

Constructive Episodic Simulation: Temporal Distance and Detail of Past and Future Events Modulate Hippocampal Engagement

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ABSTRACT: Behavioral, lesion and neuroimaging evidence show striking commonalities between remembering past events and imagining future events. In a recent event-related fMRI study, we instructed participants to construct a past or future event in response to a cue. Once an event was in mind, participants made a button press, then generated details (elaboration) and rated them. The elaboration of past and future events recruited a common neural network. However, regions within this network may respond differentially to event characteristics, such as the amount of detail generated and temporal distance, depending on whether the event is in the past or future. To investigate this further, we conducted parametric modulation analyses, with temporal distance and detail as covariates, and focused on the medial temporal lobes and frontopolar cortex. The analysis of detail (independent of temporal distance) showed that the left posterior hippocampus was responsive to the amount of detail comprising both past and future events. In contrast, the left anterior hippocampus responded differentially to the amount of detail comprising future events, possibly reflecting the recombination of details into a novel future event. The analysis of temporal distance revealed that the increasing recency of past events correlated with activity in the right parahippocampus gyrus (Brodmann area (BA) 35/36), while activity in the bilateral hippocampus was significantly correlated with the increasing remoteness of future events. We propose that the hippocampal response to the distance of future events reflects the increasing disparateness of details likely included in remote future events, and the intensive relational processing required for integrating such details into a coherent episodic simulation of the future. These findings provide further support for the *constructive episodic simulation hypothesis* (Schacter and Addis (2007) *Philos Trans R Soc Lond B Biol Sci* 362:773–786) and highlight the involvement of the hippocampus in relational processing during elaboration of future events. © 2007 Wiley-Liss, Inc.

KEY WORDS: episodic; autobiographical memory; future; fMRI; parametric modulation

INTRODUCTION

Traditionally, memory research has focused on the past—on identifying and understanding the cognitive processes and neural structures that support the ability to encode, retain, and remember past events.

Recently, a number of neuroimaging and patient studies have begun to examine the broader role episodic memory plays in the simulation of possible future events. One conceptual framework that has been advanced to explain the role of memory in the simulation of future events is the *constructive episodic simulation hypothesis* (Schacter and Addis, 2007a,b; see also Suddendorf and Corballis, 1997, 2007; Buckner and Carroll, 2007; Hassabis and Maguire, 2007). This hypothesis contends that (a) episodic memory provides a source of details for future-event simulations and (b) the constructive nature of the episodic memory system allows the flexible recombination of such details into a coherent simulation of a novel event. By this view, because remembering past events and imagining future events relies on similar information stored in episodic memory and similar cognitive processes during event construction, such as relational processing, there should be evidence of cognitive and neural overlap between past and future events.

Converging lines of evidence suggest that retrieving past events and generating future events are likely mediated by common cognitive processes and neural substrates (for reviews, see Buckner and Carroll, 2007; Schacter et al., 2007; Suddendorf and Corballis, 2007). Amnesic patients K.C. (Tulving, 1985) and D.B. (Klein et al., 2002) exhibit an extensive loss of episodic memory and substantial difficulties imagining personal future events. Recently, Hassabis et al. (2007) examined systematically the ability of five amnesic patients with bilateral hippocampal damage to imagine novel experiences and found that the patients' imaginary scenarios were greatly reduced in richness relative to controls. Moreover, the patients' imaginary constructions lacked an overall spatial coherence, tending to consist of isolated fragments of information rather than connected scenes, possibly as a result of impaired hippocampal function and relational processing. Consistent with these observations, Addis et al. (in press) found that healthy older adults generate significantly fewer episode-specific details relative to young adults when describing past and future events. Furthermore, the ability of older adults to generate episodic details for both past and future events was correlated with their ability to integrate information and form relations between items (i.e., relational memory, Cohen et al., 1997; Eichenbaum, 2001).

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Grant sponsor: National Institute of Mental Health (NIMH); Grant number: MH060941.

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Accepted for publication 27 November 2007
DOI 10.1002/hipo.20405

Published online 21 December 2007 in Wiley InterScience (www.interscience.wiley.com).

These data again suggest that the simulation of future episodes draws on relational processes, mediated by the hippocampus, that enable flexible recombination of details from past events into novel scenarios.

Several recent neuroimaging studies examining the neural correlates of remembering the past and imagining the future have demonstrated striking overlap in the regions engaged by these two tasks (Okuda et al., 2003; Addis et al., 2007; Szpunar et al., 2007). The common neural network includes medial prefrontal cortex (PFC), medial parietal cortex extending into the retrosplenial cortex and precuneus, and medial temporal lobes (MTL) including the hippocampus. Addis et al. (2007) found that engagement of this core network changed over the course of generating an event. During the initial construction of a past or future event, the only component of this network engaged was the left hippocampus. However, once participants began elaborating upon the event and generating as much detail as possible, there was a striking overlap: the entire core network strongly activated for both past and future events.

In addition, direct contrasts of the past and future tasks have revealed consistently greater neural activity when imagining future events relative to past events (Okuda et al., 2003; Addis et al., 2007; Szpunar et al., 2007). In particular, such differences have been noted in frontopolar and MTL regions (Addis et al., 2007; Okuda et al., 2003), and Addis et al. found that future-specific activity was only evident during the early, construction phase of event generation. Schacter and Addis (2007a) proposed that this finding of greater neural activity for future relative to past events might reflect the more intensive constructive processes required by imagining future events relative to retrieving past events. Both past and future event tasks require the retrieval of information from memory, engaging common memory networks. However, only the future task requires that event details gleaned from various past events are flexibly recombined into a novel future event. Thus, additional regions supporting these processes may be recruited by the future-event tasks.

