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Core Network Contributions to Remembering the Past, Imagining the Future, and Thinking Creatively

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Abstract

The core network refers to a set of neural regions that have been consistently associated with episodic memory retrieval and episodic future simulation. This network is thought to support the constructive thought processes that allow the retrieval and flexible combination of stored information to reconstruct past and construct novel future experiences. Recent behavioral research points to an overlap between these constructive processes and those also engaged during divergent thinking—the ability to think creatively and generate novel ideas—but the extent to which they involve common neural correlates remains unclear. Using functional magnetic resonance imaging, we sought to address this question by assessing brain activity as participants recalled past experiences, simulated future experiences, or engaged in divergent thinking. Consistent with past work, we found that episodic retrieval and future simulation activated the core network compared to a semantic control condition. Critically, a triple conjunction of episodic retrieval, future simulation, and divergent thinking revealed common engagement of core network regions, including bilateral hippocampus and parahippocampal gyrus, as well as other regions involved in memory retrieval (inferior frontal gyrus) and mental imagery (middle occipital gyrus). The results provide further insight into the roles of the hippocampus and the core network in episodic memory retrieval, future simulation, and divergent thinking, and extend recent work highlighting the involvement of constructive episodic processes in creative cognition.

Keywords

creativity; default network; divergent thinking; episodic memory; future imagination; hippocampus

The human brain has the remarkable capacity to retrieve and flexibly combine stored information to reconstruct past experiences (episodic memory retrieval; Tulving, 2002), imagine new experiences that have not yet occurred (episodic simulation/future thinking; Atance & O'Neil, 2001; Schacter, Addis, & Buckner, 2008), and generate creative solutions

to open-ended problems (divergent thinking; Guilford, 1967). Although both cognitive and neuroimaging studies suggest commonalities among these three forms of constructive processing (Beaty, Benedek, Silvia, & Schacter, 2016; Benedek et al., 2018; Madore, Thakral, Beaty, Addis, & Schacter, 2017), no prior study has directly investigated the extent to which they involve common regions of the brain. Here we report such an investigation.

During the past decade, a large number of studies have highlighted striking cognitive and neural similarities between remembering past experiences and imagining possible future experiences (for recent reviews, see; Schacter et al., 2012; Schacter, Benoit, & Szpunar, 2017). One of the most consistently observed similarities involves the recruitment of a common core network of brain regions when people remember past experiences, imagine or simulate future experiences, and engage in related forms of mental simulation (Andrews-Hanna, Smallwood, & Spreng, 2014; Buckner & Carroll, 2007; Demblon, Bahri, & D'Argembeau, 2015; Hassabis & Maguire, 2007; Konishi, McLaren, Engen, & Smallwood, 2015; Schacter, Addis, & Buckner, 2007; Spreng, Mar, & Kim, 2009; Stawarczyk & D'Argembeau, 2015). This common core network for remembering and imagining (for a recent meta-analysis, see Benoit & Schacter, 2015) largely overlaps with the extensively studied default network (cf., Andrews-Hanna, 2012; Buckner, Andrews-Hanna, & Schacter, 2008; Raichle, MacLeod, Snyder, Powers, Gusnard, & Shulman, 2001; Axelrod, Rees, & Bar, 2017) and includes the medial prefrontal cortex, posterior cingulate/retrosplenial cortex, lateral temporal and parietal regions, and parts of the medial temporal lobes, including the hippocampus. According to the constructive episodic simulation hypothesis (Schacter & Addis, 2007), these neural similarities, and many of the cognitive similarities between remembering the past and imagining the future (Schacter et al., 2012; Szpunar, 2010), reflect to a large extent the role of episodic memory (Tulving, 2002) in supporting simulations of future and other hypothetical experiences. Schacter and Addis (2007) suggest that episodic memory includes flexible retrieval processes that allow people to recombine elements of past events to generate simulations of novel future events that they have not yet experienced.

Consistent with the constructive episodic simulation hypothesis, several recent studies using an *episodic specificity induction* (ESI)—brief training in recollecting specific details of a recent experience—have shown that the ESI selectively and similarly boosts retrieval of episodic (but not semantic) details on subsequent tasks that require remembering past experiences and imagining future experiences, compared with various control conditions (Jing, Madore, & Schacter, 2016, 2017; Madore, Gaesser, & Schacter, 2014; Madore & Schacter, 2016; McFarland, Primosch, Maxson, & Stewart, 2017; for review, see Schacter & Madore, 2016). Moreover, recent evidence from a functional magnetic resonance imaging (fMRI) study indicates that when participants are scanned while performing a future imagining task after receiving an ESI versus a control induction, several core network regions previously linked to retrieval of episodic details, including the left anterior hippocampus and right inferior parietal lobule, show increased activity (Madore, Szpunar, Addis, & Schacter, 2016).

