Conjunction Analysis of Cortical Activations Common to Encoding and Retrieval

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KEY WORDS spatial memory; positron emission tomography (PET); overlap; parietal cortex; episodic encoding; episodic retrieval

ABSTRACT The notion of overlap between encoding and retrieval processes is central in cognitive theories of episodic memory, but to date most functional neuroimaging studies have emphasized differences between these processes. In the present study, overlap between encoding and retrieval processes was investigated by analyzing data from a positron emission tomography (PET) study of encoding and retrieval of different kinds of event information. Using a conjunction analysis, we specifically aimed at identifying overlap in activation patterns for encoding and retrieval of three classes of event information: item, temporal, and spatial. It was found that both encoding and retrieval of spatial information activated posterior parietal areas bilaterally. In addition, item encoding and retrieval were associated with increased activity in the right temporal pole, and temporal encoding and retrieval with left inferior frontal and left inferior temporal regions. These findings suggest that when specific episodic information is retrieved from memory, regions involved in encoding of the same information are engaged. *Microsc. Res. Tech. 51: 39–44, 2000.*

INTRODUCTION

The development of functional neuroimaging techniques like positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) has made it possible to measure whole-brain activity while subjects are performing various mental operations. Although the specifics differ, both PET and fMRI are hemodynamic techniques; they estimate brain activity by measuring blood flow changes (see Buckner and Logan, in press). During recent years, PET and fMRI have been used extensively to study the functional neuroanatomy of many different cognitive functions (for a recent review, see Cabeza and Nyberg, 2000). In the present report we are concerned with PET studies of episodic memory.

Episodic memory refers to memory for personally experienced events (Tulving, 1983). It is recognized that episodic memory consists of many different subprocesses, and a major distinction can be made between encoding (acquisition) and retrieval processes. Cognitive theories of episodic memory hold that a match between encoding and retrieval is crucial for successful memory performance. One example is the encoding specificity principle proposed by Tulving and Thomson (1973). According to this principle, effective cues at retrieval are those that were associated with the target information at encoding. Another example is the transfer appropriate processing account (Morris et al., 1977), which states that the similarities between processing at encoding and test determine memory performance. In a similar way, Craik (1983) has hypothesized that retrieval operations represents an attempt to recapitulate the initial perceptual processes activated at encoding.

Craik et al. (1996) pointed out that the overlap between encoding and retrieval at the cognitive level should translate into overlap at the neural level. To date, however, functional imaging studies have highlighted differences rather than similarities between neural correlates of encoding and retrieval. One example of this is the hemispheric encoding/retrieval asymmetry (HERA) model proposed by Tulving and colleagues (Nyberg et al., 1996a; Tulving et al., 1994). The HERA model states that the left prefrontal cortex is differentially more involved in semantic memory retrieval and episodic memory encoding than is the right prefrontal cortex. By contrast, right prefrontal cortex is differentially more involved in episodic retrieval than is the left prefrontal cortex. Another example is the hippocampal encoding/retrieval (HIPER) model (Lepage et al., 1998). The HIPER model summarises PET data showing that encoding activations tend to be located in rostral parts of the medial-temporal lobes, whereas retrieval activations tend to occupy caudal parts of the medial temporal lobes (for further discussion of the HIPER model, see Schacter and Wagner, 1999).

Taken together, although there are some exceptions (e.g., Grasby et al., 1993; McDermott et al., 1999; Nyberg et al., 1996b), the majority of functional neuroimaging studies published to date have focused on differences rather than similarities between episodic encoding and retrieval. By contrast, in the present study we explicitly address the issue of whether encoding and

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Received 30 November 1999; accepted in revised form 3 April 2000

retrieval of spatial location activate specific overlapping regions. The processing of spatial information is known to activate regions in the dorsal visual processing stream (see Ungerleider and Haxby, 1994), notably parietal cortical regions (Köhler et al. 1995). On the basis of these prior studies, we predicted that overlap in activation patterns would be observed in parietal cortex. In addition to spatial information, two other classes of event information were examined: item and temporal information. We had no anatomical predictions for the site(s) of overlap for these classes of information, but we expected that encoding-retrieval overlap in activity would be a general feature regardless of the type of event information.

