Weaving the past into an imagined future: Episodic future thinking relies on working memory as a cognitive interface with episodic memory

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ABSTRACT

Converging cognitive and neuroimaging evidence reveals that episodic memory and episodic future thinking (EFT) share component processes. Much less is known about the relationship between EFT and working memory (WM) processes. We hypothesized that WM capacity might provide a crucial componential cognitive role during EFT by supporting the translation of information from discrete episodic memories into a novel future event. We tested this hypothesis in two studies. In Study 1, we collected functional magnetic resonance imaging data during a dual-task interference paradigm that varied WM load and processing demands during EFT. Events imagined while actively maintaining bound item-location representations were less vivid than those imagined during low WM load control trials. Measures of functional and effective connectivity indicated that this behavioral effect corresponded with reduced coupling between the dorsomedial prefrontal cortex and right temporoparietal junction. Events imagined while simultaneously manipulating items in WM took longer to construct than events imagined during control trials and were associated with less functional coupling between the right hippocampus and posterior visuospatial regions. In Study 2, participants completed a similar WM dual-task while simultaneously recalling past events or imagining future events during scalp-recorded encephalography (EEG). As in Study 1, future events imagined while maintaining item-location representations were less vivid than control trials. This effect was specific to future events and corresponded to reduced theta reactivity over bilateral temporoparietal sites. Relative to episodic memory, EFT was associated with alpha synchronization over frontal and parietal sites as well as greater theta-gamma phase amplitude coupling in the right dorsolateral prefrontal cortex. In contrast, episodic memory was associated with greater cross-frequency coupling between frontal theta and occipital gamma oscillations. These results provide novel empirical support for previous theoretical accounts suggesting that WM capacity provides the cognitive workspace necessary to temporarily store and recombine details from discrete episodes into a future event representation.

GENERAL AUDIENCE ABSTRACT

This study used neuroimaging and behavioral techniques to identify how long-term and short-term memory processes interact to support the ability to imagine future events. The results suggest that short-term memory serves as a mental stage on which memories of the past are held and transformed into imagined scenes.

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Behavioral and neuroimaging studies have revealed striking similarities and extensive functional overlap between remembering the past and imagining the future, known as episodic future thinking (EFT; for review, see Schacter et al., 2012). Episodic memory and EFT are both consistently observed to activate a core set of brain regions corresponding to the brain's default network (see Benoit & Schacter, 2015; Spreng, Mar, & Kim, 2009). Schacter and Addis (2007a; 2007b) have proposed a theoretical framework for how the two systems interact that emphasizes the constructive nature of each process. According to their *constructive episodic simulation hypothesis*, details retrieved from episodic memory are flexibly recombined in order to create novel mental depictions representing hypothetical future events (Schacter & Addis, 2007b). Overlap between episodic memory and EFT can therefore be traced back to the shared reliance on constructive mechanisms and event details. In an alternative proposal, episodic memory and EFT are suggested to engage overlapping component processes involved with (re)constructing and maintaining mental scenes representing a past or future event (Hassabis & Maguire, 2007; 2009).

Given the constructive and generative nature of EFT proposed by these theoretical frameworks, imagining a contextually specific future event should involve significant demands on working memory (WM), broadly defined as a limited capacity system that supports the temporary storage and processing of information, because it requires selectively retrieving, organizing, and recombining disparate details into a novel event depiction. However, relatively little is known about the functional relationship between EFT and WM processes. The current studies seek to directly identify the roles of specific WM processes supporting episodic retrieval and recombination during EFT (Study 1) and the degree to which WM demands imposed by EFT differ from those recruited during episodic memory (Study 2).

WM contributions to EFT vs. Episodic Memory

The initial construction of a novel future event elicits a stronger neural response in the right anterior hippocampus (HPc), dorsomedial prefrontal cortex (dMPFC), and ventrolateral and dorsolateral prefrontal cortex compared to recalling the past (Addis, Wong, & Schacter, 2007; Addis, Pan, Vu, Laiser, & Schacter, 2009; Benoit & Schacter, 2015; Okuda et al., 2003). In contrast, mentally elaborating on a previously constructed event produces minimal dissociations except with regard to the selective modulation of left anterior HPc, left amygdala, and right frontopolar activity by the amount of self-reported details comprising future events, but not past (Addis & Schacter, 2008). Increased MTL and prefrontal activity during EFT construction is consistent with the WM and executive control demands suggested by the recombination of disparate event details into a novel episodic representation (Addis et al., 2009; Benoit & Schacter, 2015; Schacter & Addis, 2007a; Thakral, Benoit, & Schacter, 2017). Dorsolateral and ventrolateral prefrontal cortex have both been implicated in studies that require organization of items maintained in WM.

Consistent with the hypothesis that increased activation in prefrontal cortex reflects increased WM demands in EFT as opposed to episodic memory, sustained neural activity in several putative frontoparietal control regions, including dorsolateral prefrontal cortex, angular gyrus, and medial parietal lobe, is modulated by the number of disparate event details comprising a simulated event depiction, potentially reflecting the controlled processing demands of maintaining detailed representations in WM (Thakral et al., 2017). Furthermore, impaired function in regions selectively modulated by the amount of details comprising a future event

(Addis & Schacter, 2008) – left anterior HPc and right frontopolar cortex — is thought to underlie age-related deficits in feature binding in WM (Mitchell, Johnson, Raye, & D'Esposito, 2000).

Although the neural results reviewed above offer support for the engagement of WM during episodic simulation, the conclusions are largely based on reverse inference of hippocampal and frontoparietal network function. Behavioral and neuropsychological studies provide more direct data regarding the role of WM in EFT.

Behavioral Evidence for WM modulation of EFT

Previous behavioral findings demonstrate that individual differences in executive control and WM capacity predict EFT over and above similar measures of memory retrieval (D'Argembeau, Ortoleva, Jumentier, & Van der Linden, 2010; Hill & Emery, 2013). D'Argembeau et al. (2010) observed that executive retrieval processes uniquely predicted the ability to produce contextually specific future events, but not the ability to retrieve contextually specific past events. Unlike the past, future events can be imagined to occur in any number of spatiotemporal contexts. Additional executive resources may be necessary to organize and monitor the recombination of disparate autobiographical and episodic details into a coherent and plausible event depiction (D'Argembeau et al., 2010). Hill and Emery (2013) observed that a component measure of WM capacity similarly predicted the ability to produce contextually specific future events, but not past. The unique predictive role of WM capacity was limited to the *construction* of specific future events and did not similarly predict the ability to retrieve generic autobiographical information or vividly elaborate on already constructed events (Hill & Emery, 2013).

Neuropsychological Evidence for the role of WM in EFT

Lifespan developmental approaches have identified overlapping trajectories in the maturation and decline of EFT, executive function, and WM (Abram, Picard, Navarro, & Piolino, 2014; Zavagnin, Beni, Borella, & Carretti, 2015), suggesting commonalities between these cognitive skills. As described above, age-related deficits in WM feature binding are associated with neural dysfunction in regions that are also responsive to the amount of details comprising a future event (Addis & Schacter, 2008; Mitchell et al., 2000). Impaired WM abilities may therefore account for age-related differences in future event construction (Rendell et al., 2012; for review, see Schacter, Gaesser, & Addis, 2013; but also see Romero & Moscovitch, 2012).

Similarly, patients with frontal-based executive dysfunction show deficits in EFT. Parkinson’s patients with no memory impairments were observed to produce significantly fewer episodic details when imagining the future compared to control participants, and this effect was most robust among those patients exhibiting higher rates of executive dysfunction (de Vito et al., 2012). Likewise, diminished WM maintenance capacity following traumatic brain injury is observed to predict EFT deficits, but not the ability to imagine abstract future events or recall past events (Coste et al., 2015).

Study 1

Existing evidence indicates a relationship between EFT and WM processes, but the precise WM demands imposed during EFT, as well as their neural basis, remain poorly understood. We predicted that different component processes of WM (maintenance and manipulation) contribute to distinct retrieval and recombination stages of EFT construction. To test this prediction, we used a dual-task interference paradigm to identify EFT performance decrements as well as changes to the brain’s functional architecture in response to concurrent

WM demands. We predicted that MTL and frontal regions that are consistently observed to be more strongly engaged during EFT than episodic memory would also demonstrate disrupted functional connectivity with the putative core recollection and EFT network when either WM maintenance or manipulation demands increased.

Participants performed a modified Sternberg WM task as they simultaneously imagined specific future episodic events over a 10 s delay period. The WM dual-task included three conditions meant to recruit different aspects of WM load: (1) active maintenance of three bound item-location representations (maintenance trials), (2) active manipulation of three items to determine the single item that needed to be maintained (manipulation trials), and (3) active maintenance of a single, unbound, predetermined item during delay (low WM control trials). This dual-task interference paradigm was designed to test the respective contributions of WM maintenance and manipulation to future event construction in an effort to understand the cognitive mechanisms that drive EFT. If proactive interference of a secondary WM task disrupts EFT performance, we can infer that the two tasks compete for limited capacity resources.

Materials and Methods

Participants

Twenty-six members of the Virginia Tech community (20 females) were recruited and given monetary compensation for participating. All participants were right handed. Two female participants were excluded from fMRI data analysis due to stimulus presentation timing and syncing errors leading to a final N of 24 (mean age = 23, range 19-29).

Experimental Procedure

Stimuli. Sixty-three nouns with similar scores on normative indices of imageability (*M* = 5.86, *SD* = 0.33), concreteness (*M* = 6.87, *SD* = 0.22), and frequency of use (*M* = 1.74, *SD* =

0.26) were used as EFT cues (Addis et al., 2007; Clark & Paivio, 2004). EFT cues were randomly assigned to one of three lists; Analyses of Variance (ANOVA) confirmed that these lists did not significantly differ on imageability [$F_{(1,61)} = .49$, $p = .49$], concreteness [$F_{(1,61)} = 1.33$, $p = .25$], or frequency of use [$F_{(1,61)} = .22$, $p = .64$]. These lists were then assigned to one of three functional runs for each participant in a counterbalanced fashion. During each run, words were randomly assigned to a trial.

Stimuli for the Sternberg interference task consisted of images of 67 objects on a solid white background (300 x 282 pixels). Images were qualitatively inspected and chosen for similarity in object complexity. Items were grouped into three orthogonal categories based on their relative weights: light (e.g., apple, button), medium (e.g., chair, dog) or heavy (e.g., bus, piano). The items in each category were inspected by the experimenters to ensure that the relative weights across categories were unambiguous. Items presented in the Sternberg task were randomized with replacement on a trial by trial basis.

Prior to scanning, the task instructions were explained to participants and they had an opportunity to perform a minimum of three practice trials for each condition (9 trials total). Participants were allowed to repeat the practice trials until they were comfortable with the instructions and timing. During these practice trials we asked participants to imagine future events aloud so that we could assess the episodic specificity of envisaged events and provide feedback when necessary.

Participants completed three runs of the EFT task, during which fMRI data were collected, each lasting approximately 8 mins and 30 s in duration. Each run included 20 EFT trials. The 20 trials in each run consisted of 10 trials from 2 of the 3 task conditions (i.e., maintenance-control, manipulation-control, and manipulation-maintenance). Behavioral piloting indicated that performance accuracy on the Sternberg WM task was vastly improved when the task was broken into blocks consisting of 2 rather than 3 trial types due to the additional demands created by maintaining three sets of task instructions.

Trials were 20 s in duration and consisted of a WM cuing phase, an EFT cuing phase, a WM probe, and an event rating phase (see Figure 1A for trial timing and layout). Each trial was separated by a jittered ITI with an average duration of 4 s. Trial order and ITI lengths were determined by an optimization simulation using the optseq2 program (http://surfer.nmr.mgh.harvard.edu/optseq/). Stimuli were projected onto a screen viewed by participants on a mirror attached to the head-coil. Presentation® software (Version 16.1, www.neurobs.com) was used for the presentation and timing of stimuli and to record behavioral responses during scanning.

WM Cuing. At the onset of each trial, three images were presented along with cues indicating which item(s) were to be remembered for the duration of the trial (Figure 1B). During maintenance trials, arrows pointing to each of the items indicated that all three items and their locations on the screen were to be remembered. During manipulation trials, participants were instructed to determine the relative weights of each of the presented items and to then remember the middle weighted object (as indicated by the cue ‘middle’ at the top of the screen) independent of spatial arrangement. Instead of varying the relative weight of the to-be-remembered item (i.e., lightest, middle, heaviest), we opted to require participants to always pick the middle weighted object. This ensured that all three items had to be evaluated and compared in order to select the appropriate to-be-remembered stimulus and therefore maximized the manipulation of information required by the task. During control trials, a single arrow indicated the to-be-remembered item. Participants were instructed that during control trials, they were only required to remember the indicated item, without respect to spatial locations or the other items on the screen.

EFT Phase. Immediately following the WM cuing phase, participants were prompted to imagine a future event using an event construction-elaboration paradigm (Addis et al., 2007; 2009). Participants were instructed to imagine a novel future event in response to a cue word (e.g. “coffee”) presented in the center of the screen for the duration of the 10 s EFT phase. As with prior studies (Addis et al., 2007; 2009), participants were instructed to imagine plausible future events specific in place and time, lasting a few minutes or hours but less than one day. Events were not required to directly correspond to the cue word; instead, participants were encouraged to imagine the first event that came to mind. Participants were also encouraged to imagine events from a first-person field perspective. The experimenter provided feedback during the practice trials to ensure that these directions were understood.

Participants were instructed to respond via a button box once they had successfully brought a single contextually specific event to mind (e.g., “I can imagine camping at the Outer Banks with friends this July 4th weekend” in response to the EFT cue “BEACH”). Participants were informed that imagined events did not need to be richly detailed before making this response. The reaction time for this response was recorded and indicated the transition from event *construction* to event *elaboration* (Figure 1C). At this point, participants were instructed to mentally elaborate on the sensory and contextual details of the envisaged event for the remainder of the 10 s EFT phase.

WM Probe. The end of the EFT phase was signaled by the presentation of the WM probe, which consisted of one of the three stimuli from the WM cuing phase. Participants made a yes/no response to indicate whether the WM probe matched the to-be-remembered stimulus from the encoding phase (Figure 1B). During maintenance trials, the probe stimulus was presented in one of the three original screen locations. Participants were required to indicate whether the location of the probe item matched that item's location during the WM cuing phase. Successful performance on the maintenance task therefore required participants to maintain three items and their associated spatial information in short-term storage throughout the duration of the EFT cue phase. In manipulation and control trials, participants indicated whether the probe stimulus matched the middle weighted (manipulation trials) or explicitly indicated (control trials) item. Successful performance on the manipulation task therefore required participants to analyze three items according to semantic characteristics and make a judgment regarding their relative sizes but then maintain only a single item throughout the duration of the EFT cue phase. Successful performance on the control task did not require such analysis but again required ongoing storage of a single unbound item.

The maintenance and manipulation tasks differed from control trials in terms of the types of WM load they preferentially engaged. That is, the maintenance and manipulation tasks (compared to control) functionally differed in terms of the relative *capacity* (maintenance > control) and *processing* (manipulation > control) necessary for successful WM performance (Table 1). Maintenance and control tasks both required active storage of stimuli in WM but varied in terms of capacity (multiple bound item-location representations vs. single unbound item). In contrast, manipulation and control tasks involved equal capacity demands (single unbound item) but differed in terms of the processing required to select the to-be-remembered item.

Subjective Ratings. During the ratings phase participants were presented with two 4-pt scales to rate the qualitative features of the imagined events. Participants rated both the degree of vividness (i.e., amount of detail associated with each envisaged event) and the novelty (i.e., degree of similarity to previously experienced events) of each imagined event on a 4-point scale (1 = not at all; 4 = very).

MRI data acquisition

MRI data were acquired at the Virginia Tech Carillion Research Institute Human Neuroimaging Lab using a 3T Siemens Tim Trio scanner equipped with a 12-channel head coil. Prescreening interviews were conducted to ensure safety in the scanner, and headphones were provided to attenuate acoustic noise from the scanner. Padding and adjustable head restraints minimized head movement. Functional data collection consisted of a gradient echoplanar imaging (EPI) sequence (repetition time/TR = 2000 ms; echo time/TE = 23 ms; field of view = 220). Each volume included 40 slices with a thickness of 3.4 mm and no interslice gap. Voxel size for functional images was 3.4 x 3.4 x 3.4 mm. Anatomical images were collected using an MPRAGE sequence (voxel size = 0.9 x 0.9 x 0.9 mm).

Preprocessing and Analysis

All imaging preprocessing and analysis was performed using Statistical Parametric Mapping (SPM8) software (Wellcome Trust Centre for Neuroimaging, London). EPI data were slice-time corrected with sinc interpolation to account for differences in the timing of adjacent slice acquisition. Then, the functional images for a single participant were brought into spatial alignment by using a six-parameter, rigid-body transformation. Following realignment, the high-resolution MPRAGE structural image for each participant was co-registered to the mean EPI for each participant. Spatial normalization was conducted using a segmentation-based procedure. First, the unified segmentation tool in SPM8 was used to calculate normalization parameters based on each participant’s co-registered high-resolution MPRAGE. These normalization parameters were then applied to the EPI images to transform them into Montreal Neurological Institute (MNI) template space. Finally, the images were spatially smoothed with an 8 mm full-width at half-maximum Gaussian filter.

Blood oxygenation-level dependent (BOLD) signal was measured with maintenance and manipulation trials being compared to control trials. We conducted separate GLMs corresponding to one of the two cognitive events of interest: (1) the TR corresponding to the initial onset of the EFT cue word (EFT onset), and (2) the TR immediately preceding the participant button box response signifying an event had been brought to mind (event production) (Figure 1C). Within each GLM, each trial was modeled with a single stick function convolved with the canonical hemodynamic response function (HRF). We suggest that the temporal dynamics and protracted nature of generative event construction (Conway & Pleydell-Pearce, 2000; D’Argembeau & Mathy, 2011) are captured collectively by the EFT onset and event production phases which correspond to strategic autobiographical retrieval operations and the integration of event features and details into a unitary representation, respectively. Note that the terms construction and elaboration defined in prior studies using the same paradigm correspond with the terms EFT onset and event production, respectively, used in this study (Addis et al., 2007; 2009).

Run order and motion parameter outliers were modeled as covariates of no interest. Motion parameter outliers were identified at the individual-subject level using the Artifact Detection Tools (http://gablab.mit.edu/index.php/software) in SPM8 with thresholds for global signal intensity ($z = 5$), translational movement (0.5 mm), and rotational movement (0.005 rad).

