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Differential components of prospective memory? Evidence from fMRI

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Abstract

Two of the principal components of prospective memory (i.e., remembering to carry out delayed intentions) are recognizing the appropriate context to act ("cue identification") and remembering the action to be performed ("intention retrieval"). In this experiment, the demands on these components were manipulated while measuring brain activity using fMRI to explore whether the two components share a common neural basis. The results showed significant behavioral differences between the cue identification and intention retrieval conditions. However, a consistent pattern of hemodynamic changes was found in both prospective memory conditions in anterior prefrontal cortex (BA 10), with lateral BA 10 activation accompanied by medial BA 10 deactivation. These effects were more pronounced when demands on intention retrieval were high. This is consistent with the hypothesis that anterior prefrontal cortex (area 10) supports the biasing of attention between external events (e.g., identifying the cue amid distracting stimuli) and internal thought processes (i.e., maintaining the intention and remembering the intended actions). Together, the results suggest that whilst cue identification and intention retrieval may be behaviorally separable, they share at least some common neural basis in anterior prefrontal cortex.

Keywords: Anterior prefrontal cortex; Rostral prefrontal cortex; Frontal lobes; Functional magnetic resonance imaging (fMRI); Executive function

1. Introduction

Prospective memory (PM[1]), remembering to perform an intended action after a delay (Meacham & Singer, 1977), may involve a number of processing stages: forming an intention, maintaining the intention in memory over an interval while being engaged in another (or ongoing) task, executing the intended action at the appropriate moment, and evaluating the outcome (Freud, 1901; Ellis, 1996). Much research into PM has focused on the third of these stages, involving recognition of the appropriate moment to act and remembering what action was to be performed (see Table 1 in Burgess, Scott, & Frith, 2003, for a list of cardinal properties of PM). The most often studied example is where an action needs to be performed when an external event occurs, such as remembering to stop and buy a loaf of bread when you drive past the grocery store ("event-based PM"; Einstein, Holland, McDaniel, & Guynn, 1992). McDaniel and Einstein (1992) proposed a division of event-based PM into two components: cue identification and intention retrieval. Cue identification involves the detection of the cue event (e.g., the grocery store) signaling that the intended action should be performed; intention retrieval involves the subsequent recovery of that intention (e.g., buying the bread) from memory. There are a considerable number of behavioral studies that have investigated these components (e.g., Brandimonte & Passolunghi, 1994; Cohen, West, & Craik, 2001; Marsh, Hicks, Cook, Hansen, & Pallos, 2003; Einstein et al., 1992; Einstein, McDaniel, Manzi, Cochran, & Baker, 2000; Ellis & Milne, 1996; West, Herndon, & Crewdson, 2001; West & Ross-Munroe, 2002; West, Wymbs, Jakubek, & Herndon, 2003).

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[1] Delegates at the 2nd International Conference on Prospective Memory, Zurich, July 2005, voted that the use of the abbreviation "PM" for prospective memory was preferable to other extant forms.

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Much of this research has focused on one or other of the two components, such as on the effect of cue characteristics in triggering a response. It has been shown that cues that are particularly salient tend to be noticed more frequently (Einstein et al., 2000), that unfamiliar cues benefit prospective remembering (Brandimonte & Passolunghi, 1994), and that when an intention has been formed to respond to a particular category of cues, highly typical category members evoke the intention more often than less typical exemplars (Ellis & Milne, 1996). Studies of intention retrieval have concentrated primarily on the association between the cue and the stored intention. When this association is strong, retrieval may be relatively automatic, as opposed to more effortful processing when the association is weak (McDaniel & Einstein, 2000; McDaniel, Einstein, Guynn, & Breneiser, 2004).

Despite the extensive research on PM processes, however, relatively few studies have investigated whether cue identification and intention retrieval might rely on separable cognitive processes. Cohen et al. (2001) evaluated in separate experiments the hypothesis that cue identification and intention retrieval are primarily supported by stimulus-driven and conceptually driven processes, respectively. Cue identification was manipulated by a change in format of the cue from study session to test session and, in a second experiment, intention retrieval was manipulated by a change in semantic relatedness between the cue and the intention from study session to test session. The authors found that a change in cue format reduced the number of PM cues detected, while semantically unrelated intentions were less often correctly recalled upon detection of the cue, consistent with their hypothesis. However, only accuracy data were reported, although many PM studies have reported an effect of prospective memory retrieval on reaction times (e.g., Burgess, Scott, & Frith, 2003; Marsh, Hicks, & Watson, 2002; Marsh et al., 2003; West et al., 2001). Marsh et al. (2003) examined reaction times while investigating the extent to which maintenance of a PM intention might affect cognitive processing of the ongoing task at the time a PM cue is encountered (see also Smith, 2003). Marsh et al. manipulated cue identification and intention retrieval demands separately and found differential effects on reaction times in the ongoing task. However, despite showing a differential effect of maintaining a PM intention on performance of the ongoing task, these authors did not study the effect of manipulating cue identification and intention retrieval on the PM task itself.

