Encoding the future: Successful processing of intentions engages predictive brain networks

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ABSTRACT

Evidence from cognitive, patient and neuroimaging research indicates that "remembering to remember" intentions, i.e., prospective memory (PM) retrieval, requires both general memory systems involving the medial temporal lobes and an executive system involving rostral PFC (BA 10). However, it is not known how prospective memories are initially formed. Using fMRI, we investigated whether brain activity during encoding of future intentions and present actions differentially predicted later memory for those same intentions (PM) and actions (retrospective memory). We identified two significant patterns of neural activity: a network linked to overall memory and another linked specifically to PM. While overall memory success was predicted by temporal lobe activations that included the hippocampus, PM success was also uniquely predicted by activations in additional regions, including left rostrolateral PFC and the right parahippocampal gyrus. This finding extends the role of these structures to the formation of individual intentions. It also provides the first evidence that PM encoding, like PM retrieval, is supported by both a common episodic memory network and an executive network specifically recruited by future-oriented processing.

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Introduction

The faculty for acting out postponed intentions at the appropriate time, i.e., "remembering to remember," is described as prospective memory (PM). Intact PM has been linked with numerous abilities including multitasking, strategic navigation, normal social behavior and planning in general (Kliegel et al., 2007). An understanding of the brain basis of PM has begun to emerge from various neuroimaging-based comparisons of PM and retrospective memory (RM), i.e., memory for the past. For instance, event-related potential (ERP) evidence indicates that neural responses can distinguish successful from unsuccessful PM encoding (West and Ross-Munroe, 2002; West et al., 2003) and PM from RM encoding (Leynes et al., 2003). However, as most functional neuroimaging investigations have focused on PM retrieval – the realization of an intention and concomitant retrieval of the intention from memory – the specific mechanisms by which the brain initially encodes intentions is not well understood. As this ability appears poised at the intersection of a number of emerging research areas in cognitive neuroscience, such as mental time travel and the mental generation of future events (Schacter et al., 2007; Suddendorf and Corballis, 2007; Tulving, 2008),

better understanding of PM formation appears a ripe topic for exploration. Here, we present the first investigation of the processes underlying successful intention formation to employ functional magnetic resonance imaging (fMRI).

Ideas have varied regarding the relationship of PM to other forms of memory. Early discussion focused on whether PM was merely a special application of RM (Crowder, 1996; Dalla Barba, 1993; c.f. Kvavilashvili, 1987; Ellis, 1996). More recently, cognitive psychologists have favored the view that PM is supported by interactions between a general memory system and a system supporting timely retrieval (Graf and Uttl, 2001; McDaniel and Einstein, 2000). Consistent with this view, a recent study utilizing ERPs identified two neural networks associated with retrieval: one linked to both PM and RM, and a second to PM only (West and Krompinger, 2005).

The notion that PM depends on interactions with a general RM system has been substantiated further by evidence highlighting the role of prefrontal cortex (PFC), especially rostral PFC (BA 10), in complementing the function of the medial temporal lobes (MTL). Temporal lobe patients have impairments in both PM and RM; in contrast, frontal lobe patients demonstrate impaired PM but relatively preserved RM when appropriate cues are available (Burgess et al., 2007a), although aspects of RM may still be impaired (Stuss and Alexander, 2005; Wheeler et al., 1995). Activation of both rostral PFC and the MTL is often observed in neuroimaging contrasts of PM against various baselines (Burgess et al., 2001; Okuda et al., 1998,

2003; Simons et al., 2006), especially rostrolateral PFC, which is linked with the stimulus independent thought that may be necessary for setting up internal contingencies (Burgess et al., 2007b). Sustained ERPs over frontal scalp regions predict later PM (Leynes et al., 2003; West and Ross-Munroe, 2002; West et al., 2003), also suggesting that frontal areas are involved in forming intentions. In light of such evidence, some have proposed that MTL supports both memory types with additional support for PM from rostral PFC (Cohen and O'Reilly, 1996; Okuda et al., 2003). This proposal is consistent with the view that the frontal lobes play a role in organizing hippocampal input and output (Moscovitch, 1994) and maintaining a temporal context for episodes (Milner, 1982; Milner et al., 1991; Moscovitch, 1992). Notably, it is also consistent with evidence showing that both the hippocampus and rostral PFC contribute to the construction of future events (Addis et al., 2007).

What remains unclear is the role these systems play in initially forming intentions. For instance, it is unknown what processes involved in forming intentions are unique or are shared with those normally required for imagining actions; it is also not known what brain areas might be involved. Accordingly, in the current study, we explored the neural predictors of successful PM and RM encoding using fMRI. PM is believed to depend on both successful association of prospective cues with an intention, in addition to full retrieval of that specific intention (Cohen et al., 2001; McDaniel and Einstein, 2000). It is generally understood that successful PM retrieval depends first on the identification of the prospective cue (that is, remembering that *something* must be done) and second on the ability to remember and perform the appropriate action. The present study deals only with the first phase; the second phase is usually considered to reflect standard RM processes. As conventional tests for prospective remembering, such as those used in an fMRI study by Eschen et al. (2007), have yielded insufficient prospective responses to support a neuroimaging contrast of remembered and forgotten trials, we limited the scope of our test to the identification of prospective cues as an initial step towards understanding how PM is encoded. To provide an RM reference condition, we also explored successful identification of imagined actions. Based on observations that both RM and PM retrieval are impaired by MTL damage, we predicted that MTL activation would be linked with both successful RM and PM encoding. Based on evidence linking both PM and future event construction to rostrolateral PFC, we predicted that activation in this area would be linked specifically with successful PM encoding.

