ALTHOUGH numerous neuroimaging studies have examined the functional neuroanatomy supporting episodic memory for verbal material, there have been few investigations of non-verbal episodic encoding and retrieval. We used fMRI to directly compare prefrontal activation elicited by verbal and non-verbal material during encoding and during retrieval. Regardless of the mnemonic operation (encoding/retrieval), inferior prefrontal activation lateralized based on material type. Verbal encoding and retrieval resulted in greater left inferior prefrontal activation, whereas non-verbal encoding and retrieval resulted in greater right inferior prefrontal activation. The similarity between inferior prefrontal activity during encoding and during retrieval indicates that these mnemonic operations depend on shared processes mediated by inferior prefrontal regions. *NeuroReport* 9: 3711–3717 © 1998 Lippincott Williams & Wilkins.

Key words: Declarative memory; Encoding specificity; Episodic memory; Explicit memory; fMRI; Prefrontal cortex; Working memory

Material-specific lateralization of prefrontal activation during episodic encoding and retrieval

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Introduction

Episodic memory is a form of long-term memory that supports the conscious remembrance of everyday experiences.[1] The ability to consciously remember an experience requires its initial encoding into long-term memory and its subsequent retrieval from long-term memory. Episodic encoding and retrieval both depend on multiple component processes. For example, retrieval is thought to include the representation of retrieval cues and products in working memory, the generation and initiation of a retrieval search, the recovery of information from episodic memory, and the evaluation of the relevance of retrieved information to the current task goal.

Functional neuroimaging studies using PET and functional MRI (fMRI) indicate that regions in prefrontal cortex contribute to episodic encoding and retrieval.[2–4] Regions in left inferior prefrontal cortex, including a posterior and dorsal region (Brodmann areas [BA] 44/6) and an anterior and ventral region (BA 47/45), consistently demonstrate greater activation during the performance of encoding tasks yielding higher levels of subsequent memory.[5–7] In contrast, regions in right dorsolateral (BA 46/9) and frontopolar (BA 10) prefrontal cortices, consistently demonstrate greater activation during the performance of retrieval tasks relative to non-retrieval baseline tasks.[2–4,8] This pattern of prefrontal activation led to the proposal of the hemispheric encoding/retrieval asymmetry (HERA) framework, which posits that the functional contributions of prefrontal cortex lateralize based on the nature of the mnemonic operations engaged.[2,9] Left prefrontal regions are posited to be differentially more involved in encoding operations, whereas right prefrontal regions are posited to be differentially more involved in retrieval operations.

Although numerous neuroimaging studies have yielded results consistent with the HERA pattern,[2,9] most of these studies examined either the encoding or the retrieval of verbal stimuli, such as words and pictures of nameable objects. In contrast to verbal episodic memory, considerably less is known about the contributions of specific prefrontal regions to non-verbal episodic memory. The few available studies of non-verbal encoding have revealed a disparate pattern of results, with one study demonstrating involvement of left prefrontal cortices,[10] others demonstrating involvement of right prefrontal cortices,[11–13] and yet others implicating bilateral prefrontal cortices.[14,15] These findings suggest that, relative to verbal encoding, non-verbal encoding may be more dependent on right prefrontal regions. One possibility is that the contributions of specific prefrontal regions to episodic memory depends on

the nature of the material being processed.[12,13,16] To test this hypothesis, direct comparisons between verbal and non-verbal conditions are required. We are aware of only one neuroimaging study that directly compared verbal and non-verbal encoding within the same subjects,[12] and of no study that directly compared verbal and non-verbal retrieval within the same subjects.

