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Dissociable Neural Routes to Successful Prospective Memory

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Abstract

Identifying the processes by which people remember to execute an intention at an appropriate moment (*prospective memory*) remains a fundamental theoretical challenge. According to one account, top-down attentional control is required to maintain activation of the intention, initiate intention retrieval, or support monitoring. A diverging account suggests that bottom-up, spontaneous retrieval can be triggered by cues that have been associated with the intention and that sustained attentional processes are not required. We used a specialized experimental design and functional MRI methods to selectively marshal and identify each process. Results revealed a clear dissociation. One prospective-memory task recruited sustained activity in attentional-control areas, such as the anterior prefrontal cortex; the other engaged purely transient activity in parietal and ventral brain regions associated with attentional capture, target detection, and episodic retrieval. These patterns provide critical evidence that there are two neural routes to prospective memory, with each route emerging under different circumstances.

Keywords

memory, cognitive neuroscience

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In planning to go to the grocery store later that day, Thelma intended to take reusable bags to use for packing her groceries. As preparation, she placed the bags in a basket beside her front door. On returning home from work, she gathered her shopping list, fed the dog, and was thinking about some unresolved business as she left the house to drive to the grocery. When paying for the groceries, she realized that she had forgotten to bring her reusable bags.

This vignette illustrates the common failure of a particular memory function, termed *prospective memory* (PM), that is ubiquitous in everyday life. PM involves remembering to execute an intention at an appropriate point in the future. In the present study, we examined a current debate regarding the neural and cognitive processes that support PM. A standard account of PM is that it requires sustained, top-down attentional control: processes that serve to maintain activation of the intention

while carrying out other ongoing activities (e.g., Burgess, Quayle, & Frith, 2001), to initiate periodic retrieval of the intention (Craik, 1986), or to support monitoring for the environmental event (or events) that signal appropriate execution of the intention (Smith, 2003). On this account, Thelma failed to remember her intention to take her reusable bags to the grocery store because she did not sustain the control processes that support prospective remembering (i.e., she was distracted by the ongoing demands of the day).

A contrasting perspective, known as the multiprocess theory, suggests that a second mechanism can support PM retrieval (McDaniel & Einstein, 2000). This mechanism, bottom-up spontaneous retrieval, does not require

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monitoring or other sustained attentional processes but, instead, is a transient process that is triggered by stimulus cues with strong associations to the PM intention (McDaniel, Guynn, Einstein, & Breneiser, 2004). An important but unresolved theoretical issue concerns whether PM can in fact be supported by a spontaneous retrieval route that does not require sustained attentional control (e.g., see Smith, 2003). Returning to the vignette, the idea is that on leaving the house, Thelma's intention to take the grocery bags might have been spontaneously retrieved if she had been attending fully to the basket or, perhaps, if she had strongly linked exiting the front door with her intention to take her reusable bags.

Viewed from the theoretical perspectives just described, PM emerges as a compelling paradigm for encapsulating general issues of planned versus stimulus-driven behavior or, alternatively, proactive versus reactive control (Braver, 2012; Bugg, McDaniel, & Einstein, 2013). Consequently, the extent to which prospective remembering primarily requires sustained (proactive) control versus transient (spontaneous and reactive) control not only bears critically on understanding PM (and its failure) but also may help to inform more general issues of goal-driven behavior. Unfortunately, behavioral research methods, such as estimating the cost of a PM task to ongoing performance, have not been able to convincingly adjudicate between these views, leaving the current debate unresolved in the literature (see Einstein & McDaniel, 2010; Smith, 2010).

In the present experiment, we introduced a novel approach to illuminate these theoretical processes in PM. Using powerful functional MRI (fMRI) methods, we contrasted two PM conditions that were identical except in one subtle way. In both conditions, participants busily engaged in an ongoing semantic-classification task, but were additionally instructed that if they ever encountered a particular target event, they should try to remember to perform the PM task. The two PM conditions differed only in terms of the stimulus cue that designated the PM trial: In one condition, the PM trial was indicated by a particular word (e.g., "table"), and in the other, the PM trial was indicated by a particular syllable (e.g., "tor," as in *tornado*, *actor*, or *history*). Following the literature, we refer to the word-cue task as the *focal-PM task* because processing the word (and its meaning) is focal to the ongoing task of semantic processing. Conversely, we refer to the syllable-cue task as the *nonfocal-PM task* because identifying a particular syllable is not focal to the ongoing task of semantic processing (Einstein et al., 2005).

The fMRI analysis was specifically optimized to dissociate sustained versus transient neural-activity dynamics using a mixed-block/event-related design. This design enables separate identification and categorization of

brain regions, distinguishing patterns of activity that are sustained (i.e., stably maintained across trials during specific task blocks) from those that are transient (i.e., event related or active only on specific task trials). Prior fMRI studies of PM have consistently shown neural-activation patterns associated with sustained attentional control, with the anterior prefrontal cortex (aPFC) being the primary system involved, along with other components of the frontoparietal attention system (Burgess, Gonen-Yaacovi, & Volle, 2011). However, these studies have been limited in that the fMRI methods have not typically enabled a direct assessment of whether the activity dynamics in these regions are sustained or transient (see Reynolds, West, & Braver, 2009, for an exception). Moreover, the experimental designs have uniformly employed target events that are nonfocal to the demands of the ongoing task (Burgess et al., 2001; Reynolds et al., 2009; for a possible exception, see Gilbert, Gollwitzer, Cohen, Oettingen, & Burgess, 2009), precluding a comparison of activation patterns and dynamics under nonfocal versus focal PM. Thus, the current study design and method represent a considerable advance over those in the prior literature.

