fMRI Evidence for Separable and Lateralized Prefrontal Memory Monitoring Processes

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Abstract

■ Source memory research suggests that attempting to remember specific contextual aspects surrounding prior stimulus encounters results in greater left prefrontal cortex (PFC) activity than simple item-based old/new recognition judgments. Here, we tested a complementary hypothesis that predicts increases in the right PFC with tasks requiring close monitoring of item familiarity. More specifically, we compared a judgment of frequency (JOF) task to an item memory task, in which the former required estimating the number of previous picture encounters and the latter required discriminating old from new exemplars of previously seen items. In comparison to standard old/new recognition, both source memory and the JOF task examined here require more precise mnemonic judgments. However, in contrast to source memory, cognitive models suggest the JOF task relies heavily upon item familiarity, not specific contextual recollections. Event-related fMRI demonstrated greater recruitment of right, not left, dorsolateral and frontopolar PFC regions during the JOF compared to item memory task. These data suggest a role for right PFC in the close monitoring of the familiarity of objects, which becomes critical when contextual recollection is ineffective in satisfying a memory demand. ■

INTRODUCTION

Memory demands vary considerably in the amount of contextual information required for success. At one end of the spectrum, many laboratory tasks of recognition can be accomplished via judgments of item familiarity (or novelty). During these tasks, subjects encounter words or objects in a "study" list and then must later discriminate between these and items that were not previously presented. Signal detection and computational models suggest that these tasks can potentially be accomplished by simply relying upon a continuous item strength or familiarity signal, which builds monotonically with item exposures, without resorting to recovering specific contextual aspects regarding the previous encounter with each item (Hintzman, Nozawa, & Irmscher, 1982; Atkinson & Juola, 1974; Banks, 1970). In contrast, for some tasks, recovery of detailed contextual information is necessary for success. For example, in typical source memory tasks, items are shown in one of a number of encoding contexts (e.g., male or female voicing, different locations, different orientating tasks, etc.) and subjects are represented the items at test and must determine from which specific source each originated. Because the items have been exposed to the same degree, closely attending to differences in familiarity is unhelpful. Instead, subjects must recover or recollect different contextual aspects of the previous encounters in sufficient detail to make a source attribution. Thus, the relative utility of recollection and familiarity processes is heavily influenced by the task design, with some designs requiring more extreme reliance on one or the other process.

Recent comparisons of source and item memory tasks using functional imaging have led to a consistent pattern of prefrontal cortex (PFC) response. In general, these studies have found increases in the left PFC when source memory is compared to item memory (Dobbins, Foley, Schacter, & Wagner, 2002; Raye, Johnson, Mitchell, Nolde, & D'Esposito, 2000; Rugg, Fletcher, Chua, & Dolan, 1999; Nolde, Johnson, & D'Esposito, 1998). This typically left-lateralized increase has been observed for pictures as well as words and can also be seen when other contextually demanding retrieval tasks, such as item cued recall, are compared with simple item memory (Cabeza, Locantore, & Anderson, 2003). Advocates of the source monitoring framework have interpreted these findings as indicative of the need for more "reflective" or "systematic" processing for source compared with item memory, involving more subprocesses or more monitoring of more specific information (Raye et al., 2000; Nolde et al., 1998; Johnson, Hashtroudi, & Lindsay, 1993). Similarly, in a recent study by Ranganath, Johnson, and D'Esposito (2000), the authors interpreted increased left anterior PFC activity in terms of the demand for more contextually or perceptually specific information during retrieval attempt for source versus general item memory tasks. In general, these accounts lead to the prediction

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that increases in the specificity of contextual information required during retrieval will also lead to increased activity in the left PFC. Additionally, the source monitoring framework has been used to suggest that regions in the right PFC may instead support more "heuristic" memory processes that have been characterized as relatively simple, quick processes sufficient for less reflectively demanding tasks such as memory judgments based on familiarity (Nolde et al., 1998).

An alternate conceptualization of PFC responses during recognition has been developed to account for increases in the right PFC during recognition. For example, Henson and colleagues used the remember/know technique (Tulving, 1985) in an attempt to separate memory endorsements based upon contextual recollection (remembered) from those merely relying upon a sense of item familiarity (known) (Henson, Rugg, Shallice, Josephs, & Dolan, 1999). When successful "know" reports were compared to successful "remember" reports, greater activity was observed in the right dorsolateral PFC (see also Eldridge, Knowlton, Furmanski, Bookheimer, & Engel, 2000). In addition, low confidence recognition reports, which are typically assumed to rely on familiarity in isolation, also lead to increased activity in the right dorsolateral PFC (Henson, Rugg, Shallice, & Dolan, 2000). These observations led to the suggestion that the right dorsolateral PFC may be involved in the "retrieval monitoring" of items that are close to the response criterion. A somewhat related idea is that the right PFC is critical for the "postretrieval monitoring" of mnemonic content (Rugg & Wilding, 2000; Rugg, Otten, & Henson, 2002; Rugg, Henson, & Robb, 2003; Schacter, Buckner, Koutstaal, Dale, & Rosen, 1997). From this perspective, the right dorsolateral PFC is particularly involved in the monitoring of recovered memory content in order to verify whether it satisfies a current memory demand. Such postretrieval monitoring requirements may be elevated when the recovered information is of an impoverished nature such as during low-confidence reporting, when relying upon memories devoid of much contextual content (i.e., "know" responses), or under situations requiring the close scrutiny of potentially diagnostic information regarding prior sources (Rugg et al., 2002, 2003).