GLM contrast images were thresholded at $p < .001$, uncorrected, with a 14 voxel extent-threshold which was determined to yield a cluster-wise corrected threshold of $p < .05$ (3dClustSim, AFNI version 16.3.04).

Partial Least Squares. In order to assess whether the dual-task conditions engaged distinct WM subprocesses we submitted the fMRI and behavioral WM data to a spatiotemporal partial least squares (PLS) analysis (McIntosh & Lobaugh, 2004). Spatiotemporal PLS is a multivariate technique that analyzes covariance between patterns of whole brain activity and the experimental task design (task PLS) or a behavioral measure(s) of interest (behavioral PLS). This covariance is decomposed using singular value decomposition in order to identify orthogonal latent variables (LVs) that describe the optimal fit between brain activity and cognitive tasks (task PLS) or between brain activity and behavioral performance (behavioral PLS). We elected to use a non-rotated multiblock PLS analysis which is a combination of task and behavioral PLS. This allowed us to identify spatiotemporal patterns of brain activity that simultaneously reflect differences between task-based conditions and behaviorally-based WM performance measures (i.e., WM accuracy and response time). This analysis also allowed for the specification of a priori contrasts between the three WM conditions.

The statistical significance of each LV was determined using 500 permutation tests that randomly reordered and decomposed the data to calculate new sets of LVs. Each original LV was assigned a probability based on the number of times a statistic (i.e., amount of covariance explained or singular value) from the permuted data exceeded the original values. Each brain voxel was assigned a weighted salience value that was proportional to its covariance with the onset of the EFT task and behavioral measures of WM performance (WM accuracy and response time) at each TR of the pre-specified 18 *s* (9 TR) temporal window. The reliability of voxel salience within a LV were determined using bootstrap resampling with replacement to estimate standard errors in 300 bootstrap samples. Unlike traditional univariate techniques, PLS is computed in a single analytic step, negating the need to correct for multiple comparisons. Clusters of 20 or more voxels in which the bootstrap-to-standard-error ratio (similar to a z-score) was greater than 3.2 (approximate p = .001) are reported.

Psychophysiological interaction analyses. We performed a series of psychophysiological interaction (PPI) analyses (Friston et al., 1997; O'Reilly et al., 2012) in order to identify brain regions demonstrating reduced functional connectivity in response to the maintenance and manipulation WM tasks as compared to low WM load control trials. We performed separate PPI analyses for maintenance and manipulation conditions at EFT onset and event production. We selected the right anterior HPc (28, -10, -16) and dMPFC (4, 61, 25) as our seed regions of interest (ROIs). These ROIs were identified by Addis et al (2007) as being more active during the construction of future relative to past events and were proposed to reflect the increased cognitive demands of future thinking (Addis et al., 2007; 2009; Hill & Emery, 2013; Schacter & Addis, 2007a). ROIs were defined for each participant as the hippocampal and PFC peak activations from the EFT onset manipulation > control contrast closest to those reported by Addis et al. (2007; all peaks were within 10 mm). These peaks then served as the center of spherical ROIs (radius = 6 mm). The first eigenvariate of each ROI served as the physiological variable in each analysis (i.e., the first principal component of the voxel time series). Given our interest in altered functional coupling in response to the maintenance and manipulation WM tasks compared to low load control trials, we defined the psychological variables as the two reverse random-effects contrasts (i.e., control > maintenance, control > manipulation) separately for the two cognitive events: EFT onset and event production. We entered these two regressors and their interaction term into a first-level GLM for each participant. The contrast images for the PPI regressors were then entered into a second-level random effects GLM to determine functional coupling at the group level.

Because of the high degree of multicollinearity between PPI regressors, PPI analyses are known to lack statistical power. To account for inflated false negative rates, we report areas of activation surviving a voxel-wise threshold of $p < .005$, uncorrected, with a 29 voxel extend threshold (yielding cluster-wise corrected $p < .05$). This threshold is in line with prior studies reporting on PPI analyses (e.g., Gu et al., 2010; Humbert & McLaren, 2014; Yang et al., 2017).

Dynamic Causal Modelling. We next used Dynamic Causal Modelling (DCM) in order to uncover how concurrent WM load influences the flow of information between functionally coupled regions identified by the PPI analysis. DCM provides an estimate of effective connectivity by describing how activity in one brain region causes a change in activity in another brain region and how these relationships change in varying contexts (Friston, Harrison, & Penny, 2003; Stephan et al., 2010). Thus, DCM can be used to estimate the direction and context-dependent modulation of connections between a set of neuronal populations.

For the purpose of these analyses, we focused on the event production phase. Since manipulation effects were minimal during this phase, the primary focus of the DCM analyses was on context-dependent changes in effective connectivity as a function of varying WM capacity between the maintenance and control dual-tasks.

The first step of DCM involves generating a set of plausible causal models (Stephan et al., 2010). Each model consisted of three nodes. The DMPFC seed node was the same as that used as a seed ROI in the PPI analyses. Two additional right lateralized nodes located in the dorsolateral prefrontal cortex and temporoparietal junction (TPJ) were also used. These nodes were identified by the event production maintenance > control and control > maintenance PPI contrasts respectively (Section 3.3.2). We specified reciprocal intrinsic connections between the DMPFC and DLPFC nodes and between the DMPFC and TPJ nodes. ROI BOLD time series data were extracted from the corresponding 1st level PPI contrasts. For each participant, we located the peak activation within 10mm of the ROI centers. These peaks were used as the centers when generating spherical ROIs (radius = 6mm). The first eigenvariate from each ROI (i.e., the first principal component of the time-series of the voxels included within the sphere) was extracted.

For each model, event production onsets were entered as direct (i.e., evoke a local response) and modulatory (i.e., context-dependent modulation of connectivity between nodes) inputs. The design matrices consisted of: (1) maintenance trial production, (2) control trial production, and (3) EFT trial production (i.e., concatenation of all WM trial types). Each trial type was entered as direct and/or modulatory inputs in various models (Figure 2). All models had the same intrinsic connections but differed in terms of: (1) sites of the direct inputs and (2) modulatory effects.

In a follow-up DCM analysis, self-reported event vividness was entered as a fourth parametric modulatory input to the optimal model structure from the first DCM analysis (see Figure 7). Data from one participant was dropped from this analysis due to an insufficient number of vividness ratings.

Random effects Bayesian model selection was used to perform group-level inference on the optimal model structure (Stephan et al., 2010). This method identifies a model from the set of all alternative plausible models that best optimizes the balance between relative fit of the data and model complexity (Penny, Stephan, Mechelli, & Friston, 2004). To further clarify the optimal model structure, the model space was partitioned into families based on (1) the pattern of direct and modulatory inputs (families FA-FC) and (2) the directions and patterns of effective connectivity between nodes (families F1-F7). Random effects family-level inference was used to compare model families.

Results

Behavioral Results

Performance on the WM tasks was measured by response time (WM-RT) and accuracy (i.e., proportion of correct WM probe responses) during the WM probe phase. One-way ANOVAs revealed a significant effect of WM condition on WM-RT [$F_{(2,1412)} = 39.20$, $p < .001$] but not response accuracy [$F_{(2,69)} = 2.19$, $p = .120$]. Post hoc Tukey HSD pairwise comparisons indicated that WM-RT latencies were significantly longer during maintenance (*M* = 1532.59 ms, *SD* = 495.98 ms) trials compared to manipulation (*M* = 1341.83 ms, *SD* = 463.27) and control (*M* = 1271.79 ms, *SD* = 444.65) trials at $p < .0001$. WM-RT was numerically greater for manipulation trials compared to control, though this difference was slightly beyond traditional significance thresholds after correcting for multiple comparisons ($p = .056$). Though the main effect of condition on WM response accuracy was not significant, we do note that the proportion of correct trials was numerically lower for maintenance (*M* = .78, *SD* = .19) and manipulation (*M* = .84, *SD* = .23) trials compared to control (*M* = .90, *SD* = .18) trials. These behavioral measures suggest greater difficulty associated with the maintenance and manipulation conditions compared to low WM load control trials.

Behavioral measures of EFT included the response latency between EFT onset and the button press indicating successful event construction (EFT-RT) and self-reported event vividness and novelty ratings. In order to examine the relationship between WM and behavioral features of

EFT we used the lmerTest R package (Bates, Maechler, Bolker, & Walker, 2015; Kuznetsova, Brockhoff, & Christensen, 2014) to run separate repeated measures linear mixed effects models using each behavioral measure as an outcome variable (see Magezi, 2015 for a review of the use of linear mixed-effects models for repeated measures designs in cognitive neuroscience). Results of the analyses are presented in Table 2. Intraclass correlation coefficients (ICC) indicated that much of the variance in the behavioral measures could be accounted for by intra-subject clustering ($\text{ICC}_{\text{EFT-RT}}$ = .68, $\text{ICC}_{\text{Vividness}}$ = .24, $\text{ICC}_{\text{Novelty}}$ = .18). In order to account for this dependence, we entered subject as a random effects, random intercept predictor (Model 1). In subsequent models we entered WM condition (Model 2) and WM accuracy (correct, incorrect; Model 3) and the condition x accuracy interaction term (Model 4) as additional categorical fixed effects predictors in a nested, stepwise fashion. All categorical predictors were dummy coded (control and correct trials treated as reference group). Nested models were compared using maximum likelihood ratio tests in order to determine whether the addition of WM condition and accuracy significantly contributed to the model fit for each of the behavioral outcome variables. Post-hoc pairwise comparisons of the conditional means for each factor level, corrected for multiple comparisons (Tukey HSD), were performed using the lsmeans R package (Lenth, 2016). All comparisons surviving a $p < .05$ significance threshold are reported in the text below.

Behavioral analysis of EFT-RT revealed significant main effects of WM condition ($\chi2$ = 7.96 (2), p = .019) and WM accuracy ($\chi2$ = 18.54 (1), p < .001). Post-hoc analyses of these effects revealed that events imagined during manipulation trials (*M* = 4596.07 ms, *SE* = 401.29 ms) took significantly longer to construct than events imagined during control trials (*M* = 4354.88 ms, *SE* = 401.50 ms) and that events imagined during incorrect WM trials (*M* = 4903.40 ms, *SE* = 410.62 ms) took significantly longer to construct than those imagined during correct

WM trials (*M* = 4422.42 ms, *SE* = 397.31 ms) (Figure 3A, left panel). We also observed a significant condition x accuracy interaction (χ2 = 6.28 (2), *p* = .043) which indicated that increased EFT-RT during the manipulation task was driven by performance on incorrect (*M* = 5334.79 ms, *SE* = 431.77 ms) compared to correct (*M* = 4469.64 ms, *SE* = 401.02 ms) WM trials (Figure 3B, left panel). Taken together, this pattern of results suggests that the organizational demands associated with manipulation trials may have interfered with processes supporting event construction (e.g., retrieval and binding of details into a novel event).

Behavioral analysis of self-reported event vividness revealed nonsignificant main effects of WM condition (χ2 = 549 (2), *p* = .064) and WM accuracy (χ2 = .36 (1), *p* = .546). We observed a significant interaction between WM condition and accuracy (χ2 = 6.97 (2), *p* = .031). Post-hoc analyses revealed that events imagined during maintenance trials (*M* = 2.86, *SE* = .09) were less vivid than those imagined during control trials (*M* = 2.97, *SE* = .09) but this effect was only significant on correct WM trials (Figure 3, middle panels). These results suggest that the successful maintenance of bound item-location representations in WM may interfere with the ability to construct detailed event representations.

We did not observe a significant effect of WM condition (χ2 = .52 (2), *p* = .770), WM accuracy (χ2 = .07 (1), *p* = .790) or their interaction (χ2 = .00 (2), *p* = .981) on self-reported event novelty. These results suggest that the concurrent WM tasks used in this study does not interfere with the ability to construct and elaborate on a novel future event depiction.

In summary, the behavioral data indicate that the need to actively evaluate and organize the contents of WM during the manipulation task resulted in slower EFT-RT compared to control trials that required similar maintenance demands but did not require organizing the contents of WM. This effect was largely driven by incorrect performance on the manipulation task. In contrast, events imagined during the successful maintenance of bound multimodal representations (maintenance task) were less vivid than those imagined while maintaining an unbound unimodal representation (control task) in WM.

fMRI Results

Spatiotemporal PLS Results. We hypothesized that the maintenance and manipulation dual-tasks would engage distinct WM subprocesses, both behaviorally and neurally. To test this hypothesis, we used a non-rotated multiblock PLS analysis in order to identify spatiotemporal patterns of brain activity that simultaneously reflect changes in mean activity between WM conditions as well as brain activity related to behavioral measures of WM performance (i.e., WM accuracy and WM-RT). This analysis identified a significant pattern of latent brain activity reflecting both overlapping and dissociable neural profiles across the three task conditions (p =.008; 61.87% variance explained; Table 3). The EFT phase across all dual-task conditions was well characterized by increased brain activity in a number of default network regions, including the ventromedial prefrontal cortex, posterior cingulate, middle temporal gyrus, and bilateral MTL (including HPc and parahippocampal cortex) (Figure 4A, left panel). Activity in these regions is ubiquitously observed in neuroimaging studies of EFT (Schacter et al., 2012; Spreng & Grady, 2010; Spreng et al., 2009).

The behavioral portion of the multiblock analysis demonstrated that successful performance on the WM tasks was associated with dissociable patterns of brain activity. The same pattern of default network and MTL activity, reported above, that covaried with the EFT task in all three conditions was positively correlated with accuracy on the maintenance (r = .32) and control (r = .39) tasks as well as WM-RT in the maintenance trial task (r = .46) (Figure 4A, middle and right panels). That is, successful performance on the maintenance and control WM secondary tasks was associated with increased default network and MTL activity (Figure 4B, left panel).

The PLS analysis identified a separate pattern of brain activity that covaried with accuracy on the manipulation task (r = -.33) (Figure 4A, middle panel). Successful performance on the manipulation task was associated with increased activity in predominantly right-lateralized regions including anterior insula, ventrolateral and anterior prefrontal cortex, dorsal anterior cingulate, superior parietal lobule, precuneus, somatosensory and motor cortices, and bilateral fusiform gyri (Figure 4B, right panel). Therefore, accuracy on the secondary task that required manipulation was associated with a distinct pattern of brain activity during EFT as compared to accuracy on the maintenance and control tasks.

This pattern of results indicates that successful performance on the maintenance and control tasks engage overlapping neural resources which are distinct from those recruited during successful manipulation trials. Given the functional load distinctions between the WM dual-tasks (Table 1), these results likely reflect the unique *processing* demands associated with each task (i.e. active maintenance vs. manipulation) and not the effects of increased *capacity* (which would presumably show similar manipulation and control correlations). Moreover, the consistency of the default network and MTL activations across all three conditions likely reflects the common dimension of EFT in all three tasks.

GLM Results. The PLS analysis discussed in the previous section (3.2.1) identified dissociable brain regions that covaried with performance on the secondary WM tasks over the entire duration of the EFT task. However, because construction latencies were inherently variable between trials, this analysis did not permit us to model neural activity phase-locked with distinct cognitive events during the protracted event construction epoch (cf. Addis et al., 2009).

Our next fMRI analysis utilized separate GLM random-effects contrasts of WM and control trials (as well as direct contrasts of the two WM tasks) to model separate patterns of brain activity evoked by the dual-task processing demands coinciding with EFT onset and event production, respectively. All brain regions that survived a threshold of $p < .001$, uncorrected, with a minimum of 14 contiguous voxels (see section 2.4) are reported in Table 4.

We hypothesized that EFT onset would be characterized by heightened activity during maintenance and manipulation trials as compared to control trials due to the increased capacity (maintenance trials) and organizational processing demands (manipulation trials) of the immediately preceding WM cuing phase. During manipulation trials we observed increased brain activity in right inferior temporal gyrus (xyz = 48, -54, -19), left inferior occipital gyrus (xyz = -44, -75, -6), and left orbital frontal cortex (xyz = -20, 38, -16) in comparison to control trials. Activity in these areas is consistent with the need to assess and evaluate the semantic characteristics of the WM stimuli during manipulation trials (Mazard, Laou, Joliot, & Mellet, 2005; Pins, Meyer, Foucher, Humphreys, & Boucart, 2004; Saccuman et al., 2006). Maintenance trials were characterized by increased activity in the left middle occipital gyrus (xyz = -27, -98, 4) and right middle frontal gyrus (xyz = 27, 34, 18) as compared to control trials. The middle frontal gyrus is often implicated in neuroimaging studies of WM (Altamura et al., 2007; D’Esposito, Postle, Ballard, & Lease, 1999; Owen et al., 1998). A direct contrast of the two WM conditions did not reveal any significant activations.

Event production contrasts did not reveal any significant increases in neural responses during manipulation or maintenance trials as compared to control trials. Instead, reverse contrasts revealed increased activity in several posterior visuospatial regions during both WM trial types compared to control. During event production, control trials led to greater activity in the left superior occipital gyrus (xyz = -24, -81, 42) compared to manipulation trials and greater activity in the left lingual gyrus (xyz = -20, -85, -13), left fusiform gyrus (xyz = -17, -37, -16), and left insula (xyz = -41, -3, 1) compared to maintenance trials. These regions are commonly reported in studies of mnemonic mental simulation and likely reflect mental imagery processes (Gardini, Cornoldi, De Beni, & Venneri, 2006; Gerlach et al., 2011; Hassabis, Kumaran, & Maguire, 2007; Sherrill et al., 2013; Summerfield, Hassabis, & Maguire, 2010; Xu, Evensmoen, Lehn, Pintzka, & Haberg, 2010).

A contrast of the two WM tasks (maintenance > manipulation) revealed greater activity in the left lingual gyrus (xyz = -20, -85, -13) during the maintenance compared to manipulation tasks. The reverse manipulation > maintenance contrast did not reveal any significant activations.

PPI Results. The next analysis addressed the question of functional connectivity between WM and EFT regions during the dual-task paradigm. In particular, we ran a series of PPI analyses to search for previously-identified EFT regions that demonstrated altered functional connectivity in the face of increased WM demands (Figure 5A). Given the near ceiling performance (90 ± 18%), we infer that the control WM task represents these regions' typical connectivity during EFT and that any *reduced* connectivity reflects interference due to additional WM demands of either type. We also ran the reverse PPI contrasts in order to determine whether any brain areas demonstrated *increased* functional connectivity with the EFT-related seed ROIs during maintenance and manipulation trials but not control trials.

