

Retrieval Success is Accompanied by Enhanced Activation in Anterior Prefrontal Cortex During Recognition Memory: An Event-Related fMRI Study

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Abstract

■ Neural regions associated with retrieval success were identified using event-related fMRI procedures and randomly ordered trials on a recognition memory test. Differences between hits and correct rejections (CRs) occurred in multiple regions, including bilateral anterior and right dorsolateral prefrontal cortex, bilateral inferior parietal cortex, and right superior parietal cortex (all hits > CRs), and right occipital cortex (CRs > hits). The hit > CR pattern is not compromised by time-on-task explanations because response latencies for correctly rejected words exceeded those for hits. Converging evidence for the claim that the hit > CR pattern identified neural correlates of retrieval success was obtained by unconfounding item history and retrieval

success. That is, we implemented a third condition in which nonstudied words were presented, yet retrieval success was hypothesized to facilitate CRs of these lures. Specifically, when confronted with a familiar, yet nonstudied word, (e.g., nosebleed after studying nosebleed and skydive), subjects might adopt a strategy whereby they recall the studied word(s) that gave rise to the familiarity (nosebleed, skydive) and thereby reject the lure. This method of instantiating retrieval success under conditions in which the target word had not been studied offers converging evidence for the claim that anterior-prefrontal cortex (among other regions) demonstrates enhanced activation during retrieval success. ■

INTRODUCTION

The present study was designed with the goal of identifying neural correlates of retrieval success. Specifically, we asked the fundamental question of whether different patterns of activation occur for items that are correctly recognized as having been previously studied (hits) and those correctly classified as not previously studied (correct rejections, CRs) under conditions in which item types occur in an unpredictable order (as permitted by fMRI). The question was asked in relation to the whole brain, but special interest centered upon a region of right

anterior prefrontal cortex (in or near BA 10), which has been shown to be activated during memory retrieval (e.g., McDermott, Buckner, Kelley, Petersen, & Sanders, 1999a; Buckner, Raichle, Miezin, & Petersen, 1996; Tulving, Kapur, Craik, Markowitsch, & Houle, 1994; Squire et al., 1992; see Desgranges, Baron, & Eustache, 1998; Fletcher, Frith, & Rugg, 1997; Buckner, 1996 for review). Debate has swirled with respect to the functional role of this region. Some researchers have posited that the “set” or “mode” of intending to retrieve the past elicits activity in this region and that no item-related differences occur

here (e.g., LePage, Ghaffar, Nyberg, & Tulving, 2000; Düzel et al., 1999; Wagner, Desmond, Glover, & Gabrieli, 1998; Kapur et al., 1995; Nyberg et al., 1995). Others have proposed that the level of effort required during retrieval tasks modulates the level of activity in this region (e.g., Schacter, Alpert, Savage, Rauch, & Albert, 1996). Still others have argued for item-level differences, such that this region serves as a neural correlate of successful recollection because previously studied words can elicit greater activity than nonstudied words (e.g., Rugg, Fletcher, Frith, Frackowiak, & Dolan, 1996; Rugg et al., 1998; Tulving et al., 1994). However, these latter studies are accompanied by interpretive difficulties in that the blocked designs they used do not permit for a clean separation between item level and set effects; differences between blocks of previously studied items and blocks of nonstudied items could arise from differences in studied and nonstudied items per se or from differences in processing strategies emerging from the different contexts in which the items occur. In a recent study not plagued by these difficulties (Henson, Rugg, Shallice, Josephs, & Dolan, 1999a), no differences were observed in anterior prefrontal cortex as a function of whether an item had previously been studied (or whether it was vividly “remembered” or just “known” to have been studied in Tulving’s [1985] framework), although many other brain regions differed as a function of the remember, know, and new categories.

Thus, the primary question in the present study was whether differences between hits and CRs would be manifested in right anterior prefrontal cortex (or anywhere in the brain) using rapid event-related fMRI procedures and linear modeling techniques (see Donaldson & Buckner, in press for a review). The benefit of these procedures is that they permitted trials to occur every several seconds in an order that was undetectable from the standpoint of the subjects. All but one previous attempts to obtain such differences using event-related fMRI procedures have exhibited null effects (McDermott et al., 1999a, 1999b; Buckner et al., 1998; Schacter, Buckner, Koutstaal, Dale, & Rosen, 1997; although see Henson et al., 1999a, as discussed previously).

In an effort to provide converging evidence for the regions correlated with retrieval success (as identified by the hit > CR pattern), we created a third condition in which lures related to the studied words were presented; these lures were recombined lexical components of compound words that had been studied. That is, we presented subjects with compound words (e.g., nosebleed, skydive) during the study phase and then later recombined lexical subunits of the words to make a new compound word (nosedive) on the test phase. Prior work had shown that this approach, the conjunction paradigm, reliably induces higher probabilities of false alarms to the recombined (or conjunction) words than to standard, unrelated lures,

although the majority of these recombined words are correctly classified as nonstudied (Kroll, Knight, Metcalfe, Wolf, & Tulving, 1996; Reinitz, Lammers, & Cochran, 1992; Underwood & Zimmerman, 1973). One hypothesis of how subjects achieve a high CR rate in this difficult condition is that they adopt a recall-to-reject approach, especially following multiple study presentations and when long response deadlines are used during retrieval (Benjamin, in press; Jones & Jacoby, in press; see also Yonelinas, 1997; Brainerd, Reyna, & Kneer, 1995; Clark 1992). That is, although the conjunction lure (e.g., nosedive) might seem familiar, which would lead subjects to initially want to classify it as having been studied, recollection that nosebleed, not nosedive, had been studied would lead subjects to correctly reject the lure. Jones and Jacoby provide evidence for such a process by varying the response deadline during the recognition test. Specifically, following multiple presentations of studied words, subjects made fewer false alarms to conjunction lures when allowed more time to respond (2,900 msec after stimulus onset) than when given a shorter deadline (1,300 msec). The present study used a long deadline (3,800 msec after stimulus onset) in an effort to encourage a recall-to-reject strategy in the conjunction condition. In summary, we attempted to create a situation in which recollection might take place, albeit in response to lures; by comparing hits and CRs of conjunction words, we sought converging evidence for regions of the brain correlated with retrieval success.

