

The neural correlates of correctly rejecting lures during memory retrieval: the role of item relatedness

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Abstract Successful memory retrieval is predicated not only on recognizing old information, but also on correctly rejecting new information (lures) in order to avoid false memories. Correctly rejecting lures is more difficult when they are perceptually or semantically related to information presented at study as compared to when lures are distinct from previously studied information. This behavioral difference suggests that the cognitive and neural basis of correct rejections differs with respect to the relatedness between lures and studied items. The present study sought to identify neural activity that aids in suppressing false memories by examining the network of brain regions underlying correct rejection of related and unrelated lures. Results showed neural overlap in the right hippocampus and anterior parahippocampal gyrus associated with both related and unrelated correct rejections, indicating that some neural regions support correctly rejecting lures regardless of their semantic/perceptual characteristics. Direct comparisons between related and unrelated correct rejections showed that unrelated correct rejections were associated with greater activity in bilateral middle and inferior temporal cortices, regions that have been associated with categorical processing and semantic labels. Related correct rejections showed greater activation in visual and lateral prefrontal cortices, which have been associated with

perceptual processing and retrieval monitoring. Thus, while related and unrelated correct rejections show some common neural correlates, related correct rejections are driven by greater perceptual processing whereas unrelated correct rejections show greater reliance on salient categorical cues to support quick and accurate memory decisions.

Keywords Episodic memory · fMRI · Novelty detection · Retrieval · Medial temporal lobes

Introduction

Memory success is typically measured by one's ability to remember past experiences. However, successful memory also depends on the ability to suppress false memories by correctly rejecting new information that has not been previously encountered (Gallo et al. 2004, 2006). A wealth of behavioral evidence has suggested that individuals have greater difficulty suppressing false memories for new information that shares semantic or perceptual features with previously encountered information (i.e., related lures) compared to new information that is distinct (i.e., unrelated lures) (e.g., Arndt and Reder 2003; Deese 1959; Gallo et al. 2001; Gutchess and Park 2009; Meade et al. 2007; Seamon et al. 2002). As such, previous findings support the idea that false memory suppression for these two types of lures is mediated by dissociable cognitive and neural mechanisms. While previous neuroimaging studies have focused on elucidating the neural processes that support false memories for related and unrelated lures (for review see Dennis et al. 2015), little research has examined the cognitive and neural processes that support memory success through the correct rejection of these two types of lures. The present study sought to fill this gap in the literature by identifying

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the cognitive and neural processes involved in suppressing false memories both (a) when retrieval lures share perceptual and semantic features with studied information and (b) when they are relatively distinct.

With respect to retrieval lures, most memory studies have utilized what can be considered ‘unrelated lures.’ That is, when testing true memory, studies have typically used lures that share little perceptual or semantic overlap with items shown at encoding. As such, these items are relatively easy to correctly reject and false memory rates are typically low (e.g., Begg and Wickelgren 1974; Shepard 1967). Neuroimaging studies investigating responses to unrelated lures have found that such lures elicit increased activity in anterior portions of the medial temporal lobes (MTL) compared to true memories (Danckert et al. 2007; Daselaar et al. 2006a, b; Dudukovic and Wagner 2007; Kirchoff et al. 2000; Kohler et al. 2005; Tulving et al. 1996). As such, activity in the anterior MTL is posited to reflect a bottom-up novelty signal that is ‘triggered’ with the presentation of previously un-encountered information. Similar MTL increases have sometimes been found for new information that bears resemblance to studied information (Kumaran and Maguire 2006, 2007a). Researchers posit that this increase in activation reflects a mismatch or recall-to-reject signal within the MTL (Kumaran and Maguire 2007a, b, 2009) beyond that found for item novelty alone (Brown and Aggleton 2001). Such studies suggest that related lures might invoke a novelty signal in the MTL greater than that seen for unrelated novelty. However, given that previous studies have not examined the perceptual/semantic relatedness between lures, it remains unclear whether the strength of the MTL novelty signal is influenced by the relatedness between lures and targets.

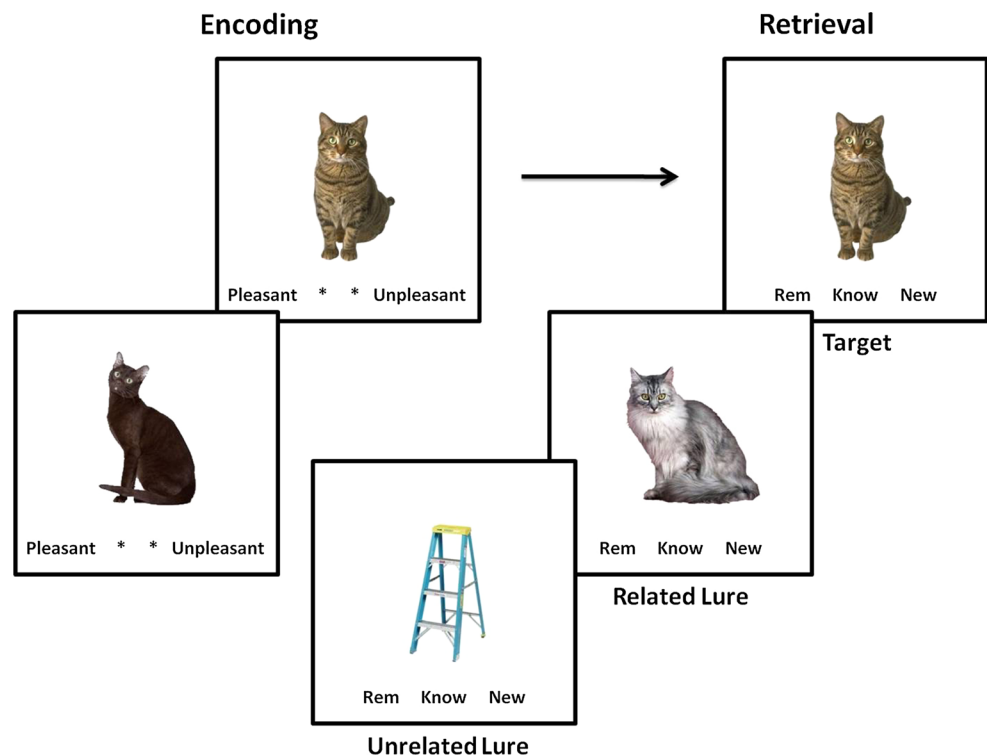
In addition to novelty detection processes within the MTL, studies investigating false memory suppression have identified monitoring and control processes that contribute to rejecting retrieval lures. Focusing on correct rejections for inaccurate associative information as compared to item information (Achim and Lepage 2005) as well as correct rejections of inaccurate source information (Gallo et al. 2006, 2010), results of these studies suggest an important role of retrieval monitoring processes subserved by the dorsolateral prefrontal cortex (DLPFC) in suppressing false memories. In addition to processing in DLPFC, previous studies have also found correct rejections to be mediated by activity within ventrolateral PFC (VLPFC) (Achim and Lepage 2005; Gallo et al. 2006). While associated with many functions, VLPFC has been posited to resolve interference between items that share semantic properties (Atkins and Reuter-Lorenz 2011; Badre and Wagner 2005; Nee et al. 2007; Postle et al. 2004; Wimber et al. 2009). Together, such frontally mediated control processes are

