

Ventrolateral prefrontal cortex and self-initiated semantic elaboration during memory retrieval

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ABSTRACT

Left ventrolateral prefrontal cortex (LVPFC) is often implicated in neuroimaging studies of context memory retrieval. This activation has been argued to reflect proactive semantic processing that facilitates recollection of past events, or instead to reflect a reactive response to experienced episodic interference. We investigated these characterizations in an fMRI study that manipulated the relative distinctiveness of encoding across subsequent targets and lures by varying encoding task manipulations. Critically, during later testing, retrieval queries and prior target processing were held constant across the distinctive and non-distinctive testing conditions, and therefore any differences in cortical activity would be linked to subject-initiated retrieval strategies. We found that LVPFC activity was specific to context retrieval under distinctive conditions even though this condition demonstrated the least interference. The results suggest that this region is critical for self-initiated semantic elaboration during retrieval, and this conclusion was bolstered by finding that LVPFC activity predicted individual differences in context memory discrimination. In line with Tulving's Encoding Specificity Principle, we suggest that subjects actively construct semantic retrieval cues, reflected in increased LVPFC activation, in an attempt to isolate the distinctive semantic features of hypothetical experiences when possible. If successful, this improves the match between retrieval cue and engram and facilitates performance.

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1. Introduction

Left ventrolateral prefrontal cortex (LVPFC; BA 45/47) activation has been observed during semantic processing, particularly when semantic judgments are loosely constrained and non-automatic (Badre & Wagner, 2002; Cabeza & Nyberg, 2000; Gold & Buckner, 2002; Petersen, Fox, Posner, Mintun, & Raichle, 1988; Poldrack & Wagner, 2004; Thompson-Schill, 2003; Wagner, Paré-Blagoev, Clark, & Poldrack, 2001). A less appreciated regularity is the finding of LVPFC activity across a range of episodic retrieval judgments (Buckner, 1996; Buckner & Wheeler, 2001; Lepage, Ghaffar, Nyberg, & Tulving, 2000; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). Notably, activation has been reported in a variety of context memory tasks, in which participants attempt to retrieve specific episodic details regarding prior stimulus encounters, such as deciding if probe items were presented during a particular prior rating or decision task. In contrast, when memory judgments are based on item familiarity or novelty (e.g. determining if the item had simply been presented before regardless of context) minimal LVPFC activation

is observed (Dobbins, Foley, Schacter, & Wagner, 2002; Dobbins, Rice, Wagner, & Schacter, 2003; Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Nolde, Johnson, & Raye, 1998; Ranganath, Johnson, & D'Esposito, 2000; Rugg, Fletcher, Chua, & Dolan, 1999; Rugg, Henson, & Robb, 2003; Yonelinas, 2002). The increased recruitment of LVPFC during context relative to item memory has been interpreted as reflecting controlled semantic operations that facilitate the intentional recollection of specific details about a past event. Although some research has been devoted to understanding the role of LVPFC in cognitive control of contextual memory, the nature of its contribution remains unclear.

Recent studies have argued for a multi-process model of the LVPFC, proposing important functional distinctions within this region (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Danker, Gunn, & Anderson, 2008; Dobbins & Wagner, 2005; Gold et al., 2006). Specifically, several research reports have suggested that anterior LVPFC (BA 47/45) is involved with the controlled retrieval of semantic information (Badre et al., 2005; Fiez, 1997; Poldrack et al., 1999; Wagner et al., 2001) whereas posterior LVPFC (BA 45/44) is perhaps more involved in the selection of task-relevant information amongst irrelevant competing representations, regardless of whether those representations are semantic, episodic, or phonological (Buckner, 2003; Moss et al., 2005; Thompson-Schill, D'Esposito,

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Aguirre, & Farah, 1997; Thompson-Schill, D'Esposito, & Kan, 1999; Thompson-Schill, Bedny, & Goldberg, 2005). Although conceptually similar, these controlled semantic retrieval and general selection hypotheses differ in important ways in terms of their characterizations of activation during episodic memory retrieval. More specifically, the general selection account suggests that activation reflects a reactive control mechanism used to overcome interference and conflict among episodic representations. The engagement of the selection process would occur transiently, rather than in a sustained fashion, only when irrelevant information to perform the task is accidentally retrieved (Braver, Gray, & Burgess, 2007; Snyder, Feigenson, & Thompson-Schill, 2007). This type of mechanism has also been termed a “back-end” monitoring strategy whereby subjects rely on post-retrieval selection or monitoring processes to resolve ambiguous retrieval outcomes (Velanova, Lustig, Jacoby, & Buckner, 2007).

In contrast, the controlled semantic retrieval hypothesis posits a top-down mechanism employed as subjects build descriptive retrieval cues to aid episodic retrieval in a goal-directed manner. These proactive processes are thought to play a key role in episodic remembering as they permit the retrieval or attentional foregrounding of semantic information that would have been highly relevant during hypothetical prior encounters. If successful, this elaborative process increases overlap between the semantic information being considered during the retrieval attempts, and that which would have been central had the probe actually been encountered. This in turn is expected to increase the odds of recollection in the case of positive memory probes and also to reduce the likelihood false endorsement for negative probes. The importance of the relationship between encoding and retrieval operations has remained central in episodic memory research since the landmark work of Tulving et al. demonstrating that recollection depends on the extent to which the information provided by the retrieval cues overlaps with that which was central during the encoding of prior experiences (Tulving, 1983; Tulving & Thomson, 1973). Tulving and colleagues termed the importance of this match the “Encoding Specificity Principle” (see also Morris, Bransford, & Franks, 1977; Weldon & Roediger, 1987). To quote Tulving (1983) “The engram of an event stored in the episodic system, and the retrieval cue, as interpreted or encoded in light of the information in the semantic system, must be compatible for remembering to occur” (italics added p. 224). Thus, from this perspective, the potential for success during episodic retrieval attempt critically relies upon the nature of the semantic processing that subjects engage in during retrieval attempt.

Herein, we refer to the semantic processing occurring during episodic retrieval attempt as “semantic elaboration” and assume that these semantic operations are similar to those that are often critical for the original encoding of episodes (e.g., Kahn, Davachi, & Wagner, 2004; Nyberg, Habib, McIntosh, & Tulving, 2000; Nyberg et al., 1996; Vaidya, Zhao, Desmond, & Gabrieli, 2002). A critical difference however between the semantic operations executed during encoding, and those that the Encoding Specificity Principle assumes critical during retrieval, is that the former are typically more heavily constrained or dictated by the encoding environment whereas the latter depend upon subject's inferences about the types of information likely central for the putative prior experiences, and their belief that considering this information may trigger recollection of the actual event.

Consistent with the view that anterior LVPFC aids semantic elaboration during retrieval is the finding that activation in this region during source memory tasks is present when the conceptual details of the probes are relevant to the possible prior source contexts (e.g. remembering having made a pleasant/nonpleasant versus a living/nonliving judgment at encoding for presented test items),

but not when it was the prior perceptual features that were critical for the current memory judgment (e.g. whether the object had appeared in a large or small size at encoding; Dobbins & Wagner, 2005). Since this retrieval activation overlaps with that reported in semantic retrieval studies (Dobbins et al., 2002; Ranganath et al., 2000; Wagner et al., 1998), this suggests that that recruitment of this region depends on the nature of the to-be-recalled details, with subjects choosing to semantically process retrieval items only when the sought remembrances are linked to the semantic features of the probes. According to these findings, anterior LVPFC is critical during some contextual recollection tasks because it enables retrieval of semantic attributes of the probe items most closely related to the desired episodic information. Furthermore, subjects are assumed to flexibly weight different features of the probes during remembering, depending upon their belief about the information that is most diagnostic for identifying the origin of a memory (Dobbins, Kroll, Yonelinas, & Lui, 1998; Johnson, Hashtroudi, & Lindsay, 1993). Such proactive strategies enable the access and active maintenance of semantic featural information that is task-relevant and presumably require the subjects' awareness that semantic analysis of the targets and lures should aid remembering (Braver et al., 2007; Wagner et al., 2001).