The present fMRI study examined prefrontal activation during episodic encoding and retrieval, with the goal of determining whether prefrontal activation lateralizes based on the nature of the target material. Memory processes were examined for two classes of stimuli that differed in their nameability and meaningfulness. One class of stimuli consisted of words, which are easy to verbally label and have pre-experimental meaning. The other class consisted of abstract visual textures, which are difficult to verbally label and lack semantic content (Fig. 1). Importantly, material-specific effects were examined both at the time of stimulus encoding and at the time of retrieval. In the first scan, participants alternated between the intentional encoding of blocks of words and of blocks of textures. In the second scan, participants alternated between the intentional retrieval of blocks of words and of blocks of textures.

Two main outcomes were possible. To the extent that prefrontal mnemonic functions are organized by encoding and retrieval processes and that these processes are similarly engaged regardless of material, we expected little if any activation to be observed in these scans. To the extent that prefrontal mnemonic functions are organized by materials, we expected primarily left prefrontal activation during the word conditions and right prefrontal activation during the texture conditions.

Materials and Methods

Subjects: Subjects were nine right-handed volunteers (six females, three males) from the Stanford University community who participated for $30. All subjects were native speakers of English. Informed consent was obtained from each subject prior to participation in this study, which was approved by the Institutional Review Board at Stanford University.

Materials, design and procedures: Stimuli consisted of 108 abstract, high frequency (mean frequency of $138.7/10^6$)[17] 4–8 letter long (mean length of 6.0) words and 108 chromatic visual textures that were difficult to verbally label (Fig. 1). Stimuli were divided into three 36-item word sets and three 36-item texture sets. From these sets, 144-item experimental lists were created for scanning purposes by combining two word sets and two texture sets. Each experimental list was broken into six cycles that alternated between blocks of 12 words and blocks of 12 textures (the order of conditions – word/texture or texture/word – was counterbalanced across subjects). Each block consisted of six items from one of the three 36-item sets and six items from a different 36-item set. Each subject was presented two experimental lists, one during an encoding scan and another during a retrieval scan. Half of the items encountered during encoding (i.e. items from one 36-item set) reappeared
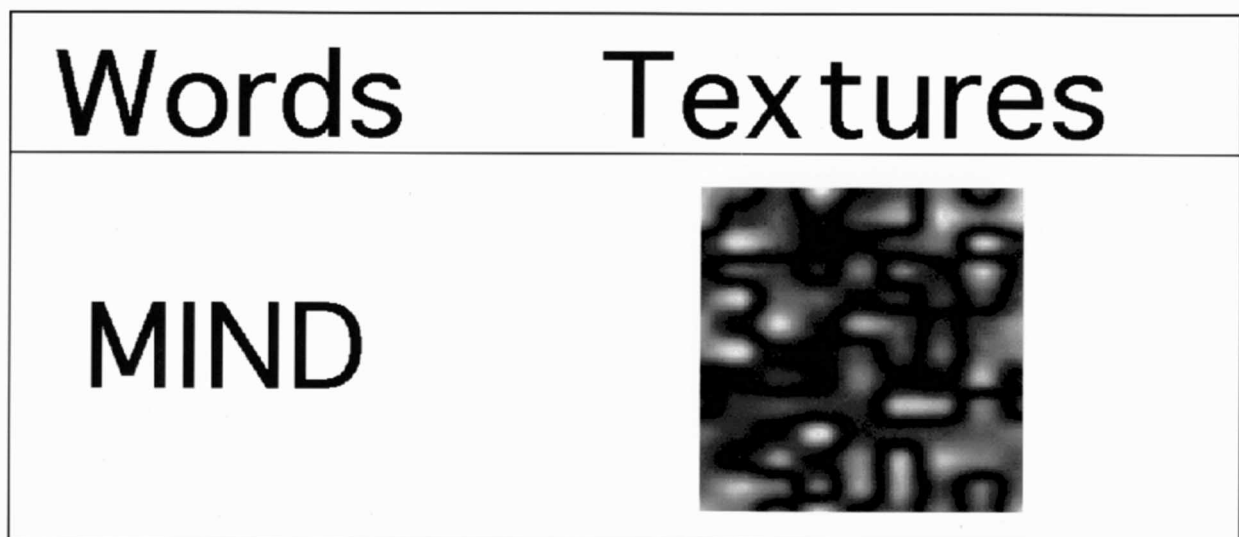