The few available results thus suggest that cue identification and intention retrieval might be separable behaviorally, in that manipulating the demand on the two components may differentially affect error rates and/or reaction times. However, even if this is the case, it may not necessarily follow that the two components are supported by exclusively different brain regions. Previous neuroimaging studies of PM have used a variety of paradigms which, although not designed to manipulate cue identification and intention retrieval as experimental variables, have nevertheless involved cue identification and intention retrieval processes to differing extents. In all of these studies, a consistent pattern of activation has been observed, involving particularly anterior prefrontal cortex (approximating Brodmann area 10) (Burgess, Quayle, & Frith, 2001; Burgess et al., 2003; den Ouden, Frith, Frith, & Blakemore, 2005; Okuda et al., 1998). It is not clear, therefore, whether the anterior prefrontal cortex network is involved in PM function to a similar degree irrespective of the demands on cue identification and intention retrieval, or whether varying cue identification and intention retrieval as experimental variables will reveal that the key neural correlate of PM reflects processing relating to one of the hypothesized components more than the other.

The experiment presented here examined these issues by scanning participants using fMRI while they were undertaking a task in which PM trials were embedded in an ongoing task in such a way as to prevent participants from actively rehearsing the intentions. Two PM conditions were used, one with high cue identification demand and low intention retrieval demand (the 'cue identification PM condition'), and one with low cue identification demand and high intention retrieval demand (the 'intention retrieval PM condition'). Cue identification was manipulated by altering the perceptual salience of the PM cues (Brandimonte & Passolunghi, 1994; Einstein et al., 2000). In the low cue identification demand condition, the cues were perceptually distinct from the ongoing trials, while in the high demand condition, the cues were perceptually similar but conceptually distinct. Intention retrieval demand was manipulated by varying the number of actions participants needed to perform in order to determine the appropriate response. If, as predicted by previous neuroimaging studies (Okuda et al., 1998; Burgess et al., 2001, 2003; den Ouden et al., 2005), an anterior prefrontal cortex network supports PM function regardless of the demands on cue identification and intention retrieval, then substantial overlap can be expected between the patterns of activation associated with each PM condition.

The use of word and shape versions of the task enabled analysis involving conjunction contrasts across tasks to identify brain regions that are commonly activated across stimulus types, and might be considered to reflect "central", task-independent PM processes, as opposed to those that might be specific to a particular stimulus type or task. In addition, to examine the effect of maintaining a PM intention on performance of the ongoing task (Marsh et al., 2003; Smith, 2003), a session consisting solely of ongoing trials was included at the beginning of the experiment, before participants had received any instructions concerning PM trials. Previous studies have shown that once instructed about a PM condition, the expectation that a PM trial will occur continues even if participants are subsequently instructed that there will be no PM trials in the upcoming block (Burgess et al., 2003; Einstein et al., 2005; Holbrook, Bost, & Cave, 2003). Ongoing trials presented before exposure to a PM condition should not be contaminated by the expectation of a PM trial, so were termed 'uncontaminated' ongoing trials, with ongoing trials occurring after presentation of PM instructions termed 'contaminated' ongoing trials. Burgess et al. (2001) have shown that not only the execution, but also the expectation, of a PM trial can be associated with lateral anterior prefrontal cortex activation. If this region is involved in maintenance of the PM intention, it should show greater activation in the present experiment during contaminated versus uncontaminated ongoing trials and, indeed, between contaminated ongoing trials in the intention retrieval versus cue identification PM conditions.

2. Methods

2.1. Participants

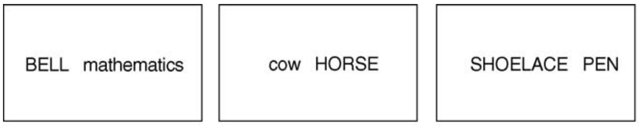
Sixteen right-handed native speakers of English (eight males, eight females, mean age 23.4 years, range 18–30 years) volunteered to take part in the experiment. They were screened using a comprehensive medical questionnaire and written informed consent was obtained before participating.

2.2. Design and materials

Two PM tasks, a word and a shape task, were administered to each participant. Each task consisted of ongoing trials, prospective memory trials with high cue identification and low intention retrieval demands (termed cue identification PM trials), and prospective memory trials with low cue identification and high intention retrieval demands (termed intention retrieval PM trials). The two PM conditions occurred in separate sessions.

Each trial in the word task consisted of two nouns presented in the middle of the screen, one of which was written in upper case and the other in lower case letters (see Fig. 1). Words were drawn from the MRC Psycholinguistic Database (Wilson, 1988), and were matched for written frequency, familiarity, and concreteness. For ongoing trials, participants were instructed to indicate using a keypad whether the left or the right of the two words contained more letters. In the cue identification PM condition, in which trials were perceptually similar but conceptually distinct from the ongoing condition, a different key was to be pressed if the words belonged to the same semantic category, for example cow and horse. Conversely, in the intention retrieval PM condition, in which trials were perceptually distinct from the ongoing condition, words were written in the same case and participants were required to retrieve a greater number of actions than in the cue identification PM condition: count up the syllables of both words and press one key if the total was four or less, or another key if the total was higher than four. To avoid interference between the instructions, words of the same semantic category were never written in the same case.

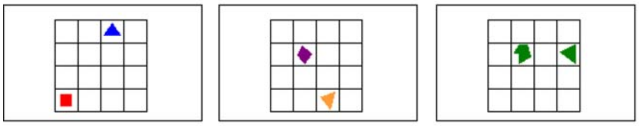
The shape task consisted of a 4 × 4 grid, in which a colored triangle and a random other shape, such as a pentagon, were presented (see Fig. 1). Each shape was drawn in a different color, selected from six possible hues. Irregular shapes were used to avoid recognition at first glance. For ongoing trials, participants were instructed to indicate whether the shape other than the triangle was presented to the left or the right of the triangle (see Fig. 1). In the cue identification PM condition in which, as before, trials were perceptually similar but conceptually distinct from the ongoing condition, a different key was to be pressed if the two shapes were a chess knight's move away from each other. In the intention retrieval condition, in which trials were perceptually distinct from the ongoing condition, the two shapes were of the same color and participants were required to retrieve a greater number of actions than in the cue identification PM condition: determine the number of sides of the shape other than the triangle, and press one key if this number was five or less, and another key if this number was higher than five. Again, to avoid conflicting instructions, shapes were never both a knight's move away from each other and drawn in the same color.



