Similarity between Brain Activity at Encoding and Retrieval Predicts Successful Realization of Delayed Intentions

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Abstract

■ Remembering delayed intentions can be highly demanding. Accuracy in laboratory paradigms assessing prospective memory (PM) is typically well below ceiling, and failure to remember intended behaviors after a delay is a common occurrence in everyday life. However, relatively little is known of the potential differences in brain activity that distinguish successful versus unsuccessful PM. In this fMRI study, participants repeatedly encoded, stored, and then had the opportunity to retrieve intended behaviors while engaged in a distracting ongoing task. This yielded a success rate of approximately two thirds. Overall levels of brain activity distinguished successful versus unsuccessful trials at all three stages (encoding, storage, and retrieval), suggesting multiple neural determinants of PM success. In addition, the voxelwise similarity between patterns of brain activity at encoding and retrieval was greater for successful than unsuccessful trials. This was true even in posterior cingulate, which showed opposite patterns of signal change between encoding and retrieval. Thus, successful realization of delayed intentions may be associated with reinstatement of encoding context at the time of retrieval. ■

INTRODUCTION

Living a purposeful, independent life requires the ability to form intentions for future behavior and then act on those intentions after a delay. This ability is often termed "prospective memory" (PM; Kliegel, McDaniel, & Einstein, 2008; McDaniel & Einstein, 2000; Brandimonte, Einstein, & McDaniel, 1996; Ellis, 1996; Harris, 1984; Meacham & Dumitru, 1976). However, PM frequently goes awry, even in healthy young adults: Everyone has had the experience of forgetting to post a letter, pass on a message, or attend an appointment. More severe deficits in PM have been observed in healthy aging (Uttl, 2011), following brain injury (Uretzky & Gilboa, 2010), and in clinical disorders such as autism (Jones et al., 2010; Altgassen, Williams, Bölte, & Kliegel, 2009), schizophrenia (Wang et al., 2009), and Parkinson's disease (Kliegel, Altgassen, Hering, & Rose, 2011). Yet the neurological determinants of PM success versus failure are not currently well understood. In this study, we investigated patterns of brain activity that distinguished successful versus unsuccessful performance of a PM task.

One of the reasons for the difficulty of PM tasks is that retrieval cues do not directly trigger intended actions. Instead, successful realization of delayed intentions requires self-initiated behavior, at least to some degree. This difficulty might be mitigated in at least two ways, at different points in time. First, one could encode the intention more effectively to begin with, so that it is more likely to be triggered when the appropriate cue is presented (Gilbert, Gollwitzer, Cohen, Oettingen, & Burgess, 2009; Gollwitzer, 1999). Alternatively (or in addition), one could rehearse one's intention and/or monitor the environment for retrieval cues more effectively over the retention interval (i.e., period between encoding and retrieval) to maximize the chances of retrieval success (Smith, 2003). Therefore, one aim of this study was to investigate whether brain activity differentiating successful versus unsuccessful PM can be found at the point of encoding an intention, and/or during intention storage. To do this, we used event-based fMRI to investigate a task divided into stages requiring encoding, storage, and retrieval of delayed intentions. We then categorized trials according to PM success and searched for brain regions showing differential activity between hits and misses, separately for all three stages.

Evidence from a related paradigm comes from West and Ross-Munroe (2002), who investigated event-related brain potentials associated with PM encoding and subsequent PM retrieval trials. Encoding trials associated with a subsequent hit elicited a greater slow wave negativity over frontal electrodes than trials associated with a subsequent miss. At retrieval, a negative peak over occipital-parietal electrodes approximately 300 msec after stimulus onset was greater for hits than misses. These findings indicate that brain activity related to successful versus unsuccessful PM can be distinguished both at encoding and retrieval. However, it is not clear whether such effects also apply to the delay period between encoding and retrieval, during which participants perform an ongoing task. Although ERP evidence distinguishes ongoing activity under

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PM versus ongoing-only conditions (West, Scolaro, & Bailey, 2011; Stokes, Thompson, Cusack, & Duncan, 2009; West, Bowry, & Krompinger, 2006), it is not clear whether these effects are related to PM success (for fMRI evidence, see also Reynolds, West, & Braver, 2009; Simons, Scholvinck, Gilbert, Frith, & Burgess, 2006; Burgess, Scott, & Frith, 2003; Burgess, Quayle, & Frith, 2001). Furthermore, it is difficult to draw conclusions on the anatomical basis of these effects from electrophysiological approaches.

Another purpose of the present study was to examine the relationship between brain activity at encoding and retrieval rather than looking at these two stages separately. Behavioral evidence suggests that the similarity of encoding and retrieval contexts can exert a powerful influence on PM success (Marsh, Hicks, & Cook, 2008). McDaniel, Robinson-Riegler, and Einstein (1998) found that PM success was reduced when participants encoded their intentions in one room and had the opportunity to realize them in another. McGann, Ellis, and Milne (2003) presented evidence that PM success was reduced when items were presented in different fonts at encoding and retrieval or when homonyms (e.g., "bank") were presented in different semantic contexts (money vs. river). Nowinski and Dismukes (2005) found that participants were more likely to realize intentions when performing the task that they had first performed when they learned that intention. We, therefore, investigated whether similarity of brain activity at encoding and retrieval was related to PM success.

Consistent with this possibility, "cortical reinstatement" theories of memory suggest that recall of a stimulus is associated with reinstatement of brain activity that occurred when it was encoded (Rugg, Johnson, Park, & Uncapher, 2008; Polyn, Natu, Cohen, & Norman, 2005). Evidence for such accounts comes from fMRI studies, in which participants are exposed to items in two or more encoding contexts and then asked to make memory judgments on those items in a single retrieval context. Cortical reinstatement is then demonstrated by activity at retrieval that reflects each item's earlier encoding context. For example, in a study by Johnson and Rugg (2007), participants viewed a series of words and either imagined the referent of that word in a visual scene or imagined a sentence containing it. Later, the same words were presented in a randomized order within a single retrieval context. In some regions (e.g., left occipital cortex), retrieval-related activity was greater for words initially encountered in the scene versus the sentence context; the same region also showed greater activity during scene encoding versus sentence encoding. Other regions (e.g., ventromedial pFC) showed the reverse pattern. Thus, retrieval-related activity in some regions mirrored the activity elicited when the item was first encountered.