PPI analyses examine the task-specific time course correlations between seed ROIs and other brain regions. We searched for correlations that were evident during control trials but not during maintenance or manipulation trials separately at the EFT onset and event production phases. Regions identified by this analysis were assumed to reflect reduced or disrupted network connectivity in response to the WM tasks. We also searched for patterns of increased functional connectivity in response to the WM tasks (i.e., correlations with seed ROIs during the maintenance or manipulation tasks but not control). The peak activations for each PPI contrast are listed in Tables 5a and 5b.

EFT Onset PPI. We hypothesized that on control trials, when WM load is low and performance was near ceiling, the EFT onset phase should correspond to typical memory search and retrieval operations involved with accessing the details from episodic memory that will be reorganized into a future event depiction. Given the slower event construction latencies observed during manipulation trials, we propose that the manipulation condition will produce reduced functional connectivity between areas that are critical for the initial construction of future events and areas that support WM manipulation. In line with this prediction, we observed reduced coupling between the dMPFC seed and a cluster of voxels within the left temporal pole (xyz = -44, 7, -23), right lingual gyrus (xyz = 27, -68, -2) and left fusiform gyrus (xyz = -30, -54, -16) as well as between the right HPc seed and right calcarine gyrus (xyz = 10, -68, 15). Manipulation trials were also associated with reduced coupling between the right HPc and a cluster of voxels centered in right lateral orbitofrontal cortex (xyz = 24, 38, -16) and a second cluster of voxels with local maxima in the right inferior frontal gyrus (IFG; xyz = 48, 31, 21) and extending dorsally into the middle frontal gyrus during manipulation trials compared to control; however, these regions did not survive cluster-wise corrections (Figure 5B).

We did not observe any regions of reduced functional connectivity with the seed ROIs during EFT onset on maintenance trials, even at less conservative uncorrected thresholds. The lack of reduced or disrupted functional connectivity was particularly surprising because the maintenance task was the most difficult WM task as indexed by WM-RT (see section 3.1).

However, the behavioral data also indicate that maintenance did not affect initial event construction latency but rather vividness ratings. Therefore, any disruption from the maintenance WM task may occur at later time points in the EFT task. Our data suggest that concurrent WM demands do not affect the onset of future thinking when those demands involve maintaining bound multimodal representations rather than item manipulation.

Event Production PPI. During event production, which was defined in our study as the 2-second period prior to the key press indicating that the participant had an event in mind, manipulation trials were associated with reduced connectivity compared to control trials between the right HPc seed and a cluster of voxels in the left postcentral gyrus (xyz = -44, -30, 49) extending caudally into the inferior parietal lobule (xyz = -54, -47, 49) (Figure 5B). We also observed reduced coupling between the right HPc and a cluster of voxels within dorsal aspects of the left inferior frontal gyrus (xyz = -41, 34, 21) which was similar to the right inferior frontal gyrus location observed at EFT onset, though this did not survive cluster-wise correction.

Maintenance trials were also associated with altered connectivity patterns during the event production phase. In particular, the dMPFC seed showed *reduced* coupling with the right angular gyrus (xyz = 51, -58, 21) overlapping with the temporoparietal junction (TPJ) (Figure 5C) as well as *increased* coupling with right (xyz = 44, 48, 11) and left (xyz = -37, 44, 25) middle frontal gyri compared to control trials. We also observed increased connectivity between the right HPc seed and a number of posterior visuospatial and lateral parietal regions in response to the maintenance task. This particular pattern of extensive increased functional connectivity during this stage is consistent with behavioral indications that the maintenance task was the most difficult of the WM tasks and may reflect the allocation of executive and imagery resources away from episodic construction processes, leading to reduced vividness.

DCM Results. PPI analyses revealed patterns of altered functional connectivity in response to concurrent WM load. These analyses provide novel insights into the functional architecture underlying WM interactions with EFT; however, these analyses do not indicate the deterministic relationship between these neural systems. The primary aim of the DCM analysis was to begin developing an information processing model of EFT under varying WM load. In particular, we focused on identifying the optimal model structure underlying altered connectivity during the event production phase in response to the increased capacity demands of the maintenance dual-task. Random effects model selection identified a winning model that was optimal for 21 of the 23 subjects (Figure 6). In this model structure, EFT trials (regardless of concurrent WM demands) evoked a local response in the DMPFC ROI, while maintenance trials evoked activity in the right DLPFC. Moreover, maintenance and control trials modulated bidirectional DMPFC-DLPFC and DMPFC-TPJ functional connectivity, respectively.

In a second DCM analysis, we examined the degree to which self-reported event vividness (collapsed across all WM trials) parametrically modulated the bidirectional DMPFC-DLPFC and DMPFC-TPJ connectivity identified in the initial winning model. Random effects model selection identified two winning models which were collectively optimal for 19 of 22 subjects (Figure 7). In both models, EFT vividness modulated DLPFC to DMPFC communication. EFT vividness additionally modulated the bidirectional flow of information between the DMPFC and TPJ seeds in Model 15.

Study 1 Discussion

Although the interactions between EFT and other memory systems, including episodic memory and semantic memory, have been studied, much less is known about the functional and mechanistic relationship between EFT and WM. The results from Study 1 provide novel insights into the functional relationship between WM and EFT as well as the neural basis of WM subcomponents as they interact with EFT. Future events imagined during a concurrent WM task that required participants to actively manipulate and organize items in WM took longer to construct than events imagined during low WM load control trials. A PPI analysis revealed that this manipulation task led to reduced functional connectivity between brain regions associated with semantic retrieval and cortical reinstatement of modality specific episodic details. In contrast, events imagined while actively maintaining bound item-location representations in WM were less vivid than those imagined during low WM load control trials but did not produce delayed event construction. A PPI analysis indicated that this behavioral effect corresponded with reduced functional connectivity between the dMPFC seed and right TPJ. These patterns of altered functional coupling and behavioral EFT performance during concurrent WM load demands provide preliminary evidence for the hypothesis that distinct WM subcomponents may support distinct processes required to translate information from episodic memory into a novel envisaged event.

WM Manipulation

Successful performance on manipulation trials required participants to evaluate, organize, and select items maintained in WM based on their semantic characteristics. Random-effects contrasts comparing manipulation to control trials during each of the cognitive phases indicated that manipulation demands were maximal during the EFT onset phase. This is consistent with behavioral results indicating that WM interference from the manipulation task led to significantly longer event construction latencies compared to the less cognitively demanding control trials.

We ran a series of PPI analyses in order to identify patterns of altered functional connectivity with EFT ROIs in response to the increased processing demands associated with the manipulation dual-task. Consistent with behavioral and GLM results, the PPI analyses indicated that altered functional connectivity was maximal during EFT onset which we speculate corresponds with strategic mnemonic retrieval.

We observed reduced functional coupling between the dMPFC seed and left temporal pole at EFT onset. Atrophy in regions proximal to these has been observed to correspond with parallel deficits in semantic memory and EFT among semantic dementia patients (Irish, Addis, Hodges, & Piguet, 2012; Viard et al., 2014). It is possible that this pattern of results reflects disrupted semantic retrieval during early stages of EFT construction. Access to semantic autobiographical knowledge (e.g., self-schema and personal goals) has been suggested to provide the contextual framework for retrieving increasingly specific episodic and sensory details when constructing an autobiographially plausible and salient future event (Conway & Pleydell-Pearce, 2000; D’Argembeau & Mathy, 2011; Irish et al., 2012). The manipulation subcomponent of WM may support the retrieval and reorganization of semantic and contextual information when constructing an autobiographically plausible and salient future event. Future studies carefully controlling for cognitive load and information processing demands may help clarify the role of semantic memory during future simulation and degree to which WM is involved.

Unlike recalling the past, imagining the future involves integrating details from discrete experiences into a novel, unitary event representation (Addis et al., 2009; Schacter & Addis, 2007b; Weiler, Suchan, & Daum, 2010). Moreover, whereas past events are situated in a specific place and time, future events can be placed in any number of spatiotemporal contexts (D’Argembeau et al., 2010). Accordingly, imagining the future has been observed to differentially draw on executive resources involved with organizing and monitoring the strategic retrieval of contextually accurate details from long-term memory (Conway & Pleydell-Pearce, 2000; D'Argembeau & Mathy, 2011; de Vito et al., 2012; Jeunehomme & D'Argembeau; 2015). Reduced functional coupling between the HPc seed and posterior visuospatial regions may reflect disrupted cortical reinstatement involved with accessing disparate episodic and sensory details comprising an imagined event.

Another possibility is that reduced coupling between the right HPc and visuospatial regions as well as between the dMPFC and temporal pole may reflect interference with the organization and binding of disparate episodic and semantic details maintained in WM into a unitary event depiction. Increased activity in the right anterior HPc is observed in response to relational binding of novel stimuli (Kholer, Danckert, Gati, & Menon, 2005; Preston, Shrager, Dudukovic, & Gabrieli, 2004) as well as when imagining events comprised of highly disparate details (Addis, Cheng, Roberts, & Schacter, 2011; Weiler et al., 2010). The preferential increase in right anterior HPc activity during future relative to past event construction might therefore reflect the increased relational processing demands of recombining highly disparate event features from discrete past experiences into a novel and unitary event depiction (Addis et al., 2007; Weiler et al., 2010). The manipulation subcomponent of WM may therefore support the organization and strengthening of inter-item associations between disparate semantic and episodic details retrieved from long-term memory into a coherent spatiotemporal context during future simulation. Future studies exploiting the relative congruence between details comprising an envisaged event may help clarify the precise functional role of WM manipulation during EFT.

Notably, the manipulation task did not involve ongoing organization of information throughout the EFT trial. Therefore we may have underestimated the importance of such processing in later stages of EFT, after the organization required for the manipulation task was complete. Further research is needed into the role of WM manipulation demands during EFT production and elaboration stages.

WM Maintenance

Measures of functional and effective connectivity indicated that attenuated event vividness during the maintenance task corresponded with reduced bidirectional connectivity between the dMPFC and TPJ in favor of increased connectivity between dMPFC and bilateral middle frontal gyri during the event production phase. The dMPFC seed used in these analyses was selected based on previous observations of increased activity in this region during future relative to past event construction (Addis et al., 2007; 2009; Okuda et al., 2003). Notably, this region is proximal to frontopolar regions previously identified as being active during the maintenance of integrated vs. unintegrated cross-modal stimuli, leading to speculation that the region is a candidate site of the episodic buffer component of WM (Prabhakaran et al., 2000; Rudner et al., 2007; Zhang et al., 2004). A DCM analysis indicated that EFT trials – regardless of concurrent WM load – evoked a local response in the dMPFC, corroborating the functional importance of this region during EFT.

Patterns of reduced and enhanced functional coupling with the dMPFC in response to heightened maintenance load is largely consistent with the heterogeneity of the episodic buffer (Nobre et al., 2013) and may reflect the different types of stimuli being maintained in WM during control and maintenance trials (Baddeley et al., 2010). For example, during low WM load control trials (speculated to reflect baseline EFT), we observed greater dMPFC-TPJ connectivity. The dMPFC and TPJ are components of a distinct functional-anatomic subsystem within the default network supporting self-reflection and evaluation of personally salient information during autobiographical thought (Andrews-Hanna et al., 2010; 2014). During the more cognitively demanding maintenance trials, dMPFC-TPJ connectivity was reduced in favor of heightened functional coupling between the dMPFC seed and bilateral middle frontal gyri. Activity in bilateral middle frontal gyri is commonly reported in studies of WM that require the maintenance and manipulation of exogenously presented stimuli (Blumenfeld & Ranganath, 2006; D'Esposito et al., 1999; Ranganath et al., 2003). We suggest that the pattern of altered functional coupling in response to heightened WM capacity demands of maintenance trials may indicate a shift between endogenously retrieved autobiographical information being maintained in WM in response to the EFT task (during the control WM task) and exogenously provided information being actively maintained in WM (during the maintenance task).

In addition to supporting self-reflective aspects of autobiographical past and future thought, dMPFC and TPJ activity is commonly observed in response to Theory-of-Mind tasks that require subjects to infer the mental states of others (Andrews-Hanna, Saxe et al., 2014; Rabin, Gilboa, Stuss, Mar, & Rosenbaum, 2010; Spreng & Grady, 2010; Spreng et al., 2009). Activity in these regions has been specifically linked to the increased cognitive control necessary to maintain conflicting mental states during a false-belief Theory-of-Mind task (Hartwright, Apperly, & Hansen, 2014). Accordingly, imagining a future event may require holding in mind a novel event that is at odds with the current reality. Likewise, frontal regions are also suggested to enable mental time travel by encoding the subjective awareness of time (Nyberg, Kim, Habib, Levine, & Tulving, 2010; Szpunar, 2011; Tulving, 2002; Wheeler, Stuss, & Tulving, 1997). Altered dMPFC-TPJ connectivity during maintenance trials may therefore reflect the meta-representational demands of thinking about oneself in the distant future (Perner, 2000; Spreng et al., 2009).

Interestingly, successful performance on the maintenance dual-task was positively correlated with activity in the default network and bilateral MTL. This finding is seemingly at odds with the prevailing view of the default network as a “task-negative” network. However, hthere is growing evidence that upregulation of the default network may actually facilitate performance on cognitively demanding tasks that require control of autobiographical or internal mnemonic representations (Gerlach et al., 2011; 2013; Spreng et al., 2010; 2014). We suggest that the dual-task demands of maintaining bound item-location representations diverted limited capacity resources away from the similar demands of maintaining rich episodic representations within the focus of attention during EFT.

Study 2

The results of Study 1 provide novel insights into the functional and neurobiological basis of WM processes during EFT but did not directly compare WM during EFT to episodic memory. Hypotheses for the functional role of WM during EFT are largely motivated by behavioral (D’Argembeau et al., 2010; Hill & Emery, 2013) and neural (Addis et al., 2007; Benoit & Schacter, 2015) differences between EFT and episodic memory. Specifically, growing evidence suggests that EFT might uniquely recruit WM resources over and above those imposed by episodic memory. Study 2 will directly address this hypothesis by testing the prediction that concurrent WM dual-tasks will interfere with EFT to a greater degree than episodic memory.

Neuroimaging studies using fMRI and PET methodologies, along with neuropsychological studies of patient populations, have provided valuable insights into the neural substrates of EFT. In contrast, the electrophysiological basis of EFT remains poorly understood. Although the electrophysiological correlates of episodic memory and WM have been well established, there has only been one study attempting to link EFT with traditional electroencephalogram (EEG) frequency bands. In a recent study, Hsu and Sonuga-Barke (2016) used EEG power and coherence measures to characterize default network activity as participants vividly imagined spending money in the future. Compared to a resting condition, EFT was associated with reduced EEG power over the medial prefrontal cortex across the delta, theta, alpha, and beta frequency bands. Reduced activity compared to resting state may reflect task-evoked deactivation in response to the increased mental effort associated with imagining a novel future event. Increased power was also observed over lateral temporal sites in the delta, theta, and alpha frequency bands, as well as phase synchrony between prefrontal, temporal, and parietal sources overlapping the default network in the delta and theta frequency ranges. These results corroborate prior neuroimaging studies by showing that interactions between functionally heterogeneous cortices are important for EFT (Hsu & Sonuga-Barke, 2016).

In two prior EEG studies, differences in event-related regional brain activity indexed by low-frequency (< 1 Hz) slow-cortical shifts have been observed between real and imagined (counterfactual and future) events. Examining construction of episodic and counterfactual (i.e., imagined) memories, Conway and colleagues (2003) observed overlap in left frontal regions in response to both tasks but greater activity over occipto-temporal regions as participants recalled previously experienced episodes. Greater activity over posterior visual processing areas is also observed as participants vividly elaborate on previously experienced past events compared to imagined future events (Weiler, Suchan, & Daum, 2011). In contrast, elaborating on hypothetical future events was associated with greater temporo-parietal activity (Weiler et al., 2011). The authors of these studies suggest that real and imagined events might draw on similar control processes but differ in terms of the sensory content comprising an event depiction, with stronger activation over posterior visual processing cortices during memory for real events reflecting cortical reinstatement of the original perceptual experience.

Study 2 was motivated by two aims: (1) identify the unique WM demands imposed by EFT and episodic memory and (2) clarify how EFT and episodic memory interactions with WM manifest within traditional EEG frequency bands. To carry out these aims, scalp EEG signals were recorded as participants were cued to recall events from their past and imagine hypothetical events in their future while performing a simultaneous Sternberg interference task. The WM dual-task conditions used in Study 2 were the same as those used in Study 1.

Materials & Methods

Participants

Twenty-six members of the Virginia Tech community (15 females, 11 males) were recruited through the department of psychology SONA system and were given extra credit for participating. Data from 4 male and 1 female participants were excluded from EEG data analysis due to technical or participant error leading to a final N of 21 (mean age = 18.86, SD = 1.06*)*. Participants from Study 1 were excluded from participating in Study 2.

Experimental Procedure

Experimental procedures in Study 2 were the same as those in Study 1 with a few notable exceptions. The primary difference was the inclusion of an episodic memory condition. Participants were prompted to recall events from their past (episodic memory) and imagine events in their future (EFT) during a concurrent WM dual-task. The stimuli used for Study 2 were the same as those used in Study 1 but with the inclusion of additional episodic cues to account for a greater number of trials. The trial structure and timing was slightly altered to conform with EEG acquisition (Figure 8).

Stimuli. EFT cues from Study 1 were also used as episodic memory and EFT cues (hereafter episodic cues) in Study 2. An additional 60 cue words were selected to account for the additional number of trials in Study 2. Episodic cues had mean imageability of 6.48 (*SD* = .25), mean concreteness of 6.79 (*SD* = .30), and mean frequency of use of 1.73 (*SD* = .29) (Addis et al., 2007; Clark & Paivio, 2004). Cue words were randomly assigned to one of six lists; Analyses of Variance (ANOVA) confirmed that these lists did not significantly differ on imageability [$F(_{5, 114)} = .81$, $p = .545$] but did significantly differ on normative concreteness [$F_{(5, 114)} = 10.33$, $p < .001$] and frequency of use [$F(_{5, 114)} = 5.08$, $p < .001$]. Cue lists were assigned to one of six EEG blocks, counterbalanced across participants. During each EEG block, words were randomly assigned to a trial for each participant.

