The Medial Temporal Lobe and the Left Inferior Prefrontal Cortex Jointly Support Interference Resolution in Verbal Working Memory

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Abstract

■ During working memory retrieval, proactive interference (PI) can be induced by semantic similarity and episodic familiarity. Here, we used fMRI to test hypotheses about the role of the left inferior frontal gyrus (LIFG) and the medial temporal lobe (MTL) regions in successful resolution of PI. Participants studied six-word lists and responded to a recognition probe after a short distracter period. We induced semantic PI by using study lists containing words within the same semantic category (e.g., animals). We also measured PI induced by recent study, which should increase episodic familiarity, by comparing recent negative probes (lures studied in previous trial) to distant negative probes (lures that had not been presented within a block). Resolving both types of PI resulted in enhanced activation in LIFG and MTL regions. We propose that the LIFG and the MTL support successful resolution of interference via controlled retrieval processes that serve to recover detailed episodic (e.g., list-specific or source) information: Specifically, the data suggest that BOLD activation in the LIFG reflects the deployment of controlled retrieval operations, regardless of whether the retrieval attempt succeeds in recovering the target information, whereas MTL activation specifically reflects access to relevant episodic information that serves to successfully resolve PI. ■

INTRODUCTION

Most complex cognitive skills require access to representations formed as the products of recent perceptual and cognitive operations. As with long-term representations, the successful retrieval of recently formed representations is strongly affected by different sources of interference (e.g., Anderson & Neely, 1996; Crowder, 1976). Proactive interference (PI), which stems from learning prior to the to-be-retrieved material (e.g., Keppel & Underwood, 1962), has major effects on retrieval dynamics. The present study focuses on the neural mechanisms that underlie PI resolution in verbal working memory (WM).

Much of the work on the neural bases of interference resolution in WM has come from investigations of interference effects stemming from episodic familiarity induced by recent study, using a recent negative (RN) probe paradigm (Monsell, 1978). In this paradigm, the high residual familiarity of a recently studied lure (typically from a previous study list) induces either longer response times for correct rejection or an increased likelihood of false recognition (e.g., McElree & Dosher, 1989; Monsell, 1978). Neuroimaging studies have found more activation in the ventral left inferior frontal gyrus (LIFG) for an RN probe (lure from the study list of the previous trial) compared to an unstudied probe in item recognition (e.g., Badre & Wagner, 2005; Jonides, Badre, Curtis, Thompson-Schill, & Smith, 2002; Jonides et al., 2000; Jonides, Smith, Marshuetz, & Koeppe, 1998). In addition, this enhanced activation in the LIFG is specific to the retrieval stage of the RN probe (D'Esposito, Postle, Jonides, & Smith, 1999). That the LIFG plays a crucial role in successful interference resolution is further supported by studies demonstrating that patients with LIFG damage are more susceptibility to RN probes than healthy control groups (e.g., Thompson-Schill et al., 2002), and by a recent study showing that repetitive transcranial magnetic stimulation of the LIFG impairs correct rejection of RN probes (Feredoes, Tononi, & Postle, 2006).

These studies establish that the LIFG plays an important role in resolving interference that arises from episodic familiarity, but they also raise the possibility that this region could have a critical role in interference resolution in general. Interference induced by episodic familiarity is but one type of PI effect. Indeed, a long tradition of behavioral research on PI effects has focused on the build up of PI results from the prior learning of semantically similar study material. The negative effect of semantically similar material on memory accuracy is most evident in the release from PI paradigm. In this paradigm,

participants are presented with study lists consisting of semantically similar items, such as exemplars from the same semantic category. As the number of words presented from the same category increases, performance decreases due to a build up of PI. When the category is then switched, performance returns to baseline, suggesting that this shift to a new category "releases" PI. Comparable results indicating PI's detrimental effect on retrieval success have been obtained in investigations of both recall (e.g., Tehan & Humphreys, 1996; Watkins & Watkins, 1975; Gardiner, Craik, & Birstwistle, 1972; Craik & Birtwistle, 1971; Wickens, 1970), and recognition (e.g., Öztekin & McElree, 2007; Petrusic & Dillon, 1972).

Behavioral work has identified important properties of the processes operative in the build up and release from PI in this paradigm. Research indicates that PI selectively affects retrieval with no or minor effect on encoding or storage processes (e.g., Tehan & Humphreys, 1996; Watkins & Watkins, 1975; Gardiner et al., 1972). Accordingly, it has been suggested that build up of PI decreases memory performance by reducing discriminability of the target material at retrieval (e.g., Crowder, 1976). Recently, using a probe-recognition variant of the release from PI paradigm comparable to the fMRI study we report here, Öztekin and McElree (2007) demonstrated that PI decreases the diagnosticity of familiarity information, but that it has no measurable effects on the recovery of more detailed episodic information. These findings suggest that recovery of detailed episodic information (e.g., source memory) may be used to compensate for the negative impact of PI on memory performance, at least in item recognition.

Studies examining responses to RN probes indicate that successfully resolving interference caused by episodic familiarity may rely on similar compensation mechanisms. Behavioral studies investigating the time course of recognition (e.g., Öztekin & McElree, 2007; Hintzman, Caulton, & Levitin, 1998; McElree, 1998; Hintzman & Curran, 1994; McElree & Dosher, 1989) have demonstrated that an RN probe induces high false alarm rates early in retrieval compared to a non-RN probe, due to its high residual familiarity. However, false alarm rates diminish later in retrieval when participants are able to recover more detailed episodic information (i.e., either that the probe was not a member of current study list, or that it was studied on previous trial). Thus, extant behavioral evidence suggests that controlled retrieval processes, which recover detailed episodic information, may serve to alleviate the adverse effects of both types of interference.

Despite the extensive behavioral work, the neural bases of PI resolution induced by semantic similarity are understudied. To our knowledge, only one neuroimaging study (Postle, Brush, & Nick, 2004; see also Postle & Brush, 2004 for comparable results) applied a related paradigm. In that study, stimulus domain (e.g.,

words, letters, colors, digits) was modified across a number of blocks. Within each stimulus domain, increased activation in the LIFG was observed across the first two trials of the block, indicating that the LIFG is sensitive to interference that arises from repeated exposure of a class of stimuli. Additionally, the LIFG has been implicated in controlled semantic processing (e.g., Thompson-Schill, 2003; Thompson-Schill et al., 1998) and strategic retrieval of information from semantic memory (e.g., Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997).