Even though the majority of past–future differences evident in this small set of studies have revealed more intense neural activity for future relative to past events, one study reported some unique activity associated with past events. Okuda et al. (2003) found that the temporal distance of events modulated activity in the left medial PFC and MTL (parahippocampal gyrus extending into the hippocampus), such that there was greater activity in these regions during construction of events closer to the present than more temporally distant events (i.e., a recency effect); notably, this effect was greater for past events relative to future events. Although this is the only study to report a unique neural signature for past events, note that Okuda et al. did not obtain data concerning the qualities of the events reported by their participants, such as the amount of detail in past and future events. The absence of such phenomenological data raises some questions. First, it is known that past events tend to be more detailed than future events, simply because these representations reflect real experiences (Johnson et al., 1988; Conway et al., 2003; D'Argembeau and van der Linden, 2004; Addis et al., in press; Szpunar and McDermott,

in press). Second, the recency effect reported in this study might not reflect temporal distance per se, but rather the fact that more remote past and future events tend to be less detailed (Piefke et al., 2003; Addis et al., 2004; D'Argembeau and van der Linden, 2004; Szpunar and McDermott, in press) and more abstract (Trope and Liberman, 2003) than recent events. These are important considerations, given that the level of detail of past events has been shown to modulate activity in the left MTL, including the hippocampus (Addis et al., 2004).

The present study was aimed at better characterizing the MTL activity associated with the elaboration of past and future events. Specifically, we investigated whether past and future task-related activity could be differentiated during the elaboration phase. Even though previous direct contrasts of the elaboration-phase data had revealed activation of a core network and no task differences (Addis et al., 2007), it is possible that this common neural machinery is used in different ways according to whether the event is located in the past or the future. Here, we reanalyzed these data according to the amount of detail generated and the temporal distance of each event from the present using parametric modulation analyses. Given that relational processing is thought to be critical to the generation of both past and future events (Schacter and Addis, 2007a,b), we hypothesized that both the integration of increasing amounts of detail for either a past or future event would be associated with increasing levels of hippocampal activity (Addis et al., 2004; Eichenbaum, 2001). However, as future events are thought to require more intensive processing to recombine disparate details into a coherent event, the hippocampal response to increasing amounts of future-event detail should be larger than that for past-event detail. In addition to the MTL, activity in the right frontal pole, thought to play a role in prospective thinking (Burgess et al., 2000, 2001), should also correlate with future-event detail if it is involved in the generation of future details. Finally, if a neural hallmark of past events is a greater hippocampal response to temporally close events than that evident for future events (Okuda et al., 2003), we should find this difference even when the level of detail is taken into account.

METHODS

The present study is based on a new analysis of data collected in the study described by Addis et al. (2007). Only a brief description of paradigm is provided here; for a full description, refer to Addis et al. (2007).

Participants

Sixteen healthy, right-handed adults (seven male; mean age, 23 yr; range, 18–33 yr) with no prior history of neurological or psychiatric impairment participated in the study. Two participants were excluded because of an insufficient number of responses during the scan and postscan interview. All partici-

pants gave informed written consent in a manner approved by the Harvard and Massachusetts General Hospital Institutional Review Boards.

fMRI Paradigm

All participants completed six runs of functional neuroimaging, each 10 min and 24 s in duration. Within each run, 16 trials were randomly presented; this number comprised 4 trials from each condition (past event, future event, semantic retrieval, and visual imagery). Note that data from the control tasks are not considered in the current analyses, and thus these tasks are not described in detail. Each trial consisted of a construction and elaboration phase (20 s) and three rating scales (5 s each). Trials were separated by a rest period during which a fixation cross was presented for a mean duration of 4 s (jittered between 2 and 6 s). All stimuli were presented in black text on a white background and projected on a screen viewed by participants on a mirror incorporated into the head-coil. E-Prime software (Psychology Software Tools, Pittsburgh, PA) was used for the presentation and timing of stimuli and collection of reaction times and response data. Responses were made on an MR-compatible five-button response box.

Past- and future-event tasks

Twenty-four past- and 24 future-event trials were presented randomly across the entire scanning session. Each trial was 35 s in duration and began with a 20-s construction and elaboration phase, during which a modified version of the Crovitz cueing procedure (Crovitz and Schiffman, 1974) was used. A cueing slide was presented for the duration of this phase and comprised three lines: (1) task instructions (“recall past event” or “envisage future event”); (2) the timeframe for the event (“last week” or “next week”; “last year” or “next year”; or “last 5–20 years” or “next 5–20 years”); and (3) a cue word. Cue words were nouns selected from the Clark and Pavio extended norms (Clark and Paivio, 2004), high in Thorndike-Lorge frequency (Mean = 1.66, SD = 0.290), imageability (Mean = 5.85, SD = 0.330), and concreteness (Mean = 6.83, SD = 0.342). Lists of 24 cue words cycled through conditions; lists did not differ significantly in frequency, imageability, or concreteness.

