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Cognitive Brain Research 13 (2002) 261–265

COGNITIVE BRAIN RESEARCH

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Short communication

Relating semantic and episodic memory systems

Vinod Menon[a,b,c,*], Jesse M. Boyett-Anderson[a], Alan F. Schatzberg[a,b,c], Allan L. Reiss[a,b,c]

[a]Department of Psychiatry & Behavioral Sciences, 401 Quarry Road, Stanford University School of Medicine, Stanford, CA 94305-5719, USA

[b]Program in Neuroscience, Stanford University School of Medicine, Stanford, CA 94305, USA

[c]Stanford Brain Research Center, Stanford University School of Medicine, Stanford, CA 94305, USA

Accepted 5 November 2001

Abstract

Episodic and semantic memory are two forms of declarative memory which appear to function in distinct yet interdependent ways. Here we provide direct evidence for a functional relationship between these two memory systems by showing that left lateral temporal lobe regions involved in semantic memory play an important role in accurate episodic memory retrieval.

Theme: Neural basis of behavior

Topic: Learning and memory: systems and functions

Keywords: Episodic memory; Semantic memory; fMRI; Temporal lobe; Hippocampus

Declarative memory involves the encoding, storage and recollection of knowledge under conscious control [22]. In 1972, Tulving described two forms of declarative memory — episodic memory that deals with specific, personally experienced events, and semantic memory that deals with a relatively permanent store of general world knowledge that accrues over the years and is not tied to specific events [22,25]. It is now well-established that episodic memory for events and words encoded during semantic categorization (deep encoding) exceeds recognition memory for events and words encoded during non-semantic episodic (shallow encoding) [1,5]. Thus, words encoded while a subject assigns each word to a semantically defined category; e.g. living vs. non-living, are remembered much better than words encoded while subjects discriminate between surface features; e.g. capitalization of the words. These behavioral findings suggest a close relationship between semantic and episodic memory [6].

The relationship between the neural systems subserving semantic and episodic memory is poorly understood, as brain imaging and lesion studies have focused on dissociating brain areas involved in these two forms of declarative memory. These studies have shown that medial temporal lobe (MTL) structures, particularly the hippocampus, are involved in episodic memory [4], that the left lateral temporal lobe (LTL) is involved in semantic memory [7], and that the left inferior frontal cortex plays a key role in both memory systems [4,7]. In this study, we investigated the relationship between episodic and semantic memory systems by examining the correlation between brain activation and accurate memory performance during episodic retrieval of words that had been encoded during a semantic categorization task.

Twelve healthy, right-handed subjects (five males) aged 18–48 years (mean age=26) participated in the study after giving informed consent. Each subject performed both encoding and retrieval tasks in the MRI scanner. These tasks were separated by a distracter task lasting 5 to 10 min. During both the encoding and retrieval tasks, nouns were visually presented to subjects in a blocked fMRI paradigm with alternating experimental and control conditions. In the experimental condition of the encoding task, subjects were instructed to remember 40 unique nouns while assigning each one to a semantic category (living or non-living). In the experimental condition of the retrieval task, subjects made old/new recognition memory judgments on 48 words (32 previously seen, old, words; and 16 new words) by pressing two different keys. In the control

*Corresponding author. Tel.: +1-650-498-6737; fax: +1-520-244-6474.

E-mail address: menon@stanford.edu (V. Menon).

