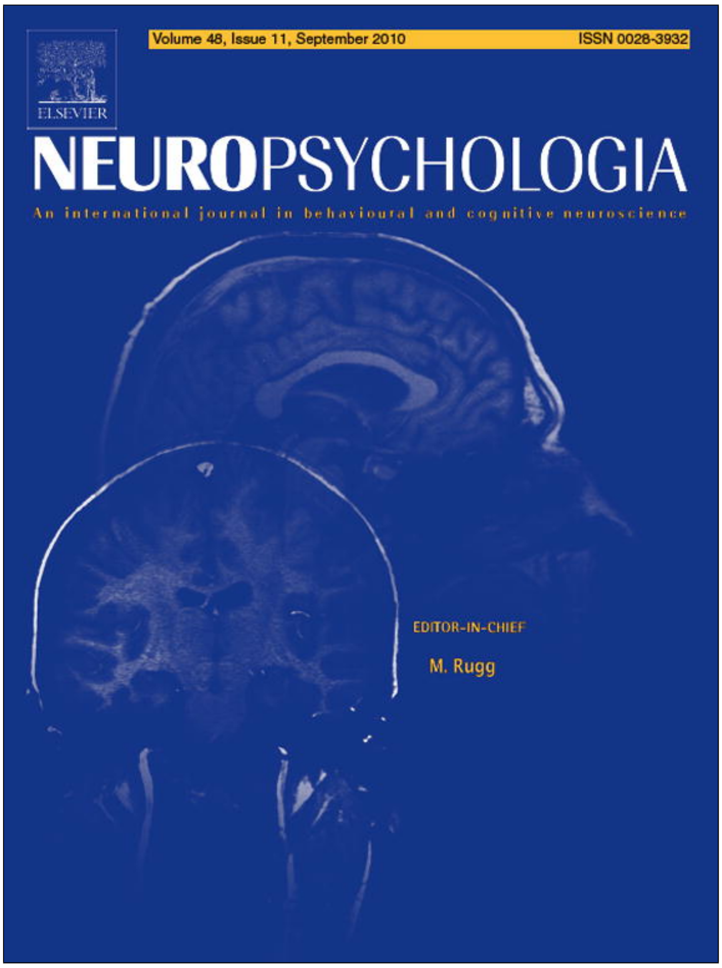
Volume 48, Issue 11, September 2010
ISSN 0028-3932
ELSEVIER
NEUROPSYCHOLOGIA
An international journal in behavioural and cognitive neuroscience
EDITOR-IN-CHIEF
M. Rugg

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).

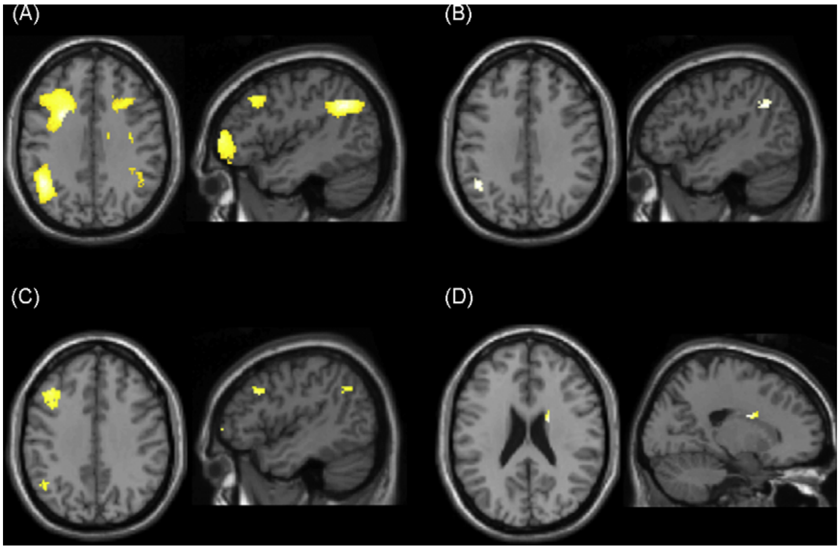

Fig. 1. (A) Horizontal and sagittal views of activation in the Repeated–New contrast, thresholded at $p < .001$ uncorrected for multiple comparisons, revealing activation in left posterior parietal cortex and bilateral medial frontal gyrus as a function of incidental episodic retrieval. (B) Horizontal and sagittal views of Repeated–New contrast thresholded at $p < .05$ corrected for multiple comparisons. The left posterior parietal cortex is the only region that survives this more stringent threshold. (C) Horizontal and sagittal views of left posterior parietal cortex and the anterior and posterior extents of the middle frontal gyrus. Activity in these regions, thresholded at $p < .001$ uncorrected for multiple comparisons, was greater in the Repeated-LL condition than in the Repeated-SL condition. (D) Horizontal and sagittal views of the right caudate nucleus. Activity in this region, thresholded at $p < .001$ uncorrected for multiple comparisons, was greater in the Repeated-SL condition than in the Repeated-LL condition.