Materials and methods

The current study was conducted in three phases: (1) a pre-scanning familiarization phase, in which participants were shown various scenes; (2) a scanned study phase during which participants associated scenes with either future intentions or present imagined actions; and (3) a post-scanning phase in which participants completed a cue identification task. The first phase allowed us to include familiar lures as a test of the cue identification task without sacrificing scanner time. During fMRI scanning in phase 2, we asked participants to study scenes for a later memory test either as cues for intentions or as settings for imagined actions. In a third phase that followed scanning, we tested their ability to distinguish prospective cues from other scenes. Data from the phase 3 cue identification task served to categorize encoded scenes from phase 2 as either hits or misses.

Participants

Thirteen right-handed volunteers from the Greater Toronto Area, all fluent in English with normal or corrected-to-normal vision and hearing, participated in the experiment (9 female; aged 22–35 years, mean age 25.8). Participants were screened for the absence of neurological and psychiatric conditions and received financial remuneration for their participation. In addition to these 13, one person participated but was excluded for not following instructions, another for chance-level performance on the behavioral task, and a third due to excess imaging artifact. The protocol for this experiment was approved by the Research Ethics Board at Baycrest Hospital in Toronto.

Stimulus materials

A collection of 384 indoor and outdoor scenes was prepared. Pictures were selected from photographs containing emotionally neutral landscapes and objects that featured no human or animal subjects nor any well-known landmarks (320 × 240 pixels). For each participant, this collection of scenes was randomly split into two sets of 192 images: a "familiarization" set and a "novelty" set.

Experimental tasks

Participants were informed that the study consisted of three parts that together would take approximately two and a half hours to complete, and that their memory would be tested at the end of the experiment. In the phase 1 pre-scanning familiarization task, participants viewed the familiarization set of scenes in a mock fMRI scanner (Fig. 1). This setting was used in order to maximize the contextual match between familiarization and the study phase, which involved fMRI scanning. Participants were informed that their memory would not be tested for the stimuli presented in this phase, but that they were to view each of the scenes in order to familiarize themselves with the stimulus set. Each image was presented for 2.2 s and was followed by a 0.8 s fixation. The full set of familiarization scenes was presented in random sequence three times. To ensure that participants were alert for this task, they were occasionally prompted to press a button to continue.

During fMRI scanning in phase 2, participants responded to scenes under "action" or "intention" instructions (Fig. 1). The particular task to perform for short series of images was specified by the word "action" or "intention" appearing both before each series and above each image. For scenes associated with action instructions, participants were instructed to imagine themselves performing any action in the scene as they viewed it. Participants were not informed that these items would appear later in the experiment. For scenes associated with intention instructions, participants were instructed to use the scene as a reminder to perform any action the next time it appeared. That is, they were explicitly told that the intention scenes would appear again in the experiment and that they would need to remember their generated intentions spontaneously. Following the presentation of each scene, participants were asked to press a key on an MR-compatible keypad to indicate successful generation of an action or intention. Participants practiced both phase 2 tasks prior to the beginning of scanning and were asked to provide examples of actions and intentions that they generated during the practice session. They were given feedback as to whether these actions and intentions were appropriate, and when they were not, participants were given further coaching until they mastered the tasks.

Because both the action and intention task involved viewing randomly allocated visual scenes and generating a self-performed action, the tasks were similar in terms of perceptual processing, motor planning and autobiographical focus. In addition, verbal reports from two additional participants tested outside the scanner indicated that generated actions and intentions both overwhelmingly reflected the basic utilization of prominent objects in the scenes. For example, for a scene featuring swings, "playing on the swings" was described as an action. For a scene with a desk and phone, "make a phone call when I see the phone again" was described as an intention. In scenes that did not feature a utilizable object, responses still reflected simple actions that could be immediately performed in the scenes. For a scene featuring a forest, "bird-watching in the woods" was described as an
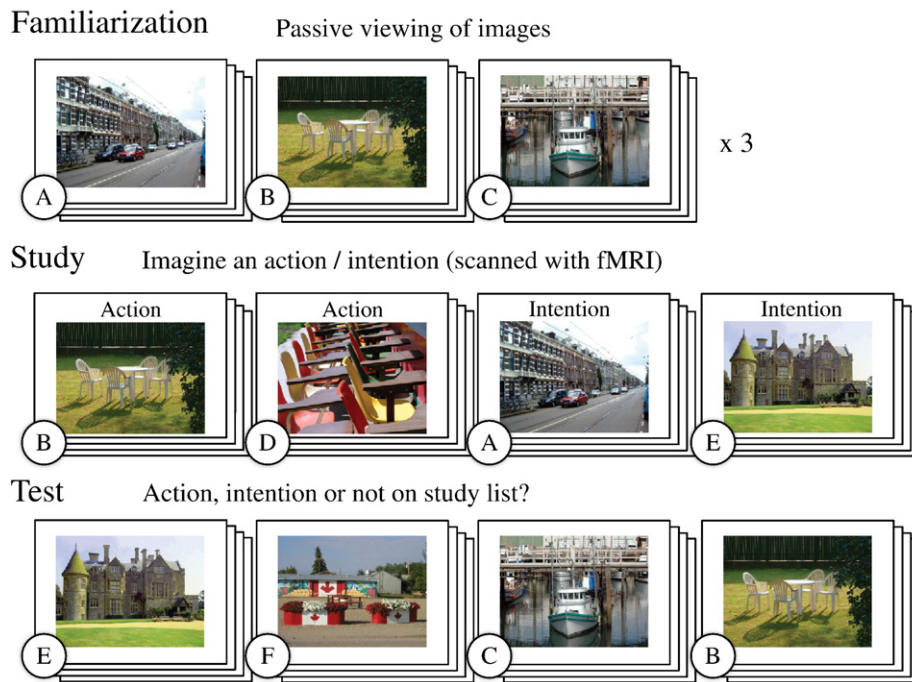
Fig. 1. Schematic of experimental design. The experiment consisted of three phases: familiarization, study and test. In the familiarization phase (top), participants passively viewed images in a mock fMRI scanner (A–C). In the study phase (middle), participants studied familiar (A, B) and novel (D, E) scenes under either "action" or "intention" instructions while being scanned in a real fMRI scanner. In the test phase (bottom), participants decided at a computer whether each scene was studied as an action (B), studied as an intention (E), or was not studied in the study phase (C, F).