The multiprocess theory suggests a number of strong predictions regarding brain-activity patterns in focal and nonfocal PM (McDaniel & Einstein, 2011). First, we predicted that the neural signature of top-down attentional control—sustained activity in the aPFC and other frontoparietal regions—should be observed only in nonfocal conditions. Second, we hypothesized that such top-down control would be necessary during nonfocal PM to preactivate the system to notice the PM target event and successfully retrieve the stored intention. We tested this hypothesis by examining functional-connectivity patterns between the aPFC and retrieval-related regions (e.g., the parietal cortex; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Wagner, Shannon, Kahn, & Buckner, 2005) that were specific to successful PM trials, predicting that connectivity patterns would be stronger under nonfocal conditions.

In the focal-PM conditions, a different pattern of activity dynamics and connectivity was expected. Here, transient, reactive control is sufficient because processing of the stimulus cue as part of the ongoing task should by itself capture attention and spontaneously trigger PM retrieval. Accordingly, our third prediction was that the focal-PM condition would not produce sustained activation but, instead, would be associated with increased transient activity during PM trials (i.e., trials on which the focal stimulus cue was presented) in a widely distributed set of brain regions that support bottom-up processes (e.g., attentional capture, target detection, and episodic retrieval). Finally, our fourth prediction was that focal-PM trials would be associated with a unique pattern of aPFC

functional connectivity, reflecting a bottom-up rather than top-down mode of PM intention retrieval and implementation.

Method

Participants

Forty-five adults (age range = 18–37 years) participated, with 25 randomly assigned to the nonfocal-PM condition and 20 to the focal-PM condition. Participants were right-handed native English speakers with normal or corrected-to-normal vision who had no history of neurological or psychiatric disorders or illicit drug use (see the Method section in the Supplemental Material available online for additional details).

Procedure

Participants in both conditions performed an ongoing semantic-classification task. The task required judgments of whether visually presented target words (appearing in lowercase) matched the semantic category indicated by an immediately preceding uppercase cue word (example match trial: cue = “COLOR,” target = “green”; example nonmatch trial: cue = “FURNITURE,” target = “grape”). Participants responded by pressing a button with the index or middle finger of their right hand. PM and control (i.e., non-PM) blocks were administered in both conditions. In the PM blocks, participants were given the additional task of trying to remember to make a response (by pressing a third button with their right ring finger) when the PM target appeared. The only difference between the focal- and nonfocal-PM blocks was the specification of the PM target: In the focal-PM blocks, it was a particular word (e.g., “table”); in the nonfocal-PM blocks, it was a particular syllable (e.g., “tor”).

Participants first practiced to familiarize themselves with the ongoing task. The experimental session, which participants performed while they underwent fMRI scans, consisted of 10 scanning runs (8.5 min each) that included 3 control and 7 PM runs (with order counterbalanced across participants). Each scanning run was composed of alternating task blocks (three blocks lasting approximately 2 min each) and resting-fixation blocks (four blocks lasting approximately 30 s each), with 25 trials per task block (total trials: 225 in control blocks, 525 in PM blocks). A total of 20 PM trials were randomly interspersed among the 525 ongoing-PM block trials (i.e., each block contained 0, 1, or 2 PM trials).

To facilitate identification of event-related brain activation, we jittered the interval between category cue and target using an exponential distribution (range = 2,500–20,500 ms). We varied the category-target interval rather than the intertrial interval (which was held constant at

1,500 ms) to ensure that participants would be focused on actively maintaining the category cue rather than rehearsing the PM goal during the unfilled jitter intervals. We treated the short interval between the target and the next trial’s category cue as a single event for purposes of event-related modeling.

fMRI data analysis

Details on fMRI data acquisition and preprocessing are available in the Method section in the Supplemental Material. A general-linear-model approach (Friston, Frith, Frackowiak, & Turner, 1995) was used in combination with a mixed-block/event-related design (Reynolds et al., 2009; Visscher et al., 2003). This design enables simultaneous and independent estimation of brain-activation responses, differentiating those that are sustained (i.e., stably increased across trials during task blocks) from those that are transient (i.e., event related). Sustained task-related activity was estimated separately for PM and control blocks. Event-related (transient) activity was estimated for PM trials and ongoing trials, yielding three separate event types (PM, ongoing PM, and ongoing control). These estimates were restricted to correct trials only because there were too few error trials to provide reliable estimates.

We had a strong a priori hypothesis that sustained activity would be selectively increased during the nonfocal-PM task in brain regions supporting top-down attentional control and monitoring. As such, we focused our analysis of sustained activity on a canonical set of frontoparietal regions of interest (ROIs) that have been identified through meta-analyses of working memory and cognitive-control tasks (Owen, McMillan, Laird, & Bullmore, 2005; Wager & Smith, 2003; see Fig. S1 in the Supplemental Material). In addition, we included an aPFC ROI that has been associated with sustained attentional monitoring in previous PM studies (Gilbert et al., 2006). We tested each of these ROIs to determine whether they showed increased sustained activity in the PM relative to control blocks and whether this activity was specific to the nonfocal condition. We also conducted a whole-brain analysis, testing for the presence of any additional regions showing the reverse effect, that is, sustained activity increased only in the focal condition.

Because we had less strong hypotheses regarding transient, PM-related activation, these analyses were conducted in an exploratory, whole-brain fashion (using appropriate familywise error corrections when testing for statistical significance). Regions were identified that showed activation on PM trials relative to ongoing trials (in both PM and control blocks) in the focal and nonfocal conditions. Identified regions were then further tested for either overlap (conjunction) or differential activation across the two conditions. We conducted an analysis of

this type for the aPFC ROI as well because of our theoretical interest in sustained versus transient activity within this region.