0926-6410/02/$ – see front matter
PII: S0926-6410(01)00120-3

condition for both the encoding and retrieval tasks, subjects responded with alternating key presses while viewing two alternating nouns. Each word was presented for 2.5 s with a 0.5-s inter-stimulus interval. fMRI data were acquired using a 3T GE scanner and a spiral pulse sequence [9].

fMRI data were analyzed using techniques implemented in SPM99 (Wellcome Department of Cognitive Neurology), including motion correction, spatial normalization, and spatial smoothing (FWHM=4 mm) [26]. For each subject, brain regions that showed increased activity during correct memory retrieval were determined using linear regression and a covariate derived from behavioral performance. To construct the behavioral covariate of interest, each temporal frame was assigned one of three values: $\alpha=1/$(number of correct responses) if the image was acquired during a correct response, $\beta=-1/$(number of incorrect responses) if the image was acquired during an incorrect response and 0 for all other time points. The choice of α and β was based on the need to have the covariate sum to zero, thereby preventing any confounding effects of task by covariate interaction. Note that this also results in equal levels of weighting for the correct and incorrect responses, irrespective of the number of actual correct and incorrect responses. Contrast images reflecting brain activation correlated with this covariate were determined for each subject. A random effects model [10] was then used to determine precise brain areas that showed significant group activation. Overall brain activation related to encoding and retrieval was also determined for each subject by contrasting the respective experimental and control conditions. Group activation during encoding and retrieval was then examined using a random effects model. Significant clusters of activation were determined using the joint expected probability distribution of height and extent of Z scores [16], with height ($Z>1.96$; $P<0.05$) and extent threshold ($P<0.05$). Consistent with other related studies, hippocampal activations are reported without extent corrections [17,24].

Subjects performed both the retrieval and the encoding task with a high degree of accuracy (Table 1). During encoding, accuracy in the semantic categorization task was greater than 90% and reaction times (RT) for living vs. non-living judgments were significantly different ($t(11)=2.47$; $P=0.03$). In the retrieval task, accuracy was not significantly different for previously studied and novel words ($t(11)=-1.328$; $P>0.05$). ANOVA of RT with factors 'studied' (studied, novel) and 'accuracy' (correct, incorrect) revealed a significant main effect of accuracy on RT (correct RT<incorrect RT; $F(1,11)=30.682$; $P=0.00018$). There was no interaction between studied words and accuracy ($F(1,11)=0.466$; $P=0.51$) and no main effect of studied versus novel words ($F(1,11)=3.699$; $P=0.081$). The comparable RTs for correctly identified previously studied and novel words suggest that common mechanisms may be involved in the processing of both.

During the encoding task, significant activation clusters were detected in the left middle frontal gyrus (MFG) extending into the inferior frontal gyrus (IFG) (BA 9/45/47; Talaraich coordinates: −40, 14, 28), left MFG (BA 8; −40, 22, 50), left superior frontal gyrus (BA 6; −24, −8, 64), right IFG (BA 47; 28, 28, −2), left LTL (BA 22; −62, −22, 2), right cerebellum (30, −70, −16) together with right fusiform/lingual gyrus (BA 18; 18, −88, −14), left cerebellum/vermis (−6, −60, −16) (Fig. 1, top row) as well as the left (−30, −12, −18) and right hippocampus (34, −12, −16) (Fig. 2, left panel). During the retrieval task, when performance was not considered, significant activation clusters were detected in the left IFG (BA 47; −28, 24, −4), left MFG/IFG extending into the anterior cingulate cortex (BA 9/44/24; −36, 12, 28), right IFG (BA 44; 56, 16, 24 and BA 47; 36, 20, −10), left supramarginal gyrus (BA 40; −34, −46, 42), right putamen and caudate (16, 10, 2), right cerebellum (36, −74, −18) together with right fusiform/lingual gyrus (BA 18; 28, −90, −6) and vermis (−2, −62, −40) (Fig. 1, middle row) as well as the right hippocampus (26, −4, 22) (Fig. 2, right panel). During retrieval, brain activation related to accurate memory performance was observed in the left LTL (Fig. 1, bottom row), with peak activation in the middle temporal gyrus (BA 21 and 22; −50, −38, −4) extending into the superior and inferior temporal gyri. No activation clusters were detected in the prefrontal cortex, hippocampus, or other MTL structures. No brain regions showed negative correlations with behavioral performance.

