Human Memory

Volume 2

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HUMAN MEMORY

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Remembering the Past and Imagining the Future: Common and Distinct Neural Substrates during Event Construction and Elaboration

Donna Rose Addis, Alana T. Wong and Daniel L. Schacter

Episodic memory allows individuals to project themselves backward in time and recollect many aspects of their previous experiences (Tulving, 1983). Numerous cognitive and neuroimaging studies have attempted to delineate the psychological and biological properties of episodic memory. One common assumption in such studies is that episodic memory is primarily or entirely concerned with the past. However, a growing number of investigators have begun to approach episodic memory in a broader context, one that emphasizes both the ability of individuals to re-experience episodes from the past and also imagine or pre-experience episodes that may occur in the future (Atance & O'Neill, 2001, 2005; Buckner & Carroll, in press; D'Argembeau & Van der Linden, 2004; Gilbert, 2006; Hancock, 2005; Klein & Loftus, 2002; Schacter & Addis, in press; Suddendorf & Busby, 2005; Tulving, 1983, 2002; Williams et al., 1996). From this perspective, both past and future event representations can be episodic in nature, containing rich contextual details about events that are specific in time and place.

Some evidence for this close linkage of past and future events comes from studies of patients with episodic memory deficits. For example, Tulving (1985) reported that patient K.C., a patient who suffered from total loss of episodic memory as a result of head injury that produced damage to the medial temporal

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and frontal lobes. Consequently, he was unable to imagine specific events in his personal future (Tulving, 1985) despite no loss in general imagery abilities (Rosenbaum, McKinnon, Levine, & Moscovitch, 2004). A more systematic investigation in another amnesic patient, D.B. (Klein & Loftus, 2002) revealed that he, too, exhibited deficits in both retrieving past events and imagining future events. Interestingly, this deficit in imagining the future was specific to D.B.'s *personal* future; he could still imagine possible future events in the public domain (e.g., political events and issues). Taken together, the pattern of deficits in these patients suggest there may be something unique about imagining personal future events above and beyond the general processes involved in constructing non-personal events and generating images.

Another population exhibiting episodic memory impairments – suicidally depressed individuals – show reduced specificity of both past and future autobiographical events, and notably, the reduction in specificity of past and future events is significantly correlated (Williams et al., 1996). Moreover, Williams and colleagues demonstrated that in healthy individuals, manipulations that reduced the specificity of past events (e.g., instructions or cues which induce a general retrieval style) also reduced the specificity of subsequently generated future events. Furthermore, factors that influence the phenomenology of past events also influence future events in the same way. For example, D'Argembeau and Van der Linden (2004) investigated how event valence and temporal distance from the present affects phenomenological qualities of past and future events. Positive events were associated with subjective ratings of greater re-experiencing and pre-experiencing than negative events, and temporally close events comprised more sensory and contextual details than temporally distant events.

These converging lines of evidence suggest a great deal of overlap between the retrieval of past events and the imagining of future events. What cognitive mechanisms and neural substrates underlie such overlap? When remembering the past and imagining the future, one must draw upon similar types of information. Events in one's past and future are inherently personal and thus should be comprised of autobiographical information. Furthermore, both tasks involve the construction of an event representation, and thus should include conceptual and visuospatial information known to comprise event representations (e.g., Greenberg & Rubin, 2003). Conceptual and semantic information about the self and one's life (e.g., familiar people, common activities) is thought to be mediated by anterior temporal regions (Addis, McIntosh, Moscovitch, Crawley, & McAndrews, 2004; Fink et al., 1996; Graham, Lee, Brett, & Patterson, 2003). Episodic and contextual imagery should feature in both types of event, thus requiring activation of precuneus (Fletcher et al., 1995) and parahippocampal/retrosplenial cortices (Bar & Aminoff, 2003), respectively. Finally, both retrieving past events and imagining future events requires the binding of details into a coherent event: either the reintegration of a memory trace, or the novel integration of disparate details into a coherent future event. Given the known role of the hippocampus in relational processing in memory (Cohen & Eichenbaum, 1993; Eichenbaum, 2001) and specifically, the reintegration of recollective details in autobiographical memories (Addis, McIntosh et al., 2004), it is likely this structure will also bind event details for novel future scenarios. Finally, the personal nature of both past and future events should engage regions mediating self-referential processing (e.g., left medial PFC, Craik et al., 1999; Gilboa, 2004; Gusnard, Akbudak, Shulman, & Raichle, 2001). Consistent with these suppositions, the one neuroimaging study that has compared directly the neural correlates of past and future events found common engagement of bilateral medial PFC, hippocampus and parahippocampus and the left precuneus (Okuda et al., 2003).