WM stimuli for the Sternberg interference task were the same as those used in Study 1. Unlike Study 1, WM stimuli were randomized *without* replacement during each EEG study block.

Procedure. Prior to beginning the task, instructions were explained and participants were required to perform a minimum of three practice trials for each WM dual-task condition (9 trials total). Participants were allowed to repeat the practice trials until they were comfortable with the instructions and timing.

The experiment was divided into six task blocks during which EEG data were collected. Each block lasted approximately 10-12 minutes. Each block consisted of 20 episodic trials. As before, the 20 trials in each block consisted of 10 trials from 2 of the 3 task conditions (i.e., maintenance-control, manipulation-control, manipulation-maintenance). Moreover, each block consisted of trials from only one temporal direction (i.e., past or future). The entire experiment consisted of 120 trials (60 trials from each temporal direction, 40 trials from each WM dual-task condition).

The trial timing and layout was the same as in Study 1 with three exceptions (Figure 8). At the beginning of each trial, a self-paced “Ready” screen was presented that cued the onset of a new trial. Participants were instructed to make any movements or adjustments at this time and to respond when ready to begin. The “Ready” phase was terminated by a participant initiated button press.

The WM cuing and WM probe phases were the same as in Study 1 and are not discussed in detail here. The episodic cuing phase was analogous to the EFT cuing phase in Study 1 but with the addition of episodic memory trials. Episodic cues and temporal direction (i.e., “Remember Past” or “Imagine Future”) remained on screen for the duration of the 10 s episodic cuing phase. As in Study 1, participants were instructed to respond once an episodic event was successfully brought to mind during the episodic cuing phase. Response times were collected and served as a behavioral measure of event construction latencies.

During the ratings phase participants were presented with five 5-pt scales to rate the qualitative features of the imagined events. Participants rated the degree of vividness, novelty, positive valence, personal significance, and emotionality of each past or future event on a 5-point scale (1 = not at all; 5 = very). Unlike Study 1, the Ratings phase in Study 2 was self-paced.

Presentation® software (Version 16.1, www.neurobs.com) was used for the presentation and timing of stimuli and to record behavioral responses during the experiment.

EEG Data Acquisition, Preprocessing, and Analysis

Electrophysiological data were recording using a BioSemi ActiveTwo system with 32 active Ag/AgCl electrodes mounted in an elastic cap according to the international 10/20 system.

Additional electrodes were placed on the left and right temples and above and below the right eye to monitor horizontal and vertical eye movements. The on-line sampling rate for EEG data collection was 1024 Hz.

All off-line preprocessing steps were performed with the EEGLAB toolbox (Delorme & Makeig, 2004) for MATLAB (Version 2012a). All electrodes were referenced after recording to the average of the two mastoid channels. Continuous EEG data were resampled to 512 Hz and segmented into fixed-length epochs time-locked to the onset of the Episodic Cue phase. Epochs corresponded to a time period spanning 200 ms prior to the presentation of the Episodic Cue until the end of the Episodic Cue phase (10 s following cue onset). Epochs were baseline corrected and filtered using an IIR Butterworth band-pass filter with a high-pass cutoff of .2 Hz and a low-pass cutoff of 50 Hz. Data were decomposed using Independent Component Analysis (ICA) to identify and manually remove eye blink and muscle artifacts. Data were further segmented into fixed-length epochs corresponding with each of the six experimental conditions. For each condition and participant, fixed-length epochs time-locked to the presentation of the episodic cue and lasting the entire 10 s duration of the Episodic Cue phase were generated. Epochs corresponding with the cognitive events modelled in Study 1 (i.e., EFT onset and event production) were also generated. Episodic onset epochs were time-locked to the initial presentation of the episodic cues. Event production epochs were time-locked to a 2 s period immediately preceding participant button response indicating the successful construction of a past or future event.

To increase statistical power, 26 electrodes were selected a priori and grouped into four bilateral regions of interest (ROIs): MPFC (FP1, FP2, AF3, AF4, Fz), DLPFC (F3, F4, F7, F8,

FC1, FC2, FC5, FC6), TPJ (CP5, CP6, P7, P8, T7, T8), and posterior occipital (O1, O2, PO3, PO4, P3, P4, Oz).

Power spectral analyses were performed to quantify the effects of WM dual-task condition and temporal direction on brain activity in the four bilateral ROIs: MPFC, DLPFC, TPJ, and posterior Occipital cortex. Data were analyzed in the theta (4-8 Hz), alpha (8-12 Hz), and gamma (30-40 Hz) frequency ranges for the entire trial duration as well as for the episodic onset and event production phases. Repeated measures ANOVAs were conducted separately for each ROI and frequency range combination, with WM condition (maintenance, manipulation, and control), temporal direction (past, future), and their interaction as within-subjects variables. Averaged theta, alpha, and gamma oscillatory power served as the outcome variables.

Cross-frequency phase amplitude coupling (PAC) was analyzed using the pacpy package for Python (https://github.com/voytekresearch/pacpy). PAC measures the degree to which local high-frequency amplitude is modulated by the phase of low-frequency oscillations and is thought to provide a mechanism for coordinating neuronal communication and information integration across distinct temporal and spatial scales (Canolty & Knight, 2010). Theta/gamma PAC in the hippocampus and cerebral cortex has been functionally linked with episodic memory (Friese et al., 2013; Lega, Burke, Jacobs, & Kahana, 2016) and WM (Axmacher et al., 2010; Roux & Uhlhaas, 2014) processes. One hypothesis is that theta/gamma PAC reflects a neural code for representing multiple items in an ordered manner (Lisman & Jensen, 2013). Theta/gamma PAC might provide a mechanism by which constituent episodic details are organized and integrated within a broader semantic context during episodic event construction.

Theta/gamma PAC was measured within and between the Fz, F4, T8, Pz, CP6, and Oz electrodes. We elected to use single electrodes instead of the aforementioned ROIs to account for the smaller spatial scale of the high-frequency gamma oscillations. The spatial extent of phase synchronization varies by frequency-band, with low-frequency oscillations modulating neural activity over large spatial regions and high-frequency oscillations modulating activity over smaller neural assemblies (Canolty & Knight, 2010; von Stein & Sarnthein, 2000). By measuring PAC at single electrode sites we hoped to increase the specificity of the PAC analyses. These analyses yielded a single phase locking value (Mormann et al., 2005; Vanhatalo et al., 2004) for each participant, condition, and electrode. Phase locking PAC values were analyzed using repeated measures ANOVAs to determine degree to which theta/gamma PAC modulated by WM dual-task and temporal direction. Correlations between PAC and behavioral measures were also explored.

Results

Behavioral Results

WM performance (i.e., accuracy and RT during the WM probe phase) was analyzed using separate 3 (WM condition) x 2 (temporal direction) ANOVAs. These analyses revealed significant main effects of WM condition [$F_{(2,150)} = 33.60$, $p < .001$] but not temporal direction [$F_{(1,151)} = 0.06$, $p = .802$] on WM accuracy. Post-hoc Tukey HSD pairwise comparisons indicated that WM accuracy was significantly lower on maintenance ($M = 47 \pm 3\%$) compared to manipulation ($M = 82 \pm 3\%$) and control ($M = 75 \pm 3\%$) trials. WM accuracy on manipulation and control trials were not significantly different. Analysis of WM probe RT revealed a significant main effect of WM condition [$F_{(2,2600)} = 84.91$, $p < .001$] but not temporal direction [$F_{(2,2601)} = .19$, $p = .661$]. Post-hoc Tukey HSD pairwise comparisons indicated that WM-RT was significantly greater on maintenance ($M = 1730.48$ ms, $SE = 18.17$ ms) compared to manipulation ($M = 1506.19$ ms, $SE = 17.55$ ms) and control ($M = 1405.64$ ms, $SE = 17.88$ ms) trials. Likewise, manipulation WM-RT was significantly greater than control WM-R. Increased WM-RT (maintenance and manipulation trials) and lowered WM accuracy (maintenance trials) suggest greater difficulty than the low WM load control trials.

The behavioral effects of concurrent WM demands on EFT were analyzed using repeated measures linear mixed effects models as in Study 1 but with the addition of temporal direction as a categorical fixed effect predictor as well as self-reported event valence, arousal, and salience as additional outcome variables. As in Study 1, much of the variance in the behavioral measures could be accounted for by intra-subject clustering (ICC_{RT} = .52, $ICC_{Vividness}$ = .12, $ICC_{Novelty}$ = .12). $ICC_{Valence}$ = .04, $ICC_{Arousal}$ = .11, $ICC_{Salience}$ = .13). In order to account for this dependence, we entered subject as a random effects, random intercept predictor (Model 1). In subsequent models we entered WM condition (Model 2) and temporal direction (Model 3) and the condition x temporal direction interaction term (Model 4) as additional categorical fixed effects predictors in a nested, stepwise fashion. All categorical predictors were dummy coded (control and future trials treated as reference group). Nested models were compared using maximum likelihood ratio tests in order to determine whether the addition of WM condition and temporal direction significantly contributed to the model fit for each of the behavioral outcome variables. All post-hoc pairwise comparisons surviving a $p < .05$ significance threshold after correcting for multiple comparisons are reported in the text and Table 6.

Behavioral analysis of self-reported event vividness revealed significant main effects of WM condition ($\chi 2$ = 11.78 (2), $p = .003$) and temporal direction ($\chi 2$ = 186.33 (1), $p < .001$). Post-hoc analyses revealed that, as in Study 1, events imagined during maintenance trials (*M* = 3.36, *SE* = .09) were significantly less vivid than those imagined during manipulation (*M* = 3.50, *SE* = .09) or control (*M* = 3.54, *SE* = .09) trials. Future events (*M* = 3.16, *SE* = .11) were generally less vivid than past ($M = 3.24$, $SE = .11$) events but this effect was not significant after correcting for multiple comparisons ($p = .158$). A significant interaction between WM condition and temporal direction ($\chi2 = 180.14$ (2), $p < .001$) revealed that reduced vividness during maintenance trials was unique to future events. As with Study 1, these results suggest that successful maintenance of bound item-location representations in WM may interfere with the ability to construct detailed event representations and that this might be unique to the construction of novel future events.

Behavioral analysis of event construction RT revealed a marginally significant effect of WM condition ($\chi2 = 5.81$ (2), $p = .055$) but not temporal direction ($\chi2 = 0.37$ (1), $p = .543$), or their interaction ($\chi2 = 2.60$ (2), $p = .273$). As in Study 1, manipulation trials took longer to construct ($M = 4794.18$ ms, $SE = 338.73$) than control ($M = 4636.00$ ms, $SE = 338.65$) and maintenance ($M = 4628.53$ ms, $SE = 338.88$) trials, though these effects were not significant after correcting for multiple comparisons. An identical pattern of results was observed when controlling for WM accuracy.

There were no significant main effects of WM condition on event novelty ($\chi2 = 4.05$ (2), $p = .132$), valence ($\chi2 = 2.11$ (2), $p = .347$), arousal ($\chi2 = 0.95$ (2), $p = .623$), or salience ($\chi2 = 1.65$ (2), $p = .439$). In contrast, there were significant main effects of temporal direction on event novelty ($\chi2 = 5.08$ (1), $p = .024$), valence ($\chi2 = 48.15$ (1), $p < .001$), arousal ($\chi2 = 28.46$ (1), $p < .001$), and salience ($\chi2 = 40.84$ (1), $p < .001$). Post-hoc analyses revealed that future events were significantly more novel ($M_{Future} = 3.16$, $SE_{Future} = .09$; $M_{Past} = 3.06$, $SE_{Past} = .10$), positive ($M_{Future} = 3.37$, $SE_{Future} = .06$; $M_{Past} = 3.05$, $SE_{Past} = .06$), emotionally arousing ($M_{Future} = 2.86$, $SE_{Future} = .09$; $M_{Past} = 2.63$, $SE_{Past} = .09$), and personally significant ($M_{Future} = 2.85$, $SE_{Future} = .10$; $M_{Past} = 2.57$, $SE_{Past} = .10$) than past events. An interaction between temporal direction and WM condition on the emotional arousal measure ($\chi 2$ = 7.47 (2), *p* = .024) revealed that future events were rated as more emotionally intense during manipulation and control trials but not during maintenance trials. Interactions between temporal direction and WM condition were not significant for measures of event novelty, valence, or salience (all *p*'s > .448).

EEG Results

Power Spectral Analysis. Power spectral analyses were performed to quantify the effects of WM dual-task condition and temporal direction on brain activity in four bilateral ROIs: MPFC, DLPFC, TPJ, and posterior Occipital cortex. Data were analyzed in the theta (4-8 Hz), alpha (8-12 Hz), and gamma (30-40 Hz) frequency ranges for the entire trial duration as well as for the EFT onset and event production phases. Repeated measures ANOVAs were conducted separately for each ROI and frequency range combination, with WM condition (maintenance, manipulation, and control), temporal direction (past, future), and their interaction as within-subjects variables. Averaged theta, alpha, and gamma oscillatory power served as the outcome variables. Greenhouse-Geisser corrections are reported when the WM condition factor violated sphericity assumptions.

Full Trial. Analyses of the full EFT-WM trial identified a significant main effect of temporal direction in the alpha frequency range for the MPFC [*F*(1, 20) = 8.81, *p* = .008], DLPFC, [*F*(1, 20) = 4.64, *p* = .043] and TPJ [*F*(1, 20) = 7.36, *p* = .013] ROIs, but not the Occipital ROI [*F*(1, 20) = 3.36, *p* = .082]. A post-hoc analysis revealed increased alpha power (i.e., alpha synchronization) during EFT trials compared to episodic memory (Figure 10). There was also a significant main effect of WM condition in the alpha frequency range in the posterior occipital ROI [*F*(2, 40) = 6.22, *p* = .004]. Post-hoc analyses revealed alpha desynchronization (i.e., reduced alpha power) during maintenance trials compared to manipulation and control trials. Main effects of WM condition were not significant in any of the other ROIs in the alpha frequency band (all *p*’s > .19).

There was a significant temporal direction by WM condition interaction in the gamma frequency range in the TPJ ROI [*F*(2, 40) = 3.75, *p* = .032]. A post-hoc analysis revealed that EFT gamma power was greater than episodic memory during low WM load control trials, but did not differ during maintenance or manipulation trials.

There were no significant main effects of temporal direction or WM condition in the theta frequency range.

EFT Onset. Analyses of the EFT onset phase identified a significant main effect of WM condition in the alpha frequency range for the posterior Occipital ROI [*F*(2, 40) = 5.03, *p* = .011]. A post-hoc analysis revealed that alpha power was lower during maintenance trials compared to manipulation and control trials.

There was a significant main effect of WM condition in the gamma frequency range for the TPJ ROI [*F*(2, 40) = 6.92, *p* = .003]. A post-hoc analysis revealed greater gamma power during manipulation trials compared to maintenance and control trials. There was also a significant temporal direction by WM condition interaction in the TPJ ROI [*F*(2, 40) = 10.80, *p* < .001]. A post-hoc analysis revealed a selective Episodic Memory > EFT effect during manipulation trials (Figure 11).

There were no significant main effects of WM condition or temporal direction in any of the other ROIs or frequency bands.

Event Production. Analyses of the event production phase identified significant main effects of WM condition in the alpha frequency range for the MPFC [*F*(2, 38) = 3.25, *p* = .050], DLPFC [*F*(2, 38) = 4.47, *p* = .018], TPJ [*F*(2, 38) = 3.51, *p* = .040], and Occipital [*F*(2, 38) =

6.96, *p* = .003] ROIs. Post-hoc analyses revealed that, among all ROIs, alpha power was greater during control trials compared to maintenance and manipulation trials [Figure 12, left panel].

Significant temporal direction by WM condition interactions in the theta frequency range were observed in the DLPFC [*F*(2, 38) = 3.65, *p* = .036] and TPJ [*F*(2, 38) = 4.62, *p* = .016] ROIs. Post-hoc analyses of these results revealed differing patterns of results. Within the DLPFC ROI, theta power during low WM load control trials was greater during EFT compared to episodic memory trials (Figure 12, middle panel). In contrast, within the TPJ ROI, theta power during the maintenance dual-task was greater during episodic memory compared to EFT trials (Figure 12, right panel).

Phase-Amplitude Coupling. There was a significant main effect of temporal direction on local theta/gamma PAC in the F4 electrode [*F*(1, 20) = 9.33, *p* = .006] (Figure 13, left panel). A post-hoc analysis revealed that theta/gamma PAC was greater during EFT compared to episodic memory. We also analyzed global (i.e., inter-electrode) PAC to identify how frontal (Fz and F4) theta phase modulated posterior (T8, Pz, Oz, CP6) gamma amplitude. These analyses revealed a significant main effect of temporal direction on theta/gamma PAC between the F4 and Oz electrodes [*F*(1, 20) = 16.61, *p* < .001] as well as between the Fz and Oz electrodes [*F*(1, 20) = 11.95, *p* = .002]. In both cases, theta/gamma PAC was lower during EFT compared to episodic memory (Figure 13, middle panel). There was also a significant condition x temporal direction interaction for Fz-Oz PAC [*F*(2, 40) = 3.93, *p* = .028]. Post-hoc analyses revealed that theta/gamma PAC was greater for episodic memory than EFT during the manipulation and control tasks, but not maintenance (Figure 13, right panel).

There was a significant negative correlation between emotional arousal and theta/gamma PAC between the F4 and CP6 electrodes. There were also weak but nonsignificant negative relationships between CP6 theta/gamma PAC and event vividness, arousal, and salience (Table 7). One potential limitation to identifying robust PAC-behavior correlations is the relatively narrow gamma-band range used in these analyses (30-40 Hz). Follow-up analyses parsing low- (~30 – 70 Hz) and high- (~70 – 128 Hz) gamma frequency ranges may provide a more nuanced account of how cross-frequency coupling contributes to phenomenological features of episodic memory and EFT.

Study 2 Discussion

Events imagined while actively maintaining bound item-location representations in WM were less vivid than those imagined during low WM load control trials. This effect was specific to EFT; vividness of past events was not impaired by concurrent WM capacity demands. Study 2 therefore replicates and extends the behavioral WM maintenance findings from Study 1. The specificity of this result to EFT supports the hypothesis that EFT recruits WM resources over and above those recruited by episodic memory.