Although the hippocampus and the prefrontal cortex showed significant activation during both the encoding and retrieval tasks, no significant performance-related activation was detected in these regions during retrieval. This may be due to several factors. These regions may be involved in (1) retrieval effort rather than success; (2) re-encoding of previously seen words; or (3) encoding of novel words. Both veridical and illusory recognition are known to activate the hippocampus and the prefrontal cortex [18]. Nyberg et al. [14] have suggested that activation in the hippocampus increases with retrieval

Table 1
Subjects performed both tasks with a high degree of accuracy. Retrieval accuracy did not differ significantly between previously studied and novel words. Reaction times for correct and incorrect choices during retrieval were significantly different. There were no significant interactions between either accuracy or reaction time and the studied/non-studied-dichotomy

	Total	Previously studied	Novel
Encoding			
Accuracy	95%±4%		
Retrieval			
Accuracy	85%±9%	87%±7%	81%±10%
Reaction times			
Correct	1107±145	1072±144	1142±143
Incorrect	1409±338	1323±195	1495±429

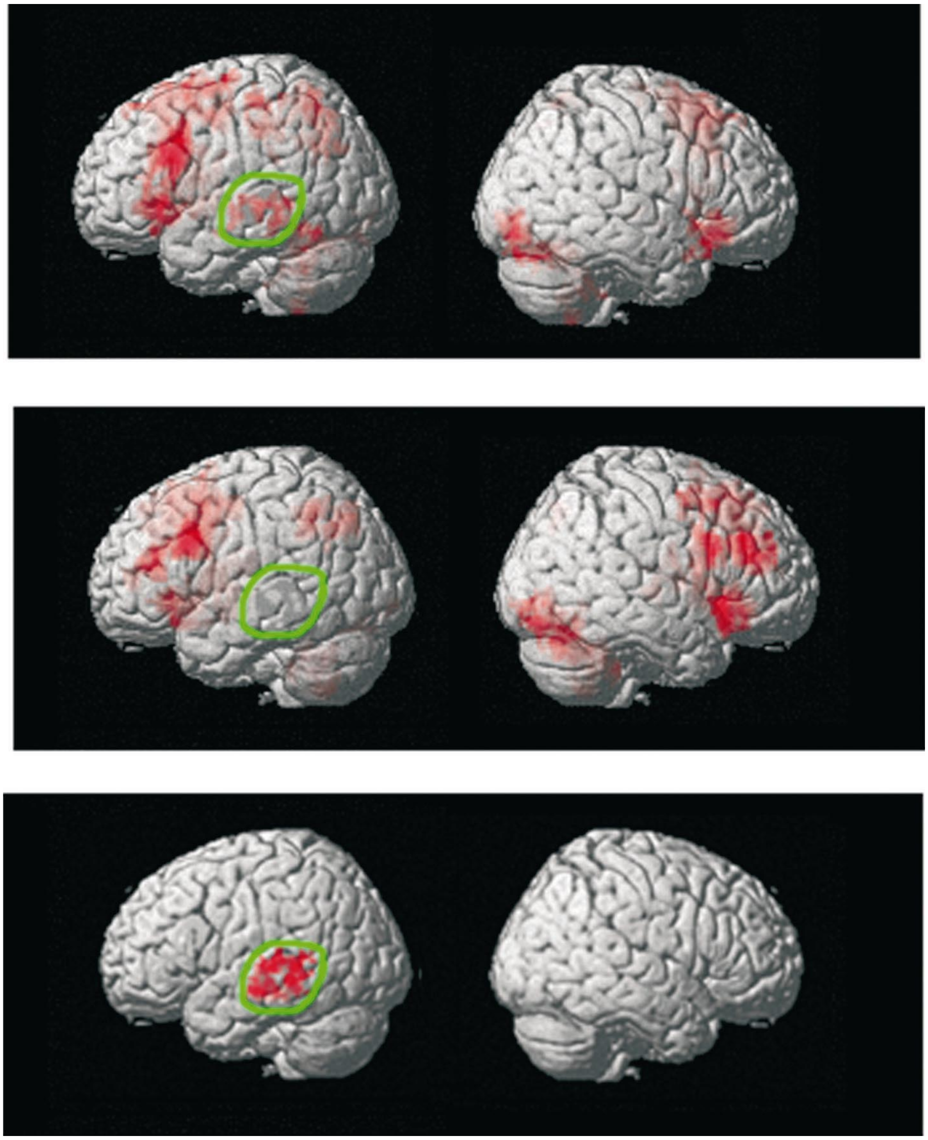

Fig. 1. Top row, brain areas that showed significant activation during the encoding task included the left lateral temporal cortex, prefrontal cortex and the hippocampus. Middle row, brain areas that showed significant activation during the retrieval task when performance was not considered include the frontal cortex, and parietal lobe (both accurate and inaccurate trials were included). Bottom row, the only brain area that showed increased activation with accurate memory retrieval was the left lateral temporal cortex (BA 21/22).

accuracy, however several other studies based on event-related analyses have failed to replicate this finding [2]. Furthermore, encoding processes during tasks nominally labeled as retrieval tasks by the experimenter may also result in greater activation of left prefrontal cortex [3]. Additional encoding processes may involve the left inferior frontal gyrus as well as the hippocampus [15]. Together with the present results, these findings suggest that while the hippocampus and prefrontal cortex are involved in multiple operations during memory retrieval tasks, the left LTL may only be involved in accurate memory performance for semantically encoded material.

Our results indicate that accurate performance (correct recognition of previously studied words and correct rejection of novel words) during this episodic memory retrieval task engages the left LTL. This region also showed significant activation during the semantic categorization (encoding) task. Lesion and imaging studies have shown that left LTL regions are crucial for storage of semantic knowledge and semantic processing of words [4,20]. Lesion and imaging studies have also suggested that although left inferior prefrontal cortex is involved in semantic processing, the left LTL plays a more prominent role in the storage and retrieval of semantic knowledge [12,24].

Activation of the left LTL during semantic categorization and its reactivation during accurate episodic retrieval provides evidence for a link between the neural processes