action and "go for a walk when I see the forest" was an intention. This approach seems appropriate, as high relatedness between cues and intentions has been shown to enhance PM performance (Cohen et al., 2001).

Data were collected in a mixed design over four functional runs, each containing eight study blocks of eight images. Half of the blocks contained scenes studied in phase 1 and the remaining blocks contained previously unseen images. Each block was preceded by 2 s of instruction and 2 s of fixation and was followed by 12 s of fixation. Each image was presented for 4 s and followed by 2 s of fixation. In total, 256 pictures were presented in phase 2, 64 in each of the four block types: novel action, novel intention, familiar action and familiar intention; each run contained two blocks of each type presented in a random sequence. Only 64 images from the familiarization phase and 64 additional novel scenes were not presented during phase 2. A different random allocation of scenes to the various conditions was made for each participant.

In a cue identification test in phase 3 that took place in a quiet testing room, participants viewed on a computer all 384 of the images from the familiarization and novelty sets in a random sequence. This included both the 256 images encountered during scanning in phase 2 as well as 64 familiar lure images (presented in phase 1) and 64 entirely novel lure images (not presented during phases 1 or 2) that were not presented during scanning (Fig. 1). Each image was presented for a maximum of 4 s and was followed by 1 s of fixation. For each image, participants were asked to indicate whether the scene was studied as an intention, studied as an action, or not studied during scanning. When participants signaled that a picture was studied, they were prompted to report whether they remembered the specific action or intention associated with the picture, or knew that the picture was an action or intention but without a specific recollection. Participants were given unlimited time to make this decision.

MRI acquisition

All imaging was performed on a 3-Tesla whole-body MRI system (Siemens, Erlangen, Germany). For each participant, 28 contiguous 5-mm-thick axial oblique slices were obtained that were positioned to captured the entire brain volume (determined based on initial scout images). The field of view was 200 by 200 cm (64×64 matrix) providing an in-plane resolution of 3 mm. T2-weighted EPI image acquisition was used for all functional scans (TE = 30 ms; TR = 2000 ms; flip angle = 70°). Each run involved the acquisition of eight initial stabilization volumes that were discarded and 264 task volumes (33 volumes per block with eight blocks). An additional T1-weighted high-resolution MRI volume was obtained for the display of neuroanatomy during the same experimental session using a 3D MPRAGE pulse sequence in the same orientation as the functional scans (160 slices; 1 mm thick; FOV = 256×256 mm; 192×256 matrix; 1 mm in-plane resolution).

Preprocessing

Initial image preprocessing was performed using FSL (FMRIB Software Library version 4) (see Smith et al., 2004). Following motion correction of the T2-weighted functional images, Probabilistic Independent Component Analysis (ICA) was conducted on a run-by-run basis to identify and remove high-amplitude time course spikes as well as residual motion artifacts, high-frequency scanner noise and artifacts attributable to gradient timing errors. This step was performed upon the data using a semi-automatic procedure involving MELODIC (Beckmann and Smith, 2004) and detailed inspection of ICA components by two raters. Timing differences between slices in the same volume were corrected using SPM software (Statistical Parametric Mapping version 5). Functional data were then transformed into standardized MNI space (Cocosco et al., 1997), resampled into isotropic voxels ($3 \times 3 \times 3$ mm), and smoothed using a 3D Gaussian kernel with a full-width at half maximum value of 6 mm.

Statistical analysis

To evaluate how task and encoding success characterized participant neural responses during the encoding phase, we conducted a multivariate assessment of the event-related data, which permitted comparisons using the post-scan cue identification task in

phase three. Because remembered and forgotten cues from this task were sequenced approximately randomly within each block (as determined by participants' performance), jittered timing was not needed for this analysis. We examined the percent signal change in each event from 2 to 10 s following each stimulus onset relative to onset of a reference scan, as taken 2 s after trial onset, to allow for a haemodynamic return to baseline from the preceding trial. We determined that this window was optimal for response detection on the basis of hemodynamic response function modeling as well as inspection of global intensity data.