critical to rejecting lures that are not associated with a bottom-up novelty signal (e.g., related lures), given that they share properties with information presented at study. However, while previous research has provided evidence for the role of lateral PFC regions in rejecting complex lures, this work has been done outside the context of traditional false memory paradigms (but see Atkins and Reuter-Lorenz 2011 for a short term memory study). As such, the role of frontal regions in supporting false memory suppression across levels of semantic and perceptual relatedness remains unclear.

Neuroimaging studies utilizing related lures (e.g., new items that share perceptual or semantic overlap with old items) have typically done so in order to examine neural processes leading to false memories as opposed to those supporting the suppression of false memories (i.e., correct rejections). Results from these studies suggest that while both true and false memories are supported by reconstructive retrieval processes mediated by the MTL and frontoparietal regions (Atkins and Reuter-Lorenz 2011; Cabeza et al. 2001; Dennis et al. 2012; Garoff-Eaton et al. 2006, 2007; Gutchess and Schacter 2012; Schacter et al. 1997), true compared to false memories are often associated with increased activity within the MTL (Cabeza et al. 2001; Dennis et al. 2012; Kim and Cabeza 2007) and sensory cortices (Atkins and Reuter-Lorenz 2011; Dennis et al. 2012; Schacter et al. 1996; Slotnick and Schacter 2004). These neuroimaging findings are consistent with behavioral studies demonstrating that true compared to false memories are associated with a greater degree of perceptual detail (Marche et al. 2010; Mather et al. 1997; Norman and Schacter 1997). Thus, due to the semantic and perceptual overlap between targets and related lures, processing of specific item features is needed to support successful (true) memory. With respect to processes supporting correct rejections, when targets and lures are derived from the same category, retrieval of specific perceptual details from encoding may also support the detection of perceptual differences between these similar items, aiding in the correct identification of novel information and the suppression of false memories.

While item-specific details have been shown to separate true from false memories, false memories for related lures are often associated with enhanced processing of the overall theme or category (i.e., semantic gist) of the lure, mediated by middle and superior temporal cortices (Dennis et al. 2008, 2014a; Price 2000, 2010). While categorical overlap has been identified as a contributing factor to related false memories, it has also been suggested that categorical processing is sufficient to distinguish between new and old items when there is a distinct categorical boundary that separates targets and lures (Koutstaal 2006). As such, it follows that categorical processing is an effective means

Fig. 1 Stimuli presentation. During study, participants viewed eight exemplars from 90 categories (e.g., cats) and made pleasantness ratings for each item. At retrieval, participants saw items from encoding (targets), new items from categories presented during encoding (related lures), and new items from non-presented categories (unrelated lures). Participants made memory responses using the Remember–Know–New procedure for each item



to distinguish unrelated lures from both related lures and targets, as there is a low degree of shared semantic gist between these items. That is, gist is typically built up across a number of items within a single category, thus producing a high degree of gist that can lead to false memories. In the case of unrelated lures, it is exactly this lack of common gist between targets and lures that allows participants to make successful decisions based on semantic or categorical information alone. However, while previous findings indicate that lateral temporal regions may support false recognition of unrelated as compared to related lures (Garoff-Eaton et al. 2006), the role of these regions in supporting correct responses (i.e., correct rejections) to unrelated items remains unclear.