Thus, the goal of the present study was to identify specific regions that reflect differences as a function of retrieval success using rapid event-related fMRI procedures. To this end, subjects studied compound words (three times each) and were tested (old/new recognition memory) on the intact versions of these words (hereafter “studied” words), on recombined versions of the words (“conjunction” lures), and on compound words novel with respect to the experiment (“unrelated” lures).

RESULTS AND DISCUSSION

Behavioral

Table 1 displays the probability of calling an item “old” as a function of the three condition types. These probabilities differed reliably among conditions, $F(2, 46) =$

Table 1. Examples of Study and Test Stimuli and Behavioral Data as a Function of Item History

Study	Test	Item Type	p “Old”	Response Latency
kickstand	kickstand	Studied	.89	1172 ms
nosebleed	lifeguard	Unrelated Lure	.08	1317 ms
skydive	nosedive	Conjunction Lure	.27	1486 ms

319.6, $MSe = .013$; the false alarm rate for the conjunction words (0.27) exceeded that for the unrelated words (0.08), $F(1, 23) = 69.0$, $MSe = .006$, but did not approach the hit rate (0.89), $F(1, 23) = 206.8$, $MSe = .022$. Mean response latencies differed among conditions, too, $F(2, 46) = 21.96$, $MSe = 26,935.9$. Conjunction words elicited the longest mean response latencies (1,486 msec), unrelated nonstudied items an intermediate latency (1,317 msec), and studied items received the fastest responses (1,172 msec). Contrasts among response latencies showed reliable differences such that conjunction lures elicited longer latencies than did unrelated lures, $F(1,23) = 26.3$, $MSe = 13,091$, which elicited longer latencies than did studied items, $F(1,23) = 9.4$, $MSe = 26,718$. Similar conclusions are reached when responses are taken into account; conjunction CRs took the longest (1,514 msec), unrelated CRs were

intermediate (1,295 msec), and hits (1,133 msec) were fastest, all F 's(1, 23) > 13.0.

fMRI

Overall Analysis of Variance (ANOVA)

To identify regions of interest, the fMRI data were analyzed with a one-way ANOVA with three factors (item history: studied, nonstudied, conjunction) on a voxel-by-voxel basis across the whole brain (i.e., subjects' responses were not included as a factor in the initial fMRI analyses to determine the regions of interest). Multiple regions demonstrated differences in activation patterns among the three types of words. These results are summarized in Figure 1 (top panel) and in Table 2. The top panel of Figure 1 is nondirectional and shows regions that differ among condi-