All analyses were performed using mean-centred partial least squares (PLS) analysis in PLSGUI (McIntosh and Lobaugh, 2004). This procedure produced a set of latent variables (LVs) representing the strongest overall patterns expressed in the fMRI data that may be described by a contrast of the experimental tasks. Mean-centering was applied to the fMRI data matrix to generate an input matrix with signal values expressed as deviations from zero. Singular value decomposition was performed upon the input matrix to identify LVs, which consisted of a singular image, singular profile and singular value (SV). The singular profile described a best-fit contrast of all experimental conditions that was used to generate a singular image describing the relationship of all voxels to the contrast over the full time course. Each LV was evaluated as a whole for significance using the SV, an index of the covariance between the singular image and singular profile as well as an index of the percentage of overall covariance between the brain data and the design accounted for by the LV. The threshold for LVs identified in these analyses was set at $P<0.05$, as computations were not done on a voxel-by-voxel basis but on the entire pattern. Five hundred permutation tests were run to establish the significance of each SV and 100 bootstrap tests were used to estimate voxel standard error. For the purpose of identifying brain voxels contributing to the pattern expressed in an LV, maps were created to express the ratio of voxel salience over estimated standard error (i.e., bootstrap ratio; BSR.).

In order to characterize LVs in terms of a specific spatial distribution, we inspected BSR maps of LVs for clusters of reliably differentiated voxels. A cluster was defined as any 24 or more contiguous cortical or subcortical voxels above a BSR of 2.575 and a peak of 3.29 (approximately corresponding to a minimum spatial extent of 648 mm³, a 99% confidence interval and a 99.9% confidence interval) that was no closer than 12 mm to another cluster. In the event-related analysis, we specifically identified those clusters activating during the peak hemodynamic response at 4–6 s after stimulus onset. Labels for identified clusters were obtained by transforming peak MNI coordinates into Talairach coordinates using a best-fit icbm2tal transform (Lancaster et al., 2007) and localizing these coordinates in a Talairach brain atlas (Mai et al., 2004).

Results

Behavioral results

Participants successfully created actions and intentions for nearly all of the presented items, as measured by the proportion of items to which participants responded during fMRI scanning ($M=0.96$, SD = 0.04). In support of the notion that forming and encoding an intention requires further preparatory processes beyond those normally required to imagine and encode an action, all but one of the participants later indicated that it took more effort to create intentions. Consistent with this claim, participants indicated more successful generations of a response under action instructions, $M=0.98$, SD = 0.02, than under intention instructions, $M=0.94$, SD = 0.06, $t(12)=2.97$, $P<0.05$, although no significant differences in reaction time were observed between pictures studied under action instructions, $M=2783$ ms, SD = 640 ms, and those studied under intention instructions, $M=2895$ ms, SD = 501 ms, $t(12)=1.60$,

$P=$ n.s. Items for which no response was collected during the study phase (i.e., items for which the participant had generated neither an action nor an intention) were omitted from further behavioral and functional neuroimaging analysis.

To confirm objectively that all participants successfully encoded the scenes presented during the study phase, a picture accuracy score was obtained for each participant using scores from the post-scanning phase 3 cue identification task. Accuracy scores were computed for each condition by calculating the proportion of hits among studied items and subtracting the rate of false alarms to lures. Participants obtained accuracy scores that were well above chance, $t(12)=8.36$, $P<0.001$, although accuracy scores were higher for scenes presented under action instructions, $M=0.47$, SD = 0.19, chance = 0, than for those presented under intention instructions, $M=0.35$, SD = 0.15, $t(12)=3.90$, $P<0.005$. While this pattern appears to run counter to observations of "intention superiority" in the PM literature (Goschke and Kuhl, 1993), the intention superiority effect describes memory for intentions observed during their retention interval (Maylor et al., 2000), whereas we investigated the cued retrieval of intentions. In addition, intention memory is known to be reduced by additional cognitive demands during encoding (Einstein et al., 1997). The demanding study environment (a noisy fMRI scanner) and task (involving a large number of items) may have reduced the overall efficacy of intention formation.

Functional neuroimaging results

We sought to identify the neural predictors of encoding success for intentions and actions as measured in the subsequent cue identification task in phase 3. To this end, we ran an event-related PLS analysis on the fMRI data, using the subsequent memory data to classify items as hits or misses for each subject in each of the four block types (instructions × novelty). Scenes correctly identified as action or intention cues were classified as hits; all other responses, including null responses, were classified as misses. It should be noted that no pair-wise comparisons were tested in our analysis; only multivariate statistical analyses were performed. Our data-driven analysis specifically (1) identified those orthogonal spatiotemporal patterns and designs that captured the greatest amount of brain variance, and (2) isolated patterns among these that captured a greater-than-chance proportion of the total variance. No further tests were performed to evaluate other possible contrasts, in line with the rationale of this multivariate approach (McIntosh and Lobaugh, 2004). Our analysis revealed two significant patterns of neural activity.

The singular profile of the first pattern of neural activity (LV1) dissociated hits and misses on the cue identification task across block types, $SV=17.96$, crossblock = 25.45%, $P<0.05$ (Fig. 2). We interpreted this pattern as an overall predictor of encoding success. Inspection of the BSR map associated with the pattern revealed that voxel clusters associated with this general encoding network were primarily located in the right temporal lobe. These included clusters in the right posterior hippocampus and right fusiform gyrus (Fig. 2a,b) as well as bilateral clusters in the posterior inferior temporal gyrus (Table 1). Decreases in activity at the right temporoparietal junction also predicted successful encoding (see Uncapher and Wagner, 2009 for a review of negative subsequent memory effects in this area). Outside of the temporal lobe, the only cluster associated with this first neural network was located in the right lateral occipital gyrus.