Based on the behavioral work that suggests both types of PI are resolved with similar compensatory processes, and based on the Postle et al. (2004) study, we hypothesized that the LIFG, which has been found to be involved in resolving episodic familiarity interference, would likewise be involved in the resolution of PI induced by semantic similarity. This should particularly be the case if the LIFG supports controlled retrieval processes that are essential for resolving both types of interference. Indeed, the LIFG has been implicated in the retrieval or selection of both long-term (Miller & Cohen, 2001; Thompson-Schill et al., 1997; Demb, Desmond, Wagner, & Chandan, 1995) and WM representations (e.g., Öztekin, McElree, Staresina, & Davachi, 2008), suggesting that this region may be critical in domain-general retrieval operations. In addition, Badre and Wagner (2005) suggested that interference resolution in the RN probe paradigm may be accomplished through episodic retrieval, and that enhanced activation in the LIFG for RN probes may reflect the increased demand on controlled episodic retrieval processes.

Our second goal was to examine the contribution of medial temporal lobe (MTL) regions to PI resolution. The MTL is known to be critical in encoding and retrieval of long-term episodic memories (for review, see Mayes, Montaldi, & Migo, 2007; Davachi, 2006). However, the MTL has also been implicated in maintenance (Cabeza, Dolcos, Graham, & Nyberg, 2002; Davachi & Wagner, 2002; Ranganath & D'Esposito, 2001) and retrieval of WM representations as well (e.g., Öztekin et al., 2008; Karlsgodt, Shirinyan, van Erp, Cohen, & Cannon, 2005), indicating its contribution to both WM and LTM processes. Consistent with previous work suggesting that episodic retrieval is engaged to resolve interference (e.g., Öztekin & McElree, 2007; Badre & Wagner, 2005), we expected to also observe enhanced activation in the MTL for conditions that require access to relevant episodic information (e.g., source memory) in order to resolve PI, regardless of whether it is induced by episodic familiarity or semantic similarity.

To test these hypotheses, we conjointly applied the release from PI paradigm, and the RN probe paradigm in a short-term probe recognition task (e.g., Öztekin & McElree, 2007), and examined neural activation in LIFG and MTL regions using fMRI.

METHODS

Participants

Fifteen healthy right-handed adults (7 women, ages between 18 and 36 years) participated in the study. Informed consent was obtained in accordance with the institutional review board at New York University. Participants were native speakers of English, had normal or corrected-to-normal vision, and were paid for their time.

Design and Stimuli

Stimuli consisted of 21 instances of 36 categories from the category norms of Van Overschelde, Rawson, and Dunlosky (2004). The experiment consisted of five 10-min blocks. Each block contained 60 experimental trials, in which participants studied a six-item list, solved a math problem, and executed a recognition memory judgment to a test word. To induce PI via semantic similarity, words from the same category were presented for three consecutive trials. A category was pseudorandomly selected from the 36 categories. The same category was not repeated within a block.

Positive and negative test probes were presented equally often. Positive probes were randomly chosen from the six serial positions of the study list, with the constraint to be twice as likely drawn from Positions 1 to 3 than Positions 4 to 6.[1] Negative probes consisted of distant negatives (DNs) and recent negatives (RNs). DNs were drawn from members of the same semantic category of the studied items, but had not been presented within the current block. RNs were selected randomly from the six serial positions of the previous trial. For List 2 and List 3 trials, negative probes were half the time DNs and half the time RNs. For List 1 trials, negative probes consisted of only DNs, as these trials involved the first instance of a category. This design structure (illustrated in Figure 1A) resulted in 50 positive probe trials for each of the three lists, 50 DN trials for List 1, 25 DN and 25 RN trials for List 2, and 25 DN and 25 RN trials for List 3 upon completion of the experiment.

Participants completed a 1-hr behavioral practice session before doing the task in the MRI scanner.

Procedure

Figure 1B shows the sequence of events in a single trial. Each trial began with the presentation of a six-word study list, presented sequentially for 400 msec each. Next, a math problem consisting of either addition or subtraction of two randomly selected two-digit numbers was presented for 1600 msec. Participants indicated whether the solution to the problem was correct or not by pressing either the middle or index finger on the button box. Following the math problem, a test word was presented for 2000 msec, and participants indicated whether the word was a member of the current study list or not by pressing either the middle or index finger on the button box. The intertrial interval consisted of the presentation of a fixation point on the center of the screen for 4000 msec.

fMRI Protocol

A Siemens Allegra 3-T head-only scanner was used to acquire functional and anatomical images. Thirty-six axial slices were obtained with a voxel size of 3 mm × 3 mm × 3 mm (TR = 2 sec; TE = 30 msec; flip angle = 90°). Following the functional runs, T1-weighted high-resolution anatomical images (MP-RAGE) were obtained for anatomical localization.

Image Processing

Image processing and data analysis were performed using SPM2 (www.fil.ion.ucl.ac.uk/spm/). Preprocessing of images consisted of (a) correction of slice acquisition timing across slices, (b) realigning the images to the first volume in each fMRI run to correct for head movement, (c) normalization of functional and anatomical images to a standard template EPI provided by SPM2, and (d) smoothing images with a 6-mm full-width half-maximum isotropic Gaussian kernel.

fMRI Data Analysis

Data analysis was conducted using the General Linear Model implemented in SPM2. To identify regions that were engaged by our task in an unbiased manner, all trials (including correct and incorrect trials across all conditions) were modeled using a canonical hemodynamic response function and its temporal derivative. Data across runs were concatenated and modeled as one session with mean signal and scanner drift entered into the model as covariates. For each participant, a task effects contrast was derived using a subject-specific fixed-effects model.