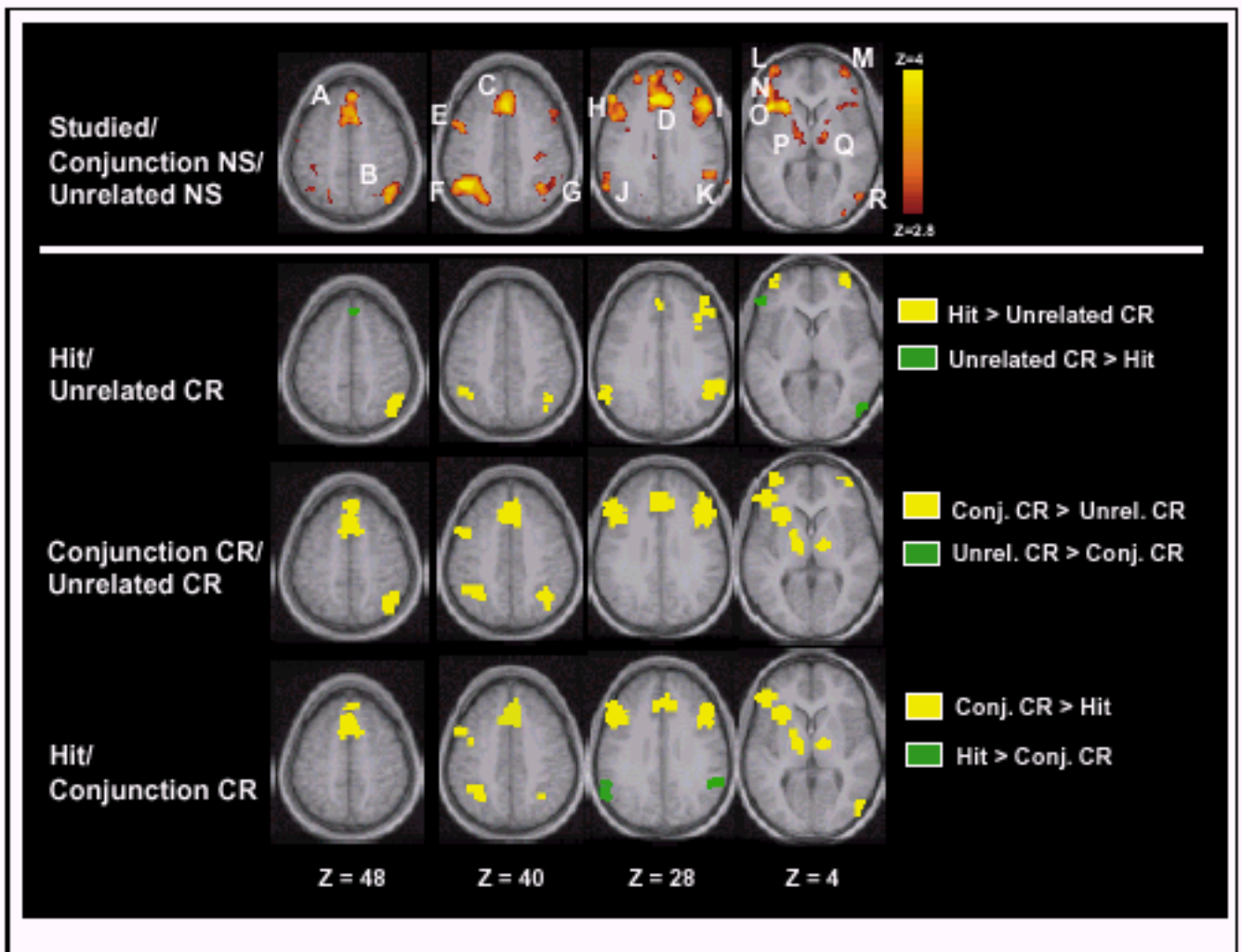


Figure 1. Top panel: Regions that differed among the three item types as determined by the overall ANOVA. Colored pixels represent statistically significant differences, which are displayed on the corresponding structural scans in atlas space (Talairach & Tournoux, 1988). Atlas coordinates and the direction of differences corresponding to each region can be obtained from Table 1. The left sides of the images correspond to the left side of the brain. Bottom panel: Results from the specific contrasts between item types; the specific patterns of results can be gleaned from Table 1. The left sides of the images correspond to the left side of the brain. For purposes of Figure 1, we considered only voxels within regions that had been identified in the region-of-interest analysis. We performed the specific contrasts (thresholded to $p < .05$) on voxels within these regions, and this panel displays voxels that met significance under both procedures.

Table 2. Regions Identified by the Whole-Brain One-Way ANOVA on Response Magnitudes and Follow-up Contrasts on These Regions

Region	Figure 1 label	Peak	Response magnitude (% signal change)			Overall ANOVA [F(2, 46)]	Contrasts [F(1, 23)]				Overall pattern
			Hit	Unrel. CR	Conj. CR		Hit/Unrel. CR	Hit/Conj. CR	Unrel. CR/Conj. CR		
Medial frontal BA 8	A	3,37,48	.18	.10	.37	11.49	< 1, <i>ns</i>	9.86	31.05	CCR > Hit, UCR	
R superior parietal BA 7	B	41,- 57,48	.20	-.09	.13	8.19	12.19	< 1, <i>ns</i>	15.16	CCR, Hit > UCR	
Anterior cingulate (dorsal) BA 32	C	1,21,42	.16	.07	.29	7.96	< 1, <i>ns</i>	7.83	15.00	CCR > Hit, UCR	
Anterior cingulate (ventral) BA 32	D	- 3,29,30	.03	-.18	.10	9.16	2.93, <i>p</i> < .10	6.53	18.10	CCR > Hit, UCR	
L middle frontal (dorsolateral PFC) BA 9/6	E	- 43,1,40	.33	.34	.58	5.69	< 1, <i>ns</i>	9.40	5.89	CCR > Hit, UCR	
L inferior parietal BA 40	F	- 37,- 51,36	.22	.08	.31	12.77	5.20	8.48	21.70	CCR > Hit > UCR	
R inferior parietal BA 40	G	35,- 55,42	.24	.06	.27	5.80	4.46	1.66, <i>ns</i>	13.25	CCR, Hit > UCR	
L middle frontal (dorsolateral PFC) BA 9/46	H	- 49,31,24	.21	.22	.49	12.03	< 1, <i>ns</i>	18.01	14.60	CCR > Hit, UCR	
R middle frontal (dorsolateral PFC) BA 9/46	I	45,23,30	.14	.04	.30	13.94	4.26	8.68	34.02	CCR > Hit > UCR	
L inferior parietal/middle temporal BA 39	J	- 59,- 61,24	-.18	-.40	-.46	6.28	8.34	10.19	< 1, <i>ns</i>	Hit > UCR, CCR	
R inferior parietal BA 40	K	47,- 49,30	-.01	-.24	-.18	9.44	22.38	7.68	1.49, <i>ns</i>	Hit > UCR, CCR	
L middle frontal (anterior PFC) BA 10	L	- 37,53,10	.25	.01	.27	6.18	4.86	2.02, <i>ns</i>	12.02	CCR, Hit > UCR	
R middle frontal (anterior PFC) BA 10	M	35,51,4	.34	.04	.19	4.84	8.91	< 1, <i>ns</i>	5.23	CCR, Hit > UCR	
L inferior frontal BA 46	N	- 45,37,8	.06	.11	.37	22.49	5.89	37.10	17.21	CCR > UCR > Hit	
L anterior insula BA 47	O	- 39,17,2	.16	.11	.36	15.45	< 1, <i>ns</i>	29.36	22.54	CCR > Hit, UCR	
L thalamus	P	- 13,- 13,4	.20	.16	.36	9.86	< 1, <i>ns</i>	10.30	14.20	CCR > Hit, UCR	
R thalamus	Q	13,- 13,4	.13	.11	.25	8.36	< 1, <i>ns</i>	10.64	12.65	CCR > Hit, UCR	
R extrastriate BA 19/39	R	51,- 73,6	.08	.35	.39	8.10	14.63	8.79	< 1, <i>ns</i>	CCR, UCR, CCR > Hit	

Figure 1 labels refer to labels in the top panel of Figure 1. Peak coordinates are in Talairach and Tournoux (1988) space. BA = approximate Brodmann's area; PFC = prefrontal cortex; Hit = studied words correctly classified as studied; Unrel. CR = unrelated nonstudied words correctly rejected as nonstudied; Conj. CR = conjunction items correctly rejected as new; *ns* = nonsignificant.

tions (studied, nonstudied, conjunction). Differences among the three item types were manifested in regions within medial frontal cortex (A), right superior parietal cortex (B), dorsal and ventral anterior cingulate (C, D), multiple regions within bilateral inferior parietal cortex (F, G, J, K), bilateral dorsolateral prefrontal extending into posterior frontal cortex (E, H, I), bilateral anterior prefrontal cortex (L, M), left inferior frontal cortex (N, O), thalamus (P, Q), and right extrastriate visual cortex (R).