Although prior work suggests that LVPFC contributes to semantic elaboration during retrieval, characterizing this process as self-initiated or strategic is perhaps premature because the type of the to-be-remembered information has been usually fairly evident given the retrieval query alone. For example, in Dobbins et al. (2002) subjects were prompted to select the one of three retrieval probes previously encountered during a pleasant/unpleasant rating task using the prompt “Pleasant Item?”. Under these settings, although the processing can be characterized as semantic elaboration, it is not clear to what extent one would want to refer to it as strategic or self-initiated because the retrieval prompt itself clearly identifies what type of probe information is most relevant, namely, semantic features linked to item pleasantness. That is, to the extent the critical item features are made explicit by the retrieval cue or prompt, this minimizes any demand for the subjects to recruit elaborative strategies in a self-initiated fashion. Since it is generally accepted that self-initiation of control processes plays a key role in supporting memory (Bissig & Lustig, 2007; Braver et al., 2007; Craik & Byrd, 1982; Derwinger, Neely, & Bäckman, 2005; Kapur et al., 1996; Mäntylä & Nilsson, 1983; Velanova et al., 2007) this represents a notable potential shortcoming. For example, Kirchoff and Buckner (2006) examined patterns of encoding activity when subjects were unconstrained intentional encoding instructions. The data demonstrated that individuals' self-initiated use of various encoding strategies predicted later retrieval accuracy. Significantly, the engagement of verbal/semantic elaboration was associated with activation in a network of regions that included LVPFC, while perceptual inspection strategies elicited extrastriate activation (Kirchoff & Buckner, 2006). Thus, evidence suggests that during episodic encoding, anterior regions of the LVPFC may contribute to self-initiated, proactive semantic elaboration processes at encoding. Interestingly, the tendency to self-initiate this strategy, at least during encoding, can be influenced by prior training (Derwinger et al., 2005; Bissig & Lustig, 2007). Studies targeting retrieval tasks in episodic memory have not yet tested if such self-initiated semantic elaboration predicts memory performance and how it correlates with PFC activation patterns.

Here we investigate semantic elaboration and general selection characterizations of the role of the LVPFC during retrieval, in an event-related fMRI study. During encoding subjects saw two sequential lists of words and performed either the same semantic rating task across the two lists (non-distinctive encoding) or different semantic tasks across the lists (distinctive encoding).

CONTEXT MEMORY JUDGMENT

(A) *Distinctive condition*

Pleasant? Yes/No	Concrete? Yes/No	List 1? Yes/No
List 1 words	List 2 words	List 1, List 2, & New words

(B) *Non-distinctive condition*

Pleasant? Yes/No	Pleasant? Yes/No	List 1? Yes/No
List 1 words	List 2 words	List 1, List 2, & New words

Fig. 1. Experimental design. During encoding, subjects saw two lists of words. In the first list, they performed a pleasantness judgment on each word, while in the second list they made either a concreteness judgment (A) or a pleasantness judgment (B). During context memory retrieval, subjects were asked to decide whether each word had been presented in the first list of encoding (“List 1?”).

This design enabled us to render the processing of the first list either distinctive, or non-distinctive with respect the second list (Fig. 1). During subsequent context retrieval, participants were presented with words from the previous encoding lists and new words and were asked to decide whether each presented word was from a particular list (Is this word from List 1?). Critically, in the non-distinctive condition, retrieval of the prior semantic tasks performed on the items poorly discriminated the list origins (because it was the same across lists) whereas during the distinctive case such memory content was predicted to be of substantial benefit. Because the retrieval prompt remained the same across distinctive and non-distinctive testing conditions (i.e., Is this word from List 1?), any differences in controlled processing between conditions should reflect subject-initiated changes in adopted retrieval strategies. We hypothesized that PFC regions critical for the self-initiated semantic elaboration of the probes, should demonstrate increased activity for the distinctive relative to the non-distinctive condition. In contrast, regions involved in general selection demands should demonstrate greater activation in the non-distinctive compared to the distinctive condition, given the greater difficulty in contextual responding due to the high similarity of the episodic representations.

2. Methods

2.1. Subjects

Eighteen English-speaking volunteers (18–31 years old, 12 females) were included in the study. Informed consent was obtained in a manner approved by the Institutional Review Board of Duke University Medical Center. Two volunteers were excluded from the analyses, given that their behavioral performance was at chance.

2.2. Materials

A total of 480 words were drawn randomly from a pool of 1216 words. From this set, six lists of 80 items were constructed for use in six study/test cycles. The items in the pool were, on average, 7.09 letters and 2.34 syllables long, with a Kucera-Francis corpus frequency of 8.85.

2.3. Procedure

Each subject underwent six study/test cycles during which both the study and immediately following test periods were scanned. Two of the cycles tested simple item recognition whereas four of the cycles examined context memory judgments. Half of the subjects completed the context memory cycles first, followed by the item memory cycles. For the other half, the order was reversed. During each study phase, subjects were presented with two sequential lists of written words and asked to make semantic judgments on each word. During the first list in all cycles, subjects performed a pleasant/unpleasant judgment on each word. The nature of the second list processing determined whether the first list processing was retrospectively rendered distinctive or not. More specifically, during the second list they were asked to

make either pleasant/unpleasant decisions matching the task performed in the first list (non-distinctive encoding) or instead were asked to make concrete/abstract decisions which were assumed to target different features of the probes relative to the first list pleasantness ratings (distinctive encoding). For the pleasantness judgment, subjects simply indicated whether or not they felt the word’s meaning was pleasant. It was stressed that there were no correct or incorrect responses to the query and that they should indicate their personal preference. For the concreteness judgment, subjects indicated whether the word denoted a concrete object or an abstract concept. Subjects responded via button box using the left hand and were given 3 s to respond. The encoding prompt and word remained on the screen for 2500 ms, followed by a blank screen of 500 ms prior to the appearance of the following item. Each study list consisted of 30 words and 10 fixation baseline trials intermixed. During fixation trials, a cross was presented in the middle of the screen and subjects were instructed to relax. In total, each subject studied 360 words equally distributed across six study/test cycles. Half of the cycles consisted of distinctive encoding and the other half of non-distinctive encoding, presented in alternating order (Fig. 1).

Immediately following each study phase, a memory test was administered to assess either context or item memory. Subjects were presented with single words that were either taken from the previous encoding lists or were new words. During the context memory task, subjects were asked to decide whether each word had been presented in the first encoding list (“List 1?”). Subjects were given 4 s to respond to each item by pressing a left and right key with the left hand. They were to respond “no” to both new items and items originating from the inappropriate List 2 context. In the item memory task, subjects had to decide whether each word was simply studied or not, regardless of prior task (“Old?”). Thus subjects were to respond “yes” to both List 1 and List 2 items and “no” to new items. Subjects were given 4 s to respond to each item. Whereas responses during context memory were simple choice (“yes” or “no”) responses, item memory incorporated confidence assessments indicating both the nature (“yes” or “no”) and confidence (“high” or “low”) of the response using four buttons (e.g., “high-yes”–“low-yes”–“low-no”–“high-no”). Incorporating confidence during item memory was done in order to match prior item-memory studies (e.g. Dobbins et al., 1998; Gold et al., 2006; Henson, Rugg, Shallice, Josephs, & Dolan, 2000; Yonelinas, Otten, Shaw, & Rugg, 2005). Aside from the response differences all other aspects of testing were matched across item and context memory tests (Fig. 1).