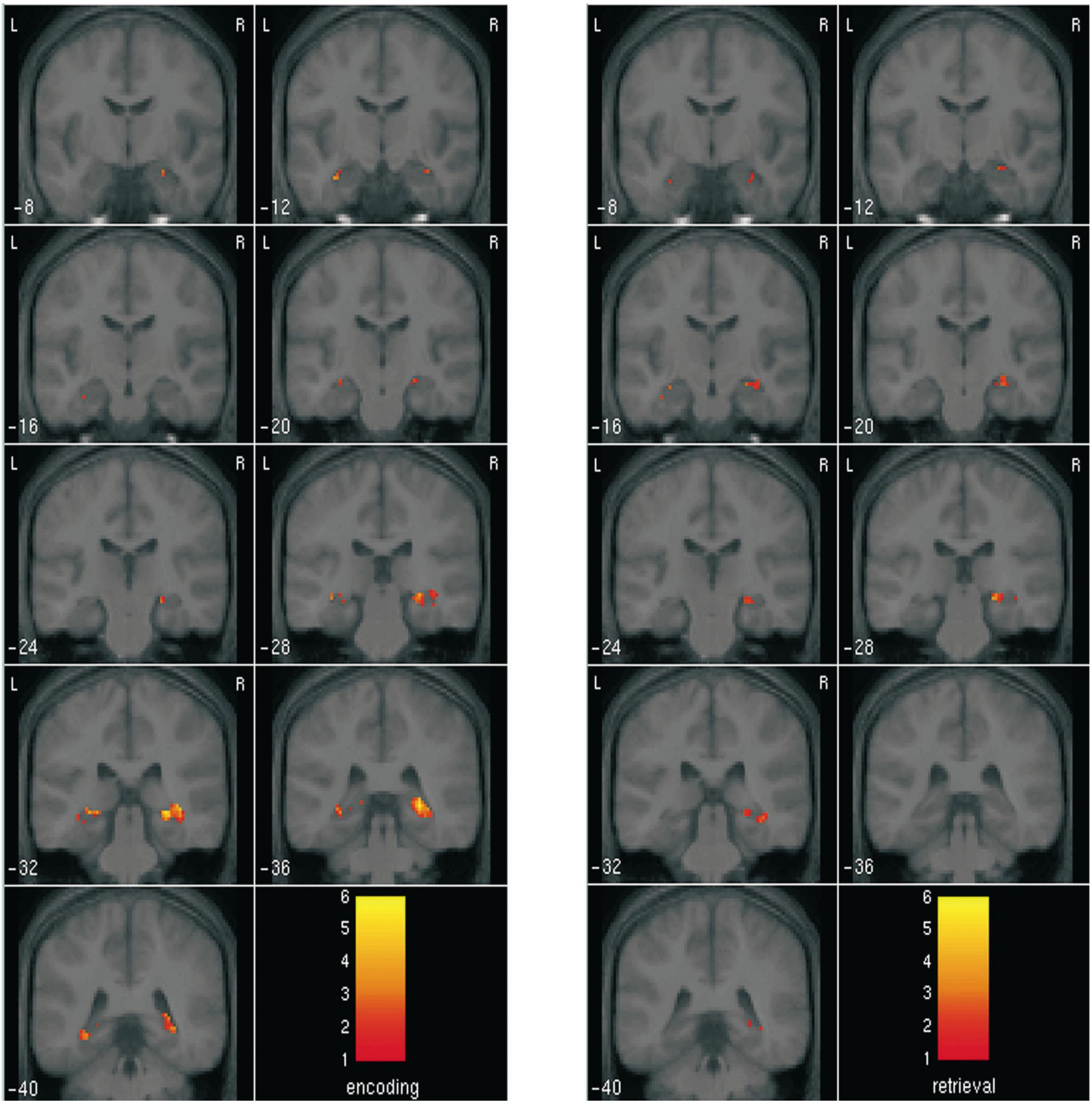

Fig. 2. Hippocampal activation during (left panel) encoding and (right panel) retrieval. The hippocampus did not show increased activation with accurate memory retrieval. Numbers in the lower left corner of each coronal section refer to Talaraich y-coordinate.

underlying episodic and semantic memory. Further support for this relationship comes from lesion studies, which have shown that damage to the left LTL can result in disrupted episodic memory [21]. In addition, amnesic patients, with lesions to MTL regions involved in episodic memory, are impaired in the acquisition of new semantic memories [8]. Access to and interaction with brain areas involved in semantic processing may underlie the superior episodic memory for words that were subjected to semantic analysis during encoding [6]. The precise neural mechanisms by which activation of semantic processing areas contribute to accurate episodic retrieval performance however remain unknown. Semantic processing during episodic encoding may create a stronger or more elaborate memory trace. During retrieval, the semantic memory trace may be used to reconstruct the prior encoding episode [22]. In addition, evidence suggests that mechanisms of veridical episodic memory can be used to suppress false recognition [19]. Thus, comparing the recognition cue to the semantic memory trace may aid in accurately identifying novel words. In agreement with this interpretation, imaging studies have found no difference in left LTL activation during correct recognition of previously studied words and correct identification of novel words [11,13].

In summary, our findings indicate that left lateral LTL regions involved in semantic memory also play a role in accurate episodic memory performance. We hypothesize that the functional interaction between the lateral and medial temporal lobes contributes to improved episodic memory retrieval. While access to semantic memory may aid in episodic recognition of previously studied material, it is also possible that, through repetition and rehearsal, new information is abstracted from its episodic context and represented as semantic memory [23].

Acknowledgements

Supported by NIH Grants HD 40761, MH01142, HD31715 and MH50047.

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