjective recollection experience via activation of a gist trace, rather than retrieval of contextual information. In this account, familiarity-based representations produce the subjective experience of recollection even in the absence of contextual retrieval (Brainerd et al., 2001). This account does not propose an origin for contextual details that are reported with a falsely remembered item. We infer that it would predict fundamental differences in the neural correlates of context information retrieved in response to a critical lure and that retrieved in response to a studied item because recollection of the critical lure is driven by familiarity (Arndt, 2010). That is, retrieval of context information in response to a critical lure should be equivalent to guessing or incorrect context retrieval in response to a studied item and therefore activation associated with false recollection should be comparable to that associated with incorrect retrieval.

In order to test the predictions highlighted in Table 1, the current study will compare the neural correlates of false recollection to source memory for studied items under three conditions: 1. when context information is correctly retrieved, 2. when context information is borrowed from similar items on the study list, and 3. when context information is judged incorrectly. Although previous studies have examined the neural correlates of incorrect source retrieval in response to studied items (Karanian & Slotnick, 2014a, 2014b), to our knowledge no prior studies have examined the neural correlates of incorrect source retrieval in response to falsely remembered items. In addition, prior studies of the neural correlates of incorrect source retrieval have not differentiated between incorrect source memories in general and those driven by context borrowing from similar items.

The current study used the DRM paradigm in combination with manipulated source information (four different background colors). The use of more than two contexts allows us to identify context borrowing separately from incorrect source judgments of unknown basis. We also used a new manipulation in which a subset of critical lures were shown to participants during the study phase, as opposed to typical critical lures which are not studied. These “studied” critical lures² were presented as part of an unrelated list of words with a different background color from the semantically-related DRM list words. Studied critical lures allowed us to compare context borrowing in studied items to context borrowing in unstudied items. Neuroimaging data were collected during retrieval while participants were asked to make old or new judgments and source memory decisions (“What was the background color of this word?”) to all words identified as studied, including critical lures.

Method

Participants

The participants were 25 students at Virginia Tech who were compensated monetarily for their time. Participants were 32% male and 68% female. Participants were screened for MRI safety requirements. Of the 25 fMRI participants, 17 were included in the analyses described below. Three participants’ data sets were corrupted or incomplete due to technological problems. An additional two participants were excluded due to excessive movement which was defined as greater than 10% fMRI signal outlier trials. A final three participants were excluded due to insufficient false memories (defined as fewer than 4 unstudied critical lures judged to be “old”). Although these participants’ performance was more accurate than those remaining, they did not have sufficient trial numbers to be included in the fMRI analysis of falsely remembered items.

Procedure

Participants studied 120 lists of 7 words each. These lists were split into two study/test sequences with the proportions of stimuli, described below, equally divided between the two sessions. Of the lists studied, 70 were DRM lists (54 lists reported by Roediger, Watson, McDermott & Gallo, 2001; 16 lists created by the experimenter). Each DRM list was matched to a critical lure, the word with the highest backward-association-strength to the other items on the list. We selected a “secondary” critical lure for 20 of the DRM lists (16 experimenter-created and 4 from Roediger, Watson, et al., 2001) in order to increase the pool of stimuli for this experiment to a total of 90 critical lures. This secondary critical lure was the word with the second highest backward-association-strength to the list words.

We included both traditional critical lures (unstudied but highly related to studied items) and a new condition of studied critical lures whose purpose was to assess rates of context borrowing in true memories. The 50 studied critical lures were each studied within an unrelated list composed of randomly selected filler words. The words formed the “studied critical lure” condition. . The 40 traditional critical lures were not studied in the experiment

²Note that the studied critical lures were not, in fact, lures but rather studied items. We use the term “critical lure” to refer to this condition in order to identify these studied items as words that would be unstudied in a typical DRM paradigm.

(as is typical for the DRM procedure) and formed the “unstudied critical lure” condition. The difference in trial numbers for these two conditions was designed to balance trial numbers at retrieval when the studied critical lures were divided into three conditions (correct source, lure source, and incorrect source) whereas the unstudied critical lures were only divided into two conditions (lure source and incorrect source). Each blocked study list (7 words per list) was presented on one of four background colors. The colors were randomized with the caveat that each unrelated list was presented on a different color than the DRM list that matched its studied critical lure. That is, if the DRM list whose critical lure is “sleep” was studied on a red background, the unrelated list that contained the word sleep was studied in one of the remaining three colors. This manipulation allowed us to determine which source list (DRM list or unrelated list) the participant was retrieving during the test phase.

Participants were informed prior to beginning the study lists that they would be tested on both the words and their background colors. They were given 2 seconds to view each word, during which they were asked to judge how well the background color “fit” the word, using the numbers 1 through 4 on the keyboard to indicate their decision. This task was intended to ensure attention to each word. A fixation cross appeared between words for 250 milliseconds. All seven items from a single list were presented sequentially and with the same background color. A 2.8-second interval occurred between lists. The order of the seven words within each list and of the lists themselves was randomized across participants. fMRI data collection took place only during the test lists. Test lists were composed of all 50 studied critical lures, 50 studied filler items (from the unrelated lists), 40 studied DRM list items, 40 unstudied critical lures, and 160 new and randomly selected words. The test lists were therefore composed of 140 studied items, 40 unstudied but likely to be falsely recognized critical lures, and 160 new items. The number of new items was chosen to be approximately equivalent to the number of old items given a “perceived old” rate of 50% for the unstudied critical lures.