FIG. 1. Example stimuli from the word and texture conditions.

in the retrieval scan as studied items. The other half of the items in the retrieval scan were unstudied (i.e. the items from the 36-item set that did not appear in the encoding list). Across subjects, all items served in the encoding scan, as studied items in the retrieval scan, and as unstudied items in the retrieval scan. Each stimulus was presented for 1500 ms and was followed by a 1250 ms interstimulus interval, yielding a block duration of 33 s.

Subjects participated in one scanning session lasting ~90 min. Across the session, four functional scans were administered, two of which are reported here (the other two embody a separate experiment that will be reported elsewhere). In the encoding scan, subjects were presented an experimental list. For word blocks, subjects were instructed to read each word silently and to try to remember each word for a later memory test. For texture blocks, subjects were instructed to try to remember each texture for a later memory test. In the retrieval scan, subjects were presented a different experimental list. For each stimulus, subjects were instructed to determine whether or not they recognized the item as having been studied in the encoding scan. Subjects pressed a response button using their right index finger when they recognized the test item. Stimuli were generated by a Macintosh computer, back-projected onto a screen located above the subject's neck and viewed via a mirror mounted above the subject's head.

fMRI procedures: Imaging was performed with a 1.5T whole-body GE Signa scanner. A prototype receive-only whole-head coil was used for signal reception. Head movement was minimized using a 'bite-bar' formed with each participant's dental impression. A T2*-sensitive gradient echo spiral sequence was used for functional imaging with parameters of TE = 40 ms, TR = 900 ms, flip angle = 70°, FOV = 36 cm, and in-plane resolution = 2.35 mm. Four spiral interleaves were obtained for each image, for a total acquisition time of 360 ms per image slice (3600 ms per image volume). The experimental presentation program controlled the scanner onset. In each experiment, 10 6 mm thick slices were acquired separately in the coronal plane of the Talairach atlas[18] from the anterior commissure to the frontal pole, with a 1 mm interslice space. Functional images were acquired continuously every 3.6 s over the course of each 396 s experiment, for a total of 110 images per slice. T1-weighted flow-compensated spin-echo anatomy images were acquired for each of the slices imaged in the functional scans.

Functional image processing was performed offline after transferring the raw data to a Sun SparcStation. Raw functional images were motion-corrected in the in-plane dimensions using AIR 3.0,[19] and then spatially filtered in three dimensions using a Gaussian filter (5 mm full width at half-maximum). The data were then analysed using a cross-correlation method. The activity of each pixel was correlated to a reference function obtained by convolving the square wave describing the task alternation with an estimate of the participant's hemodynamic response function.[20] For each scan in the present experiment, the frequency of the square wave describing the task alternation was 0.015152 Hz (six cycles/396 s). These correlation values were then normalized to create a functional image (SPM{Z}). Averaged functional images across the nine subjects were formed by warping the functional images for each participant onto a reference template from the Talairach atlas.[21] Averaged functional activation maps were constructed by selecting pixels whose averaged correlation values exceeded a criterion of $Z \geq 1.96$ or $Z \leq -1.96$ ($p = 0.05$, two-tailed) following application of a median filter of six pixels. Cluster maxima included in the activation tables below exceeded the statistical threshold, contained at least six contiguous significant pixels, and were at least two slices away from the nearest maximum in the same cluster. To assess whether the pattern of activation was similar across the encoding and the retrieval scans, an across-scan statistical analysis was performed by creating a difference Z map that reflects an across-subject average of the paired difference image between the encoding and retrieval SPM{Z} maps for each subject.[22]

Results

Behavioral results: Behavioral data were collected during the recognition scan. Memory for the words and textures was comparable, with recognition accuracy (P_{hits}–$P_{false alarms}$) not differing between word (0.42) and texture (0.41) blocks (F < 1.0). Recognition response latencies were also comparable for the word (856 ms) and texture (878 ms) blocks (F < 1.0).

fMRI results: Table 1 presents the Talairach locations of regions demonstrating an effect of material type during the encoding scan, and Table 2 presents the locations of regions demonstrating an effect of material type during the retrieval scan. Figure 2 presents the averaged functional activation maps for selected slices from the encoding and retrieval scans.