The current study sought to investigate neural mechanisms supporting false memory suppression by using data collected as part of a perceptual false memory study (Dennis et al. 2012) that examined retrieval processes using both related and unrelated lures. Related lures were drawn from the same categories as items shown at encoding (e.g., cats, balloons, clocks), thereby sharing both semantic and perceptual similarities with studied items, whereas unrelated lures were drawn from unique categories not presented during encoding (see Fig. 1). As a first step, we examined the neural basis of correct rejections independent of item relatedness by comparing both related and unrelated correct rejections to false recognitions, a contrast which controlled for the true history of the item (new) while assessing neural responses supporting memory accuracy. Given the

aforementioned findings regarding the neural basis of false memories and bottom-up novelty signals, we predicted that both related and unrelated correct rejections would be associated with neural activity in anterior MTL regions as well as visual cortex. With respect to distinct neural mechanisms supporting rejection of lures that differ in their relatedness to targets, we predicted that the correct rejection of unrelated lures, compared to correct rejection of related lures, would be supported by greater engagement of regions associated with semantic or categorical processing, including regions of lateral temporal cortex. We also predicted that, compared to unrelated lures, the correct rejection of related lures would assert greater demands on neural regions supporting item-specific perceptual processing and require greater monitoring processing to negotiate semantic and perceptual inference. Specifically, we predicted that, compared to unrelated correct rejections, related correct rejections would result in increased activity within early visual cortices sensitive to recapitulation of sensory details, as well as frontal regions associated with control and monitoring processes (Gallo et al. 2006, 2010; Vincent et al. 2008).

Methods

Participants

Twenty right-handed native English speakers were recruited from the Pennsylvania State University community.

Participants were screened for history of neurological disorders and psychiatric illness, alcoholism, drug use, and learning disabilities. Two participants were excluded from the analysis due to head motion in excess of 4 mm and one was excluded for performing below chance on the memory test, resulting in data from 17 participants reported in all analyses (11 females; $M = 21.28$ yrs, $SD = 1.79$). All participants provided written informed consent and received financial compensation for their participation. All experimental procedures were approved by the Pennsylvania State University's Institutional Review Board for the ethical treatment of human participants.

Stimuli

Stimuli consisted of 1092 color photographs of common objects. Images were obtained from an internet image search. All backgrounds were removed, and pictures were cropped and resized to an approximate size of 480×480 pixels. Images were presented focally and were equated for resolution. Seven hundred twenty images were presented during encoding, including 90 categories of stimuli with eight exemplars per category (see Fig. 1 for example stimuli). Stimuli included categories such as cats, balloons, and clocks. No superordinate categories (e.g., furniture) were used such that category exemplars would be varied (i.e., couches, chairs, tables). Six hundred forty two images were presented at retrieval including (a) 270 targets (three of the eight exemplars from each category), (b) 270 related lures (3 novel images associated with each encoding category), and (c) 102 unrelated lures (including three novel images from each of 34 unrelated categories). Items selected as targets were counterbalanced between participants.

Procedure

Encoding and retrieval both took place in the scanner with approximately 24 h separating the two memory phases. The 24-h delay was included both to increase the number of false recognitions made and to prevent fatigue associated with extended time in the scanner. Encoding was incidental, and participants were instructed to make subjective pleasantness ratings of objects as they were presented. Encoding images were presented for 1 s, and participants were given an additional 1 s to make their pleasantness rating, followed by a variable interstimulus interval ($M = 2$ s, range 1.5–3 s). Data analysis from only the retrieval phase will be presented in the current publication. During retrieval, participants completed six runs, each approximately 8 min in length. Each image was displayed for 2.5 s, while participants made memory responses using the 'Remember–Know–New' paradigm followed by a variable interstimulus interval ($M = 2$ s, range 1.5–3 s). In accord with

typical task instructions, participants were told to respond 'Remember' if they could recollect specific details about the object such as its shape, color, or their thoughts or feelings during its initial presentation. Participants were told to respond 'Know' if the picture looked familiar, but they could not recollect any specific details of its prior presentation. They were told to respond 'New' if they believed the picture was not presented during the encoding session. The images were pseudorandomly sorted, ensuring that no more than three images from any one category appeared in a row. Behavioral responses were recorded using a four-button response box. Images were displayed by COGENT in MATLAB (Mathworks). Scanner noise was reduced with headphones and earplugs, and cushioning was used in the head coil to minimize head motion.

Image acquisition

Images were acquired using a Siemens 3T scanner equipped with a 12-channel head coil. A T1-weighted sagittal localizer was acquired to locate the anterior (AC) and posterior (PC) commissures. Images were then prescribed parallel to the AC–PC plane. An MPRAGE was acquired with a 2300 ms TR, 3.41 ms TE, 230 mm field of view (FOV), 256^2 matrix, 160 axial slices, and 0.9 mm slice thickness for each participant. Echoplanar functional images were acquired using an interleaved acquisition, 2000 ms TR, 30 ms TE, 240 mm FOV, a 64^2 matrix, and 34 axial slices with 3.8 mm slice thickness, resulting in 3.8-mm isotropic voxels.

Behavioral analyses

To determine the effects of item relatedness on memory accuracy, 'New' response rates to targets, related lures, and unrelated lures were entered into a one-way, repeated-measures ANOVA. A similar analysis was used to measure the effects of relatedness on reaction time. Where appropriate, a Greenhouse–Geisser correction for sphericity was included to account for differences in variance between conditions. Post hoc *t* tests were used to probe significant interactions using an uncorrected threshold of $p < 0.0167$, resulting in a Bonferroni correction for multiple comparisons of $p < 0.05$.

fMRI analyses

Functional data were preprocessed and analyzed with SPM8 (Statistical Parametric Mapping; Wellcome Department of Cognitive Neurology, <http://www.fil.ion.ucl.ac.uk/spm>). Images were first checked for scanner and movement artifacts using a time-series diagnostic function TSDiffAna (Freiburg Brain Imaging) in MATLAB (Mathworks).

Time-series data were corrected for differences in slice acquisition times and realigned. Images were then co-registered to the individual's T1 image before being spatially normalized to a standard stereotaxic space using the Montreal Neurological Institute (MNI) EPI template implemented in SPM8. Finally, the volumes were spatially smoothed using an 8-mm isotropic Gaussian kernel.