The analysis revealed that response times significantly differed across the three conditions: ($F(2,22) = 5.75$, $p < .01$). Bonferroni-adjusted paired samples t-tests revealed that the response times in the New condition were significantly slower ($M = 1091.65$) than the response times in the Repeated-SL ($M = 999.56$, $p < .01$) condition but not different from the response times in the Repeated-LL ($M = 1007.82$) condition. There was no difference in response times between the two Repeated conditions. Corrected performance (hits–false alarms) on the post-scan recognition tests was also examined with a repeated measures ANOVA. The ANOVA revealed that recognition performance significantly differed across the three conditions ($F(2,22) = 15.84$, $p < .001$). Bonferroni-adjusted paired samples t-tests revealed that corrected recognition performance was significantly greater in both Repeated conditions (Repeated-SL, $M = 0.86$, $p < .01$; Repeated-LL, $M = 0.88$, $p < .01$) than in the New ($M = 0.76$) condition; recognition performance did not differ, however, between the two Repeated conditions.

To determine whether performance during the encoding task was related to performance during the post-scan recognition test, differences in response times during encoding between the two Repeated conditions and the New condition were correlated, across subjects, with differences in corrected recognition performance between the two Repeated conditions and the New condition (c.f. Wagner, Maril, & Schacter, 2000). The correlations between differences in response time and differences in corrected recognition performance in both Repeated conditions did not reach statistical significant (Repeated-LL $r = -0.23$; Repeated-SL $r = -0.01$; both $Ps > .05$). Thus, any advantage in response time conferred from the repeated presentation of the pictures during the encoding scan did not translate into better post-scan recognition performance.

3.2. PET activations

To examine brain regions involved in incidental retrieval of old pictures, brain activity averaged over the two Repeated ($2 \times$ Repeated-LL $+ 2 \times$ Repeated-SL) conditions was contrasted with brain activity averaged over the New ($4 \times$ New) condition. Greater activity for incidental retrieval of repeated pictures was found in the left inferior parietal lobule, bilateral supramarginal gyrus, bilateral middle frontal gyrus, left anterior and right posterior cingulate, left middle temporal gyrus, right medial and superior frontal gyri, right precentral gyrus, the right caudate body and thalamus (see Fig. 1A and B, and Table 1).

We next examined whether activity within the set of regions involved in incidental episodic retrieval of old pictures was modulated by the delay between the initial and subsequent presentation of the stimuli. For this analysis, we performed a direct comparison between the two Repeated conditions, Repeated-LL and Repeated-SL, inclusively masked with the aforementioned Repeated–New contrast (to restrict the search space to only those regions activated in the Repeated–New contrast). These analyses revealed

Table 1
Table of coordinates in Repeated (Repeated-SL + Repeated-LL)–New contrast.

Region	BA[a]	X[b]	Y[b]	Z[b]	Z-score[c]
Inferior parietal lobule	40	−38	−33	31	3.25
Supramarginal gyrus	40	−44	−49	34	4.86
	40	40	−37	30	3.55
	40	48	−47	34	3.32
Middle frontal gyrus		−26	11	31	4.96
	10	−44	52	−1	4.36
	9	28	19	27	3.85
		38	26	24	3.75
Anterior cingulate	32	−20	28	21	4.50
Posterior cingulate gyrus	31	16	−40	22	3.73
Middle temporal gyrus		−53	−37	−5	3.59
Medial frontal gyrus	10	24	49	9	4.47
Superior frontal gyrus	10	14	68	8	4.38
	10	34	58	−5	4.08
Precentral gyrus	6	36	−10	34	3.55
Caudate body		16	−8	28	3.76
		18	15	21	4.85
Thalamus		12	−22	20	4.24

[a] BA = Brodmann area.

[b] X, Y, Z coordinate are in the Talairach and Tournoux (1988) stereotaxic space. Negative X values refer to sites in the left hemisphere.