Evidence for retrieval-related cortical reinstatement also comes from fMRI studies using multivoxel pattern analysis (MVPA). In such studies, results are typically investigated on an individual participant basis, using unsmoothed, un-normalized data. It is then possible to investigate whether patterns of activity across a set of voxels differ between experimental conditions (Norman, Polyn, Detre, & Haxby, 2006), potentially in the absence of any overall differences in activation between conditions at the group level (e.g., Soon, Brass, Heinze, & Haynes, 2008). In a study by Johnson, McDuff, Rugg, and Norman (2009), participants were exposed to items in the context of three different encoding tasks. A pattern classifier was trained to predict which of the three encoding tasks was being performed, using data from this encoding phase. In the retrieval phase, all items were presented in a single context, randomly intermixed. Nevertheless, when presented with the items in this manner, the pattern classifier was able to identify, at above chance levels, which encoding task had been used, although it was trained only on data from the encoding phase. Furthermore, classification accuracy was significantly higher for correctly recalled items than forgotten items or items associated only with a sense of familiarity.

Further evidence linking cortical reinstatement with retrieval success comes from a study by Xue et al. (2010), also using an MVPA approach. In a series of experiments, Xue et al. exposed participants to multiple presentations of various visual stimuli (faces, words). Subsequently, participants' memory for these stimuli was tested outside the scanner. Xue et al. found that the pattern of activity elicited by multiple presentations of the same item was more similar for items that were subsequently remembered than for items that were subsequently forgotten. This suggests that reinstatement of patterns of brain activity elicited by multiple presentations of the same stimulus may be functionally linked with subsequent memory for that stimulus. In the present study, we investigated similarity between brain activity elicited at encoding versus retrieval of items in a PM paradigm, to see if encoding-retrieval similarity could be linked with PM success in a similar manner. Like Xue et al., we used an MVPA approach to conduct a representational similarity analysis (Kriegeskorte, Mur, & Bandettini, 2008). However, unlike Xue et al., we compared similarity of brain activity between encoding and retrieval trials rather than investigating similarity between multiple encoding trials.

METHODS

The data set investigated in the present study was previously reported by Gilbert (2011). This previous report collapsed over trials involving correct and incorrect performance. Here, we focus on the direct comparison between successful and unsuccessful trials.

Participants

Thirty-two right-handed participants took part in the study (18 men; mean age = 25 years, range = 19–38 years). The experiment was approved by the local ethics committee, and all participants provided written informed consent before taking part.

Behavioral Task

A paradigm was developed in which participants repeatedly (a) formed, (b) maintained, and then (c) realized delayed intentions while engaged in an unrelated ongoing task. By pseudorandomly manipulating the duration of the maintenance period, it was possible to disambiguate these three phases (cf. Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000; see Figure 1). Participants performed a two-back task throughout the experiment, indicating on each trial whether the stimulus matched the item presented two trials previously (ISI = 2.7 sec). A PM task was embedded within this two-back task (cf. Reynolds et al., 2009). The stimuli consisted of pictures in half of the blocks and words in the other half. On *PM encode trials*, the stimulus was surrounded by a colored border (red or blue, counterbalanced across participants). On such trials, participants performed the two-back task as usual. However, they were asked to remember the stimulus and to press a third button rather than one of the buttons used for the two-back task, should they notice the same stimulus on a subsequent trial. Between two and six trials after each PM encode trial, the relevant stimulus was repeated (*PM retrieve trials*), after which it was not shown again. Thus, on PM retrieve trials, participants were required to interrupt their ongoing performance of the two-back task and instead press a different button to indicate that they had noticed the stimulus that they had encoded on the previous PM encoding trial. Crucially, the stimuli presented on PM retrieve trials were no different in appearance to those presented on other trials, and a two-back response to such stimuli would be possible if they were not detected as targets. Correct responses on PM retrieve trials, therefore, had to be self-initiated on the occurrence of the appropriate item rather than being strongly cued by the stimulus characteristics. This is one of the defining features of laboratory paradigms assessing PM, as opposed to other forms of dual-task paradigm (Burgess et al., 2003). The trials between PM encoding and PM retrieval trials were denoted *PM store trials*. During these trials, participants had to maintain a representation of the stimulus presented on the PM encode trial so that they could interrupt their performance of the two-back task when it was presented again on a PM retrieve trial.

On *baseline encode trials*, the stimulus was also surrounded by a different colored border (blue or red, counterbalanced across participants), but participants were instructed to treat these trials identically to any other without a border. These baseline encode trials were followed by *baseline store trials* and *baseline retrieve trials* in an identical manner to the PM trials, but there were no task requirements associated with these trials apart from the two-back task. Thus, baseline trials were matched perceptually with PM trials, but they did not require encoding, storage, or retrieval of delayed intentions.

Two different versions of the tasks were performed by two groups of 16 participants. The first version of the task was as above. In the second version of the task, there were four possible colored borders (red, green, blue, and yellow) and two PM response buttons instead of one. In this version of the task, two colors instructed participants to press one of two PM response buttons on the subsequent PM retrieval trial; the other two colors served as baselines. Thus, in this version participants had to remember which response to make, as well as which cue to detect. In all other respects, the two versions of the task were identical. For the present study, as in Gilbert (2011), results for the two task versions were collapsed.
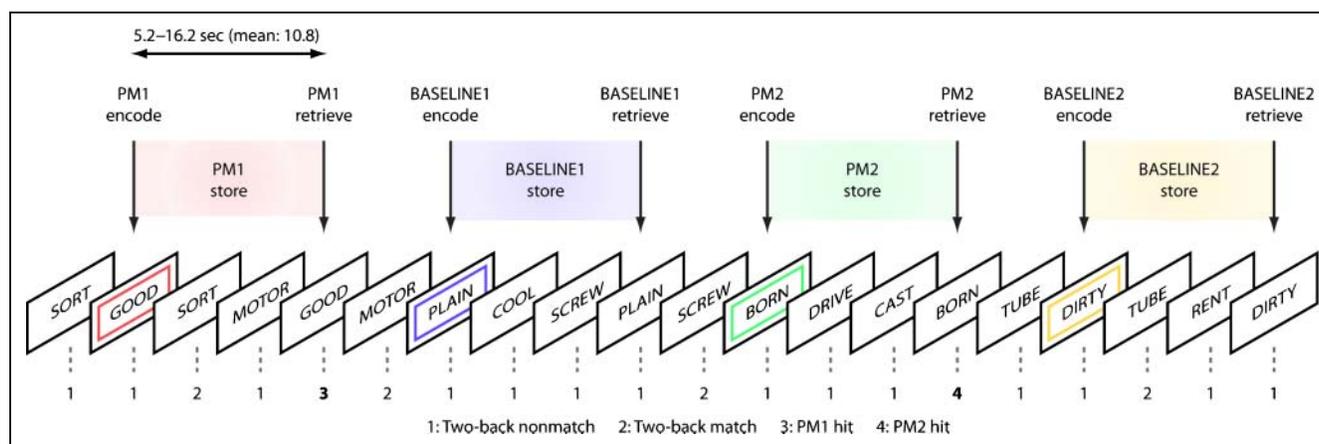
Figure 1. Schematic illustration of the task (reproduced from Gilbert, 2011, Figure 1). Participants performed a two-back task (responding with Button 1 to two-back nonmatches and Button 2 to two-back matches). Encode–store–retrieve cycles were embedded within this task. Stimuli were surrounded by colored borders on encode trials, with the assignment of colors to conditions counterbalanced between participants, for example, red: PM1 encode (press Button 3 when you encounter the stimulus again), green: PM2 encode (press Button 4 when you encounter the stimulus again), and blue and yellow: Baselines 1 and 2, respectively (no additional task requirements). PM and baseline cycles alternated. Version 1 of the task included PM1 and Baseline1 conditions only. In Version 2 of the task, the selection of PM1 versus PM2 for a particular PM cycle and Baseline1 versus Baseline2 for a particular baseline cycle was pseudorandomized. In half of the blocks, stimuli consisted of words, as illustrated; in the other half of blocks, picture stimuli were used.