Regions of interests (ROIs) were defined from the task effects contrast for each participant. Voxels in each participant's individual ROIs were restricted to the most active 20 voxels within an anatomically defined region. Specifically, the anatomical boundaries for the inferior frontal gyrus ROI consisted of the inferior frontal sulcus dorsally and rostrally, and the precentral sulcus caudally. The hippocampal region included the dentate gyrus, the uncus, the hippocampus proper, and was limited caudally by the parahippocampal ramus of the collateral fissure. The parahippocampal region contained the parahippocampal gyrus and parahippocampal uncus (including both the entorhinal and the perirhinal cortices), and it was limited caudally by the parieto-occipital sulcus, and ventrally by the collateral sulcus (Tzourio-Mazoyer et al., 2002). To model activation across conditions in these ROIs, correct trials (incorrect trials were excluded
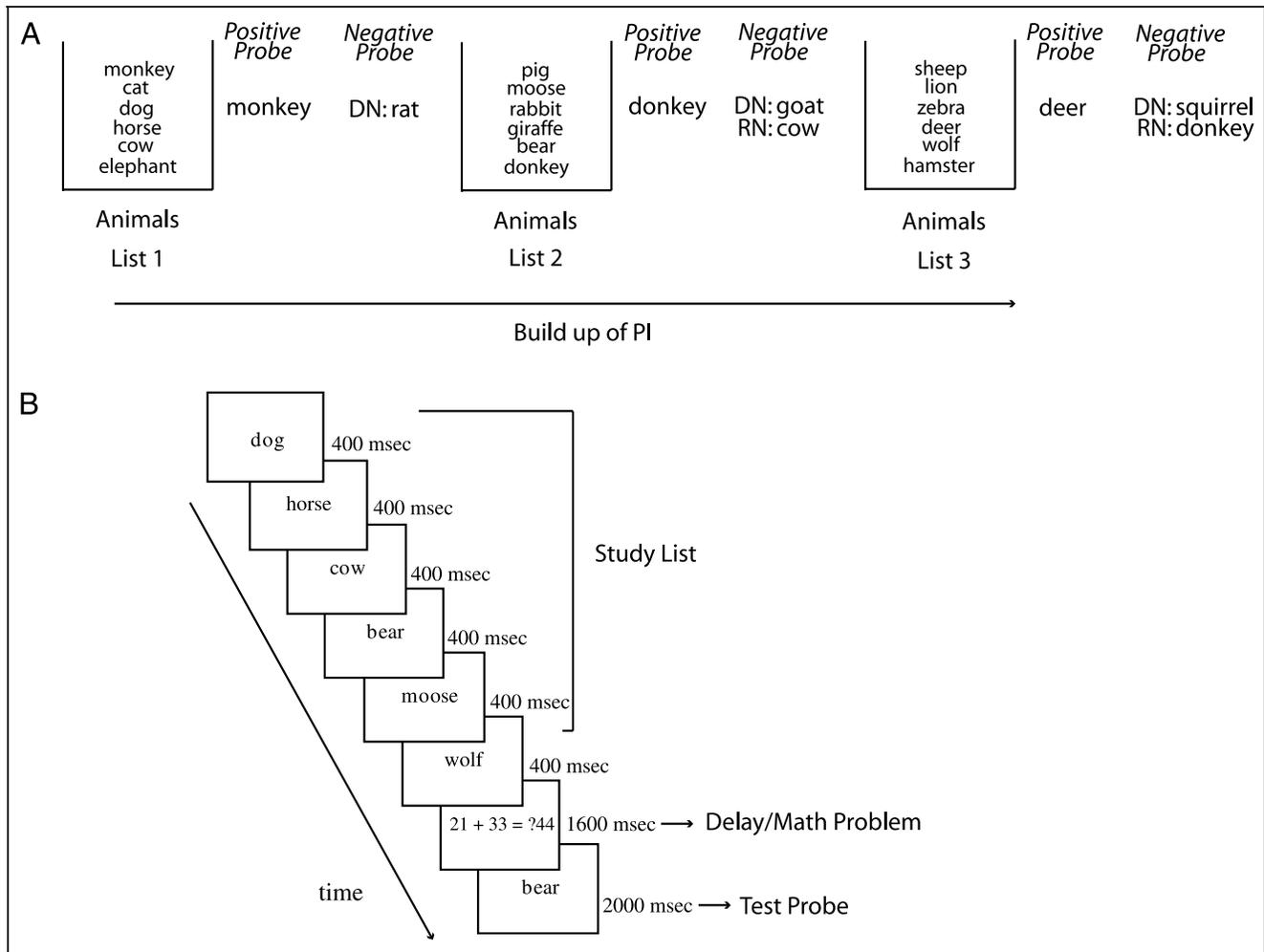
Figure 1. Experimental design and trial organization. (A) Illustration of PI manipulation and list structure. DN = distant negative; RN = recent negative. (B) A sample sequence and timing for an experimental trial.

from this model) were sorted according to conditions of interest (list and type of test probe) and were modeled with a finite impulse response function using seven regressors to model activity for 14 sec after the trial onset. Using this model, ROIs were further analyzed with the MarsBaR ROI toolbox for SPM (Brett, Anton, Valabregue, & Poline, 2002; http://marsbar.sourceforge.net/). Percent BOLD signal change across participants was subjected to mixed ANOVAs, treating condition (list and type of test probe) and time (TRs) as repeated measures, and subjects as a random effect. To reveal the statistical pattern across conditions, additional comparisons on the peak time point of activation were conducted.

RESULTS

Behavioral Data

Positive Probes

A repeated measures ANOVA conducted on the hit rates across the three lists indicated a reliable reduction in accuracy as PI built up [$F(2, 28) = 4.732, p < .017$] (illus-trated in Figure 2A). Pairwise comparisons indicated a significant decrease in hit rates between Lists 1 and 3 [$t(14) = 2.212, p < .044$] and Lists 2 and 3 [$t(14) = 2.639, p < .019$]. There was also a slight increase in reaction time (RT) across the three lists (Figure 2B) as PI built up, however, this trend was not reliable.