Ongoing task: Press key in direction of longer word

Cue Identification PM trial: Press different key if words are semantically related

Intention Retrieval PM trial: If words same case, count total syllables, press left key if <=4, right key if >4



Ongoing task: Press key in direction of shape other than triangle

Cue Identification PM trial: Press different key if shapes are a knight's move apart

Intention Retrieval PM trial: If shapes same colour, count sides of shape other than triangle, press left key if <=5, right key if >5

Fig. 1. The words (top) and shapes (bottom) experimental tasks. An ongoing trial, a cue identification PM trial, and an intention retrieval PM trial are shown for each task.

Word and shape tasks were administered in short blocks of approximately 35 s, interrupted by approximately 10 s of an unrelated task which was used as a baseline condition, common to all scanning sessions, against which hemodynamic activity relating to the different experimental conditions could be contrasted across sessions. In the unrelated task, participants were asked to press two keys alternately to make a row of Xs flip as quickly as possible between a horizontal and a vertical configuration. The inter-trial interval in the unrelated task was varied randomly between 300 and 700 ms to induce subjects to pay attention to the stimuli.

2.3. Procedure

Each trial consisted of 500 ms of a fixation cross, followed by presentation of the stimulus (the two words or shapes) for a maximum of 3000 ms. The tasks were subject-paced to prevent rehearsal of the given instructions (cf. Burgess et al., 2003) and ensure variable onset times of the trials, which improves fMRI design estimation efficiency (Henson, 2003). There was an inter-trial interval of 250 ms.

The tasks were administered in six sessions. The first two sessions (one words, one shapes, with task order counterbalanced between subjects) consisted of "uncontaminated" ongoing trials only without any expectation of a PM trial (no mention of PM conditions was made in the instructions for these first sessions). Two PM sessions then followed for each task, one session containing "contaminated" ongoing and cue identification PM trials, and one session containing "contaminated" ongoing and intention retrieval PM trials. The order of the PM conditions was also counterbalanced between subjects. Each session consisted of blocks of approximately 35 s of task (range 34–36 s, randomized) alternating with around 10 s of the unrelated task (range 9–11 s, randomized), with a 1 s pause between blocks. All sessions were preceded by instructions and a practice round. Each of the four PM sessions (two PM conditions for each of the two tasks) consisted of a number of ongoing trials interspersed with one group of four PM trials per 35 s block. This group of PM trials was always presented after approximately 20 s of ongoing task, to ensure that the participant would be fully engaged in the ongoing task and to control for the time between the last PM trial of a group and the first PM trial of the next group. To minimize the possibility that the appearance of the PM trials could be anticipated, two of the 35 s blocks in each condition did not contain any PM trials at all, and in two other 35 s blocks the PM trials were presented close to the beginning of the block. Anticipation of the PM task on a trial to trial basis was reduced further by placing an extra ongoing trial randomly somewhere in between the four PM trials and by varying the position of the group of PM trials within the block. In total, 32 PM trials were presented per session. The four PM sessions each lasted 517 s.

2.4. Image acquisition and data analysis

T2-weighted echo-planar functional images were acquired using a 3T Siemens Allegra system. For each subject, two time series of 21 followed by four time series of 227 whole-brain images were obtained (TR = 2.34 s, TE = 30 ms, 36 sequential axial slices aligned at approximately 10° to the AC–PC transverse plane, 2 mm thickness, 1 mm inter-slice skip). The first six images of each session were discarded to allow for T1 equilibration. Prior to the actual experiment, a magnetic fieldmap was acquired for each subject, which was used in the preprocessing of the functional images to reduce the distorting effects of the sinus area on the prefrontal cortex.

FMRI data were pre-processed and analyzed using the statistical parametric mapping procedure as implemented in SPM2 (Wellcome Department of Imaging Neuroscience, London). All images were realigned to the first image to correct for motion (using 4th-degree B-spline interpolation), after which the magnetic fieldmap was used to create a mean undistorted image. After realignment, all images were resampled in time to match the middle slice, to correct for differences in slice acquisition timing. The images were then normalized to an EPI template in MNI stereotactic space (Cocosco, Kollokian, Kwan, & Evans, 1997). Normalized images were resampled into 3 mm cubic voxels and smoothed using a Gaussian filter (8 mm FWHM kernel). A high-pass filter of 1/128 Hz was used to remove low-frequency noise, and an AR(1) + white noise model corrected for temporal autocorrelation. Finally, the time series was scaled to a grand mean of 100 across voxels and scans within each session.