On presentation of this cueing slide, participants were required to recall a past event that occurred during the specified timeframe or imagine a future event that could occur within the timeframe. The event did not have to strictly involve the object named by the cue. Events were, however, required to be temporally and contextually specific, occurring over minutes or hours, but not more than 1 day (i.e., episodic events). Future events had to be novel (i.e., not been previously experienced by the participant) and plausible given the participant’s plans for the future. Further, participants were instructed to experience events from a field perspective (i.e., seeing the event from the perspective of being there) rather than from an observer perspective (i.e., observing the self from an external vantage point). Once participants had the event in mind (i.e., an event had been retrieved or imagined), they pressed a button

on the response box. This response time was recorded and marked the end of event construction and the beginning of elaboration. Participants were instructed prior to scanning that once they made this response, they were then to elaborate, that is, expand the event representation by silently retrieving or generating as much detail as possible until the end of the phase (i.e., until the rating task appears). The cueing slide remained onscreen for the entire 20-s duration, irrespective of when the response was made. If no response was made within the 20 s, the next phase of the trial (rating tasks) began. During the *ratings phase* of each event trial, participants rated the contents of the event. Three rating scales were presented (detail, emotionality, and field/observer perspective), each for 5 s. Relevant here, the amount of detail retrieved or imagined was rated on a five-point scale (1 = vague with no/few details; 5 = vivid and highly detailed).

Postscan interview

Immediately following scanning, participants completed an interview in which they were prompted with each cue shown in the past- and future-event conditions. They were required to think back to the event they retrieved or imagined in the scanner, and to describe the event to the experimenter. Only those events that were specific in both time and place were included in analyses. Participants provided their age (or predicted age) at the time of the event for those events in the 5- to 20-yr timeframe.

Data Acquisition

Images were acquired on a 3-T Siemens Sonata MRI scanner. Detailed anatomical data were collected using a multiplanar rapidly acquired gradient echo sequence. Functional images were acquired using a T2*-weighted echo planar imaging sequence (TR = 2,000 ms, TE = 23 ms, FOV = 200 mm, flip angle = 90°). Twenty-five coronal oblique slices (5-mm thick) were acquired at an angle perpendicular to the long axis of the hippocampus in an interleaved fashion.

Data Processing and Statistical Analyses

All preprocessing and analyses of imaging data were performed using SPM2 (Wellcome Department of Cognitive Neurology, London, UK). Standard preprocessing of functional images was performed, including discarding the first four functional images to allow scanner equilibrium effects, rigid-body motion correction and unwarping, slice timing correction, spatial normalization to the Montreal Neurological Institute (MNI) template (resampled at $2 \times 2 \times 2$ mm³ voxels), and spatial smoothing (using an 8-mm full-width half maximum isotropic Gaussian kernel). Linear slope was removed to correct for drift. Each event was modeled by SPM2’s canonical hemodynamic response function (hrf). Only the elaboration phase of each trial was analyzed here. Thus, the canonical hrf was applied 1 s before the response time on each trial, based on electrophysiological evidence, indicating that neural changes

associated with the formation of an autobiographical memory begin typically 800–1,000 ms before a manual response is made (Conway et al., 2001). This should therefore coincide with the decision that a past or future event had been retrieved or imagined and to begin elaborating on the event. Neural activity related to the elaboration of events was modeled only at this single time-point rather than across the entire phase (i.e., as an extended event of variable duration) to reduce contamination by other cognitive processes, including the potential decreases in effort and participant engagement across the duration of elaboration phase (Addis et al., 2007).

Fixed-effects parametric modulation analyses

To investigate how detail and temporal distance contribute to neural activity during the elaboration phase, and whether these effects differed according to whether the event was in the past or future, a series of parametric modulation analyses were first conducted at the fixed-effects level. First, two parametric modulation analyses were performed (one each for past and future events), with the amount of detail generated (rated on a five-point scale) entered as a covariate of interest (modeled linearly). These analyses permitted identification of regions where activity was correlated positively with the amount of detail generated (e.g., higher amounts of neural activity during the elaboration of events rated as more detailed). Inclusion of the temporal distance of the event (number of years from the present) as a nuisance variable meant that this analysis revealed the orthogonal contribution of detail to patterns of neural activity, independent of any contribution of temporal distance. Second, we also sought to identify those regions in which activity correlated with temporal distance of past and future events, independent of the amount of detail generated. Thus, a further two parametric modulation analyses were conducted (one each for past and future events), with temporal distance entered as the covariate of interest and detail ratings entered as a nuisance variable (modeled linearly). These analyses permitted identification of regions where activity modulated with temporal distance in a positive (i.e., showing an effect of temporal remoteness, such that activity increases as remoteness of the event from the present increases) or negative (i.e., showing an effect of temporal closeness, such that activity increases as the remoteness of the event decreases) manner.

Random-effects conjunction analyses

Conjunction analyses were computed to identify regions in which parametric responses to either detail or temporal distance were similar across past and future events. Relevant contrast images from fixed-effects parametric modulation analyses were entered into one of two conjunction analysis: (1) contrast images from parametric modulation analyses for detail (independent of temporal distance) of past events and future events were entered into the past–future conjunction analysis for detail and (2) contrast images from parametric modulation analyses

for temporal distance (independent of detail) of past events and future events were entered into the past–future conjunction analysis for temporal distance.