The singular profile of the second pattern of neural activity (LV2) also dissociated hits and misses on the cue identification task, but only for items encoded under intention instructions, $SV=16.09$, crossblock = 20.41%, $P<0.05$ (Fig. 3). One of the two miss conditions in the action task loaded positively onto the pattern, hinting at an interaction (i.e., poor encoding of actions when the observed neural network is active), although the other action miss conditions did not share this pattern. We interpreted this pattern as specifically
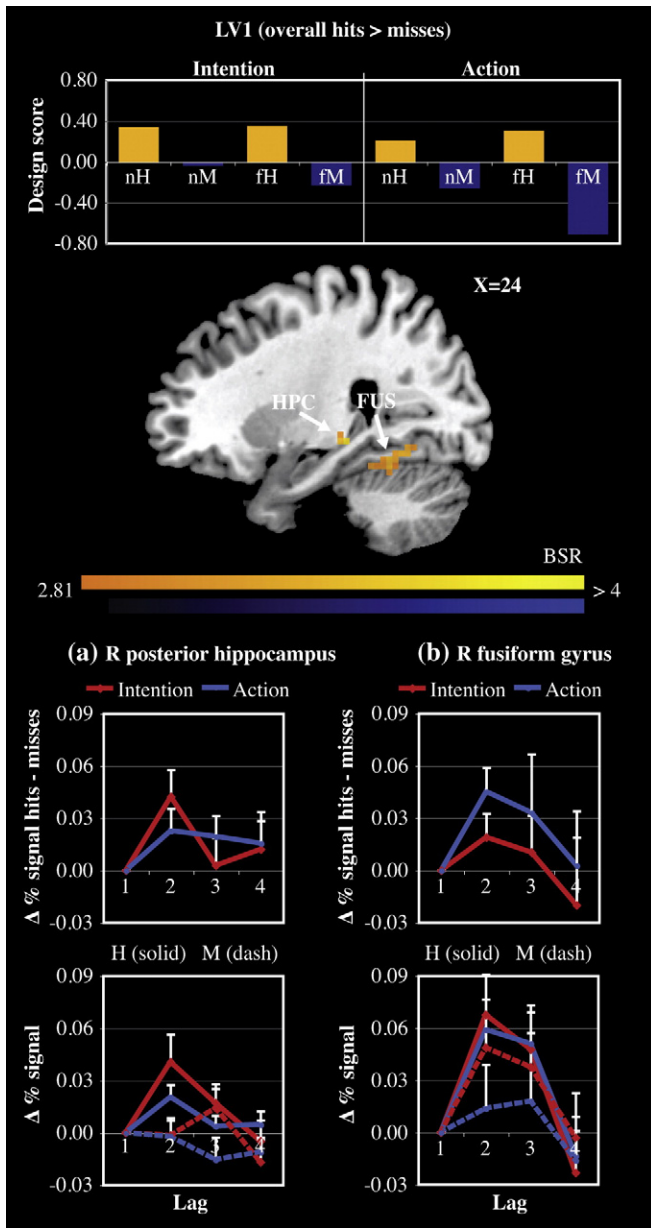
Fig. 2. Episodic memory network associated with both RM and PM. At top is a bar plot of design scores indicating how strongly each condition covaries with responses of the network described in Table 1 (hits, H, and misses, M, in novel and familiar conditions are designated by the prefixes "n" or "f" respectively). This profile can be interpreted as an overall encoding network that supported subsequent memory for all types of material. The sagittal brain image depicts voxel clusters that reliably covaried with this contrast profile in (a) the right hippocampus (HPC) and (b) the right fusiform gyrus (FUS) (anterior is left; positive covariances are in orange; negative in blue), overlaid on an MNI anatomical template brain. The line plots at bottom depict the subsequent memory effects (difference in percent signal change between hits and misses + 1 SE) that were associated with action and intention items in the peak voxel of the indicated region.

predicting later PM. Notably, no significant pattern was present that uniquely predicted subsequent memory for items studied under action instructions. In other words, memory for actions and intentions was predicted by a common neural network (LV1), but memory for intentions was also supported by a second neural network (LV2). This latter network was associated with a more spatially distributed set of brain responses (Table 2) than was observed in the first network. Regions that specifically predicted successful memory for intentions included a lateral PFC region that included left lateral

rostral PFC (Fig. 3a), a region overlapping the left frontal operculum and insular gyrus, and bilateral premotor cortex. In the temporal lobe, the network included the left posterior superior temporal gyrus and the right parahippocampal gyrus (PHG, Fig. 3b); visual and parietal areas were also present. Activation in a separate set of regions characterized by a medial tendency negatively predicted subsequent memory for intentions. These included the cingulate gyrus, left superior parietal lobule and occipital cortex; more lateral regions included right parietal and occipital cortices.