Random effects statistical analysis was undertaken twice, once using a block design to estimate the main effects of interest, and once using an event-related design to allow investigation of effects that might be correlated with reaction time. Each analysis was conducted in two stages of a mixed effects model. In the first analysis, 16 conditions were defined: baseline and ongoing conditions for all six sessions, and a PM condition in the last four sessions. Blocks of PM condition lasted from the moment that the first PM trial which the subject responded correctly to appeared on the screen until the subject responded to the last PM trial in a group. Blocks of all conditions were modeled by convolving a boxcar that had a specific onset time and duration with a canonical haemodynamic response function. In the second analysis, the aforementioned conditions were re-defined as event-types for separate trials; a separate regressor coded for missed responses in each session. In both analyses, parameter values for each covariate were then estimated using a subject-specific fixed-effects model. Movement parameters in the three directions of motion and 3° of rotation were included as confounds, as well as a single covariate representing the mean session effect. In the event-related analysis, RTs were included as a parametric modulator of each event-type regressor.

Subject-specific estimates for the contrasts of interest were obtained using linear contrasts across sessions. To control for between-session signal differences, the effects of interest within each session were contrasted against the baseline condition from that same session. These estimates were entered into the second stage of analysis treating subjects as a random effect, using a one-sample *t*-test across subjects. Since activations that were independent of the type of stimuli involved (words or shapes) were of principal theoretical interest, a cognitive conjunction analysis was applied to the data which identifies as significant only those brain regions that are commonly activated in both tasks. Statistical parametric maps of the independent word and shape contrasts of interest were constructed and a one-way ANOVA on the 16 subjects was used to reveal brain regions significantly activated across both tasks, at an uncorrected threshold of $p < 0.001$. The anatomical locations and approximate Brodmann areas of significant cluster maxima of at least five contiguous voxels were localized using the Talairach and Tournoux atlas (Talairach & Tournoux, 1988) after adjusting coordinates to allow for differences between the MNI and Talairach templates (Brett, Christoff, Cusack, & Lancaster, 2001). The activation in prefrontal cortex associated with both PM conditions was examined in more detail by extracting mean percentage signal change magnitude relative to the baseline conditions from the subject-specific parameter estimates of cluster maxima, and subjecting them to a repeated-measures analysis that included region (left lateral BA 10, right lateral BA 10, and medial BA 10) and PM condition as repeated factors.

3. Results

3.1. Behavioral results

The accuracy and reaction time data as a function of task and condition are displayed in Table 1. There was no main effect of task in terms of accuracy, $F(1,15) = 0.67$, n.s., but a significant main effect of condition, $F(3,45) = 102.74$, $p < 0.0001$, and a trend towards an interaction between the two factors, $F(3,45) = 2.73$, $p = 0.055$. Accuracy scores were lower on PM trials compared to both types of ongoing trials, $F(1,15) = 53.57$, $p < 0.0001$. The accuracy difference between the cue identification and intention retrieval PM conditions was also significant, participants being less accurate in the intention retrieval PM condition compared to the cue identification PM condition, $F(1,15) = 15.44$, $p < 0.001$.

Table 1
Accuracy (%) and reaction time (ms) data per task (standard deviations in parentheses)

	Words task	Shapes task
Uncontaminated ongoing		
Accuracy	98.9 (1.7)	97.4 (3.0)
RT	566 (151)	720 (129)
Contaminated ongoing		
Accuracy	97.0 (1.7)	96.8 (2.2)
RT	991 (260)	839 (102)
Cue identification PM		
Accuracy	80.6 (12.0)	83.3 (13.6)
RT	1133 (169)	836 (113)
Intention retrieval PM		
Accuracy	75.9 (10.2)	68.3 (7.9)
RT	1596 (190)	1394 (207)

Uncontaminated ongoing: ongoing trials where no PM trial was expected. Contaminated ongoing: ongoing trials where a PM trial was expected. Cue identification PM: prospective memory trials with high demand on cue identification and low demand on intention retrieval. Intention retrieval PM: prospective memory trials with high demand on intention retrieval and low demand on cue identification.

Reaction times were significantly increased in the word compared to the shape task, $F(1,15) = 23.34$, $p < 0.0001$, and showed a main effect of condition, $F(3,45) = 145.20$, $p < 0.0001$, and an interaction, $F(3,45) = 23.07$, $p < 0.0001$. Both tasks showed an increase in reaction times between uncontaminated and contaminated ongoing trials, $F(1,15) = 38.08$, $p < 0.0001$, and between cue identification PM and intention retrieval PM trials, $F(1,15) = 191.08$, $p < 0.0001$. A comparison between the contaminated ongoing trials in the two PM conditions revealed that ongoing trials in the cue identification PM condition were associated with significantly longer RTs than in the intention retrieval PM condition, $t(15) = 4.55$, $p < 0.001$, though when separated per task this difference was only significant in the words task, $t(15) = 4.93$, $p < 0.001$.

3.2. Neuroimaging results

The results from the block analysis are reported first.[2] To identify the brain areas involved in prospective memory, each of the PM conditions in the word and shape tasks was contrasted with the uncontaminated ongoing condition, with between-session differences controlled for using the common baseline condition as described in the Methods section. Because we are interested in the brain regions associated with prospective memory that are not dependent on the kind of task used, a conjunction contrast was used to identify activations that were common to both word and shape tasks. The conjunction contrast revealed a remarkably consistent pattern of significant activation in both the cue identification and intention retrieval PM

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[2] An event-related analysis was also conducted as verification, which produced activation in similar brain regions as the block analysis with reduced effect sizes, consistent with the lower statistical power associated with event-related designs (Henson, 2003).