Behavioral Procedure

Participants performed the task for six sessions, three featuring word stimuli and the other three featuring picture stimuli. Material type (words or pictures) alternated with each session and was counterbalanced across participants for the first session. In each session, participants viewed a series of 123 stimuli at the center of a screen, viewable via a mirror. Pictures were randomly selected images from the photographic collection "20,000 Photos" (Focus Multimedia Limited, Staffs, UK), including animals, cityscapes, landscapes, buildings, and vehicles, at a size of approximately 5° tall and wide. Words were randomly selected from the MRC Psycholinguistic database with the constraint that they were three to five letters long, associated with a familiarity rating of 400–600 and an imagability rating of 400–700. Words were presented in capital letters, Arial typeface, approximately 1° tall. On each trial, the stimulus was presented for 1.35 sec, followed by a blank screen for 1.35 sec. Participants could respond at any point in the trial.

To select stimuli for each session, random items were first assigned to each of the 123 trials. Following this, on a randomly selected 50% of trials, the item was replaced with the stimulus that was presented two trials previously; that is, these trials were made into two-back hits. The PM and baseline encoding and retrieval trials were then inserted. The first encoding event occurred on the second trial of each session, with the nature of the trial (PM or baseline) randomly chosen. On these trials, the stimulus was surrounded by a colored border (red or blue in Version 1 of the task and red, blue, green, or yellow in Version 2 of the task; the assignment of colors to conditions was counterbalanced across participants). Following this encoding event, there were between one and five store trials selected from a uniform distribution. The same stimulus that was presented in the encoding trial was then presented, followed by one filler trial and then the next encoding trial. Successive encoding trials always alternated between PM and baseline conditions. In Version 2 of the task, the two categories of PM and baseline conditions were randomly selected, with the constraint that they occurred in equal number within every session and no more than three in a row were of the same category (e.g., PM1, Baseline2, PM1, Baseline1, PM1, Baseline2 would necessarily be followed by a PM2 event). A total of 20 encode–store–retrieve cycles were presented in each session, preceded by one filler trial (the first trial of the session) and followed by two filler trials (the last two trials of the session) to yield a total of 123 trials in each session: three filler trials plus 20 cycles consisting of an encoding trial between one and five store trials (mean = 3), a retrieval trial, and one filler trial (i.e., 20 cycles averaging six trials each).

MRI Scanning

A 1.5 T Siemens TIM Avanto scanner with 32-channel head coil was used to acquire both T1-weighted structural images and T2*-weighted EPIs (64 × 64; 3.5 × 3.5 mm pixels; echo time = 40 msec) with BOLD contrast. Each volume comprised 31 axial slices (3.5 mm thick, oriented approximately to the AC–PC plane). Functional scans were acquired in six sessions, each comprising 135 volumes (approximately 6 min). Volumes were acquired continuously with an effective repetition time of 2.5 sec per volume. The first four volumes in each session were discarded to allow for T1 equilibration effects. Between the third and fourth functional scan, a 6-min T1-weighted structural scan was performed.

Data Analysis

Univariate Analyses

fMRI data were analyzed using the SPM8 software (www.fil.ion.ucl.ac.uk/spm/software/spm8/). The volumes were realigned, corrected for different slice acquisition times, normalized into 3 mm^3 voxels using the Montreal Neurological Institute (MNI) reference brain and fourth degree B-spline interpolation, and smoothed with an isotropic 8-mm FWHM Gaussian kernel. The volumes acquired during the three sessions with word stimuli were concatenated and modeled as one time series; the three sessions with picture stimuli were concatenated and modeled as a second time series. This was necessary because the data from some participants did not include both hits and misses in every session. The variance in the BOLD signal was decomposed with a set of regressors in a general linear model (Friston et al., 1995), using a mixed blocked and event-related design (Visscher et al., 2003). Within each of the two time series, separate regressors coded for (a) PM encode, (b) PM retrieve, (c) baseline encode, and (d) baseline retrieve events, using delta functions aligned to the onset of each event. In Version 2 of the experiment (with two different colors associated with the PM and baseline conditions), PM and baseline events were each coded with two separate regressors. Additional boxcar regressors coded for (a) PM storage and (b) baseline storage periods (again with additional regressors in Version 2 of the experiment), indicating the period between relevant encoding and retrieval events (mean duration = 10.8 sec, range = 5.2–16.2 sec). By pseudorandomly manipulating the duration of the storage periods, activity associated with these periods was distinguished from activity associated with the encode and retrieve events (Rowe et al., 2000). Each of these regressors was entered into the model twice, convolved with a canonical hemodynamic response function: once coding for encoding, storage, and retrieval of intentions associated with successful PM responses, and once coding for unsuccessful trials. Additional regressors modeled the mean of each concatenated run and the transitions between these runs. These regressors, together with the regressors representing residual movement-related artifacts and the mean over scans, comprised the full model for each session. The data and model were high-pass filtered to a cutoff of 1/128 Hz.