The first important finding from these results is that recent prior experience with items (or the absence of recent experience) was manifested in different activation patterns on the randomly ordered recognition test. As noted in the Introduction, several reports have published failures to identify such differences, with one notable exception. The item-level differences revealed here tended to occur in many of the regions typically activated by memory retrieval tests (see Desgranges et al., 1998; Cabeza & Nyberg, 1997; Fletcher et al., 1997 for review), and the possible roles of these regions will be considered after a description of the specific patterns of results obtained.

Contrasts

To quantify the specific patterns of results statistically, the regions identified in the overall ANOVA were further explored using contrasts that took into account subjects' classification of these items (i.e., hits/unrelated CRs; hits/conjunction CRs; conjunction CRs/unrelated CRs); the quantification of these contrasts can be seen in Table 2, where the response magnitudes are presented as a function of the three conditions.

The follow-up contrasts were performed by one-way ANOVAs (with two factors) using the regions identified by the overall (three-factor) ANOVA. For illustrative purposes, these contrasts were also performed on a whole-brain voxel-by-voxel basis, and the resulting regional differences are displayed in the bottom panel of Figure 1, which displays all voxels significant in the specific contrast with the stipulation that only voxels previously identified in the region-of-interest step (from the overall ANOVA) were included. The data of most interest are the contrasts in Table 2, which can be understood by examining the mean response magnitudes entered into the contrasts (columns 4–6) and the resulting *F* values (columns 8–10). The combination of these factors is presented schematically in the final column of the table.

Several patterns of results emerged. We note first that regions manifesting the pattern conjunction CRs > unrelated CRs > hits would have to have been interpreted cautiously because this pattern could have arisen solely from response latency differences (see D'Esposito et al., 1997 for a discussion of this problem). However, this specific pattern of results was

observed in only one of the 18 regions in Table 2 (the regions on which the contrasts were performed)—left inferior frontal cortex (Region N, BA 46). Correctly rejected conjunction lures did tend to produce the greatest level of activation of the three conditions, however, which could have been due to the lengthy response latencies elicited by these lures or by the enhanced monitoring/retrieval demands elicited by the condition, which in turn produced the lengthy response latencies. For this reason, our discussion focuses primarily upon differences in the direction of hits > unrelated CRs. This pattern is opposite that for the latency data, and, therefore, these data are not compromised by such concerns. The regions exhibiting the conjunction CR > unrelated CR pattern are then considered in an attempt to provide converging evidence with respect to the regions involved in retrieval success insofar as the recall-to-reject approach was adopted by subjects in this condition.

We consider regions exhibiting greater activation for hits than unrelated CRs as reflecting retrieval success. The following regions demonstrated greater activation for hits than unrelated CRs: right superior parietal cortex (BA 7, region B in Figure 1), several regions within bilateral inferior parietal cortex (BA 40, regions F, G, J, and K), right dorsolateral prefrontal cortex (BA 9/46, region I), and bilateral anterior prefrontal cortex (BA 10, regions L and M). Of these regions, some showed further activation for correctly rejected conjunction lures (conjunction CRs > hits > unrelated CRs): left inferior parietal cortex (region F), right dorsolateral prefrontal cortex (region I), and others did not differentially activate for conjunction CRs and hits: right superior parietal cortex (region B), right inferior parietal cortex (region G), and bilateral anterior prefrontal cortex (regions L and M). We interpret these data as demonstrating regions associated with retrieval success; the primary pattern leading to this conclusion is that of hit > unrelated CR. Complementing this finding is the outcome that most of the regions showing the hit > unrelated CR pattern also showed the conjunction CR > unrelated CR pattern. (The two regions not confirmed in this analysis, regions J and K in Figure 1, also exhibited other characteristics that make them difficult to interpret, as will be discussed.) In summary, the two conditions thought to be involved in retrieval success activated regions within the following areas to a greater extent than the condition representing a relative lack of retrieval success: right superior parietal cortex, bilateral inferior parietal cortex, right dorsolateral prefrontal cortex, and bilateral anterior prefrontal cortex.

The timecourses of activation for some of these regions (labeled as F, I, L, and M in Figure 1) are shown in Figure 2, in which the differential activation levels for the three conditions of interest can be seen. The primary point to be taken from this figure is that the