[c] All Z-scores are significant at $p < .001$ uncorrected for multiple comparisons.

that incidental retrieval of repeated pictures following a long lag (Repeated-LL) relative to a short lag (Repeated-SL) resulted in greater overall activation in three left hemisphere regions: the left inferior parietal lobule (*XYZ* = −48 −56 38; *Z* = 2.75; BA 40), and the anterior and posterior extents of the left middle frontal gyrus (anterior: *XYZ* = −26 63 8; *Z* = 3.35; BA 10; posterior: *XYZ* = −40 27 28; *Z* = 2.99; BA 9). The reverse contrast, Repeated-SL–Repeated-LL inclusively masked by the Repeated–New contrast, resulted in activity in only one region: the right caudate body (*XYZ* = 20 1 22; *Z* = 3.58; see Fig. 1C and D).

4. Discussion

Much recent research has focused on the role of the left posterior parietal cortex in intentional episodic retrieval (Cabeza et al., 2008; Ciaramelli et al., 2008; Vilberg & Rugg, 2008; Wagner et al., 2005). A small number of studies have also identified activity in the left posterior parietal cortex when subjects encounter old information on tasks that do not explicitly require episodic retrieval (Dolan & Fletcher, 1997; Phillips et al., 2009). Based on the latter observation, we wondered whether the PPC would also be activated during incidental study-phase episodic retrieval and whether this activity, if present, would be modulated as a function of the lag between the initial and subsequent presentations of the stimuli. In studies that have examined the role of the PPC in episodic memory retrieval (Cabeza et al., 2008; Ciaramelli et al., 2008; Vilberg & Rugg, 2008; Wagner et al., 2005), greater PPC activity is observed when test stimuli are old than when they are new (Old–New contrast; Wagner et al., 2005). In such situations, however, it is unclear whether activity in the PPC is driven by the demands of the task (i.e. intentional retrieval), by the nature of the stimuli (i.e. the old retrieval cues), or by a combination of the two. Thus, we hypothesized, based on prior cognitive (Greene, 1989, 1992; Hintzman & Block, 1973; Hintzman et al., 1975) and neuroimaging (Dolan & Fletcher, 1997; Phillips et al., 2009) research, that the presence of old stimuli would incidentally initiate episodic retrieval processes to repeated stimuli and result in activation of the left posterior parietal cortex.

To test this hypothesis, we performed a PET study in which subjects were scanned while making simple decisions about new pictures or pictures they had previously seen following two different lags. We hypothesized that the presence of repeated pictures may initiate episodic retrieval – what has previously been referred to as incidental study-phase episodic retrieval – of the original presentation of the pictures without any intention on the part of the subjects to explicitly remember the items, as when a memory simply "pops to mind." The contrast between the average of the two Repeated conditions (Repeated-SL and Repeated-LL) and the New condition resulted in an extensive bilateral pattern of brain activity that involved frontal, temporal, and parietal brain regions. The left posterior parietal cortex, including the left inferior parietal lobule and the left supramarginal gyrus, was one of the strongest activated regions in this pattern, and the only one that survived a $p < .05$ threshold that was corrected for multiple comparisons (see Fig. 1B). This result, then, is consistent with previous studies of incidental retrieval (Dolan & Fletcher, 1997; Phillips et al., 2009) and confirms our hypothesis that the presence of repeated information on a task that does not explicitly require retrieval from episodic memory is sufficient to activate the posterior parietal cortex.

The PPC activation we observed in the Repeated–New contrast was situated in the inferior parietal lobule (*XYZ* = −38 −33 31) and the supramarginal gyrus (*XYZ* = −44 −49 34), both regions located within the ventral posterior parietal cortex. Several past studies have found nearby activations when contrasting intentional retrieval of old information to attempted intentional retrieval of new information. For example, Shannon and Buckner (2004) found activation in the left inferior parietal lobule (*XYZ* = −44 −61 42) when contrasting hits to correct rejections for both pictures and sounds. Similarly, Guerin and Miller (2009) reported activation in left lateral parietal cortex (*XYZ* = −42 −57 48) when comparing hits to correct rejections for both words and faces. Similar activation of the left lateral parietal cortex when comparing intentional retrieval of old versus new information has been reported in several other studies as well (Wheeler & Buckner, 2003; Phillips et al., 2009; Vilberg & Rugg, 2009a). Activation in the ventral posterior parietal cortex has also been observed when intentional retrieval accompanied by recollection is contrasted with intentional retrieval accompanied only by familiarity (i.e. Remember–Know comparisons). For example, Henson, Rugg, Shallice, Josephs, & Dolan (1999) reported activation in the left lateral inferior parietal cortex (*XYZ* = −57 −51 39) when contrasting Remember responses to Know responses for words. Similarly, Eldridge, Knowlton, Furmanski, Bookheimer, & Engel (2000) observed activity in the left inferior parietal gyrus (*XYZ* = −43 −56 40) when contrasting retrieval of words accompanied by Remember responses to retrieval of words accompanied by Know responses. Similar findings of activation in the ventral posterior parietal cortex when intentional retrieval accompanied by recollection is contrasted with intentional retrieval accompanied by familiarity have been reported in several other studies (Daselaar, Fleck, & Cabeza, 2006; Vilberg & Rugg, 2009b, 2009c; Yonelinas, Otten, Shaw, & Rugg, 2005).