On each test trial, participants viewed a word and were asked first to indicate whether that word had been studied on a confidence scale ranging “sure new”, “unsure new”, and “unsure old” to “sure old”. If the word was judged to be old, participants were asked to identify the background color that had appeared with it during the study phase. During color decisions, four boxes of color corresponding to the four buttons appeared on the screen to indicate the response button mappings. The old/new and color decision screens were presented for 2 seconds each, followed by a jittered intertrial interval that ranged from 2 to 6 seconds. The color response could be given at any time from the beginning of the color decision screen to the end of the intertrial interval, at which point the next trial began. The intertrial interval and condition order at test was determined using the optseq2 optimization simulation (<http://surfer.nmr.mgh.harvard.edu/optseq/>). Test words were randomly assigned to trials within the condition order determined by optseq2.

MRI data were acquired at the Virginia Tech Corporate Research Center Human Neuroimaging Lab using a 3T Siemens Trio scanner equipped with a 12-channel phased array head coil. Functional data were obtained with a gradient echoplanar imaging (EPI) sequence (repetition time/TR, 2000 ms; echo time/TE, 25 ms; field of view, 220); each

volume had 36 axial slices, with a thickness of 3.4 mm and no interslice gap, resulting in a voxel size of $3.4 \times 3.4 \times 3.4$ mm. Additionally, T1-weighted images coplanar with the EPIs were acquired using an MPRAGE sequence (field of view, 243; voxel size = $1 \times 1 \times 1$ mm; number of slices = 192). Preprocessing was performed with Statistical Parametric Mapping (SPM8) software. EPI data were slice-time corrected with sinc interpolation to account for timing differences in acquisition of adjacent slices. The data were then realigned using a six-parameter, rigid-body transformation. Following realignment, the high-resolution structural image for each participant was coregistered to the mean EPI image for that participant. The unified segmentation tool in SPM8 was applied to the high-resolution structural image to calculate normalization parameters for each participant. The normalization parameters calculated during segmentation were applied to the EPI images. Finally, the images were spatially smoothed with an 8-mm full-width at half-maximum Gaussian filter.

The preprocessed data were analyzed with a general linear model in SPM8. All trials were modeled as a single TR (2 sec) with an onset at the beginning of the test probe and convolved with the canonical hemodynamic response function (HRF). Trials were sorted according to the stimulus type (e.g. DRM list item) and retrieval accuracy (e.g. correct source, meaning the background color was correctly identified). The primary contrasts of interest given the predictions by theories of false memory were those of context borrowing (i.e. lure source judgments) as compared to correct source judgments for both studied and unstudied critical lures.

Outliers were identified in the data using the Artifact Detection Tools (<http://gablabs.mit.edu/index.php/software>) in SPM8, with thresholds for global signal intensity ($z = 5$), translational movement (.5 mm), and rotational movement (0.05 rad). The outlier TRs were modeled as covariates of no interest. The overall alpha level was $p < .05$ which was achieved from a combination of p thresholds and cluster thresholds. The MTL cluster threshold was determined by a Monte Carlo simulation, as implemented in the 3dClustSim program in the AFNI software package, version 16.3.04 (Cox, 1996). MTL regions, for which we had *a priori* predictions, were assigned a minimum cluster size of 10 voxels at $p < .005$. Regions outside the MTL were assigned a voxel threshold of $p < .001$ which was combined with an FWE-corrected cluster threshold of $p < .05$ (as implemented in SPM8). Reported coordinates are based on the Montreal Neurological Institute (MNI) template brain.

Results

Behavioral Results

Overall memory for the studied words was significantly better than chance ($M = 66.8\%$, $t(16) = 6.10$, $p < .001$). Participants failed to give background color judgments to an average of 1.7% of items judged as old. These skipped source judgments were not included in the analyses reported below. Overall memory for the background color (source accuracy) was significantly better than the chance level of 25% ($M = 31.7\%$, $t(16) = 4.32$, $p < .001$). In order to validate our experimenter-created stimuli, we compared the old/new ratings for the primary critical lures from the original DRM lists to the DRM lists we created and found that the mean rating was 2.2 (with 1 being “sure old” and 4 being “sure new”) for both types. We also compared the old/new ratings for the 20 secondary critical lures to the primary

critical lures. Although the secondary critical lures produced fewer false memories, likely due to having lower BAS than the primary critical lures, the average old/new ratings did not differ significantly between the stimulus types ($M_{\text{primary}} = 2.3$, $M_{\text{secondary}} = 2.6$, $t(16) = 1.31$, $p = .90$).

We next assessed behavioral accuracy (see Table 2) and reaction times (see Table 3) for individual conditions of interest. DRM list items produced mean word accuracy of 64.9% and mean color accuracy of 43.1%, both significantly greater than chance (word: $t(16) = 4.94$, $p < .001$, color: $t(16) = 4.88$, $p < .001$, average of 12.17 trials per participant). Studied DRM critical lures, which were studied on unrelated lists, produced mean word accuracy of 70.0%. These items were sorted into three conditions based on the accuracy of the follow-up source judgment. Correct source judgments (i.e. the background color that corresponded to the unrelated list on which they were studied) were given on 33.3% of trials, which was significantly greater than chance ($t(16) = 3.23$, $p = .005$, average of 12 trials per participant). Participants chose the “lure source” (i.e. the background color that corresponded with the relevant DRM list rather than the unrelated list on which the critical lure was studied) significantly more often than would be expected by chance ($M = 33.1$, $t(16) = 2.96$, $p < .01$, average of 11.29 trials per participant). Finally, participants gave incorrect source judgments on 33.6% of trials with an average of 14.53 trials per participant.