Each test list consisted of 100 trials: 20 words from encoding List 1, 20 from encoding List 2, 20 new words, 20 fixation trials and 20 active control trials. In the active control trials subjects were instructed to press a specific button. These trials involved similar visual and motor demands as the experimental items, but no recognition memory was required. The order of the event types was determined by using an optimal sequencing program (Wager & Nichols, 2003).

Thus in total there were six cycles, four comprised of context memory task and two of item memory task. The total number of test items for context memory was 240 (80 old words from encoding List 1, 80 words from encoding List 2 and 80 new words) and the total for item memory was 120 words (40 old words from encoding List 1, 40 words from encoding List 2 and 40 new words). The test items were equally distributed across the distinctive and non-distinctive conditions. Critically, even though the encoding tasks were blocked, it is unlikely that subjects adopted intentional strategies during encoding of List 1 items that differed across the conditions, as they did not know in advance the nature of the processing in List 2 or the type of memory test they would be given at retrieval. Thus the nature of the encoding operations in List 1 was assumed identical for all test conditions and therefore any differences observed between distinctive and non-distinctive conditions at test would reflect processes that took place after List 1 items’ encoding.

Finally, following the scanning session, subjects were given a surprise item memory decision task for words that had been presented in the retrieval scans as new items. This post-scanning list was comprised of 240 words, half of which had been presented earlier in the experiment, while the other half were novel words. Subjects had 4 s to respond to each item by pressing a left and right key in the keyboard.

2.4. fMRI acquisition and analyses

Scanning was performed on a 3T General Electric (Waukesha, WI) scanner using a standard head coil. Functional data were acquired by using an echo-planar sequence (TR = 2000 ms, TE = 31 ms, 34 axial slices parallel to the AC-PC plane with near-isotropic voxels 3.75 mm × 3.75 mm × 3.8 mm, no gap) designed to minimize susceptibility artifacts (Guo & Song, 2003). Before functional data collection, four dummy volumes were discarded to allow for T1 equilibrium. High-resolution T1-weighted anatomical images (3D spoiled gradient recalled acquisition [SPGR]) were acquired for visualization.

Our main analyses focused on the retrieval scans. However, encoding data were also examined to verify that encoding operations during List 1 were similar across the distinctive and non-distinctive conditions. Data were processed using Statistical Parametric Mapping (SPM2: www.fil.ion.ucl.ac.uk/spm/). Slice acquisition timing was corrected by resampling all slices in time relative to the middle slice collected, followed by rigid body motion correction across all runs. Functional data were spatially normalized to a canonical echo-planar imaging template using a 12-parameter affine and nonlinear transformation, and then spatially smoothed with an 8 mm Gaussian kernel. For each scan type (source distinctive, source non-distinctive, item

distinctive and item non-distinctive) we modeled the correct responses to each retrieval condition (List 1, List 2, New, and control trials) separately. In addition, to investigate retrieval outcome effects we also modeled incorrect responses to List 2 words. However, for List 1 and New trials incorrect responses were too infrequent for most subjects and therefore were not included separately in the model. A separate analysis was performed for the encoding scans of List 1 items. In this analysis, we modeled the processing of List 1 items in the distinctive, and non-distinctive conditions. The remaining analysis parameters were the same as for the retrieval scans.

Subjects were treated as random effect. For the analyses, volumes were treated as temporally corrected time series and modeled by convolving a canonical hemodynamic response function (HRF) with time derivatives. The resulting functions were used as covariates in a general linear model, along with a basis set of cosine functions that were used to high-pass filter the data and a covariate representing sessions' effects. The least squares parameter estimates of the best-fitting canonical HRF for each condition of interest were used in pairwise contrasts and stored as a separate image for each subject. These images were then tested against the null hypothesis of no difference between contrast conditions using one-tailed *t*-tests. Activations were considered significant if they consisted of five or more contiguous resampled voxels (2 mm isotropic) and exceeded an alpha threshold of .001 for simple contrasts. This threshold is consistent with numerous prior reports (e.g. Badre et al., 2005; Dobbins & Wagner, 2005; Dobbins et al., 2003; Wagner et al., 2001) and facilitates comparisons with prior results. Functional regions of interest were extracted using MARSBAR peristimulus time averaging for the functional data (Brett, Anton, Valabregue, & Poline, 2002). Percent signal averages were obtained for the significant voxels within a cluster as defined by an 8 mm radius around each SPM identified maxima for the relevant maps. These extracted and averaged data were further analysed using off-line statistical software.

Due to technical problems approximately 15% of the behavioral responses throughout the experiment were not recorded. As described in greater detail below, the number of non-responses (due to the computer fault and/or subject's failure to respond in time) was identical across all conditions in both context and item memory. Therefore the behavioral pattern should not be affected by this fault.

3. Results

3.1. Behavioral data

Fig. 2 illustrates the mean “yes” rates for the three item origins during the context and item memory tasks. During both tasks, “yes” responses to List 1 items are correct responses (empty

boxes) and “yes” responses to new items are incorrect (solid boxes). However the tasks differ in terms of the correctness of “yes” responses to List 2 items. These responses are incorrect during the context task and reflect List 2 intrusion errors. During the item memory task these indicate correct recognition for the List 2 items. Separate two-way ANOVAs were conducted on the “yes” rates from each task examining the factors of Item-Origin (List 1, List 2 and New) and Encoding Condition (Distinctive or Non-Distinctive).

During context memory there were main effects of Item-Origin ($F(2,30)=103.65, p<.001$) and Encoding Condition ($F(1,15)=6.96, p<.05$). The former indicates that the correct and incorrect response rates differed, whereas the latter indicates that the “yes” rate was higher during Non-Distinctive compared to Distinctive conditions. More importantly, there was an Item-Origin by Encoding Condition interaction ($F(2,30)=4.93, p<.05$) suggesting that the effects of the distinctiveness manipulation were dissimilar across the items from the three possible sources. Post hoc pairwise comparisons confirmed that neither the correct detection of List 1 items, nor the false alarm rates to new items differed as a function of prior encoding distinctiveness (t 's <1). In contrast, List 2 intrusion errors were significantly higher following Non-Distinctive compared to Distinctive encoding ($t(15)=3.04, p<.01$) (Fig. 2). Finally, the ability to discriminate List 1 and List 2 items for the two Encoding Conditions was directly examined by contrasting the List 1 detection and List 2 intrusion rates. Discrimination between List 1 targets and List 2 lures was well above chance following Distinctive encoding ($t(15)=3.62, p<.01$) and also was above chance following Non-Distinctive encoding ($t(15)=2.86, p<.05$), though necessarily lower given the increased List 2 intrusion rate noted above. Overall, these data demonstrate that the sole effect of the distinctiveness manipulation was on the intrusion rate for List 2 items. As expected, errors to List 2 items increased in the condition in which the semantic processing matched List 1 (Non-Distinctive) compared to when the semantic processing differed from List 1 (Distinctive).