Each of these two conjunction analyses involved using the masking function of SPM2 to select voxels to include or exclude. Thus, a one-sample *t*-test for one contrast of interest was computed, and the activated voxels from this analysis were used to form a mask. A second one-sample *t*-test for the other contrast of interest was computed, and the mask from the first analysis was applied, such that the resulting conjunction revealed regions active in both contrasts of interest. The individual one-sample *t*-tests were thresholded at $P < 0.05$ and $P < 0.01$, such that the conjoint probability of the conjunction analysis, estimated using Fisher's method (Fisher, 1950; Lazar et al., 2002), was $P < 0.005$ (uncorrected), in keeping with other parametric modulation studies (e.g., Rombouts et al., 1999; Addis et al., 2004). An extent threshold of five contiguously activated voxels ($2 \times 2 \times 2 \text{ mm}^3$) was applied, except in our two a priori regions of interest, the bilateral hippocampus (Okuda et al., 2003; Addis et al., 2004) and the right frontal pole (Okuda et al., 2003).

Random-effects contrast analyses

To identify regions showing differential responses to detail or temporal distance depending on whether the event is in the past or the future, relevant contrast images from past and future parametric modulation analyses were entered into a random-effects model, and paired *t*-tests of the parametric effects (i.e., the slope of the regression line) for past and future events were computed. These contrasts identify voxels for which the slope of the regression line for the covariate of interest differs significantly between past and future events. This approach can therefore detect voxels in which the slope of the regression line is opposite in sign (e.g., the parametric effect is negative for past events but positive for future events) or of the same sign but significantly different in magnitude (e.g., the parametric effect is weakly positive for past events and strongly positive for future events). To clarify the nature of any significant differences and to distinguish between these two scenarios (i.e., whether the slope is of opposite sign or of same sign but different magnitude), the average estimated slope of the regression line for each condition was extracted from relevant beta images. Note that these values are scaled differently across the different variables (i.e., detail and temporal distance) and are thus not directly comparable, and any apparent differences in these values do not necessarily reflect a difference in magnitude of effect.

Additionally, even if significant past–future differences emerged, the effects themselves (i.e., for past and for future) may not be significantly different from zero. We therefore probed further any regions exhibiting a past–future difference to determine by computing a whole-brain one-sample random-effects *t*-test for each modulation effect. Thus, four one-sample *t*-tests were computed: parametric modulation effects of (1) past detail and (2) future detail, independent of temporal distance; and parametric

TABLE 1.

Medial Temporal and Frontopolar Regions Exhibiting Common and Differential Parametric Responses to the Level of Detail (Independent of Temporal Distance) of Past and Future Events

Region	Coordinates			Z-score	Mean beta	
	x	y	z		Past	Future
A. Common past–future responses to detail						
Positive modulations (i.e., increasing activity with increasing level of detail)						
L. hippocampus ^a	–18	–34	1	1.95	5.03*	7.74*
L. parahippocampal gyrus (BA 27)	–14	–46	6	1.98	11.97*	13.25*
B. Differential past–future responses to detail						
Future events (positive modulations) > past events (positive or negative modulations)						
R. frontal pole (BA10) ^b	20	63	10	3.01	–5.83	6.09*
L. amygdala ^b	–14	–8	–11	2.93	–3.77	13.41*
L. hippocampus ^c	–20	–22	–6	2.58	3.59	12.64*

All activations reported survive a threshold of $P < 0.005$, uncorrected for multiple comparisons. For each cluster of activation, the Talairach coordinates of the maximally activated voxel within each different structure are reported, as indicated by the highest Z score. BA, Brodmann area; L, left; R, right.

^aProximal (within 3 mm) to the peak voxel modulated by the level of detail of past events in Addis et al. (2004).

^bVoxels in which the significant past–future difference in the slope of the parametric modulation by detail reflected a significant positive slope for future events and negative but nonsignificant slope for past events.

^cVoxels in which the significant past–future difference in the slope of the parametric modulation by detail reflected a significant positive slope for future events and nonsignificant positive slope for past events.

*In voxels identified by conjunction analyses, the modulation effect for both past and future events is significant (with a conjoint probability of $P < 0.005$). In voxels identified by contrast analyses, the asterisk indicates which parametric modulation effects are significantly different from zero (as determined by a one-sample t -test, $P < 0.005$).

modulation effects of the temporal distance of (3) past and (4) future events, independent of detail.

The significance threshold for all contrast analyses was also set at $P < 0.005$ (uncorrected) and, again, an extent threshold of five contiguously activated voxels ($2 \times 2 \times 2 \text{ mm}^3$) was applied except in our two a priori regions of interest (bilateral hippocampus and right frontal pole; Okuda et al., 2003; Addis et al., 2004). For all analyses, the peak MNI coordinates of active regions were converted to Talairach space, and regions of activations were localized in reference to a standard stereotaxic atlas (Talairach and Tournoux, 1988).

RESULTS

Behavioral Results

Each participant contributed an average of 20.24 past (SD = 2.61) and 19.14 future events (SD = 2.66), all of which were specific in time and place. Past and future events did not differ in frequency of field and observer ratings ($\chi^2 = 2.33$, $P = 0.127$), ratings of detail ($U = 68.50$, $P = 0.174$), or temporal distance (in years, $t = -0.350$, $P = 0.729$). Spearman correlations of detail and temporal distance ratings revealed that these dimensions were uncorrelated for both past ($r_s = 0.102$, $P = 0.729$) and future ($r_s = 0.405$, $P = 0.151$) events.

Common and Differential Neural Responses to Amount of Past- and Future-Event Detail

A conjunction of the past and future parametric modulation analyses was computed to identify those regions exhibiting common neural responses to the level of detail, independent of any effects of temporal distance (see Table 1a and Fig. 1a). This analysis indicated that activity in two regions in the left MTL showed positive correlations with the level of past and future detail generated: the left posterior hippocampus and the left parahippocampal gyrus (Brodmann area (BA) 27). Notably, the hippocampal region modulated by past and future detail is proximal (within 3 mm) to the region reported by Addis et al. (2004) as responsive to the amount of detail comprising past events.