During the past few years, some parallel observations have been made concerning a form of creativity known as *divergent thinking*: generating creative ideas by combining diverse kinds of information in novel ways (Guilford, 1967). Several neuroimaging studies have provided

evidence that divergent thinking, like episodic simulation and memory, can recruit regions within the core network such as the hippocampus (e.g., Benedek et al., 2014, 2018; Ellamil, Dobson, Beeman, & Christoff, 2012). Moreover, several behavioral studies have suggested a link between divergent thinking on the one hand and episodic memory and simulation on the other. Duff, Kurzcek, Rubin, Cohen, and Tranel (2013) found that amnesic patients with severe impairments of episodic memory are also impaired on the Torrance Tests of Creative Thinking, which provide a broad assessment of divergent thinking. Healthy young adults occasionally draw on episodic memories when performing the Alternate Uses Task (AUT), a frequently used measure of divergent thinking that requires people to generate unusual uses of common objects, primarily during the early phases of task performance (Gilhooly, Fioratou, Anthony, & Wynn, 2007). Addis, Pan, Musicaro, and Schacter (2016) reported a study of young and older adults that revealed that performance on the AUT is positively correlated with the number of episodic details that participants report when they imagine possible future experiences.

Madore, Addis, and Schacter (2015) also linked episodic retrieval and AUT performance during experiments in which participants received an ESI prior to performing the AUT. Madore et al. (2015) replicated the effect of the specificity induction on an episodic simulation task and, critically, showed that the specificity induction also selectively boosts performance on the AUT, compared with an object association control task and the Remote Associates Test (Mednick, 1962), which require little divergent thinking. A subsequent study replicated the ESI effect on AUT performance in young adults, and further reported enhanced AUT performance following the ESI in older adults (Madore, Jing, & Schacter, 2016).

A recent fMRI study directly examined neural underpinnings of episodic processing during divergent thinking (Madore et al., 2017) by administering an ESI in the scanner prior to functional imaging; participants then completed the AUT and an object association task during fMRI. Consistent with past work, participants generated more object uses (but not object associations) following the ESI compared to a control induction. FMRI evidence showed that following ESI, during AUT performance there was increased activity within the same left anterior hippocampal region noted earlier that showed ESI-related increases during future imagining. These findings, along with the behavioral evidence described above, suggest that episodic processing may play a critical role in creative idea production. Moreover, they extend recent evidence linking hippocampal cortices to complex generative cognition (Moscovitch, Cabeza, Winocour, & Nadel, 2016) and provide further evidence for the role of constructive episodic processing in divergent creative thinking (Beaty & Schacter, 2017, 2018; Madore et al., 2015, 2016, 2017).

The Present Research

All of the foregoing studies suggest that episodic memory, future simulation, and divergent creative thinking share some common characteristics and may recruit some of the same core network regions. However, no neuroimaging study to-date has examined brain activity within the same individuals when they remember past experiences, imagine future experiences, and engage in divergent creative thinking. In the present research, we sought to

address this question by directly contrasting brain activity associated with these three forms of constructive cognition. To this end, we presented participants with a series of common objects during fMRI and asked them to use these objects as cue words to recall past experiences, imagine future experiences, or generate alternate uses (i.e., divergent thinking). We then assessed common patterns of brain activation associated with these three conditions against a common semantic control condition. Consistent with past work, we hypothesized that episodic retrieval and future simulation would be related to greater core network activity compared to the control condition. Critically, we further hypothesized that a triple conjunction of memory retrieval, future simulation, and divergent thinking would reveal common activity within the core network compared to the control condition, such as the hippocampus.

Method

Participants

A total of 33 young adults participated in the study. Participants received cash payment for their involvement in the study. All participants were right-handed with normal or corrected-to-normal vision and reported no history of neurological disorder. Four participants were excluded for excessive head movement during functional imaging ($> 5\text{mm}$), resulting in a final sample of 29 (12 females; mean age: 21.79, age range: 18–30). The study was approved by the Harvard University Institutional Review Board. Informed consent was obtained prior to participation.

Procedure

The experimental procedure consisted of four task conditions: *Memory*, *Future*, *Create*, and *Sentence*. In all conditions, participants were presented with common objects which served as cue words. In the *Memory* condition, participants were asked to recall a recent past experience related to the cue word; in the *Future* condition, they were asked to imagine a novel and plausible event that could happen in the near future but has not yet occurred; in the *Create* condition, they were asked to think of a novel and unusual use for the object (i.e., divergent thinking); in the *Sentence* (control) condition, they were asked to think of two related words and construct a sentence based on their size (e.g., *Paper* is bigger than *stapler* which is bigger than *pen*; Addis, Pan, Vu, Laiser, & Schacter, 2009). The *Sentence* condition served as a baseline to control for brain activity related to semantic processing and mental imagery (Beaty et al., 2015; Fink et al., 2009; Kleibeuker et al., 2013) and it has been widely used in numerous previous studies as a comparison relative to episodic retrieval and future simulation (e.g., Benoit & Schacter, 2015).