For item memory response rates the Item-Origin by Encoding Condition ANOVA yielded only a main effect of Item-Origin

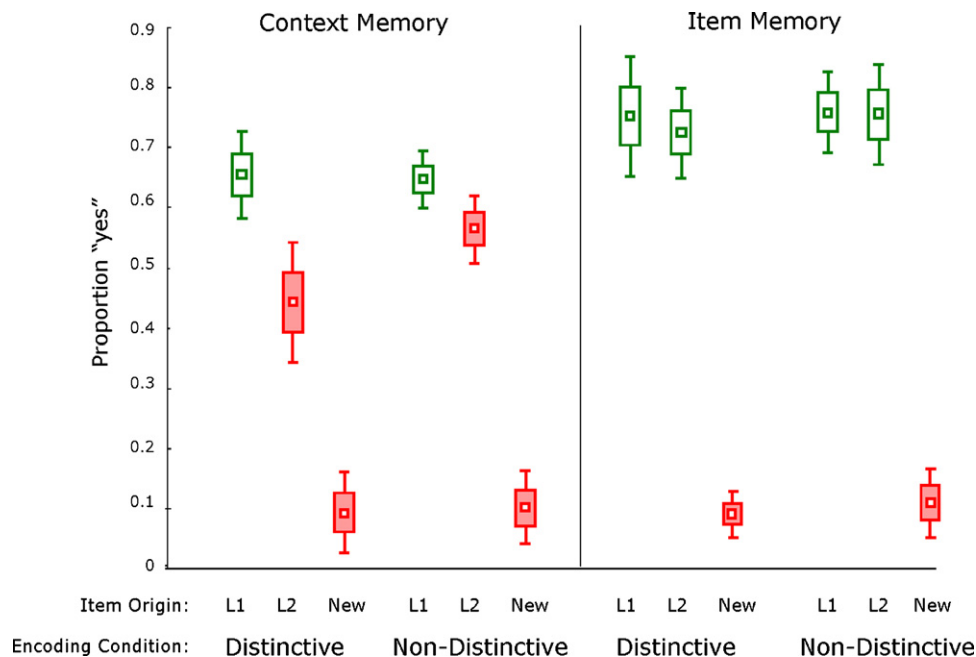


Fig. 2. Discrimination accuracy during context and item memory retrieval for List 1, List 2 and New items in the Distinctive and Non-Distinctive conditions. Each box plot denotes the mean, mean + S.E. (box), and mean + 2 × S.E. (whisker). L1 = List 1, L2 = List 2. Empty boxes denote correct responding whereas solid boxes denote incorrect responding.

($F(2,30) = 207.82, p < .001$) merely indicating the correct and incorrect response rates differed. Importantly however, no other effects were present ($F_s < 1$) demonstrating that the response rates did not differ as a function of the distinctiveness manipulation (Fig. 2). Furthermore, within both distinctiveness conditions, the recognition hit rate for List 1 items did not differ from that for List 2 items ($t_s < 1$) demonstrating that subsequent recognition was similar regardless of whether an item appeared in List 1 or List 2. This suggests the items were equally familiar regardless of whether they came from List 1 or List 2 and regardless of whether the processing matched or mismatched across List 1 or List 2.

As noted in the methods, due to technical problems approximately 15% of the responses throughout the experiment were not recorded. Importantly, the number of non-responses, due to computer malfunction and/or subjects' failure to respond in time was identical across conditions in the context memory task (.15 for List 1, .17 for List 2, and .15 for New items in the Distinctive condition; .16 for List 1, .15 for List 2, and .15 for New items in Non-Distinctive condition) and item memory task (.17 for List 1, .16 for List 2, and .17 for New items in the Distinctive condition; .16 for List 1, .13 for List 2, and .14 for New items in Non-Distinctive condition), with $p > .05$ in all cases. Thus the results above were likely unaffected by this computer fault.

Analysis of reaction times (RTs) was restricted to correct responses and again conducted separately for context and item memory tasks. During context memory, ANOVAs performed on mean RT for correct trials yielded a main effect of Encoding Condition. Subjects were slower to correctly respond to the items previously encoded under the distinctive relative to the non-distinctive condition ($F(1,15) = 8.35, p < .01$). There was also a main effect of Item-Origin ($F(1,15) = 5.67, p < .01$), with slower RTs for context decisions about words that came specifically from List 2 compared to both List 1 and New Items. Similar analyses carried out for item memory decisions showed an effect of Item-Origin ($F(2,30) = 7.36, p < .005$), with significantly slower responses for New items than List 1 or List 2 items.

Overall, the behavioral data showed that shifting the encoding task across Lists 1 and 2 (i.e. distinctive condition) significantly improved later context memory discrimination. In particular, subjects were better at rejecting distractors from List 2 when the encoding tasks were different than when they were the same. In contrast, this manipulation had no effect on the ability to subsequently recognize the items during item memory tests. This pattern of findings has different implications for the semantic elaboration and general selection hypotheses and the prediction of LVPFC activation. Under the semantic elaboration hypothesis this leads to the prediction that LVPFC activation will only be observed under the Distinctive condition, because here the semantic properties of the probe are potentially useful in recovering the prior useful recollections. In contrast, the general selection account implies a mechanism that reacts to episodic interference and an attempt to resolve competition among similar representations. Thus this hypothesis suggests that LVPFC activation should increase as discrimination declines and hence should be most robust under the Non-Distinctive condition where subjects are having increased difficulty disambiguating the episodic representations of List 1 and List 2.

3.2. Functional imaging data

3.2.1. Encoding scans

The primary purpose of the encoding analysis was to verify that List 1 item processing did not differ as a function of whether subsequent List 2 processing was distinctive or non-distinctive relative

to List 1. If so, then this would have complicated the interpretation of retrieval differences across these items during testing. We contrasted activation during the processing of List 1 items in Distinctive and Non-Distinctive conditions for each memory task, and found no significant differences in activation even at a liberal threshold of $p = .01$. In addition, we analysed the time courses of activation in our ROI, the LVPFC. These data were drawn from the LVPFC region that showed differential activation during retrieval of List 1 words in Distinctive and Non-Distinctive conditions (as described in Section 3.2.2 below). ANOVAs were carried out on the mean activity (from 6 to 10 s) in this region during processing of List 1 examining the factors of Encoding Condition (Distinctive or Non-Distinctive) and Memory Task (Context and Item Memory). Results showed no significant main or interaction effects ($F(1,15) < 1.5, p > .2$ in all cases). These results suggest that subjects did not differentially engage LVPFC for List 1 items across the two distinctiveness conditions. This was an expected result since the design precluded subjects from knowing the type of processing that would be performed in the upcoming List 2 and the type of memory test that would follow at retrieval. Thus, any differences between Distinctive and Non-Distinctive conditions during retrieval of List 1 words cannot be attributed to differences in prior encoding operations. Instead, such differences must be the result of processes that take place after List 1 items' encoding. The processing of List 2 items during encoding was not examined since the encoding tasks differed across Distinctive and Non-Distinctive conditions. Furthermore, activation for these items during later retrieval played a minimal role in the interpretation of the findings.