Overall, the "systematic/heuristic" and postretrieval monitoring characterizations potentially conflict with respect to explaining the laterality of PFC response during episodic retrieval. Whereas the systematic/heuristic characterization suggests that contextually demanding retrieval tasks will preferentially recruit the left PFC, these same tasks are presumed heavily dependent on the right dorsolateral PFC under the postretrieval monitoring framework. Here, similar to the systematic/heuristic view, we suggest that the role of the right PFC may be tied to monitoring a specific type of memory signal, namely, that based on the individual familiarity of the item itself. This hypothesis would then explain why activity is observed under conditions where memory endorsements are made in the absence of recovered contextual information such as "know" and low confidence reports. Under these conditions, subjects would have to closely attend to or monitor the familiarity signal in order to make the memory decision. There is limited additional support for the role of the right PFC in familiarity monitoring from neuropsychological research on patient B.G. Patient B.G., who suffered stroke related damage to the posterior dorsal region of the right PFC, shows an aberrant response pattern in simple item-recognition paradigms, generating large numbers of incorrect endorsements for novel lure items (false alarms) (Curran, Schacter, Norman, & Galluccio, 1997; Schacter, Curran, Galluccio, & Milberg, 1996). Such a pattern is consistent with the idea that this patient has difficulty effectively monitoring familiarity such that the low familiarity of lures does not lead to rapid rejection. Additionally, repetitive transcranial magnetic stimulation (TMS) over the right dorsolateral PFC during picture recognition has been shown to elevate false alarm rates to new items (Rossi et al., 2001). Finally, Dobbins et al. (unpublished data) observed greater activity in the right dorsolateral and frontopolar PFC in a comparison of novelty detection (which of three objects was new) relative to conceptual source memory (remembering the particular semantic task associated one of three objects) across identically constructed picture sets. Thus, there seems to be growing support for the notion that right prefrontal regions may be recruited when subjects closely monitor the item novelty/familiarity dimension during retrieval tasks.

We directly tested the familiarity-monitoring hypothesis using a demanding retrieval task that requires a more precise judgment regarding previous exposure than standard old/new recognition, namely, judgment of frequency (JOF). We compared the JOF task with an item memory task in which the subjects simply decided whether the test probe was the same or a different exemplar of the item studied. During the JOF task, subjects encounter particular items different numbers of times and must subsequently estimate the frequency of prior encounter for each of the items during a later memory test. It is important to note that although the JOF task makes reference to more precise episodic information than standard old/new recognition, there are psychological and computational reasons to believe that subjects typically accomplish this task via reliance on item familiarity without the retrieval of specific contextual information (Hintzman & Curran, 1994; Hintzman, 1984; Hintzman et al., 1982). That is, although both source and JOF tasks are more demanding than old/new recognition, we assume that each requires the increased monitoring of fundamentally different types of mnemonic content. Psychologically, the familiarity-based characterization of the JOF task makes sense, given the stereotypy of each encounter. That is, there may be little in the way of specific contextual content that could be recollected and would be useful for discriminating an item seen, for example, three times, from one seen six (see also Wagner, Maril, & Schacter, 2000). Furthermore, the deliberate encoding of individual item frequencies may be virtually impossible given the constraints of working memory. For example, consider an experiment where items are seen two, four, or six times before testing. Typically subjects are told to ignore these repetitions and perform some type of orienting task. However, it is important to consider whether they could reasonably employ any strategy to explicitly encode the frequency of separate items. Even a cursory task analysis indicates that the working memory load of such a task far exceeds the assumed capabilities of subjects. For example, subjects would have to not only track the running frequency tally of each individual item, they would also have to somehow actively note when an item "failed" to recur beyond a particular frequency. That is, remembering seeing an item at a lower frequency, say twice, is nondiagnostic because all items appeared twice and because this recollection does not indicate that the item did not also appear in later exposures. Instead, what would be necessary is remembering that an item occurred twice *and* that it did not occur at a greater frequency. Such explicit encoding of nonoccurrence for an earlier seen item is unlikely to occur while engaged in the active encoding of different items; This, combined with the likelihood that maintaining a running frequency tally during encoding vastly exceeds working memory capacity, makes it likely that explicit encoding of frequency rarely occurs. This assumption is also consistent with work showing that levels of processing and attentional manipulations that increase or impede explicit recollection have little impact in the encoding of frequency information, which appears largely automatic (Hasher, Zacks, Rose, & Sanft, 1987; Hasher & Zacks, 1984; Zacks, Hasher, & Sanft, 1982; Hasher & Chromiak, 1977). Thus, the JOF task potentially serves as the complement to standard source memory tasks. In source memory tasks the familiarity of the items is assumed to be similar, but the encoding context of each differs in some critical fashion. In contrast, during JOF tasks, the encoding context is typically held relatively fixed but the item familiarities systematically differ.

Overall, both the JOF and item memory (same or different?) conditions are expected to involve an item-based feature judgment, namely, determining if the test picture is the same or a different exemplar than what was shown before. Additionally, however, from a familiarity-monitoring viewpoint, the JOF task requires monitoring of the familiarity signal, over and above any such monitoring that may occur in the item memory task, in order to estimate the prior presentation frequency. That is, under the item memory task, any monitoring can stop once an item is determined to be old or new, further inspection of its familiarity in order to estimate frequency is unnecessary. Given these considerations, we predicted that the JOF task would yield increased activity in the right PFC compared to the item memory task.

RESULTS

Behavioral

Table 1 shows the accuracy data across the conditions using the signal detection measure d'. In general, subjects were less accurate on the frequency estimation than the item memory tasks, $t(15) = 10.47$, $p < .001$. Furthermore, within the item memory task, increasing frequency improved accuracy, $t(15) = 6.88$, $p < .001$, whereas within the JOF task, changing to a different exemplar impaired performance, $t(15) = 6.14$, $p < .001$.

Table 2 shows the median reaction time data for the subjects for correct responses. Overall, subjects were slower on correct JOF decisions than on item memory decisions, $t(15) = 12.75$, $p < .001$. Separate Item Frequency × Picture Format ANOVAs were conducted separately for each retrieval task. Within the item memory task, there was a main effect of frequency, with quicker responding to more frequently seen items, $F(1,15) = 18.70$, $p < .001$, and an interaction between item format and frequency. This interaction occurred because the correct identification of different pictures was not altered by exposure frequency, whereas the correct identification of the same pictures was significantly faster with the higher exposure frequency, $F(1,15) = 9.06$, $p < .01$. Within the JOF task, there was a main effect of item format with quicker JOFs to items that were the same versus those that were different, $F(1,15) = 112.43$, $p < .001$, and a main effect of frequency with quicker responses to the high frequency

Table 1. Behavioral Accuracy

		Accuracy	
	Twice	*Six*	*Overall*
IM("different")			
Different	.87	.88	.88
Same	.38	.16	.27
d'	1.56	2.28	1.84
	Same	*Different*	*Overall*
JOF("six times")			
Six	.79	.63	.71
Two	.32	.35	.34
d'	1.35	.77	1.02

IM = item memory; JOF = judgment of frequency.

