Neuropsychologia 48 (2010) 3317–3322

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Stimulus-driven incidental episodic retrieval involves activation of the left posterior parietal cortex

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ARTICLE INFO

Article history:
Received 15 October 2009
Received in revised form 22 June 2010
Accepted 10 July 2010
Available online 16 July 2010

Keywords:
Episodic memory
Posterior parietal cortex
Incidental retrieval
Novel
Repeated
Lag
Delay
Study-phase retrieval
Spacing effect

ABSTRACT

Recent reviews have highlighted the important role that the posterior parietal cortex (PPC) serves during episodic memory retrieval. A handful of studies have also noted that the PPC is active when old information is present on tasks that do not require overt episodic retrieval. Based on this observation, we examined whether incidental study-phase retrieval, cued by the repeated presence of stimuli, was sufficient to activate the PPC and whether this activation would be modulated by the lag between the initial and repeated presentation of those stimuli. Blood flow was measured with positron emission tomography (PET) while subjects classified pictures that were either new, repeated following a short lag, or repeated following a long lag. Activity in the left inferior parietal lobule (IPL, BA 40), amongst other regions, was greater for repeated than new pictures, and was greater following a long lag than a short lag, even though intentional retrieval was not required. These results suggest that the presence of repeated stimuli is sufficient to initiate left PPC mediated episodic retrieval.

1. Introduction

Though the posterior parietal cortex (PPC) is typically associated with attention (Corbetta & Shulman, 2002; Posner & Peterson, 1990), spatial abilities (Mishkin, Ungerleider, & Macko, 1983) and numerical calculation (Zamarian, Ischebeck, & Delazer, 2009), recent reviews have highlighted the involvement of this region during episodic memory retrieval (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). Wagner et al. (2005) noted that during episodic memory retrieval, the PPC is active when test items are old (old–new comparisons), incorrectly classified as old (false alarm–correct rejection comparisons), and when retrieval is accompanied by recollective experience (remember/know). Contrasts within the remember/know paradigm have shown that ventral parietal cortex (VPC), defined as the inferior parietal lobule, including the supramarginal and angular gyri, extending to the temporo-parietal junction, shows greater activity when items are endorsed as Remembered, whereas the dorsal parietal cortex (DPC), defined as the superior parietal lobule and the intraparietal sulcus, shows greater activity when items are familiar (know responses) but not accompanied with recollection (Cabeza et al., 2008; Ciaramelli et al., 2008).

Within the context of episodic memory, retrieval is typically intentional. That is, on standard tests of episodic memory such as recognition and cued recall, subjects are instructed to use retrieval cues to remember items from an earlier study episode. While less common, retrieval from episodic memory may also be involuntary or unintentional, as when a memory simply "pops to mind." While the term incidental retrieval is typically used in the context of implicit memory, it may also be used to describe this form of involuntary or unintentional retrieval of episodic memories. One approach to examining incidental episodic retrieval is to contrast previously experienced stimuli with novel stimuli on a task that does not explicitly require subjects to remember stimuli from the earlier study episode. Indeed, it has been hypothesized that the second presentation of an item during encoding may "remind" individuals of the earlier presentation of that item even in the absence of a deliberate intention to retrieve that earlier item (Greene, 1989). Greene (1989) refers to this process as study-phase retrieval and it is one theory underlying the spacing effect—the finding that memory performance is positively correlated with the lag between repeated iterations of an item. Hintzman and Block (1973) stated "...assume that one typical effect of the second presentation of a word is to retrieve the trace of the first... The second occurrence of the word during the study phase of the experiment thus produces what is essentially an implicit judgment of the recency of the word's first occurrence." Findings from several brain imag-