Table 2
Regions of increased and decreased activation in the contrast between the cue identification PM condition and the uncontaminated ongoing condition, combining across the word and shape tasks

Brain region	Coordinates			*Z*	Voxels
	x	*y*	*z*		
Cue identification PM > uncontaminated ongoing					
Left middle frontal gyrus (BA 10)	−39	57	3	3.9	6
Right middle frontal gyrus (BA 10)	42	57	9	4.4	23
Right inferior frontal gyrus (BA 47)	54	21	−6	3.9	21
Left inferior frontal gyrus (BA 47)	−42	18	−6	3.9	9
Right insula (BA 13)	48	15	12	3.7	8
Left insula (BA 13)	−39	0	27	4.4	15
Right inferior parietal lobule (BA 40)	45	−42	51	4.1	37
Right superior parietal lobule (BA 7)	33	−57	51	4.4	25
Right angular gyrus (BA 39)	42	−57	48	3.7	8
Uncontaminated ongoing > cue identification PM					
Medial anterior prefrontal cortex (BA 10)	0	48	−6	3.9	23
Right superior frontal gyrus (BA 8)	30	39	51	3.4	5
Right cingulate gyrus (BA 24)	6	12	36	3.9	7
Left precentral gyrus (BA 4/3)	−42	−15	42	4.2	11
Left medial frontal gyrus (BA 6/31)	−3	−21	57	3.7	17
Right medial frontal gyrus (BA 6)	6	−24	69	3.9	19
Right precentral gyrus (BA 4)	24	−24	72	3.6	11
Right precuneus (BA 7)	3	−33	54	3.7	13
Left precuneus (BA 7)	−3	−48	60	3.5	14
Right lingual gyrus (BA 18/19)	12	−51	6	3.6	17
Left lingual gyrus/cuneus (BA 18/30)	−9	−63	12	4.0	24

Coordinates are in MNI atlas space (Cocosco et al., 1997), with brain regions and Brodmann areas (BA) estimated from the Talairach and Tournoux (1988) atlas.

Table 3
Regions of increased and decreased activation in the contrast between the intention retrieval PM condition and the uncontaminated ongoing condition, combining across the word and shape tasks

Brain region	Coordinates			*Z*	Voxels
	x	*y*	*z*		
Intention retrieval PM > uncontaminated ongoing					
Left middle frontal gyrus (BA 10)	−39	57	3	3.6	8
Right middle frontal gyrus (BA 10)	39	54	15	5.1	203
Right middle/superior frontal gyrus (BA 11)	27	54	−12	3.7	16
Right inferior frontal gyrus (BA 47)	45	21	−15	4.1	22
Right medial frontal gyrus (BA 8)	9	21	48	3.6	15
Left insula (BA 13)	−39	18	−6	3.9	20
Right precentral gyrus (BA 9)	45	12	39	3.7	24
Right precentral gyrus/insula (BA 44)	51	12	9	4.0	36
Left inferior/middle central gyrus (BA 9)	−51	9	39	4.5	31
Left precentral gyrus (BA 6)	−42	3	27	5.1	54
Right inferior parietal lobule (BA 40)	45	−42	51	5.2	199
Left inferior parietal lobule (BA 40)	−48	−45	48	5.0	155
Right precuneus (BA 19)	12	−66	39	4.3	12
Right inferior occipital gyrus (BA 18)	36	−90	−12	4.0	46
Uncontaminated ongoing > intention retrieval PM					
Medial anterior prefrontal cortex (BA 10)	0	48	−6	5.3	243
Right cingulate gyrus (BA 24)	6	12	36	3.7	5
Right lateral parietal cortex (BA 3)	54	−12	57	4.4	30
Left precentral gyrus (BA 4/3)	−42	−15	45	3.6	13
Left medial frontal gyrus (BA 6/31)	−3	−18	57	4.0	19
Right medial frontal gyrus (BA 6/4)	6	−30	72	3.7	13
Right precuneus (BA 7)	3	−33	57	3.6	8
Right lingual gyrus (BA 18)	12	−51	6	3.6	8
Left lingual gyrus/cuneus (BA 30)	−6	−57	15	4.7	48
Right cuneus (BA 18)	6	−87	24	3.7	6

Coordinates are in MNI atlas space (Cocosco et al., 1997), with brain regions and Brodmann areas (BA) estimated from the Talairach and Tournoux (1988) atlas.

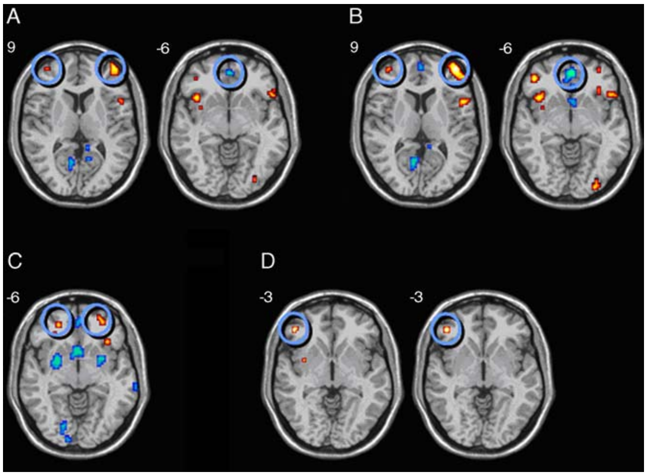

Fig. 2. Group functional activation maps of percentage signal change, in a conjunction across the word and the shape task. Activations are shown in yellow/red, deactivations are shown in blue, with activations of particular interest circled. *Z* coordinates are shown in top left corner. (A) In the cue identification PM > uncontaminated ongoing contrast, bilateral BA 10 activation and medial BA 10 deactivation was observed. A highly similar pattern was observed in (B) the intention retrieval PM > uncontaminated ongoing contrast. Differences between conditions emerge in (C), the direct intention retrieval PM > cue identification PM contrast, with significantly greater activation in anterior prefrontal cortex bilaterally in the intention retrieval PM condition, and evidence of deactivation in medial anterior BA 10. Left lateral BA 10 activation was found in (D) the contaminated ongoing > uncontaminated ongoing condition (left: cue identification PM ongoing condition; right: intention retrieval PM ongoing condition) (for interpretation of the references to color in this figure legend, the reader is referred to the web version of the article).