Trial-related activity was modeled in the general linear model (GLM) with a stick function corresponding to trial onsets convolved with a canonical hemodynamic response function (hrf). Statistical parametric maps were identified for each participant by applying linear contrasts to the beta weights for the events of interest. Individual regressors were created for each response option ('Remember,' 'Know,' and 'New') for each trial type (target, related lure, unrelated lure), resulting in nine trial regressors. In addition, regressors for 'no response' trials and motion parameters were also modeled as regressors of no interest. For a complete listing of the mean number of trials in each regressor, see Supplemental Table 1.

False memory suppression was operationalized by contrasting correct rejections with false alarms. Specifically, related correct rejections (RCR) (i.e., 'New' responses to related lures) were compared to false recollections to related lures (i.e., 'Remember' responses to related lures). A similar contrast using a related false recollection baseline was used to examine neural responses associated with successful rejection of unrelated lures¹ (i.e., unrelated correct rejection > related false recollection). This contrast had several benefits. First, it allowed us to parallel traditional successful retrieval contrasts, which contrast accurate memories with forgetting (i.e., hits > misses). Additionally, the contrast allowed us to control for neural processes associated with viewing a lure at retrieval while isolating brain regions that are associated with a correct 'New' response. Previous analyses show different neural underpinnings associated with false recollection as compared to familiarity (Dennis et al. 2012). As such, we chose to use false recollection as a baseline for identifying novelty effects in order to control for active remembering processes that can be associated with lures but that lead to an erroneous (i.e., false alarm) as opposed to successful (i.e., correct rejection) response. We also ran a similar analysis collapsing across remember and know false alarms in the baseline. Results generally mirrored those reported below. Please see Supplemental Table 2 for detailed results of this analysis. To determine overlap

between processes contributing to related and unrelated correct rejections (i.e., common correct rejection activity), we performed a conjunction of the above-described success contrasts (Friston et al. 2005; Nichols et al. 2005). To determine neural activity that showed differential responses to related and unrelated correct rejections, we performed direct comparisons between these two trial types.

Across all contrasts, in order to obtain results that were corrected for multiple comparisons, we used Monte Carlo simulations (<https://www2.bc.edu/sd-slotnick/scripts.htm>) to define individual voxel and cluster extent thresholds (e.g., Forman et al. 1995; Garoff-Eaton et al. 2007; Quadflieg et al. 2008; Slotnick and Schacter 2004). This procedure takes into account the acquisition matrix (64x64), number of slices (34), voxel dimensions ($3.8 \times 3.8 \times 3.8$ mm), intrinsic smoothness (18 mm), and resampling of voxels (none in the current study) in order to simulate data and estimate the rate of Type I error given the protocol parameters. In this study, an individual voxel threshold of $p < 0.005$ was used in combination with a cluster extent threshold of 18 voxels (988 mm³) in order to identify results corrected for multiple comparisons at $p < 0.05$. In addition, we used the aal pickatlas (Maldjian et al. 2003; Tzourio-Mazoyer et al. 2002) to restrict all analyses to cortical and subcortical regions. This whole-brain mask ensured that no cluster contained spurious activity in white matter or cerebrospinal fluid.

Results

Behavioral

Behavioral responses from the study phase of the task showed that the mean response rate was 98 % (SD = 4 %), suggesting that participants actively engaged with the encoding task. Behavioral responses to targets, related lures, and unrelated lures during the retrieval phase are presented in Table 1. A repeated-measures ANOVA of 'New' responses to each trial type (i.e., misses, related correct rejections, and unrelated correct rejections) revealed a significant effect of memory response [$F(1.5, 24) = 183.12$, $p < 0.001$ with Greenhouse–Geisser correction]. Participants correctly identified related lures [$t(16) = 9.94$, $p < 0.001$] and unrelated lures [$t(16) = 15.19$, $p < 0.001$] as 'New' at a higher rate than they misidentified targets as 'New.' Participants were also more likely to correctly identify unrelated lures as 'New' compared to related lures [$t(16) = 12.58$, $p < 0.001$]. Thus, as expected, participants showed better behavioral performance for unrelated compared to related lures due to the reduced categorical interference associated with unrelated items. A similar ANOVA

¹ While unrelated false alarms were included in the model, they were ultimately treated as a regressor of no interest as many participants had an insufficient number of trials to extract an adequate neural signal. See also "Limitations and future directions" section.

Table 1 Behavioral results—retrieval

	Targets	Related lures	Unrelated lures
<i>Accuracy</i>			
New	0.19 (0.10)	0.49 (0.12)	0.90 (0.12)
Know	0.31 (0.11)	0.29 (0.14)	0.04 (0.03)
Remember	0.47 (0.10)	0.19 (0.11)	0.04 (0.05)
No response	0.03 (0.06)	0.02 (0.06)	0.03 (0.06)
<i>Reaction times</i>			
New	1500 (174)	1434 (121)	1152 (148)
Know	1526 (195)	1553 (188)	1568 (364)
Remember	1288 (145)	1355 (164)	1484 (263)

The table reports mean response rates to targets, related lures, and unrelated lures as well as their respective mean reaction times in milliseconds (and SD) during the retrieval task

on reaction times also revealed a significant effect of memory response [$F(3,48) = 32.52$, $p < 0.001$]. Participants were significantly faster in responding ‘New’ to unrelated lures than responding ‘New’ to related lures [$t(16) = 8.13$, $p < 0.001$], ‘New’ to target items [$t(16) = 6.55$, $p < 0.001$], or ‘old’ to related lures [$t(16) = 7.58$, $p < 0.001$]. That is, participants made faster unrelated correct rejection responses compared to other types of ‘New’ responses as well as related false alarms. No other differences in reaction time were significant.