3.2.2. Retrieval scans

We first investigated the neural regions associated with context retrieval by comparing successful retrieval of List 1 words in the context memory scans (collapsed across distinctiveness of encoding) with the motor control task finding a mainly left-lateralized network including activation in L ventrolateral, dorsolateral and medial PFC regions. In addition, activation was found in L insula, bilateral middle/anterior cingulate, fusiform gyrus, middle occipital lobe, superior parietal lobule, and R ventrolateral PFC. This result replicates previous context memory research (e.g. Dobbins & Han, 2006; Rugg et al., 1999), suggesting that our task and materials tapped into a network potentially subserving episodic retrieval (Fig. 3A). In contrast to the extensive network in Fig. 3A, the contrast for correct item memory decisions on List 1 words relative to the motor control task demonstrated activation in only a subset of the above regions including L posterior lateral PFC, pars opercularis, precentral gyrus, bilateral fusiform gyrus, bilateral middle occipital cortex, and supplementary motor area (Fig. 3B). These findings were substantiated by a direct comparison of the two contrasts. Context memory (minus motor control) relative to item memory (minus motor control) revealed increased activation in posterior middle ventral and dorsal regions of the lateral PFC, as well as bilateral inferior occipital gyrus (Fig. 3C). The reverse contrast identified two small clusters in L middle occipital gyrus and L supramarginal gyrus, respectively. Complementing the behavioral data and consistent with prior fMRI literature, these findings indicate a neural dissociation between context and item memory tasks, with the former imposing greater demands on left PFC regions. Subsequent analyses focused on the context memory decisions only.

To specifically explore the differential effects of prior encoding distinctiveness upon later context retrieval processes, we contrasted activity during successful detection of List 1 items (hits) and the correct detection of new words (correct rejections) under distinctive versus non-distinctive prior encoding conditions. The analysis focused on List 1 words because the distinctiveness

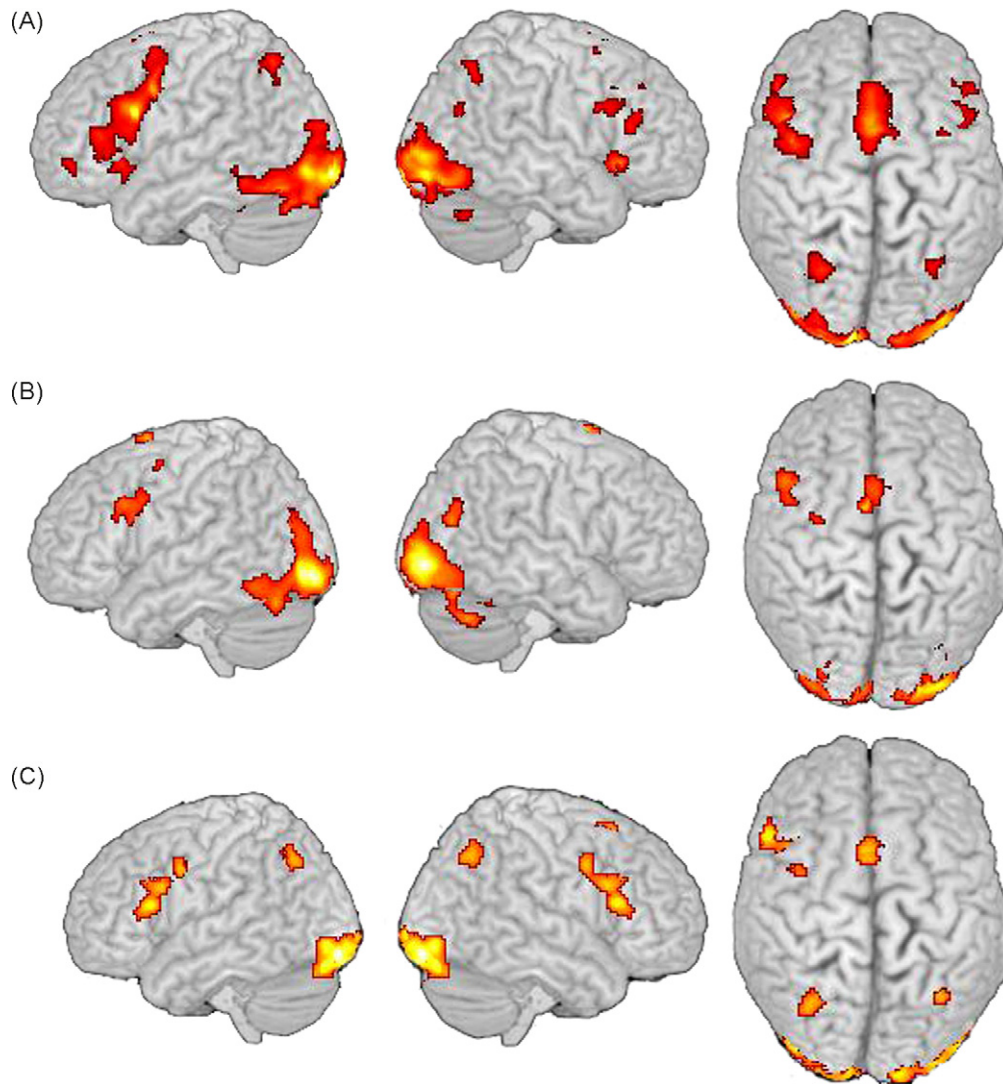


Fig. 3. (A) Regions demonstrating significant increases in response to successful context retrieval for List 1 words compared to motor control task. (B) Regions demonstrating significant increases in response to successful item retrieval for List 1 words compared to motor control task. Activations are overlaid on a canonical brain and thresholded at .001, five voxels. (C) Regions demonstrating significant increases in response to List 1 words in context retrieval (minus motor control) compared to item retrieval (minus motor control). Activations are overlaid on a canonical brain and thresholded at .005, 32 voxels, for display purposes.

manipulation was subsequent to the encoding of this list, and therefore prior encoding processes were assumed identical across the two conditions for these items. If L lateral PFC regions mediate the self-initiated use of semantic elaboration strategies at retrieval, then significant activation should be observed in this region for the distinctive scans, since elaboration of the semantic features of the probes should facilitate recollection of which task was previously performed on the probes. Since the two different tasks are exclusive to the two lists, recovery of task information is equivalent to list identification. Consistent with this hypothesis, we found increased activation in the left regions of PFC including the middle/anterior ventrolateral (BA 45/47), anterior ventrolateral (BA 10/47), and medial PFC (BA 6/32) for List 1 compared to new items under the Distinctive condition. In addition, L insula, precuneus (BA 7), L inferior parietal lobule (BA 7) and bilateral posterior cingulate gyrus (BA 23) were also more active for List 1 words compared to novel items (Fig. 4A, Table 1). In contrast, following the Non-Distinctive encoding condition differential activation for List 1 compared to New words in left lateral PFC was absent, although medial superior frontal cortex (BA 32), L inferior parietal (BA 40) and anterior and

posterior cingulate gyrus (BA 32 and 23, respectively) regions were differentially active (Fig. 4B, Table 1). These findings demonstrate that increased recruitment of LVPFC only occurred for familiar material following Distinctive encoding. Moreover, since activation in this region did not differ during encoding of List 1 words, we can confidently say that anterior LVPFC recruitment reflected retrieval, rather than encoding processes.