Parameter estimates for each regressor were calculated from least mean squares fit of the model to the data. Effects of interest were assessed in a random effects analysis as follows. Each contrast of interest was performed separately for the word and picture stimuli. The two resulting contrast images were then entered into a repeated measures ANOVA using nonsphericity correction (Friston et al., 2002) for assessment of results at the group level. All analyses averaged over the word and picture stimuli. An uncorrected height threshold of $p < .005$ was used in conjunction with an extent threshold determined by SPM8 to achieve $p < .05$ family-wise error correction for multiple comparisons across the whole brain volume.

Representational Similarity Analysis

In this analysis, preprocessing did not include normalization or smoothing. First-level models were generated for each participant in SPM8 as above. However, instead of four regressors coding for PM encode, PM retrieve, baseline encode, and baseline retrieve trials (or eight regressors in Version 2 of the task), every encode and retrieve trial was modeled with a separate regressor, that is, a total of 240 regressors (six sessions, each consisting of 10 PM encode, 10 PM retrieve, 10 baseline encode, and 10 baseline retrieve regressors). A searchlight approach was used, calculating pattern similarity for a sphere of voxels centered on each voxel in the brain in turn; this analysis was conducted twice: once for the three blocks with word stimuli and once for the blocks with picture stimuli. At each voxel, a spherical ROI was generated (radius = 3 voxels). Parameter estimates for each voxel within the ROI were extracted, for every encode-and-retrieve trial. Similarity between patterns of activity on each encode trial and its paired retrieve trial was assessed with the Pearson correlation coefficient (Xue et al., 2010) between parameter estimates for the two trials. This was calculated separately for each encode–retrieve pair. The mean similarity for unsuccessful PM trials was then subtracted from the mean similarity for successful PM trials; this difference score was assigned to the central voxel of the ROI. The resulting maps, consisting of a difference score for each voxel, were then normalized into MNI space (using the same normalization parameters as the univariate analyses) and smoothed using a Gaussian kernel (FWHM, 4 mm). This relatively small kernel size was used to avoid excessive smoothing, seeing as the searchlight analysis already imposes spatial smoothing on the data. The two resulting images (one from the word blocks and one from the picture blocks) were entered into a repeated measures ANOVA (within-subject factor: stimulus type) for assessment of results at the group level.

RESULTS

Behavioral Results

Accuracy in the two-back task was relatively high, marginally higher for words than pictures (words: 88%; pictures: 87%;

$F(1, 30) = 3.3, p = .08$). Mean RTs to words were marginally faster than to pictures in this task (words: 850 msec; pictures: 870 msec; $F(1, 30) = 2.95, p = .096$). On PM retrieve trials, participants successfully pressed the correct PM button approximately two thirds of the time, with higher accuracy for picture than word stimuli (pictures: 70%; words: 64%; $F(1, 30) = 5.9; p = .02$). The mean number of intervening trials between encode and store trials did not differ significantly between PM hits and PM misses (hits: 3.01; misses: 2.95; $F(1, 30) = 0.4, p = .54$).

Previous studies have suggested that RTs during an ongoing task can increase whereas participants maintain PM intentions, indexing a cognitive cost associated with storing intentions and/or monitoring for targets (Einstein et al., 2005; Smith, 2003). To test for this possibility, RTs during baseline store periods were compared with RTs during PM store periods, separately for PM store periods associated with subsequent PM hits versus misses. RTs during storage periods associated with both hits and misses (873 and 884 msec, respectively) were significantly slower than RTs during baseline storage periods (842 msec; $F(1, 30) > 18.2, p < .001$). However, RTs did not differ significantly between PM storage periods associated with subsequent hits versus misses ($F(1, 30) = 2.0, p = .166$). Thus, PM storage periods associated with subsequent hits versus misses yielded comparable intention maintenance costs. This pattern of results has previously been argued to suggest relatively automatic triggering of PM responses by the appropriate cue (Loft & Yeo, 2007). PM encode trials associated with subsequent hits had significantly faster RTs than those associated with subsequent misses (918 vs. 954 msec; $F(1, 28) = 7.6, p = .01$; two participants were excluded from this analysis because of missing data). Likewise, RTs on successful PM retrieve trials were significantly faster than those on unsuccessful PM retrieve trials (894 vs. 987 msec; $F(1, 30) = 15.5, p = .0004$).

fMRI Results: Univariate Analyses

Full results of the contrasts between PM and baseline conditions, separately for encode, store, and baseline trials, are described in Gilbert (2011). Briefly, the contrast of PM encode versus baseline encode trials was associated with widespread occipital, medial and lateral temporal, medial and lateral parietal, and subcortical activity. The contrast of PM store versus baseline store revealed prominent bilateral lateral frontal activation, along with activity in parietal cortex and cerebellum. The contrast of PM retrieve versus baseline retrieve trials revealed activation in bilateral pre- and postcentral gyrus, bilateral cerebellum, and posterior cingulate.

For the present study, the main contrasts of interest are between PM conditions associated with PM hits versus misses rather than contrasts between PM and baseline conditions. These results are summarized in Table 1 and Figure 2. There were no regions associated with greater

encoding-related activity for hits than misses. The reverse contrast identified a region of posterior cingulate showing greater activity associated with subsequently missed items than subsequently remembered items. During the store period, greater activity in superior parietal and premotor cortices was associated with subsequent PM hits; a region of posterior cingulate superior to the region identified in the analysis of encode trials was associated with subsequent misses. Finally, on PM retrieve trials, hits were associated with increased activation in pre- and postcentral gyrus, caudate, cerebellum, occipito-temporal cortex, posterior cingulate, and medial rostral pFC; misses were associated with increased activation in lateral pFC.