Lures

There were two types of lures: DNs, unstudied lures that were from the same category of the studied items, and RNs, lures presented from the preceding trial. Hence, a DN presented in List 1 induced a low amount of PI, whereas DNs presented in Lists 2 and 3 induced high amounts of PI due to semantic similarity. Note that there were no RN probes in List 1 trials because this was the first presentation of the current category. RNs presented in List 2 (lures selected from members of List 1) induced high episodic familiarity and moderate amount of PI from semantic similarity, and RNs presented in List 3 (lures selected from studied items in List 2) induced high episodic familiarity and high amounts of semantic PI.
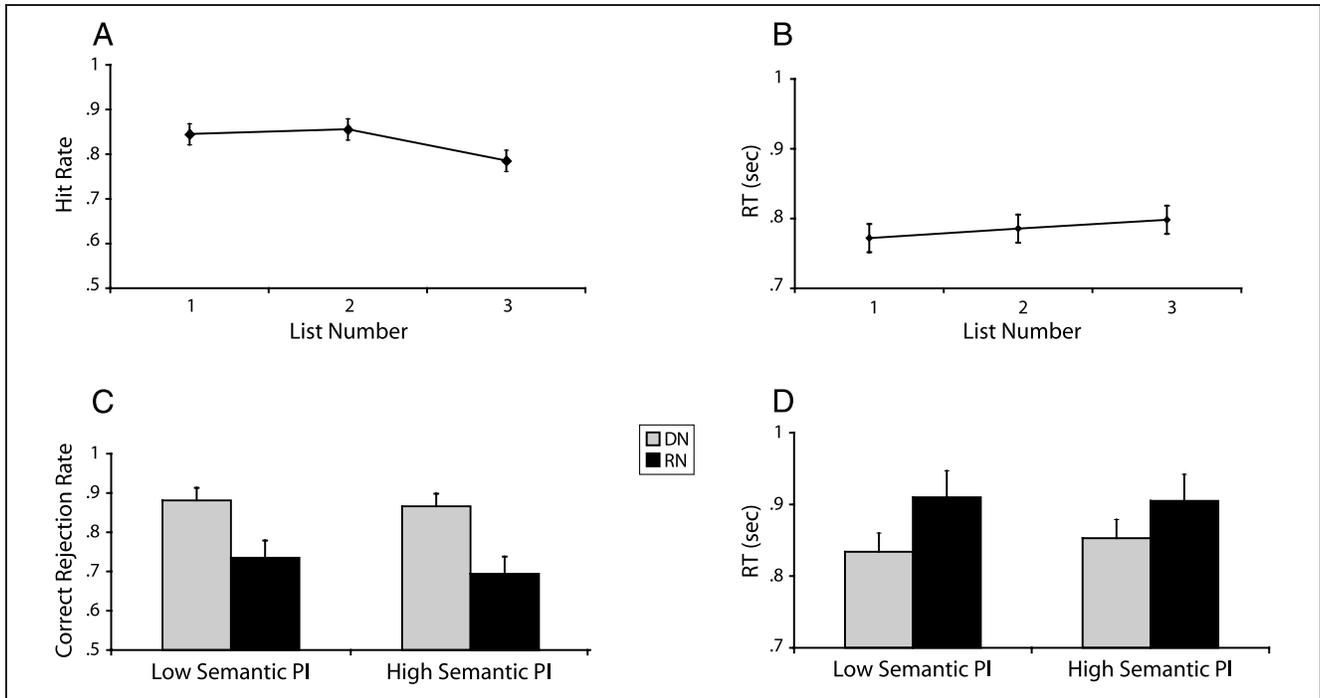
Figure 2. Behavioral data. (A) Accuracy for positive test probes (measured in hit rate) as a function of list. (B) RT for positive test probes as a function of list. (C) Accuracy for negative test probes (measured in correct rejection rate) for DN versus RN probes broken into when semantic PI was low (i.e., DN in List 1 compared to RN in List 2 [lure drawn from List 1]) and when semantic PI was high (i.e., DN in Lists 2 and 3 compared to RN presented in List 3 [lure drawn from List 2]). (D) RT for DN versus RN probes broken into low versus high semantic PI. Error bars indicate standard error of the mean.

Consequently, to compare the effects of type of probe as a function of amount of semantic PI in the retrieval context, we compared DNs in List 1 to RNs in List 2 (lures that were selected from studied items in List 1) as these conditions induced low amounts of semantic PI, and concatenated DNs in Lists 2 and 3, and compared them against RNs in List 3 as these conditions induced high amounts of semantic PI.

A 2 (low semantic PI vs. high semantic PI) × 2 (DN probe vs. RN probe) repeated measures ANOVA conducted on correct rejection rates indicated a main effect of probe type [$F(1, 14) = 38.101, p < .001$] with reduced accuracy for RNs compared to DNs (Figure 2C). Pairwise comparisons indicated that RNs were less accurate than DNs when amount of PI was both low [$t(14) = -4.430, p < .001$] and when PI was high [$t(14) = -4.236, p < .001$]. RTs for RNs were also marginally slower compared to DNs [$F(1, 14) = 3.932, p < .067$] (Figure 2D). Pairwise comparisons revealed that the RT difference was significant when semantic PI was low [$t(14) = 2.543, p < .023$] but was not reliable when amount of semantic PI was high.

Neuroimaging Data

Behavioral results demonstrate that the task successfully induced PI based on both episodic familiarity and se-

mantic similarity. Specifically, semantic similarity reduced accuracy as it built up across the lists, and RN probes exhibited lower accuracy and slower response times compared to DN probes. We next turn to our neuroimaging data to assess the contributions of LIFG and MTL regions in successful resolution of both types of PI.

Left Inferior Frontal Gyrus

Positive probes. Linear contrasts conducted on peak percent signal change in the LIFG across the three lists revealed that activation in List 1 was significantly reduced compared to List 2 [$F(1, 308) = 13.56, p < .001$] and List 3 [$F(1, 308) = 4.37, p < .038$]. Hence, in line with our prediction, LIFG activation increased when semantic PI was high, consistent with the hypothesis that the LIFG contributes to the resolution of semantic PI.

Lures. A 2 (low semantic PI vs. high semantic PI) × 2 (DN vs. RN) repeated measures ANOVA conducted on peak percent signal change activation in the LIFG indicated a marginal interaction between type of probe and the amount of semantic PI [$F(1, 14) = 4.29, p < .057$]. Further linear contrasts indicated that when semantic PI was low, RNs exhibited *more* activation than DNs [$F(1, 616) = 6.73, p < .001$], replicating previous neuroimaging studies. However, when semantic PI was high,

RNs exhibited *less* LIFG activation than DNs, although this comparison was not statistically reliable (Figure 3C). In order to investigate whether the amount of activation was modulated by individual differences in the behavioral data, we computed differences in RT between RN and DN probes when semantic PI was low and when semantic PI was high. The resultant difference scores were regressed on the corresponding difference in peak percent signal change (across RN and DN probes). The increase in LIFG activation for RNs compared to DNs when semantic PI was low was reliably predicted from the corresponding difference in RT between the probes $[r(14) = .654, p < .008]^2$ (Figure 3D), with enhanced LIFG activation for RNs being associated with *slower RTs* for RNs. This relationship is consistent with LIFG activation reflecting the compensation mechanisms that are engaged to resolve PI. A comparable relationship was not present in accuracy data ($r = .003, p = .991$). There was also no reliable relationship with behavioral performance and neural activation for high semantic PI conditions. As reported above, the episodic familiarity effect (reflected from higher activation for RN compared to DN probes) in the LIFG was not present under high semantic PI.

Medial Temporal Lobe

Positive probes. Peak percent signal change increased as PI built up in the left parahippocampal gyrus (Fig-

ure 4C): Activation in List 1 was reliably less than List 2 $[F(1, 308) = 6.53, p < .011]$ and List 3 $[F(1, 308) = 4.82, p < .029]$. Peak percent signal change in the left hippocampus exhibited the same pattern [List 1 < List 2, $F(1, 308) = 7.01, p < .009$; List 1 < List 3, $F(1, 308) = 3.62, p < .058$] (Figure 4D). Hence, as predicted, MTL regions also appear to contribute to the resolution of semantic PI.

Lures. A significant interaction of probe type and PI was evident in peak percent signal change in the left parahippocampal gyrus $[F(1, 14) = 5.92, p < .029]$. Further comparisons indicated that neural activation for RNs was marginally greater than DNs when semantic PI was low $[F(1, 616) = 3.05 p < .081]$ and, in contrast, was marginally reduced when semantic PI was high $[F(1, 616) = 2.99 p < .084]$ (Figure 4E). A similar nonsignificant interaction was observed in the left hippocampus ROI as well (Figure 4F).