Imaging

Regions showing common activity for correct rejections of related and unrelated lures included right anterior MTL (hippocampus and parahippocampal gyrus) and right early visual cortex (see Table 2; Fig. 2). Activity associated with unrelated correct rejections as compared to related correct rejections included bilateral inferior temporal gyrus and bilateral middle temporal gyrus (see Fig. 3a). Activity associated with related correct rejections as compared to unrelated correct rejections included bilateral VLPFC, bilateral fusiform gyrus, and bilateral early and late visual cortex (see Fig. 3b). For a complete listing of neural regions distinguishing related and unrelated correct rejections, see Table 3.

Discussion

The present study sought to identify neural activity that aids in suppressing false memories by examining the network of brain regions underlying correct rejection of retrieval lures. In doing so, we also examined the role of relatedness between targets and lures in the suppression of false memories. Consistent with previous studies utilizing false memory paradigms, behavioral results showed that participants rejected related lures at a lower rate than unrelated lures, supporting the notion that correctly rejecting related lures represents a more difficult memory decision than that of unrelated lures. With regard to neural processes, and consistent with the prediction that successful rejection of lures is associated with enhanced novelty signals, we found that, independent of relatedness, accurate memory responses to lures were associated with activity in the right MTL and early visual cortex. Additionally, when related and unrelated correct rejections were compared directly, unrelated correct rejections showed greater engagement of bilateral middle and inferior temporal cortices, which was consistent with the prediction that unrelated correct rejections are supported by categorical processing. Related correct rejections, in contrast, showed greater engagement of bilateral early and late visual cortices and bilateral VLPFC, suggesting greater processing of novel perceptual features of related lures compared to unrelated lures. Each of these findings is discussed in turn.

Common correct rejection activity

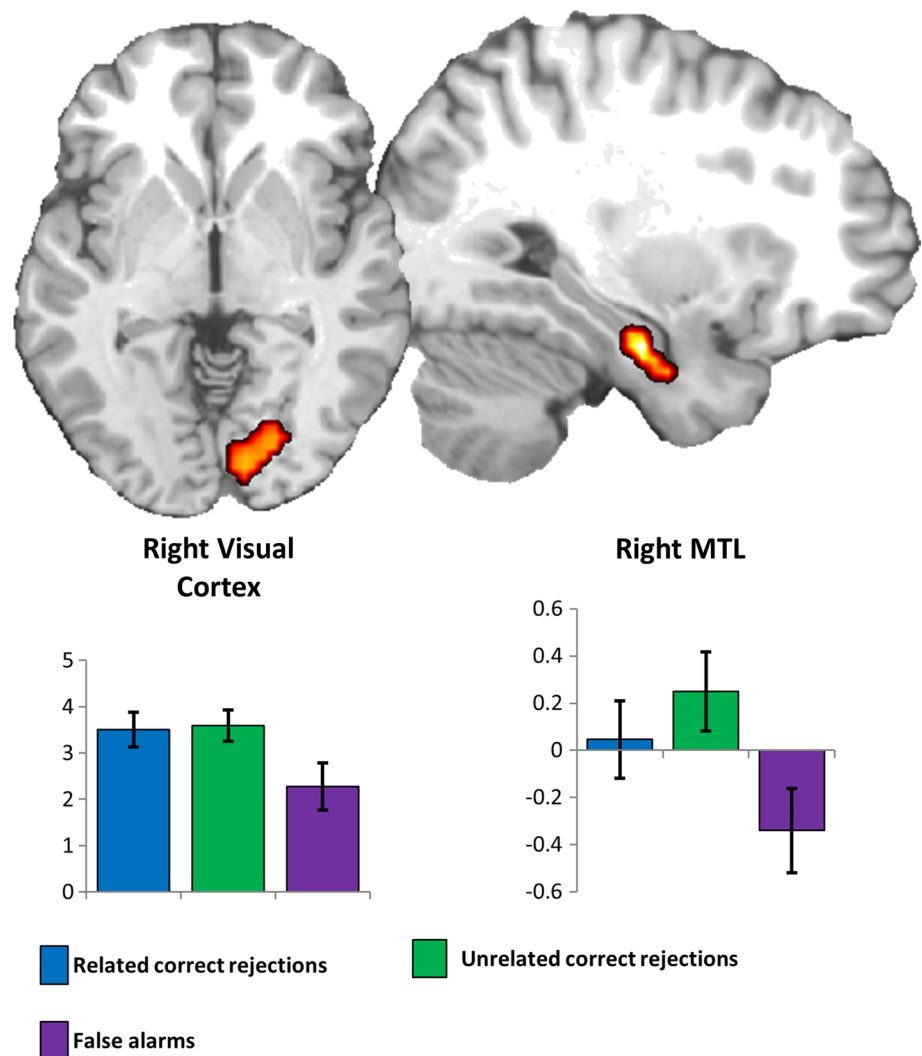
Our first goal was to identify the neural basis of successful correct rejections regardless of whether or not retrieval lures were perceptually and categorically related to previously studied items. The finding that neural activity in early visual cortex supports successful suppression of false memories is consistent with previous studies’ findings that visual regions differentiate new from old items at retrieval (Dobbins and Wagner 2005; Dudukovic and Wagner 2007; Gur et al. 2007; Kirchhoff et al. 2000). In particular, activity in early visual cortex during retrieval has been associated with reinstatement of previously encountered perceptual details (Dennis et al. 2012; Slotnick and Schacter 2004; Vaidya

Table 2 Brain regions showing common activation for related and unrelated correct rejections compared to false recognitions