During the encoding scan, left prefrontal regions demonstrated greater activation during the encoding of words relative to textures. These regions included left precentral gyrus bordering the posterior extent of inferior frontal gyrus (BA 6), posterior left inferior frontal gyrus (BA 44), anterior left inferior frontal gyrus (BA 45/47), and left frontal operculum

Table 1. Regions demonstrating differential activation during the encoding of words and textures.

Region	Talairach coordinates			Max Z	BA
	x	y	z		
Words > textures					
L inferior frontal	−53	21	8	3.96	45,47
L frontal operculum/inferior frontal	−37	28	1	3.76	47,45
L precentral	−43	0	49	3.51	6
L frontal operculum	−47	14	0	3.42	47
L inferior frontal	−52	7	18	3.28	44
L superior frontal/pre-SMA	−3	14	57	3.20	6
L inferior frontal	−52	7	7	3.14	44
L middle frontal	−28	14	55	2.83	8,9
L superior frontal	−6	56	21	2.77	9
L middle frontal	−34	42	22	2.72	9
L orbital frontal	13	56	−15	2.67	11
Textures > words					
R inferior frontal	48	28	16	−3.56	45
Anterior cingulate	0	42	10	−3.05	32
Medial frontal	−8	42	−2	−2.97	10,32
R precentral	39	0	34	−2.89	6

Table 2. Regions demonstrating differential activation during the retrieval of words and textures.

Region	Talairach coordinates			Max Z	BA
	x	y	z		
Words > textures					
L inferior frontal/frontal operculum	−46	14	13	5.06	44,47,45
L frontal operculum/inferior frontal	−48	28	−3	4.30	47,45
L precentral	−40	0	39	3.56	6
L superior frontal/pre-SMA	−4	14	53	3.39	6,8
L superior frontal	−13	56	26	3.05	9
L inferior frontal	−48	7	17	2.89	44
Medial frontal	−5	56	−9	2.77	10,11
R orbital frontal	12	56	−2	2.77	10,11
L superior frontal	−17	42	31	2.66	9
R superior frontal	10	63	20	2.66	9,10
R middle frontal	24	49	6	2.63	46,10
L middle frontal	−25	49	2	2.60	10
L superior frontal	−7	49	17	2.60	9
Textures > words					
R precentral/inferior frontal	44	7	23	−3.11	44,6
R inferior frontal	48	28	14	−2.89	45
L inferior frontal	−40	35	9	−2.86	45
R orbital frontal	18	28	−14	−2.66	11

(BA 47/45). In contrast, right prefrontal regions demonstrated greater activation during the encoding of textures relative to the encoding of words. These regions included right precentral gyrus bordering the posterior extent of inferior frontal gyrus (BA 6) and anterior right inferior frontal gyrus (BA 45).