In our final analysis, we tested for PM-related changes in functional connectivity specific to either the focal or nonfocal condition using the psychophysiological-interaction (PPI) approach (for details, see the Method section in the Supplemental Material). The aPFC region was used as an ROI seed in the PPI analysis. Regions were identified that showed significant increases in functional connectivity with the aPFC on PM trials for which participants remembered to respond (correct PM trials) and were specific to the focal or nonfocal condition. Target regions identified through this analysis were then further examined in terms of their activation profile on trials of the different task types.

Results

Behavioral Results

Participants in the focal and nonfocal conditions performed the ongoing task at a high level of accuracy in PM (> 90% for both focal and nonfocal) and control (92%) blocks. PM performance was lower in the nonfocal condition (mean accuracy = 74%) than in the focal condition (mean accuracy = 89%), $t(43) = 3.33$, $p < .05$; this result was consistent with the assumption that identifying the nonfocal-PM target required processing that overlapped less with the ongoing task than did identifying a focal-PM target. Moreover, replicating prior findings (Einstein et al., 2005), results showed that monitoring costs (slower ongoing-task reaction times, RTs, in PM relative to control blocks) were present for the nonfocal task (mean RT = 71 ms), $t(24) = 8.52$, $p < .001$, and were significantly greater than those observed in the focal condition (mean RT = 40 ms)—Condition \times Block interaction: $F(1, 43) = 5.96$, $p < .05$, $\eta_p^2 = .122$. This pattern supports the interpretation that the nonfocal condition placed greater demands on sustained attentional-monitoring processes. However, the behavioral data were not definitive on this point, again replicating prior findings (see Experiment 3 in Scullin, McDaniel, Shelton, & Lee, 2010), in that significant RT monitoring costs were also observed in the focal condition, $t(19) = 4.15$, $p = .001$ (see Table S1 in the Supplemental Material for more details about behavioral performance). To more directly address the question of whether focal and nonfocal PM reflected different mechanisms of task performance, we turned to the neuroimaging data.

Sustained brain activation

Our primary hypothesis was that the two PM conditions would demonstrate differential sustained activity in brain

regions reflecting attentional monitoring. Tests for evidence of sustained activation conducted separately in the two conditions showed a strikingly different pattern of findings. During nonfocal PM, sustained activation was found in a number of a priori–defined ROIs that make up the canonical frontoparietal cognitive-control network (see Fig. 1; also see Table S2 in the Supplemental Material), as well as in the left aPFC region that has been most consistently associated with attentional-monitoring activity in the prior PM neuroimaging literature (see Fig. 2). In contrast, during the focal-PM task, there was no evidence of sustained activation anywhere in the brain, even when a liberal statistical threshold was employed. We formally confirmed a significant Condition (focal, nonfocal) \times Block (PM, control) interaction ($p < .05$) in all identified nonfocal ROIs.¹

Transient brain activation

We next turned to the transient (event-related) activation that was increased on correct PM trials relative to ongoing trials (in both PM and control blocks). Here, a very different pattern emerged. A widely distributed pattern of activation was found (see Fig. 1; also see Table S3 in the Supplemental Material) in areas including dorsal frontoparietal regions associated with top-down attentional control that were also identified in the nonfocal sustained analysis (e.g., the superior frontal cortex near the frontal eye fields). However, we also observed transient activation in ventral brain regions typically engaged by bottom-up shifts of attention and detection of salient target stimuli (e.g., the ventral parietal cortex and the cingulo-opercular “salience” network; Cabeza et al., 2008; Corbetta & Shulman, 2002; Seeley et al., 2007). This pattern of transient activity was equally prominent in the focal and nonfocal conditions as confirmed via an overlap analysis (see Table S3 in the Supplemental Material). The analysis did not reveal any regions that exhibited differential patterns of PM-related transient activation across the two conditions (via an interaction contrast with statistical significance thresholded to correct for whole-brain family-wise error). Thus, transient PM-related activity (on correct PM trials) was present and equivalent in both the focal- and nonfocal-PM conditions, whereas sustained activity was observed only in the nonfocal condition.

Functional connectivity

Our initial analyses suggested that the focal and nonfocal conditions were not strongly differentiated in terms of transient activity on PM trials. Indeed, this pattern extended to the left aPFC region, which exhibited sustained activation specific to the nonfocal condition but also showed a significant transient increase on correct PM trials that was equivalent in both the focal