Note. d' values based on individual subjects not aggregate proportions. In order to calculate accuracy, different exemplar items were arbitrarily classified as targets during item memory, and the items seen six times were arbitrarily classified as targets for JOFs.

Table 2. Behavioral Reaction Times

	Reaction Time (msec)		
	Twice	*Six*	*Overall*
IM			
Different	1755	1721	
Same	1794	1595	1716
	Same	*Different*	
JOF			
six	1698	2054	
two	2094	2245	2022

IM = item memory; JOF = judgment of frequency.
Reaction times are for median correct responding only.

items, $F(1,15) = 30.34$, $p < .001$. There was also an interaction between item format and frequency, which resulted because the slowing that occurred with different pictures was more severe for high frequency than low frequency items, $F(1,15) = 14.16$, $p < .01$.

fMRI

JOF Relative Increases

Bilateral prefrontal (dorsolateral and anterior), inferior parietal, and midline regions demonstrated greater signal during correct responses on the JOF task compared to the item memory task, collapsed across potential changes in item format (same or different) (Figure 1, Table 3). However, inspection of the extracted time courses for ROIs in the left and right PFC regions suggested that the hemispheres potentially differed in the nature of JOF task response as a function of item format (same or different). More specifically, if one restricts attention to the task response for items that remained the same across encounters, the main evidence for an increased activity in JOF task appears predominantly in the right PFC; the hemodynamic responses to the retrieval tasks in the left hemisphere look quite similar to one another (solid lines, Figure 1). In contrast, when attention is restricted to items that changed between study and test, there appears to be a bilaterally increased PFC response for the JOF compared to item memory tasks.

To confirm this impression statistically, we analyzed the peak response (6 sec post stimulus onset) from

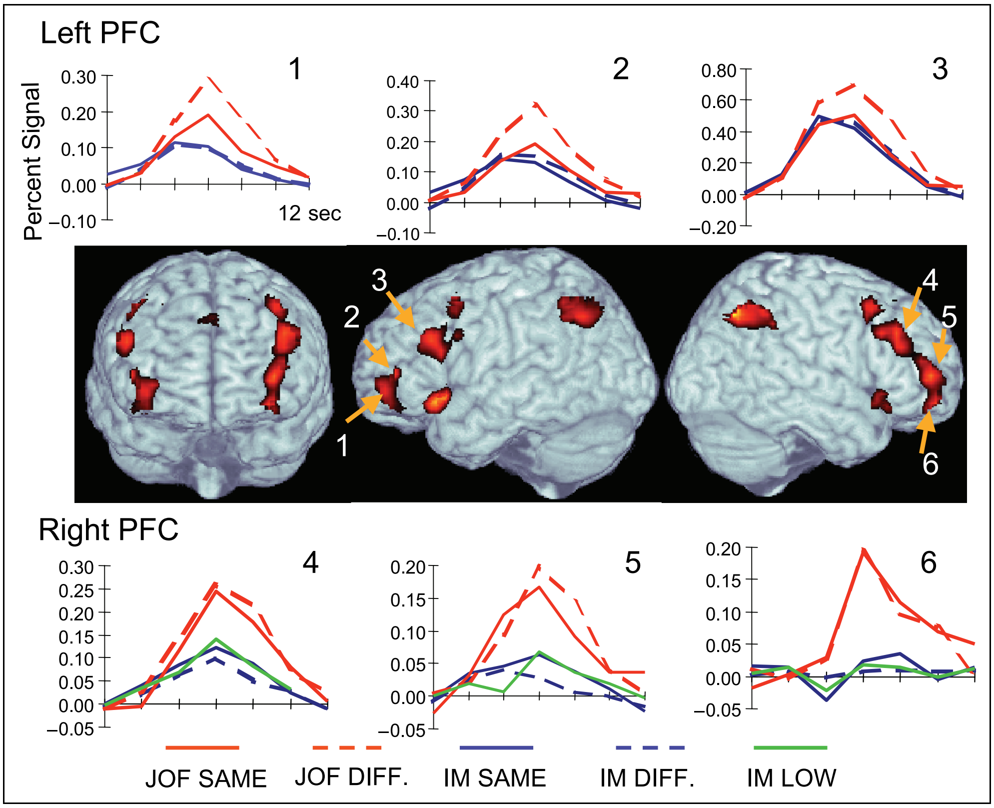
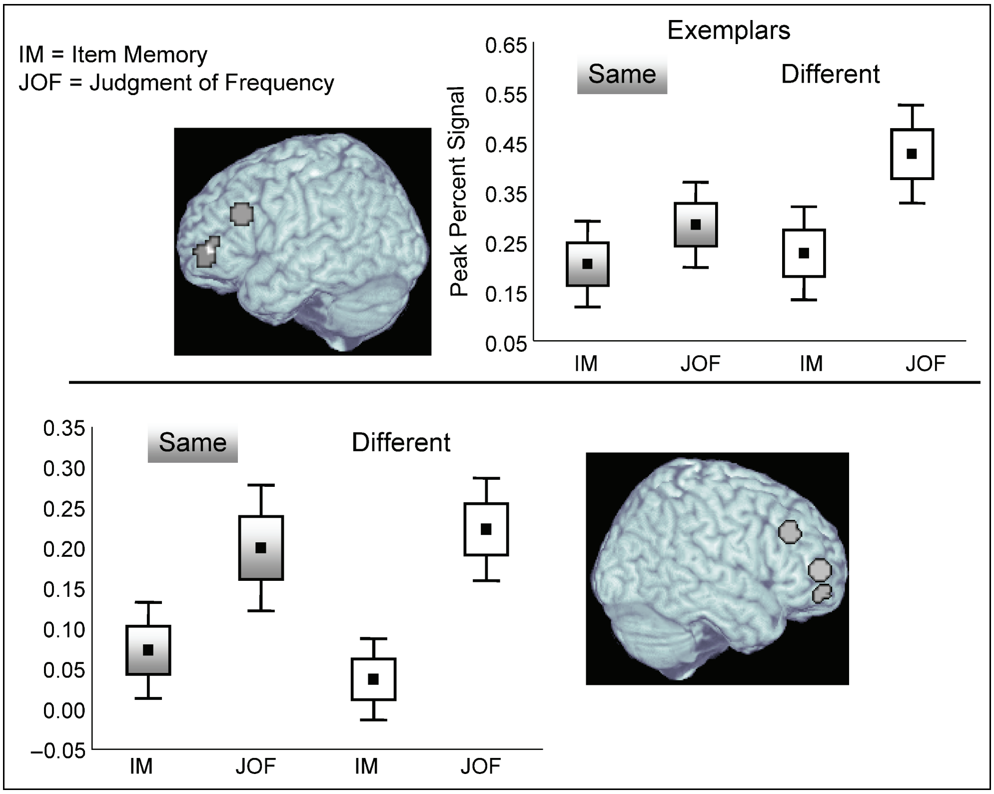