MATERIALS AND METHODS

The basis for the present report is a re-analysis of data from a study reported by Nyberg and colleagues (1996b). Of main interest was data from three encoding conditions and three retrieval conditions. During the encoding conditions, single words were presented either at the left or at the right side of a computer screen in two different study lists. In the item encoding condition, subjects were instructed to remember the words for a subsequent test (they did not have to remember on which side or in which list the words appeared). In the location encoding condition, subjects were instructed to try to remember the words and their spatial location (left/right). In the temporal encoding condition, subjects were instructed to try to remember the words and their temporal appearance (list 1/list 2). Each encoding condition was followed by a retrieval condition. During these conditions, words were presented at the center of a computer screen. The subjects were instructed to determine if the words had been presented before (item retrieval), if they had been presented on the left or right side of the computer screen (spatial retrieval), or if the words appeared in the first or second study list (temporal retrieval). For further procedural details see Nyberg et al. (1996b).

PET was used to monitor regional cerebral blood flow (rCBF) in 12 subjects while they performed these six conditions (and two additional conditions not discussed here). Image analysis was performed using the statistical parametric mapping (SPM) software (Friston et al., 1995). All statistical analyses were carried out using SPM for windows. The PET scanning procedure and image analyses are described in more detail in Nyberg et al. (1996b).

In the original report, separate analyses were conducted for the different encoding and retrieval conditions. That is, each of the encoding conditions was contrasted with the other two. These analyses revealed that encoding of spatial location activated a region in the right inferior parietal cortex when compared to encoding of item and temporal information, and that retrieval of spatial information activated a region in left middle frontal gyrus when compared with retrieval of item and temporal information. Encoding of item information compared to location and temporal information was associated with activity in left hippocampus, and retrieval of item information compared to location and temporal information was associated with right middle temporal and right inferior frontal activation. Finally, encoding of temporal information compared to item and location information revealed increased activity in left fusiform gyrus, and retrieval of temporal information compared to item and location information revealed increased activity in anterior cingulate gyrus. Thus, these analyses provided no support for overlap in activation patterns for encoding and retrieval of different kinds of event information. Here our strategy for data-analysis was to maximize our chances for finding encoding-retrieval overlap.

The traditional way of analyzing neuroimaging data, the subtraction method, is a method in which two tasks are designed in such a way that they only differ in the components of interest. These two tasks are then contrasted so that the brain regions associated with the components of interest are isolated. Here, a cognitive conjunction analysis (Price and Friston, 1997) was used to reveal common areas of activation in three pair of contrasts involving: (1) spatial information (encoding and retrieval), (2) temporal information (encoding and retriaval), and (3) item information (encoding and retrieval). Cognitive conjunction studies are designed such that a pair of contrasts share a processing difference, and regions that are differentially activated in one of the two contrasts are excluded. Instead, this method for data analysis identify regions that are activated in *both* contrasts. By identifying overlapping activation patterns, it is possible to associate these with a shared processing component, in this case processing of specific (material-dependent) event information.

RESULTS

Voxels were considered as significantly activated if they passed a height threshold of $Z = 2.58$ ($P < 0.005$, uncorrected for multiple comparisons) and belonged to a cluster of at least 100 activated voxels. In line with our expectations, the conjunction analysis revealed that encoding and retrieval of spatial information, compared to encoding and retrieval of item and temporal information, differentially activated regions in bilateral inferior parietal cortex (Fig. 1). No other significant activations were found. The specific location of the peak activations, according to the atlas of Talairach and Tournoux (1988), was [x,y,z = −34, −46, 20] in the left hemisphere and [x,y,z = 46, −24, 24] in the right hemisphere, Brodmann area (BA) 39/40 in both hemispheres. Increased activity in right inferior temporal cortex [x,y,z = 44, 10, −36], BA 38, was observed when item encoding and retrieval was compared to encoding and retrieval of spatial and temporal information. Temporal encoding and retrieval compared to encoding and retrieval of item and spatial information was associated with increased activity in left inferior temporal cortex [x,y,z = −48, 28, −28], BA 21/38, and left inferior frontal cortex [x,y,x = −20, 56, 4], BA 10 (Fig. 1).

DISCUSSION

Based on predictions from cognitive theories, this study aimed at investigating whether some brain regions are activated during *both* encoding and retrieval of specific event information. The results from analyses of three different classes of event information—item, spatial, and temporal—provide support for overlap in activation patterns. Importantly, overlap was not observed in the same areas for all three event classes.