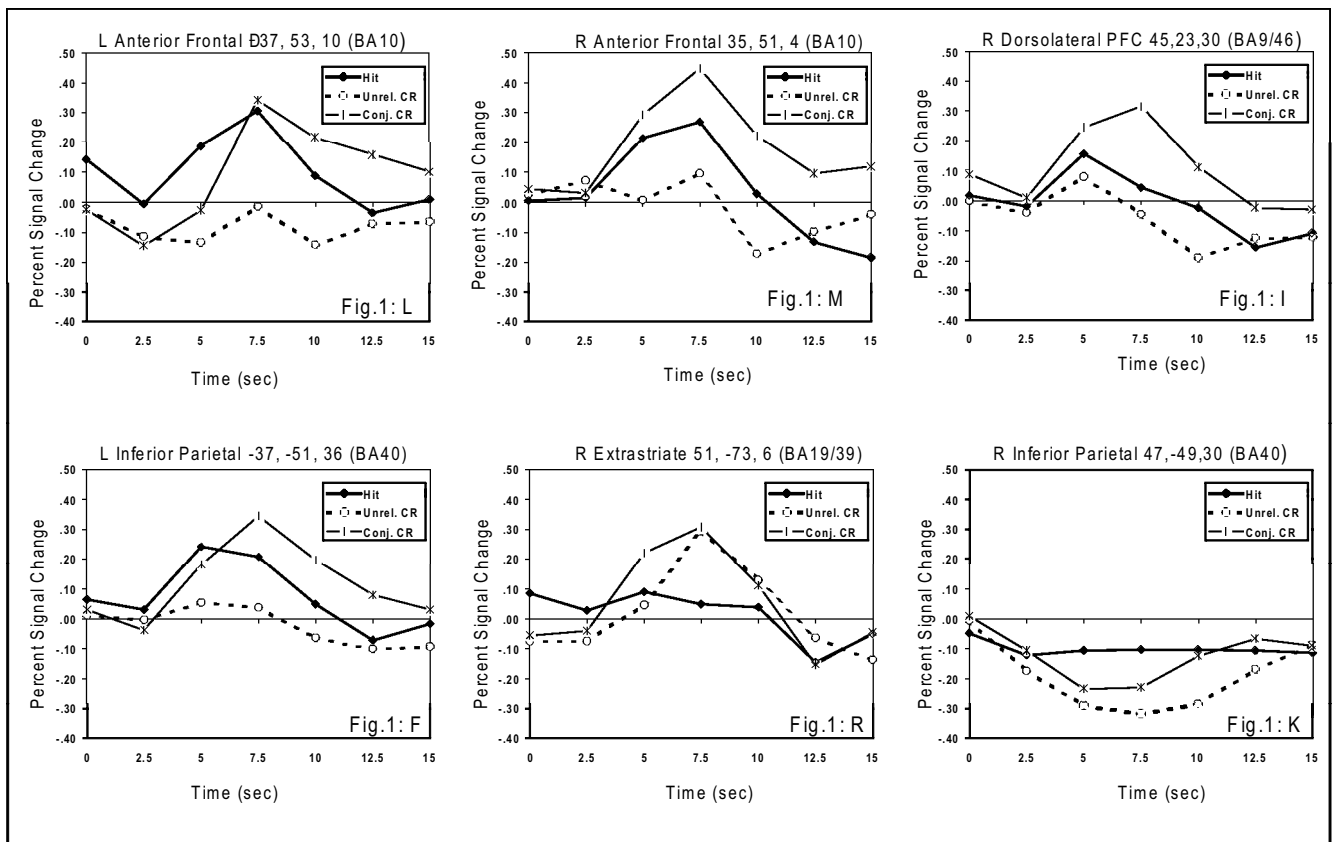


Figure 2. Percent signal change for hits, unrelated correct rejections (Unrel. CR), and conjunction correct rejections (Conj. CR) as a function of time for selected regions from Figure 1. Because each TR (whole-brain scan) lasted 2.5 sec, timepoints shown correspond to the onset of the TRs within each trial (e.g., the third scan spanned from 5 to 7.5 sec and is plotted at 5 sec).

regions discussed above show regular timecourses, similar to those typically seen in event-related fMRI studies.

Several other noteworthy patterns were obtained. A region in right extrastriate visual cortex (BA 19/39), region R demonstrated greater activation for unrelated CRs than hits and conjunction CRs, as can be seen in Figure 1 and Table 2, and in the timecourse data for this region in Figure 2. This pattern is of interest because this region has been shown to manifest a neural correlate of perceptual priming such that recently encountered words give rise to less activation here than do nonstudied words (see Schacter & Buckner, 1998 for a review). The typical explanation is that less neural effort is required to resolve the perceptual features of recently seen words. Conjunction words have generally been reported not to produce perceptual priming (Reinitz & Alexander, 1996), although there have been occasional reports of small levels of priming (Reinitz & Demb, 1994). To the extent that our data speak to the issue, they are more consistent with the failures to find perceptual priming in that no diminution of activation was observed for the conjunction CRs in the extrastriate-visual region that demonstrated priming for hits. That is, visual cortex was activated to an equivalent extent for

the correctly rejected conjunction lures and the unrelated lures.

Two regions manifested greater activation for hits than for both types of CRs, which did not differ. Both regions exhibiting this pattern (i.e., left inferior parietal/middle temporal cortex, BA 39 and right inferior parietal cortex, BA 40, labeled J and K in Figure 1) showed negative magnitudes (i.e., decreases in activation) for all conditions. (In addition to examining the magnitudes in Table 1, this pattern can be seen for the right inferior parietal region by examining its timecourse in Figure 2.) Note that these parietal regions are ventral and lateral to other positively activated regions in bilateral inferior parietal cortex (F and G in Figure 1). This pattern of increases occurring in regions of bilateral inferior parietal cortex closely apposed to other regions, which show decreases, has been reported in previous studies of memory retrieval (e.g., McDermott et al., 1999a; McDermott et al., 1999b; Buckner et al., 1996). That is, increases are seen within lateral (and often medial) inferior parietal cortex at approximately 40 mm above the plane intersecting the anterior and posterior commissures, and decreases are seen in regions further lateral and sometimes ventral and anterior). The novel finding here is that the level of deactivation differs as a

function of prior experience with the items. However, this type of pattern is particularly difficult to interpret because its interpretation hinges upon the understanding of deactivation. Whether or not decreases are taken to represent an active process dictates how these results would be interpreted. Resolution of the issue of how to interpret deactivation of the blood oxygenation level dependent (BOLD) signal will have to await further research and conceptual development.