Remembering the past and imagining the future differ, at least with respect to temporal orientation, and thus some unique cognitive processes and neural regions should be associated with each. The retrieval of past events is known to activate right lateral prefrontal regions supporting memory search and post-retrieval processing (Fletcher & Dolan, 1999; Fletcher & Henson, 2001; Rugg, Otten, & Henson, 2002; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994), as well as lateral parietal cortex, whose function in memory retrieval may involve orienting attention to internal representations (Wagner, Shannon, Kahn, & Buckner, 2005). In contrast, future events are expected to engage generative processing mediated by left lateral prefrontal cortex (Poldrack et al., 1999) to support the creation of novel events, and frontopolar cortex mediating prospective thinking and future planning (Burgess, Quayle, & Frith, 2001; Burgess, Veitch, de Lacy Costello, & Shallice, 2000; Okuda et al., 1998). Damage to this latter region has been associated with deficits in advantageous decision making and awareness of future consequences (Bechara, Damasio, Damasio, & Anderson, 1994). Okuda et al. (2003) report that right anteromedial frontal pole (BA 10) was more active for future than past events, and that activity in this region correlated with the number of references to intentions.

Notably, however, Okuda et al. (2003) used a blocked design that did not allow a direct linkage between specific events and neural activity; participants were instructed to talk freely regarding events in certain time periods, and it is unclear whether the events were truly episodic (i.e., specific in time and place). Previous research has shown that specificity of past autobiographical events can influence regions engaged during retrieval (Addis, McIntosh et al., 2004; Graham et al., 2003). Moreover, it is possible that in the study by Okuda and colleagues, the phenomenological qualities of past and future events differed, particularly in light of behavioral evidence demonstrating that past events are typically more detailed and more strongly re-experienced than future events (D'Argembeau & Van der Linden, 2004). Importantly, neuroimaging findings indicate that these qualities can modulate activity in regions supporting autobiographical memory retrieval (Addis, Moscovitch, Crawley, & McAndrews, 2005).

The present study used event-related functional magnetic resonance imaging (fMRI) to examine the neural correlates of past and future events that are truly episodic in nature (i.e., specific in time and place) and of equivalent phenomenology. To this end, we employed an objective rating for the episodic specificity of events generated during scanning, and collected subjective ratings of the level of detail, emotionality, personal significance and field/observer perspective. Furthermore, we exploit the advantages of event-related fMRI to examine patterns of neural activity associated with the construction (i.e., the search and reconstruction of a past event or the creation of a future event) and subsequent elaboration (i.e., retrieving or imagining supplementary details) of past and future events. It is hypothesized that past and future events will be maximally differentiated during the construction phase, when cognitive processes specific to each event type should be engaged. Specifically, past events are predicted to activate regions supporting a strategic memory search, including cue-specification processes (e.g., ventrolateral PFC, BA 47, Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1998; Moscovitch & Winocur, 2002), and orienting attention to internal memorial representations (e.g., lateral parietal cortex, Wagner et al., 2005). In contrast, future events are expected to recruit regions related to generative processing and prospective thinking, namely the left lateral PFC (Poldrack et al., 1999) and right frontal polar cortex (Okuda et al., 2003), respectively.

Patterns of neural activity common to past and future events are expected at both the construction and elaboration phases. For instance, self-referential processing and associated left medial PFC activity should be sustained throughout both phases. Even so, we predict that overlap will be maximal during the elaboration phase. At this point, episodic and contextual imagery processes should be fully engaged for both event types, drawing on the resources of precuneus, retrosplenial and parahippocampal cortices. Further, the hippocampus should bind details retrieved or imagined during the elaboration phase, irrespective of whether the event is located in the past or future.