During the retrieval scan, inferior prefrontal activation lateralized in a similar material-specific manner. Left prefrontal regions demonstrating greater activation during the retrieval of words relative to textures included left precentral gyrus bordering the posterior extent of inferior frontal gyrus (BA 6), posterior left inferior frontal gyrus (BA 44), anterior left inferior frontal gyrus (BA 45/47), and left frontal operculum (BA 47/45). Right prefrontal regions demonstrating greater activation during the retrieval of textures relative to words included right precentral and posterior inferior frontal gyri (BA 44/6) and anterior right inferior frontal gyrus (BA 45). In contrast to the encoding scan, there was greater activation during word relative to texture retrieval in frontopolar prefrontal cortex situated bilaterally in the middle frontal gyrus (BA 10/46). However, the across-scan comparison of encoding versus retrieval
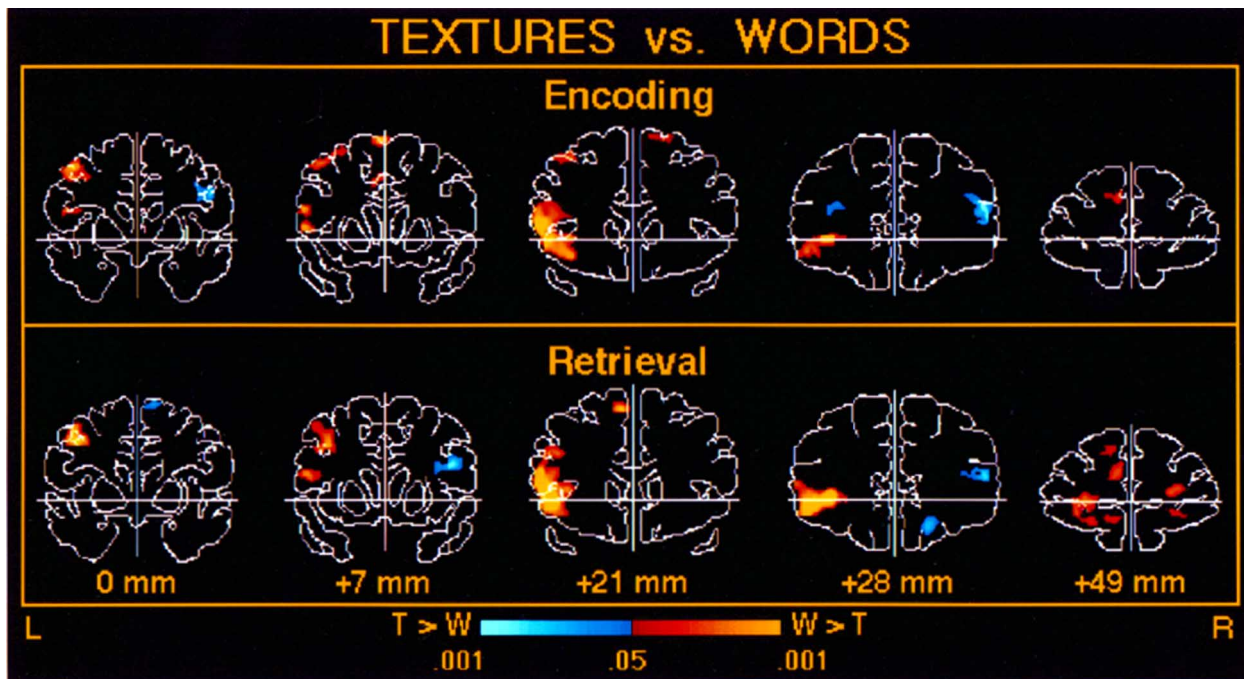
FIG. 2. Composite activation images from five coronal sections. The left side of each image corresponds to the left side of the brain. The upper row displays the data from the encoding scan, the lower row that from the retrieval scan. Each column displays the composite from one section (mm rostral to the anterior commissure indicated at the bottom). All composites reflect Z-scores averaged across all participants. Regions that demonstrated greater activation during the word condition (W > T) are displayed in the red-to-yellow color scale; regions demonstrating greater activation during the texture condition (T > W) are displayed in the blue-to-white color scale. Inferior frontal regions demonstrated a material-specific pattern of lateralization that was similar in the encoding and retrieval scans (first four columns). Bilateral frontopolar prefrontal activation was greater during the retrieval of words relative to textures (fifth column).

did not reveal any reliable differences in the pattern of material-specific activation.