Unstudied critical lures, which are new items, were judged to be old on 51.2% of trials. Of those false memories, the lure source (i.e. the background color that was used for the relevant DRM list) was selected significantly more often than chance ($M = 43.1\%$, $t(16) = 4.43$, $p < .001$, an average of 8.18 trials per participant). Therefore, we conclude that false source memory can be driven by relevant information and is not sufficiently explained as “guessing”. Reaction times to unstudied critical lures identified as old were consistently slower than the same judgments given to studied critical lures.

fMRI Results

We first compared studied critical lures assigned the correct source to DRM list items assigned the correct source (which served as a baseline measure of correct contextual retrieval). This contrast served to identify any differences in correct source recollection due to the association status of critical lures. In this analysis we found greater hippocampal activation, shown in Figure 1A, in both the left ($x = -24$, $y = -7$, $z = -26$) and right hemispheres ($x = 31$, $y = -10$, $z = -26$) for correct source retrieval with a studied critical lure than correct source retrieval with a DRM list item. Retrieval of the correct source for a critical lure requires that the participant overcome the strong competing associations of the matching DRM list and its conflicting source information. Therefore, it is not surprising that correct responses in this condition are associated with greater hippocampal activation than correct responses to relatively easy source judgments, such as the DRM list items, which did not have interfering source information. Previous studies have also found increased hippocampal activation associated with more difficult recollection tasks (Shrager, Kirwan, & Squire, 2008). Reaction times were slower for studied critical lures assigned the correct source than for DRM list items given a correct source judgment, consistent with a more

difficult decision, but the difference was not statistically significant ($t(16) = 1.38, p = .19$). Table 4 reports the complete list of activations for this contrast.

In order to test the predictions from the theories of false memory described earlier, the key comparison is between context borrowing (both to studied and unstudied items) and baseline correct source recognition, as seen in Table 1. Activation monitoring theory predicts reduced context-related activation (PHc and V1) whereas global matching models predict no difference between the two conditions and SAC predicts greater context-related activation. First, we investigated the neural processes that drive context borrowing for studied critical lures, which had higher trial numbers than the unstudied critical lure conditions. We compared context borrowing for studied critical lures to our baseline measure of correct source recognition: DRM list items given correct source judgments. As predicted by SAC, we found greater PHc activation, seen in Figure 1B (peak $t = 4.12$, cluster = 17, $p < .001$, $x = 34$, $y = -44$, $z = -9$) associated with retrieval of the lure source information in response to the studied critical lure. This activation suggests that there was stronger contextual retrieval for studied critical lures incorrectly assigned to the lure source than for correct source judgments. No other clusters survived the FWE correction and there were no suprathreshold clusters of activation in the reverse contrast.

We next compared context borrowing for studied critical lures to context borrowing for unstudied critical lures, in which the background color for the relevant DRM list was chosen for an unstudied critical lure that was incorrectly judged to be old. Prior to the study, we predicted that the two processes would be similar because both involve source information being retrieved from the encoding episodes of similar studied items rather than the item currently being accessed in memory. In fact, we did not find any regions that survived the cluster threshold in this contrast (in either direction), even when differences in reaction time between the conditions (see Table 2) were accounted for. Thus, we did not find any evidence in this paradigm for neural differences between context borrowing associated with studied items and unstudied items although this may be due to insufficient power or other idiosyncratic factors.

Given our finding that the context borrowing conditions for both types of critical lure produced similar neural signatures and given the differences in trial numbers (studied critical lure context borrowing = 11.29 trials; unstudied critical lure context borrowing = 8.26) we infer that, given sufficient power, context borrowing might produce similar findings to those of studied critical lures. We did exploratory analyses to investigate context borrowing for unstudied critical lures, specifically within MTL regions, but note that these contrasts rely on small trial numbers and therefore may not be representative of all differences.

The comparison between unstudied critical lures given a lure source judgment and studied critical lures given correct source judgments provides a test of the theories presented in Table 1. We found that studied critical lures assigned to the correct source produced greater right anterior hippocampal activation (cluster = 15, peak $t = 3.48$, $p = .001$, $x = 24$, $y = -10$, $z = -16$) than did unstudied critical lures given a lure source judgment. No other clusters of activation were found in this contrast or the reverse contrast. None of the theories reviewed predicted greater hippocampal activation for context borrowing than correct recollection.

Unstudied critical lures given a lure source judgment were next compared to all critical lures (including both studied and unstudied) given an incorrect source judgment. This contrast provides a measurement of the difference between context borrowing and failed context retrieval. The contrast revealed bilateral posterior occipital activation (cluster = 1816, cluster $p_{FWE} < .001$, peak $t = 8.29$, peak $p < .001$, $x = 10$, $y = -98$, $z = 11$, and $x = -3$, $y = -95$, $z = 11$), shown in Figure 2, in response to unstudied critical lures assigned the lure source as compared to studied items assigned an incorrect source. This finding is consistent with SAC's prediction of strong contextual memory for false recollection, which should result in perceptual reinstatement effects. We also found a significant cluster of activation for this contrast in right intraparietal sulcus (cluster = 111, cluster $p_{FWE} = .013$, peak $t = 5.71$, peak $p < .001$, $x = 38$, $y = -61$, $z = 42$).

We compared studied critical lures assigned the lure source to studied critical lures assigned the incorrect source in a direct test of fuzzy trace theory, which predicts no difference between context borrowing and incorrect source memory. Consistent with fuzzy trace theory, there were no significant areas of activation that were greater for lure source judgments than incorrect source judgments when the studied critical lures were examined.

Finally, we conducted several analyses of false memory that do not speak directly to the theories being assessed here. The first contrast compared activation associated with trials on which unstudied critical lures were incorrectly judged to be old to those on which unstudied critical lures were correctly judged to be new. Table 5 lists all findings for this contrast. We found significant clusters of activation in the left precentral gyrus/motor cortex and the left medial superior frontal gyrus. The second contrast reflects “anti-false memory” in that it compares the neural correlates of correct rejection of an unstudied critical lure with correct rejection of an unrelated new item. Critical lures might be more difficult to reject than other new items given their similarity to many list items. The reaction times in these two conditions did not differ significantly ($t(16) = 1.21$, $p = .24$), which does not support a difference in difficulty, however the numerical difference was in the expected direction (see Table 3). The fMRI contrast revealed left dlPFC activation (cluster = 153, cluster $p_{FWE} = .002$, peak $t = 6.84$, peak $p < .001$, $x = -47$, $y = 7$, $z = 42$) that was greater for correctly rejected critical lures as compared to new items. This suggests that rejecting critical lures requires more analysis and manipulation of retrieved information, potentially reflecting more attempts at recollection. No other significant clusters of activation were identified in this contrast.