Discussion

Current theoretical proposals about PM posit that memory for intentions is supported by both a generic memory system and an executive system (Graf and Uttl, 2001; McDaniel and Einstein, 2000). PLS was ideally suited for testing this hypothesis due to its ability to cluster or dissociate cognitive events on the basis of brain activity. Along these lines, by loading responses from the phase 3 cue identification task onto an event-related analysis, we found that the greatest proportion of covariance was accounted for by a network predicting subsequent memory for both actions and intentions, followed by a network that predicted memory for intentions only. No stable network was present that predicted memory for actions only. While the two networks were statistically distinct both spatially and in terms of their singular profile, it is reasonable to conceptualize them as an integrated system supporting PM, considering that statistically orthogonal patterns of brain activity have been found to interact in other applications of PLS (McIntosh et al., 2003). This result is comparable to a recent PLS analysis of event-related potential data collected during retrieval of RM and PM, which revealed one network associated with RM and PM hits and a second associated with PM hits only (West and Krompinger, 2005). The current study is unique, however, in that it provides the first evidence these same dynamics are associated with memory encoding. Moreover, as overall memory was superior for actions over intentions, the additional activity we found to be associated with PM cannot be dismissed as a levels of processing effect, where superior memory is linked with additional cognitive and neural processing (Craik and Lockhart, 1972). Rather, and in line with functional neuroimaging observations revealing overlap in that the brain areas that support RM encoding and retrieval (Persson and Nyberg, 2000; Polyn et al., 2005; Wheeler et al., 2000), our result strongly suggests that a common encoding and retrieval system underlie PM that involve both generic episodic memory

Table 1
Activated voxel clusters in LV1 of the event-related fMRI analysis.

Region	BA	Hemi.	Peak coordinates			Peak BSR	Spatial extent (mm³)
			X	Y	Z		
Hits > misses (overall)							
Temporal lobe							
Hippocampus	–	R	27	−30	−6	3.73	945
Inferior temporal gyrus	37	L	−60	−60	−18	4.11	783
	37	R	54	−63	−21	4.50	702
Fusiform gyrus	19/37	R	21	−63	−9	4.21	3132
Occipital lobe							
Occipital gyrus	18	R	15	−105	12	3.88	1026
Misses > hits (overall)							
Temporal lobe							
Superior temporal gyrus	39	R	66	−51	27	6.30	800

This LV corresponded to a contrast of hits and misses across instruction conditions.
Note: Peak locations are described using MNI standardized space (Cocoso et al., 1997). Clusters were thresholded at BSR 2.575 (P<0.01) with a minimum extent of 24 voxels and a minimum peak of BSR 3.5 (P<0.001).
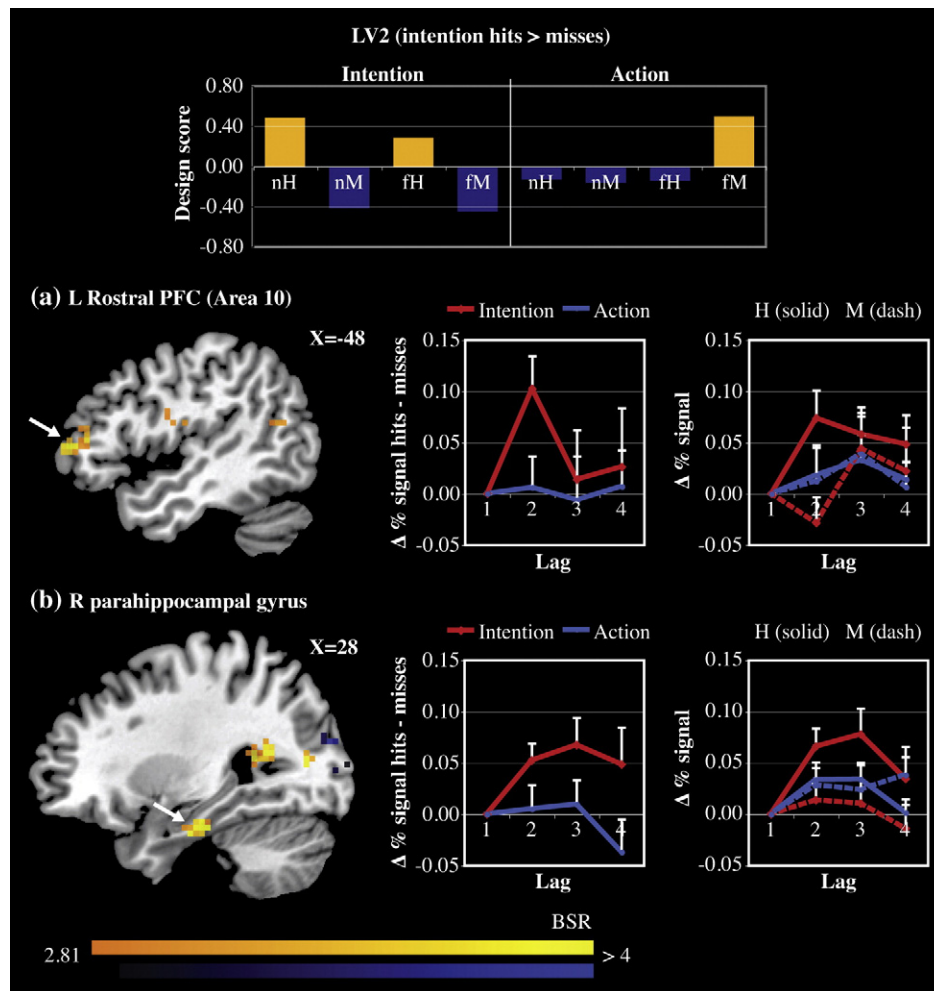
Fig. 3. Supplemental executive network associated with PM only. At top is a bar plot of design scores indicating how strongly each condition covaries with responses of the network described in Table 2. This profile can be interpreted as a network that supplemented the overall encoding network (Fig. 2) to support PM but not RM encoding. The sagittal brain images depict voxel clusters that reliably covaried with this contrast profile in (a) left rostral PFC and (b) right PHG (anterior is left; positive covariances are in orange; negative in blue), overlaid on an MNI anatomical template brain. The line plot adjacent to each brain image depicts the respective subsequent memory effects (difference in percent signal change between hits and misses + 1 SE) associated with action and intention items in the peak voxel of the indicated region.

resources and additional executive resources needed for future-oriented processing.