Representational Similarity Analysis

The analysis of pattern similarity between encode and retrieve trials revealed regions in medial rostral pFC, posterior cingulate, and medial and lateral parietal cortex, where pattern similarity between encode and retrieve trials was greater for hits than misses. These are illustrated in Figure 3A and summarized in Table 2. Thus, several brain regions exhibited greater similarity between patterns of response at encoding and retrieval for successful versus unsuccessful trials. There were no regions showing the reverse pattern (i.e., greater similarity for unsuccessful than successful trials) nor did the pattern similarity between encode and store or between

Table 1. Regions Showing Significant Differences in Activity for PM Hits versus PM Misses, Separately for Encode, Store, and Retrieve Phases

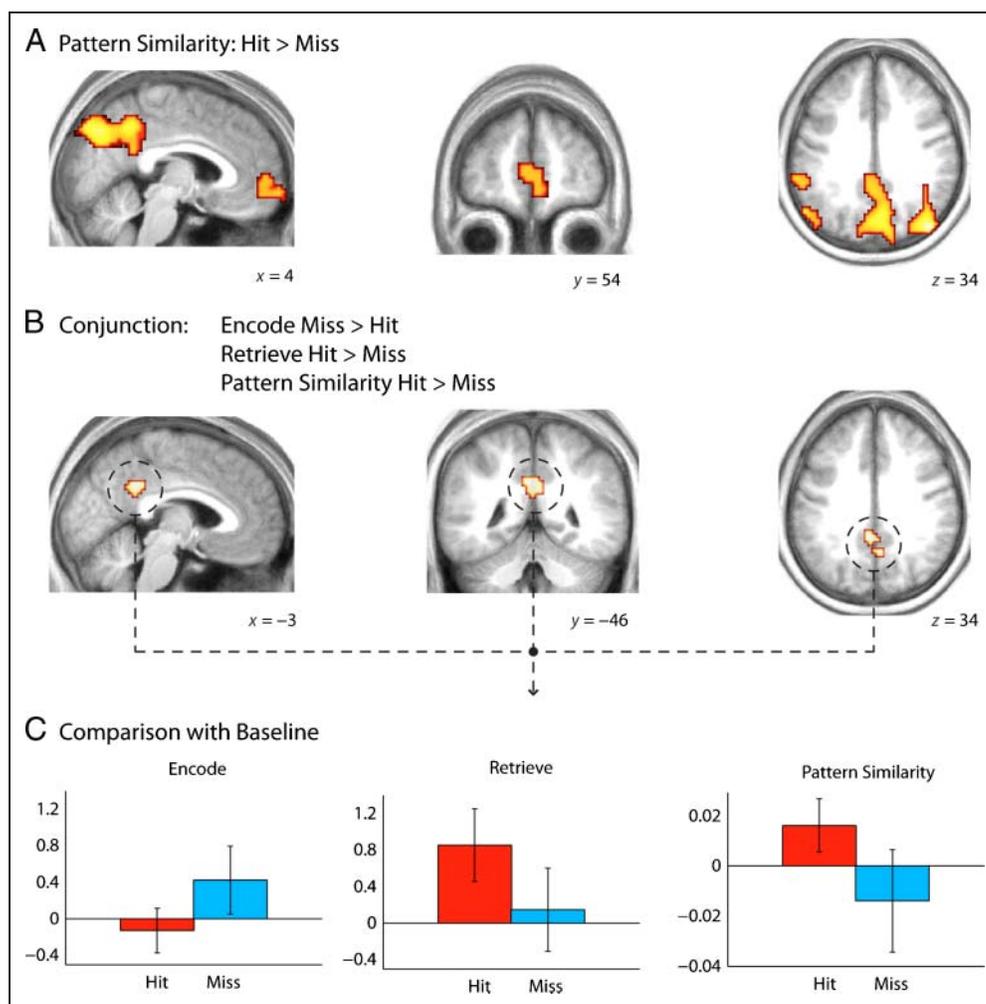| Region	BA	Coordinates	Z_{max}	Voxels (n)
Encode Hit > Miss				
No significant activations				
Encode Miss > Hit				
Posterior cingulate	23/31	0, −43, 28*	4.02	254
Store Hit > Miss				
Medial/lateral parietal cortex, premotor cortex	6/7/40	−45, −34, 52*	5.12	1128
Lateral parietal cortex	40	42, −43, 37*	3.99	164
Store Miss > Hit				
Posterior cingulate	30	6, −52, 7	4.38	505
Medial pFC	9/10	−3, 53, −5*	4.38	868
Lateral occipito-parietal cortex	18/19/39	−18, −85, 13	3.71	301
Retrieve Hit > Miss				
Pre-/postcentral gyrus	3/4	−36, −43, 58	5.42	828
Caudate	–	6, 23, −2	4.36	318
Caudate/thalamus/posterior cingulate	23	−27, 5, 22	4.34	634
Cerebellum	–	3, −67, −17	4.20	322
Medial pFC	9/10	3, 68, 19*	4.14	406
Postcentral gyrus	3	63, −13, 37*	4.07	419
Occipito-temporal cortex	19/37	−36, −76, 1	3.80	292
Retrieve Miss > Hit				
Lateral pFC	44	−45, 14, 28	3.81	290

BA = Brodmann's area.

*Significantly greater pattern similarity between encode and retrieve events for PM hits than PM misses ($p < .05$).
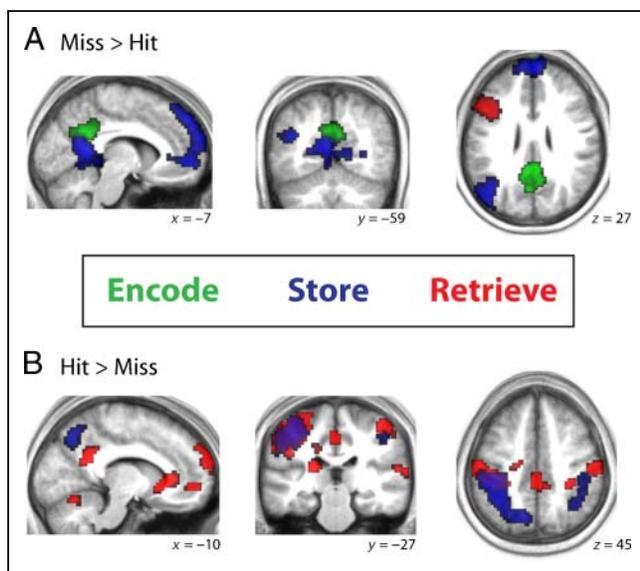
Figure 2. Regions showing significant differences in activity for PM hits versus PM misses, separately for encode, store, and retrieve phases. Results are plotted on the mean structural scan.

retrieve and store differ in any region between hits and misses.

As noted above, RTs for successful PM encode and retrieve trials were faster than corresponding RTs for unsuccessful trials. Might the pattern similarity results reflect this behavioral difference? To answer this question, the pattern similarity analyses were repeated after removing PM hit trials on a participant-by-participant basis so that RTs were matched between hits and misses ($F < 1$). In this analysis, the difference in pattern similarity between hits and misses remained significant in all five regions listed in Table 2 (PM hit > PM miss) at $p < .005$. Thus, these results do not simply reflect behavioral differences between hits and misses.