The proximity of the left ventral posterior parietal cortex activity in the present study to those observed in past studies of intentional retrieval suggests that if the left inferior parietal cortex activation observed in the Repeated–New comparison in the present study is indeed a reflection of incidental episodic retrieval, as we have hypothesized, then this is the same retrieval mechanism that is recruited during intentional episodic retrieval tests such as cued recall and recognition. That is, the only difference between episodic retrieval in the present study and those in past studies is how the retrieval mechanism is initiated: intentionally via task instruction in previous studies versus incidentally (stimulus-driven) by the presence of repeated items in the present study. We do not claim that the retrieval process in the present study differs in any meaningful way from what has been ascribed to the left posterior parietal cortex in past studies.

The attention to memory (AtoM; Cabeza et al., 2008; Ciaramelli et al., 2008) hypothesis proposes that dorsal and ventral extents of the PPC are functionally distinct. Activity within the dorsal parietal cortex has been attributed to top-down, goal-directed memory retrieval (Cabeza et al., 2008; Ciaramelli et al., 2008), whereas activity within the ventral parietal cortex is hypothesized to reflect bottom-up reflexive responses to salient stimuli (Cabeza et al., 2008; Ciaramelli et al., 2008). Salient memory stimuli include items that are remembered with high confidence or with contextual details and when the cue and target are identical (Ciaramelli et al., 2008). Indeed, as reviewed above, studies employing the remember/know paradigm have found greater VPC activity to items that are recollected compared to item retrieval that is only accompanied by familiarity. Activity in the Repeated–New contrast in the present study was also noted in the VPC. While we did not inquire about the nature of the retrieval experience (recollection or familiarity) on the recognition tests following each PET scan, we assume, given the high level of recognition performance even after a 24-h delay and the high likelihood that picture stimuli like the ones used in the present study are associated with a recollection response (Rajaram, 1993), that the VPC activity in the present study was likely due to the salience of the picture stimuli as predicted by the AtoM model. Conspicuously absent in the present study was activation in the dorsal posterior parietal cortex. Given that dorsal parietal activity has been hypothesized to reflect goal-directed top-down retrieval, its absence may reflect the fact that retrieval was incidental rather than intentional—that is, the task that subjects were engaged did not require intentional retrieval of past information.

The direct comparison between the Repeated-LL and Repeated-SL conditions resulted in greater activity in three foci in the Repeated-LL condition: left inferior parietal lobule, posterior extent of the middle frontal gyrus, and the anterior extent of the middle frontal gyrus, and one activation in the in the Repeated-SL condition: right caudate nucleus. Only a handful of studies have examined brain activity differences as a function of the lag between the initial and repeated presentation of stimuli. Wagner et al. (2000) reported an fMRI study that examined incidental encoding (concrete/abstract classification) of novel words, words repeated after a short lag, and words repeated after a long lag. The authors reported greater activity in the left anterior inferior prefrontal cortex ($XYZ = -46\ 28\ 15$), a site near the posterior middle frontal gyrus activation observed in the Repeated-LL condition ($XYZ = -40\ 27\ 28$) in the present study, following a long delay between the initial and repeated presentation of the words relative to a short delay. A critical difference between the present study and Wagner et al.'s (2000), however, is that in the present study activity in the left middle frontal gyrus was greater in both Repeated conditions relative to the New condition, whereas in Wagner et al.'s (2000) study, activity in the left anterior inferior prefrontal cortex was greater in their new condition relative to their repeated conditions. For this reason, Wagner et al. (2000) ascribed their finding to neural priming, whereas the activity in the present study was ascribed to incidental episodic retrieval. A study examining naming of novel and repeated black-and-white line drawings found greater activity in the left basal ganglia when repeated drawings were named following a short delay compared to a long delay (van Turennout, Bielamowicz, & Martin, 2003). The site of this activation ($XYZ = -16\ -2\ 16$) was near the caudate nucleus activation in the Repeated-SL condition of the present study ($XYZ = 20\ 1\ 22$), albeit in the opposite hemisphere. The hemispheric difference between the present study and van Turennout et al.'s (2003) may be related to the nature of the response required on each task. While subjects were required to process non-verbal stimuli in both studies, van Turennout et al.'s (2003) required subjects to name the objects depicted in the line drawings while subjects in the present study were required to decide whether people were present in the photographs. Thus, the left hemisphere activation in the van Turennout et al. (2003) study may reflect the verbal nature of the responses subjects were required to make, while the right hemisphere activation in the present study may reflect the non-verbal nature of the responses subjects were required to provide on our task. Neither the study by Wagner et al. (2000) nor the study by van Turennout et al. (2003) reported a difference in the left inferior parietal cortex as a function of delay. Thus, while there appears to be some similarity with respect to the regions that respond to different lags between the initial and repeated presentation of different types of stimuli (words, black-and-white line drawings, and color photographs) across different imaging methodologies (PET and fMRI), there also appear to be significant differences that will require further testing to resolve.