There was also a significant correlation between the difference in neural activation across RN and DN probes in the left parahippocampal gyrus and the corresponding difference in correct rejection rates $[r(14) = .587, p < .021^3]$: activation was enhanced for RNs compared to DNs when there was *less* difference in accuracy between the RN and DN probes (Figure 4G). This relationship provides evidence that the MTL contributes to the successful resolution of episodic familiarity interference.
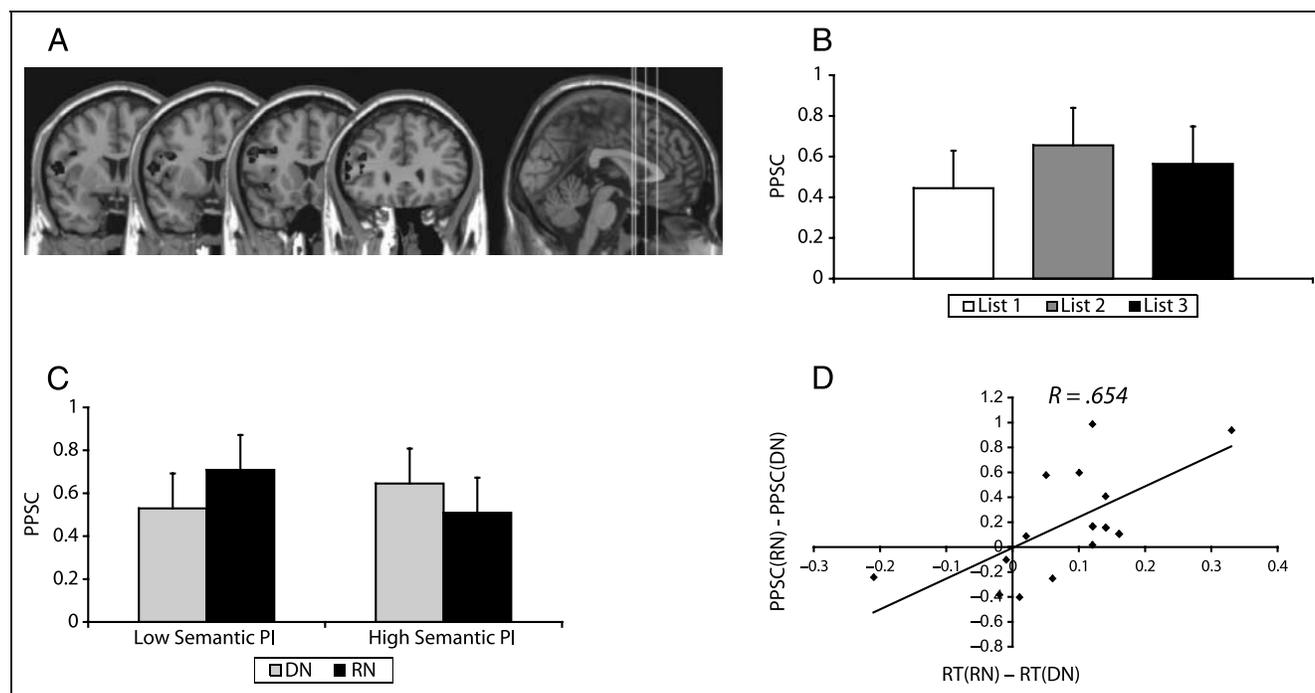

Figure 3. Neuroimaging data for the left inferior frontal gyrus (LIFG) ROI. (A) Multislice coronal view of the LIFG ROI across participants. (B) Peak percent signal change activation in this ROI for positive test probes as a function of list. (C) Peak percent signal change activation in this ROI for DN versus RN probes broken into low versus high semantic PI. (D) Scatterplot of difference in peak percent signal change in this region between RN and DN probes when semantic PI was low as a function of the corresponding RT difference across participants. Error bars indicate 95% confidence intervals. PPSC = Peak percent signal change; RT = reaction time; DN = distant negative; RN = recent negative.
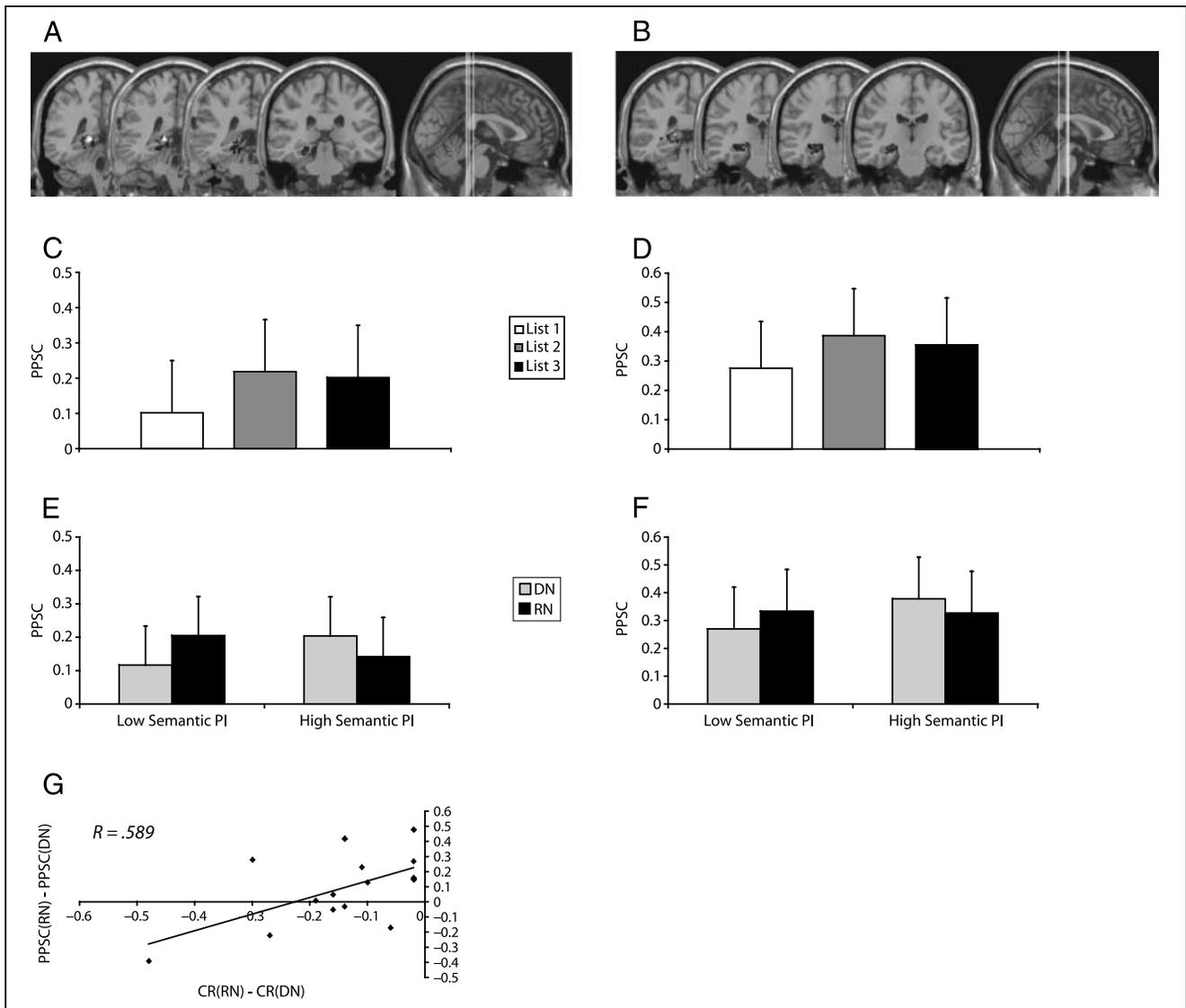
Figure 4. Neuroimaging data for medial temporal lobe (MTL) ROIs. (A) Multislice coronal view of the left parahippocampal gyrus ROI across participants. (B) Multislice coronal view of the left hippocampus ROI across participants. (C) Peak percent signal change (PPSC) activation in the left parahippocampal gyrus ROI for positive test probes as a function of list. (D) Peak percent signal change activation in the left hippocampus ROI for positive test probes as a function of list. (E) Peak percent signal change activation in the left parahippocampal gyrus ROI for DN versus RN probes broken into low versus high semantic PI. (F) Peak percent signal change activation in the left hippocampus ROI for DN versus RN probes broken into low versus high semantic PI. (G) Scatterplot of difference in peak percent signal change activation across RN and DN probes in the left parahippocampal gyrus ROI as a function of the corresponding difference in correct rejection rates under low semantic PI. Note that activation is enhanced for RNs compared to DNs when there is *less* difference in accuracy between the RN and DN probes. Error bars indicate 95% confidence intervals. PPSC = peak percent signal change; CR = correct rejection rate; DN = distant negative; RN = recent negative.