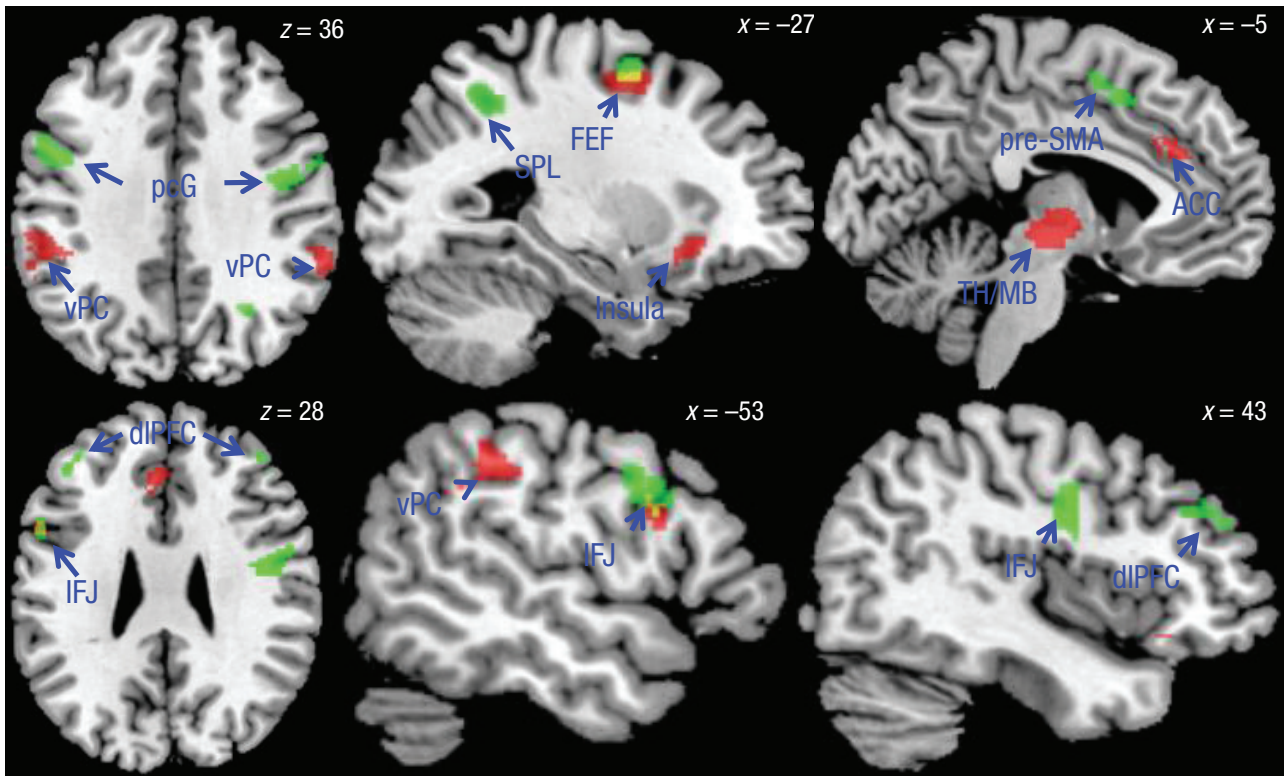


Fig. 1. Sustained activations specific to nonfocal prospective memory (PM; green), overlap of transient activations for both focal and nonfocal PM (red), and overlap of regions showing sustained activations for nonfocal PM and transient activations for both focal and nonfocal PM (yellow). The x and z values are Montreal Neurological Institute coordinates specifying the sites of brain activations. ACC = anterior cingulate cortex; dIPFC = dorsolateral prefrontal cortex; FEF = frontal eye field; IFJ = inferior frontal junction; pcG = precentral gyrus; pre-SMA = pre-supplementary motor area; SPL = superior parietal lobe; TH/MB = thalamus/midbrain; vPC = ventral parietal cortex.

and nonfocal conditions (see Fig. 2). Nevertheless, we hypothesized that the aPFC might play distinct functional roles in the two conditions through interactions with other brain regions that trigger the retrieval and implementation of PM intentions in either a top-down (i.e., initiated from sustained attentional monitoring) or a bottom-up (i.e., triggered by attentional capture from a salient stimulus event) manner. Therefore, we conducted a PPI analysis to test whether the aPFC showed differential functional connectivity with other brain regions in focal versus nonfocal conditions during correct PM trials. It is important to note that examining transient connectivity changes on correct PM trials (rather than sustained or block-related connectivity) provides a stricter test for dissociable effects, given that aPFC activity was equivalent across the two conditions. The PPI analysis revealed a double dissociation in which the aPFC exhibited stronger connectivity with the precuneus on correct nonfocal PM trials and with the right middle temporal gyrus on correct focal PM trials. This double dissociation was confirmed through the presence of a significant Region (precuneus,

middle temporal) \times Condition interaction, $F(1, 41) = 19.28, p < .001, \eta_p^2 = .320$ (see Fig. 3).

We also examined these two target regions identified by PPI to determine their pattern of transient activation in PM and ongoing (non-PM) trials in both conditions. Interestingly, in both regions, we found that activation on PM trials was stronger in the focal compared with the nonfocal condition, $ps < .05$. It is worth pointing out that these transient-activation effects were detectable only in ROI-based analyses (i.e., they did not meet the threshold for significance in the initial whole-brain voxelwise analysis) because of the enhanced statistical power afforded by this analysis.

Discussion

There has been an ongoing theoretical debate regarding the cognitive processes that support prospective remembering, and it has proven difficult to resolve via purely behavioral measures. One account holds that people must sustain attentional-control processes to support PM