While nothing is known about the neural processes underlying the construction and elaboration of future events, very little is known about past event construction versus elaboration. The designs of neuroimaging studies examining retrieval of past events have typically precluded the analysis of construction and elaboration phases. Most often studies are designed to allow participants to gain access directly to personal memories without a retrieval search (Addis, Moscovitch et al., 2004; Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004; Maguire, Mummery, & Buchel, 2000; Piefke, Weiss, Zilles, Markowitsch, & Fink, 2003; Ryan et al., 2001; Steinvorth, Corkin, & Halgren, 2006). Those studies that do invoke a retrieval search have used blocked designs, thus collapsing across the construction and elaboration phases (Conway et al., 1999; Graham et al., 2003; Rekkas & Constable, 2005). Two previous event-related studies that explored the construction and elaboration of past events utilized electroencephalography (Conway, Pleydell-Pearce, & Whitecross, 2001; Conway, Pleydell-Pearce, Whitecross, & Sharpe, 2003). While construction and elaboration were differentiated electrophysiologically, with the former engaging left PFC and the latter activating bilateral posterior cortices, these studies failed to detect hippocampal activity at either stage. We expect that direct comparisons of event construction and elaboration will reveal a similar pattern of cortical activation, but that with use of fMRI, we will also be able to characterize hippocampal engagement during these phases.

1. Methods

1.1. Participants

Sixteen healthy, right-handed adults (seven male; mean age, 23 years; range, 18–33 years) with no prior history of neurological or psychiatric impairment participated in the study. Two participants were excluded due to an insufficient number of responses during the scan and post-scan interview. All participants gave informed written consent in a manner approved by the Harvard and Massachusetts General Hospital Institutional Review Boards.

1.2. Stimuli

Ninety-six nouns were selected from the Clark and Pavio extended norms (Clark & Paivio, 2004) for use as cue-words in this study. All were high in Thorndike-Lorge frequency ($M = 1.66$, $SD = .290$), imageability ($M = 5.85$, $SD = .330$) and concreteness ($M = 6.83$, $SD = .342$) in order to increase the likelihood that an event could be retrieved or imagined, and also so that each word could be used in all conditions in a fully counterbalanced design (i.e., only imageable words can be used in the visual imagery task; see below). The cue-words were divided into four lists of 24 and Analyses of Variance (ANOVA) confirmed the lists did not differ significantly with respect to frequency [$F(3,92) = .842$, $p = .940$], imageability [$F(3,92) = .133$, $p = .940$] or concreteness [$F(3,92) = .951$, $p = .419$]. The word lists cycled through conditions in a fully counterbalanced design, and each participant was randomly assigned to a counterbalanced version.

1.3. Scanning

Immediately prior to scanning, the experimental tasks were explained to participants and they completed two practice trials for each condition (eight in total). The contents of the all events retrieved or imagined during this practice session were then probed to confirm that participants understood the instructions (e.g., that events generated were specific in time and place). Participants were aware that following the scan they would be required to describe the events generated in response to each cue word presented during scanning.

In the MRI environment, 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). 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, Inc., 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.

1.3.1. 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 & 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"); (3) a cue word.

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. Participants were encouraged to freely associate so that they were successful in generating an event. 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). Examples were provided to illustrate this requirement (e.g., remembering a 3-week trip to France versus remembering visiting the Eiffel Tower on one specific day; imagining one's future child versus imagining the birth of one's future child). 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, to ensure the projection of the self over time (e.g., if one is not planning to have children, she should not imagine giving birth). 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 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. Note that all elaboration of detail was completed silently.

During the *ratings phase* of each event trial, participants rated the contents of the event. Three rating scales were presented, each for 5 s: (1) a five-point scale of the amount of detail they retrieved or imagined (1 = vague with no/few details; 5 = vivid and highly detailed); (2) a five-point scale of the intensity of emotion experienced upon retrieving or imagining this event (1 = detachment; 5 = highly emotional); (3) a binary scale regarding whether the event was experienced primarily from a field or observer perspective (1 = saw event through my own eyes; 5 = saw myself from an external perspective). These particular scales were presented during scanning as these ratings depended directly on the phenomenology of the event generated during the preceding construction and elaboration phase and could potentially change if made after scanning.