A final pattern exhibited greater activation for conjunction CRs than for either hits or unrelated CRs, which did not differ. This pattern was manifested by medial frontal cortex, ventral anterior cingulate, left dorsolateral prefrontal cortex (BA 46/9/6), and left anterior insula.

We note that although we are buttressing our primary pattern of interest (hit > unrelated CR) with the conjunction CR condition (conjunction CR > unrelated CR), it is not the case that hits and conjunction CRs behaved identically, as can be seen in the contrast of the two conditions in Figure 1 and in Table 2. Although the two conditions are thought to contain a recollective component that is greater than that in the unrelated CR condition, the items clearly differ in other processing components they engender. Conjunction CRs probably necessitate more cognitive control, which may explain enhanced activation in regions generally thought to be involved in controlled processing (bilateral dorsolateral prefrontal cortex and anterior cingulate). Further, it is impossible to know which condition (hits or conjunction CRs) elicits greater recollective activity. One might expect that hits would do so because the target is presented at test; however, in the conjunction condition, recollection is used to override familiarity and lead to CRs (Jones & Jacoby, in press; see also Benjamin, in press); in addition, there are two items that correspond to each target word in the conjunction condition, but only one in the studied condition. Therefore, the claim is not that hits and conjunction CRs are identical. Rather, the finding that all but two regions identified with the hit > unrelated CR pattern were also shown to exhibit the conjunction CR > unrelated CR pattern offers a tentative convergence point for the claim that we have indeed identified regions correlated with retrieval success.

Relation to the Existing Literature

We now consider these results in relation to the literature and hypotheses about the underlying processing that may be performed by these regions. The region of primary interest in neuroimaging studies of episodic retrieval has been right anterior prefrontal cortex; left anterior prefrontal cortex and right dorsolateral prefrontal cortex have also been examined, but to a lesser extent. Whether and how these three regions might differ with respect to their functional roles in memory retrieval is a matter of debate (see Rugg & Wilding, 2000;

Ranganath & Paller, 1999; Rugg, Fletcher, Chua, & Dolan, 1999; Nolde, & D'Esposito, 1998; Nolde, Johnson, & Raye, 1999). We concentrate here on right anterior prefrontal cortex, noting that three principal hypotheses have been forwarded to explain its role in retrieval (as discussed in the Introduction). The first hypothesis arises from a series of null effects when blocks of studied items (or blocks containing predominantly studied items) are compared to blocks of new (or predominantly new) items. On this basis, it has been argued that the goal (or mental set, or mode) of trying to retrieve elicits activation here, and the level of success one may have in meeting this goal, or the level of effort put forth in service of this goal, do not modulate activation in this region (LePage et al., 2000; Düzel et al., 1999; Kapur et al., 1995; Nyberg et al., 1995). Our data are clearly inconsistent with this hypothesis (at least in its strong form, whereby null effects of item history are predicted) because item-level differences were indeed obtained on the recognition memory test. Further, these differences cannot be explained by calling upon global strategy shifts because the intermixing of item types precludes such an explanation. Note that we are not claiming that the mental set of trying to retrieve the past has no influence on activation in this region; we believe that it does, although the current data do not speak to this issue. What we have shown is that over and above any effects of overall, global mental set, item-level differences indicative of retrieval success are manifested within the right-anterior-prefrontal cortex during memory retrieval.

The second main hypothesis in explaining the role of anterior prefrontal cortex in memory retrieval is that the level of effort put forth in attempting to retrieve modulates activation of the region (Schacter et al., 1996). To the extent that the level of effort can be quantified by response latencies, our data are inconsistent with this explanation; the pattern of response latencies (conjunction CRs > unrelated CRs > hits) was inconsistent with the pattern of activation observed in anterior prefrontal cortex (conjunction CRs, hits > unrelated CRs). One might question whether reaction time is indeed a valid index of effort, although this argument has been forwarded. Regardless of the relation between latency and effort, we have shown that level of activation in anterior-prefrontal cortex need not track with response latency.

The third principal hypothesis—that activation in anterior prefrontal cortex can be modulated by retrieval success—receives strong support from this dataset. That is, hits elicited greater activation than did correctly rejected unrelated lures despite response latencies showing the opposite pattern. Hence, our results demonstrate that hit/unrelated CR (and studied/nonstudied) differences can indeed occur in an anterior-prefrontal region under conditions in which global strategy shifts can be ruled out. Retrieval success correlated with the level of activation in this region.

Although the assumption that retrieval success was instantiated by a condition in which lures were correctly rejected may at first glance seem paradoxical, we have noted that there is no necessary relation between subjects' responses and retrieval success. In fact, although this is especially true in the conjunction condition, there may be some low level of retrieval success that tends to occur in unrelated CRs (cf. McDermott et al., 1999b). On the basis of Jones and Jacoby's (in press) results, there is good reason to believe that retrieval success would be high in the conjunction condition as implemented in this experiment, especially for those conjunctions correctly classified as nonstudied. That is, in order to reject the conjunction items under experimental conditions similar to those used here, subjects have been found to adopt an approach that elicits recall of studied items related to the target word, which was not itself studied.

It is puzzling why the single published experiment demonstrating item-related differences in retrieval using event-related fMRI failed to find item-level effects in the region of anterior prefrontal cortex under consideration here (and typically activated during retrieval studies). Henson et al. (1999a), too, were puzzled by this null effect and offered two possible explanations: that (1) this region does not actually reflect item-level differences during recognition memory (and instead responds to the state or set of retrieval attempt); and/or (2) susceptibility artifacts in this region may have diminished power to detect a response in this region. We can offer no insight with respect to this discrepancy and acknowledge that our own results are presently the outlier in event-related fMRI studies of recognition memory. Nevertheless, we have no reason to doubt our findings; future studies will be necessary to complete understanding of the boundary conditions of this effect.