Region	BA	H	Coordinates (T & T)			T	mm ³
			x	y	z		
<i>Common activity for related and unrelated correct rejections</i>							
Anterior hippocampus/PHG	28/32/36	R	30	−7	−19	6.82	1262
Early visual cortex	17/18	R	11	−86	4	4.00	2963

BA Brodmann’s area, H hemisphere, T & T coordinates from Talairach and Tournoux (1988), L left, R right, PHG parahippocampal gyrus

Fig. 2 Common novelty success activity. Brain regions showing common activity for related and unrelated correct rejections, including right anterior MTL. Bar graphs depict parameter estimates for related correct rejections, unrelated correct rejections, and related false alarms extracted from the peak voxel of each cluster. See Table 2 for coordinates of peak activation. *MTL* medial temporal lobe



et al. 2002; Wheeler et al. 2000). As such, results support the notion that detection of perceptual mismatch between target and lures is a critical component of correctly rejecting retrieval lures (see below for more discussion regarding the role of the visual cortex in memory retrieval). Further, given that we controlled for the true novelty of the item by comparing correct rejections to false recollections, we have extended previous findings by showing that the detection of perceptual mismatch not only supports implicit differences between new and old items, but also contributes to the successful suppression of false memories in order to correctly reject lures.

Activity in right anterior MTL, including the anterior hippocampus and parahippocampal gyrus, was also shown to support similar retrieval accuracy effects for both related and unrelated correct rejections. This finding is consistent with a wide range of neuroimaging and physiological work demonstrating greater activity in anterior MTL associated with retrieval lures compared to old items (e.g., Daselaar

et al. 2006a; Dudukovic and Wagner 2007; Henson et al. 2003; O’Kane et al. 2005; Strange et al. 2005; Yassa and Stark 2008), suggesting that this region supports a bottom-up novelty signal. Importantly, direct comparisons between related and unrelated correct rejections (discussed below) revealed no evidence for differential MTL processing. The lack of differences in anterior hippocampus and parahippocampal gyrus provides evidence that processing of lures in the anterior MTL is not dependent upon the semantic and/or perceptual features of stimuli, but rather contributes to successful memory responses to retrieval lures in a more universal manner.

In addition to explicit memory signals contributing to rejecting related and unrelated lures, increased MTL processing associated with lures may reflect encoding processes, as previous research has shown encoding success effects in the MTL during retrieval tasks (Stark and Okado 2003; Wing et al. 2013) that are greater for new compared to old items (Kirchhoff et al. 2000; Tulving et al. 1996).

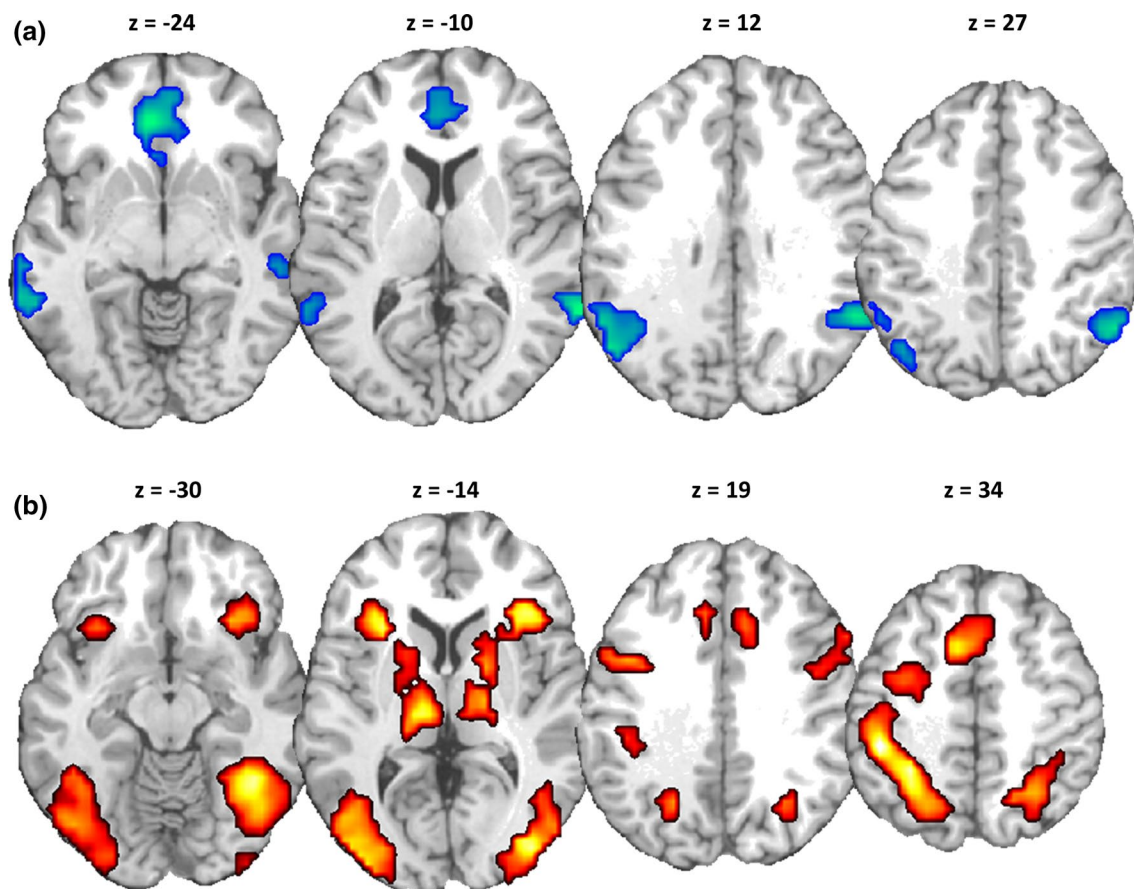


Fig. 3 Differential novelty activity. **a** Brain regions showing greater activity for related compared to unrelated correct rejections including ventrolateral prefrontal cortex and occipital cortex. **b** Brain regions showing greater activity for unrelated compared to related correct rejections

including bilateral inferior and middle temporal gyri and the anterior cingulate. Regions in *red* show greater activity for related compared to unrelated correct rejections. Regions in *blue* show greater activity for unrelated compared to related correct rejections (colour figure online)

However, while encoding of both related and unrelated lures may contribute to novelty activity in the MTL, the present design does not allow for the analysis of subsequent memory effects stemming from new items. Thus, while the present results demonstrate that activity in the MTL contributes to successful responses to lures, further research is necessary to establish the relative roles of encoding and retrieval processes associated with such accurate responses.