Figure 1. Cortical regions demonstrating greater activity for the JOF task in comparison to the item memory (IM) task (collapsed across differences in item format). Activity maps are thresholded at .001 5-voxels one-tailed, overlaid on a canonical high-resolution structural image in MNI space (MRICRO software, www.psychology.nottingham. ac.uk/staff/cr1/mricro.html). Upper insets show reconstructed hemodynamic responses across conditions of interest for the left PFC whereas lower insets plot the same responses for the right PFC. *y*-axis is percent signal change, *x*-axis is poststimulus onset time in 2-sec increments out to 12 sec. Solid lines indicate task performance for items that remained same between study and test; broken lines indicate performance for items that were different exemplars than those studied. Red lines indicate JOF response, blue lines IM response. The green line shows IM response at a lower level of behavioral performance comparable to JOF performance (IM for items seen twice collapsed across same/different condition).

Figure 2. Data for Hemisphere (left or right) × Retrieval Task (JOF or IM) × Item Format (same or different) interaction observed in anterior PFC regions. Image overlays demonstrate the left and right regions that constituted each ROI. Box plots show the peak response (6 sec post stimulus onset) averaged across each subject for the conditions of interest. Box is one standard error of the mean and box plus whiskers is two standard errors. Shaded boxes show task-related response when the item format remained the same across study and test; open boxes show the response when the items were different exemplars.



regions of interest (ROIs) in the left and right dorsolateral and frontopolar areas. These ROIs were drawn from the dorsolateral and frontopolar regions implicated in the JOF greater than item memory contrast. Each ROI (left and right) contained significant voxels within three 8-mm-diameter spheres centered on the three SPM-identified maxima in each hemisphere. The left-hemisphere ROI contained 130 voxels and the right contained 138 voxels (Figure 2). These peak responses were then entered into a Hemisphere (Left or Right) × Retrieval Task (Item Memory or JOF) × Item Format (Same or Different) three-way ANOVA (Figure 2). Because these regions were selected without respect to item format, they are unbiased with respect to any potential Item Format × Hemisphere interactions.

Main Effects

The results yielded main effects of hemisphere, left > right; $F(1,15) = 14.50$, $MSE = .051$, $p < .01$, and retrieval task, $F(1,15) = 135.82$, $MSE = .005$, $p < .001$. Additionally, the main effect of item format, different > same; $F(1,15) = 4.41$, $MSE = .010$, $p = .053$, approached significance. The main effect of hemisphere must be interpreted cautiously because it assumes the responses of the two hemispheres are scaled similarly (i.e., ratio scaling with same range). However, given this assumption, the data suggest that on average the left hemisphere was engaged to a greater extent than the right hemisphere (.28 vs .13). The main effect of retrieval task simply confirms that these ROIs were drawn from the original frequency > item memory contrast. Finally, the main effect of item format demonstrates slightly greater activity for exemplars that are different versus those that remain the same across study and test (.23 vs .19).