Paired t -tests were used to compare the neural responses to the level of detail of past and future events (see Table 1b and Fig. 1b). This analysis revealed two medial temporal regions in which the parametric response to detail (i.e., the slope of the regression line) was significantly greater for future relative to past events. In the left anterior hippocampus, this significant difference represented a stronger positive modulation of activation by the amount of detail comprising future events relative to past events, and accordingly, only the modulation effect for future events was significantly different from zero (as indicated by the results of one-sample t -tests of the parametric effects of future detail and past detail). In the left amygdala as well as the right frontal pole, a slightly different pattern emerged. The

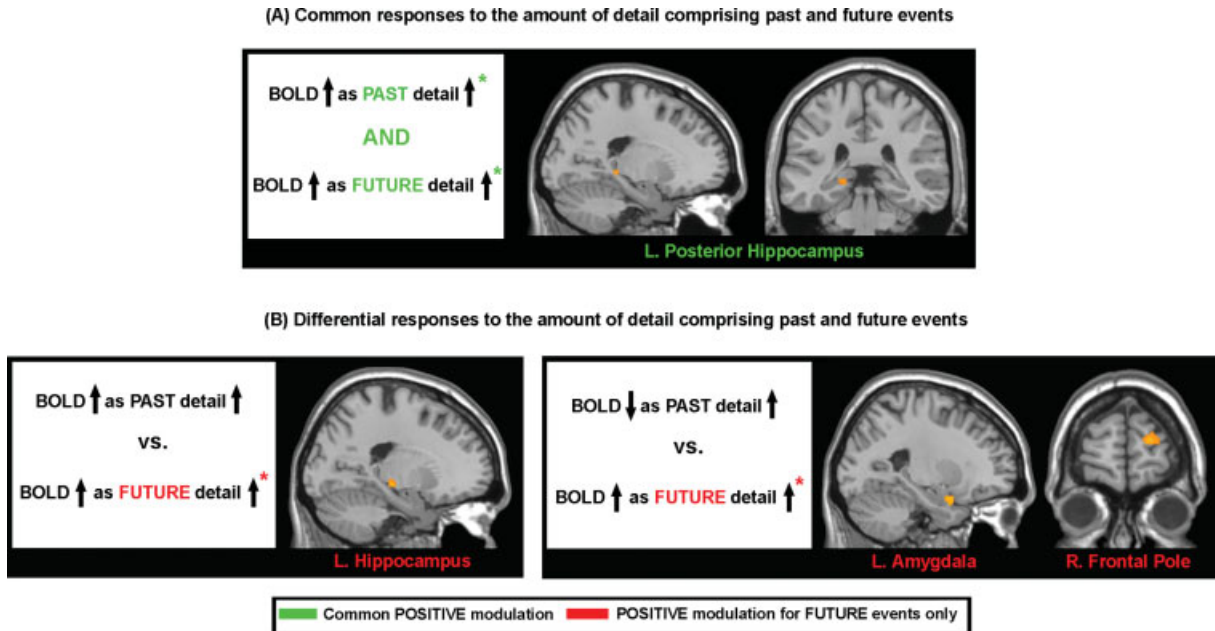


FIGURE 1. Medial temporal and frontopolar regions exhibiting common and differential parametric responses to the level of detail (independent of temporal distance) of past and future events. (A) Engagement of the left posterior hippocampus ($xyz = -18, -34, 1$) was positively correlated with the amount of detail comprising past and future events, such that activity in this region was significantly increased during the elaboration of more detailed events. (B) Regions of the left medial temporal lobe and right frontopolar cortex exhibiting differential responses to the amount of past and future event detail generated. In the left anterior hippocampus ($xyz = -20, -22, -6$), this past–future difference reflected a significant positive correlation between activity and the

amount of detail comprising future but not past events. In the left amygdala ($xyz = -14, -8, -11$) and right frontal pole (BA 10, $xyz = 20, 63, 10$), this past–future difference was due to negative correlations with the amount of past detail and positive correlations with the amount of future detail; in both regions, only the latter correlation was significant. *In voxels identified by conjunction analyses, the modulation effect for both past and future events is significant (with a conjoint probability of $P < 0.005$). In voxels identified by contrast analyses, the asterisk indicates which parametric modulation effects are significantly different from zero (as determined by a one-sample t -test, $P < 0.005$).

significant past–future difference reflected opposite modulation effects: a significant positive correlation for future events (i.e., increasing neural activity with increasing detail) and a nonsignificant negative correlation for past events.

Common and Differential Neural Responses to the Temporal Distance of Past and Future Events

We were interested in identifying medial temporal regions that respond commonly and differentially to the temporal distance of both past and future events, independent of any contributions of detail. A conjunction of contrast images from the past and future parametric modulation analyses did not reveal any regions exhibiting similar responses to distance. However, paired t -tests revealed a number of regions in which the parametric response to temporal distance (i.e., the slope of the regression line) was significantly greater for future relative to past events (see Table 2 and Fig. 2). Extraction of the average estimated slope of the regression line for each condition from relevant beta images indicated that in all peak voxels, the significant difference represented opposite modulation effects: the effect was *positive* for future events (i.e., increasing neural activity with increasing temporal distance from the present) and

negative for past events (i.e., increasing neural activity with decreasing temporal distance, “recency effect”). One-sample random-effects t -tests for each of the modulation effects (i.e., for past and future events) revealed that engagement of medial temporal structures, namely bilateral hippocampus, right amygdala, and right parahippocampus (BA 30) correlated significantly with increasing temporal distance of *future* events. In contrast, the recency effect for past events (i.e., the negative correlation of neural activity and neural activity) was significant in another aspect of the right parahippocampal gyrus (BA 35/36). Note that in the left parahippocampal gyrus, neither the past or future modulation effect was significantly different from zero.