Discussion

The goal of this study was to investigate how contextual details come to be retrieved with the wrong item and how contextual details can be associated with items that were not studied. Activation monitoring, global matching models, and SAC all provide different hypotheses with respect to these questions. Our behavioral results indicate that context borrowing does occur for both studied and unstudied items. Unstudied critical lures and studied critical lures were both significantly more likely to be associated with a context detail that belonged to the relevant DRM list than would be expected by chance. In the case of unstudied critical lures, this context detail is the most plausible, as there is no correct choice. In the case of studied

critical lures, this context detail overrode the correct background color that occurred for the unrelated list. We interpret this finding as evidence that false source recollection is not purely driven by guessing processes but rather can be based on information encoded in highly related episodes.

For studied critical lures, we found that choosing the “lure source” produced greater right PHc activation than did choosing the correct source for a studied list item. This finding suggests stronger context retrieval in the absence of episodic binding for context borrowing than for correct source memory. Studied critical lures that were assigned to the correct source category produced greater bilateral hippocampal activation than correct source judgments for studied list items. This finding suggests that studied critical lures, which were seen with a different background color than the associated DRM list items, needed to have strong episodic retrieval in order to be assigned to the correct source. DRM list items, in contrast, could be retrieved based on general or gist-based contextual retrieval for the list of related items and therefore did not rely as heavily on hippocampal activation. Our findings for unstudied critical lures must be cautiously interpreted given the small trial numbers. However, we did find that unstudied critical lures assigned to the lure source (i.e. the background color for the associated DRM list) produced less right anterior hippocampus activation than did correct source judgments for studied critical lures. This suggests that false source recollection is associated with reduced activation of the encoded episodic binding. There were no differences in MTL cortical regions in this contrast.

Current data in comparison to a meta-analysis of false memory fMRI studies

A recent meta-analysis and review by Kurkela and Dennis (2016) provides a thorough accounting of known neural correlates of false memories that we will compare with the current findings. Consistent with the current study, MTL activation did not reliably distinguish between true and false memories. Although some of the included studies found increased MTL activation for true memories as compared to false memories (e.g. Dennis, Bowman, & Vandekar, 2012; Kim & Cabeza, 2007), others found no differences in MTL (e.g. Dennis et al., 2012; S. M. Stark, Yassa, & Stark, 2010). The meta-analysis did not identify common regions of perceptual activation across studies, likely due to differences in the perceptual characteristics across studies, but individual studies have consistently found that perceptual activation distinguishes between true and false source memories (e.g. Gonsalves et al., 2004; Okado & Stark, 2003; C. E. L. Stark et al., 2010). As in the current study, true memories for visually-presented stimuli activate the occipital lobe more strongly than false memories during retrieval (Okado & Stark, 2003).

Our most puzzling finding: left precentral gyrus activation that was greater for unstudied critical lures labeled old than those labeled new, is also consistent with Kurkela and Dennis' (2016) meta-analysis. They found that left precentral gyrus activation was common to false retrieval in general as well as a number of more specific contrasts. This region is known to be involved in planning and coordination of motor movements which makes it a surprising finding in a purely cognitive task. They raise the possibility that planning and executing a motor response involves greater effort for false memories than true memories but also suggest that the effect could be due to confounding differences in reaction times between

true and false memories. Our findings shed some light on this proposal. With respect to reaction time, we found slower reaction times for correctly rejected unstudied critical lures than those that were falsely remembered, but this difference was not statistically significant. Also, in the current study, unstudied critical lures that were falsely remembered were followed by a source memory judgment that required a right-handed motor response whereas critical lures that were rejected required no further response. Although this right-handed button press fell outside the time window modeled in our analysis, we suggest that participants either began planning the movement immediately or used an explicit motor movement as a form of working memory. That is, participants may have moved their finger to the chosen source button immediately upon judging that the critical lure had been studied. Although this specific explanation likely does not apply to all of the studies analyzed by Kurkela and Dennis, it is consistent with their proposal that differences in motor planning for a button press response might explain the left precentral gyrus activation.

Assessing theories of false memory with respect to the current findings

We proposed mechanisms by which cognitive accounts of false memory might explain false source recollection via context borrowing in the DRM paradigm and translated these mechanisms into neuroimaging predictions via the BIC theory's account of MTL subregion function. The key results for these predictions are the comparisons of context borrowing for both studied and unstudied critical lures to correct source recognition. Although the overall pattern of findings does not precisely fit with any of the accounts discussed, some accounts provide a better fit than others. First, we found behavioral evidence for context borrowing which suggests that false recollection is not equivalent to uninformed guessing. Therefore, fuzzy trace theory is inconsistent with our behavioral findings.

Second, we found evidence that hippocampal activation drives correct source retrieval but is diminished for context borrowing. None of the theories we discussed explicitly predict reduced episodic binding in context borrowing.

Third, we found evidence that context borrowing for studied critical lures was associated with greater PHc activation than correct source retrieval. This finding contradicts the prediction from activation-monitoring theory that the context representation would be degraded in context borrowing. However, this finding is predicted by SAC because the theory proposes that context information must be exceptionally strong to drive spurious recollection of the episode during context borrowing.