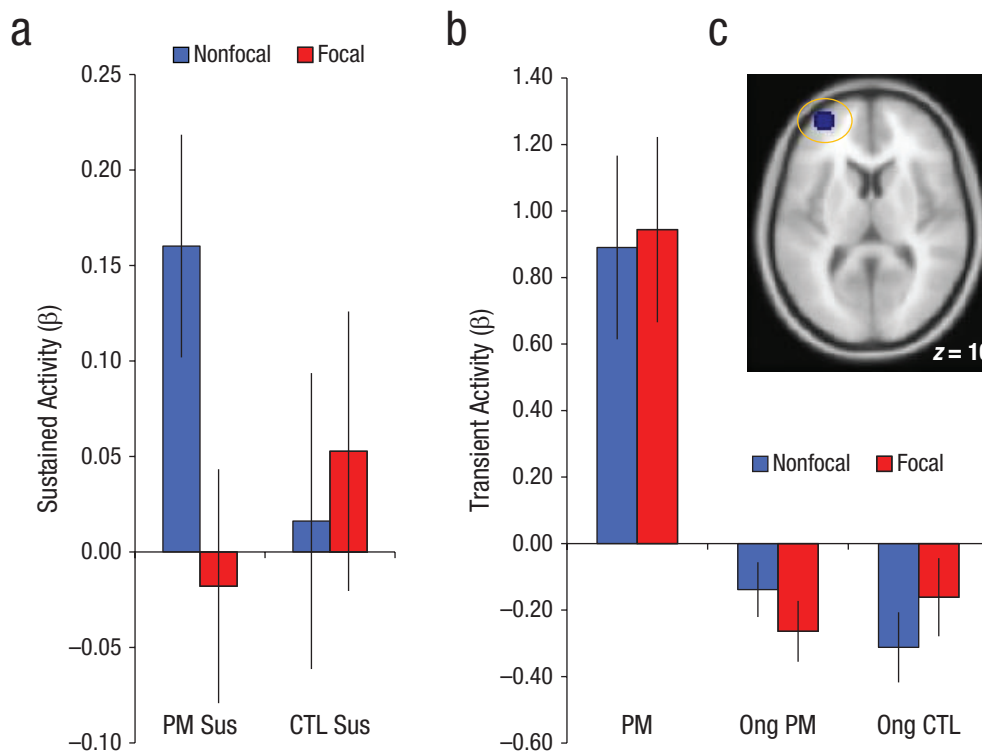


Fig. 2. Sustained (a) and transient (b) activity in the left anterior prefrontal cortex region of interest (c; 8-mm sphere at Montreal Neurological Institute, MNI, coordinates $x = -34$, $y = 56$, $z = 9$) for focal and nonfocal prospective memory (PM). The z value indicates the millimeter value of the z coordinate, or axial dimension, of the MNI coordinate system. PM Sus = sustained activity in PM blocks; CTL Sus = sustained activity in control blocks; PM = transient activity on PM trials (correct trials only); Ong PM = transient activity for category-decision-task trials (ongoing trials) during the PM block; Ong CTL = transient activity for ongoing trials during the control block. Error bars represent standard errors of the mean.

(as suggested in the opening vignette). The other account posits that environmental stimuli (e.g., a cue linked to the intention during encoding) can often spontaneously prompt PM retrieval, thereby obviating the need for sustaining attentional-control processes. The present fMRI study provides critical new evidence suggesting that both routes can lead to successful PM, but under different circumstances.

The central finding was that subtle shifts in the PM task—shifts motivated by previous theoretical analyses (e.g., McDaniel & Einstein, 2000, 2011)—led to dramatic shifts in the neural systems, activation dynamics, and connectivity patterns associated with task performance. First, consider the nonfocal-PM condition. Our interpretation is that when PM trials are signaled by nonfocal cues, sustained attentional control is recruited to enable recognition of the cue as a PM target. In line with this interpretation, we observed activation in the frontoparietal control network, including the aPFC region that has been most consistently associated with top-down attentional

control in PM tasks (Burgess et al., 2011). Here, we definitively demonstrated that the PM-related activity was sustained, replicating a prior finding by Reynolds et al. (2009) but additionally showing that such sustained activity patterns are highly specific to nonfocal PM (rather than a general property of all PM tasks).

In addition, on nonfocal PM trials, the aPFC showed a particular change in connectivity that may have enabled more efficient detection of the target cue, and retrieval of the associated PM intention, via top-down biasing. Specifically, the aPFC showed selectively increased connectivity (the PPI effect) with the precuneus, a medial parietal region that may link retrospective memory and PM (Buckner & Carroll, 2007; Cavanna & Trimble, 2006; Wagner et al., 2005). Although the PPI effect does not indicate the directionality of the connectivity increase, it is consistent with the idea that PM retrieval was primed by sustained attentional control subserved by the aPFC. One might think of sustained activation in the aPFC as placing the system in a retrieval mode (Guynn, 2003;

Lepage, Ghaffar, Nyberg, & Tulving, 2000), such that the nonfocal cue on PM trials would be appropriately interpreted with respect to the PM-retrieval goals. Moreover, this retrieval mode would presumably attenuate the transient activation of this retrieval system when the cue was encountered because the system would already be primed and so would require less bottom-up activation to be fully engaged. Converging with this theoretical analysis, results revealed that the precuneus showed reduced transient activation in response to nonfocal-PM trials relative to focal-PM trials (see Fig. 3).

The most novel findings of the study were observed in the focal-PM condition, and they suggest that the processes engaged during nonfocal PM are only one route by which successful PM retrieval can occur. Under focal-PM conditions, there was no sustained activity in the aPFC, the frontoparietal control network, or elsewhere in the brain, which suggests an absence of top-down attentional monitoring; nevertheless, very high levels of PM

performance were obtained. In contrast, transient activation on correct PM trials was equally strong in most regions (relative to activation on nonfocal-PM trials). The similar transient activation pattern for focal and nonfocal PM is consistent with the idea that processes in addition to intention retrieval are necessary to complete execution of the PM task on a PM trial; such processes may include disengagement and interruption of ongoing activity, as well as coordination of the PM response (Marsh, Hicks, & Watson, 2002; McDaniel & Einstein, 2011). Moreover, this pattern also likely reflects the fact that some retrieval processes may be involved on both focal and nonfocal PM trials (McDaniel & Einstein, 2000).