We next investigated whether the regions showing significant differences in pattern similarity between PM hits and misses also showed differences in overall levels of activation for hits versus misses, separately for encode and retrieve trials. This analysis used small volume corrections on the basis of 10-mm-radius spheres centered on the five peak coordinates listed in Table 2 for PM hit > PM miss. At this liberal threshold, two of the five regions showed significantly greater retrieval-related activity for hits than

Figure 3. (A) Regions showing significantly greater pattern similarity between encoding and retrieval trials for PM hits than PM misses. (B) Results of conjunction analysis showing common activation in posterior cingulate for the contrast shown in A, along with encode miss > hit and retrieve hit > miss. Results are plotted on the mean structural scan. (C) Contrast estimates for the comparisons of encode miss > hit and retrieve hit > miss and mean encoding-retrieval pattern similarity (Pearson correlation coefficient) for PM hits and misses. All analyses are normalized so that zero corresponds to the baseline condition. Error bars show within-subject 95% confidence intervals (Loftus & Masson, 1994) for the comparison between each bar and the baseline condition; thus, bars are significantly different from the baseline level when error bars do not cross the zero point. Note that all comparisons between hit and miss were significant; the error bars refer to the more conservative comparison between each condition and baseline.

Table 2. Results of Representational Similarity Analysis

Region	BA	Coordinate	Z_{max}	Voxels (n)
PM Hit > PM Miss				
Occipito-parietal cortex	19/39	45, −79, 34	4.09	369
Precuneus/posterior cingulate	7/23	−9, −79, 43	3.97	846
Lateral parietal cortex	39	−60, −67, 31	3.45	115
Lateral parietal cortex	40	−60, −43, 43	3.06	113
Medial pFC	10	−3, 53, 4	2.85	111
PM (Hits and Misses) > Baseline				
Occipito-parietal cortex	19/39	−30, −76, 34	4.01	254
Lateral parietal cortex	40	−45, −49, 46	3.59	95
Occipito-parietal cortex	19/39	36, −70, 31	3.63	163
PM Hit > Baseline				
Occipito-parietal cortex	19/39	36, −70, 31	4.61	1758
Lateral parietal cortex	40	−45, −49, 46	4.35	358
PM Miss > Baseline				
No significant voxels				

The table shows regions showing significantly greater pattern similarity between encoding and retrieval trials depending on trial type: PM hit, PM miss, or baseline. BA = Brodmann's area.

misses (45, −79, 34; −3, 53, 4). No region showed any significant difference at encoding between trials associated with subsequent hits versus misses. Thus, in at least three of the five regions listed in Table 2 (PM hit > PM miss), the pattern similarity results cannot be attributed to overall differences in mean activity between PM hits and misses on encode and retrieve trials.

These results indicate that the regions showing the most significant difference in pattern similarity between hits and misses generally did not differ in overall activation level on successful versus unsuccessful trials. What about the regions that did show significant differences in activation level between hits and misses, in the univariate analyses? Of the 14 regions identified in Table 1, six showed significantly greater encode–retrieve pattern similarity for hits than misses at an uncorrected threshold of $p < .05$ (these regions are marked with asterisks). Thus, there was partial overlap between the regions identified in the univariate and representational similarity analyses.

For comparison against pattern similarity results in the PM condition, we also investigated similarity between encode and retrieve trials in the baseline condition (i.e., trials perceptually matched to PM encode and retrieve events, but without the requirement to encode or retrieve a delayed intention; see Table 2). Collapsing over hits and misses, similarity between encode and retrieve trials was greater in the PM than baseline condition in occipito-

parietal regions. Similar regions showed greater pattern similarity for PM hit than baseline trials, but no regions showed greater pattern similarity for PM miss than baseline trials.

Within-item versus Cross-item Similarity

As well as investigating pattern similarity between corresponding encoding and retrieval events, we also investigated similarity between encoding and retrieval events associated with different items. This allowed us to investigate whether the pattern similarity results might represent state-dependent effects (e.g., an abstract PM "tag" representation, applied to all successful PM encode and retrieve trials, regardless of the stimulus) rather than item-specific representations. If pattern similarity between successful encode and retrieve trials reflects a general PM tag or a distinctive attentional state, then the similarity between encode and retrieve events from two successful trials might be more similar than the encode and retrieve events from two unsuccessful trials, even when the encode and retrieve events involved different stimuli. We, therefore, compared encode and retrieve events for (a) distinct pairs of items both associated with a PM miss and (b) distinct pairs of items both associated with a PM hit.

Seeing as fMRI time series are intrinsically autocorrelated, it was important for these analyses to match the

temporal interval separating hit–hit and miss–miss pairs; otherwise, results might reflect differences in similarity between pairs of trials that are close together versus far apart. To do so, each session was examined separately. Every possible pairwise combination of miss trials within that session was then considered. For each of these pairs, the hit trials within the same session were searched so that a pair could be found that were separated by the same number of trials. Only when this criterion was met were the relevant trials included in the analysis. When more than one pair of hit trials was found that were separated by the appropriate number of trials, a single pair was randomly selected. In this way, a set of cross-item miss–miss and hit–hit pairs was derived within each session, with matched intertrial intervals. The pattern similarities between encode and retrieve events for these trial pairs were then calculated, separately for hit–hit and miss–miss pairs, and analyzed as above. In this cross-item analysis, there were no regions showing significantly greater encode–retrieve similarity for hit–hit than miss–miss trials. This was true even after applying small-volume corrections to 10 mm spheres centered on the five peak coordinates from the original hit > miss pattern similarity analysis. Thus, greater encoding-retrieval similarity for PM hits than PM misses could only be detected on a within-item basis in the present study.

Overlapping Effects in Posterior Cingulate

Inspection of Figures 2 and 3 suggests that a common region of posterior cingulate showed significant effects of (a) greater activity associated with encode miss than encode hit, (b) greater activity associated with retrieve hit than retrieve miss, and (c) greater pattern similarity between encoding- and retrieval-related activity for hits than misses. To evaluate overlap between these three effects, a conjunction analysis was performed, with each contrast thresholded as standard (height threshold of $p < .005$ combined with a cluster threshold to achieve $p < .05$ FWE corrected). This revealed a cluster of 64 voxels in posterior cingulate significantly activated in all three analyses (peak MNI coordinate: $-3, -46, 34$), illustrated in Figure 3B. In a further analysis, we investigated signal change (or representational similarity) at the peak coordinate identified in the conjunction analysis (Figure 3C). For this analysis, we compared PM hit and PM miss trials separately to the baseline condition. At encoding, signal in posterior cingulate was significantly greater for PM miss than baseline ($t(31) = 2.3, p = .03$) but not significantly different between PM hit and baseline ($t(31) = 1.1, p = .3$). At retrieval, signal in posterior cingulate was significantly greater for PM hit than baseline ($t(31) = 4.4, p < .001$) but not significantly different between PM miss and baseline ($t(31) = .7, p = .5$). Representational similarity was significantly greater for PM hit than baseline ($t(31) = 3.1, p = .004$) but not significantly different between PM miss and baseline ($t(31) = 1.4, p = .18$).