We have thus far focused discussion primarily on anterior prefrontal cortex because this region (especially on the right) has received the most attention in the neuroimaging literature with respect to episodic memory retrieval. However, activation of anterior prefrontal cortex in or near BA 10 during retrieval is often accompanied by activation of right dorsolateral prefrontal cortex in or near BA 46/9 (Nolde et al., 1998; Wagner et al., 1998), as it was in this dataset. Rugg et al. (1996) identified these regions, along with anterior cingulate, as being regions correlated with retrieval success (although see LePage et al., 2000 for a conflicting conclusion). Our results complement those of Rugg et al., who drew this conclusion by parametrically manipulating the ratio of old/new items on a recognition memory test. Although they used a blocked design, they took steps to overcome the problem of context effects/set differences across conditions. However, as they note, difficulties with this attempt occurred. The four regions mentioned above were sensitive to the density of old items, a finding that led Rugg et al. to conclude that these regions are indeed

more active for previously studied items than for non-studied items. The present study complements their findings in that (with the exception of anterior cingulate) highly similar regions (with peak coordinates very close to those reported by Rugg et al.) demonstrated effects sensitive to retrieval success in a design in which context effects can be dismissed. Retrieval success effects in frontal cortex are also obtained in the event-related potential literature (e.g., Allan & Rugg, 1996; Wilding & Rugg, 1996).

We emphasize that it may not be the phenomenological experience of conscious recollection that gives rise to the hit > unrelated CR pattern in some of these regions but rather a process or class of processes that tend to be invoked more often (or to a greater extent) for old items than for new items. Specifically, it has been proposed that postretrieval monitoring may underlie such effects (Henson et al., 1999a; Henson, Shallice, & Dolan, 1999b; Schacter et al., 1997; Rugg et al., 1996; Rugg et al., 1998). As alluded to previously, postretrieval monitoring refers to a complex set of processes lying somewhere at the intersection of source memory, working memory, decision processes, and conscious recollection and holds that once an item or trace is retrieved, the rememberer must work with that item and evaluate its appropriateness for current task goals (Moscovitch, 1994). When attempting retrieval, a person makes contact with some form of the to-be-remembered event and then must hold that information in mind (the working memory component) while analyzing it to determine whether it meets the criterion to be classified as having previously occurred. Such a process would be enhanced in the conjunction condition, and other similar conditions in which familiarity must be overridden in order to maximize recollective processing (see Henson et al., 1999a for a similar argument).

Rugg et al. (1996) point out that it is unlikely that these frontal "retrieval" regions all perform the same processes and argue that it would be informative to investigate possible dissociations among the regions. There are hints of such dissociations in our dataset, but we hesitate to draw any conclusions from them, especially since the dissociations lie in the form of null effects (e.g., hits and conjunction CRs are statistically equivalent in anterior frontal cortex, but differ in right dorsolateral prefrontal cortex). This pattern is consistent with some recent claims that right dorsolateral prefrontal cortex is especially important for postretrieval monitoring (Henson et al., 1999a). It will be interesting to see if future work bears out differences that, when combined with these, might inform understanding of the differential contributions of separate regions within frontal cortex to memory retrieval.

The item-level differences seen here (and in Henson et al., 1999a) suggest that it will be worth revisiting other questions in which item-level effects (independent of

context effects) may appear (e.g., whether false alarms that are compelling and phenomenologically similar to hits, cf. Roediger & McDermott, 1995, differ from hits at the neural level). Why no item-level differences have been manifested previously between hits and CRs (or studied and nonstudied items) in event-related fMRI (McDermott et al., 1999a; McDermott et al., 1999b; Buckner et al., 1998; Schacter et al., 1997) is unclear, but may be related to reduced power accompanying the slow, fixed-interval event-related designs, which might alter subjects' strategies, weaken mental sets, or may simply lead to boredom, all of which could affect neural activation. Regardless of the reason for the differences, our study (along with that of Henson et al.) points to the promise of rapid event-related procedures in informing understanding of memory retrieval through the use of tightly controlled experimental designs.

METHODS

Subjects

Subjects ($N = 24$, 12 males, 12 females, mean age 21.75, range 18–32 years) were recruited from the Washington University community in return for a payment. All were right-handed native speakers of English, who had normal or corrected-to-normal vision and reported no history of significant neurological problems. They provided informed consent in accordance with the guidelines set by the Washington University Human Studies Committee.

Materials

A total of 216 compound words forming 72 sets of triplets served as stimuli. Each set of triplets contained a target word (e.g., checkpoint) and two words that overlapped with the target with respect to its two lexical features (e.g., checklist, needlepoint). Counterbalancing for each stimulus type was achieved by dividing the triplets into three sets (of 24 triplets); sets were rotated across conditions (studied, conjunction, unrelated nonstudied) across subjects. That is, in the studied condition, the target (e.g., checkpoint) was studied, in the conjunction condition, the two primes (e.g., checklist, needlepoint) were studied, and in the unrelated nonstudied condition, none of the three items were encountered prior to the recognition test, on which the target item appeared.

Procedure

Scans were obtained on a 1.5-T Siemens Vision System (Erlangen, Germany) with a standard circularly polarized head coil. A Power Macintosh computer (Apple, Cupertino, CA) and Psyscope software (Cohen, MacWhinney, Flatt, & Provost, 1993) displayed the visual stimuli. An LCD projector (Ampro, model LCD-150) shielded with

copper wire displayed stimuli on a screen placed at the head of the bore. Subjects viewed the screen via a mirror fastened to the head coil. Responses were made by subjects during retrieval by pushing one of two keys on a fiber optic switch connected to a Psyscope Button Box (Carnegie Mellon University, Pittsburgh, PA). A pillow and surgical tape were used to minimize head movement. Headphones dampened scanner noise and enabled communication with subjects.