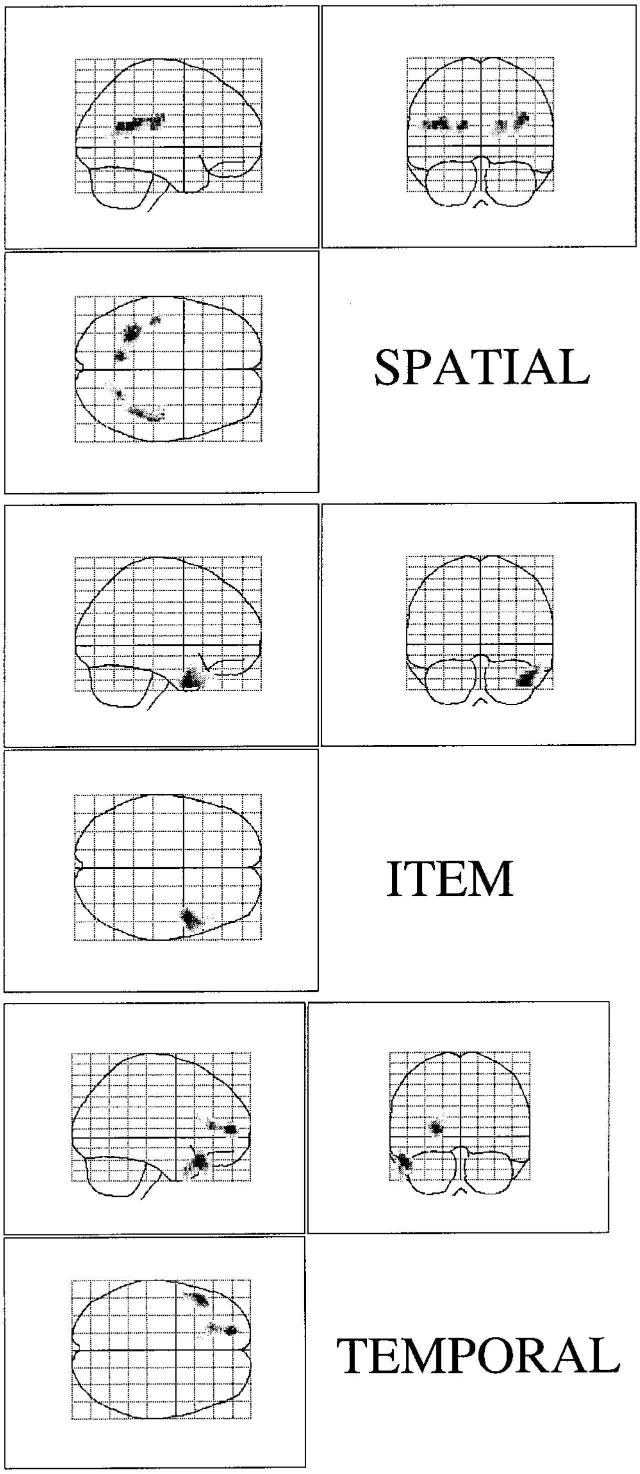

Fig. 1. Statistical parametric maps (SPM) of brain regions that show increased activation in the conjunction analyses for encoding and retrieval of (**a**) spatial, (**b**) item, and (**c**) temporal information. The peaks of activations are plotted onto glass-brain projections of the brain in standardized space (Talairach and Tournoux, 1988), viewed from the right (sagittal view), from the back (coronal view), and from the top (transverse view). The images were thresholded at 0.005 (uncorrected). Darkness in center of highlighted images indicates stronger activity. (Note: color version of artwork is available online.)

Rather, our findings appear to indicate that encoding-retrieval overlap in brain activity is material-specific.

Information about spatial location was associated with bilateral posterior parietal activation during both encoding and retrieval. This is in line with previous neuroimaging studies that have provided evidence for posterior parietal cortex as a key region in various kinds of spatial processing. The bilateral activation as well as the specific site of parietal activation deserves comment. For the purpose of this discussion, we have summarized results from several studies investigating spatial cognition that have obtained posterior parietal activations (Table 1). For each study, the target and reference tasks are indicated along with Brodmann's area designations and right/left hemisphere location.