DISCUSSION

This study showed clear differences in brain activity associated with successful versus unsuccessful realization of delayed intentions. Regional differences in overall levels of activity associated with PM success were evident during encoding of delayed intentions (mean = 11 sec before retrieval opportunity), during storage of delayed intentions and also during retrieval itself. Furthermore, the present results demonstrate the importance of the relationship between encoding- and retrieval-related activity, not just overall levels of activation, seeing as successful PM was associated with greater similarity between patterns of activity at encoding and retrieval.

PM Success versus Failure: Differences in Overall Regional Activity

The finding that brain activity at the point of intention encoding predicted subsequent PM success suggests one reason for unsuccessful PM performance: a failure to adequately encode the intention to begin with. This corroborates previous electrophysiological evidence demonstrating differences in brain activity between PM encoding trials associated with subsequent hits versus misses (West & Ross-Munroe, 2002). However, a simplistic model whereby the sole determinant of PM success is whether an intention was encoded into memory to begin with can be ruled out. Even on PM store trials preceding unsuccessful retrieval, RTs were slowed down relative to baseline store trials. Indeed, this slowing was statistically equivalent to the slowing observed on PM store trials preceding successful retrieval. Thus, even PM store trials before retrieval failure were associated with an intention maintenance cost (Smith, 2003), suggesting that an intention was encoded into memory on at least a proportion of unsuccessful PM trials. Regional levels of brain activity during store trials were also predictive of subsequent PM success versus failure. This suggests a second determinant of PM success: the extent to which participants rehearsed their PM intentions and/or monitored for PM retrieval cues, during the retention interval. Consistent with this suggestion, previous behavioral studies have indicated that PM success can be predicted from fluctuations in RT on trials before target presentation (West, Krompinger, & Bowry, 2005). Finally, and least surprisingly, regional brain activity differed between successful and unsuccessful PM retrieve trials. However, this finding is harder to interpret, seeing as successful and unsuccessful PM retrieve trials were associated with different motor responses and unsuccessful trials may have been associated with additional processes such as error detection or conflict monitoring.

It is notable that analysis of both encode and store trials yielded regions that showed greater activity associated with subsequent misses than hits, that is, a "subsequent forgetting" effect. Indeed, although distinct regions predicted subsequent memory and subsequent forgetting on

store trials, only regions associated with subsequent forgetting were identified at encoding. This suggests that unsuccessful PM might be associated with a "failure to deactivate" certain brain regions. One explanation for this might be that subsequent forgetting effects reflect activity in brain regions associated with performance of the ongoing (two-back) task at the expense of the embedded PM task. Alternatively, activity in these regions might reflect task-unrelated cognitive processes (e.g., mindwandering; Smallwood & Schooler, 2006). However, it is unclear how these accounts can explain the finding that subsequent forgetting was associated with activity in different regions at encoding and storage, which may play functionally distinct roles (Leech, Kamourieh, Beckmann, & Sharp, 2011). Whereas activity on store trials in a relatively dorsal region of posterior cingulate was associated with subsequent forgetting, a relatively ventral region was associated with subsequent forgetting on encoding trials, with virtually no overlap between the two regions (Figure 2). If these subsequent forgetting effects reflected activity related to the ongoing task or entirely task-unrelated activity, it is unclear why this activity should differ according to the factor that relates only to the PM task (phase: encoding or storage).

An alternative account might be that regions exhibiting a subsequent forgetting effect play a functional role in the PM task, despite higher levels of BOLD signal being associated with poorer performance. For example, one of the regions that showed greater activity during PM store trials associated with subsequent retrieval failure was medial rostral pFC. In the earlier study by Gilbert (2011), also analyzing the present data set, medial rostral pFC was found to maintain a representation of the forthcoming cue for action during store periods. This suggests that it played a functional role in the task, seeing as it represented task-relevant information. Thus, there is no necessary contradiction between a region being functionally involved in a task and also showing reduced overall levels of activity associated with better performance.

Comparison between signal in posterior cingulate for PM miss, PM hit, and baseline encode trials showed that PM miss trials were associated with significantly greater activity than baseline trials, with statistically equivalent activity for PM hit and baseline trials. This pattern of results is somewhat perplexing: Compared with the baseline condition, the PM condition led to greater encoding-related activation, but only for stimuli that were subsequently forgotten. One interpretation might be that the PM condition led to an overall increase in posterior cingulate activity, across both hits and misses (e.g., because of detection of the salient PM encode cue). In addition to this, successful encoding may have suppressed activation, compared with unsuccessful encoding. These two effects might cancel out on hit trials, leading to significant signal change only in the comparison between PM miss and baseline trials. By contrast, on retrieve trials, posterior cingulate activation was greater for PM hits than baseline trials, with statistically equivalent activation for PM miss and baseline trials.

PM Success versus Failure: Pattern Similarity between Encoding and Retrieval

As well as regions exhibiting overall differences in activity between trials associated with PM success versus failure, the present study also identified several regions in which patterns of activity were more similar between encoding and retrieval for successful than unsuccessful PM. This was not because of RT differences between successful and unsuccessful trials, seeing as these results remained significant even after RTs were matched between successful and unsuccessful trials. Additionally these findings were not reducible to overall differences in activity between successful and unsuccessful trials, which were absent in most regions at retrieval and all regions at encoding. Furthermore, the length of the retrieval interval (i.e., the number of intervening trials between encode and retrieve events) had no impact on PM success, ruling this out as a potential explanation of these results. Of course, different responses were associated with successful versus unsuccessful PM retrieve trials, by definition. However, this seems unlikely to explain the pattern similarity results, seeing as successful trials were associated with dissimilar responses on encode (ongoing) and retrieve (PM) trials, yet had greater pattern similarity than PM misses, which received an ongoing response for both retrieve and encode trials.