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doi:10.1016/j.neuropsychologia.2010.07.015

ing studies are relevant to the question of whether the posterior parietal cortex participates in incidental study-phase retrieval. For example, Dolan and Fletcher (1997); see also Fletcher & Dolan, 1999) contrasted encoding of old category-exemplar word pairs with encoding of new category-exemplar word pairs. In both conditions, subjects were simply told to study the word pairs for a later memory test; there was no requirement for the subjects to explicitly retrieve information about the earlier presentation of the old word pairs during the encoding task. With positron emission tomography (PET), Dolan and Fletcher (1997) observed that during encoding, when word pairs were old, greater activity was observed in the left inferior parietal cortex than when the word pairs were new. Pairs that included one old item and one new item also resulted in greater bilateral lateral parietal cortex activity than novel word pairs. Similar findings showing greater posterior parietal cortex activity when old stimuli are contrasted with new stimuli during incidental episodic retrieval have been reported by Phillips, Velanova, Wolk, & Wheeler (2009) on a semantic categorization (living/non-living decision) task.

The motivation behind the present study was to examine the role of the PPC during incidental study-phase retrieval as a function of the lag between the initial and subsequent presentation of a set of stimuli. If, as hinted at by prior research (Dolan & Fletcher, 1997; Phillips et al., 2009), PPC activity was observed during this task, it would complement existing literature on the role of the PPC during intentional episodic memory retrieval. Specifically, such an outcome would suggest that the presence of a repeated stimulus would be sufficient to activate the PPC, possibly reflecting incidental study-phase episodic retrieval of the initial experience of that stimulus. The implication from such an outcome, then, would be that episodic retrieval-related activity within the PPC may either be goal-driven *or* stimulus-driven. To this end, subjects were scanned with PET while performing an encoding task on a set of novel and repeated picture stimuli. The repeated pictures were initially presented to the subjects either the evening prior to the scanning session (Repeated Long-Lag) or immediately prior to the scanning session (Repeated Short-Lag). To the extent that memory performance would be expected to be superior following the Long-Lag condition than the Short-Lag condition as predicted by the spacing effect (Greene, 1989; Hintzman & Block, 1973; Hintzman, Summers, & Block, 1975), it was predicted that activity in the PPC, if observed during the incidental retrieval task, would be greater in the Long-Lag than the Short-Lag condition.

2. Methods

2.1. Subjects

Fourteen right-handed subjects (eight female; age range 20–28) participated in the experiment. Two subjects (two males) were excluded from the analyses due to average head movement in excess of 4 mm across the scanning session. Each subject was paid $50. The study was approved by the ethics committee of Baycrest Centre for Geriatric Care, University of Toronto.

2.2. Procedure

The experiment consisted of three phases (familiarization, encoding, and recognition) and three conditions (New/Repeated Short-Lag/Repeated Long-Lag). These three experimental conditions comprised an eight scan PET protocol that was counterbalanced across subjects such that each condition appeared in each scan position and was followed and preceded by every other condition just once.

Stimuli consisted of 552 color photographs (640 × 420 pixels) downloaded from the internet with approximately half-containing people. Photographs included, but were not limited to, scenes of beaches, forests and landscapes. Stimuli in each condition were presented in the center of a black computer screen and subjects were required to indicate, with the press of a mouse button, whether people were present in each picture. The stimuli were presented on the screen for a period of 3 s with a 1 s inter-stimulus-interval. In addition, subjects were informed that one unusual stimulus would appear amongst the series of photographs and they were to look for it. The task for this unusual stimulus (a black-and-white picture of a famous person) was the same as all other stimuli (decide if a person is present in the picture). The results of this analysis will not be discussed in this paper.

In order to create the two Repeated (Short-Lag and Long-Lag) conditions, two separate familiarization phases were carried out. Pictures in the Repeated Long-Lag (Repeated-LL) condition were initially presented to subjects the night prior to scanning, while the pictures in the Repeated Short-Lag (Repeated-SL) condition were initially presented to subjects during the transmission scan immediately prior to experimental scans. During both familiarization phases, subjects encoded a set of pictures (89 stimuli per session) by indicating whether a person was present in each. A brief recognition test for a subset of the studied pictures (10 old and 10 new items) immediately followed the encoding task. These two tasks were each performed twice, with the same set of stimuli during each familiarization phase, in order to thoroughly familiarize subjects with the stimuli and the procedures.