In line with our observations, a few previously observed activations were bilateral (Courtney et al. 1996; Haxby et al., 1994; Lacquaniti et al., 1997), but there is a strong tendency for activations in BA 40 to be right lateralized (see Table 1). Specifically, of the 18 listed activations, 4 were located in the left hemisphere (3 of these were bilateral) and 14 in the right. This indicates a special role for right parietal area 40 in spatial processing, which is in agreement with previous suggestions based on neuroimaging (Corbetta et al., 1993; Moscovitch et al., 1995) and lesion (Pigott and Milner, 1993; Smith and Milner, 1981) studies. For example, the great majority of studies investigating spatial neglect and topographic disorientation have found right-sided parietal lesions to be more critical for these types of tasks than left-sided lesions (for a review, see Aguirre and D'Esposito, 1999).

Turning to the specific site of activation, our parietal activations were located in inferior rather than superior portions of the parietal lobes. This can be related to the suggestion by Milner and Goodale (1995) of a functional division within the parietal lobes. By their view, the parietal cortex is divided between spatial cognition and spatial visuo-motor control. Inferior parts of the parietal cortex are specifically involved in spatial cognition, whereas superior parts of the parietal cortex are more associated with visuo-motor control. In contrast, several studies investigating spatial cognition have found superior parietal activations (e.g., Aguirre and D'Esposito, 1997; Corbetta et al., 1995; Moscovitch et al., 1995). These latter studies question the validity of a functional division between superior and inferior parietal regions as related to spatial cognition and visuo-motor control. Similarly, the summary in Table 1 provides no support for such a division (nine of the studies investigating spatial cognition reported inferior activation and seven reported superior activation). This distributed nature of parietal activations raises the problem of specifying the relative contribution of each region to spatial memory, and makes it difficult to draw any general conclusions about a functional division within the parietal cortex.

We also found encoding-retrieval overlap in brain activation when item and temporal information were investigated. During encoding as well as retrieval of temporal information, left inferior temporal and left inferior frontal cortex were differentially activated. The finding of overlap in frontal cortex for temporal information is especially interesting to note in light of results from patients' studies. In a series of studies,

TABLE 1. Studies with parietal activations related to spatial processing

		Talairach coordinates (xyz)			
Study	Contrasts	R/L	BA 7	R/L	BA 40
Episodic retrieval					
Köhler et al. (1998)	Spatial processing > object processing			R	52, −48, 32
Moscovitch et al. (1995)	Object location—perceptual matching			R	22, −64, 32
				R	28, −50, 48
Johnsrude et al. (1999)	Object location—visuomotor control	L	−28, −62, 41		
		R	35, −66, 44		
Episodic encoding					
Aguirre et al. (1997)	Position—appearance	L	−34, −52, 60	R	38, −48, 49
Maguire et al. (1998)	Explore virtual environment—view image	L	−22, −64, 48		
Maguire et al. (1996)	Navigation—non-navigation	R	18, −68, 36		
Owen et al. (1996)	Object location—object features	L	−29, −78, 33	R	13, −64, 48
Perception					
Haxby et al. (1994)	Location matching—face matching	R	10, −58, 44	R	32, −38, 36
		L	−16, −64, 48	L	−36, −44, 36
Attention					
Coull and Nobre (1998) (PET)	Spatial orientation—rest			R	62, −46, 32
Coull and Nobre (1998) (fMRI)	Spatial orientation—rest			R	48, −48, 20
Corbetta et al. (1993)	Spatial attention—central detection			R	23, −33, 46
Corbetta et al. (1995)	Spatial search—rest	R	33, −69, 50		
		L	−27, −59, 56		
Lacquaniti et al. (1997)	Point to spatial targets—visual detection	R	22, −52, 52	L	−28, −34, 24
				R	24, −38, 32
Gitelman et al. (1999)	Spatial detection—central detection	L	−21, −60, 57		
		R	27, −68, 57		
		L	−6, −60, 57		
		R	3, −54, 57		
Corbetta et al. (1998)	Spatial attention—fixation	R	25, −59, 56		
		L	−25, −55, 50		
Imagery					
Ghaem et al. (1997)	Imagery navigation—rest	L	−14, −70, 36		
Mellet et al. (1996)	Spatial mental imagery—rest			R	42, −46, 40
Working memory					
Jonides et al. (1993)	Spatial memory—perception			R	42, −40, 36
Courtney et al. (1996)	Location memory—face memory			R	42, −31, 40
				L	−44, −32, 40
		R	8, −60, 44		
		L	−14, −64, 44		