DISCUSSION

The major finding of the present study is that although the elaboration of past and future events engages a common neural network, MTL regions comprising this network respond differentially to the amount of detail and temporal distance of past and future events. This observation suggests that the core net-

TABLE 2.

Medial Temporal Regions Exhibiting Differential Parametric Responses to the Temporal Distance (Independent of Detail) of Past and Future Events

Region	Coordinates			Z-score	Mean beta	
	x	y	z		Past	Future
Differential past–future responses to temporal distance						
Future events (positive modulation) > past events (negative modulation) ^a						
L. hippocampus	-32	-28	-12	3.44	-2.65	1.84*
R. hippocampus	38	-37	-2	3.76	-1.50	2.85*
R. amygdala	18	-6	-13	2.77	-2.74	3.09*
L. parahippocampal gyrus (BA 19)	-26	-51	-4	3.07	-3.18	1.76
R. parahippocampal gyrus (BA 35/36)	22	-37	-8	3.15	-3.73*	1.40
R. parahippocampal gyrus (BA 30)	26	-43	-8	3.13	-2.73	2.10*

All contrast effects are significant at $P < 0.005$ (uncorrected for multiple comparisons). BA, Brodmann area; L, left; R, right.

^aIn all cases, significant differences reflect opposite modulatory responses to temporal detail of past and future events (i.e., a positive correlation for future events and a negative correlation for past events).

*In voxels identified by contrast analyses, the asterisk indicates which parametric modulation effects are significantly different from zero (as determined by a one-sample t -test, $P < 0.005$).

work supporting past and future thinking (Schacter et al., 2007) can be recruited in different ways depending on whether the event being generated is in the past or future. Although we previously found neural differences only during the *construction* phase (Addis et al., 2007), using a parametric approach we have now identified distinct neural correlates of the *elaboration* of past and future events. Moreover, the differences we found previously at construction were limited to unique activity for *future* events; using this approach, we have identified a neural signature unique to the elaboration of *past* events.

Neural Responses to the Amount of Detail

The findings of this study provide further support for the constructive episodic simulation hypothesis (Schacter and Addis, 2007a,b) and converge with recent findings, suggesting that relational processing is a critical component of the episodic simulation of future events. For instance, Addis et al. (in press) found that the number of episodic details comprising past and future events in older adults correlated with their relational memory abilities. Furthermore, Hassabis et al. (2007) reported that hippocampal amnesic patients exhibit significant difficulty

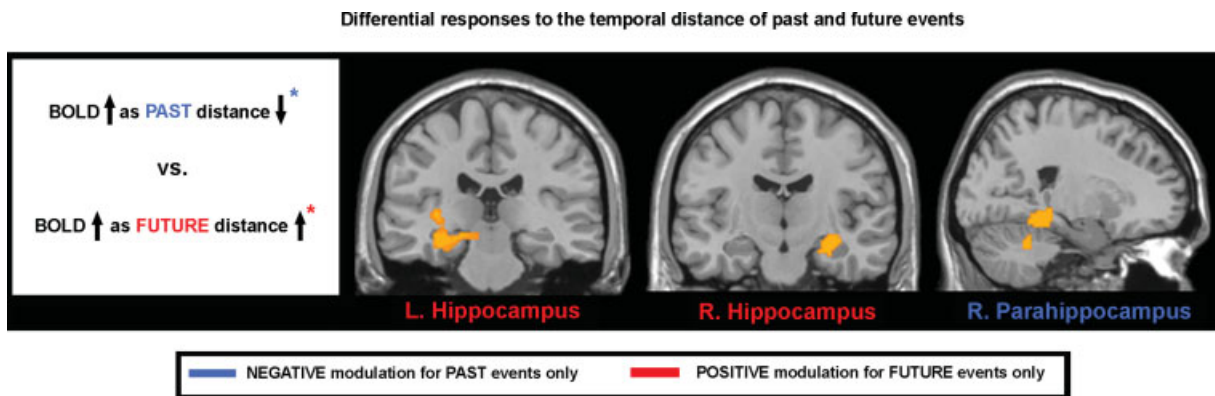


FIGURE 2. Medial temporal regions exhibiting differential responses to the temporal distance of past and future events. In all cases, this past–future difference reflected opposite modulatory responses for past and future events: activity was positively correlated with the temporal distance of future events, but negatively correlated with the temporal distance of past events (i.e., a recency effect). One sample t -tests of these modulatory effects revealed that the recency effect for past events was only significant in the right

parahippocampal gyrus (BA 35/36, $xyz = 22, -37, -8$), while the temporal distance effect for future events was significant in bilateral hippocampus ($xyz = -32, -28, -12$ and $38, -37, -2$) and right parahippocampal gyrus (BA 30, $xyz = 26, -43, -8$). *In voxels identified by the contrast analyses, the asterisk indicates which parametric modulation effects are significantly different from zero (as determined by a one-sample t -test, $P < 0.005$).

in generating and integrating details when attempting to simulate novel scenarios. Both studies suggest that the role of relational processes, supported by the hippocampus (Cohen et al., 1999; Eichenbaum, 2001), are not limited to memory per se, but also enable the flexible recombination of details from past events into representations of novel scenarios. Here, our finding that the hippocampus responds to the amount of detail integrated into a coherent representation of an autobiographical event, irrespective of whether the event is in the past or the future, also provides support for this idea. Interestingly, the region identified within the left posterior hippocampus ($xyz = -18, -34, 1$) is in close proximity to the region responsive to the amount of detail comprising past events—a study by Addis et al. (2004; $xyz = -20, -37, 0$, thus peak voxels are within 3 mm of each other).