conditions in anterior prefrontal cortex (BA 10), with activation bilaterally in lateral BA 10 and deactivation in medial BA 10 (see Fig. 2A and B). Examination of the signal confirmed that there was no significant effect of PM condition on activation in the anterior prefrontal cortex clusters identified, $F(1,15) = 3.22$, n.s. Significant activation was also found in a number of other areas including ventrolateral prefrontal and lateral parietal cortex in both PM conditions, and dorsolateral prefrontal cortex and orbitofrontal cortex in the intention retrieval PM condition (see Tables 2 and 3).

Separate examination of the word and shape task contrasts revealed additional, potentially task-dependent, activation associated with cue identification in left premotor cortex, precuneus, and occipital cortex for words, and parahippocampal cortex for shapes. Similarly, the intention retrieval PM condition was associated with additional activation in left cingulate gyrus, premotor cortex, and precuneus for words, and a more anterior part of cingulate gyrus and postcentral gyrus for shapes.

Returning to the task-independent conjunction contrasts, despite the similarities in activation patterns associated with the two PM conditions versus the uncontaminated ongoing condition, a number of brain regions were identified in the direct task-independent contrast between cue identification PM and intention retrieval PM (see Fig. 2C). These results provide evidence of additional differential BA 10 involvement in the PM conditions. Significantly greater activation was found in the intention retrieval PM condition bilaterally in regions of BA 10 that peaked slightly less laterally than those observed in the contrasts above. Medial BA 10 appeared to be more active in the cue identification PM condition (see blue activation in Fig. 2C), although this effect did not exceed the whole-brain threshold of $p < 0.001$. At a threshold of $p < 0.05$ corrected for the voxels in an 8-mm sphere around the peak that was identified in both the cue identification PM versus ongoing and intention retrieval PM versus ongoing contrasts (0, 48, −6; see Tables 2 and 3), however, significant medial BA 10 activation did emerge in the cue identification versus intention retrieval PM contrast (0, 45, −9; $Z = 3.5$; voxels = 19). Other brain regions which were more active at the whole-brain threshold in the cue identification PM condition included the anterior cingulate, whereas in the intention retrieval PM condition more extensive areas of the cingulate gyri were among regions showing greater activation (see Table 4).

Since the behavioral data showed longer RTs in the intention retrieval PM than in the cue identification PM condition, it is possible that the greater bilateral BA 10 activation in the intention retrieval PM condition might be attributable to differences in time on task. To test this possibility, a second analysis was conducted including RT as a parametric modulator to identify brain regions where activation was positively or negatively correlated with RTs. No significant correlation was found between RT and activation in the regions of BA 10 identified in the previous contrasts, even when the threshold was dropped to $p < 0.1$ uncorrected. It thus seems safe to attribute the greater bilateral BA 10 activation during intention retrieval PM trials primarily to the demands on recovering the delayed intention.

To examine the effect of maintaining a PM intention on performance of the ongoing task, the contaminated ongoing trials in both PM conditions were contrasted with the uncontaminated ongoing trials. In both PM conditions, contaminated ongoing trials were associated with greater activation in left lateral BA 10/47 (−48, 39, 0 for cue identification; −48, 42, −3 for intention retrieval; see Fig. 2D). Again, no correlation was found between RTs and activation in these regions in the analysis that included RT as a parametric modulator. Contrasting directly the contaminated ongoing trials in both PM conditions, significantly greater activation in left lateral BA 10 was observed during the intention retrieval PM condition than the cue identification PM condition (see Table 5). This is consistent with the idea that activation in this region reflects maintenance of the intended PM actions (Burgess et al., 2001).

4. Discussion

The main finding of the present experiment was that, despite behavioral differences between the cue identification and intention retrieval PM conditions, a strikingly similar pattern of hemodynamic changes, involving anterior prefrontal cortex (BA 10), was observed across both conditions. Finding such consistent results even when the demands on cue identification and intention retrieval were manipulated sufficiently to produce significant behavioral effects, confirms the view from previous neuroimaging studies that this region is likely to be of central importance to prospective memory (Okuda et al., 1998; Burgess et al., 2001, 2003; den Ouden et al., 2005).