Effects of relatedness on correct rejections

Unrelated correct rejections

Despite processes shared by both related and unrelated correct rejections, comparisons between the two revealed several neural differences. Specifically, consistent with the categorical differences between unrelated lures and targets, unrelated correct rejections were found to elicit greater activity in bilateral inferior and middle temporal gyri, regions associated with categorical or gist processing

(Galton et al. 2001; Mummery et al. 2000; Price 2000, 2010). Within the context of false memories, activation in lateral temporal gyri has most often been associated with false recognitions of related lures (Dennis et al. 2007, 2014a; Garoff et al. 2005; Gutchess and Schacter 2012; Slotnick and Schacter 2004). This finding has been interpreted within the context of the fuzzy-trace theory of memory, which suggests that reliance on gist information can lead to confusion between targets and lures if more specific verbatim traces (item-specific details) are not also retrieved (Brainerd and Reyna 1990). However, as we originally posited, with respect to suppressing false memories for unrelated lures, utilizing categorical or semantic labels is a sufficient and highly effective means to support a correct memory decision because unrelated lures differ from targets and related lures at a categorical level. That is, the low degree of common gist between targets and unrelated lures makes using general semantic labels a viable strategy for quick and less effortful memory decisions without compromising accuracy. Behavioral data support this theoretical

Table 3 Brain regions showing differential activation for related and unrelated correct rejections

Region	BA	H	Coordinates (T & T)			T	mm ³
			x	y	z		
<i>Related correct rejections > unrelated correct rejections</i>							
Inferior frontal gyrus (ventrolateral PFC)	47/45	R	37	30	−5	7.00	13,553
	47/45	L	−37	23	−2	5.11	12,730
	44	R	56	6	20	4.42	4938
	44	L	−52	10	26	5.57	9987
Middle frontal gyrus	8/9	L	−30	0	48	3.97	1097
Superior frontal gyrus	6/8	M	−7	11	51	5.62	9438
Insula	−	L	−30	24	5	6.61	3128
	−	R	30	23	−5	7.07	3018
Cingulate gyrus	32	M	7	21	36	4.84	2359
Postcentral gyrus	3/2/1	L	−45	−33	49	7.78	5048
Inferior parietal cortex	40	L	−45	−33	46	8.63	16,352
Precuneus	31	R	15	−63	16	6.08	5213
	31	L	−15	−71	17	5.11	1811
Fusiform gyrus	37	L	−37	−43	−21	4.88	3347
	37	R	37	−54	−7	6.39	5487
Early/late visual cortex	18/19	R	41	−82	10	6.87	36,270
	18/19	L	−41	−89	4	7.66	20,412
Cerebellum	−	L	−33	−43	−24	6.47	8121
	−	R	26	−43	−24	7.31	16,242
<i>Unrelated correct rejections > related correct rejections</i>							
ACC/Ventromedial PFC	32/24/11	M	−4	37	−9	5.1	14,102
Inferior temporal gyrus	20	R	56	−11	−32	6.23	4884
	20	L	−41	−36	−11	5.07	5377
Middle temporal gyrus	21	R	56	−32	−9	3.74	1756
	21	L	−67	−42	1	4.41	4061
Temporoparietal cortex	22/40	R	67	−49	12	6.13	9164
Inferior parietal cortex	40	R	56	−54	47	4.98	2798
	39/40	L	−56	−63	30	4.69	5926

BA Brodmann's area, H hemisphere, T & T coordinates from Talairach and Tournoux (1988), L left, R right, M medial, PFC prefrontal cortex, ACC anterior cingulate cortex

account by showing both the highest accuracy and the quickest reaction times for unrelated correct rejections.

It is also possible that activation within lateral temporal regions reflects a bottom-up novelty detection response that is greater for unrelated as compared to related correct rejections, that is not necessarily semantically based (Dobbins and Wagner 2005; Tulving et al. 1994; Wright et al. 2003). This interpretation is supported by the fact that unrelated correct rejections also elicited greater activity in the ACC, which is a region commonly associated with novelty, but not semantic, processing (Berns et al. 1997; Kiehl et al. 2001; Tulving et al. 1994, 1996). As such, future research is needed to disentangle the roles of semantic labeling and bottom-up novelty processing in reject lures that are highly distinct from studied items.