Participants were asked to think of one response for each of the four conditions. For each trial of the *Memory* and *Future* conditions, they were instructed to think of one event that was personal, specific in time and place, and lasting no longer than a day (Addis et al., 2007). As soon as their response was in mind, they were instructed to make a button press with their right thumb and then to elaborate (i.e., fill in more details) on their response until the end of the trial. The same procedure was followed for the *Create* and *Sentence* conditions, i.e., participants were asked to press a button when their response was in mind,

and to elaborate on it until the end of the trial. Elaboration in the *Create* condition involved thinking about how the use could be applied; elaboration in the *Sentence* condition involved thinking about the meaning or definition of the words including visually imagining the objects (Addis et al., 2009). Participants received thorough training on all tasks and completed 20 practice trials prior to scanning. To ensure task compliance, participants were presented with all cue words from the scanner and asked to type brief descriptions of their responses in a post-scan behavioral session. If they could not recall a given response, they were instructed to type “don’t recall”; if they did not have a response for a trial, they typed “no response.”

The experimental protocol consisted of a jittered fixation cross (4–8s), a condition cue (*Memory*, *Future*, *Create*, or *Sentence*) paired with an object in text (e.g., “key”; 2s), a thinking period presenting a fixation cross (8s), and a response period requiring a button press to indicate whether a response was successfully generated (1 = *yes*, 2 = *no*; 3s). The duration of the thinking period was based on behavioral pilot testing indicating that participants could reliably produce a response across all four conditions within the allotted time. The thinking period was relatively brief because we were interested in isolating brain activity related to the construction of a single response (cf., Benoit, Szpunar, & Schacter, 2014; Szpunar, St. Jacques, Robbins, Wig, & Schacter, 2014).

Stimuli consisted of 200 concrete nouns, the majority of which have been used in past research on divergent thinking (e.g., Benedek et al., 2014; Fink et al., 2009) and episodic retrieval, which has found that single words are sufficient for cueing personal experiences (e.g., Addis et al., 2007). Participants completed the tasks in four runs (50 trials per run). Each run consisted of 10 *Memory*, 10 *Future*, 10 *Sentence*, and 20 *Create* trials. Experimental stimuli were assigned to the four conditions (fixed across participants) and presented randomly within-run in an event-related design^{1,2}

MRI Data Acquisition and Preprocessing

Whole-brain imaging was performed on a 3T Siemens Magnetom Prisma MRI system (Siemens Medical Systems, Erlangen, Germany) using a 32-channel head coil. Blood oxygen level-dependent (BOLD) data were acquired with a T2*-weighted multiband echo planar imaging (EPI) sequence that incorporated multiband radiofrequency pulses and

¹Twice as many *Create* trials were included to increase the probability of participants spontaneously producing an equal number of “old” and “new” ideas; these data were collected for an exploratory analysis outside the scope of the current study.

²We tested whether cues differed across the four conditions in terms of several lexical characteristics that may impact task difficulty or mental imagery: concreteness, mean number of associations, word frequency, and valance. We analyzed concreteness ratings using the Brysbaert, Warriner, and Kuperman (2014) concreteness norms for those cues included in the database: *Future* ($n = 34$; $M = 4.82$, $SD = 0.15$), *Memory* ($n = 29$; $M = 4.84$, $SD = .29$), *Create* ($n = 61$; $M = 4.86$, $SD = 0.12$), and *Sentence* ($n = 29$; $M = 4.81$, $SD = 0.18$). A one-way ANOVA yielded a non-significant effect of condition on concreteness ratings, $F(3, 149) = .59$, $p = .61$, indicating that this subset of cues was rated as similarly concrete across the four conditions. We analyzed mean number of associations using the Nelson, McEvoy, and Schreiber (1998) free association norms for the cues included in the database: *Memory* ($n = 18$; $M = 13.39$, $SD = 4.07$), *Future* ($n = 17$; $M = 11.76$, $SD = 4.13$), *Create* ($n = 41$; $M = 13.71$, $SD = 4.84$), and *Sentence* ($n = 13$; $M = 14.54$, $SD = 4.44$). This analysis yielded a non-significant effect of condition on number of associations, $F(3, 85) = 1.08$, $p = .36$. Regarding cue word frequency, we ran a one-way ANOVA to test for mean differences using the same subset of cue words available in the Nelson et al. database: *Memory* ($M = 50.17$, $SD = 89.98$), *Future* ($M = 16.18$, $SD = 22.03$), *Create* ($M = 20.78$, $SD = 33.14$), and *Sentence* ($M = 27.31$, $SD = 34.63$). A one-way ANOVA yielded a non-significant effect of condition on cue word frequency, $F(3, 85) = 1.84$, $p = .14$. Regarding valance, we ran a one-way ANOVA to test for mean differences using the available cue words in the Warriner et al. database—*Memory* ($n = 20$; $M = 5.66$, $SD = 1.01$), *Future* ($n = 22$; $M = 5.58$, $SD = .75$), *Create* ($n = 42$; $M = 5.55$, $SD = .68$), and *Sentence* ($n = 15$; $M = 5.40$, $SD = .95$)—and found a non-significant effect of condition on valance, $F(3, 95) = 1.08$, $p = .36$.

simultaneous multislice (SMS) acquisition (Feinberg et al. 2010; Moeller et al. 2010; Xu et al. 2013). The EPI parameters included 84 interleaved axial-oblique slices, Repetition Time (TR) = 2000 ms, Echo Time (TE) = 30 ms, flip angle = 80°, 1.5-mm³ nominal voxels, 6/8 partial Fourier, Field of View (FoV) = 204mm, SMS = 3. The first two volumes were discarded to allow for T1 equilibration effects. Anatomical images were acquired with a T1-weighted magnetization prepared rapid gradient multiecho sequence (176 sagittal slices; TR = 2530 ms; TE = 1.64ms; flip angle = 7°; 1-mm³ voxels; FoV = 256mm).