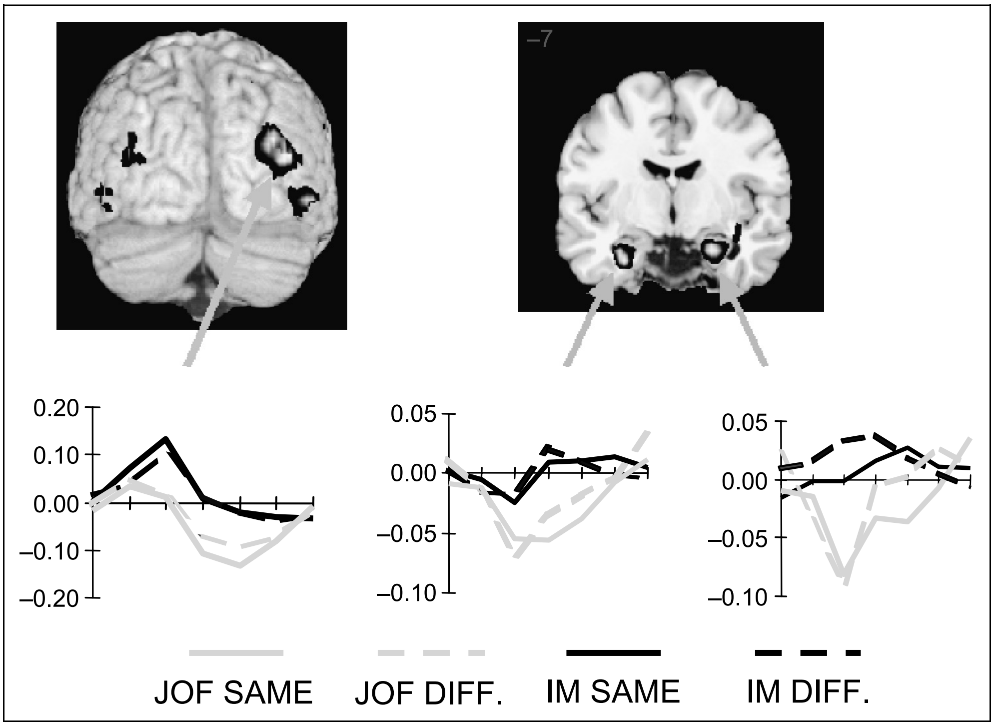
Two-Way Interactions

There were significant Hemisphere × Item Format, $F(1,15) = 25.04$, $MSE = .002$, $p < .001$, and Retrieval Task × Item Format, $F(1,15) = 7.28$, $MSE = .009$, $p < .05$, interactions. Post hoc Tukey's HSD comparisons indicated that the Hemisphere × Item Format interaction occurred because there was greater activity for different versus same items in the left hemisphere (.33 vs. .24, $p < .001$) but no item format differences in the right (.13 vs. .14, *ns*). Post hocs for the Retrieval Task × Item Format interaction indicated that it occurred because item format did not affect the activity level during item memory judgments (.14 vs .13; same vs. different), whereas the different items yielded more signal than same items during the JOF task (.32 vs. .24, $p < .05$).

Three-Way Interaction

There was a Hemisphere × Retrieval Task × Item Format interaction, $F(1,15) = 5.86$, $MSE = .001$, $p < .05$ (Figure 2). Post hoc interaction analyses were conducted separately for the left and right hemispheres. In the left hemisphere, there was a main effect of retrieval

Figure 3. Regions showing a greater response during item memory versus judgments of frequency (collapsed across differences in item format). Activity maps are thresholded at .001 5-voxels one-tailed, overlaid on a canonical high-resolution structural image in MNI space (MRICRO software http://www.psychology.nottingham.ac.uk/staff/cr1/mricro.html). See Figure 1 caption for additional information.



task, $F(1,15) = 126.32$, $MSE = .002$, $p < .001$, a main effect of item format, $F(1,15) = 14.13$, $MSE = .008$, $p < .01$; different > same, and a significant Retrieval Task × Item Format Interaction, $F(1,15) = 8.90$, $MSE = .006$, $p < .01$. Follow-up Tukey's HSD comparisons demonstrated that the interaction occurred because there was a greater signal for the JOF in comparison to the item memory task for items that differed between study and test ($p < .001$); however, the retrieval tasks did not significantly differ when items remained the same between study and test. In the right hemisphere, there was the expected main effect of retrieval task, $F(1,15) = 80.10$, $MSE = .005$, $p < .001$, but no main effect of item format, $F < 1$ or Retrieval Task × Item Format interaction, $F(1,15) = 3.88$, $MSE = .004$, $p > .06$. Because the interaction approached significance, post hoc Tukey's comparisons were conducted to confirm that the pattern was different from the left hemisphere. These demonstrated that unlike the left, there was a significant increase for the JOF in comparison to the item memory task, regardless of item format (*p*s < .001).

Overall, this pattern of results suggests that the right PFC is engaged in a particular type of memory monitoring that is required regardless of whether the test item serves as an exact replica (copy cue) or a more symbolic cue regarding the frequency of prior encounters. That is, unlike the left hemisphere, this region is reliably engaged to a greater extent regardless of the item format during JOFs. The fact that the level of response during the JOF task appears similar regardless of item format also suggests that this region is not merely reflecting general effort since this manipulation produced a large behavioral decline in performance in the task (Table 1). We further examine "difficulty" or "effort" explanations in the discussion.

A statistically different response pattern was observed in the left PFC. When activity was compared across the tasks for items that were the same between study and test, no significant differences were observed. In contrast, strong task differences were observed for items that were different between study and test, with a selective increase observed for the JOF task. Similar left dorsolateral and frontopolar responses have been implicated in contextual source and paired associate retrieval paradigms (Maril, Simons, Mitchell, Schwartz, & Schacter, 2003; Dobbins, Rice, Wagner, & Schacter, 2003; Dobbins et al., 2002) and for source judgments based on perceptual characteristics of stimuli (Ranganath et al., 2000). Furthermore, the overall level of activity was higher in the left than the right dorsolateral and frontopolar regions, although this must be interpreted cautiously.

Item Memory Relative Increases

For the reverse comparisons, item memory versus JOF (collapsed across item format), no above baseline activity differences were observed in the PFC (Table 4). However, there were extrastriate, IT, and MTL regions that demonstrated consistently greater signal during item memory compared to JOFs (Figure 3). In addition

Table 3. SPM Results—JOF versus Item Memory Contrast

			Talairach				
Hemisphere	*Region*	*BA*	*x*	*y*	*z*	*Voxels*	*Z score*
Left	IFG	47	−33	23	−9	72	4.91
*	IFG/MFG	10	−45	47	3	15	4.29
*	MFG	45/46	−48	27	24	60	4.43
	MFG	9	−42	13	27	19	3.58
*	MFG	10	−39	52	−5	55	4.11
	MFG	6	−42	14	46	19	3.93
	IPL	7/39	−36	−59	42	58	4.33
	IPL	40	−45	−47	49	24	3.95
	Cingulate	32	−6	25	37	67	4.54
	Posterior cingulate	23	0	−19	29	60	4.76
	Posterior cingulate	23	−6	−25	26	38	4.37
	Posterior cingulate	23	−6	−37	21	13	3.44
	Precuneus	7	−3	−65	36	79	4.35
	Precuneus	7	−12	−59	36	33	3.79
	Thalamus		−12	−17	9	32	3.96
	Thalamus		−9	−15	−2	22	3.90
	Thalamus		−18	−14	3	26	3.74
	Brain stem		−3	−30	−19	15	4.08
Right	IFG	47	30	26	−9	61	4.67
*	MFG	10	39	53	3	57	4.58
*	MFG	9/46	45	33	29	57	4.46
*	MFG	11	36	55	−13	24	4.39
	MFG	9	45	25	29	50	4.24
	MFG	10	45	47	11	29	3.91
	MFG	8	39	20	43	40	4.2
	SFG	9	9	36	26	52	4.29
	IPL	7/40	42	−62	45	35	5.12
	IPL	40	53	−44	46	31	4.22
	IPL/Supramarginal	40	50	−39	38	21	4.01
	Cingulate	32	9	25	37	43	4.14
	Posterior cingulate	23	6	−37	21	32	4.24
	Posterior cingulate	29	9	−43	10	7	3.59
	Precuneus	31	15	−54	30	59	5.64
	Thalamus		12	−11	12	30	4.04
	Caudate		9	0	3	11	3.30
	Caudate		15	6	11	5	3.34
	Brain stem		6	−30	−19	8	3.66
	Brain stem		0	−31	−29	5	3.39
	Brain stem		12	14	−8	7	3.38

Note. Asterisks denote regions contributing to ROIs. IFG = inferior frontal gyrus; MFG = middle frontal gyrus; SFG = superior frontal gyrus; IPL = inferior parietal lobule; BA = approximate Brodmann's location. Coordinates are in Talairach space transformed from the original MNI.