Discussion

The present study revealed a pattern of material-specific activation that was similar during episodic encoding and episodic retrieval. During encoding, left inferior prefrontal cortices (LIPC) were more active for words, whereas right inferior prefrontal cortices (RIPC) were more active for non-verbal visual textures. These material-specific differences likely are not attributable to differences in encoding efficacy because subsequent recognition memory for the words and textures was comparable. During retrieval, a similar pattern of lateralized inferior prefrontal activation based on material type was observed. These material-specific differences cannot be attributable to differences in retrieval success or retrieval effort because recognition accuracy and response latency were comparable for the word and texture conditions. Thus, in contrast to HERA,[2,9] activation in inferior prefrontal cortices was lateralized primarily based on the nature of the material (verbal or non-verbal), rather than the stage of episodic operations (encoding or retrieval). These results are consistent

with neuropsychological demonstrations that left and right frontal lesions differentially impact verbal and non-verbal episodic memory.[16]

The vast majority of prior PET and fMRI studies of episodic memory have examined memory for verbal stimuli, such as words and pictures of everyday objects. Consistent with the present findings, studies of verbal encoding have demonstrated activation in posterior LIPC (BA 44/6), near Broca's area, and in anterior LIPC (BA 47/45).[2–4] The magnitude of encoding activation in these regions has been shown to predict whether or not a verbal experience will be subsequently remembered or forgotten, directly implicating these regions in verbal memory formation.[23] It is important to note, however, that LIPC activation has also been noted in previous studies of verbal episodic retrieval.[8,24] The present results provide strong evidence that the same LIPC regions engaged during verbal encoding are also engaged during verbal retrieval.

Posterior LIPC and anterior LIPC activations have been posited to reflect the processing of phonological and semantic stimulus characteristics, respectively.[4,8,25,26] Posterior LIPC may mediate phonological working memory processes such as the retrieval and maintenance of lexical and phono-

logical aspects of stimuli,[27] whereas anterior LIPC may mediate semantic working memory processes such as the retrieval, maintenance, or evaluation of semantic knowledge that is represented elsewhere in cortex.[2,5–7,28] Phonological and semantic working memory processes appear to be recruited in the service of both verbal encoding and retrieval.

Although considerably less is known about non-verbal encoding and retrieval, the few studies to date provide convergent evidence that regions in RIPC contribute to non-verbal episodic memory. Consistent with the present results, material-specific lateralized prefrontal activation was noted in a study directly comparing word and face encoding: posterior LIPC was active during word encoding but not face encoding, whereas posterior RIPC was active during face encoding but not word encoding.[12] Similarly, posterior right prefrontal activation was noted during the learning of pairs of non-verbal visual patterns and sounds relative to when these pattern-sound pairings were over-learned.[13] Finally, the magnitude of encoding activation in RIPC has been shown to predict whether or not complex visual scenes will be subsequently remembered or forgotten, directly implicating RIPC in non-verbal memory encoding.[11] The present findings provide strong evidence that the same RIPC regions are recruited both during non-verbal encoding and retrieval. RIPC regions may subserve visuo-spatial working memory processes that mediate the maintenance of visual, icon-like representations of visual stimuli and of the position of stimuli in visual space.[29,30] Visuo-spatial working memory processes appear to be recruited in the service of both non-verbal encoding and retrieval.

The similarity between the inferior prefrontal regions engaged during encoding and those engaged during retrieval indicates that these mnemonic operations recruit the same material or content-specific working memory processes. This overlap in component processes provides a potential neural mechanism for the encoding specificity effect. Behavioral studies have demonstrated an interdependence between encoding and retrieval operations, such that retrieval will be more successful when the conditions of encoding and retrieval are most similar:[31,32] "In its broadest form the [encoding specificity] principle asserts that only that can be retrieved that has been stored, and that how it can be retrieved depends on how it was stored" (p.359).[31] The present results suggest that how information is stored and how it is retrieved jointly depend on processes mediated by specific inferior prefrontal regions. Depending on the content of an experience, both encoding and retrieval appear to be associated with phonological coding, semantic retrieval and evaluation, and attention to visuo-spatial characteristics. Future research is neces-

sary to determine whether retrieval is most successful when the overlap in prefrontal activation during encoding and retrieval is maximal.