Functional image preprocessing included slice-time correction, spatial re-alignment to the mean image across sessions, coregistration to the individual anatomical image, and spatial normalization into Montreal Neurological Institute (MNI) space using the TPM template supplied by SPM12. Functional data were smoothed with a 6 mm³ isotropic Gaussian kernel. Univariate analysis was conducted on the preprocessed functional data in a two-stage mixed effects general linear model. In the first stage, each participant's BOLD response was modeled as a boxcar for the cue period (2s), the thinking period of the four task conditions (*Memory*, *Future*, *Create*, and *Sentence*; 8s), and response period (3s). Trials that participants responded 'No' to producing a response during the *Response* period were modeled as a regressor of no interest (mean proportion of 'No' response rate collapsed across conditions of 8.33%), along with six subject-specific movement parameters for each run. In the second analysis stage, subject-specific parameter estimates for each condition (i.e., *Memory*, *Future*, *Create*, and *Sentence*), corresponding to the 8-second thinking period of the trial, were taken forward to a repeated measures ANOVA model as implemented in SPM12.

For all analyses, an individual voxel threshold of $p < .001$ was employed corrected for multiple comparisons to $p < .05$ with a cluster extent threshold of 19 voxels (Slotnick, Moo, Segal, & Hart Jr., 2003; Slotnick, 2017, for a recent example of this approach, see Thakral, Benoit, & Schacter, 2017a). This cluster extent was computed using a Monte Carlo simulation with 10,000 iterations with an estimated spatial autocorrelation value of 21.06 mm (i.e., the full-width-half-maximum of the image corresponding to the standard error of the ANOVA model).

Conjunction analyses were conducted to examine common activation patterns for the episodic conditions (*Memory* and *Future*) and divergent thinking (*Create*). Specifically, contrast images were computed for the main pairwise comparisons of interest (i.e., *Memory* > *Sentence*, *Future* > *Sentence*, and *Create* > *Sentence*) and entered as inclusive masks into the conjunction analysis. Each contrast that entered into a conjunction was thresholded at $p < .001$.

Results

Behavioral Results

We assessed reaction time (RT) during the thinking period across conditions, i.e., the amount of time (in milliseconds) between the trial onset and participants' button press: *Memory* ($M = 2360.19$, $SD = 933.93$), *Future* ($M = 2463.28$, $SD = 1084.09$), *Create* ($M = 2865.13$, $SD = 977.74$), and *Sentence* ($M = 3687.75$, $SD = 1527.13$). A repeated-measures ANOVA of the

RT data showed a significant effect of condition ($F(3, 84) = 30.65, p < .001$). Follow-up pairwise comparisons revealed increased RT in the *Sentence* condition compared to the *Memory* ($p < .001$), *Future* ($p < .001$), and *Create* ($p < .001$) conditions, as well as increased RT in the *Create* condition compared to the *Memory* ($p < .001$) and *Future* ($p < .01$) conditions, but no significant difference between *Memory* and *Future* conditions ($p > .05$).

To assess task performance, we computed the proportion of trials that participants indicated producing a response during the *Response* period. Participants were successful in generating responses for a majority of trials across the four conditions: *Memory* ($M = 91.86\%$, $SD = 7.50$), *Future* ($M = 94.93\%$, $SD = 4.95$), *Create* ($M = 87.80\%$, $SD = 9.40$), and *Sentence* ($M = 92.07\%$, $SD = 11.09$). A repeated-measures ANOVA of the performance data showed a significant effect of condition ($F(3, 84) = 6.22, p < .001$). Follow-up pairwise comparisons revealed higher performance in the *Future* condition compared to the *Create* ($p < .001$) and *Memory* ($p < .05$) conditions; higher performance in the *Memory* condition compared to the *Create* ($p < .05$) condition; and higher performance in the *Sentence* condition compared to the *Create* ($p < .05$) condition but not the *Memory* ($p > .05$) or *Future* ($p > .05$) conditions. Thus, although participants took significantly longer to produce a response in the *Sentence* condition, performance was slightly higher in this condition compared to the *Create* condition and not significantly different from the *Memory* or *Future* conditions.

fMRI Analyses

Conjunction analyses—To identify core network regions jointly recruited during memory and simulation (see Benoit & Schacter, 2015), we began by conducting a conjunction analysis of episodic retrieval and future simulation, ($Memory > Sentence$) $\cap$ ($Future > Sentence$). As expected, the results showed robust engagement of regions within the core network, including a large cluster peaking in medial prefrontal cortex (MPFC) and extending to bilateral hippocampus, bilateral parahippocampal gyrus, bilateral middle temporal gyrus (MTG), and bilateral superior temporal gyrus (STG); posterior cingulate cortex (PCC); and bilateral angular gyrus (AG), among other regions (see Table 1 and Figure 1).