Table 4. SPM Results—Item Memory versus JOF Contrast

			Talairach				
Hemisphere	*Region*	*BA*	*x*	*y*	*z*	*Voxels*	*Z score*
Left	PHG/Uncus		−27	−7	−25	40	4.90
	PHG/Fusiform	36	−33	−30	−11	13	4.18
	PHG/Hippocampus		−30	−15	−9	10	3.50
	Fusiform	37	−33	−47	−13	19	3.85
	SOG	19	−39	−83	24	19	4.06
	MOG	19	−33	−75	18	11	3.34
	MTG	37	−42	−61	1	10	3.94
	MOG	19	−50	−61	−4	9	3.31
Right	PHG/Uncus		24	−7	−20	60	4.92
	Fusiform	37	33	−39	−13	29	3.95
	MTG	19	48	−75	20	37	4.78
	SOG	19	39	−77	29	44	4.71
	MOG	37	42	−61	−4	30	3.76
	MOG/ITG	19/37	50	−64	−2	38	3.70
	ITG	20	39	−16	−27	13	4.15

PHG = parahippocampal gyrus; SOG = superior occipital gyrus; MOG = middle occipital gyrus; ITG = inferior temporal gyrus; MTG = middle temporal gyrus; BA = approximate Brodmann's location. Coordinates are in Talairach space transformed from the original MNI. The table lists relative activations only.

to the activity in visual association areas, there was a bilateral relative decrease in signal in an anterior portion of MTL bordering perirhinal and anterior hippocampal areas. Since the data were not globally scaled, this relative decrease is likely not a processing artifact. Although there remains controversy regarding the interpretation of relative signal decreases, we report these deactivations because of the established importance of the MTL region in recognition memory, and because although the signal differences were small, they were highly reliable. Based on the repeated observation of greater activity for new than studied items across multiple experiments, Henson, Cansino, Herron, Robb, and Rugg (2003) recently suggested that bilateral MTL regions proximal to those reported here may signal item familiarity (Henson et al., 2003). In the current study we found no evidence for familiarity modulation of these regions (see also Rugg et al., 2003). In addition to failing to distinguish different and same items within each task, these regions also did not distinguish between items seen two and six times when in the same format even at a liberal threshold (.01). There are many possible reasons for this apparent discrepancy. For example, the familiarity signal differences observed here might be considerably smaller than those observed between purely novel and old items and this may have precluded detection (see Brown & Aggleton, 2001). Regardless, in the current data, bilateral anterior MTL regions are reliably modulated by the nature of the episodic retrieval task and not the familiarity of the items. Under the assumption that MTL regions may be highly active during baseline tasks (Stark & Squire, 2001), it is possible that the ''baseline'' MTL activity seen here during the item memory task actually corresponds to active feature encoding driven by object processing activity suggested in the extrastriate and IT regions.

DISCUSSION

The current data demonstrate that judgments of frequency do not recruit the same neural substrates as tasks requiring the recovery of specific contextual content (i.e., source memory). Prior research comparing source to item memory in our laboratory has shown strikingly left lateralized prefrontal and parietal responses for contextually demanding source memory tasks using both words (Dobbins et al., 2002, 2003) and pictures (Dobbins et al., unpublished data). This tendency towards left lateralization for source memory, which has also been observed in other laboratories (Ranganath et al., 2000; Raye et al., 2000; Rugg et al., 1999; Nolde et al., 1998), has been held to indicate that the left PFC is critically tied to more contextually specific retrieval demands (Ranganath et al., 2000) compared to simple item-recognition judgments. Here we observed that the most reliable difference between the JOF and item memory tasks was seen in the right—not left—PFC. This finding suggests that simply requiring more precision in the memory discrimination, in and of itself, does not guarantee a concomitant increase in left PFC activity; instead what appears to be critical is the nature of the retrieval information that subjects choose to monitor in order to solve the memory task. Before considering this idea more fully it is important to consider whether these data can be easily explained by difficulty or effort-based accounts.

Earlier imaging studies of memory sometimes employed the construct of retrieval effort to account for activity (e.g., Schacter, Alpert, Savage, Rauch, & Albert, 1996). Therefore, retrieval effort is a potential explanation for our data given that the JOF task here was associated with less accurate and longer responses than the item memory task (for discussion, see Rugg & Wilding, 2000). However, there are numerous reasons for rejecting the effort account of the current data and perhaps PFC retrieval data in general. First, the level of activity in the right PFC during the JOF task did not appreciably change as a function of item format (Figures 1 and 2). However, this manipulation had a marked effect on behavioral accuracy, resulting in an approximately 43% decrease in performance when the picture exemplars differed between study and test. Thus, right dorsolateral and frontopolar regions are clearly not tracking "effort" in any general sense within the JOF task, at least for correct responses. Second, if we contrast performance on the item memory task for items seen twice during study ($d' = 1.56$) with that of the JOF task performed on same format items ($d' = 1.35$), the accuracies are comparable. However, there still remains a large signal difference in the previously discussed right PFC regions between the two tasks (see Figure 1, green lines). Finally, recent studies comparing source to item memory have rendered a general effort-based account largely uninformative, because these studies have demonstrated more robust increases in left and not right PFC for the more "effortful" source memory tasks (Cabeza et al., 2003; Dobbins et al., 2002, 2003; Raye et al., 2000; Rugg et al., 1999; Nolde et al., 1998) that are invariably less accurate and slower than simple old/new recognition. Thus, given the available data, knowing that one episodic memory task is less accurate or slower than another, does not indicate the expected laterality of prefrontal response.