Imagined future events were more novel, positive, emotionally arousing, and personally salient than recalled past events. This pattern of results is consistent with past studies demonstrating that imagined future events tend to be more positive and personally significant than past events (D’Argembeau & Van der Linden, 2004; 2006). These results suggest and EFT positivity bias that is more pronounced than that observed during episodic memory.

Full trial analyses revealed greater alpha power over the frontal and parietal ROIs during EFT compared to episodic memory across all three WM dual-task conditions. Alpha-band oscillations are the dominant oscillations in the human brain and putatively regarded to subserve cognitive processes related to endogenous selective attention, particularly suppression of distracting or task irrelevant details (Foxe & Snyder, 2011; Klimesch, 2012). In the WM domain, alpha-band oscillations during a WM retention interval increase linearly with WM load – both in terms of relative capacity (Busch & Herrmann, 2003; Jensen, Gelfand, Kounios, & Lisman, 2002) and top-down manipulation of WM stimuli (Sauseng et al., 2005). This has led to speculation that alpha activity may suppress or modulate the flow of information into areas involved with actively retaining items in WM (Jensen et al., 2002; Sauseng et al., 2005). Alpha-band oscillatory activity is also observed to closely correlate with the spatial and task-evoked dynamics of the default network (Knyazev, Slobodskoj-Plusnin, Bocharov, & Pylkova, 2011) and is implicated in a number of putative default network functions, including spontaneous self-referential thinking (Knyazev et al., 2011), mental imagery (Cooper, Croft, Dominey, Burgess, & Gruzelier, 2003) and egocentric orientation in time and space (Klimesch, 2012).

Heightened EFT alpha synchronization suggests greater attentional resources might be necessary when constructing a novel future event than recalling a prior episode and are consistent with growing behavioral (D'Argembeau et al., 2010; Hill & Emery, 2013) and fMRI (Addis et al., 2007; Benoit & Schacter,H 2015; Thakral et al., 2017) evidence for preferential engagement of executive and neural resources during EFT compared to episodic memory. Alpha band activity over occipital regions did not differ between episodic memory and EFT. This lack of a difference is somewhat surprising given prior EEG studies showing greater activity in visual processing regions in response to real vs. imagined events (Conway et al., 2003; Weiler et al., 2011). Instead, alpha power over the occipital ROI was significantly reduced during the maintenance WM dual-task, regardless of temporal direction. Alpha desynchronization (i.e., reduced power) is largely believed to reflect a release from inhibition (and thus reflect neuronal excitability). This effect may therefore reflect the enhanced visuospatial processing demands of retaining bound item-location representations in WM.

Neural oscillations from different frequency bands often occur simultaneously, with high-frequency oscillations nested within lower-frequency phase. PAC is believed to provide an important neural mechanism for coordinating neuronal communication and information integration across distinct temporal and spatial scales. Theta/gamma PAC is associated with WM (Axmacher et al., 2010; Roux & Uhlaas, 2014) and episodic memory (Friese et al., 2013; Lega et al., 2016) performance and believed to facilitate retention and organization of multi-item representations (Lisman & Jensen, 2013). Thus, we hypothesized that theta/gamma PAC might be particularly important during EFT, which requires maintaining and integrating disparate episodic details into a unitary event representations. To our knowledge, theta/gamma PAC has never been investigated during EFT.

Patterns of cross-frequency theta/gamma PAC also differed between EFT and episodic memory. However, because PAC did not vary as a function of WM load, the functional significance of these differences are interpreted cautiously.

Increased theta/gamma PAC over the right DLPFC during EFT compared to episodic memory is also consistent with the increased neurocognitive demands imposed by EFT. One possibility is that heightened theta/gamma PAC during EFT reflects the greater organizational and binding demands of integrating disparate semantic and episodic details maintained in WM into a unitary future event depiction. Lateral prefrontal activations are among the regions preferentially active during future event construction (Addis et al., 2007; 2009) and are commonly observed to be involved with monitoring and organizing information being actively maintained in WM (Blumenfeld & Ranganath, 2006; D’Esposito et al., 1999). Hierarchically organized theta/gamma oscillations provide a potential mechanism for integrating items within WM (Lisman & Jensen, 2013). According to this model, neurons that fire simultaneously during a gamma cycle represent a single, distinct item. These items are then nested within the slower theta phase to form organized, multi-item representations. Prefrontal theta/gamma PAC may reflect the organization and strengthening of inter-item associations between disparate semantic and episodic details into a coherent spatiotemporal context during EFT.

Interestingly, theta/gamma coupling between frontal and occipital electrodes was greater during episodic memory. Similar interactions between frontal theta and posterior gamma oscillations have been observed during successful memory encoding (Friese et al., 2013). One possible interpretation is that frontal theta oscillations might preferentially modulate retrieval of visual sensory content during episodic memory compared to EFT. Increased frontal-occipital PAC during episodic memory may reflect the heightened sensory-perceptual imagery associated with recalling previously experienced events. Past events tend to include more sensory and contextual details (D'Argembeau & Van der Linden, 2004; 2006) and are also observed to differentially draw on visual components of mental imagery (de Vito, Buonocore, Bonnefon, & Sala, 2014; 2015). Stronger electrophysiological activation over posterior visual processing cortices during memory compared to imagination is speculated to reflect cortical reinstatement of the original perceptual experience (Conway et al., 2003; Weiler et al., 2011).

Episodic Onset

The behavioral and PPI results from Study 1 indicated that the manipulation dual-task interfered with the initial EFT event construction phase whereas interference from the maintenance task was comparatively minimal or nonexistent. This pattern of results was partially replicated in Study 2. As in Study 1, construction latencies were longer during the manipulation task compared to maintenance and control; however, this effect was not statistically significant after correcting for multiple comparisons. In contrast to Study 1, the maintenance task in Study 2 was associated with occipital alpha-band desynchronization compared to manipulation and control. This result may reflect the increased visuospatial processing demands of retaining item-location representations in WM, regardless of temporal direction.

Manipulation trials were associated with increased gamma power over the TPJ sites; however, this effect was unique to episodic memory trials, not EFT. Parietal gamma synchronization has been previously observed during manipulation and organization of multimodal representations in WM (Morgan et al., 2011). One possibility is that, compared to EFT, recalling a past event that can be precisely located in space and time loads more heavily on gamma-band cognitive control processes. However, this interpretation seems unlikely. Imagining a novel event requires novel integration of disparate event features and has been shown to recruit cognitive control resources over and above those active when recalling a past event (D'Argembeau et al., 2010; Hill & Emery, 2010). Another possibility is that EFT and episodic memory differ in terms of their relative recruitment of feature binding. Gamma-band oscillations have long been linked to perceptual feature binding (Fries, 2009; Nyhus & Curran, 2010), and patients with parietal lobe damage exhibit featuring binding deficits (Humphreys, Hodsoll, Riddoch, 2009; Robertson, 2003).

Event Production

Alpha power was greater during the low WM load control trials compared to the maintenance and manipulation dual-task conditions, but did not differ as a function of temporal direction. This result is surprising given the presumed functional link between alpha-band activity and top-down attentional control. The event production phase is hypothesized to correspond with the integration of event features into a coherent and unitary episodic representation. Accordingly, we expected the greater WM load associated with the maintenance and manipulation dual-tasks to elicit stronger alpha activity than the low WM load control trials. One possibility is that reduced alpha power reflects increased neural excitability (i.e., release from inhibition) during the more demanding maintenance and manipulation tasks.

Differences at event production were also observed in the theta frequency range. Distributed cortical theta activity is suggested to support and coordinate a variety of mnemonic processes by mediating dynamic cortico-hippocampal interactions (Anderson, Rajasimhan, Ghacibeh, Meador, & Ding, 2010; Bastiaansen & Hagoort, 2003; Cashdollar et al., 2009; Jones & Wilson, 2005; Miller, 1991; Nyhus & Curran, 2011). Prior studies indicate a frontal-parietal distinction in theta-band function, with theta power over frontal areas reflecting attentional control (Nyhus & Curran, 2010) and theta-power over parietal sites reflecting short-term storage of items and mental representations (Baastiaansen, Posthuma, Groot, & de Geus, 2002; Raghavachari et al., 2006). The distinct patterns of theta reactivity observed in Study 2 may thus reflect differential engagement of top-down control and storage processes, respectively.

Theta power over the DLPFC ROI was greater during EFT compared to episodic memory during the low WM load control trials. One possibility is that under baseline conditions, EFT recruits greater mnemonic control processes compared to episodic memory, but this effect is attenuated or lost during the more cognitively demanding WM dual-tasks. In contrast, theta power over the TPJ ROI was reduced during the maintenance dual-task, but only for EFT. This result mirrors the behavioral finding of reduced event vividness during maintenance trials. This effect may therefore reflect disrupted retention and integration of details comprising an imagined future event.

Conclusion

As in Study 1, events imagined while simultaneously maintaining bound item-location representations in WM were less vivid than those imagined while retaining a single, unbound representation. A similar effect was not observed when recalling past events. This behavioral effect corresponds with patterns of theta desynchronization over temporo-parietal regions during event production. Episodic memory and EFT both involve retrieval and recombination of episodic details (Schacter & Addis, 2007b; Hassabis & Maguire, 2007). However, unlike episodic memory, EFT involves novel recombination of contextual and episodic details spanning discrete past experiences (Addis et al., 2009). The WM demands imposed by retaining and binding disparate details comprising a novel future event are likely greater than those involved with recalling a past event.

The effects of WM load were not as clear in Study 2. Instead, the results primarily indicated behavioral and neural differences between EFT and episodic memory. EFT was associated with greater cortical alpha-band power over frontal and parietal sites as well as heightened frontal theta/gamma PAC. These findings corroborate and extend existing behavioral and neuroimaging evidence that EFT recruits additional neurocognitive resources over and above episodic memory.

General Discussion

The behavioral and neural similarities between episodic memory and EFT have received considerable attention over the past decade. Several theoretical frameworks emphasizing the constructive and generative nature of the declarative memory system (i.e., episodic and semantic memory) have been proposed to explain this functional correspondence. Schacter and Addis (2007a; 2007b) proposed that details retrieved from episodic memory are flexibly recombined when mentally simulating a hypothetical future event. According to this hypothesis, episodic memory and EFT each rely on the same constructive mechanisms and draw from a shared pool of episodic details. In an alternative proposal, episodic memory and EFT are suggested to engage overlapping component processes involved with (re)constructing and maintaining mental scenes comprised of relevant semantic, episodic, and sensory details (Hassabis & Maguire, 2007; 2009). Semantic memory is proposed to provide a unique but complimentary role to episodic memory during EFT by providing the contextual framework for retrieving increasingly specific episodic and sensory details when constructing a plausible and salient future event (D'Argembeau & Mathy, 2011; Irish et al., 2012; Irish & Piguet, 2013; La Corte & Piolino, 2016).

Although the interactions between EFT and other memory systems, including episodic memory and semantic memory, have been studied, much less is known about the functional and mechanistic relationship between EFT and WM. The results from the current studies provide novel insights into the functional relationship between WM and EFT as well as the neurocognitive basis of WM subcomponents as they interact with EFT and episodic memory.

Though an empirically based model of WM function during EFT remains elusive, several hypothetical frameworks have been proposed. For example, WM capacity has been speculated to provide the cognitive workspace or "stage" on which disparate information retrieved from episodic memory can be temporarily maintained and combined into a unitary event depiction (Addis et al., 2009; Schacter & Addis, 2007a; Suddendorf & Corballis, 2007). Buffer demands are likely greater when holding and recombining details from discrete episodes into a novel event compared to reconsolidation of a previously established memory trace. Results indicating that the increased capacity demands of the maintenance dual-task selectively interfered with EFT support this view.

Alternatively, executive WM subprocesses may help facilitate controlled mnemonic retrieval operations necessary for accessing the source material comprising an event representation (D’Argembeau et al., 2010). Whereas past events can be precisely located in space and time, novel future events can be imagined to occur within any number of spatiotemporal contexts. The boundlessness of imagining unique item-context associations might place greater demands on executive processes involved with initiating and monitoring memory search and retrieval. According to this view, the increased processing demands of the manipulation dual-task should selectively interfere with EFT construction. In the following sections, we discuss current evidence for and against these proposals.

WM Maintenance as a Cognitive Stage

Successful performance on the maintenance dual-task required participants to maintain bound object-location pairings for the duration of the EFT trial. Across both studies, interference from this task affected the vividness and amount of details comprising future events, but not past. This pattern of results largely supports the cognitive stage account of WM interactions with EFT (Suddendorf & Corballis, 2007). Though episodic memory and EFT both involve reinstating and integrating details into a unitary representation, imagining a novel future event involves accessing details from discrete episodes (Addis et al., 2009). Constructing and holding a mental representation comprised of disparate details (e.g., imagining a person or item in a unique context) may load on WM buffer resources more heavily than a past event composed of contextually congruent details.

The episodic buffer subcomponent of WM was originally introduced by Baddeley (2000) as a limited capacity system involved with the transient storage and integration of diverse multimodal information into a unitary (and often novel) episodic representation. In order to conform with emerging empirical evidence, the construct has since been revised to depict a passive store capable of holding multidimensional representations formed by mechanisms outside of WM that vary depending on the specific type of stimuli being bound (Baddeley, Allen, & Hitch, 2010). Baddeley (2000) speculated that the episodic buffer might support the creation of novel mental models and scenes via the reactivation and recombination of existing memory traces (e.g., retrieving and manipulating existing knowledge of elephants and hockey in order to imagine a novel scene involving an elephant playing hockey). The purported function and structure of the episodic buffer makes it well suited to serve as the cognitive modelling space on which disparate episodic, semantic, and sensory details are recombined into a novel future event depiction (Schacter & Addis, 2007a; Suddendorf & Corballis, 2007).

Prior neuroimaging studies have consistently reported stronger frontoparietal reactivity during EFT compared to episodic memory (Addis et al., 2007; 2009; Benoit & Schacter, 2015). However, the functional significance of frontoparietal activity during EFT has been largely based on reverse inference. The neural results from these studies provide converging evidence and novel insights into the functional significance of frontoparietal activity during EFT. In Study 1, concurrent maintenance load and self-reported event vividness were observed to modulate bidirectional frontoparietal connectivity. In Study 2, maintenance interference over bilateral parietal sites selectively interfered with theta reactivity during EFT but not episodic memory, a pattern which complemented the behavioral vividness results. Notably, the neural effects of the maintenance task were observed during the event production phase which is speculated to signify the (re)combination of details into a coherent and unitary event depiction. Taken together, these results offer compelling support for the cognitive stage hypothesis; increased frontoparietal activity during EFT may reflect the heightened cognitive demands of maintaining and integrating disparate details into an imagined event.

One potential caveat of our buffer interpretation is the lack of a clear relationship between WM load and EFT related activity. Our dual-task conditions only included two levels of relative WM capacity [i.e., high (maintenance task) and low (manipulation and control tasks)]. We were therefore unable to identify parametric relationships between the number of items being maintained in WM and brain activity. We are encouraged by the results of a recent paper by Thakral et al. (2017) that varied the number of details comprising a future simulation. The authors observed that sustained neural activity in several frontoparietal control regions was modulated by the number of details comprising a future simulation, potentially reflecting the controlled processing demands of maintaining detailed representations in WM. We believe that this provides a compelling paradigm for continued exploration into the functional basis of a buffer component during episodic simulation.

WM Manipulation and Strategic Retrieval

Successful performance on the manipulation task required participants to evaluate, organize, and select items maintained in WM based on their semantic characteristics. We predicted that the increased processing demands of organizing stimuli maintained in WM would draw limited capacity resources away from strategic retrieval and monitoring operations necessary to access the content comprising an episodic representation. Whereas past events are situated in a specific place and time, future events can be placed in any number of spatiotemporal contexts (D’Argembeau et al., 2010). Accordingly, imagining the future has been observed to differentially draw on executive resources involved with organizing and monitoring the strategic retrieval of contextually accurate details from long-term memory (Conway & Pleydell-Pearce, 2000; D’Argembeau & Mathy, 2011; de Vito et al., 2012; Jeunehomme & D’Argembeau; 2015). We therefore predicted that the manipulation WM subcomponent would interfere with EFT to a greater degree than episodic memory and that this effect would be pronounced during the early event construction phase. This hypothesis is only partially supported by the current results.

In Study 1, the concurrent WM processing demands of the manipulation task resulted in longer event construction latencies; however, this effect was driven by performance on incorrect WM trials. Thus, the degree to which concurrent WM load drew limited capacity resources away from EFT construction remains unclear. Likewise, interference from the manipulation task was associated with reduced functional connectivity within neural circuits associated with semantic and episodic retrieval. As predicted, neural effects associated with the manipulation task were maximal during early event construction.

The behavioral and neural results from Study 2 were less conclusive. As in Study 1, event construction latencies were longer during the manipulation task, and this effect was more pronounced when constructing future compared to past events. However, the effect size was small and not significant. Stronger theta reactivity over bilateral parietal sites was observed during episodic memory trials, whereas EFT reactivity was not significantly modulated by concurrent WM load across any of the frequency bands tested. As in Study 1, this effect occurred during the early stages of event construction; however, contrary to our initial prediction, this effect was not stronger for EFT.

Frontal Cross-Frequency Coupling and Detail Recombination

The DLPFC is among the regions that are more strongly engaged by EFT (Addis et al., 2007; Benoit & Schacter, 2015), a finding that was generally supported by results in Study 2. The lateral prefrontal cortex is implicated in studies that require organization of items maintained in WM and activity in these regions has been observed to aid long-term memory formation, perhaps by strengthening the associations between items (Blumenfeld & Ranganath, 2006).

The preferential theta/gamma coupling over this region during EFT is consistent with the WM and executive control demands suggested by the constructive recombination of disparate event details into a novel episodic representation (Addis et al., 2009; Benoit & Schacter, 2015; Schacter & Addis, 2007a; Thakral, Benoit, & Schacter, 2017). One possibility is that frontal PAC provides a neural mechanism for integrating episodic and sensory details within a broader autobiographical or spatiotemporal context. Although this effect could not be directly tied to the maintenance or manipulation WM tasks, it provides novel evidence for increased cognitive processing during EFT. Uncovering the functional significance of cross-frequency dynamics during EFT will be a promising area for follow-up investigation.