Related correct rejections

While unrelated lures can be rejected based on category-level information, related lures differ from targets primarily in terms of specific perceptual details associated with individual exemplars of items drawn from the same categories (e.g., cats, balloons). Further, while relatedness between items at study has been shown to facilitate encoding processes (e.g., Gutchess and Park 2009; Leshikar et al. 2010), relatedness at retrieval leads to increased interference and reduced memory sensitivity. Consistent with this explanation, related lures were associated with both reduced behavioral accuracy as well as increased neural activity in bilateral early visual cortices and bilateral VLPFC compared to unrelated lures. Previous studies of

false memory have shown that early visual cortex distinguishes between true and related false memories (Dennis et al. 2012; Dennis et al. 2014b; Slotnick and Schacter 2004). This differential activity has been interpreted as a sensory signal reflecting the reactivation of perceptual details associated with targets viewed at encoding that helps distinguish between similar items presented during retrieval (Dennis et al. 2012; Slotnick and Schacter 2004; Vaidya et al. 2002). The current results extend this work by suggesting that visual cortex may support both perceptual reactivation and detection of perceptual differences between targets and lures during memory retrieval. That is, the observed occipital activity for related compared to unrelated correct rejections may represent a sensory signal associated with retrieval of the original, related target item. When reactivated and compared to the related lure, target information provides sufficient perceptual mismatch to elicit a ‘New’ response. Thus, while previous false memory studies have demonstrated that sensory recapitulation supports true recollection (Abe et al. 2008; Atkins and Reuter-Lorenz 2011; Dennis et al. 2012; Schacter et al. 1996), the present study extends these findings by showing that this sensory signal also supports suppression of related false memories. Further, the current results demonstrate that while this sensory mismatch signal may support all correct rejections to some degree (see common activity), it is relatively more important when lures cannot be distinguished from targets based on categorical distinctions alone (as is the case with unrelated lures), but rather require retrieval of specific perceptual details to differentiate old and new information.

Finally, consistent with our predictions that the correct identification of related lures would elicit greater monitoring and evaluation processes than that of unrelated lures, the present results showed greater neural activity in bilateral VLPFC associated with related correct rejections. Previous studies of false memory suppression have found lateral PFC engagement associated with the successful rejection of information that is familiar (Achim and Lepage 2005; Lepage et al. 2003) or that requires retrieval of the item’s source (Gallo et al. 2006, 2010). Thus, the current results support previous findings showing that the lateral PFC supports relatively complex retrieval decisions, likely reflecting control and monitoring processes that serve to evaluate the products of retrieval (for review see Mitchell and Johnson 2009).

While previous studies of false memory suppression have often found activity in VLPFC associated with rejecting retrieval lures (Atkins and Reuter-Lorenz 2011; Gallo et al. 2006; Lepage et al. 2003), the role of the DLPFC has typically been the primary point of discussion when evaluating the neural basis of correct rejections (Achim and Lepage 2005; Gallo et al. 2006, 2010; Lepage et al.

2003). As noted in the Introduction, along with the DLPFC, the VLPFC has been posited to support the resolution of semantic or perceptual interference (Badre and Wagner 2005; Nee et al. 2007; Postle et al. 2004; Wimber et al. 2009). The present study extends this previous work by highlighting the role of VLPFC in false memory suppression for lures that share a high degree of semantic and perceptual gist with items presented at encoding. Specifically, given the overlap in semantic labeling/gist in the related condition, the VLPFC is called upon to negotiate interference with this shared labeling in order to distinguish such lures from highly overlapping studied information. Thus, the present study suggests that the features of lures may have an important influence on the types of monitoring strategies necessary to suppress false memories. That is, interference caused by semantic overlap is resolved via engagement of VLPFC, whereas other types of complexity (e.g., associative and source memory) engage other types of control mediated by the DLPFC. However, future research is needed to directly compare how features of lures influence the neural basis of frontally mediated retrieval monitoring in false memory suppression.

Limitations and future directions

As the present study is the first neuroimaging study to separate neural responses to retrieval lures both in terms of relatedness between new and old items and in terms of behavioral accuracy, several findings will require replication and further elucidation in future studies. Notably, although a baseline of related false alarms served our purpose of controlling for true novelty while investigating common correct rejection activity, a more complete design would include unrelated false alarms as a baseline for unrelated correct rejections. This analysis would allow for the estimation of separate accuracy effects within related and unrelated lures before determining overlap between their activation maps. We were unable to include such a baseline in the current study due to insufficient trials in this category across most participants (mean = 7.4, range 0–24 trials per participant). Such a design would be of interest both in refining our understanding of unrelated correct rejections presented here, but also to further our understanding of neural activity subserving unrelated as distinct from related false recognitions. However, as unrelated false alarms are rare in the context of false memory paradigms, it has been a challenge for neuroimaging studies to obtain sufficient related and unrelated false alarms to extract neural signal while maintaining adequate memory performance overall (but see Duarte et al. 2010; Garoff-Eaton et al. 2006; Iidaka et al. 2012). Nonetheless, this fully crossed design represents a critical next step in fully elucidating the neural basis

of false memory suppression stemming from related and unrelated lures at retrieval.

Conclusions

The present study sought to elucidate the neural mechanisms that support false memory suppression by measuring accurate responses to related and unrelated lures at retrieval. Results revealed that regions previously associated with new–old differences, including anterior MTL regions, also showed differential activity for accurate compared to inaccurate responses to lures across levels of relatedness. This work extends previous literature by showing that, despite differences in the bottom-up features and overall behavioral accuracy associated with related and unrelated lures, both are associated with a common MTL-mediated memory success effect. In addition to common regions supporting successful responses to related and unrelated lures, several regions were differentially active for related and unrelated correct rejections. Specifically, direct comparisons between neural activity supporting related and unrelated correct rejections showed that unrelated lures could be efficiently rejected based on processing of general semantic and categorical differences from items presented at study. However, the correct rejection of related lures required increased engagement of both sensory processing and control processing regions. Taken together, results suggest that, in addition to common processes supporting correct rejections, the relationship between lures and targets affects the cognitive processes necessary to successfully reject lures at retrieval. These results provide a framework for understanding how individuals avoid false recognitions in order to correctly reject lures when they are either similar or distinct from information stored in memory.

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