An important further finding, however, was that transient activation was significantly increased on correct focal-PM trials (relative to nonfocal-PM trials) in two additional regions (the precuneus and the right middle temporal gyrus, as indicated by the ROI analysis; see Fig. 3). This double dissociation between sustained and

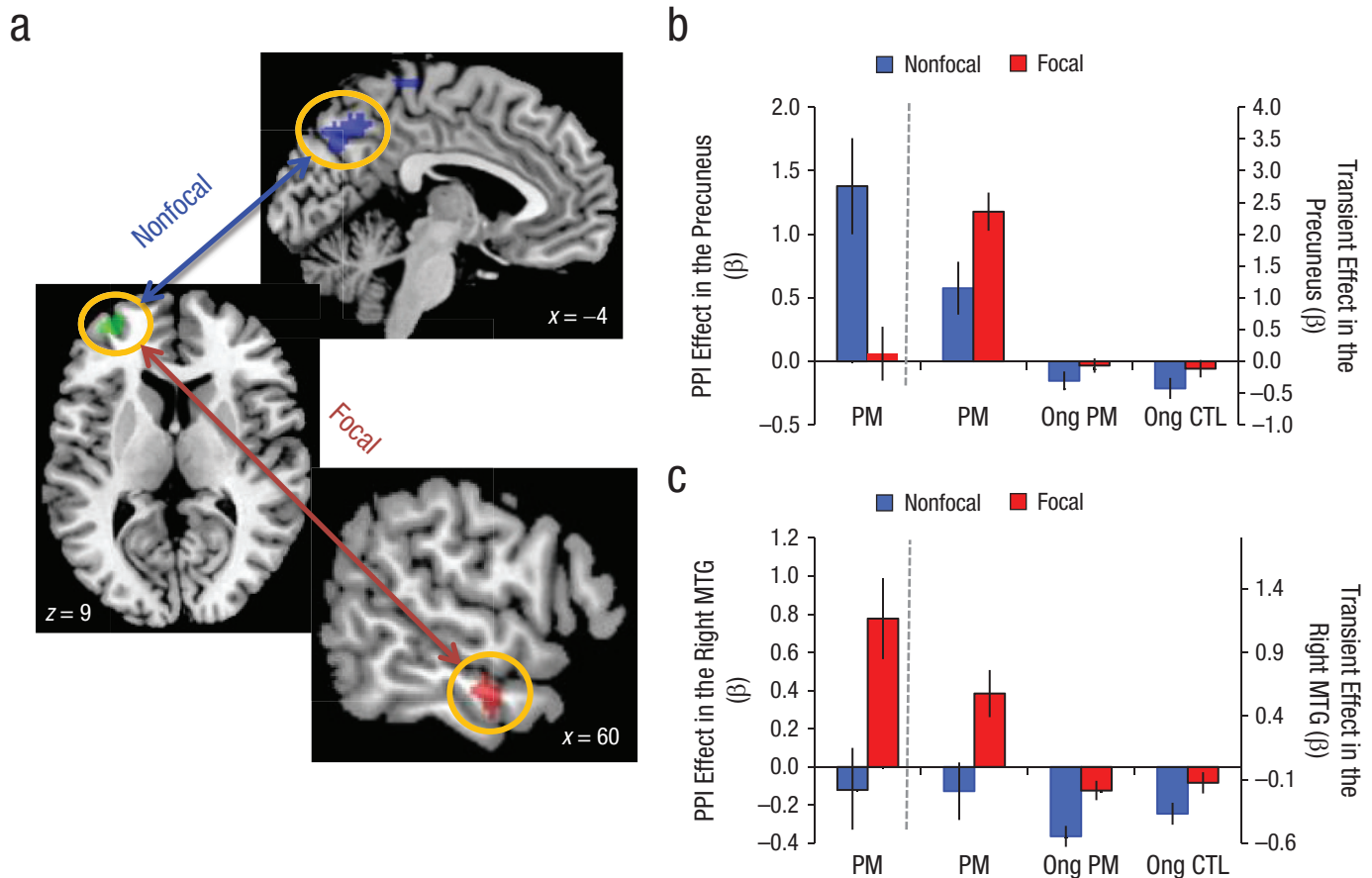


Fig. 3. Psychophysiological interaction (PPI) effects for PM trials (a) between the right middle temporal gyrus (Montreal Neurological Institute, MNI, coordinates: $x = 62, y = 12, z = 16$) and precuneus ($x = 2, y = 72, z = 40$) and the left anterior prefrontal cortex (aPFC), and PPI and transient effects in (b) the precuneus and (c) the right middle temporal gyrus (MTG) as a function of trial type. The x and z values are MNI coordinates specifying the sites of brain activations. PM = transient effect on PM trials (correct trials only); Ong PM = transient effect for category-decision-task trials (ongoing trials) during the PM block; Ong CTL = transient effect for ongoing trials during the control block. Error bars represent standard errors of the mean.

transient activity across nonfocal and focal tasks supports the proposal that two distinct types of processing (retrieval) strategies can support PM. This interpretation is additionally supported by the widely distributed pattern of increased transient activity observed on correct focal-PM trials, centered on parietal and ventral brain regions—not only the middle temporal gyrus and the precuneus but also the ventral parietal cortex and the cingulo-opercular network, brain areas that are widely thought to be involved with the detection of salient target events and bottom-up shifts of attention (Cabeza et al., 2008; Seeley et al., 2007).

We suggest that in focal-PM conditions, the retrieval of the PM intention is primarily a bottom-up phenomenon initiated by detection of salient target cues. The increased activity observed in the precuneus during focal-PM trials supports the idea that the episodic retrieval processes engaged during these trials may be spontaneous, that is, occurring in the absence of sustained aPFC activation (Beck, Ruge, Walser, & Goschke, 2013). Although we do not have a strong interpretation regarding the connectivity pattern observed between the right middle temporal gyrus and the aPFC during focal PM, we speculate that it may reflect a bottom-up retrieval process initiated by the temporal cortex that may enable the suspension of ongoing processing, shifting focus toward the retrieval-related significance of the cue. Although the role of the right middle temporal gyrus is not typically emphasized in studies of memory and attention, it is a reliable component of brain networks engaged by target-detection or novelty tasks (Linden et al., 1999), response inhibition (Swick, Ashley, & Turken, 2011), and episodic- or autobiographical-memory tasks (Burianova, McIntosh, & Grady, 2010; Svoboda, McKinnon, & Levine, 2006). Thus, further research will be needed to more clearly understand the functional interaction between these two regions.