Finally, we found widespread visual perceptual activation in response to unstudied critical lures being assigned to the lure source as compared to studied items given incorrect source judgments. Although previous studies have identified greater occipital activation for true memories compared to false memories (C. E. L. Stark et al., 2010), recent papers have argued that occipital lobe activation depends on perceptual vividness and therefore can be equal for both true and false memories (Karanian & Slotnick, 2014b). This may explain why we found stronger perceptual activation for a falsely remembered item that was assigned an appropriate (although misattributed) source detail over a correctly remembered item that was assigned an incorrect source detail. Our finding suggests that perceptual reinstatement associated with true memories in previous experiments may have been driven by retrieval of

particular perceptual details (in this case, background color) rather than item information (the word itself).

The finding of increased occipital activation in context borrowing is inconsistent with fuzzy trace theory's prediction that context borrowing for critical lures should be equivalent to guessing for studied items. This finding is also inconsistent with our predictions from activation-monitoring theory, which state that perceptual reinstatement during context borrowing will be degraded. Global-matching models predict equivalent perceptual reinstatement for constructed memory probes that garner sufficient matching strength from encoded memory traces and therefore does not predict a difference in this contrast. However, this finding is consistent with SAC's somewhat counterintuitive prediction that context borrowing should be driven by relatively greater perceptual feature activation than other types of judgments. This is because the active context features must be strong enough to drive the context and episode nodes above threshold even though activation is not spreading from the concept node as it would typically.

Specifying a mechanism for false recollection with context borrowing

We conclude that our results are perhaps best predicted by a combination of the SAC and BIC theories. Although we did not predict reduced episodic activation for context borrowing via SAC, the theory can plausibly account for this finding if we assume that the atypical activation of the episode node, in the absence of an active concept node, generally results in lower episodic activation despite surpassing the threshold for recollection. Correct source recollection is driven by spreading activation from both the concept and context nodes to the episode node which is likely to produce higher activation of that episode node than under conditions of context borrowing. When this assumption is made, BIC theory interprets SAC's predictions as consistent with our results. Thus, the mechanism for context borrowing in both studied and unstudied critical lures most closely matches the SAC proposal that activation of context information, in the absence of item activation, allows retrieval of the episode for related items in response to a critical lure. Thus, the context information is retrieved in response to the critical lure as a “dissociated source” accompanying a non-specified item.

The dissociated source mechanism is similar to a number of previously suggested proposals, including the “prototype-familiarity illusion” that fluent processing of an item (as in the critical lure) can allow nonconscious attribution of that item to a source that is plausible (Jacoby, Kelley, & Dywan, 1989; Whittlesea, 2002). Dissociated source is consistent with “feature borrowing” which Gallo & Roediger (2003) propose as an alternative explanation for their findings and which they derived from earlier proposals about constructive retrieval (Schacter, Norman, & Koutstaal, 1998). Our proposal is also consistent with “familiarity plus corroboration”, which takes place via borrowing of context details from presented items (Lampinen, Neuschatz, & Payne, 1999; Reyna & Titcomb, 1997). This account relies on “partially recollected” memories of related items with the recollected context details attributed to the unstudied critical lure. Finally, a recent study (Doss, Bluestone, & Gallo, 2016) used the term “perceptual recombination” to refer to partial recollection of context

features in the absence of accurate item retrieval, which is again consistent with our dissociated source proposal.

Conclusions

This study is the first to examine the neural correlates of context borrowing during retrieval. We found that falsely remembered items derived source information from semantically-related study items. We also found that source information associated with studied items could be overridden by source information from semantically-related study items. Our neuroimaging results support a “dissociated source” account of context borrowing. We found that increased PHc activation, thought to indicate context retrieval, occurred during context borrowing as compared to typical source retrieval whereas increased hippocampal activation, thought to indicate retrieval of an episodic binding, occurred during correct source retrieval. Strong context retrieval during context borrowing was also indicated by increased perceptual activation for context borrowing as compared to other incorrect source judgments. The pattern of findings suggests that context borrowing can be conceptualized as strong activation of a related item's contextual features that drives relatively weak retrieval of the associated episodic binding. This type of dissociated source retrieval may occur under other conditions and suggests that context-driven episodic retrieval need not inevitably lead to item retrieval. It also suggests that context features as processed via PHc are not item-specific but rather can be incorporated into differing events.

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References

- Anastasi JS, Rhodes MG, Burns MC. Distinguishing between memory illusions and actual memories using phenomenological measurements and explicit warnings. *The American Journal of Psychology*. 2000; 113(1):1–26. [PubMed: 10742841]
- Arndt J. The role of memory activation in creating false memories of encoding context. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2010; 36(1):66–79. <https://doi.org/10.1037/a0017394>.
- Arndt, J. *Psychology of Learning and Motivation*. Vol. 56. Elsevier; 2012. False Recollection: Empirical findings and their theoretical implications.; p. 81-124. Retrieved from <http://linkinghub.elsevier.com/retrieve/pii/B9780123943934000030>
- Arndt J, Hirshman E. True and false recognition in MINERVA2: Explanations from a global matching perspective. *Journal of Memory and Language*. 1998; 39(3):371–391. <https://doi.org/10.1006/jmla.1998.2581>.
- Arndt J, Reder LM. The effect of distinctive visual information on false recognition. *Journal of Memory and Language*. 2003; 48(1):1–15. [https://doi.org/10.1016/S0749-596X\(02\)00518-1](https://doi.org/10.1016/S0749-596X(02)00518-1).
- Brainerd CJ, Wright R, Reyna VF, Mojardin AH. Conjoint recognition and phantom recollection. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2001; 27(2):307.
- Cirelli LK, Dickinson J, Poirier M. Using Implicit Instructional Cues to Influence False Memory Induction. *Journal of Psycholinguistic Research*. 2015; 44(5):485–494. <https://doi.org/10.1007/s10936-014-9301-y>. [PubMed: 24807061]
- Collins AM, Loftus EF. A spreading-activation theory of semantic processing. *Psychological Review*. 1975; 82(6):407–428. <https://doi.org/10.1037/0033-295X.82.6.407>.