Milner and colleagues have shown that patients with frontal-lobe lesions are impaired in tasks involving memory for temporal order of events (McAndrews and Milner, 1991; Milner et al., 1991, 1971). Evidence for such an impairment has been obtained using a relative-recency discrimination task, where subjects are presented a long series of items sequentially and then asked to decide which of two test items appeared more recently. It has been shown that patients with frontal lobe lesions can perform as well as controls in discriminating between old and new test items, but their performance on recency discrimination is severely impaired. Therefore, it has been suggested that frontal lobe damage might interfere with encoding and retrieval of "time-tags," which are hypothesized to be imbedded in the memory for experienced events (Milner, 1971; Yntema and Trask, 1963). Regarding laterality, it has been proposed that right frontal lesions mainly impair temporal order for non-verbal material whereas left frontal lesions impair temporal-order memory for verbal material (Corsi et al., cited in Milner et al., 1991). In agreement with patient studies, a PET study by Cabeza et al. (1997) found bilateral dorsal frontal regions to be activated when subjects retrieved temporal-order information. Moreover, in our original report, temporal retrieval was associated with midline frontal activation (Nyberg et al., 1996b). These lesion and imaging results point to a specific role for frontal regions in memory for temporal event information.

Encoding and retrieval of item information was associated with increased activity in right temporal pole regions. Given that item information was present also in the spatial and temporal conditions, our finding of differential regional activation in the item condition may seem surprising. It should be noted, though, that subjects were informed that all items had been studied in the spatial and temporal retrieval conditions. Hence, the item condition, but not the spatial and temporal conditions, required the subjects to judge whether items had been presented earlier. Anterior temporal activations have been reported in a few other studies investigating retrieval of item information (Cabeza et al., 1997; Nyberg et al., 1996b), suggesting that this region is associated with memory for item-specific information. Moreover, a study by Nyberg et al. (1996c) identified left temporal pole as a brain region critically involved in higher levels of retrieval success. In line with these findings, Markowitsch (1995) has suggested that the (right) temporal pole region works in concert with (right) frontal regions during retrieval of episodic information. Here we obtained evidence for involvement of the right temporal pole during not only retrieval but also during encoding of item information.

The present finding of material-specific encoding-retrieval overlap in brain activation can be related to two findings in the original report by Nyberg and colleagues (Nyberg et al., 1996b). First, it was found that the encoding and retrieval conditions, across type of information (item, spatial, temporal), activated several common regions relative to a baseline reading condition. These regions were mainly located in bilateral prefrontal, anterior cingulate, and bilateral insular cortices, possibly reflecting increased demands on top-down/attentional operations in the encoding and retrieval conditions. Second, it was found that encoding, regardless of type of information (item, spatial, temporal), activated regions in left prefrontal and fusiform cortices. Retrieval, irrespective of what was retrieved (item, spatial, temporal information) activated right prefrontal and midbrain regions. These activation responses were seen as reflecting the operation of general (material-independent) encoding and retrieval networks. Together with the present findings, these previous analyses indicate the operation of several episodic memory networks with different characteristics: (1) a process- (encoding/retrieval) and material-independent episodic memory network (encoding and retrieval vs. baseline); (2) a process-dependent and material-independent network (encoding vs. retrieval across types of information); and (3) a process-independent and material-dependent network (material-specific activations across encoding and retrieval). Thus, the overlap response studied here is only one aspect of the neural machinery that is operating during episodic encoding and retrieval, but we believe it is a most crucial aspect.

In conclusion, the present study provides evidence that when specific event information is recovered from memory, regions involved in the initial processing of this event information are engaged. This raises the possibility that retrieval activation reflects recruitment of the sites were memory for specific event information is being represented. If true, this would provide support for the view that long-term memory representation of information involves the same brain regions as those involved when the information originally was experienced (see Squire et al., 1993).

ACKNOWLEDGMENTS

This work was supported by a grant from HSFR Sweden to L.N.

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