There was no comparable relationship between MTL activation and RT ($r = .161$, $p = .565$).

Accuracy Analysis

To follow up on the relationship between neural activation in the MTL and accuracy, and to further test whether this relationship reflected MTL's contribution to successful resolution of PI, we examined how activation in our ROIs varied for correct rejections and false alarms to RN probes.[4] This analysis indicated that activation for correct rejection trials was greater than false alarm trials

in the MTL, in both the hippocampal [$F(1, 9) = 7.16$, $p < .025$] and the parahippocampal [$F(1, 9) = 11.44$, $p < .008$] regions. A comparable effect was not present in the LIFG.

Thus, as predicted, the data indicate that both LIFG and MTL regions are involved in the resolution of both types of interference. The data further suggest that they might have different roles in supporting PI resolution. The observed relationship between RT and LIFG activation suggests that LIFG activation might be reflecting the engagement of controlled retrieval operations, regardless of whether the retrieval attempts are successful in

resolving PI (as there was no comparable relationship with accuracy). The reliable relationship between MTL activation and accuracy, on the other hand, suggests that the MTL might support PI resolution via recovering specifically the relevant episodic information that can successfully resolve PI.

Response Criterion Bias

We found increased activation to positive probes in both LIFG and MTL regions when semantic PI was present. However, in each ROI, activation was slightly less for List 3 compared to List 2, although amount of PI was presumably highest in List 3. Correspondingly, there was a reduction in hit rates from List 2 to List 3, indicating that participants were less successful in resolving PI in List 3. To investigate this pattern further, we examined whether there was a change in strategies for resolving PI in Lists 2 and 3.

We computed each participant's response criterion bias (β in an equal-Gaussian Signal Detection model) in each list. There was a marginal change in bias across Lists 2 and 3 [$t(14) = 2.02, p < .063$], reflecting a more conservative criterion in List 3 than in List 2. This finding suggests that the slight reduction in LIFG and MTL activation across Lists 2 to 3 may have been due to a more conservative response criterion, which decreased the need to engage in compensatory mechanisms (i.e., retrieval of detailed episodic information) to resolve PI. If this interpretation is correct, rather than indexing the amount of PI, neural activation in the LIFG and the MTL may reflect the compensatory mechanisms (e.g., retrieval of list-specific information) that are engaged to resolve PI.

DISCUSSION

Summary

The LIFG plays a crucial role in resolving interference (see Jonides & Nee, 2006, for a literature review). We replicated the well-established finding of enhanced LIFG activation for responses to recently studied lures. Consistent with the hypothesis that the rejection of lures with high episodic familiarity requires the retrieval of detailed episodic information (Öztekin & McElree, 2007; Badre & Wagner, 2005), we found that recently studied lures also engender enhanced activation in MTL regions. To our knowledge, MTL involvement in PI resolution with the paradigms investigated in our study (PI induced by episodic familiarity and semantic similarity) has not been previously reported. Extending prior neuroimaging investigations of PI, we examined how the build up of semantic similarity affects neural activation in both LIFG and MTL regions. In our analyses of responses to studied items in the release from PI paradigm, we found that activation increased in both the LIFG and the MTL as PI built up across the lists. These findings indicate that

both regions are involved in resolving the potentially detrimental effects of semantic similarity on memory performance, and they suggest that these regions play a general role in PI resolution. Furthermore, the data indicated a dissociation in the roles of LIFG and MTL regions in resolving PI. LIFG activation was correlated with RT measures, suggesting that the LIFG might support the controlled retrieval operations that are engaged to resolve PI, regardless of whether these operations are successful. In contrast, MTL activation correlated in an opposite direction with behavioral accuracy: MTL activation was enhanced as the accuracy difference across RNs and DNs was less, suggesting that the MTL may support access to relevant episodic information (e.g., source or list-specific information) that can successfully resolve PI.

Finally, we found evidence that the two types of interference modulate neural activation in an interactive fashion: In both LIFG and MTL regions, RNs engendered enhanced activation compared to DNs under conditions of low semantic PI, but not when semantic PI was high. Below, we highlight the implications of these findings, and we propose a tentative explanation for the observed interaction between the two interference sources.