Returning to the systematic/heuristic and postretrieval monitoring accounts discussed earlier, it appears that the current results are more easily accommodated under the former. Under the systematic/heuristic characterization, the right PFC is tied to heuristic memory judgments, which have been argued to be consistent with signal detection accounts of familiarity (Nolde et al., 1998). However, it is important to note that it is not entirely clear that the JOF task would have been classified as "heuristic" if one remained entirely within the systematic/heuristic framework, and did not also consider dual-process or statistical models of recognition directly (Yonelinas, Dobbins, Szymanski, Dhaliwal, & King, 1996; Yonelinas, 1994; Jacoby, 1991; Mandler, 1980). For example, Nolde et al. (1998) suggested that right PFC heuristic processes were relatively simple and quick compared to left PFC systematic processes (p. 3513). However, in the current paradigm, the JOF task itself is conceptually no simpler than the item memory task. More specifically, the JOF task requires that subjects understand that the current test items originated from the study episode, that there were two prior frequency categories, and that responses should be differentially assigned based on the prior frequency of the current test probe. When considered from this viewpoint, the JOF task appears no less complicated than the standard source memory task that has shown a tendency to be left lateralized in comparison to item memory (Dobbins et al., 2002, 2003; Raye et al., 2000; Rugg et al., 1999; Nolde et al., 1998). What is important from a dual process account is that recollection will be largely ineffective in making the frequency discrimination, and therefore subjects will closely monitor differences in item familiarity. Thus, although we view familiarity monitoring as consistent with a "heuristic" process it is important to emphasize that the precision of the discrimination does not directly determine the laterality of prefrontal response. In addition, the speed of responding also does not unambiguously identify the process used for recognition discrimination. Within signal detection theory, the speed of response is tied to the relative differences in the familiarities of the items discriminated (in the case of forced choice), or to the distance between an item's familiarity and an internal criterion in paradigms like the current one. From this perspective, it is possible to observe both extremely quick or slow responses based on item familiarity (Murdock & Dufty, 1972). Likewise, the ability to distinguish prior sources based on recollection can be facilitated or impaired based on the relative distinctiveness of the prior source contexts, with such effects potentially having little to do with the familiarity of the individual items and presumably greatly affecting response speed (e.g., Dobbins, Kroll, Yonelinas, & Liu, 1998). Thus, although systematic/heuristic or recollective/familiarity-based judgments are expected to differentially depend on the left and right PFC regions, respectively, this reliance cannot be simply mapped onto differences in reaction time or precision of retrieval demand across memory tasks.

The current data are less consistent with the postretrieval monitoring account of the right dorsolateral PFC

(Rugg et al., 2002, 2003). Under this account, activity in the right dorsolateral PFC is tied to the evaluation of recovered mnemonic content, and such activity should be elevated under conditions that demand a finer grained consideration of mnemonic information (e.g., exclusion vs. inclusion memory tasks). From this viewpoint, one might expect the greater activity for the JOF than item memory tasks since it requires an additional assessment regarding prior frequency of occurrence. However, one would also expect greater activity for test items that were different from the studied version compared to those that were the same, based on the idea that these items would demand greater scrutiny of the memory signal regarding both original form and prior frequency. Behavioral evidence in line with this idea is particularly strong for the JOF task. When the test item was a different exemplar than that studied, behavioral accuracy fell (Table 1) and response times were elevated (Table 2), consistent with a requirement for greater postretrieval monitoring. However, the JOF task signal for different exemplars was not significantly elevated over that for same exemplars in either right dorsolateral or frontopolar PFC. Instead, the left dorsolateral and frontopolar PFC demonstrated a large signal increase specific to this condition (Figures 1 and 2).

Another framework recently advanced to account for hemispheric differences during retrieval tasks relies upon the distinction between ''production'' and ''monitoring'' (Cabeza et al., 2003). Under this framework, the left PFC is recruited during semantically guided production operations, whereas the right PFC is more involved in monitoring and verification operations. Given the similarity between the postretrieval monitoring and ''production/monitoring'' accounts in terms of the right PFC, we also suggest these data are potentially problematic for the production/monitoring account.

A final pattern in the data worth considering was the response in left dorsolateral and frontopolar regions. It has been suggested that similar regions are critical for monitoring conceptually specific memory content regarding either the contextual source or featural characteristics of items (e.g., Dobbins et al., 2002; Ranganath et al., 2000). In the current paradigm, the results indicated that on average there was a greater level of activity in these regions in the left compared to right hemisphere, consistent with the idea that subjects attempted to recollect feature specific information for all items, in addition to monitoring the familiarity of items during JOF trials that further required participation of right PFC regions.

In summary, based on prior imaging literature suggesting a role for the right PFC in retrieval likely devoid of recollective content (Henson et al., 1999, 2000), cognitive research suggesting that JOFs are well modeled as arising from global item familiarity (Hintzman et al., 1982; Hintzman, 1984), and neuropsychological and TMS research demonstrating elevated false alarms with right PFC damage/disruption (Rossi et al., 2001; Curran et al., 1997; Schacter, Alpert, et al., 1996; Schacter, Curran, et al., 1996), we predicted the greater net activity increase observed in the right PFC during the JOF task. This prediction arose because subjects were expected to be heavily reliant upon monitoring item familiarity during testing, given that recollective detail was anticipated to be indistinct with respect to the frequency discrimination. This characterization is most consistent with the systematic/heuristic distinction of PFC contributions to episodic retrieval, and combined with prior research contrasting source and item memory; this indicates that the nature of the contents of memory monitored by each hemisphere is fundamentally different. Under this distinction, subjects may monitor memory for the familiarity of items and/or specific conceptual or qualitative characteristics of what is recovered from memory (i.e., recollective monitoring). Dobbins et al. (2002) previously suggested that left frontopolar and dorsolateral regions might be implicated in such recollective monitoring because although they were involved in source discriminations, they were not active during novelty detection or semantic encoding operations. Whether dorsolateral and frontopolar regions themselves contribute differentially to monitoring operations, however, still remains unclear. The idea that left and right prefrontal regions monitor fundamentally different memory representations is not entirely unexpected given the known differences between the hemispheres in terms of conceptual versus visuoperceptual knowledge processing.