Next, we assessed which of the above core network regions are also recruited during divergent thinking by performing a triple conjunction where divergent thinking and the episodic conditions (memory retrieval and future simulation) were each compared to the semantic control condition, ($Memory > Sentence$) $\cap$ ($Future > Sentence$) $\cap$ ($Create > Sentence$). Results of this triple conjunction analysis revealed common engagement within the MPFC; right MTG; and a large cluster peaking in right amygdala and extending to right hippocampus, right parahippocampal gyrus, and right STG. We also found a large cluster peaking in left inferior frontal gyrus (IFG) and extending to left hippocampus, left parahippocampal gyrus, and left STG. Additional clusters were found within middle occipital gyrus (MOG), pre- and postcentral gyrus, and cerebellum (see Table 2 and Figure 1).

The triple conjunction reported above provides evidence for common neural activity engaged during episodic memory, future simulation, and divergent thinking. However, it is possible that underlying differences between the three conditions remain. That is, while each

condition elicits greater activity relative to a common semantic control condition, a given 'common' activation may differ in its neural activity between episodic memory, future simulation, and divergent thinking. For example, the hippocampus and other core DN regions are known to elicit greater activity during simulation relative to memory (with this difference thought to reflect the greater recruitment of recombination/relational processing demands during simulation relative to memory; e.g., Addis et al., 2007, 2009; Benoit & Schacter, 2015; for a discussion, see Schacter et al., 2012). Moreover, a recent meta-analysis of divergent thinking (Wu et al., 2015) failed to reveal reliable activation of the MPFC (potentially due to the inclusion of control tasks with comparable demands on self-referential processing), suggesting that the activation of this region in the above conjunction may have been largely driven by the episodic conditions.

In light of these findings, we aimed to provide a strong test of commonality by statistically removing such differences. Specifically, the triple conjunction of (*Memory* > *Sentence*) $\cap$ (*Future* > *Sentence*) $\cap$ (*Create* > *Sentence*) was exclusively masked with the main effect of *Memory*, *Future*, and *Create* at the liberal threshold of $p < .05$ (i.e., the more liberal the threshold of the exclusive mask, the more conservative the approach, see also Thakral et al., 2017a). The outcome of this procedure yields clusters of activity where episodic memory, future simulation, and divergent thinking elicit greater activity relative to the non-episodic control condition while removing any statistical differences between the three former conditions.

This analysis revealed a similar pattern of activation as the triple conjunction reported previously, albeit with notably smaller clusters in several regions. Critically and consistent with the above, the results showed common activity within bilateral hippocampus and parahippocampal gyrus; superior frontal gyrus (SFG); left IFG; right MOG; bilateral postcentral gyrus; right cerebellum; and right fusiform gyrus (see Figure 1 and Table 3).

Simple contrasts—For completeness, we also report each of the individual contrasts that were entered into the above conjunctions. Consistent with past work, the contrast of *Memory* > *Sentence* revealed strong engagement within the core network, including a large cluster in MPFC extending to bilateral hippocampus, bilateral amygdala, PCC, and left IFG; left AG; and bilateral STG, among other regions. The contrast of *Future* > *Sentence* showed a largely similar activation pattern within the core network (see Figure 2 and Table 4). Regarding divergent thinking, the contrast of *Create* > *Sentence* showed increased activity within a large cluster peaking in the left insula and extending to MPFC, left IFG, left hippocampus, left parahippocampal gyrus, and left amygdala. Another large cluster peaked in the right amygdala and extended to the right hippocampus and right parahippocampal cortex. Additional clusters were found within occipital and parietal cortices, including MOG, fusiform gyrus, and postcentral gyrus, among other regions.

Discussion

The present research examined common neural correlates underlying episodic memory retrieval, episodic future stimulation, and divergent creative thinking. Consistent with past work, we found that compared to a semantic control condition, both memory retrieval and

future simulation strongly engaged the core network. Critically, the triple conjunction—which assessed common neural engagement across episodic memory, future simulation, and divergent thinking compared to the control condition—implicated several core network regions, including bilateral hippocampus. The results extend recent behavioral research on the overlap between episodic processing and divergent thinking and suggest that both cognitive processes may involve constructive retrieval mechanisms associated with the core network.

As discussed earlier, behavioral experiments have shown enhanced divergent thinking performance following an episodic specificity induction (ESI) compared to control inductions that do not impact episodic retrieval (Madore et al., 2015, 2016, 2017). Specifically, these experiments found that ESI increased fluency (i.e., the total number of responses) and flexibility (i.e., the number of conceptual categories) on a subsequent divergent thinking task—the same creativity task used in the current study. Our results also complement the recent fMRI evidence discussed in the Introduction (Madore et al., 2017) showing that when participants were scanned while engaged in divergent thinking following an ESI, there was increased activation within the left anterior hippocampus—a region involved in episodic memory that also showed ESI-related increases during future imagining (Madore et al., 2016). The present work extends this finding by demonstrating within a single experiment that the hippocampus supports episodic memory, future imagining, and divergent thinking.