- Cox RW. AFNI: software for analysis and visualization of functional magnetic resonance neuroimages. *Computers and Biomedical Research, an International Journal*. 1996; 29(3):162–173.
- Davachi L, Mitchell JP, Wagner A. Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences*. 2003; 100:2157–2162.
- Deese J. On the prediction of occurrence of particular verbal intrusions in immediate recall. *Journal of Experimental Psychology*. 1959; 58(1):17–22. <https://doi.org/10.1037/h0046671>. [PubMed: 13664879]
- Dennis NA, Bowman CR, Vandekar SN. True and phantom recollection: an fMRI investigation of similar and distinct neural correlates and connectivity. *NeuroImage*. 2012; 59(3):2982–2993. <https://doi.org/10.1016/j.neuroimage.2011.09.079>. [PubMed: 22001165]
- Diana RA, Reder LM, Arndt J, Park H. Models of recognition: A review of arguments in favor of a dual-process account. *Psychonomic Bulletin & Review*. 2006; 13(1):1–21. <https://doi.org/10.3758/BF03193807>. [PubMed: 16724763]
- Diana RA, Yonelinas AP, Ranganath C. Imaging recollection and familiarity in the medial temporal lobe: a three-component model. *Trends in Cognitive Sciences*. 2007; 11(9):379–386. <https://doi.org/10.1016/j.tics.2007.08.001>. [PubMed: 17707683]
- Doss, MK., Bluestone, MR., Gallo, DA. Two Mechanisms of Constructive Recollection: Perceptual Recombination and Conceptual Fluency. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, No Pagination Specified. 2016. <https://doi.org/10.1037/xlm0000273>
- Eichenbaum H, Yonelinas AP, Ranganath C. The medial temporal lobe and recognition memory. *Annual Review of Neuroscience*. 2007; 30:123–152. <https://doi.org/10.1146/annurev.neuro.30.051606.094328>.
- Einstein GO, Hunt RR. Levels of processing and organization: Additive effects of individual-item and relational processing. *Journal of Experimental Psychology: Human Learning and Memory*. 1980; 6(5):588–598. <https://doi.org/10.1037/0278-7393.6.5.588>.
- Gallo DA, McDermott KB, Percer JM, Roediger HL. Modality effects in false recall and false recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2001; 27(2):339–353.
- Gallo DA, Roediger HL. Variability among word lists in eliciting memory illusions: Evidence for associative activation and monitoring. *Journal of Memory and Language*. 2002; 47(3):469–497. [https://doi.org/10.1016/S0749-596X\(02\)00013-X](https://doi.org/10.1016/S0749-596X(02)00013-X).
- Gallo DA, Roediger HL. The effects of associations and aging on illusory recollection. *Memory & Cognition*. 2003; 31(7):1036–1044. [PubMed: 14704018]
- Gershman SJ, Schapiro AC, Hupbach A, Norman KA. Neural Context Reinstatement Predicts Memory Misattribution. *The Journal of Neuroscience*. 2013; 33(20):8590–8595. <https://doi.org/10.1523/JNEUROSCI.0096-13.2013>. [PubMed: 23678104]
- Gonsalves B, Reber PJ, Gitelman DR, Parrish TB, Mesulam M-M, Paller KA. Neural evidence that vivid imagining can lead to false remembering. *Psychological Science*. 2004; 15(10):655–660. <https://doi.org/10.1111/j.0956-7976.2004.00736.x>. [PubMed: 15447635]
- Hege ACG, Dodson CS. Why distinctive information reduces false memories: evidence for both impoverished relational-encoding and distinctiveness heuristic accounts. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2004; 30(4):787–795. <https://doi.org/10.1037/0278-7393.30.4.787>.
- Hicks JL, Hancock TW. Backward associative strength determines source attributions given to false memories. *Psychonomic Bulletin & Review*. 2002; 9(4):807–815. [PubMed: 12613687]
- Hicks JL, Marsh RL. Attempts to reduce the incidence of false recall with source monitoring. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 1999; 25(5):1195–1209. <https://doi.org/10.1037/0278-7393.25.5.1195>.
- Hicks JL, Marsh RL. False recognition occurs more frequently during source identification than during old-new recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2001; 27(2):375–383.