In contrast to the localized DLPFC PAC observed during EFT, episodic memory was associated with increased coupling between prefrontal theta and occipital gamma. Prior studies have observed similar frontal-posterior coupling during successful memory encoding (Friese et al. 2013) and retrieval (Koster et al., 2014). Frontal-occipital PAC may reflect the guided retrieval and binding of sensory/perceptual details which are more prominent when recalling previously experienced events (Conway et al., 2003; Weiler et al., 2011). Accordingly, the topography of PAC may vary as a function of the type of information comprising a recalled or imagined event.

Conclusions

Despite the well-established link between episodic memory and EFT, much less is known about the functional relationship between EFT and WM. Increased brain activity observed during EFT has been speculated to reflect the increased cognitive demands of flexibly retrieving and recombining details from discrete past experiences into a novel event depiction. We hypothesized that WM capacity might provide a crucial componential cognitive role during future simulation by supporting the translation of information from episodic memory into a novel future event. To test this hypothesis we used a dual-task interference paradigm (Blumenfeld & Ranganath, 2006) to parse the respective contributions of distinct executive and working memory sub-processes hypothesized to support EFT.

Existing evidence for a functional link between EFT and WM is primarily correlational. These results provide an important first step in clarifying the causal basis of WM function during EFT and provide novel mechanistic insights into the neural circuitry and executive processes involved with linking details from discrete past experiences into imagined future events. In particular, these results provide novel empirical support for previous theoretical accounts suggesting that WM capacity provides the cognitive modelling space or “stage” necessary to temporarily store and recombined autobiographical details from episodic memory into a unitary event depiction (Schacter & Addis, 2007a; Suddendorf & Corballis, 2007). In contrast, the strategic retrieval account of WM function during EFT received mixed support in the current studies. These results provide a useful context for understanding the neural and cognitive basis of co-occurring WM and EFT deficits observed across a diverse range of psychiatric, developing, and aging populations.

Not all future events are created equal and recruitment of WM and executive resources likely differs across the spectrum of imaginable events. For example, events that have been previously imagined and are temporally proximal are much easier to bring to mind (Jeunehomme & D’Argembeau, 2015). Likewise, phenomenological characteristics such as visual imagery, emotional valence, desirability, and personal salience are also known to influence the general autonoetic experience (D’Argembeau & Van der Linden, 2004; 2006) and relative ease (de Brigard, Szpunar, & Schacter, 2013; de Vito, Neroni, Gamboz, Sala, & Brandimonte, 2015; Szpunar & Schacter, 2012) of mentally simulating an event. Therefore, future studies might investigate whether WM is more involved when imagining future events that are lower on these subjective dimensions.

The functional significance of flexibly retrieving and recombining information from past experiences extends well beyond the ability to imagine the future. Humans are able to reflect on what could have been, entertain the thoughts and feelings of others, and use past knowledge to navigate novel environments. These seemingly diverse cognitive abilities are critical for guiding adaptive behavior and decision making and also contribute to our rich inner autobiographical lives. Continued exploration into the mechanistic specificity of these abilities is therefore of critical importance and interest.

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Table 1. Differential WM Load

WM Dual-Task	WM Capacity	WM Processing
Maintenance	High	Low
Manipulation	Low	High
Control	Low	Low

Table 2. Linear Mixed-Effects Results

	Model 2 (Condition)			Model 3 (Condition + Accuracy)		
	β	CI	*p*	*β*	CI	*p*
EFT-RT (ms)						
Fixed Effects						
Intercept	4354.88	3584.32 – 5125.44	**< .001**	4312.67	3545.52 – 5079.78	**< .001**
Maintenance	182.97	8.65 – 357.37	.100	116.37	-59.42 – 292.17	.398
Manipulation	241.19	66.74 – 415.63	**.019**	208.84	35.00 – 382.68	**.049**
Incorrect				266.97	266.97 – 710.19	**<.001**
Random Effects						
σ^2		17353753.31			17111000.63	
ICC		0.68			0.68	
Event Vividness						
Fixed Effects						
Intercept	2.97	2.80 – 3.14	**<.001**	2.97	2.80 – 3.14	**<.001**
Maintenance	-0.11	-0.20 - -0.02	.056	-0.11	-0.20 - -0.02	**.047**
Manipulation	-0.03	-0.12 – 0.06	.733	-0.04	-0.13 – 0.05	.710
Incorrect				0.04	-0.08 – 0.15	.547
Random Effects						
σ^2		0.486			0.485	
ICC		0.24			0.24	
Event Novelty						
Fixed Effects						
Intercept	2.42	2.21 – 2.62	**< .001**	2.42	2.21 – 2.62	**< .001**
Maintenance	0.02	-0.10 – 0.15	.930	0.02	-0.10 – 0.15	.930
Manipulation	-0.02	-0.15 – 0.10	.931	-0.02	-0.15 – 0.10	.932
				0.00	-0.16 – 0.16	.981
Random Effects						
σ^2	.	.975			.975	
ICC		0.18			0.18	

Note: Working memory condition and accuracy factor levels were dummy coded with control and correct trials treated as the reference groups, respectively. All *p* values are corrected for multiple comparisons (Tukey HSD).

Table 3. PLS Peak Coordinates

Brain Region	MNI Coordinates				
	x	y	z	BSR	Cluster Size
TR 1					
R. Middle Occipital Gyrus	27	-88	20	7.051	478
R. Fusiform Gyrus	34	-82	-17	6.903	146
L. Superior Frontal Gyrus	-14	10	68	6.659	241
L. Middle Occipital Gyrus	-54	-71	0	6.652	1193
R. Fusiform Gyrus	34	-31	-27	6.616	201
L. Inferior Temporal Gyrus	-41	-31	-24	5.982	117
L. Superior Temporal Sulcus	-65	-41	17	5.603	51
L. Putamen	-17	0	0	5.091	48
R. Postcentral Gyrus	51	-20	61	5.081	37
R. Superior Parietal Lobule	14	-61	58	4.981	27
L. SupraMarginal Gyrus	-48	-44	24	4.882	22
L. Superior Parietal Lobule	-24	-68	54	4.84	80
L. Temporal Pole	-37	3	-27	4.732	64
L. Precuneus	-3	-58	58	4.371	24
R. Lingual Gyrus	14	-58	0	3.839	20
R. SMA	14	-7	58	-4.819	179
L. Insula	-31	17	-10	-4.794	22
L. Superior Medial Gyrus	3	24	51	-4.723	41
L. Somatosensory Ctx.	-24	-34	54	-4.296	54
TR 2					
L. Inferior Occipital Gyrus	-54	-68	-3	5.816	146
L. SMA	-10	7	71	5.306	183
R. Inferior Temporal Gyrus	44	-17	-27	5.152	25
L. Cuneus	-10	-88	31	4.899	67
R. Precentral Gyrus	54	-7	48	4.776	35
R. Cerebellum	31	-51	-37	4.687	273
R. Putamen	20	10	-3	4.629	48
R. Somatosensory Ctx.	37	-31	37	4.52	21
L. Inferior Frontal Gyrus	-44	31	27	4.512	52
R. Hippocampus	44	-31	-7	4.511	25
L. Cerebellum	-27	-51	-37	4.29	74
L. Pallidum	-14	3	0	4.285	35
L. Middle Occipital Gyrus	-31	-61	34	4.245	26
L. Precuneus	0	-68	48	4.243	58
L. Rolandic Operculum	-41	-34	20	4.242	23
L. Calcarine Gyrus	0	-95	10	3.877	61
R. Inferior Frontal Gyrus	44	17	14	-6.355	46

R. Inferior Parietal Lobule	51	-58	51	-5.52	78
L. Superior Medial Gyrus	3	31	51	-4.775	30
R. Ventrolateral PFC	31	51	-3	-4.554	37
TR 3					
L. Superior Frontal Gyrus	-14	7	68	6.344	302
R. Inferior Temporal Gyrus	48	-17	-27	5.491	374
R. Precentral Gyrus	54	-3	51	5.433	24
L. Temporal Pole	-37	3	-27	5.309	362
L. Inferior Frontal Gyrus	-54	24	20	5.046	27
L. Middle Temporal Gyrus	-54	-14	-17	4.991	106
R. Inferior Frontal Gyrus	54	27	-3	4.946	30
L. Corpus Callosum	-14	17	24	4.924	118
R. Cerebellum	44	-54	-37	4.8	137
R. Striatum	17	3	-7	4.571	29
R. Caudate	17	0	17	4.556	57
L. Cerebellum	-41	-58	-34	4.554	59
L. Orbitofrontal Cortex	-17	34	-10	4.348	96
L. Precuneus	-7	-54	10	4.336	66
L. Inferior Frontal Gyrus	-54	31	3	4.074	71
L. Superior Temporal Gyrus	-44	-37	20	3.988	23
L. Angular Gyrus	-44	-61	24	3.789	27
R. Inferior Parietal Lobule	48	-54	54	-5.568	251
R. Ventrolateral PFC	31	54	-3	-4.928	89
R. Fusiform Gyrus	24	-68	-10	-4.107	22
TR 4					
L. Parahippocampal Gyrus	-31	-41	-10	5.631	152
L. SMA	-10	7	71	5.517	235
L. Inferior Frontal Gyrus	-54	24	20	5.353	84
R. Middle Occipital Gyrus	54	-71	27	4.889	20
R. Fusiform Gyrus	27	-37	-14	4.825	104
L. Ventromedial PFC	-7	51	-10	4.809	176
R. Cerebellum	37	-48	-41	4.807	43
L. Angular Gyrus	-48	-75	27	4.742	125
R. Middle Temporal Gyrus	58	-58	10	4.729	34
L. Precuneus	-3	-58	24	4.514	89
L. Middle Frontal Gyrus	-31	14	41	4.436	29
L. Pallidum	-20	0	7	4.235	102
L. Middle Temporal Gyrus	-58	-7	-17	4.226	47
L. Superior Frontal Gyrus	-17	44	27	4.159	25
R. Middle Temporal Gyrus	58	-10	-24	4.03	32
L. Inferior Frontal Gyrus	-51	24	-10	3.986	66
R. Caudate	17	0	17	3.896	22

L. Temporal Pole	-37	7	-24	3.844	22
R. Pallidum	20	0	-3	3.824	22
R. Inferior Parietal Lobule	44	-54	51	-5.443	237
R. Ventrolateral PFC	31	61	-7	-5.206	109
L. Fusiform Gyrus	-34	-75	-17	-4.822	61
R. Angular Gyrus	58	-51	27	-4.685	27
L. Superior Occipital Gyrus	-17	-92	20	-4.176	50
R. Inferior Frontal Gyrus	41	-68	-10	-3.904	29
TR 5					
L. Inferior Frontal Gyrus	-54	27	20	5.978	110
L. Thalamus	-14	-27	14	5.868	1352
L. Ventromedial PFC	-3	48	-7	5.475	237
L. Superior Frontal Gyrus	-20	44	37	5.098	126
L. Middle Temporal Gyrus	-51	-17	-7	5.077	37
R. Parahippocampal Gyrus	17	-7	-24	4.972	53
L. Cerebellum	-37	-54	-34	4.956	25
L. SMA	-7	10	61	4.883	188
L. Middle Temporal Gyrus	-41	-34	-3	4.651	72
R. Fusiform Gyrus	31	-37	-14	4.604	62
L. Precentral Gyrus	-48	0	54	4.279	63
R. Precentral Gyrus	27	-17	61	4.159	44
R. Cerebellum	34	-51	-37	3.961	21
L. Pallidum	-20	0	3	3.909	39
L. Parahippocampal Gyrus	-24	-3	-34	3.893	26
R. Ventrolateral PFC	27	61	-3	-7.041	100
R. Inferior Parietal Lobule	54	-51	54	-4.661	100
L. Precuneus	3	-75	44	-4.596	24
L. Fusiform Gyrus	-34	-75	-17	-4.575	58
R. Precuneus	7	-48	71	-4.189	31
R. Middle Frontal Gyrus	44	41	27	-4.156	34
TR 6					
L. Middle Temporal Gyrus	-44	-34	-3	6.081	559
L. Middle Frontal Gyrus	-27	44	34	6.053	2421
L. Angular Gyrus	-48	-61	27	5.619	2906
R. Parahippocampal Gyrus	17	-3	-20	5.538	61
R. Fusiform Gyrus	27	-37	-14	5.513	136
R. Cerebellum	20	-44	-37	5.287	158
L. Cerebellum	-31	-51	-34	4.953	114
R. Middle Temporal Gyrus	58	0	-24	4.682	183
R. Inferior Frontal Gyrus	58	10	24	4.627	68
L. Postcentral Gyrus	-34	-27	51	4.57	34
R. Middle Frontal Gyrus	27	48	34	4.524	60

R. Middle Temporal Gyrus	44	-27	-7	4.515	34
L. Parahippocampal Gyrus	-20	3	-27	4.511	72
L. Inferior Temporal Gyrus	-48	-24	-27	4.459	23
L. Inferior Frontal Gyrus	-58	31	-3	4.212	51
R. Superior Frontal Gyrus	34	65	0	-4.566	28
TR 7					
R. Fusiform Gyrus	34	-51	-20	7.216	9920
L. Precentral Gyrus	-37	-3	65	5.852	990
L. Ventrolateral PFC	-37	51	-7	4.658	30
L. Middle Frontal Gyrus	-31	41	34	4.386	44
L. Inferior Frontal Gyrus	-51	24	7	4.374	41
R. Inferior Frontal Gyrus	44	24	20	3.936	41
R. Middle Frontal Gyrus	34	54	31	3.817	26
R. Putamen	20	20	-7	3.748	25
R. Cerebellum	7	-48	-20	-3.807	68
TR 8					
R. Lingual Gyrus	3	-82	-3	6.492	5211
L. Corpus Callosum	-14	17	24	6.118	1166
R. Corpus Callosum	14	31	3	5.461	120
R. Superior Temporal Gyrus	71	-31	3	4.777	82
L. SMA	-3	14	65	4.363	52
R. Superior Medial Gyrus	17	58	14	4.167	21
TR 9					
R. Cerebellum	31	-65	-24	6.102	2197
L. Precentral Gyrus	-37	-7	65	6.02	68
R. Inferior Temporal Gyrus	54	-31	-20	5.794	142
L. Middle Temporal Gyrus	-44	-37	-3	5.315	324
L. Angular Gyrus	-44	-58	24	5.297	104
L. Inferior Frontal Gyrus	-20	37	-10	5.167	269
L. Superior Medial Gyrus	-10	58	20	4.994	77
R. Ventrolateral PFC	34	44	-14	4.904	177
L. Ventrolateral PFC	-41	51	-7	4.872	169
L. SMA	-3	17	65	4.847	61
B. Striatum	0	14	3	4.834	38
R. Corpus Callosum	20	10	24	4.741	166
L. Precentral Gyrus	-48	7	41	4.619	69
L. Inferior Parietal Lobule	-41	-24	31	4.491	29
R. Middle Occipital Gyrus	44	-82	3	4.469	41
L. Superior Parietal Lobule	-34	-51	58	4.3	56
L. Precentral Gyrus	-31	-27	58	4.015	44
R. Middle Temporal Gyrus	54	-51	3	3.936	26

Note: All activations survived a threshold of $p < .003$ (BSR ≥ 3.2) with a minimum cluster size of 20 contiguous voxels. TR = time to repetition, BSR = Bootstrap Ratio, L = Left, R = Right, B = Bilateral

Table 4. GLM Peak Coordinates

Brain Region	MNI Coordinates			*t*-score	k
	x	y	z		
MANIPULATION TASK					
EFT ONSET					
MANIP > CNTR					
L. Inferior Occipital Gyrus	-44	-75	-6	6.02	96
R. Inferior Temporal Gyrus	48	-54	-19	4.74	41
L. Orbitofrontal Cortex	-20	38	-16	4.69	15
L. Cerebellum	-3	-78	-26	4.41	26
CNTR > MANIP					
no suprathreshold clusters					
MANIP > MAINT					
no suprathreshold clusters					
EVENT PRODUCTION					
MANIP > CNTR					
no suprathreshold clusters					
CNTR > MANIP					
L. Superior Occipital Gyrus	-24	-81	42	5.2	15
MANIP > MAINT					
no suprathreshold clusters					
MAINTENANCE TASK					
EFT ONSET					
MAINT > CNTR					
L. Middle Occipital Gyrus	-27	-98	4	4.46	16
R. Middle Frontal Gyrus	27	34	18	4.35	14
CNTR > MAINT					
L. Lingual Gyrus	-10	-78	-6	4.33	35
MAINT > CNTR					
no suprathreshold clusters					
EVENT PRODUCTION					
MAINT > CNTR					
no suprathreshold clusters					
CNTR > MAINT					
L. Lingual Gyrus	-20	-85	-13	5.73	46
L. Fusiform Gyrus	-17	-37	-16	3.96	17
MAINT > MANIP					
L. Lingual Gyrus	-20	-85	-13	5.8	37

Note: All activations reported survive a threshold of $p < .001$, uncorrected, with a minimum of 14 contiguous voxels. L = left; R = right; B = bilateral, MANIP = manipulation; MAINT = maintenance; CNTR = control.

Table 5A. EFT PPI Peak Coordinates (Control > WM)

Brain Region	MNI Coordinates			*t*-score	k
	x	y	z		
Manipulation Trials					
EFT Onset					
R. HPc Seed					
R. Calcarine Gyrus	10	-68	15	3.73	95
dMPFC Seed					
L. Temporal Pole	-44	7	-23	4.58	36
R. Lingual Gyrus	27	-68	-2	3.57	33
L. Fusiform Gyrus	-30	-54	-16	3.35	29
Event Production					
R. HPc Seed					
L. Postcentral Gyrus	-44	-30	49	3.39	72
dMPFC Seed					
R. Cerebellum	27	-47	-33	3.55	46
L. Cerebellum	-13	-58	-30	3.40	36
Maintenance Trials					
EFT Onset					
R. HPc Seed					
no suprathreshold clusters					
dMPFC					
no suprathreshold clusters					
Event Production					
R. HPc Seed					
no suprathreshold clusters					
dMPFC Seed					
R. Temporoparietal Junction	51	-58	21	3.51	29

Note: All activations reported survive a threshold of $p < .005$, uncorrected, with a minimum of 29 contiguous voxels. HPc = hippocampus; dMPFC = dorsomedial prefrontal cortex; L = left; R = right.