In a replication of the rostral PFC involvement established in previous PM neuroimaging investigations (Burgess et al., 2001, 2003; Okuda et al., 1998, 2003, 2007; Simons et al., 2006), analysis of the subsequent memory data revealed a left lateral rostral PFC region; this region was found to predict later memory for intentions but not actions. Sustained ERPs over frontal scalp regions have been shown to predict later PM (Leynes et al., 2003; West and Ross-Munroe, 2002; West et al., 2003) and rostral PFC has been widely implicated in PM studies using neuroimaging (Burgess et al., 2007a,b). However, the current study is the first to directly link rostral PFC activity with memory for individual intentions. Aspects of rostral PFC have been associated with both the maintenance of internally-generated thought (Burgess et al., 2003) and the generation of future events (Addis et al., 2007), functions which may have been necessary to form internal representations of future actions. Left PFC is also known to support episodic memory encoding in general (Kapur et al., 1994; Habib et al., 2003); consistent with past findings, a left dorsolateral PFC region linked with successful episodic memory encoding of both actions and intentions was identified when a 16 contiguous voxel threshold was applied to the first neural network (LV1, instead of 24 contiguous voxels; peak MNI coordinates = [−33, 12, 54]; BSR = 6.39; spatial extent = 1024 mm³).

While it would be reasonable to imagine that the rostrolateral PFC activation associated with PM encoding could reflect greater overall difficulty in the intention condition, a post-hoc contrast of rostral PFC activity revealed no significant overall difference in signal intensity between the action and intention tasks in this region (BSR = 0.40, approx. $P > 0.6$). That is, the effect was driven entirely by intention encoding *success*. In addition, it would be difficult to maintain a difficulty interpretation at the level of the overall PM encoding pattern. For instance, whereas rostrolateral PFC predicted successful encoding of intentions, anterior cingulate cortex, which is consistently activated by cognitively demanding tasks (Barch et al., 1997; Sohn et al., 2007), predicted forgetting of intentions. Overall, our results are more consistent with investigations specifying PM than those manipulating task difficulty.

Recent models of executive function and PFC may offer clues as to the role of the "executive system" in PM based on this frontal evidence. According to the "gateway hypothesis," stimulus-oriented thought is linked with medial rostral PFC, whereas stimulus-independent thought is linked with more lateral aspects of rostral PFC (Burgess et al., 2007b). As in the current study, PM paradigms typically activate lateral aspects of rostral PFC relative to control conditions (Burgess et al., 2007b), suggesting that intention formation involves mental processes that are at least partly divorced from the immediate context. The current results extend this evidence by

Table 2
Activated voxel clusters in LV2 of the event-related fMRI analysis.

Region	BA	Hemi.	Peak coordinates			Peak BSR	Spatial extent (mm³)
			X	Y	Z		
Hits > misses (intention only)							
Frontal lobe							
Rostral PFC	10	L	−48	48	6	4.54	729
Frontal operculum/insular gyrus	44	L	−39	15	15	4.06	1431
Precentral gyrus	6	R	36	0	30	6.42	675
	6	L	−45	−6	18	6.57	1944
Temporal lobe							
Parahippocampal gyrus	36	R	27	−24	−24	5.38	864
Superior temporal gyrus	39	L	−51	−57	18	3.74	1431
Parietal lobe							
Angular gyrus	7	L	−39	−69	48	3.72	1620
Occipital lobe							
Occipital gyrus	19	R	30	−78	15	6.07	1026
Misses > hits (intention only)							
Frontal lobe							
Cingulate gyrus	24	L	0	−9	42	5.74	972
Parietal lobe							
Supramarginal/postcentral gyrus	2	R	51	−27	51	3.82	1404
Superior parietal lobule	7	L	−3	−51	69	3.79	1053
	7	L	−24	−63	60	4.11	1350
Occipital lobe							
Lingual gyrus	19	L	−3	−75	−9	5.83	2511
Occipital gyrus	19	R	27	−87	21	5.06	1053
	17	R	3	−90	3	4.43	1350
Limbic lobe							
Anterior cingulate gyrus	24	R	18	21	27	4.98	1134

This LV corresponded to a contrast of hits and misses for intention items only.
Note: Clusters and peak locations are described as in Table 1.

showing that activity in the rostrolateral PFC "gateway" to stimulus-independent thought is in fact linked with subsequent behavioral performance , suggesting that stimulus-independent thought may be a requirement for successful PM encoding. A different class of "hierarchical" models posits that rostral PFC enables pending tasks to be maintained while concurrent tasks are managed in more posterior areas (Botvinick, 2008), with some suggesting that left rostrolateral PFC in particular is linked to processing higher-order relationships (Bunge et al., 2009). As dorsolateral PFC was found to support both RM and PM – whereas only PM was associated with rostral PFC – it may be that dorsolateral PFC was recruited to control the mental generation of actions, whereas the special internal processes required for PM encoding required additional higher-order task management in rostral PFC. As unique predictions of both gateway and hierarchical models were met, our data do not seem to support one over the other. However, both models can be used to help interpret the observed effects.