Table 4
Regions of increased and decreased activation in the contrast between the cue identification PM condition and the intention retrieval PM condition, combining across the word and shape tasks

Brain region	Coordinates			*Z*	Voxels
	x	*y*	*z*		
Cue identification PM > intention retrieval PM					
Right anterior cingulate (BA 32/11)	3	36	−12	3.7	53
Left anterior cingulate (BA 25)	−3	15	−6	4.5	31
Left putamen	−24	0	−9	5.0	51
Right insula (BA 40)	57	−18	21	3.6	24
Left postcentral gyrus/insula (BA 40)	−54	−21	21	4.5	113
Left middle temporal gyrus (BA 39/19)	−54	−72	24	3.4	7
Left lingual gyrus (BA 18)	−21	−78	−6	3.8	17
Intention retrieval PM > cue identification PM					
Left middle frontal gyrus (BA 10)	−33	51	18	3.4	6
Right superior frontal gyrus (BA 10)	27	51	−3	3.8	12
Left medial frontal gyrus (BA 9)	−18	42	21	3.4	5
Left anterior cingulate (BA 32/24)	−12	27	27	3.9	11
Right insula (BA 13/47)	36	24	−3	4.2	13
Left cingulate gyrus (BA 32)	−3	21	45	6.3	364
Right lateral frontal cortex (BA 6)	24	12	63	4.5	118
Right cingulate gyrus (BA 24)	3	9	30	4.0	5
Left lateral frontal cortex (BA 6)	−27	6	66	5.1	46
Left middle frontal gyrus (BA 6)	−42	0	57	3.4	5
Left inferior parietal lobule (BA 40)	−45	−54	57	3.4	5
Left cuneus (BA 18)	−12	−75	33	5.8	246

Coordinates are in MNI atlas space (Cocosco et al., 1997), with brain regions and Brodmann areas (BA) estimated from the Talairach and Tournoux (1988) atlas.

For example, Okuda et al. (1998) reported activation in the left frontal pole (BA 10), as well as right dorsolateral and ventrolateral prefrontal cortex (BA 8/9/47) and anterior cingulate (BA 24), when participants remembered and acted upon a list of target words relative to performing an ongoing routine activity (word repetition). Activation in the frontal pole (BA 10, bilaterally) was also found by Burgess et al. (2001) across several cognitive tasks. In that study, activation during an ongoing task was compared to activation in two PM conditions: one in which PM trials were expected but never actually occurred, and one in which PM trials were expected and acted upon. In both PM conditions, activation in bilateral frontal pole, right lateral prefrontal and parietal cortex, plus precuneus, was found. Burgess et al. (2003) extended these results by showing that the bilateral activation of lateral BA 10 associated with retrieving a delayed intention was accompanied by deactivation in medial BA 10. Recently, den Ouden et al. (2005) reported activation in lateral BA 10, lateral parietal cortex, and precuneus, associated with

Table 5
Regions of increased and decreased activation in the contrast between the ongoing trials in the cue identification PM and intention retrieval PM condition, combining across the word and shape tasks

Brain region	Coordinates			*Z*	Voxels
	x	*y*	*z*		
Cue identification ongoing > intention retrieval ongoing					
Right inferior frontal gyrus (BA 47)	36	30	−6	4.1	31
Left insula (BA 13)	−42	21	15	4.3	9
Left precentral gyrus (BA 6)	−51	9	33	3.5	11
Left putamen	−27	6	−6	3.9	30
Left fusiform gyrus (BA 37)	−42	−48	−9	3.8	9
Left middle occipital gyrus (BA 19)	−30	−93	21	4.3	9
Left occipital lingual gyrus (BA 18)	−15	−99	−3	4.9	79
Right cuneus (BA 18)	15	−102	12	4.4	58
Intention retrieval ongoing > cue identification ongoing					
Left medial frontal gyrus (BA 10)	−21	54	6	4.2	15
Right middle frontal gyrus (BA 6)	18	18	66	3.7	8
Left paracentral lobule (BA 6)	−12	−18	60	3.8	14
Right paracentral lobule (BA 6)	12	−30	66	3.9	20
Left postcentral gyrus (BA 4)	−15	−30	66	4.0	10
Left cuneus (BA 18)	3	−75	36	3.9	6

Coordinates are in MNI atlas space (Cocosco et al., 1997), with brain regions and Brodmann areas (BA) estimated from the Talairach and Tournoux (1988) atlas.

keeping an intention in mind while performing an ongoing task responding to questions about intentions and actions.

In the present experiment, the reliability of the consistently observed lateral BA 10 activation was assessed by manipulating the demands placed on cue identification and intention retrieval processes as experimental variables. Of course, both PM conditions involved cue identification and intention retrieval to some degree; the experimental manipulation was not all-or-none. However, the demands on the two PM components were manipulated sufficiently for significant behavioral differences to emerge between them: accuracy was lower, and reaction times longer, in the intention retrieval condition than in the cue identification condition, although correlational analysis indicated that these behavioral differences could not explain the consistent hemodynamic changes observed across conditions. Significant lateral BA 10 activation was seen bilaterally in both PM conditions, confirming the characteristic nature of this activation, as reported by a number of neuroimaging studies (Okuda et al., 1998; Burgess et al., 2001, 2003; den Ouden et al., 2005). Moreover, both PM conditions were additionally associated with medial BA 10 deactivation when contrasted with ongoing trials, consistent with the findings of Burgess et al. (2003), who also observed reduced medial BA 10 activation during PM trials versus ongoing trials. Of course, the limitations of fMRI do not allow us to speculate as to whether precisely the same neurons were recruited by both PM conditions, but it does seem clear that, at the macro level of Brodmann areas at least, similar patterns of activation in BA 10 were observed during both cue identification and intention retrieval PM conditions.