Table 5B. WM PPI Peak Coordinates (WM > Control)

Brain Region	MNI Coordinates			*t*-score	k
	x	y	z		
Manipulation Trials					
EFT Onset					
R. HPc Seed					
L. Fusiform/HPc	-27	-37	-19	4.73	91
dMPFC Seed					
L. Caudate Nucleus	-10	14	11	3.77	30
Event Production					
R. HPc Seed					
L. Precuneus	-37	-47	21	3.75	82
R. Precuneus	14	-47	15	3.74	39
dMPFC Seed					
no suprathreshold clusters					
Maintenance Trials					
EFT Onset					
R. HPc Seed					
no suprathreshold clusters					
dMPFC Seed					
R. Caudate	21	27	11	4.70	45
L Inferior Frontal Gyrus	-61	4	11	3.42	54
Event Production					
R. HPc Seed					
R. Cerebellum	31	-41	-23	4.44	30
L. Supramarginal Gyrus	-44	-37	25	4.42	49
L. Fusiform Gyrus	-34	-47	-23	4.15	42
R. Inferior Occipital Gyrus	41	-85	-6	3.80	79
R. Rolandic Operculum	61	7	4	3.57	52
R. Supramarginal Gyrus	58	-17	28	3.42	66
R. Cuneus	10	-92	15	3.40	52
dMPFC Seed					
L. Middle Frontal Gyrus	-37	44	25	3.84	29
R. Middle Frontal Gyrus	44	48	11	3.63	38
B. Calcarine Gyrus	7	-98	4	3.62	35

Note: All activations reported survive a threshold of $p < .005$, uncorrected, with a minimum of 29 contiguous voxels. HPc = hippocampus; dMPFC = dorsomedial prefrontal cortex; L = left; R = right.

Table 6. Study 2 Linear Mixed-Effects Results

	Model 2 (Condition)			Model 3 (Condition + Temporal Direction)		
	β	CI	*p*	*β*	CI	*p*
EFT-RT (ms)						
Fixed Effects						
Intercept	4640	3970 – 5300	< **.001**	4660	3990 – 5320	< **.001**
Maintenance	-0.01	-0.16 – 0.14	.995	-0.01	-0.16 – 0.15	.996
Manipulation	0.16	0.01 – 0.31	.085	0.16	0.01 – 0.31	.100
Past				-0.04	-0.17 – 0.09	.543
Random Effects						
σ^2		2.64			2.64	
ICC		.52			.53	
Vividness						
Fixed Effects						
Intercept	3.54	3.35 – 3.72	< **.001**	3.52	3.33 – 3.71	< **.001**
Maintenance	-0.17	-0.28 – -0.06	**.006**	-0.17	-0.28 – -0.06	**.006**
Manipulation	-0.03	-0.14 – 0.08	.814	-0.03	-0.14 – 0.08	.818
Past				0.03	-0.06 – 0.12	.475
Random Effects						
σ^2		1.56				1.56
ICC		.11				.11
Novelty						
Fixed Effects						
Intercept	3.16	2.97 – 3.36	< **.001**	3.21	3.21 – 3.41	< **.001**
Maintenance	-0.10	-0.21 – 0.00	.142	-0.10	-0.21 – 0.00	.142
Manipulation	-0.06	-0.16 -	.519	-0.06	-0.16 – 0.05	.512
Past				-0.10	-0.18 - -0.01	**.028**
Random Effects						
σ^2		1.45			1.45	
ICC		.13			.13	
Valence						
Fixed Effects						
Intercept	3.21	3.07 – 3.34	< **.001**	3.37	3.23 – 3.51	< **.001**
Maintenance	-0.03	-0.15 – 0.08	.823	-0.03	-0.15 – 0.08	.822
Manipulation	0.05	-0.06 – 0.17	.618	0.05	-0.06 – 0.17	.637
Past				-0.33	-0.42 – -0.24	< **.001**
Random Effects						
σ^2		1.70			1.70	
ICC		.04			.04	
Emotionality						
Fixed Effects						
Intercept	2.78	2.59 – 2.96	< **.001**	2.89	2.70 – 3.08	< **.001**
Maintenance	-0.04	-0.15 – 0.07	.765	-0.04	-0.15 – 0.07	.764
Manipulation	-0.04	-0.15 – 0.07	.751	-0.04	-0.15 – 0.07	.737
Past				-0.23	-0.32 – -0.14	< **.001**
Random Effects						
σ^2		1.54			1.52	

ICC		.11			.11	
Salience						
Fixed Effects						
Intercept	2.72	2.52 – 2.92	**< .001**	2.86	2.66 – 3.07	**< .001**
Maintenance	-0.05	-0.16 – 0.06	.673	-0.05	-0.15 – 0.06	.672
Manipulation	0.01	-0.09 – 0.12	.963	0.01	-0.09 – 0.12	.969
Past				-0.28	-0.37 – -0.19	**< .001**
Random Effects						
σ^2		1.54			1.52	
ICC		.13			.13	

Note: Working memory condition and temporal direction factor levels were dummy coded with control and future trials treated as the reference groups, respectively. All *p* values are corrected for multiple comparisons (Tukey HSD).

Table 7. PAC-Behavior Correlation Matrix

Electrode(s)	Construction RT	Vividness	Novelty	Valence	Arousal	Salience
Fz	0.01	-0.06	-0.04	-0.05	-0.04	-0.04
F4	-0.15	-0.09	0.06	0.14	0.02	0.04
T8	0.00	-0.12	0.03	0.17^{t}	0.04	-0.08
Pz	0.05	-0.10	-0.04	-0.10	-0.01	-0.05
CP6	-0.14	-0.15^{t}	-0.10	0.00	-0.16^{t}	-0.15^{t}
Oz	-0.04	-0.06	0.11	0.04	0.11	0.01
Fz-T8	-0.03	-0.10	-0.03	0.00	-0.11	-0.10
Fz-Pz	-0.09	-0.09	0.08	0.01	0.03	0.03
Fz-CP6	0.05	-0.07	0.02	0.05	-0.12	-0.10
Fz-Oz	-0.06	-0.12	-0.01	-0.07	-0.10	-0.03
F4-T8	-0.13	-0.09	-0.08	0.00	-0.11	-0.09
F4-Pz	-0.11	-0.13	-0.01	0.02	-0.09	-0.11
F4-CP6	-0.03	-0.14	-0.11	0.03	-0.18*	-0.16^{t}
F4-Oz	-0.06	-0.11	0.00	-0.08	-0.14	-0.09

Note: *$p < .05$, $^{t}p < .09$

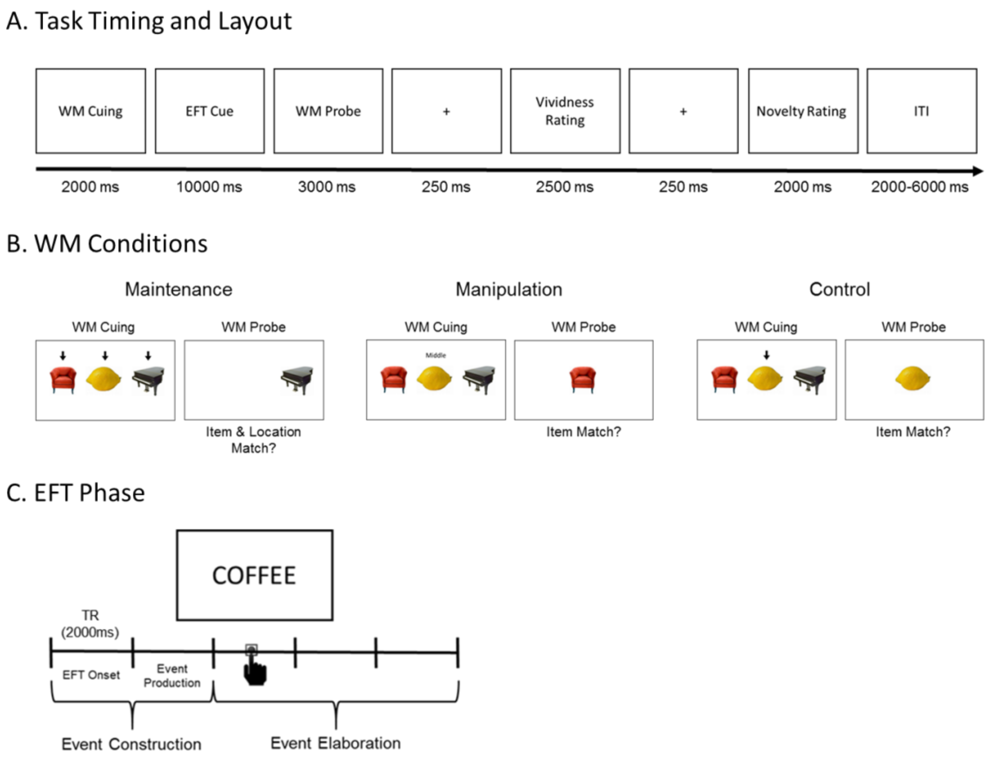

Figure 1 Task Design. (A) Structure and timing of the dual-task paradigm. **(B)** Example of the stimuli presented during the WM cuing and probe phases. During maintenance trials participants were required to remember all three items and their locations on the screen and determine whether the location of the probe stimulus at the end of the WM trial matched its location during the encoding phase. During manipulation trials participants were required to mentally organize the three stimuli based on their relative weights and to indicate whether the probe stimulus matched the middle weighted object. During control trials participants were required to maintain a single item and indicate whether the probe stimulus matched this item. **(C)** Immediately following the WM cuing phase, participants were prompted via a cue word to imagine a future event which was specific in place and time. Once a specific future event was successfully brought to mind participants responded via a button box. This response indicated the transition from event construction to event elaboration. At this point participants were instructed to mentally focus and elaborate on the details and mental imagery comprising the envisaged event for the remainder of the trial.

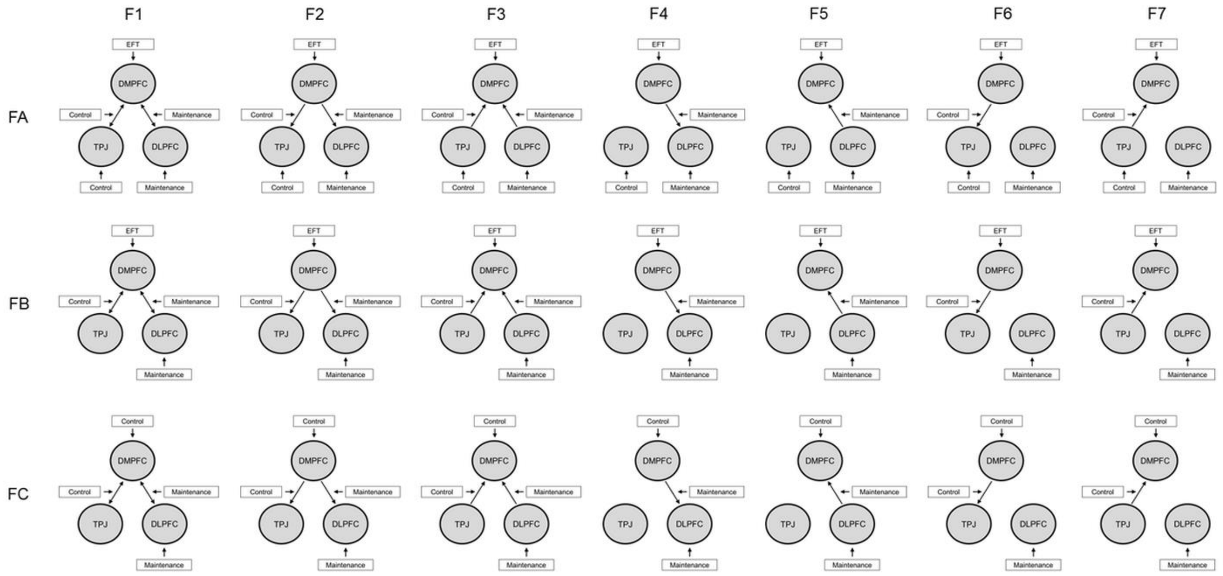

Figure 2 DCM Model Space and Family Partitioning. For each model, event production onsets were entered as direct (i.e., evoke a local response) and modulatory (i.e., context-dependent modulation of connectivity between nodes) inputs. The model space was partitioned into families that differentiated between the sites of the direct inputs (Families F1-F7, columns) and patterns of modulatory effects (Families FA-FC, rows).

A. Main Effects of WM Condition

B. Condition x Accuracy Interactions

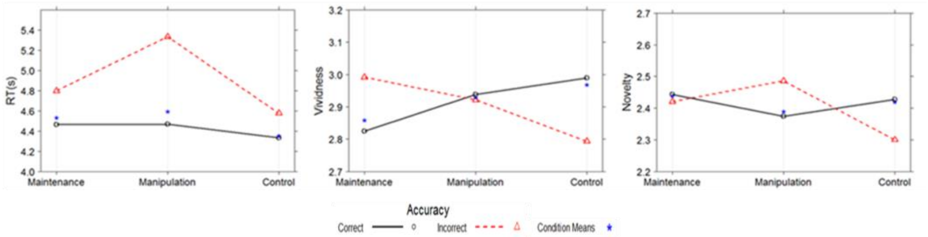

Figure 3 Behavioral Results. (A) Main effects of WM dual-task conditions on behavioral EFT measures. Events took significantly longer to construct during the manipulation and maintenance dual-tasks compared to control (left panel). Events imagined during maintenance trials were less vivid than those during control trials (middle panel), but only when controlling for WM accuracy. There were no effects of WM condition on event novelty (right panel). **(B)** Interaction between WM condition and accuracy on behavioral EFT measures. The effects of the WM tasks on EFT differed according to WM response accuracy and indicate a potential speed/phenomenology tradeoff during future event construction. Events imagined during incorrect manipulation trials took significantly longer to construct than control trials but were comparable in terms of event vividness. In contrast, events imagined during correct maintenance trials did not differ from control on construction latencies but were significantly less vivid than those imagined during correct control trials.

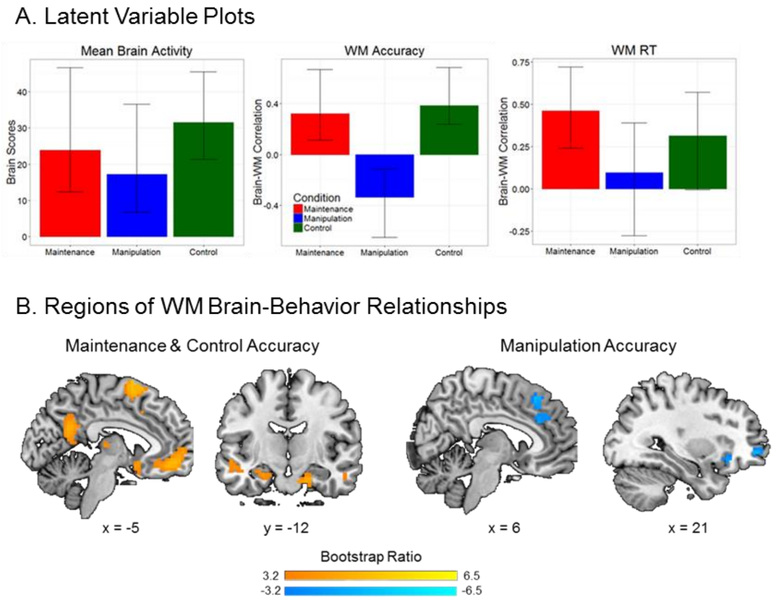

Figure 4 Spatiotemporal PLS Results. A multiblock PLS analysis identified spatiotemporal patterns of brain activity that simultaneously reflect differences between task-based conditions and behaviorally-based WM performance measures. **(A)** Plots of brain scores indicating correlations between pattern of mean brain activity corresponding to each task condition (left panel) and behavioral measures of WM accuracy (middle panel) and WM-RT (right panel). Brain scores reveal overlapping patterns of brain activity across all three conditions and differentiates behavioral performance on manipulation trials from maintenance and control trials. Error bars represent 95% confidence intervals. **(B)** The behavioral PLS revealed patterns of brain activity that differentiated between performance on the WM tasks. Maintenance and control task accuracy was positively correlated with activity in the default network and bilateral medial temporal lobes (warm colors). Accuracy on the manipulation task was positively correlated with activity in prefrontal, insular, and dorsal anterior cingulate cortices (cool colors). Areas shown were thresholded at $p = .003$ with a minimum of 20 contiguous voxels.

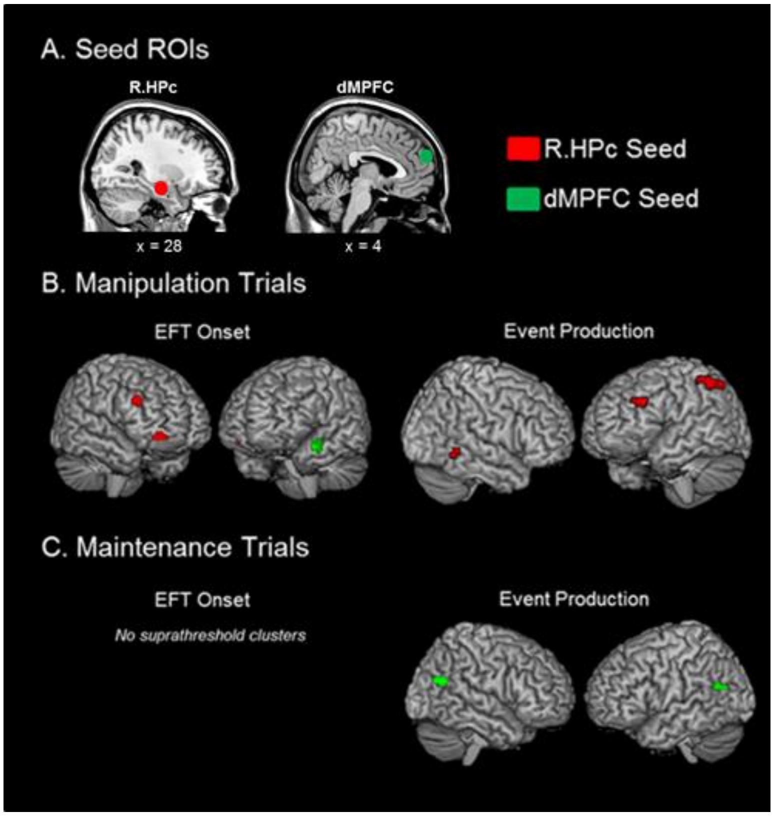

Figure 5 PPI Results. Areas of reduced functional connectivity during concurrent WM-EFT demands. ***(A)*** Seed ROIs (12-mm spheres) were located in the right anterior hippocampus (R. HPc; xyz = 28, -10, -16) and dorsomedial prefrontal cortex (dMPFC; xyz = 4, 61, 25). The PPI analysis revealed areas of increased functional connectivity with the seed ROIs during baseline EFT (control) trials but not during ***(B)*** manipulation or ***(C)*** maintenance trials. These regions thus reflect areas of reduced functional connectivity in response to concurrent WM demands. Display thresholded at $p < .005$, uncorrected, minimum 10 contiguous voxels.