To further examine the response pattern in anterior LVPFC, we extracted the time courses of the activation in this ROI (Fig. 4C) and compared the mean activity estimates from 6 to 10 s for each condition (List 1 correct, and New correct) for distinctive and non-distinctive conditions. We found that anterior L lateral PFC response was greater during retrieval of List 1 words in the Distinctive condition compared to the other three responses ($p < .01$ in all cases). Importantly, there was minimal differential activation for List 1 and New items within L lateral PFC for context decisions following Non-Distinctive encoding even though behaviorally these were more challenging (less accurate) under the non-distinctive compared to distinctive case. Thus even though performance declined and interference increased in the Non-Distinctive condition, activation

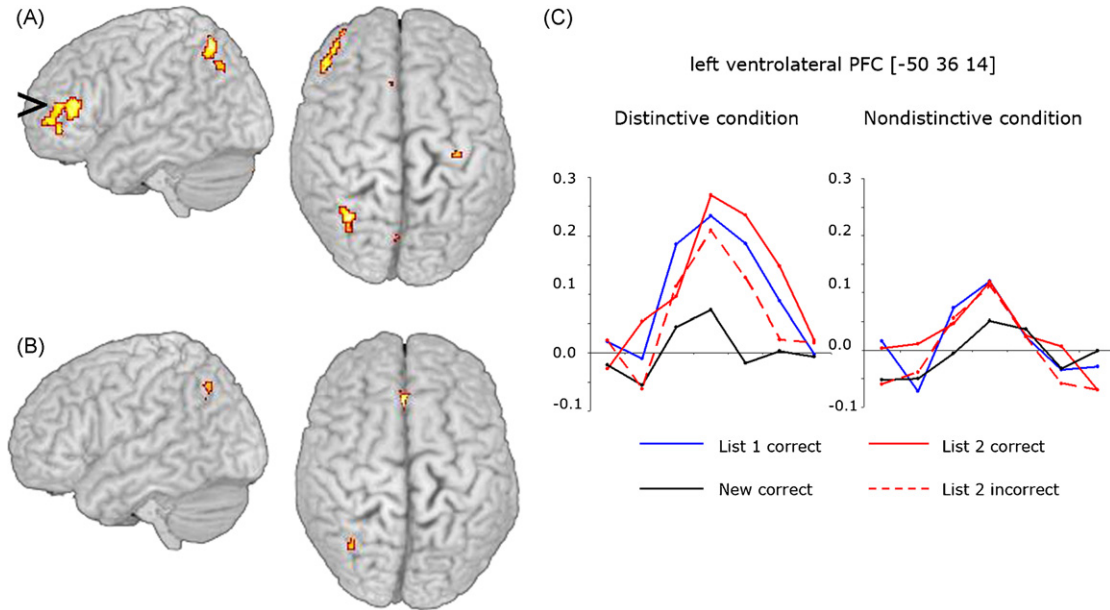


Fig. 4. (A) Regions demonstrating significant increases in response to context memory retrieval of List 1 words compared to New words for the Distinctive condition. (B) Regions demonstrating significant increases in response to context memory retrieval of List 1 words compared to New words for the Non-Distinctive condition. Activation is overlaid on a canonical brain and thresholded at .001, five voxels. (C) Extracted hemodynamic responses from a functional ROI, for the region indicated by the arrow.

of this region declined compared to the Distinctive condition. Thus, the LVPFC region is not increasingly recruited as episodic representations become increasingly similar, but instead appears to be recruited under conditions where subjects appreciate that semantic processing of the probes is potentially advantageous in eliciting useful recollections. Given that List 1 encoding was matched and the retrieval prompts were constant across Distinctive and Non-Distinctive retrieval conditions, the increased recruitment of LVPFC was subject-initiated. In contrast to familiar items from Lists 1 or 2, New items failed to engage the LVPFC region regardless of the prior distinctiveness of List 1 relative to List 2 processing (Fig. 4C black time courses) and this suggests that novel or low familiarity items are processed similarly under the two retrieval environments. In contrast, items perceived as familiar are subjected to semantic analysis only when prior processing was sufficiently distinctive to warrant this as an effective strategy.

Left anterior frontal regions have been sometimes reported to track episodic retrieval success (Henson et al., 1999; Konishi, Wheeler, Donaldson, & Buckner, 2000; Velanova et al., 2003;

Wheeler & Buckner, 2003). We found little evidence for this in the current data. For Distinctive conditions, anterior VLPFC was significantly more activated for List 2 intrusion errors than for correct detection of New items ($t(14)=4.38, p<.05$) and similar response magnitudes were observed regardless of whether erroneously responding to List 2 items or correctly endorsing List 1 items under the Distinctive retrieval condition ($p>.1$, Fig. 4C). Thus, activity in VLPFC was unique to familiar words under the distinctive condition, and it occurred both when context retrieval succeeded or ultimately failed. This is expected if subjects are semantically elaborating the familiar items, but appears inconsistent with the idea that the activation marks successful episodic retrieval. Because List 1 error rates were low for most subjects (.2 in both distinctiveness conditions) they could not be meaningfully analysed.

Overall, the analyses above indicate that the anterior LVPFC region is selectively recruited during context memory whenever participants engage in semantic elaboration processes. From this perspective, participants semantically process the retrieval probes

Table 1
Regions demonstrating significant increases in response to the contextual retrieval of List 1 words versus New words under Distinctive and Non-Distinctive conditions.

Region	BA	x	y	z	No. of voxels	Z-score
<i>Distinctive condition: List 1 > New</i>						
L superior parietal lobule	7	-34	-62	56	53	4.14
L inferior frontal gyrus	45	-50	36	14	139	3.94
R cerebellum	-	14	-84	-34	52	3.79
L cingulate gyrus	23	-4	-38	40	84	3.73
L superior frontal gyrus	32	-10	24	46	8	3.49
L inferior frontal gyrus	45	-36	22	10	10	3.48
R precentral gyrus	6	34	-22	68	11	3.42
L precuneus	30	-2	-46	16	10	3.38
R caudate	-	12	4	18	5	3.31
R cingulate gyrus	23	6	-34	28	6	3.23
L inferior parietal lobule	7	-34	-68	42	17	3.22
L cuneus	7	-6	-74	36	11	3.21
<i>Non-Distinctive condition: List 1 > New</i>						
L superior frontal gyrus	32	-4	28	38	88	4.14
R cingulate gyrus	23	6	-30	32	354	3.92
L angular gyrus	40	-34	-56	38	79	3.79

when they believe it may facilitate recollection of information (in this case semantically based rating tasks) that will be diagnostic for determining context. It is noteworthy that the retrieval cues were the same across Distinctive and Non-Distinctive scans (i.e. Is this word from List 1?) and that the targets of retrieval, List 1 items, were processed identically. Therefore, unlike prior designs, the differential LVPFC effect may be more firmly attributed to subject-initiated, as opposed to cue-instructed changes in retrieval strategy. When considered jointly with the behavioral data, these findings indicate that the use of such retrieval strategies may improve recollection, by reducing the intrusion of familiar List 2 items that are associated with the inappropriate processing task (concreteness judgment) during the Distinctive conditions. More generally, because the design encourages self-initiated elaboration for the Distinctive condition, the prediction arises that subjects who increasingly engage LVPFC during the Distinctive compared to Non-Distinctive source conditions should also show a behavioral advantage in List 1 versus List 2 context discrimination.

This hypothesis was tested using a whole brain correlation analysis examining the relationship between LVPFC recruitment and behavioral List 2 intrusion rates across distinctiveness conditions. The difference in activation for List 1 words in Distinctive versus Non-Distinctive conditions was directly contrasted in a model using the difference in the intrusion errors to List 2 items under the same conditions as a covariate. As before, results were thresholded at $p < .001$ uncorrected, five voxels (Table 2). This analysis implicated a region of the LVPFC (BA 45), which was located slightly posterior to the area found for the ROI derived from the earlier contrasts (Fig. 5A). Activation was also seen in medial regions of the superior frontal cortex and R putamen. As illustrated in Fig. 5B, individual differences in the tendency to recruit L middle VLPFC (BA 45) across the Distinctive versus Non-Distinctive conditions were associated with differences in the vulnerability to intrusion from List 2 items ($r = .75$, $p < .001$). In contrast, this region did not correlate with individual differences to false alarm rates for New items ($r = .4$, $p > .1$), corroborating its role in aiding contextual retrieval of familiar words but not novel materials. Furthermore, a more anterior ventrolateral region (BA 45/46) revealed a similar trend (Fig. 5B, right panel). In short, those subjects who showed the largest increases in anterior and mid-LVPFC responses during the Distinctive compared to Non-Distinctive retrieval conditions also showed the greatest reduction in List 2 intrusion errors. Although consistent with the semantic elaboration account, this finding is less compatible with the general selection account, at

least in these regions. If activation reflected increased selection demands in response to heightened interference, one might expect increased activation to track reduced, not improved, performance across observers.