1.3.2. Control Tasks

Twenty-four semantic memory and 24 visual imagery trials, each 35 s in duration, were randomly interspersed through the scanning session. These tasks followed the same sequence as the event tasks and thus began with a 20 s *construction and elaboration phase*, during which a cueing slide was presented. The instruction line described the task (i.e., "words – sentence/define" or "objects – triangle/imagine" for the semantic and visual imagery tasks, respectively). For the semantic task, the second line specified that "two related words" (i.e., related to the cue word) be generated; for the imagery task, the size of the two objects to be imagined was specified in relation to the cue object (i.e., "bigger/smaller"). In both tasks, the words or objects generated were required to be semantically related to the cue word, to prevent participants from simply using the same words or objects for each trial. Finally, a cue word was presented.

For the *semantic retrieval task*, participants were required to retrieve two words semantically related to the cue word, and then arrange all three words (i.e., cue word and two retrieved words) into a sentence. Thus, this control task construction phase controlled for both the generation *and* integration of information processes which feature in the construction phase of the past and future event tasks. Once a sentence was devised, participants made a button press, marking the end of construction and the beginning of elaboration. For the remainder of the 20 s cue presentation, participants generated as much detail as possible about the semantic meaning of each of the three words. For the *visual imagery task*, participants were required to imagine two objects related to the cue word, one bigger and one smaller than the object named by the cue word (i.e., a size comparison task). All three objects (i.e., the two generated objects and the cue object) were then imagined simultaneously in a triangular arrangement, and thus this task also controlled for the generation and integration of information. Once the triangular arrangement was constructed, participants made a button press and for the remainder of the 20 s cue-presentation, elaboration ensued and participants were required to generate as much detail as possible about the imagined objects. Requiring the generation of as much detail as possible meant the control elaboration phase was goal-directed in the same way as past and future elaboration.

By this design, the control tasks contained processes similar to those recruited during the event tasks: one must first retrieve information (words or objects) and integrate these together (i.e., into a sentence or a triangular arrangement), then decide that the construction phase is over and make a button press, and finally generate as much semantic or visuospatial details as possible for the remainder of the elaboration phase.

During the rating phase, three scales were presented, each for 5 s, to control for the rating scales used in the past and future event tasks: (1) a five-point scale for the average amount of detail generated during the elaboration of word meanings or visual object images (1 = no/few details; 5 = highly detailed); (2) a five-point scale for how semantically related, on average, the two words or objects they generated were to the cue word (1 = semantically unrelated; 5 = highly semantically related); (3) a binary scale for task difficulty (1 = easy; 5 = difficult).

1.4. Post-Scan 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. Pilot testing demonstrated that participants were able to reflect back on events retrieved or generated during the experiment with acceptable reliability. The episodic specificity of the event (i.e., whether it was specific in time and place) was determined by the experimenter according to a three-point episodic specificity scale (Williams, Healy, & Ellis, 1999): events specific in both time and place received a score of three; events specific in time or place received a score of two; and events general in time and place (e.g., personal semantics) received a score of one. Only those events receiving an episodic specificity score of three were included in analyses. Participants rated each event for personal significance on a five-point scale (1 = insignificant, did not change my life; 5 = personally significant and life-changing event), and provided their age (or predicted age) at the time of the event for those events in the 5–20-year timeframe. Collection of these data, in conjunction with ratings of detail, emotionality and field/observer perspective collected during scanning, allowed us to ensure that past and future events were episodic and did not differ in terms of phenomenological qualities and temporal distance. While these data may provide further insight into the nature of activations associated with past and future events (e.g., neural responses to these variables may differ according to whether the event is past or future in orientation), the focus of this paper is on construction and elaboration of events and thus imaging analyses utilizing these phenomenological data will be presented in a separate report.

1.5. Data Acquisition

Images were acquired on a 3 Tesla Siemens Sonata MRI scanner. Detailed anatomical data were collected using a multiplanar rapidly acquired gradient echo (MP-RAGE) sequence. Functional images were acquired using a T2*-weighted echo planar imaging (EPI) sequence (TR = 2000 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.

1.6. Data Processing and Statistical Analyses

All pre-processing and analyses of imaging data was performed using SPM2 (Wellcome Department of Cognitive Neurology, London, UK). Standard pre-processing 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 mm × 2 mm × 2 mm voxels) and spatial smoothing (using an 8 mm full-width half maximum isotropic Gaussian kernel). Data were high-pass filtered to account for low-frequency drifts; a cut-off value of 128 was used.