Episodic Retrieval in PI Resolution: The Contribution of the MTL

Recognition decisions can be based on an assessment of the overall quality of the match of a test probe to representations in memory—often viewed as an assessment of familiarity—or from the recovery of detailed associative (episodic and/or contextual) information, which can include source information—what is viewed as a recollective process in dual-process models (see Yonelinas, 2002, for a review). Behavioral investigations of the time course of short-term recognition memory indicate that PI primarily has a detrimental effect on decisions based on familiarity (e.g., Öztekin & McElree, 2007; McElree & Dosher, 1989). PI in the retrieval context decreases the diagnosticity of familiarity assessments, as lures that have been studied recently or that share semantic features with studied items can engender levels of familiarity comparable to list members. Under both high episodic familiarity and semantic similarity conditions, successful discrimination may require the recovery of more detailed episodic information to localize an item to a particular study context.

As MTL regions have been implicated in successful episodic retrieval (e.g., Dobbins, Rice, Wagner, & Schacter, 2003), the increased activation in MTL regions observed in the present study is consistent with behavioral research indicating greater involvement of episodic retrieval processes to counter both sources of PI. In the case of RN lures, we found a direct relationship between the difference in activation in the left parahippocampal region for recent versus distant lures and

the corresponding difference in the accuracy of rejecting the two lure types. Specifically, the difference in MTL activation between RN and DN probes was *greater* when the corresponding difference in accuracy was *less*, indicating that MTL activation is linked to *successful* resolution of episodic interference induced by the RN probes. In addition, activation in the MTL was greater for trials when an RN probe was correctly rejected, compared to trials when it was falsely recognized. Taken together, these findings implicate the role of the MTL in successful resolution of PI.

The observed patterns are also consistent with previous research that has established a relationship with MTL activation and memory success. A number of studies have indicated that activation in the MTL during encoding predicts subsequent memory (e.g., Staresina & Davachi, 2006; Davachi, Mitchell, & Wagner, 2003; Paller & Wagner, 2002) and is also enhanced for successful retrieval (e.g., Dobbins et al., 2003; Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000; Stark & Squire, 2000). Furthermore, MTL activation is correlated with WM accuracy (Öztekin et al., 2008). Hence, the relationship between accuracy and MTL activation in our current study is consistent with previous research that has established the role of the MTL in memory success, and is in line with computational models of MTL functioning (e.g., Temporal Context Model; Howard, Fotedar, Datey, & Hasselmo, 2005) that specifically assume the contribution of the MTL to recovery of relevant information (e.g., retrieval of contextual/episodic information related to an item's representation when an encoded item is represented). This relationship provides credible grounds for linking the observed enhancement of MTL activation to the deployment of episodic retrieval processes: MTL activation could be reflecting the extent of relevant episodic information recovered that serves to successfully compensate for the adverse effects of PI.

Although the direct involvement of the MTL in interference resolution in WM has not been reported before, indirect evidence suggesting susceptibility of the hippocampus to PI has been reported in a previous PET study (Curtis, Zald, Lee, & Pardo, 2000). In this study, hippocampal activation was noted while participants performed object and spatial alterations over a delay of 1 sec, suggesting that the hippocampal activation might have emerged due to the presence of PI arising from the no longer relevant information from past trials. Kirwan and Stark (2007) also noted a role of the MTL in interference resolution for recognition judgments to test probes that were perceptually similar to the studied material in a long-term episodic memory task. Critically, they found enhanced activation in the hippocampus and the parahippocampal gyrus for correct rejections compared to false alarms to perceptually similar lures. Our findings extend these results to PI induced by episodic familiarity and semantic similarity in a WM task. Collectively, these findings suggest that the MTL could help resolve inter-

ference by recovering relevant information necessary to correctly reject a similar lure. On the other hand, Sakai and Passingham (2004) found no sensitivity of the MTL to interference induced by the similarity of the distracter material to studied items in a delayed short-term recognition task. A major difference between the interference manipulations applied in this study and our study is that resolution of both types of PI (episodic familiarity and semantic similarity) in our study necessitates episodic retrieval. Taken together, these findings suggest that the MTL may contribute to PI resolution to the degree that successfully resolving interference requires the recovery of detailed episodic information.

Our findings indicate that the MTL is important in resolving PI induced by both episodic familiarity and semantic similarity in WM, and that activation is modulated by the degree to which PI is successfully resolved. This association between MTL activation and behavioral measures of successful PI resolution in WM is a novel result and adds to a growing body of work that has indicated MTL involvement in various WM operations (e.g., Öztekin et al., 2008; Cabeza et al., 2002; Davachi & Wagner, 2002; Curtis et al., 2000; Ranganath & D'Esposito, 2001; see Ranganath & Blumenfeld, 2005, for an overview). These findings collectively suggest that the MTL contributes to short-term recognition in ways comparable to its well-established role in long-term recognition memory (e.g., see Eichenbaum, Yonelinas, & Ranganath, 2007, for a review).

The Role of the LIFG

Several explanations have been proposed for the role of the LIFG in interference resolution. It has been suggested that the LIFG might be important in inhibiting or resolving responses based on familiarity (e.g., Nelson, Reuter-Lorenz, Sylvester, Jonides, & Smith, 2003; Jonides et al., 1998), or it may be involved in the selection of competing internal representations (e.g., Kan & Thompson-Schill, 2004; Thompson-Schill et al., 1997). Finally, it has been suggested that enhanced activation in the LIFG might reflect increased demand on episodic retrieval processes to resolve PI (e.g., Badre & Wagner, 2005).

We found clear evidence of enhanced LIFG activation for PI induced by both episodic familiarity and semantic similarity, suggesting that the LIFG has a general role in resolving interference in WM. Because retrieving detailed episodic information (such as source or list-specific information) takes longer than familiarity-based judgments (e.g., Öztekin & McElree, 2007; Hintzman et al., 1998; Hintzman & Curran, 1994; McElree & Dosher, 1989), the reliable relationship between the RT difference across the RN and DN probes and the corresponding difference in neural activation in the LIFG is consistent with the hypothesis that the LIFG might be contributing to the resolution of interference by supporting retrieval of detailed episodic information.

These findings do not directly speak as to which of the above accounts are correct. However, recent findings using related WM tasks (without manipulations of PI) have indicated that the LIFG is involved in episodic retrieval operations, in addition to its importance in strategic retrieval of episodic information in long-term memory (e.g., Dobbins et al., 2003). Öztekin et al. (2008) demonstrated that the LIFG and the MTL jointly contribute to WM retrieval. Enhanced activation in the LIFG and the MTL was observed for items that were not actively maintained in focal attention, hence, had to be retrieved from WM. Crucially, in a task that behavioral evidence indicates is mediated by serial search process (McElree & Dosher, 1993)—judgments of recency (which of two test items occurred more recently)—LIFG activation was modulated by the number of serial operations required to retrieve an item. This pattern suggests that activation in this region may reflect the amount of successive retrieval operations carried out to reach an accurate memory judgment. Current findings lend support to the hypothesis that the LIFG, jointly with the MTL, supports episodic retrieval processes that serve to recover detailed episodic information necessary to resolve PI, to the degree that LIFG activations observed by Öztekin et al. are comparable to those observed in the current experiment.