We found that the peak voxels of the hippocampal clusters were located in bilateral amygdala. Although the amygdala has been consistently implicated in fMRI studies of emotion-based mnemonic processing (e.g., Canli, Zhao, Brewer, Gabrieli, & Cahil, 2000; Canli, Zhao, Desmond, Glover, & Gabrieli, 1999), a recent study using direct electrical stimulation of the human amygdala found that it also contributes to memory processes in the absence of emotional content (Inman et al., 2017). In the context of Inman et al. (2017), it is unclear whether amygdala activation in the current study reflected emotion-based memory retrieval or more general mnemonic processing. Future research could clarify the role of emotion by probing the extent to which amygdala activation during episodic simulation and creative thinking correlates with self-reported emotional experiences.

The results of the triple conjunction analysis implicated a subset of core network regions engaged across the episodic and creative thinking tasks. Critically, the hippocampus survived a strong statistical test of commonality, i.e., exclusive masking the triple conjunction with the main effect of *Memory*, *Future*, and *Create*. Notably, this was not the case for the MPFC, which showed common activity in the unmasked triple conjunction but not after exclusively masking with the main effect of the three conditions. Activation of the MPFC in the unmasked conjunction (Figure 1, middle row) likely reflected greater demands on self-referential processes in the memory and simulation tasks (e.g., Addis et al., 2007) relative to the divergent thinking task, as the latter should not require the same level of self-referential processing for successful performance. By contrast, the common engagement of the hippocampus across episodic memory, future simulation, and creative thinking in the exclusively masked conjunction (Figure 1, bottom row) provides strong evidence of shared cognitive processes that may be invoked by the three tasks. How can we characterize the

precise nature of this shared process? There is now a growing body of evidence indicating that the hippocampus supports at least three dissociable processes during episodic simulation: retrieval of episodic details, recombination of those details, and encoding of recombined information (e.g., Martin, Schacter, Corballis, & Addis, 2011; Gaesser, Spreng, McLelland, Addis, & Schacter, 2013; Thakral, Benoit, & Schacter, 2017b; for reviews, see Addis & Schacter, 2012; Schacter, Addis, & Szpunar, 2017). An important avenue for future research is to specify which of these processes is shared across episodic memory, simulation, and divergent thinking. The current study provides an important step in this investigation by demonstrating that the hippocampus may benefit creative cognition by means of a domain-general process shared with episodic memory and simulation (Schacter & Addis, 2007; Schacter & Madore, 2016). Note also that our results bear on discussions of default network contributions to creative cognition (for discussion, see Beaty et al., 2016) since both hippocampus and MPFC are part of the default network.

The triple conjunction also revealed common engagement of several regions within occipital cortex that have been consistently associated with both episodic retrieval and future simulation (e.g., Addis et al., 2007, 2009; Benoit & Schacter, 2015; see Figure 2). Specifically, we found that all three conditions were related to activation of clusters within occipital cortex, including right MOG and right fusiform gyrus. Studies of divergent thinking have likewise reported activation of occipital regions, particularly the fusiform gyrus (Gonen-Yaacovi et al., 2013; Wu et al., 2015). Consistent with these prior studies, we similarly suggest that occipital activations reflect the recruitment of mental imagery processes during memory retrieval, future simulation, and divergent thinking relative to the semantic control condition, but future work is needed to address the common cognitive contribution of occipital cortex to memory, imagination, and creativity.

The triple conjunction also showed common activation of the left IFG, a region implicated in previous studies of episodic memory and simulation (Benoit & Schacter, 2015). Common engagement of the IFG is consistent with Madore et al. (2017), who reported activation within the IFG during divergent thinking following ESI. Moreover, this region has been widely implicated in neuroimaging studies on creative cognition (Gonen-Yaacovi et al., 2013). It has been proposed that this region supports such processes as the controlled retrieval of mnemonic information (see Badre & Wagner, 2007). One possibility is that left IFG activity during episodic memory, episodic simulation, and divergent thinking supports the generation of mnemonic information that is beneficial to the formation of a coherent past or future event or creative use.

Future research should further explore the extent to which creative cognition relies on episodic memory retrieval. Although our results demonstrate a common neural basis of memory and creativity within regions of the core network, the complex relationship between these cognitive processes remains poorly understood. Moreover, the extent to which other modes and domains of creative cognition rely on episodic retrieval has yet to be explored. For example, future work may investigate whether creative writing, similar to generating alternate uses, benefits from procedures that enhance episodic retrieval such as ESI (Madore et al., 2015, 2017). Such investigations may further uncover the precise role of episodic

retrieval processes to creative thought and could inform intervention paradigms aimed at enhancing imagination in specific domains of creative performance.

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Figure 1.

Conjunction analyses contrasting Memory, Future, and Create with Sentence. Clusters are projected onto surface and slice templates from MRICroGL. The left hemisphere is on the far left of each panel.