Each event was modeled by SPM2's canonical hemodynamic response function (hrf). Note that for each trial, two cognitive events were modeled: (1) the construction phase and (2) the elaboration phase. As the start of the elaboration phase was based on response times, the amount of time separating the start of the construction phase and the start of the elaboration phase was random, highly variable (*M* = 7470.12 ms, *SD* = 2212.83 ms) and thus, effectively jittered. For the construction phase, the hrf was applied after reading of the cue was completed (1.8 s after task onset for past, future and semantic tasks, and 2 s after task onset for the imagery task, as determined through behavioral piloting of five participants), ensuring that the cognitive process being sampled was indeed construction rather than the reading of the cue. With respect to the elaboration phase, 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 800–1000 ms before a manual response is made (Conway et al., 2001). Thus, it should coincide with the decision marking the end of the construction phase and the beginning of the elaboration phase, that is, the decision that a past or future event or control task items had been retrieved or generated. Neural activity related to the construction and elaboration of events was modeled at the onset of these respective phases rather than across the entire phase (i.e., as an extended event of variable duration) to reduce contamination by other cognitive processes including the possible onset of elaboration-related processes prior to the button press in the construction phase and potential decreases in effort and participant engagement across the duration of elaboration phase.

The fixed-effects model for each subject comprised eight event types corresponding to the construction and elaboration of past events, future events, semantic retrieval and visual imagery. In order to identify regions differentially engaged by past and future events, direct contrast analyses were used for both the construction and elaboration phases. Thus, four contrasts were computed for each subject: (1) past event construction > future event construction; (2) future event construction > past event construction; (3) past event elaboration > future event elaboration; (4) future event elaboration > past event elaboration. Furthermore, contrasts of the main effect of construction and elaboration, collapsed across past and future, were also computed: (1) construction > elaboration and (2) elaboration > construction. Similarly, contrasts of the interaction of temporal orientation (past or future) and the task phase (construction or elaboration) were also computed: (1) (past event construction > past event elaboration) > (future event construction > future event elaboration) and (2) (future event construction > future event elaboration) > (past event construction > past event elaboration). The contrast images for the various comparisons were subsequently entered into random-effects one-sample *t* tests. A threshold of $p < .001$, uncorrected was employed for these contrasts (e.g., Maguire & Frith, 2003; Maguire, Frith, Rudge, & Cipolotti, 2005), with an extent threshold of five contiguously activated voxels (2 mm × 2 mm × 2 mm). However, in two a priori regions of interest, the bilateral hippocampus and the right frontal pole (Okuda et al., 2003), the height threshold was set at $p < .005$, uncorrected.

Conjunction analyses were used to examine regions shared between past and future events, both at the construction and elaboration phases. To begin, four contrasts were performed at the fixed-effects level: (1) past event construction > control (imagery and semantic) task construction; (2) future event construction > control (imagery and semantic) task construction; (3) past event elaboration > control (imagery and semantic) task elaboration; (4) future event elaboration > control (imagery and semantic) task elaboration. At the random-effects level, these contrasts were used for two conjunction analyses: (1) the conjunction of event construction tasks (i.e., [past event construction > control (imagery and semantic) task construction AND future event construction > control (imagery and semantic) task construction]; (2) the conjunction of event elaboration tasks [past event elaboration > control (imagery and semantic) elaboration AND future event elaboration > control (imagery and semantic) elaboration]). This 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 $p < .01$, such that the conjoint probability of the conjunction analysis, estimated using Fisher's method (Fisher, 1950; Lazar, Luna, Sweeney, & Eddy, 2002), was $p < .001$. To examine activity in our two a priori regions of interest (bilateral hippocampus and right frontal pole; Okuda et al., 2003), the conjoint probability was set at $p < .005$, uncorrected. In all regions, an extent threshold of five contiguously activated voxels (2 mm × 2 mm × 2 mm) was applied. 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 & Tournoux, 1988). Percent signal change was extracted from activations of interest for past, future and control (collapsed across imagery and semantic tasks) construction and elaboration conditions using MarsBar toolbox for SPM (Brett, Anton, Valabregue, & Poline, 2002).

2. Results

2.1. Behavioral Results

Participants were successfully able to construct an event during scanning *and* describe the event in the post-scan interview for an average of 21.64 past ($SD = 2.17$) and 22.29 future ($SD = 1.90$) event tasks (out of a maximum of 24 of each event type). These events were then rated objectively for episodic specificity and only events with a score of 3 (i.e., specific in time and place)