The present study directly compared verbal and non-verbal memory processes, and therefore cannot reveal encoding and retrieval operations common to both verbal and non-verbal material. There have been a few reports of left[10] or bilateral[14,15] prefrontal activation during non-verbal encoding relative to control conditions suggesting that the encoding of non-verbal material may sometimes depend on the same left prefrontal operations engaged during verbal retrieval. Although at present the specific factors determining whether LIPC regions are also engaged during the encoding of non-verbal material are not known, there appears to be at least one possible source of this across-study variability: under some conditions, subjects may attempt to verbally label stimuli that on the surface appear to be difficult to label. For example, although difficult, it is conceivable that subjects may have phonologically coded the abstract visual objects used in the study by Schacter and colleagues.[15] Similarly, it is conceivable that phonological and semantic processes may be recruited during face encoding.[10] However, the extent to which subjects engage these processes when presented with faces may depend on the particular task design.[12,29] Future studies that parametrically vary the extent to which complex visual stimuli can be verbally processed or that use behavioral techniques (e.g. articulatory suppression) to assess the contributions of verbal processes during non-verbal encoding may serve to resolve this issue.

The present results provide some additional insights regarding the functional properties of frontopolar prefrontal cortices. As first highlighted by Tulving and colleagues,[9] prior studies of episodic retrieval have consistently demonstrated that right or bilateral frontopolar prefrontal cortices (BA 10) are active during verbal and non-verbal episodic retrieval.[2–4] These activations have been interpreted as reflecting the strategic evaluation of the products of retrieval to determine whether the retrieved information is from the target context.[2–4,24,33] In the present study, bilateral frontopolar prefrontal cortices were more active during verbal relative to non-verbal retrieval. Although interpretative caution may be warranted as the across-scan comparison failed to demonstrate that this effect was selective to retrieval, the presence of this pattern during retrieval is suggestive. This effect may stem from differences across material type in the pre-experimental familiarity of the targets and foils at test. The verbal stimuli used in the present study were high frequency words, and thus had high pre-experimental familiarity. In contrast, the textures were novel abstract visual patterns,

and thus had low pre-experimental familiarity. During non-verbal recognition, subjects may have been able to discriminate studied from unstudied textures based on differential familiarity because the studied textures would have been familiar and the unstudied textures completely unfamiliar. In contrast, in the verbal retrieval condition both the studied and unstudied words were familiar. Consequently, subjects may have had to make more specific memory judgements based on attribution of source or recollection of more specific item information. Thus, the differential frontopolar prefrontal activation during retrieval may not reflect the direct effects of verbal versus visuo-spatial processing, as is thought for inferior prefrontal regions. Rather, this effect may reflect the demands of contextual evaluation in deciding whether a well known, frequently encountered stimulus occurred in a particular study episode.

Conclusion

Few neuroimaging studies have examined episodic memory for non-verbal material. Through the direct comparison of verbal and non-verbal episodic memory, the present study provides strong evidence that episodic encoding and episodic retrieval depend on shared processes that are mediated by left and right prefrontal cortices. The specific inferior prefrontal regions recruited during encoding and retrieval depend on the type of material being processed, with LIPC regions mediating verbal encoding and retrieval and RIPC regions mediating non-verbal encoding and retrieval. The present results also suggest that the extent of engagement of bilateral frontopolar prefrontal regions, regions which are thought to mediate evaluative retrieval processes, depends on the demands of the particular retrieval context. Additional studies that include a low-level baseline are necessary to determine regions mediating both verbal and non-verbal episodic memory.

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