A particularly striking pattern of results was observed in posterior cingulate. The univariate analysis of results suggested that activity at encoding (miss > hit) was opposite to activity at retrieval (hit > miss). This pattern of results replicates recent studies using episodic memory paradigms (Daselaar et al., 2009; Daselaar, Prince, & Cabeza, 2004; Otten & Rugg, 2001; see also Uncapher & Wagner, 2009). In a related finding, Vannini et al. (2011) found that the magnitude of encoding-related deactivation (versus fixation) in this region predicted the magnitude of retrieval-related activation on a participant-by-participant basis. Some authors have suggested that these patterns of results constitute an exception to cortical reinstatement theories of memory, seeing as overall BOLD signal is more dissimilar between encoding and retrieval for hits than misses. However, in the present study, the representational similarity analysis showed that voxelwise patterns of activity were more similar for hits than misses, despite the "encoding-retrieval flip" (Daselaar et al., 2009) seen in overall levels of brain activity. Thus, the present results can be seen as either consistent or inconsistent with cortical reinstatement theories at different levels of analysis.

At the level of overall regional signal change, which might be conceptualized as indexing the occurrence of particular classes of cognitive process, the present results do indeed suggest the engagement of dissimilar cognitive processes between encoding and retrieval. For example, this could reflect the engagement of externally- versus internally-oriented cognitive processes (Vannini et al., 2011). But at the level of voxelwise patterns of activity, which might be conceptualized as indexing representational

content (Norman et al., 2006), the present results are consistent with cortical reinstatement accounts. Thus, the present results suggest that PM success (versus failure) is associated with relatively distinct cognitive processes between encoding and retrieval but also associated with relatively similar representational content between the two. Previous studies have shown that results from univariate and pattern analysis approaches need not mirror each other (Soon et al., 2008). The present results likewise show that recapitulation of representational content between encoding and retrieval need not imply consistent directions of overall signal change. Indeed, one interpretation of these findings, albeit speculative, is that opposite patterns of results between univariate and multivariate analyses can be seen if successful encoding and retrieval involves dissimilar cognitive processes operating on similar representational content.

The finding that greater similarity between encoding and retrieval was associated with successful PM is reminiscent of the results of Xue et al. (2010), wherein greater pattern similarity between multiple presentations of the same stimulus (i.e., multiple encoding opportunities) was associated with subsequent retrieval success. Unlike the study by Xue et al., we compared activity between encoding and retrieval events rather than multiple encoding events. However, it is of course possible that subsequent presentations of the same stimulus in the Xue et al. study were associated with memory retrieval linked to earlier presentations of the same stimulus (i.e., that encoding trials following the first presentation of the stimulus also served as retrieval trials, although this was not explicitly the task).

It is not clear from these results and the results of Xue et al. (2010) how far greater pattern similarity between trials reflects (a) a precursor to retrieval (i.e., similar brain activity on a second presentation of a stimulus to the first is itself responsible for triggering retrieval of further information about the earlier presentation, e.g., by autoassociative mechanisms; e.g., Norman & O'Reilly, 2003) or (b) a consequence of retrieval (i.e., presentation of the second stimulus triggers reinstatement of cortical activity associated with its earlier presentation, subsequently leading to similar patterns of activation between the two trials). Of course, a combination of these two effects would also be possible.

Evidence consistent with the first of these possibilities comes from PM studies reviewed in the Introduction, showing that delayed intentions are more likely to be realized when encoding and retrieval contexts overlap (Marsh et al., 2008). This suggests that similarity between brain activity at encoding and retrieval can be causally responsible for boosting PM success rather than simply a consequence of it. Evidence consistent with the second possibility comes from neuroimaging studies, in which items randomly intermixed within a single retrieval context reinstate cortical activity associated with their earlier encoding (e.g., Johnson et al., 2009; Johnson & Rugg, 2007). These studies suggest that memory retrieval may be associated with reinstate-

ment of prior cortical activity, regardless of preretrieval context.

In the present study, pattern similarity between encoding and retrieval was greater for PM hits than baseline but not significantly different between PM misses and baseline. Furthermore, after collapsing over hits and misses, pattern similarity was greater for PM than baseline trials. This suggests that the pattern similarity results, at least in part, arise from reinstatement of patterns of activation that were present at encoding, specifically on PM hit trials. In addition, the present results are consistent with the possibility that similar brain activity between encoding and retrieval is causally responsible for boosting recall of delayed intentions. In this case, a simple neurobiological mechanism suggests itself, whereby "implementation intentions" could lead to better PM performance than "goal intentions" (Gilbert et al., 2009; Gollwitzer, 1999). When we form an implementation intention, we think about a specific future cue that will allow it to be realized (e.g., "when I am in the restaurant tonight, I will order a salad"). By contrast, goal intentions are formed in the absence of such specific cues (e.g., "I intend to eat more healthily"). Seeing as imagining a particular situation can engender similar brain activity to actually being in that situation (e.g., Stokes et al., 2009), thinking about a specific cue when forming an intention will tend to increase the similarity between brain activity at encoding and retrieval. This could underlie at least part of the benefit of implementation intentions over goal intentions (although other factors are likely to be important as well; for discussion, see Ellis & Freeman, 2008).

As well as uncertainty on the temporal relationship between retrieval success and reinstatement of encoding-related brain activity, the present results are also ambiguous on what exactly is being reinstated on retrieval trials. Further studies will be required to clarify the overlap in representational content between successful encoding and retrieval trials. This overlap might reflect reinstatement of item-specific information, general contextual information shared between the two presentations of the stimulus, or an abstract "PM tag" associated with the relevance of the stimulus for the PM task. The cross-item similarity analyses showed that differences in pattern similarity between hits and misses could only be detected on a within-item basis in the present study. However, seeing as the cross-item analysis had less power than the within-item analysis (because of the temporal separation of cross-item pairs), it is premature to rule out a contribution of state-dependent effects to these results. One way to address the question of item versus state-related effects in future studies would be to include repeated presentations of the same items and then examine temporally separated within-item versus cross-item similarity.

In summary, this study identifies brain activity distinguishing successful and unsuccessful PM at several time points and in terms of both overall regional activity and specific patterns across multiple voxels. Results are consistent with the view that PM is supported by multiple underlying

cognitive mechanisms and that failures in PM can occur for different reasons (e.g., [a] inadequate or absent encoding of the intention into memory to begin with, [b] failure to maintain it effectively over time, and [c] changes in context between encoding and retrieval). This raises the possibility that PM deficits in different groups (e.g., various clinical populations) could be traced to distinct underlying problems. The present results suggest a method whereby different underlying PM deficits could be identified, even in the context of the same behavior: a failure to act on one's intentions.

Acknowledgments

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