Typically, however, imaging studies of relational memory have reported involvement of more anterior ($y < -21$) regions of the hippocampus during both encoding (Chua et al., 2007; Davachi et al., 2003; Giovanello et al., 2004; Kirwan and Stark, 2004; Jackson and Schacter, 2004) and/or recognition (Giovanello et al., 2004; Kirwan and Stark, 2004) of relational information (for a review, see Schacter and Wagner, 1999). We did find a cluster in the anterior hippocampus ($y = -22$), and notably this region was responsive specifically to the amount of detail comprising future events. This differential hippocampal activity for future events supports the prediction of the constructive episodic simulation hypothesis that simulating future events is a more intensive constructive process than retrieving past events. The construction of future events involves not only the extraction of details from various past events but the flexible recombination of these details into a coherent event, and thus it is not surprising that this requires the recruitment of additional hippocampal resources.

Findings from Preston et al. (2004) suggest that left anterior hippocampal activity ($y = -22$) is associated specifically with the novel use of elements extracted from previously learned associations. In a transitive inference design, participants first learned to associate specific faces (stimuli A) with specific houses (stimuli B), and then learned to associate another set of faces (stimuli C) with the same houses (stimuli B). Thus, each house was associated with two different faces. The A and C faces were never shown together during training, but each A and C face were related to one another through their overlapping associations with the same house (B). During scanning, the correct recognition of the A-C face pair as containing related elements significantly engaged the left anterior hippocampus relative to all other recognition conditions (i.e., successful recognition of A-B and B-C face-house pairs as “old”). Interestingly, in that same study, a region of left posterior hippocampus ($y = 30$) was engaged by all tasks requiring the retrieval of relational information (i.e., correct recognition of A-B, B-C, and A-C pairs). Both the anterior and posterior clusters reported in this study are very close to those found in the present study, and the pattern of findings reported by Preston et al. lends further support to the difference in relational processes engaged when generating past and future events. While both past and future events require the retrieval of relational information (i.e., details which were encoded as part of a mul-

ti-faceted autobiographical memory) and common engagement of left posterior hippocampus, only future events require the novel use of such details, and thus recruit the support of the left anterior hippocampus.

It is possible, however, that the differential anterior hippocampal activity for future events reflects the more active encoding of a novel representation. Even if past events elicit some level of encoding (i.e., reencoding, Nadel and Moscovitch, 1997), it likely would not be to the same level as that associated with the encoding of a newly constructed (i.e., future) event. Given that all events analyzed in this study (past or future) were successfully encoded (i.e., only events described by subjects postscan were analyzed), a difference in the level of successful encoding-associated activity cannot be ruled out. Unfortunately, an insufficient number of future events were subsequently “forgotten” in the postscan interview to enable an analysis of the contribution of encoding (i.e., a comparison of successful with unsuccessful encoding). Notably, however, Preston et al. (2004) report evidence contrary to the idea that activity in the anterior hippocampus reflects more active encoding of a novel representation. This region was not engaged during encoding of novel stimuli pairs (D-E pairs), but only when previously encoded elements were *recombined* into new pairings (A-C pairs). The idea that more novel constructions are more intensely encoded by the left anterior hippocampus is also challenged by unpublished data from our lab. Specifically, the left anterior hippocampus does not appear to be responsive to the novelty of future events (where novelty is defined in terms of previous experiences related to, and previous thoughts about, the imagined future event). Further studies designed specifically to examine the role of encoding and novelty of future events are needed to explore fully the role of left anterior hippocampus and to shed light on the neural substrates mediating the encoding of newly constructed future event representations.

The left amygdala also exhibited a differential response to the amount of detail comprising future events: there was a significant positive correlation with the amount of future detail and a negative correlation with the amount of past detail. It is unlikely that this reflects a difference in the emotional intensity of past and future events; subjective ratings on this dimension did not differ across event types (see Addis et al., 2007 for full behavioral results). It is possible, however, that the left amygdala was responding to the novelty of the future events constructed during the scan (Dubois et al., 1999; Wedig et al., 2005; Wright et al., 2006), an attribute not applicable to past events that have been previously experienced and probably also previously retrieved. Indeed, this region exhibited a negative correlation with the amount of past detail retrieved, albeit at a subthreshold level.

A similar pattern was evident in the right frontopolar cortex (BA 10), where activity was positively correlated with the amount of detail comprising future events. Our previous contrasts (Addis et al., 2007) demonstrated that this region was differentially engaged during the construction but not the elaboration of future events. Thus, the present results suggest when elaboration-related activity is broken down by the amount of detail

generated, this right frontopolar difference between past and future events persists. This result is remarkably similar to that of Okuda et al. (2003), who reported that this region was responsive to the amount of intentional information comprising the future events. Taken together with neuroimaging and lesion evidence that the right frontopolar cortex plays an important role in functions such as prospective memory (Burgess et al., 2000, 2001), it would appear this region is key to episodic *future* representation, perhaps involving the representation of intentions.