The observed relationship with LIFG activation and RT measures suggest that the LIFG might be supporting the recollective retrieval attempts that are engaged to resolve PI, regardless of whether the relevant information (i.e., source memory) is recovered, and thus, regardless of whether interference is successfully resolved. In contrast, the observed relationship with MTL activation and the accuracy measures suggest that MTL activation specifically reflects the recovery of relevant information that successfully resolves PI.

Different Sources of Interference

Our data indicate that both the LIFG and the MTL are involved in resolving interference based on episodic familiarity and semantic similarity. Interestingly, however, the effects of the two sources of interference were not additive. Rather, in the presence of high semantic similarity, RN probes no longer engendered enhanced activation in either LIFG or MTL regions, eliminating the classical RN probe effect.

Öztekin and McElree (2007) reported a corresponding interaction in a study using a behavioral analogue of the release from PI paradigm employed here. The response-signal speed–accuracy tradeoff procedure—a behavioral procedure for measuring the growth of accuracy over retrieval time—was used to investigate how PI jointly affected retrieval speed and accuracy. RNs under low levels of semantic interference (viz., a List 1 item presented as lures in List 2, as in the current study) engendered high false alarm rates early in retrieval (times less than

500 msec). However, these high false alarm rates were corrected later in retrieval (times greater than 500 msec). This time-course profile is the signature pattern of a dual-process mechanism, in which responses are first based on a fast assessment of familiarity but then modulated later in retrieval as slower accruing episodic information becomes available (see also, McElree, Dolan, & Jacoby, 1999; McElree & Dosher, 1989; for related effects based on semantic similarity, see McElree, 1998). Notably, however, the high initial false alarm rates (times less than 500 msec) for RNs were demonstrably absent under high levels of semantic interference (viz., a List 2 item presented as lures in List 3, as in the current study). This finding indicates that the presence of semantic PI in the retrieval context eliminates the early familiarity-based false alarms to the RN probe, hence, eliminating the classical episodic familiarity interference effect.

The current study does not have the temporal resolution to capture this effect. However, as the same design as Öztekin and McElree (2007) was applied here, it is reasonable to assume that the same source is responsible for the elimination of the classical episodic familiarity interference effect under high semantic PI observed in both studies. We suggest, therefore, that reduction in the difference in neural activation across our RN and DN probes under high semantic PI arises from the fact that both types of probes necessitate the engagement of episodic retrieval processes under high semantic PI.

Such an account provides a natural explanation of the diminished neural activation for RNs and the enhanced activation for DNs observed under high levels of semantic PI (Figure 3C; Figure 4E, F), which collectively eliminate the classical RN effect. Specifically, because all probe types were drawn from the same semantic categories, the build up of PI based on semantic similarity uniformly decreases the diagnosticity of familiarity information, and increases the necessity of recovering more diagnostic episodic information as a consequence. Under low levels of semantic PI, a DN can largely be rejected on the basis of low familiarity, whereas an RN would be expected to differentially engage episodic retrieval to counter residual familiarity from recent study. As semantic PI builds up, the familiarity of all test items drawn from the relevant category increases, including the familiarity of DNs. Under these conditions, DNs can no longer be rejected on the basis of low familiarity, and thus, would be expected to engage episodic retrieval to counter familiarity stemming from semantic similarity. Indirect neural support for this interpretation comes from studies that have examined the neural correlates of individual differences in PI resolution in the recent probe paradigm. Braver, Gray, and Burgess (2007) reported that in blocks that contained a high proportion of RN probe trials (80%), individuals with high fluid intelligence showed less pronounced interference effects compared to blocks that contained low proportion of interference trials (20%). Similarly, Mecklinger, Weber, Gunter, and Engle

(2003) found comparable elevated levels of LIFG activation across interference and control trials for participants with high WM capacity, whereas individuals with low WM capacity showed enhanced activation for interference trials only. Given these studies and the behavioral evidence that suggests resolution of semantic PI also necessitates controlled episodic retrieval, our data suggest that as semantic PI builds up, participants need to engage in controlled episodic retrieval for all trial types, resulting in elevated levels of LIFG and MTL activation for all trials, complementing the behavioral work (Öztekin & McElree, 2007).

Notably, our data indicate that high levels of semantic PI do not simply eliminate the classic RN effect, they reverse the effect: DNs show enhanced activation relative to RNs under these conditions. This reversal also finds a natural explanation in this framework. The source information for an RN—that it was studied in the last list, not the current list—is likely to be recovered relatively easily, and it provides a firm basis on which to reject these types of lures. In contrast, source information for a DN, given that it was not studied in the current block, is likely not recoverable. If familiarity is no longer diagnostic, the only basis for rejecting a distant lure might be attempt to recover all items on the study list to be certain that the lure was not one of them. The observed enhanced activation for DNs could reflect engagement of episodic retrieval processes that attempt to recover source information associated with it, the recovery of list items, or some mixture of the two.

Conclusion

In conclusion, we have shown that the LIFG supports successful resolution of interference effects caused by both episodic familiarity and semantic similarity, suggesting a general role of this region in resolving interference in WM (see Badre & Wagner, 2007, for a review). In addition, we report that the MTL also contributes to successful PI resolution in verbal WM. This is a novel finding that would benefit from future research. Our results further indicate that neural activation to episodic familiarity in both LIFG and MTL regions are modulated by the presence of PI induced by semantic similarity. In line with previous behavioral work, which suggests that interference resolution in the paradigms investigated in our study can be achieved via episodic retrieval, and prior neuroimaging research that has established the role of the LIFG and the MTL in memory retrieval, we suggest that these regions contribute to successfully resolving interference effects on memory performance via recovery of detailed episodic information, such as list-specific information or source memory.

Notes

1. Proactive interference has a more negative impact on memory performance for test probes drawn from earlier positions in a sequentially presented study list than the more recent ones—typically, the last three to four positions on the study list are immune to PI's effect on accuracy in immediate recognition (e.g., Öztekin & McElree, 2007). Thus, to enhance PI effects, Serial Positions 1 to 3 were tested more often than Positions 4 to 6.
2. To check that this relationship is robust, we calculated Spearman's correlation coefficient (Cohen, 2001), which also indicated a high and statistically reliable correlation, $[r(14) = .649, p < .009]$.
3. Spearman's $r(14) = .480, p < .070$.
4. Five participants (out of 15) were excluded from this analysis due to insufficient number of incorrect trials.

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