A residual question arising from the current results relates to why we observed apparent monitoring costs during focal PM (albeit reduced costs, relative to those during nonfocal PM) in the absence of sustained activation patterns. We posit that focal-PM tasks can be supported by spontaneous retrieval because full processing of the focal event is stimulated by the ongoing activity and such processing could, in principle, support a reflexive retrieval process (of the PM intention; McDaniel & Einstein, 2000, 2011). In contrast, during nonfocal PM, target events are not fully processed as a consequence of the ongoing activity. Accordingly, sustained, controlled processing must be engaged to detect the nonfocal cue as a PM target, with subsequent processes required to support retrieval of the intended activity. However, it is possible that the focal-PM condition used in our experiment, like many (if not all) real-world PM situations,

might involve a mixture of spontaneous retrieval with intermittent monitoring as well as nonfunctional cognitive processes engaged by the PM demands. These processes could lead to some cost (i.e., slower responses) during ongoing performance, as has been observed in prior studies with focal-PM tasks (e.g., Einstein et al., 2005; Meier & Rey-Mermet, 2012; Scullin et al., 2010). Nevertheless, if such monitoring or other processes were intermittent rather than stable, they would not be reflected in a reliable pattern of sustained activity that could be detected with the fMRI analysis used here.

The current study also bears on the general issue in the memory literature of whether retrieval processes require a sustained, explicit “retrieval mode” that enables the processing of current events in relation to stored memories (e.g., by reinstantiating the encoding context; Lepage et al., 2000). This issue has been difficult to adjudicate in retrospective-memory experiments because the memory instructions would always potentially switch the system to a retrieval mode. In the present paradigm, there is no requirement that the individual make a memory decision on every trial; in fact, the ongoing task does not require a memory decision. In the focal-PM condition, PM retrieval was very successful, yet there was no neural evidence that the system was in a sustained state different from that during trials in which there was no memory task. These patterns thus provide support for the claim that retrieval of episodic information (e.g., a previously formed intention) need not require activation of a memory-retrieval mode.

In closing, we note that there is functional and adaptive value to having several routes to PM retrieval (Einstein & McDaniel, 2008). PM is ubiquitous as an important daily memory activity, as illustrated in the opening vignette. Given the resource demands and somewhat fragile nature of sustained attentional control over time (e.g., Muraven & Baumeister, 2000), having to rely on this proactive control system for the myriad of PM tasks faced daily would likely be overwhelming. A complementary route to PM retrieval that is spontaneous or reactive would help support PM when resources are not available for maintaining top-down control or when distractions disrupt the ability to maintain intentions over time (as in the opening vignette). Recognizing the existence of this alternative PM route offers practical implications. For example, to support bottom-up retrieval of the intention to take reusable bags to the grocery, a person could place the bags in a location that would be fully attended when he or she left the house (e.g., under the car keys). Knowledge about how a fragile, attentionally controlled route to PM retrieval can be sidetracked might promote use of the less vulnerable bottom-up route, which could aid in rescuing retrieval of an intention that might otherwise be lost.

Author Contributions

M. A. McDaniel and T. S. Braver developed the study concept. M. A. McDaniel, T. S. Braver, and M. K. Scullin were the primary contributors to the study design, with extensive pilot testing to develop a tractable paradigm for fMRI performed by M. K. Scullin. Testing and data collection were performed by P. LaMontagne, and P. LaMontagne and S. M. Beck analyzed and interpreted the data under the supervision of T. S. Braver. M. A. McDaniel, T. S. Braver, P. LaMontagne, and S. M. Beck drafted the manuscript, S. M. Beck developed the Supplemental Material, and M. K. Scullin provided critical revisions. All authors approved the final version of the manuscript for submission.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at <http://pss.sagepub.com/content/by/supplemental-data>

Note

1. A potential alternative interpretation of the increased sustained activity in the nonfocal condition is that it reflects increased task difficulty and poorer performance and, thus, differential performance monitoring rather than PM processes per se. As described fully in the Analyses on Performance-Matched Subsample section in the Supplemental Material, we conducted an analysis that involved 15 participants in each condition who were matched on PM performance. All of the obtained effects were retained in this performance-matched subset, which suggests that this alternative interpretation is unlikely.

References

Beck, S. M., Ruge, H., Walser, M., & Goschke, T. (2013). *The functional neuroanatomy of spontaneous retrieval and strategic monitoring of delayed intentions*. Manuscript submitted for publication.