Despite finding that similar regions of BA 10 were activated (and deactivated) in both PM conditions, there was evidence that the level of activation in lateral BA 10 was greater in the intention retrieval PM condition than in the cue identification PM condition. The correlational RT analysis showed this effect was not attributable to differences in reaction time as the activations observed did not correlate with RT durations, consistent with results observed by Burgess et al. (2003). This suggests that the results cannot be explained by a simple task difficulty account, since greater difficulty (in terms at least of the amount of effort required to perform the task) could be expected to be reflected in increased RTs. Left lateral BA 10 was also significantly activated in the contrast between contaminated and uncontaminated PM trials, suggesting that activation in the region is affected by prior exposure to a PM intention. This is consistent with the finding from Burgess et al. (2001) that BA 10 activation is seen when PM trials are expected, regardless of whether they actually occur, and perhaps indicates that the region contributes to the maintenance of the delayed intention, a conclusion supported by the finding in the present experiment that BA 10 activation during contaminated ongoing trials was greater in the intention retrieval than the cue identification PM conditions. Moreover, there are echoes in these results of data from a number of electrophysiology studies which found that intention retrieval was associated with a sustained frontal slow-wave modulation that appeared to be particularly evident when retrieval of the PM intention was made more demanding (West et al., 2001; West & Ross-Munroe, 2002). Increasing the number of intentions to be remembered resulted in a larger amplitude of this frontal slow-wave (West et al., 2003). Although it is problematic to compare electrophysiological and neuroimaging results directly, there are similarities between the ERP increase over frontal sites and the present finding of greater lateral anterior prefrontal cortex activation when intention retrieval is more demanding.

The greater lateral BA 10 activation associated with intention retrieval can be conceived of in terms of differential attention towards external events and internally generated thought processes (Burgess, Simons, Dumontheil, & Gilbert, 2005; Gilbert, Frith, & Burgess, 2005; Gilbert, Simons, Frith, & Burgess, in press; Simons, Owen, Fletcher, & Burgess, 2005; Simons, Gilbert, Owen, Fletcher, & Burgess, 2005; see also Christoff & Gabrieli, 2000; Gusnard, Akbudak, Shulman, & Raichle, 2001). By this account, when one's primary aim is to detect a cue, attention must be turned towards the external world; once the cue has been detected, however, one must disengage from the external stimuli and attend to internal representations so that the relevant intention can be retrieved from memory. Thus, placing higher demands on cue identification implies biasing attention more towards external stimuli, whereas a higher load on intention retrieval implies an increase of attentional focus upon internally generated thought.

A number of previous studies have shown that lateral BA 10 plays an important role in the recollection of details about the context in which previous events occurred (Ranganath, Johnson, & D'Esposito, 2000; Rugg, Fletcher, Chua, & Dolan, 1999; Simons, Gilbert, et al., 2005; Simons, Owen, et al., 2005), an ability that requires retrieval of internally represented mnemonic information (Simons, Gilbert, et al., 2005; Simons, Owen, et al., 2005). In contrast, medial BA 10 has been associated with performance of tasks that emphasize the processing of externally presented stimuli (Gilbert et al., 2005; Janata et al., 2002; Small et al., 2003). Thus, Burgess et al. (2005) have suggested that lateral areas of BA 10 may play a role in maintaining attention towards internal cognition and more medial areas in maintaining attention towards external stimuli. The results from the PM versus ongoing contrasts in the present experiment can be interpreted along these lines, with medial BA 10 deactivation reflecting disengagement from the external ongoing task stimuli and the lateral BA 10 activation being associated with the directing of attention towards the internally represented PM intention (see Burgess et al., 2003, for a similar suggestion). Consistent with this view, lateral BA 10 activation was greater when the demands on intention retrieval were higher, and there was evidence of greater medial BA 10 activation associated with the cue identification PM condition, in which external cue processing demands were greater. Taken as a whole, these results are in agreement with the hypothesis that BA 10 acts as a "gateway", biasing attention between externally derived perceptual information used to detect the occurrence of a PM cue and internal thought processes relating to the stored PM intention (Burgess et al., 2005; Gilbert et al., 2005; Simons, Gilbert, et al., 2005).

PM-related activation was also seen in a number of areas outside the anterior PFC region of interest. When contrasted against uncontaminated ongoing trials, the cue identification and intention retrieval PM conditions provoked activation in regions of lateral PFC and parietal cortex, among other areas. A number of regions showed differential activation in the two PM conditions. These included anterior cingulate cortex, which was activated more in the cue identification PM condition, and posterior cingulate and precuneus, which showed greater activation in the intention retrieval PM condition. Activation in all these regions has been observed in previous neuroimaging studies of prospective memory (Okuda et al., 1998; Burgess et al., 2001, 2003; den Ouden et al., 2005), and has been linked with a number of processes relevant to PM retrieval. For example, lateral PFC, anterior cingulate and lateral parietal cortex have been proposed to constitute a cognitive control network involved in sustained attention and vigilance to particularly visual stimuli (Burgess et al., 2001; Coull, Frith, Frackowiak, & Grasby, 1996; Cabeza et al., 2003). Posterior cingulate, precuneus, and lateral parietal cortex have been linked in many studies with functions related to retrieval of stored mnemonic information such as recollection, retrieval confidence, and imagery (see Wagner, Shannon, Kahn, & Buckner, 2005, for a recent review).

In conclusion, the present experiment demonstrated that it is possible to tease apart behaviorally cue identification and intention retrieval components of PM, but that they may reflect the operation of similar underlying processes supported by anterior prefrontal cortex (BA 10). Evidence suggests that lateral BA 10 may reflect the maintenance and/or retrieval of the stored PM intention, showing greater activation not only during intention retrieval PM trials, but also when maintaining an intention in memory during the ongoing task.

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