- Hicks JL, Starns JJ. Remembering source evidence from associatively related items: Explanations from a global matching model. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2006; 32(5):1164–1173. <https://doi.org/10.1037/0278-7393.32.5.1164>.
- Hintzman DL. Judgments of frequency and recognition memory in a multiple-trace memory model. *Psychological Review*. 1988; 95(4):528–551. <https://doi.org/10.1037/0033-295X.95.4.528>.
- Howe ML, Wimmer MC, Gagnon N, Plumpton S. An associative-activation theory of children's and adults' memory illusions. *Journal of Memory and Language*. 2009; 60(2):229–251. <https://doi.org/10.1016/j.jml.2008.10.002>.
- Hunt RR, Einstein GO. Relational and item-specific information in memory. *Journal of Verbal Learning & Verbal Behavior*. 1981; 20(5):497–514. [https://doi.org/10.1016/S0022-5371\(81\)90138-9](https://doi.org/10.1016/S0022-5371(81)90138-9).
- Hunt RR, McDaniel MA. The enigma of organization and distinctiveness. *Journal of Memory and Language*. 1993; 32(4):421–445. <https://doi.org/10.1006/jmla.1993.1023>.
- Jacoby LL, Kelley CM, Dywan J. Memory attributions. *Varieties of Memory and Consciousness: Essays in Honour of Endel Tulving*. 1989:391–422.
- Karanian JM, Slotnick SD. False memory for context activates the parahippocampal cortex. *Cognitive Neuroscience*. 2014a; 5(3–4):186–192. <https://doi.org/10.1080/17588928.2014.938035>. [PubMed: 25012141]
- Karanian JM, Slotnick SD. The cortical basis of true memory and false memory for motion. *Neuropsychologia*. 2014b; 54:53–58. <https://doi.org/10.1016/j.neuropsychologia.2013.12.019>. [PubMed: 24389503]
- Kim H, Cabeza R. Trusting our memories: dissociating the neural correlates of confidence in veridical versus illusory memories. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*. 2007; 27(45):12190–12197. <https://doi.org/10.1523/JNEUROSCI.3408-07.2007>. [PubMed: 17989285]
- Kurkela KA, Dennis NA. Event-related fMRI studies of false memory: An Activation Likelihood Estimation meta-analysis. *Neuropsychologia*. 2016; 81:149–167. <https://doi.org/10.1016/j.neuropsychologia.2015.12.006>. [PubMed: 26683385]
- Lampinen JM, Meier CR, Arnal JD, Leding JK. Compelling untruths: content borrowing and vivid false memories. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 2005; 31(5):954–963. <https://doi.org/10.1037/0278-7393.31.5.954>.
- Lampinen JM, Neuschatz JS, Payne DG. Source attributions and false memories: a test of the demand characteristics account. *Psychonomic Bulletin & Review*. 1999; 6(1):130–135. [PubMed: 12199307]
- Mather M, Henkel LA, Johnson MK. Evaluating characteristics of false memories: remember/know judgments and memory characteristics questionnaire compared. *Memory & Cognition*. 1997; 25(6):826–837. [PubMed: 9421569]
- McCabe DP, Presmanes AG, Robertson CL, Smith AD. Item-specific processing reduces false memories. *Psychonomic Bulletin & Review*. 2004; 11(6):1074–1079. [PubMed: 15875978]
- McEvoy CL, Nelson DL, Komatsu T. What is the connection between true and false memories? The differential roles of interitem associations in recall and recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 1999; 25(5):1177–1194.
- Neuschatz JS, Payne DG, Lampinen JM, Tolia MP. Assessing the effectiveness of warnings and the phenomenological characteristics of false memories. *Memory (Hove, England)*. 2001; 9(1):53–71. <https://doi.org/10.1080/09658210042000076>.
- Norman KA, Schacter DL. False recognition in younger and older adults: Exploring the characteristics of illusory memories. *Memory & Cognition*. 1997; 25(6):838–848. <https://doi.org/10.3758/BF03211328>. [PubMed: 9421570]
- Oates, JM., Reder, LM., Cook, SP., Faunce, P. Spurious Recollection from a Dual-Process Framework The Role of Partial Matching . Raaijmakers, JGW.Criss, AH.Goldstone, RL.Nosofsky, RM., Steyvers, M., editors. Psychology Press; Hove: 2015.
- Okado Y, Stark CEL. Neural processing associated with true and false memory retrieval. *Cognitive, Affective & Behavioral Neuroscience*. 2003; 3(4):323–334.

- Payne DG, Elie CJ, Blackwell JM, Neuschatz JS. Memory illusions: Recalling, recognizing, and recollecting events that never occurred. *Journal of Memory and Language*. 1996; 35(2):261–285.
- Ranganath C, Yonelinas AP, Cohen MX, Dy CJ, Tom SM, D'Esposito M. Dissociable correlates of recollection and familiarity within the medial temporal lobes. *Neuropsychologia*. 2004; 42(1):2–13. [PubMed: 14615072]
- Reder LM, Anderson JR. A partial resolution of the paradox of interference: The role of integrating knowledge. *Cognitive Psychology*. 1980; 12(4):447–472. [https://doi.org/10.1016/0010-0285\(80\)90016-X](https://doi.org/10.1016/0010-0285(80)90016-X). [PubMed: 7418365]
- Reder LM, Ross BH. Integrated knowledge in different tasks: The role of retrieval strategy on fan effects. *Journal of Experimental Psychology: Learning, Memory, and Cognition*. 1983; 9(1):55–72. <https://doi.org/10.1037/0278-7393.9.1.55>.
- Reyna VF, Brainerd CJ. Fuzzy-trace theory: An interim synthesis. *Learning and Individual Differences*. 1995; 7(1):1–75. [https://doi.org/10.1016/1041-6080\(95\)90031-4](https://doi.org/10.1016/1041-6080(95)90031-4).
- Reyna VF, Corbin JC, Weldon RB, Brainerd CJ. How fuzzy-trace theory predicts true and false memories for words, sentences, and narratives. *Journal of Applied Research in Memory and Cognition*. 2016; 5(1):1–9. <https://doi.org/10.1016/j.jarmac.2015.12.003>. [PubMed: 27042402]
- Reyna VF, Titcomb AL. Constraints on the suggestibility of eyewitness testimony: A fuzzy-trace theory analysis. *A Synthesis of Basic and Applied Approaches to Human Memory*. 1997:157–174.
- Roediger, HL., Balota, DA., Watson, JM. Spreading activation and arousal of false memories.. In: Roediger, HL.Nairne, JS.Neath, I., Surprenant, AM., editors. *The nature of remembering: Essays in honor of Robert G. Crowder*. American Psychological Association; Washington, DC, US: 2001. p. 95-115.
- Roediger HL, McDermott KB. Creating false memories: Remembering words not presented in lists. *Journal of Experimental Psychology: Learning, Memory, & Cognition*. 1995; 21(4):803–814.
- Roediger HL, McDermott KB, Pisoni DB, Gallo DA. Illusory recollection of voices. *Memory*. 2004; 12(5):586–602. <https://doi.org/10.1080/09658210344000125>. [PubMed: 15615317]
- Roediger HL, Watson JM, McDermott KB, Gallo DA. Factors that determine false recall: A multiple regression analysis. *Psychonomic Bulletin & Review*. 2001; 8(3):385–407. <https://doi.org/10.3758/BF03196177>. [PubMed: 11700893]
- Schacter DL, Norman KA, Koutstaal W. The cognitive neuroscience of constructive memory. *Annual Review of Psychology*. 1998; 49:289–318. <https://doi.org/10.1146/annurev.psych.49.1.289>.
- Shrager Y, Kirwan CB, Squire LR. Activity in both hippocampus and perirhinal cortex predicts the memory strength of subsequently remembered information. *Neuron*. 2008; 59(4):547–553. <https://doi.org/10.1016/j.neuron.2008.07.022>. [PubMed: 18760691]
- Slotnick SD, Schacter DL. A sensory signature that distinguishes true from false memories. *Nature Neuroscience*. 2004; 7(6):664–672. <https://doi.org/10.1038/nm1252>. [PubMed: 15156146]
- St Jacques PL, Olm C, Schacter DL. Neural mechanisms of reactivation-induced updating that enhance and distort memory. *Proceedings of the National Academy of Sciences of the United States of America*. 2013; 110(49):19671–19678. <https://doi.org/10.1073/pnas.1319630110>. [PubMed: 24191059]
- Stark CEL, Okado Y, Loftus EF. Imaging the reconstruction of true and false memories using sensory reactivation and the misinformation paradigms. *Learning & Memory (Cold Spring Harbor, N.Y.)*. 2010; 17(10):485–488. <https://doi.org/10.1101/lm.1845710>.
- Stark SM, Yassa MA, Stark CEL. Individual differences in spatial pattern separation performance associated with healthy aging in humans. *Learning & Memory*. 2010; 17(6):284–288. <https://doi.org/10.1101/lm.1768110>. [PubMed: 20495062]
- Whittlesea BWA. False memory and the discrepancy-attribution hypothesis: the prototype-familiarity illusion. *Journal of Experimental Psychology. General*. 2002; 131(1):96–115. [PubMed: 11902153]