4. Discussion

The current study examined two different cognitive control hypotheses with respect to the role of LVPFC during episodic retrieval. Unlike prior studies looking at these issues, here the prior processing of target retrieval probes and the format of retrieval prompts were held constant across conditions that were predicted to differ in terms of recruitment of self-initiated semantic elaboration versus the need to select among competing episodic representations. More specifically, the semantic elaboration hypothesis predicted increased recruitment of LVPFC following Distinctive compared to Non-Distinctive processing because only in the former is such elaboration useful. In contrast, the general selection hypothesis predicts that recruitment should increase with manipulations that render episodic representations more similar, because this will necessarily increase interference and hence drive the need for selection mechanisms. Thus the general selection account predicts greater activation following Non-Distinctive encoding compared to Distinctive encoding. The data favored the semantic elaboration hypothesis and suggest a proactive, self-initiated (as opposed to reactive) control process is supported by L anterior ventrolateral PFC during retrieval.

The ability of subjects to capitalize on the relative distinctiveness of prior encoding was entirely self-initiated (proactive) as the targets and prompts at retrieval did not differ for the Distinctive and Non-Distinctive conditions. Moreover, List 1 words were encoded identically in the two conditions and an analysis of the fMRI encoding data showed no differential neural responses in LVPFC regions, even at very liberal thresholds. This suggests that the anterior LVPFC retrieval activation was not driven differences in prior encoding activation, but instead it reflected processes that occurred later during retrieval. These findings do not rule out the possibility that other nearby PFC regions may reflect bottom up reactivation of encoding processes during retrieval (Habib & Nyberg, 2008; Staresina & Davachi, 2006), however, the regions identified here are not subject to this interpretation.

Activation in LVPFC was not accompanied by activity in the L middle temporal gyrus (MTG), a region that is sometimes associated with semantic processing. However, MTG activations tend

Table 2
Regions demonstrating a significant correlation between an increase of activation for contextual retrieval of List 1 words in Distinctive versus Non-Distinctive conditions and a reduction in the intrusion scores.

Region	BA	x	y	z	No. of voxels	Z-score
<i>Brain-behavior correlation</i>						
L inferior frontal gyrus	45	-46	28	24	115	4.56
R putamen	-	26	-8	12	110	4.52
L middle frontal gyrus	44	-46	22	40	31	3.71
R superior temporal pole	38	44	18	-18	20	3.70
L superior frontal gyrus	8	-6	36	54	20	3.57
L superior frontal gyrus	6	-6	16	62	39	3.56
R precentral gyrus	6	20	-16	66	8	3.56
R inferior frontal gyrus	45	54	24	18	18	3.54
L middle frontal gyrus/precentral gyrus	6	-36	6	60	21	3.51
L precentral gyrus	6	-36	0	48	9	3.38
R superior frontal gyrus	8/32	16	18	46	10	3.35
L precentral gyrus	6	-32	-10	62	13	3.34
R superior frontal gyrus	8	6	22	66	5	3.31
R superior frontal gyrus	32	10	32	40	6	3.26
L middle frontal gyrus	8	-24	22	60	6	3.23
L superior parietal lobule	7	-36	-70	54	8	3.23
L inferior frontal gyrus	45	-44	44	0	11	3.21

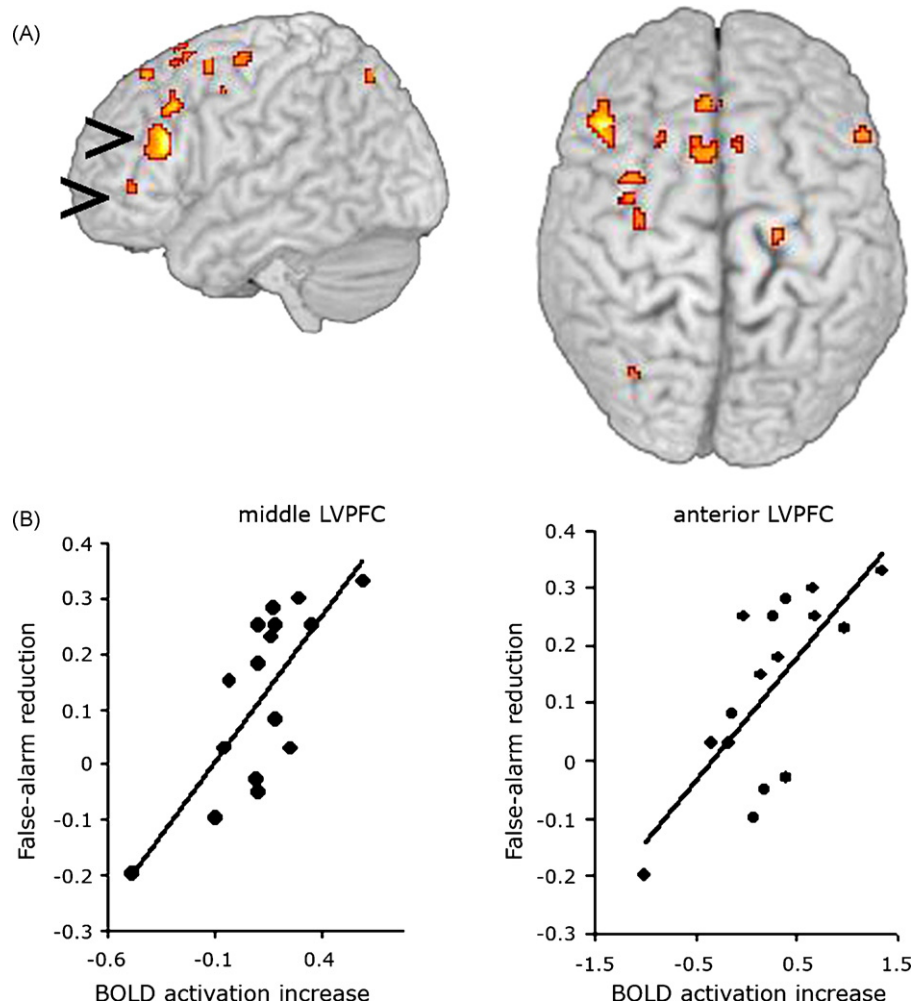


Fig. 5. (A) Regions demonstrating significant correlation between an increase of activation for contextual retrieval of List 1 words in the Distinctive relative to the Non-Distinctive conditions and reduction in intrusion scores. (B) Correlation between intrusion scores and activation in middle and anterior LVPFC. Correlations remained significant when the one potential outlier in the lower left of the plots was removed ($p < .05$). The arrows indicate the regions plotted.

to be small and show great variability across subjects, which may explain the lack of MTG activation in the current experiment. For instance, during the encoding phase, where subjects performed semantic judgment tasks, we found significant activation in bilateral fusiform gyrus, inferior occipital gyrus and PFC, but no above threshold activation in MTG. In addition, while some previous studies have reported co-activation of VLPFC and MTG (e.g. Badre et al., 2005; Dobbins & Wagner, 2005; Gold & Buckner, 2002), others have failed to find temporal activations (e.g. Dobbins et al., 2002; Konishi et al., 2000; Rugg et al., 1999). Nonetheless, our findings are consistent with results from prior studies that propose a role for anterior lateral PFC in controlled semantic retrieval (Badre et al., 2005; Badre & Wagner, 2007; Dobbins & Han, 2006; Dobbins & Wagner, 2005; Wagner et al., 2001). For example, Dobbins and Wagner (2005) have shown that attempts to recollect episodic information linked to the conceptual details of probe items elicited activation in LVPFC, while attempts to recollect prior visual perceptual details about the probes elicited RVPFC activation. These results converge on the idea that LVPFC facilitates context retrieval by supporting semantic elaboration of the probe items in a goal-directed manner and the current findings demonstrate that subjects do not have to be explicitly directed via external prompts to engage in this activity, although there are important individual differences in the propensity to do so in a self-initiated fashion (Fig. 5).