Structural images were acquired using a high-resolution sagittal MPRAGE sequence ($1.25 \times 1 \times 1$ mm voxels). Functional images were collected with an asymmetric spin-echo-planar sequence sensitive to BOLD contrast (Kwong et al., 1992; Ogawa et al., 1992). In each functional run, 110 sets of 16 contiguous, 8-mm-thick axial images ($TR = 2,500$ msec, 3.75×3.75 mm in-plane resolution) were acquired parallel to the anterior–posterior commissure plane; this procedure offered whole-brain coverage at a high signal-to-noise ratio (Conturo et al., 1996). Approximately 3 min elapsed between runs, during which time instructions were given to subjects over their headphones. At the beginning of each run, four images were acquired to permit longitudinal magnetization to stabilize; these images were not included in the functional analyses, but were used to facilitate alignment of the functional data to the structural images.

Each subject participated in two retrieval runs (each following three runs of encoding, which are not reported here). During the intentional encoding phase, each subject studied 72 words: 24 words that were later tested intact (hereafter called “studied”), and 48 words that were later tested in a recombined form; they also encountered 24 fixation trials (to introduce jitter into the design to allow for rapid event-related analyses, Dale & Buckner, 1997). Words that were later recombined to form “conjunction” lures were ordered such that the word whose first syllable was later presented in a recombined form was encountered before the word whose second syllable was later recombined (e.g., nose-bleed appeared before skydive during the study phase, and the test contained nosedive). The lag between the items of a pair varied between 1 and 5, with a mean of three intervening words. All words were studied three times (in a different order each time).

An event-related design was used for the retrieval runs. Each of the 48 trials within each run began at the onset of the TR (repetition time). Each trial spanned two TRs: The stimulus word appeared for 3,500 msec, followed by a fixation point for 1,500 msec. The deadline for responding was 3,800 msec after stimulus onset. Four types of trials (studied words, unrelated nonstudied words, conjunction words, and fixation—which introduced jitter in the timing of the hemodynamic response and allowed for extraction of the response for the other three conditions) were ordered in a balanced fashion (see Buckner et al., 1998) such that

each trial type ($N = 24$) preceded and followed each other trial type roughly the same number of times (to facilitate response modeling with the general linear model). All 24 subjects took an identical recognition test (with identical items in an identical order); the only cross-subject difference during the test phase was which words had previously been studied, which were conjunction lures, and which were unrelated nonstudied lures.

Subjects were instructed to respond with a keypress while the stimulus was on the screen (pushing one button for previously studied words and another button for words not previously studied). Subjects were told that during the fixation phase, they should look at the fixation point while remaining still.

fMRI Data Analysis

Data for each subject were subjected to the processing stream used at Washington University, which includes correction for intensity differences across odd- and even-numbered slices, interpolation to $3 \times 3 \times 3$ mm voxels, alignment to correct for slice-based within-trial differences in acquisition times, automated movement-correction within and across runs (Snyder, 1996), removal of the linear slope on a voxel-by-voxel basis to correct for frequency drift (Bandettini, Jesmanowicz, Wong, & Hyde, 1993), whole brain normalization to a common mode of 1000 to facilitate comparisons across subjects, transformation into standardized atlas space (Talairach & Tournoux, 1988), and application of a Gaussian smoothing filter (9 mm full-width half-maximum) to further accommodate variations in activation loci across subjects.

The data were analyzed using an implementation of the general linear model (Worsley & Friston, 1995; Friston, Jezzard, & Turner, 1994). The time course of each condition type (i.e., studied, unrelated nonstudied, conjunction nonstudied) was estimated in an assumption-free manner for each subject for each voxel (see Ollinger, Shulman, & Corbetta, submitted). We then cross-correlated the estimated time-course of the BOLD response to each condition at each voxel with a reference gamma function (Dale & Buckner, 1997; Boynton, Engel, Glover, & Heeger, 1996) and a latency parameter containing three values ($\gamma = 2$ sec; $\lambda = 1.25$ sec) at 1-sec steps to accommodate slight variations in the time of response onset. The greatest of the three resulting magnitudes (in percent signal change units) were then entered into an ANOVA routine, which identified voxels that demonstrated differential activation among the three conditions. The resulting composite image was then set to a threshold p level of .005, and only regions with at least 10 contiguous voxels passing this threshold were considered (Forman et al., 1995). An automated peak-search algorithm identified the location (in atlas coordinates) of peak activations on the basis of level of

statistical significance with the provision that they be separated by 8 mm, or else the peak with the smallest p value was kept. Regions around the peak activations were identified interactively by choosing contiguous voxels surpassing the threshold within the z plane of peak activity and in both of the contiguous planes.

CONCLUSIONS

We have identified neural regions that correlate with retrieval success using rapid event-related fMRI procedures and an unpredictable ordering of trial types during a recognition test. These regions have all been previously identified as contributing to episodic memory retrieval, but the novel contribution of the present experiment is to unconfound tonic set effects from those occurring at the individual item level. Especially noteworthy was the finding of greater activation for hits than unrelated CRs in anterior prefrontal cortex (in or near BA 10), which has been a region of considerable interest with respect to episodic retrieval. Correctly rejected conjunction lures, or recombined aspects of studied words, were hypothesized to lead to retrieval success in that subjects may recollect studied words in service of rejecting the familiar conjunction lures (Jones & Jacoby, in press). Consistent with this hypothesis, conjunction lures correctly classified as nonstudied exhibited greater activation than correct classifications of lures unrelated to studied words in regions identified as important in retrieval success (by the hit > unrelated CR pattern). Taken as a whole, these results enhance our understanding of some of the key regions involved in episodic memory retrieval.

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