Figure 1.

Significantly greater BOLD signal for A) studied critical lures assigned the correct source information as compared to DRM list items assigned to the correct source and B) studied critical lures assigned to the lure source information as compared to DRM list items assigned to the correct source.

Figure 2. Significantly greater BOLD signal for unstudied critical lures assigned to the lure source information as compared to DRM list items given incorrect source responses. Widespread bilateral occipital activation is evident.

Table 1

Predicted neural activations for theories of DRM false memory as interpreted by BIC theory. Direction of activation is relative to correct recollection trials.

	<u>Predicted activation relative to correct recollection</u>		
	Hippocampus	PHc	V1
Activation monitoring	=	<	<
Global-matching models	=	=	=
Source of Activation Confusion	=	>	>
Fuzzy trace	<	<	<

Table 2

Percentage of old judgments and source judgments during the retrieval task. Source memory percentages are calculated relative to the number of old responses given and therefore the number of possible source judgments.

	Old	Correct source	Lure source
Studied items			
Critical lures	70.0%	33.3%	33.1%
DRM list items	64.9%	43.1%	-
Filler items	65.3%	21.9%	-
Unstudied items			
Critical lures	51.2%	-	43.1%
Random lures	37.3%	-	-

Table 3

Reaction times (RT) for word judgments and source judgments during the retrieval task. Note that the “Old (any source)” column of reaction times includes both the data from the three columns to its right (broken out into source condition) and trials where the Color/Source judgment screen timed out and therefore no source response was given.

	Word/item judgment RT				Color/source judgment RT			
	New	Old (any source)	Old Correct source	Old Lure source	Old Incorrect source	Old Correct source	Old Lure source	Old Incorrect source
Studied items								
Critical lures	1842	* ₁₆₂₀	1612	[‡] ₁₆₀₉	1575	1550	1520	1570
DRM list items	1914	[‡] ₁₆₀₉	1557	-	1661	1498	-	1622
Filler items	1805	1604	1628	-	1598	1544	-	1508
Unstudied items								
Critical lures	1829	* ₁₇₅₃	-	[‡] ₁₇₃₀	1813	-	1490	1598
Random lures	[‡] ₁₈₀₁	1750	-	-	1750	-	-	1402

* Old judgments to studied vs. unstudied critical lures, $t(16)=3.11, p<.01$

[‡] Old judgments to list items vs. New judgments to random lures, $t(16)=5.10, p<.001$

[‡] Old judgments (with eventual Lure source judgments) to studied vs. unstudied critical lures, $t(16)=2.80, p<.05$

Table 4

Peak voxels at $p < .001$ whole-brain analyses of studied critical lure with correct source versus studied DRM list item with correct source. Reported coordinates are based on the Montreal Neurological Institute (MNI) template brain.

cluster size	cluster $p_{\text{FWE-corr}}$	peak T	peak p	x	y	z	region
247	<.001	5.35	<.001	48	-3	-16	right middle temporal gyrus
				31	-10	-26	right anterior hippocampus
110	.010	6.62	<.001	-24	-7	-26	left anterior hippocampus

Table 5

Peak voxels at $p < .001$ whole-brain analyses of accepted versus rejected unstudied critical lure. Reported coordinates are based on the Montreal Neurological Institute (MNI) template brain.

cluster size	cluster $p_{\text{FWE-corr}}$	peak T	peak p	x	y	z	region
543	<.001	4.13	<.001	-30	-24	49	left precentral gyrus
81	.036	5.56	<.001	-3	31	38	left medial superior frontal gyrus