At the level of the MTL, our finding that hippocampal activation at the time of encoding predicted overall subsequent memory is consistent with the established role of this structure in associative memory (Eichenbaum et al., 2007; Moscovitch, 2008). The right lateralization of the observed activation is consistent with previous fMRI investigations of subsequent RM for scenes (Kirchhoff et al., 2000; Stark and Okado, 2003) and may be related to the pictorial nature of the stimuli (Papanicolaou et al., 2002). In contrast to the hippocampal subsequent memory response, which was independent of task, right PHG activity selectively predicted memory for intentions. Several positron emission tomography studies employing various classes of verbal cues (words and repeated phrases) have also revealed PHG responses to various PM tasks relative to ongoing activity or RM baselines (Burgess et al., 2001; Okuda et al., 1998, 2003). The current result extends this evidence by showing that the PHG response to PM tasks is directly associated with subsequent memory for individual intentions. This link does not seem to be

limited to a particular class of cues, considering that PHG has been associated with verbal cues in the past and scene stimuli in the current study. In addition, demands on memory for the pictoral cue would have been evident in both the RM and PM conditions, whereas the PHG effect was associated only with the PM condition. Instead, we speculate that PHG may be involved in using a scene or object in a scene to signify a prospective intention, thereby tagging the object or scene as relevant for later cognition. This could be analogous to using a landmark to signify a spatial location, a known function of PHG (Spiers and Maguire, 2004).

The current results appear to bridge several related literatures: PM, mental time travel, and the mental construction of future events. Several fMRI experiments requiring participants to retrieve past events or imagine future ones have implicated both a common episodic memory network and an executive network specific to future event construction, while none found any evidence of activations specifically linked to the past (Szpunar et al., 2007; Williams et al., 1996). One study in particular showed results comparable to the current ones, linking activity in the hippocampus to a common network for past and future event construction and rostral PFC to a future-based one (Addis et al., 2007). While we observed PM formation rather than future event construction, the considerable overlap in results suggests that the processes underlying these constructs may be similar. Along these lines, it has been argued that greater area 10 (rostral PFC) volume in humans relative to other species is related to the human capacity for mental time travel (Flinn et al., 2005). Similar arguments have been made regarding PFC development in children and concurrent development of episodic future thinking abilities (Dere et al., 2008). Consistent with such brain-based evidence linking PM formation with future cognition, evidence from the cognitive PM literature suggests that PM encoding can involve the imagining of a trigger cue likely to occur at the target place and time for the intention, which has the effect of associating that trigger cue with the intention; retrieval of the intention then automatically occurs when the cue is encountered at a later time (McDaniel and Einstein, 2000; McDaniel et al., 2004). All things considered, mental simulation of the future seems likely to be important both for PM and the various faculties that appear to be linked with it, including multitasking, strategic navigation and normal social behavior (Burgess et al., 2007a). Such an extensive role of future event construction in everyday life would support the call for a re-conceptualization of memory as a support system for a "prospective brain" that makes extensive use of knowledge of the past to support cognitions that depend on prediction (Schacter et al., 2007).

In closing, the current investigation specifically explored the correlates of the cue identification portion of PM, whereas PM is believed to depend on both cue identification and intention retrieval (McDaniel and Einstein, 2000). We used this limited approach to elicit the minimum number of successfully recalled PM events necessary for a subsequent memory analysis, since full PM tests typical of cognitive studies do not seem to do so (Eschen et al., 2007); admittedly, forming the dozens of intentions necessary for an fMRI study on PM in a single intensive session is not very naturalistic, which may account for this pattern. However, cue identification and intention retrieval have been shown to share a highly similar profile of brain activation (Simons et al., 2006); participants also confirmed in a debriefing interview that they made many of their responses on the cue identification task based on the full phenomenological experience of remembering to perform intended actions. Moreover, as discussed, our results appear to converge closely with those of other PM investigations. Based on these observations, the PM correlates described here seem likely to be representative not only of cue identification processes specific to our experiment, but of PM more generally. At a minimum, these results provide a first look at processes associated with successful encoding of intentions using fMRI.

Conclusion

The current study provides the first evidence that PM encoding, like PM retrieval, is supported by both a general episodic memory network and an executive network mediating future-oriented processing. In addition, as encoding activity in the same PFC and PHG regions typically seen in PM retrieval tasks was found to predict subsequent memory for individual intentions, this study provides the first direct evidence that those regions contribute to the formation of individual intentions. Temporal lobe activations that included the right posterior hippocampus comprised the common episodic memory network, which predicted subsequent memory of both actions and intentions. In contrast, activity in the PM-only network, which included left rostral PFC and the right PHG, predicted subsequent memory for individual intentions but not for imagined actions. These network characteristics are consistent with gateway and hierarchical models of PM involving both a general memory system and executive cue-monitoring and retrieval system. They are also convergent with the neural substrates of PM retrieval, suggesting that a single PM system is associated with encoding and retrieval. Finally, the results resemble those from studies on past and future event construction, supporting the more general contention that mental simulation of the future may play a key role in supporting various human cognitions.

Acknowledgments

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