Some have argued that the medial aspects of the frontopolar cortex might be a component region of a network serving as an episodic buffer (Baddeley, 2000), acting to integrate information online (Prabhakaran et al., 2000), since it is preferentially activated during maintenance of integrated versus unintegrated information. If so, one might expect this region to be more involved when integrating information online when simulating than remembering events (Schacter and Addis, 2007c). Thus, an alternative possibility is that this region's activity, though correlated with the amount of future detail, may not reflect the process of thinking prospectively to generate such details, but rather the online integration of increasing amounts of information. These alternatives cannot be teased apart in the current study, as past and future events differed not only in terms of temporal direction (i.e., past versus future) but also in the core processes of remembering versus imagining. Further studies are required to delineate the specific contributions of regions uniquely engaged by future events—whether these regions support processes related to the temporal direction of the events (i.e., prospective thinking about the *future*) or some constructive process common to the simulation of any imaginary event (Hassabis and Maguire, 2007), such as the online integration of information in the episodic buffer.

Neural Responses to Temporal Distance

Okuda et al. (2003) found that the temporal distance of events modulated a number of regions in the PFC and MTL. This included a negative correlation in the left medial PFC and MTL (left parahippocampal gyrus extending into the hippocampus), such that there was greater activity in these regions during construction of events closer to the present than more temporally distant events (i.e., a recency effect), and this correlation was greater for past relative to future events. To date, this was the only evidence of distinct neural activity for past events when compared with future events. We hypothesized, however, that Okuda et al.'s finding might actually reflect the fact that more recent autobiographical events are typically more detailed than distant events (Piefke et al., 2003; Addis et al., 2004; D'Argembeau and van der Linden, 2004; Szpunar and McDermott, in press), given that the level of detail can modulate hippocampal activation (Addis et al., 2004). Furthermore, it was not clear whether the increased strength of the temporal distance modulation effect for past events also reflected greater detail for past events when compared with future events (Johnson et al., 1988; Conway et al., 2003; Addis et al., in press; Szpunar and McDermott, in press).

The present analyses help to clarify our understanding of MTL responses to temporal distance by ensuring that past and future events were matched for average temporal distance and ratings of detail, and by including the amount of detail generated as a covariate in the parametric modulation analysis. This analysis revealed significant past–future differences in the neural response of the bilateral hippocampus and parahippocampal gyrus to temporal distance. Interestingly, in the hippocampus, these differences reflected the presence of significant positive correlations between activity and the temporal distance of future events and a lack of significant correlations for past events. The finding that hippocampal activity increased significantly when the future events being constructed were more remote, irrespective of the amount of detail comprising these events, seems somewhat counterintuitive at first glance. However, this finding can be viewed as consistent with our constructive episodic simulation hypothesis, given the assumption that the construction of remote future events requires the integration of increasingly disparate details gleaned from a variety of sources in episodic memory. Recombination of disparate details into a coherent remote future event should thus require more intensive relational processing and hippocampal activity, irrespective of the total amount of detail integrated. Indeed, integration of unconnected pieces of information typically engages the hippocampus more than information which is already well-integrated (e.g., Preston et al., 2004). This contrasts with the construction of close future events where one can likely draw on currently relevant combinations of details (e.g., people, places, and objects), which feature in an integrated form in one's episodic memory of recent and/or current life.

Although the correlation between temporal distance and MTL activity was negative for past events (i.e., a recency effect), with detail covaried out the recency effect did not reach significance within the hippocampus. This observation contrasts with the findings of Okuda et al. (2003), and suggests their finding of a stronger hippocampal response to the recency of past than future events may have reflected other factors, such as an increased level of detail in past events. Indeed, we did find a significant recency effect for past events in the right posterior hippocampus ($xyz = 32, -37, -2, P < 0.005$, uncorrected) when detail was not included as a covariate. However, we did find the neural response to the recency of past events to be significant in other aspects of the MTL, specifically the right parahippocampal gyrus (BA 35/36). This finding is important, as it indicates the presence of a unique neural response to the elaboration of past events relative to future events. Interestingly, a different region of the right parahippocampal gyrus (BA 30) was responsive to the remoteness of future events. What this past–future difference in parahippocampal engagement reflects is unclear. However, given the role of this region in contextual processing (Bar and Aminoff, 2003), it suggests a possible distinction between the contextual processing of recent past and remote future events. This difference might reflect, for example, the difference between recollecting a recently experienced context versus trying to construct some future imaginary context.

In summary, the results presented here provide further support for the constructive episodic simulation hypothesis; in particular, the prediction that relational processing is an important component of episodic future thinking. Furthermore, our findings highlight the important contributions of hippocampal activity to the elaboration of past and future events. Specifically, engagement of the left posterior hippocampus was positively correlated with the amount of detail comprising both past and future events, possibly reflecting the retrieval of details from past events represented in episodic memory. In contrast, a more anterior region of the left hippocampus responded differentially to the amount of detail comprising future events. These observations suggest this region may support the novel use and recombination of details from various past events into a novel simulation of a future event. Moreover, activity in the bilateral hippocampus was significantly correlated with the increasing remoteness of future events. We propose that this is a reflection of the increasing disparateness of details likely included in remote future events, and the intensive relational processing required for integrating such details into a coherent episodic simulation of the future.

Acknowledgments

We thank Alana Wong and Dale Stevens for assistance with data collection.

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