Although we have interpreted the lack of LVPFC activation following Non-Distinctive encoding as reflecting an absence of self-initiated semantic elaboration, it could be argued to instead suggest that subjects simply abandoned the attempt to recollect contextual information altogether because the interference was too severe. From this perspective, general selection demands are not present following Non-Distinctive retrieval because contextual retrieval has been abandoned and hence interference does not occur. Given the current design, this amounts to assuming that subjects essentially chose to guess between the probes that were familiar during the Non-Distinctive condition. However, our behavioral data argue against this interpretation, as performance accuracy was above chance even in the Non-Distinctive condition. This indicates that subjects did not base their responses on pure probe familiarity, but instead used some degree of context recollection to respond (Fig. 2A). Furthermore, had participants completely abandoned the context retrieval task and instead chosen to rely solely upon item familiarity, then arguably their endorsement rates for List 1 and List 2 items should have resembled those during the item memory tasks, which were virtually identical (Fig. 2B). This did not occur. Thus overall, the notion that subjects abandoned a putative general selection mechanism during the Non-Distinctive context retrieval condition, and the finding that they nonetheless discriminated the items above chance, seems hard to reconcile.

The current results potentially challenge the view that anterior ventrolateral PFC is implicated in general selection processes necessary to resolve conflict between competing representations. While some studies have shown that LVPFC activation occurs in conditions of high interference (e.g. Snyder et al., 2007; Thompson-Schill et al., 1999) the region also has been shown to respond significantly more to source memory decisions than recency judgments, despite the latter being more demanding as revealed by greater error rates and longer reaction times (Dobbins et al., 2003). It is important to note that the semantic elaboration hypothesis is also potentially capable of incorporating prior findings of increased LVPFC recruitment during heightened interference conditions, provided the materials are meaningful and the subjects believe that semantic elaboration may help to resolve the interference. In contrast, any account that posits that LVPFC responses are a *necessary* consequence of interference between competing representations faces difficulty with patterns such those in the current study, where the high interference condition led to less activation than the condition demonstrating less interference.

In contrast to the differential response to familiar items following Distinctive and Non-Distinctive encoding, the LVPFC response to novel items was uniformly low across both conditions. This may reflect the fact that items perceived as novel could be uniformly rejected as inappropriate because both tasks targeted context memory. Indeed, rejection of New items was similarly efficient and rapid under both Distinctive and Non-Distinctive context memory tests and the items were also easily rejected during item memory tests (Fig. 2). Furthermore, the post-scan recognition test carried out on the New items encountered during context memory testing showed no significant differences in accuracy rates between Distinctive and Non-Distinctive conditions ($t < 1$). The results suggest that semantic elaboration strategies that improved recollection during context retrieval were not used in the processing of New items. Finally, correct rejections for novel items during the scanning task were conducted more rapidly than decisions to familiar items (from List 1 and List 2), which is also consistent with the idea that low familiarity items generally did not evoke detailed semantic processing.

The individual differences analysis suggested that subjects differed in the degree to which they up-regulated LVPFC during contextual retrieval attempts following Distinctive compared to Non-Distinctive encoding. Furthermore, these differences tracked their tendencies to effectively reject lures from List 2. In conjunction with the design of the experiment, which provided no external prompt to induce a shift in retrieval strategy, these results further demonstrate a critical role for self-initiation of semantic elaboration during retrieval tasks. The role of self-initiation of cognitive control in memory has received some attention in studies that focused on encoding (rather than retrieval) strategies. Namely, in two studies with older adults, Derwinger et al. (2005) and Bissig and Lustig (2007) have provided compelling evidence that the self-initiated use and maintenance of semantic elaboration strategies during encoding (such as relating the words to experiences in life) supported later memory. By contrast, subjects who used superficial strategies (such as rote rehearsal or mnemonic training) showed poorer performance. In a PET study with young adults, Kapur and colleagues reported that subjects' use of cognitive strategies of semantic processing during encoding, relative to simple word reading, invoked activation in L anterior inferior prefrontal cortex, and significantly improved later recollection (Kapur et al., 1996). Similarly, in an fMRI study, Kirchoff and Buckner (2006) demonstrated that subjects' self-reported use of semantic encoding strategies following testing correlated with activation in L anterior VPF, which in turn predicted memory performance. Interestingly, this region converges with that found in the current study dur-

ing context retrieval. As predicted, we found that across subjects, the magnitude activation in this prefrontal region during Distinctive versus Non-Distinctive retrieval conditions correlated with increased response accuracy reflected by an increased ability to reject familiarized lures from List 2. Furthermore, a more anterior ventrolateral region (BA 45/46) revealed a similar trend. Taken together, the results show that individual differences in retrieval strategies correlate with brain activation patterns in anterior- and middle-ventrolateral PFC regions, which in turn predict memory performance. The overlap between the ventrolateral regions implicated here and those in Kirchoff and Buckner (2006), suggests that individual differences in self-initiated semantic elaborative strategies occur not only during encoding, but also during retrieval.

Returning to Tulving's Encoding Specificity Principle that motivated the current research, the data highlight the fact that retrieval cues are actively constructed representations influenced by the subject's knowledge of the utility of processing certain types of probe features during episodic retrieval attempts. As emphasized by Tulving (1983) this runs to counter the notion that test items, such as words, maintain a fixed identity when presented as retrieval cues across different episodic retrieval situations, an assumption termed "transituational identity" by Tulving. More specifically, the current study demonstrated that two sets of identically encoded words (List 1 items), re-presented in an identical manner at test, and accompanied by the same retrieval query ("List 1?"), nonetheless were associated with considerable differences in PFC activation during retrieval attempt in the two context memory conditions examined here. This would not have occurred if the words functioned as identical copy cues in the two conditions, that is, if situational identity held. Instead, these differences reflect a subject-initiated difference in the approach to the retrieval tasks that hinges on the appreciation that because the List 1 and List 2 events were linked to different semantic features of the materials in the Distinctive condition, semantic processing of probe features at retrieval could be used to help recover episodic information disambiguating list origin during retrieval in this case. Such a strategy was not viable in the Non-Distinctive case and recruitment of LVPFC regions was greatly diminished. Interestingly, these findings may suggest that subjects have a coarse or heuristic appreciation of the Encoding Specificity Principle itself, because they were aware without instruction that processing the semantic features of probes would be useful in some situations, but less so in others. As with semantic processing during encoding events however, there appear to be considerable individual differences in the tendency to self-initiate semantic elaborative mechanisms at retrieval, and these differences appear to have considerable behavioral implications in terms of susceptibility to interference.

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