Figure 2. Univariate analyses contrasting Memory, Future, and Create with Sentence. Clusters are projected onto surface and slice templates from MRICroGL. The left hemisphere is on the far left of each panel.

Table 1

Conjunction analysis contrasting Memory and Future with Sentence

Region	BA	Peak (MNI)				k	T
		x	y	z			
Memory > Sentence $\cap$ Future > Sentence							
Medial Prefrontal Cortex ^a	10	4	52	-12	21640	15.16	
Posterior Cingulate Cortex	31	-4	-48	32	3614	13.26	
Angular Gyrus	39	-44	-70	32	1169	9.24	
Cerebellum		4	-58	-46	377	8.63	
Cerebellum		26	-86	-34	643	8.44	
Middle Occipital Gyrus	19	42	-88	6	1176	6.29	
Postcentral Gyrus	3	26	-40	62	352	5.83	
Precentral Gyrus	6	46	-10	50	370	5.77	
Angular Gyrus	39	50	-58	20	556	5.41	
Cerebellum	-	-24	-80	-34	256	5.36	
Postcentral Gyrus	5	-30	-38	62	64	5.23	
Insula	13	46	-12	22	366	5.17	
Cuneus	19	-22	-90	38	101	4.86	
Superior Temporal Gyrus	40	-62	-26	14	91	4.60	
Insula	13	-38	-28	24	34	4.43	
Middle Occipital Gyrus	19	-34	-96	14	54	4.16	
Precuneus	7	-6	-46	60	24	4.08	
Fusiform Gyrus	19	-30	-68	-10	25	4.06	
Fusiform Gyrus	19	28	-68	-10	45	3.93	
Middle Occipital Gyrus	19	-38	-84	0	53	3.88	

Notes. BA = Brodmann area, k = cluster size.

^aThe medial prefrontal cortex cluster extends to bilateral hippocampus, bilateral parahippocampal gyrus, bilateral middle temporal gyrus, and bilateral superior temporal gyrus. Anatomic locations were determined by entering coordinates into the Yale BioImage Suite Package (Papademetris et al., 2011) and Neurosynth (Yarkoni et al., 2011).

Table 2

Conjunction analysis contrasting Memory, Future, and Uses with Sentence

Region	Peak (MNI)					<i>T</i>
	BA	x	y	z	k	
<i>Memory > Sentence ∩ Future > Sentence ∩ Create> Sentence</i>						
Middle Occipital Gyrus	19	42	−88	6	645	7.15
Medial Prefrontal Cortex	10	−10	44	44	3451	6.80
Inferior Frontal Gyrus ^a	47	−36	30	−16	1021	6.19
Amygdala ^b	34	22	−4	−18	855	5.48
Postcentral Gyrus	6	56	−12	54	26	5.39
Postcentral Gyrus	40	46	−12	22	263	5.27
Postcentral Gyrus	3	46	−26	66	31	4.79
Cerebellum	−	28	−80	−32	231	5.03
Postcentral Gyrus	1	26	−40	62	76	4.48
Postcentral Gyrus	40	−54	−26	18	64	4.35
Postcentral Gyrus	1	68	−12	16	152	4.13
Middle Temporal Gyrus	19	48	−66	6	19	4.07
Fusiform Gyrus	19	28	−66	−10	30	3.61

Notes. BA = Brodmann area, k = cluster size.

^aThe left inferior frontal gyrus cluster extends to left hippocampus, left parahippocampal gyrus, and left superior temporal gyrus.

^bThe right amygdala cluster extends to right hippocampus, right parahippocampal gyrus, and right superior temporal gyrus. Anatomic locations were determined by entering coordinates into the Yale BioImage Suite Package (Papademetris et al., 2011) and Neurosynth (Yarkoni et al., 2011).

Table 3

Conjunction analysis contrasting Memory, Future, and Create with Sentence exclusively masked with the main effect of across Memory, Future, and Create

Region	Peak (MNI)					
	BA	x	y	z	k	T
<i>Memory > Sentence $\cap$ Future > Sentence $\cap$ Create > Sentence (after exclusive masking with the main effect of Memory, Future, and Create at $p < .05$)</i>						
Middle Occipital Gyrus	19	42	-88	6	571	7.15
Superior Frontal Gyrus	10	-10	44	44	145	6.80
Inferior Frontal Gyrus	47	-36	30	-16	73	6.06
Amygdala ^a	34	22	-4	-18	403	5.48
Postcentral Gyrus	6	56	-12	54	23	5.39
Amygdala ^b	34	-26	-4	-20	140	5.27
Postcentral Gyrus	40	46	-12	22	263	5.27
Postcentral Gyrus	3	46	-26	66	28	4.79
Cerebellum	–	32	-80	-34	84	4.54
Postcentral Gyrus	1	26	-40	64	57	4.48
Postcentral Gyrus	40	-54	-26	18	64	4.35
Postcentral Gyrus	1	68	-12	16	152	4.14
Middle Temporal Gyrus	19	48	-66	6	19	4.08
Fusiform Gyrus	19	28	-66	-10	30	3.61

Notes. BA = Brodmann area, k = cluster size.