- Braver, T. S. (2012). The variable nature of cognitive control: A dual mechanisms framework. *Trends in Cognitive Sciences*, *16*, 106–113.
- Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences*, *11*, 49–57.
- Bugg, J. M., McDaniel, M. A., & Einstein, G. O. (2013). Event-based prospective remembering: An integration of prospective memory and cognitive control theories. In D. Reisberg (Ed.), *The Oxford handbook of cognitive psychology* (pp. 267–282). New York, NY: Oxford University Press.
- Burgess, P. W., Gonen-Yaacovi, G., & Volle, E. (2011). Functional neuroimaging studies of prospective memory: What have we learnt so far? *Neuropsychologia*, *49*, 2246–2257.
- Burgess, P. W., Quayle, A., & Frith, C. D. (2001). Brain regions involved in prospective memory as determined by positron emission tomography. *Neuropsychologia*, *39*, 545–555.
- Burianova, H., McIntosh, A. R., & Grady, C. L. (2010). A common functional brain network for autobiographical, episodic, and semantic memory retrieval. *NeuroImage*, *49*, 865–874.
- Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: An attentional account. *Nature Reviews Neuroscience*, *9*, 613–625.
- Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain*, *129*, 564–583.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215.
- Craik, F. I. M. (1986). A functional account of age differences in memory. In F. Klix & H. Hagendorf (Eds.), *Human memory and cognitive capabilities: Mechanisms and performances* (pp. 409–422). Amsterdam, The Netherlands: North-Holland.
- Einstein, G. O., & McDaniel, M. A. (2008). Prospective memory and metamemory: The skilled use of basic attentional and memory processes. In A. S. Benjamin & B. Ross (Eds.), *The psychology of learning and motivation: Skill and strategy in memory use* (Vol. 48, pp. 145–173). San Diego, CA: Elsevier.
- Einstein, G. O., & McDaniel, M. A. (2010). Prospective memory and what costs do not reveal about retrieval processes: A commentary on Smith, Hunt, McVay, and McConnell (2007). *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *36*, 1082–1088.
- Einstein, G. O., McDaniel, M. A., Thomas, R., Mayfield, S., Shank, H., Morrisette, N., & Breneiser, J. (2005). Multiple processes in prospective memory retrieval: Factors determining monitoring versus spontaneous retrieval. *Journal of Experimental Psychology: General*, *134*, 327–342.
- Friston, K. J., Frith, C. D., Frackowiak, R. S., & Turner, R. (1995). Characterizing dynamic brain responses with fMRI: A multivariate approach. *NeuroImage*, *2*, 166–172.
- Gilbert, S. J., Gollwitzer, P. M., Cohen, A.-L., Oettingen, G., & Burgess, P. W. (2009). Separable brain systems supporting cued versus self-initiated realization of delayed intentions. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *35*, 905–915.

- Gilbert, S. J., Spengler, S., Simons, J. S., Steele, J. D., Lawrie, S. M., Frith, C. D., & Burgess, P. W. (2006). Functional specialization within rostral prefrontal cortex (area 10): A meta-analysis. *Journal of Cognitive Neuroscience*, *18*, 932–948.
- Guynn, M. J. (2003). A two-process model of strategic monitoring in event-based prospective memory: Activation/retrieval mode and checking. *International Journal of Psychology*, *38*, 245–256.
- Lepage, M., Ghaffar, O., Nyberg, L., & Tulving, E. (2000). Prefrontal cortex and episodic memory retrieval mode. *Proceedings of the National Academy of Sciences, USA*, *97*, 506–511.
- Linden, D. E., Prvulovic, D., Formisano, E., Vollinger, M., Zanella, F. E., Goebel, R., & Dierks, T. (1999). The functional neuroanatomy of target detection: An fMRI study of visual and auditory oddball tasks. *Cerebral Cortex*, *9*, 815–823.
- Marsh, R. L., Hicks, J. L., & Watson, V. (2002). The dynamics of intention retrieval and coordination of action in event-based prospective memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*, 652–659.
- McDaniel, M. A., & Einstein, G. O. (2000). Strategic and automatic processes in prospective memory retrieval: A multiprocess framework. *Applied Cognitive Psychology*, *14*, S127–S144.
- McDaniel, M. A., & Einstein, G. O. (2011). The neuropsychology of prospective memory in normal aging: A componential approach. *Neuropsychologia*, *49*, 2147–2155.
- McDaniel, M. A., Guynn, M. J., Einstein, G. O., & Breneiser, J. (2004). Cue-focused and reflexive-associative processes in prospective memory retrieval. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *30*, 605–614.
- Meier, B., & Rey-Mermet, A. (2012). Beyond monitoring: After-effects of responding to prospective memory targets. *Consciousness and Cognition*, *21*, 1644–1653.
- Muraven, M., & Baumeister, R. F. (2000). Self-regulation and depletion of limited resources: Does self-control resemble a muscle? *Psychological Bulletin*, *126*, 247–259.
- Owen, A. M., McMillan, K. M., Laird, A. R., & Bullmore, E. (2005). N-back working memory paradigm: A meta-analysis of normative functional neuroimaging studies. *Human Brain Mapping*, *25*, 46–59.
- Reynolds, J. R., West, R., & Braver, T. (2009). Distinct neural circuits support transient and sustained processes in prospective memory and working memory. *Cerebral Cortex*, *19*, 1208–1221.
- Scullin, M. K., McDaniel, M. A., Shelton, J. T., & Lee, J. H. (2010). Focal/nonfocal cue effects in prospective memory: Monitoring difficulty or different retrieval processes? *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *36*, 736–749.
- Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., . . . Greicius, M. D. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control. *Journal of Neuroscience*, *27*, 2349–2356.
- Smith, R. E. (2003). The cost of remembering to remember in event-based prospective memory: Investigating the capacity demands of delayed intention performance. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *29*, 347–361.
- Smith, R. E. (2010). What costs do reveal and moving beyond the cost debate: Reply to Einstein and McDaniel (2010). *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *36*, 1089–1095.
- Svoboda, E., McKinnon, M. C., & Levine, B. (2006). The functional neuroanatomy of autobiographical memory: A meta-analysis. *Neuropsychologia*, *44*, 2189–2208.
- Swick, D., Ashley, V., & Turken, U. (2011). Are the neural correlates of stopping and not going identical? Quantitative meta-analysis of two response inhibition tasks. *NeuroImage*, *56*, 1655–1665.
- Visscher, K. M., Miezin, F. M., Kelly, J. E., Buckner, R. L., Donaldson, D. I., McAvoy, M. P., . . . Peterson, S. E. (2003). Mixed blocked/event-related designs separate transient and sustained activity in fMRI. *NeuroImage*, *19*, 1694–1708.
- Wager, T. D., & Smith, E. E. (2003). Neuroimaging studies of working memory. *Cognitive, Affective, & Behavioral Neuroscience*, *3*, 255–274.
- Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, *9*, 445–453.