In conclusion, the current results suggest that increasing the precision of retrieval demand does not necessarily result in increases in the left PFC during retrieval attempt. Instead, demanding retrieval tasks can preferentially recruit the right PFC provided the subjects are heavily dependent upon monitoring item familiarity. Furthermore, the contribution of the left PFC, even with pictorial stimuli, seems dependent on subjects using the test items as conceptual retrieval cues in an attempt to recollect additional specific contextual or featural information surrounding previous encounters. This recollection/familiarity monitoring distinction is most consistent with the systematic/heuristic characterization of hemispheric PFC differences during retrieval based on the source-monitoring framework, and both potentially explain the strong degree of left lateralization observed with source compared to item memory tasks (e.g., Dobbins et al., 2002, 2003) while simultaneously predicting the greater involvement of the right PFC with the JOF task observed here. The observed statistical dissociation between left and right dorsolateral and frontopolar PFC regions adds to the increasing evidence that these areas make qualitatively different and important contributions during episodic retrieval attempts that cannot be accommodated within constructs such as task effort, precision, or duration.

METHODS

Subjects

Sixteen right-handed, 18- to 35-year-old, native English-speaking volunteers were paid $50 for participating in the study. Informed consent was obtained in a manner approved by the Human Studies Committee at Massachusetts General Hospital, the Committee on the Use of Humans as Experimental Subjects at MIT, and the Harvard University Committee on the use of Human Subjects in Research.

Study Materials

The stimuli consisted of 360 pairs of color pictures. The picture pairs depicted single man-made or living objects (e.g., umbrella, octopus), with the items in each pair representing perceptually different exemplars of objects with the same name, and have demonstrated a high degree of naming agreement (mean 95%) (Simons, Koutstaal, Prince, Wagner, & Schacter, 2003). Eight different versions of the task were created, which systematically counterbalanced the stimuli between subjects across three factors: study frequency (two or six presentations), test picture format (same or different), and test cue ("two<>six times?" or "same<>different?").

Task Procedures

Stimuli were back projected onto a screen at the rear of the magnet bore and were viewed with a mirror placed above the eyes. The entire experiment consisted of three study/test cycles each using 120 items. During the nonscanned study phases, subjects performed rapid living/nonliving judgments on randomized pictures shown either two or six times for 1200 msec each. Immediately following each study phase, they were scanned while making episodic memory judgments regarding the previously viewed pictures. Subjects received either JOF) ("two<>six times ?") or item memory ("same<>different ?") retrieval cues for each displayed picture. For half of the retrieval trials, the item was identical to that which had been studied, for the remaining half it was the alternate exemplar. Subjects were told that in the case of frequency estimation, if they should detect that the current item was different than that which was studied, that they should ignore this difference and attempt to remember how often they saw an item with that name (e.g., a toaster). During retrieval trials, items remained visible for 3950 msec and subjects were instructed to respond before the items disappeared from the screen. There was a 50-msec ITI between all trials. Interspersed among the retrieval trials were fixation trials varying from 2000 to 6000 msec. The order of retrieval and fixation trials was determined by an optimal sequencing program designed to maximize recovery of the BOLD signal (Dale, Greve, & Burock, 1999).

fMRI Data Acquisition

Scanning was performed on a 3T Siemens Allegra system using a standard whole-head coil. Functional data were acquired using a gradient-echo, echo-planar pulse sequence (TR = 2 sec, TE = 30 msec, 21 axial slices parallel to the AC–PC plane, 3.125 × 3.125 × 5 mm, 1-mm interslice gap). Prior to functional data collection, four dummy volumes were collected and discarded to allow for T1-equilibration effects. High-resolution T1-weighted (MP-RAGE) anatomical images were collected for visualization. Head motion was restricted by using a pillow and foam inserts.

fMRI Data Analysis

Data were preprocessed using SPM99 (Wellcome Department of Cognitive Neurology, London). Slice acquisition timing was corrected by resampling all slices in time relative to the first slice, followed by rigid body motion correction across all runs. Functional data were spatially normalized to an EPI template using a 12-parameter affine and nonlinear cosine basis function transformation. Volumes were resampled into 3-mm cubic voxels and spatially smoothed with an 8-mm FWHM isotropic Gaussian kernel. Each session was grand mean scaled such that the mean signal was 100. The data were statistically analyzed treating subjects as a random effect. For the analyses, volumes were treated as a temporally correlated time series and modeled by convolving a synthetic hemodynamic response function and its first-order time derivative using the onset times for the events. The resulting functions were used as covariates in a general linear model, along with a basis set of cosine functions that were used to high-pass filter the data, and a block covariate representing session effects. The least squares parameter estimates of height of the best fitting synthetic HRF for each condition of interest (averaged across scans) were used in pairwise contrasts and stored as a separate image for each subject. These images were then tested against the null hypothesis of no difference between contrast conditions using one-tailed t tests resulting in repeated measures t tests across subjects. Regions were considered significant and subjected to further analysis if they consisted of five or more contiguous voxels and exceeded an alpha threshold of .001 ($Z > 3.09$, uncorrected) for direct contrasts of retrieval tasks (frequency estimation vs. item memory for correct responses). This threshold has been demonstrated to adequately control for familywise error in similar studies and is comparable to that typically used in fMRI studies of memory enabling meaningful across study comparisons (Donaldson & Buckner, 1999; Buckner et al., 1998). Following this, functional ROIs were extracted using peristimulus time averaging for the event-related fMRI data surviving the retrieval task contrasts. Percent signal averages were obtained for above threshold voxels within an 8 mm radius of each of the SPM-identified maxima for the contrast. The reported ANOVAs on these data used the third time point (6 sec post stimulus onset) and are unbiased with respect to interactions involving hemispheres or item format (same or different).

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