^aThe right amygdala cluster extends to right hippocampus, right parahippocampal gyrus, and right superior temporal gyrus.

^bThe left amygdala cluster extends to left hippocampus, left parahippocampal gyrus, and left superior temporal gyrus. Anatomic locations were determined by entering coordinates into the Yale BioImage Suite Package (Papademetris et al., 2011) and Neurosynth (Yarkoni et al., 2011).

Table 4

Univariate analyses contrasting Memory, Future, and Create with Sentence

Region	BA	Peak (MNI)				k	T
		x	y	z			
Memory > Sentence							
Medial Prefrontal Cortex ^a	10	4	52	−12	31252	15.15	
Angular Gyrus	39	−44	−70	32	1298	9.24	
Cerebellum	−	4	−58	−46	587	8.62	
Cerebellum	−	26	−86	−34	708	8.44	
Middle Occipital Gyrus	19	42	−88	6	1261	6.29	
Precentral Gyrus	6	46	−10	50	390	5.77	
Superior Temporal Gyrus	39	50	−58	20	580	5.40	
Postcentral Gyrus	3	−30	−38	62	158	5.23	
Insula	13	44	−8	20	464	5.19	
Middle Occipital Gyrus	19	−22	−90	38	240	4.86	
Caudate	−	−10	2	20	90	4.84	
Superior Temporal Gyrus	40	−62	−26	14	288	4.59	
Insula	13	−40	−8	18	32	4.24	
Precentral Gyrus	6	−38	−12	50	27	4.13	
Inferior Parietal Lobe	40	68	−42	30	37	4.07	
Fusiform Gyrus	19	−30	−68	−10	42	4.06	
Fusiform Gyrus	19	28	−68	−10	49	3.92	
Middle Occipital Gyrus	18	−38	−84	0	67	3.88	
Caudate	−	6	−4	22	35	3.68	
Postcentral Gyrus	6	−26	−28	76	44	3.61	
Future > Sentence							
Medial Prefrontal Cortex ^b	10	6	50	−12	28248	14.58	
Posterior Cingulate Cortex	31	−4	−48	32	3809	12.85	
Angular Gyrus	39	−44	−70	34	1379	8.89	
Cerebellum	−	−26	−86	−34	746	8.61	
Cerebellum	−	4	−56	−46	396	7.80	
Cerebellum	−	−26	−86	−32	555	6.94	
Middle Occipital Gyrus	19	−46	−82	0	536	4.52	
Precentral Gyrus	4	52	−12	48	1259	5.62	
Inferior Frontal Gyrus	45	−56	24	6	36	4.61	
Precentral Gyrus	6	−36	−12	50	27	4.26	
Caudate	−	−16	8	20	35	4.16	
Superior Temporal Gyrus	42	−62	−26	14	93	4.14	
Insula	13	−40	−28	18	53	4.11	
Postcentral Gyrus	5	−28	−40	62	97	4.06	
Paracentral Lobule	5	−8	−46	60	49	3.92	
Cerebellum	−	46	−56	−40	45	3.86	

Region	Peak (MNI)					<i>T</i>
	BA	x	y	z	k	
Fusiform Gyrus	19	-28	-68	-10	39	3.86
Paracentral Lobule	5	16	-36	50	21	3.80
Medial Frontal Gyrus	6	-2	-22	66	46	3.69
<i>Create > Sentence</i>						
Insula ^c	13	-38	-6	16	5646	8.13
Insula	13	42	-10	0	1479	7.92
Middle Occipital Gyrus	19	42	-88	6	1200	7.15
Supramarginal Gyrus	40	-60	-28	30	903	6.02
Striatum	–	-8	2	22	163	5.64
Amygdala ^d	25	22	-4	-18	1157	5.48
Cerebellum	–	28	-80	-32	290	5.03
Cingulate Gyrus	–	-14	-34	24	120	4.99
Insula	13	-38	-28	24	24	4.69
Postcentral Gyrus	5	26	-40	62	79	4.48
Fusiform Gyrus	37	44	-40	-16	39	4.44
Cingulate Gyrus	–	20	-38	20	62	4.35
Postcentral Gyrus	5	-24	-48	76	70	4.16
Middle Occipital Gyrus	19	-46	-78	2	102	3.80
Fusiform Gyrus	19	28	-66	-10	45	3.61
Cingulate Gyrus	–	20	-38	20	62	4.35

Notes. BA = Brodmann area, k = cluster size.

^aThe medial prefrontal cluster for Memory > Sentence extends to bilateral hippocampus, bilateral angular gyrus, and posterior cingulate cortex.

^bThe medial prefrontal cluster for Future > Sentence extends to bilateral hippocampus, bilateral angular gyrus, and posterior cingulate cortex.

^cThe insula cluster for Create > Sentence extends to medial prefrontal cortex, inferior frontal gyrus, left hippocampus, and left parahippocampal gyrus.

^dThe amygdala cluster for Create > Sentence extends to right hippocampus and parahippocampal gyrus. Anatomic locations were determined by entering coordinates into the Yale BioImage Suite Package (Papademetris et al., 2011) and Neurosynth (Yarkoni et al., 2011).