Participants performed the encoding phase across eight experimental PET scans. Prior to the start of the scans, subjects were informed that they would see a series of pictures and for each they should indicate whether people were present in the pictures, as they had done during the previous familiarization phases. They were further informed that they might have seen some of the pictures before while others were new, but importantly, they were told that they should perform the encoding task in exactly the same way for all the pictures (i.e. to not treat the old and new pictures differently). Finally, subjects were told that a recognition test would immediately follow each scan. The eight scans included four scans of the New condition (consisting only of pictures subjects had not seen before), two scans of the Repeated-LL condition (consisting only of pictures subjects had seen the previous evening) and two scans of the Repeated-SL condition (consisting only of pictures subjects had seen immediately prior to the start of the experimental scans). In each scan, the task was started 1 min prior to the start of the PET scan and continued for 1 min after the completion of the 1 min PET scan. The subject was unaware of the point during this 3-min window that the PET scans were acquired. A total of 45 pictures were presented during this period (44 target stimuli and 1 famous stimulus). The famous stimulus was presented either during the period prior to the start of the scan or after the scan was completed. Immediately following each scan, subjects received a standard yes/no recognition test consisting of 20 old items from the immediately preceding encoding scan and 20 new items.

2.3. Scanning and statistical procedures

Blood flow was measured with a Scanditronix/GEMS PC 2048-15B PET Scanner using ^{15}O-water and 60 s data acquisition scans (Kapur et al., 1994; Tulving et al., 1994). Head movement was minimized with a custom-fitted thermoplastic face mask. All pre-processing steps were performed with Statistical Parametric Mapping software (SPM2, Wellcome Department of Cognitive Neurology, London). Image preprocessing involved realignment of each subject's blood flow images to their first image, spatial transformation into the standard stereotaxic atlas space of the Montreal Neurological Institute, and spatial smoothing using a 15 mm isotropic Gaussian filter. In a PET study, each subject contributes a single image to each condition. Thus, in the present protocol, each subject's data consisted of eight images: four New, two Repeated-LL, and two Repeated-SL. Random effects analyses were performed to identify activations associated with each of these conditions. Multiple images in each condition were averaged together in order to increase the signal-to-noise ratio of each condition. Two sets of analyses were carried out. The first contrasted the average of the four Repeated conditions (2 × Repeated-LL and 2 × Repeated-SL) with the average of the four New conditions in order to identify brain regions that were involved in study-phase incidental retrieval (i.e. Repeated–New). The second analysis focused on examining whether the delay between the initial and subsequent presentations of the Repeated stimuli affected brain activity related to incidental episodic retrieval. For this analysis, the Repeated-LL and Repeated-SL conditions were directly contrasted (Repeated-LL–Repeated-SL and Repeated-SL–Repeated-LL), inclusively masked by the Repeated–New contrast. This analysis revealed whether activity in any of the regions that were active for the repeated pictures was modulated by delay. The Repeated–New contrast, both by itself and when used as a mask to examine the effect of delay, was thresholded at $p < .001$ uncorrected for multiple comparisons with an extent threshold of 30 contiguous voxels. Because of the restricted search space due to the use of the Repeated–New mask, the comparison between the Repeated-LL and Repeated-SL conditions was thresholded at $p < .01$ uncorrected for multiple comparisons with an extent threshold of 20 contiguous voxels. All analyses were conducted as paired samples *t*-tests in SPM2 (Wellcome Department of Cognitive Neurology, London, UK) implemented in Matlab 6.51 (The Mathworks, Natick, Massachusetts). Coordinates were converted from Montreal Neurological Institute stereotaxic space to Talairach and Tournoux stereotaxic space using MNI2TAL Toolbox (Talairach & Tournoux, 1988; MNI2TAL, Matthew Brett). Active clusters were localized using Talairach and Tournoux Atlas (Talairach & Tournoux, 1988) and the Talairach Daemon.

3. Results

3.1. Behavioral performance

The median response times to making decisions during the encoding scans about whether the pictures contained people was examined with a repeated measures analysis of variance (ANOVA).