We have hypothesized that the VPC activity noted in the Repeated–New and Repeated-LL–Repeated-SL contrasts may reflect recollection associated with processing of the repeated stimuli. This hypothesis requires further explanation. At first glance, it appears counterintuitive to think that greater recollection would accompany items in the Long-Lag condition relative to the Short-Lag condition. However, this is exactly what would be predicted based on the Spacing Effect and is in fact what has been shown previously (Wagner et al., 2000). The Spacing Effect refers to the finding that memory performance (and presumably the accompanying recollective experience) improves as the lag between the initial and subsequent presentation of an item increases (Greene, 1989, 1992; Hintzman & Block, 1973; Hintzman et al., 1975). For example, Wagner et al. (2000) observed corrected recognition performance of 35% following their Long-Lag (24-h prior to scan) condition relative to 31% in their Short-Lag (immediately prior to scan) condition. Similarly, in the present study, corrected recognition performance in the Long-Lag condition was 88% whereas in the Short-Lag condition, it was 86%, and while the present effect did not reach statistical significance, the difference was of approximately the same magnitude that was observed by Wagner et al. (2000) and in the same direction. Furthermore, Wagner et al. (2000) observed that high-confidence recognition responses also showed a Spacing Effect: high-confidence recognition performance following a long lag (32%) was superior to high-confidence recognition performance following a short lag (25%). It is thus conceivable that the VPC activation in the present study reflects recollection associated with processing of the repeated stimuli and that this experience is greater in the Long-Lag condition than in the Short-Lag condition.

One caveat to the present interpretation should be noted. We have interpreted the greater activation in the Repeated conditions relative to the New conditions to reflect incidental study-phase episodic retrieval. This interpretation was based on the assumption that subjects would be unlikely to engage in intentional retrieval given that the encoding task simply required them to determine whether people were present in the photographs. If retrieval processes were initiated, we hypothesized that this would be unintentional and incidental, driven by the repeated stimuli, as has been previously hypothesized in the Study-Phase Retrieval theory (Greene, 1989). However, while we prefer the present interpretation, it is not possible for us to rule out the alternative—that activity in the left inferior parietal cortex reflects intentional retrieval of the original study phase. That is, subjects may have voluntarily chosen to use the encoding stimuli as retrieval cues to intentionally retrieve the details of the prior presentation of those stimuli. We think this interpretation, while plausible, is unlikely, however, given that response time performance during the encoding task was uncorrelated with performance on the post-scan recognition test. If subjects engaged in intentional retrieval during the encoding task in order to improve their response times, a positive correlation between response times and recognition performance would have been expected. Given that this was not observed, it seems unlikely that the PPC activity observed during the encoding task and attributed to incidental episodic retrieval could instead reflect intentional retrieval. This argument is similar to what Wagner et al. (2000) proposed to account for the negative correlation between their incidental retrieval and post-scan recognition tests. Future research directly manipulating the retrieval intention of the subjects will be necessary to conclusively determine whether activity in the present study reflects incidental episodic retrieval as we claim, or in fact reflects intentional episodic retrieval.

In conclusion, the results from the present study complement previous research on the role of the left posterior parietal cortex during episodic memory retrieval by demonstrating that the presence of repeated information is sufficient to initiate episodic retrieval processes, suggesting that this retrieval process, in addition to being goal-driven, may also be stimulus-driven. Activity in the posterior parietal cortex, as well as frontal and basal ganglia regions, is also sensitive to the lag between the initial and repeated presentation of the target stimuli. Greater activity in frontal and parietal regions in the Long-Lag relative to the Short-Lag condition may represent the neural signature of the Spacing Effect (see also Callan & Schweighofer, 2010).

Acknowledgements

We would like to thank D. Hussey, K. Cheung, and the staff at the PET centre at the Clarke Institute of Psychiatry for their help in data collection. This research was supported by a foundation of Anne and Max Tanenbaum in support of research in cognitive neuroscience to Endel Tulving.

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