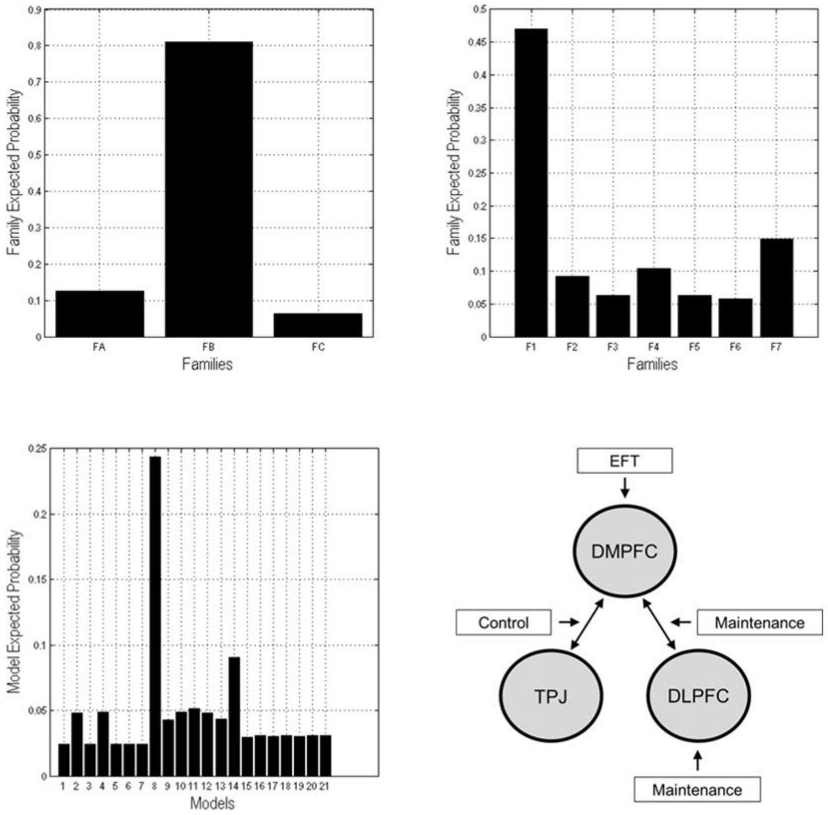

Figure 6 DCM Group-Level Family and Model Selection. Family (top panels) and model (bottom left panel) expected probabilities reflect the likelihood that a specific model or model family generated the data of a randomly chosen subject. Random effect family-level inference was used to compare model families. The data were best explained by models in which EFT and maintenance trials evoked a local DMPFC and DLPFC response, respectively (Family FB, top left) and when maintenance and control trials modulated bidirectional DMPFC-DLPFCC and DMPFC-TPJ connectivity, respectively (Family F1, top right). Random effects Bayesian model selection identified the model from the set of all alternative plausible models that best optimizes the balance between relative fit of the data and model complexity (bottom right panel). This model was optimal for 21 of 23 subjects.

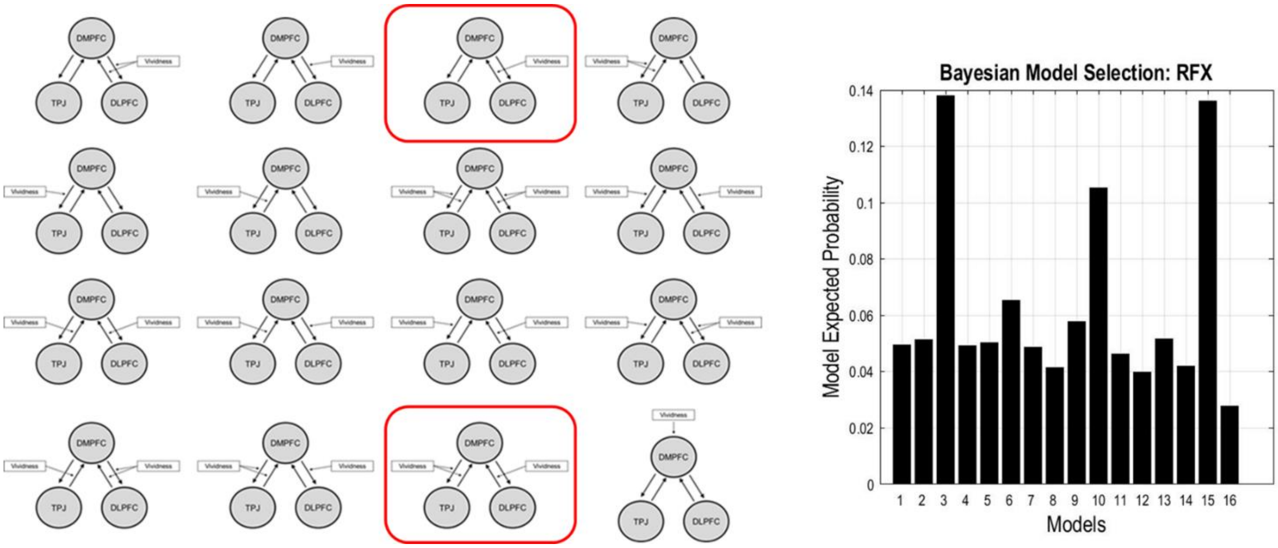

Figure 7 Vividness DCM. The model space was generated from the optimal model and family structures from the first DCM analysis. For each model, EFT and maintenance trials were entered as direct inputs to DMPFC and DLPFC activity, respectively, and maintenance and control trials were entered as modulatory inputs to reciprocal DMPFC-DLPFC and DMPFC-TPJ connectivity, respectively (inputs not shown). Event vividness was entered as an additional parametric modulatory input. Random effects model selection identified two winning model structures (red boxes) that were collectively optimal for 19 of 22 participants.

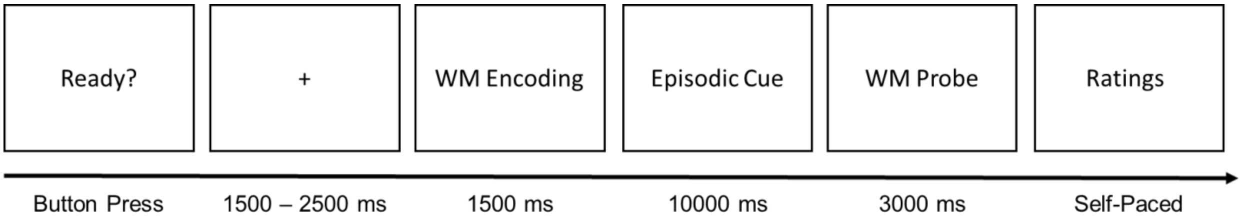

Figure 8 Task Design. Structure and timing of the dual-task paradigm.

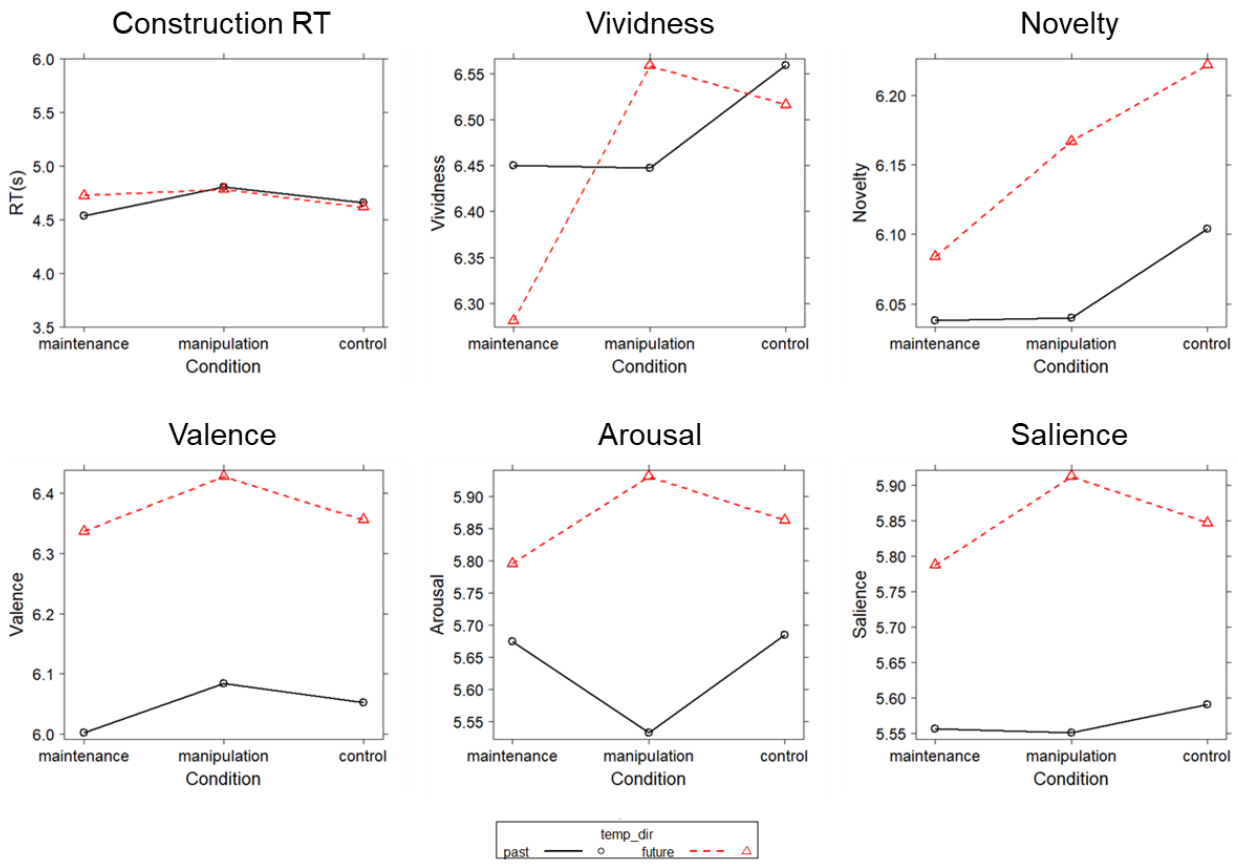

Figure 9 Study 2 Behavioral Results. Interactions between WM condition and temporal direction on behavioral measures of episodic memory and EFT. Event construction latencies did not vary as a function of WM condition or temporal direction. Future events imagined during the maintenance dual-task were less vivid than those imagined during the manipulation or control dual-tasks. This effect was specific to EFT; episodic memory vividness did not significantly vary as a function of WM condition. Across all WM conditions, future events were more novel, positively valenced, and personally salient. Future events were also rated higher in emotional arousal and this effect was most pronounced during the manipulation dual-task. Future events were also reported to be more emotionally arousing and exciting than past events and this effect was most pronounced during the manipulation dual-task.

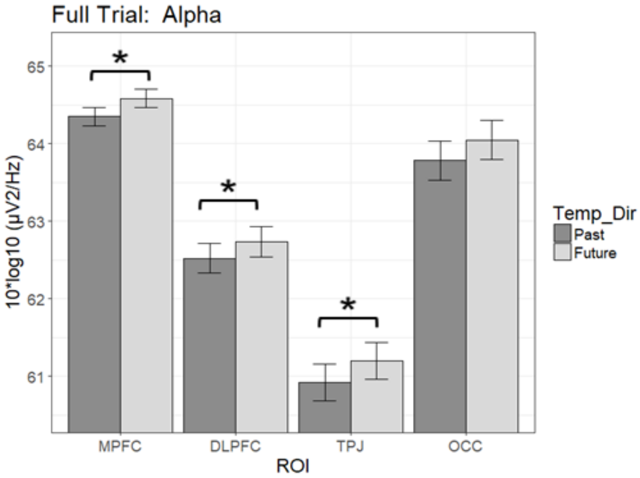

Figure 10 Alpha-Band Power Spectra. Alpha-band power was greater over frontal and temporoparietal sites during EFT compared to episodic memory across the entire 10 s Episodic Cue epoch. Error bars represent Fisher's Least Significant Difference (LSD) post-hoc comparisons.

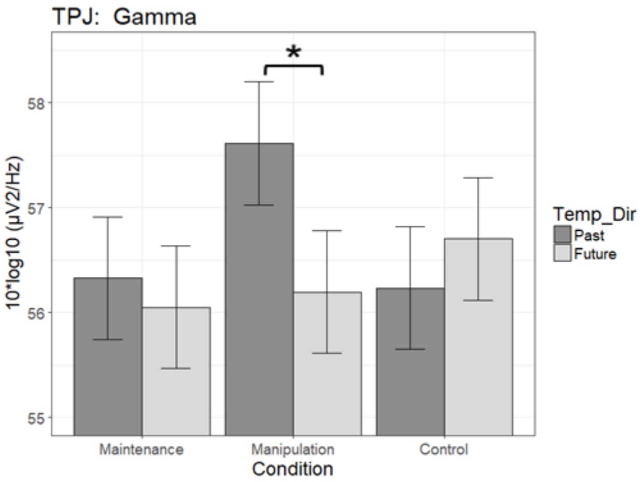

Figure 11 Gamma-Band Power Spectra. There was a significant WM condition x temporal direction interaction in gamma-band oscillatory activity during the 2 s episodic onset phase. Gamma-band reactivity over temporoparietal sites was greater during episodic memory than EFT. Error bars represent Fisher’s LSD post-hoc comparisons.

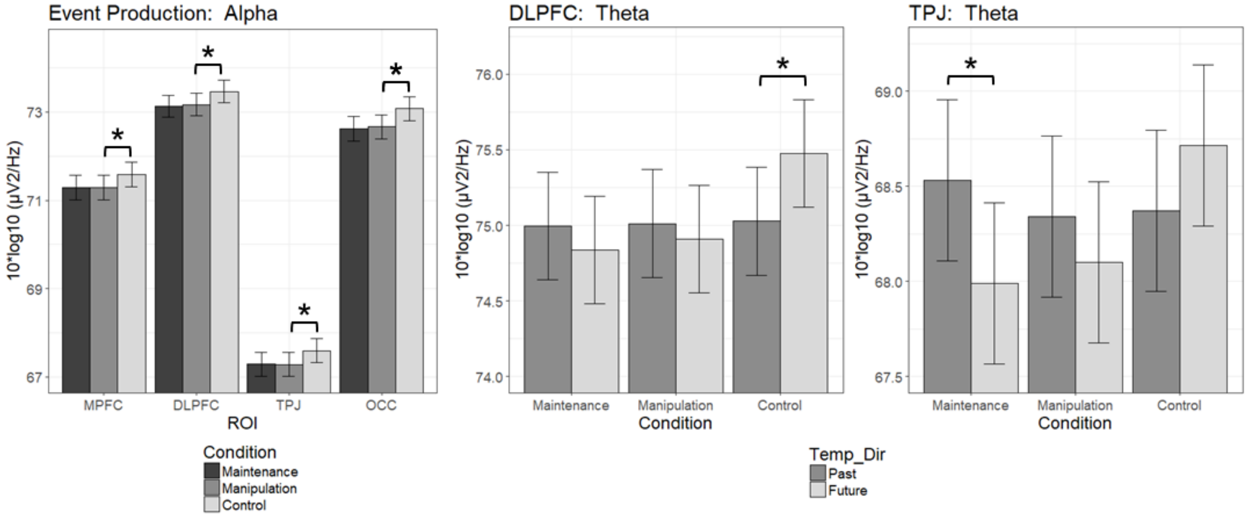

Figure 12 Event Production Power Spectra. Alpha-band power was greater over frontal, parietal, and occipital sites during low WM load control trials compared to maintenance and manipulation trials (left panel). WM condition x temporal direction interactions in theta reactivity were observed over the DLPFC (middle panel) and TPJ (right panel) ROIs. Within the DLPFC, theta power was greater during EFT, but only during the low WM load control trials. Within the TPJ, theta power was greater during episodic memory, but only during the maintenance dual-task. Error bars represent Fisher's LSD post-hoc comparisons.

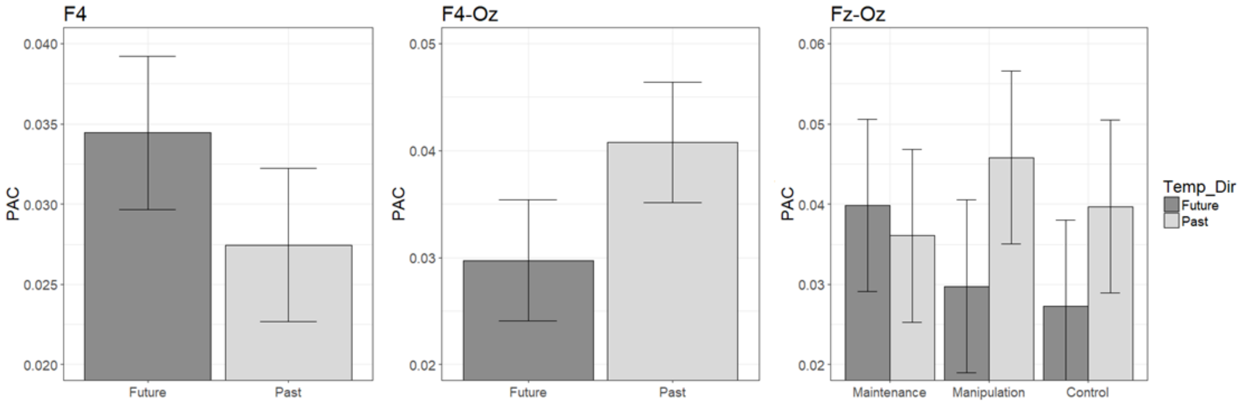

Figure 13. Theta-Gamma Phase Amplitude Coupling. Cross-frequency PAC measures the degree to which local high-frequency amplitude is modulated by the phase of low-frequency oscillations. Theta/gamma PAC in the right DLPFC was greater during EFT than episodic memory (left panel). Episodic memory was associated with greater lateral (middle panel) and medial (right panel) frontal theta modulation of occipital gamma oscillations.