Constructive episodic simulation of the future and the past: Distinct subsystems of a core brain network mediate imagining and remembering

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ABSTRACT

Recent neuroimaging studies demonstrate that remembering the past and imagining the future rely on the same core brain network. However, findings of common core network activity during remembering and imagining events and increased activity during future event simulation could reflect the recasting of past events as future events. We experimentally recombined event details from participants' own past experiences, thus preventing the recasting of past events as imagined events. Moreover, we instructed participants to imagine both future and *past* events in order to disambiguate whether future-event-specific activity found in previous studies is related specifically to *prospection* or a general demand of *imagining* episodic events. Using spatiotemporal partial-least-squares (PLS), a conjunction contrast confirmed that even when subjects are required to recombine details into imagined events (and prevented from recasting events), significant neural overlap between remembering and imagining events is evident throughout the core network. However, the PLS analysis identified two subsystems within the core network. One extensive subsystem was preferentially associated with imagining both future and past events. This finding suggests that regions previously associated with future events, such as anterior hippocampus, medial prefrontal cortex and inferior frontal gyrus, support processes general to imagining events rather than specific to prospection. This PLS analysis also identified a subsystem, including hippocampus, parahippocampal gyrus and extensive regions of posterior visual cortex that was preferentially engaged when remembering past events rich in contextual and visuospatial detail.

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Episodic memory refers to a neurocognitive system that enables individuals to remember past experiences (Tulving, 2002). Although most research on episodic memory has focused exclusively on its role in remembering, Tulving (1985) recognized that episodic memory provides a basis for "mental time travel" into both the past and future. Tulving (2002) has further theorized that episodic memory and associated capacities for mental time travel are unique to human beings, a claim that has been at the center of an intensive debate about whether non-human animals are capable of remembering the past or imagining the future (cf., Clayton, Bussey, & Dickinson, 2003; Suddendorf & Corballis, 1997, 2007; Tulving, 2002).

Compared with the considerable attention devoted to understanding how episodic memory enables remembering of past events, and the heated debate over mental time travel in non-humans, there has been far less work exploring how people use episodic memory to imagine future events. During the past couple of years, however, the situation has changed dramatically, as a rapidly growing number of studies have focused on the role of episodic memory in imagining or simulating possible future events (for recent reviews, see Schacter, Addis, & Buckner, 2007; Schacter, Addis, & Buckner, 2008). A major message of this emerging body of research is that remembering past events and imagining future events depend, to a very large extent, on shared cognitive and neural processes. Evidence favoring this claim comes from (a) cognitive studies showing that a number of experimental manipulations and individual differences affect past and future events similarly (D'Argembeau & van der Linden, 2004, 2006; Spreng & Levine, 2006; Szpunar & McDermott, 2008), (b) investigations of various patient and subject populations indicating that deficits in episodic remembering are associated with similar deficits in imagining future or novel events, including studies of amnesic (Hassabis, Kumaran, Vann, & Maguire, 2007b; Klein, Loftus, & Kihlstrom, 2002; Tulving, 1985), depressed (Dickson & Bates, 2005; Williams et al.,

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1996) and schizophrenic (D'Argembeau, Raffard, & van der Linden, 2008) patients as well as healthy older adults (Addis, Wong, & Schacter, 2008), and (c) neuroimaging studies documenting that a common *core brain network* is engaged during remembering and imagining (Schacter et al., 2007) that includes hippocampus, posterior cingulate/retrosplenial cortex, inferior parietal lobule as well as medial prefrontal and lateral temporal cortices (Addis & Schacter, 2008; Addis, Wong, & Schacter, 2007; Botzung, Dankova, & Manning, 2008; Hassabis, Kumaran, & Maguire, 2007a; Okuda et al., 2003; Szpunar, Watson, & McDermott, 2007). These studies have raised a host of new conceptual and empirical questions, and have given rise to a number of novel theoretical proposals (Buckner, Andrews-Hanna, & Schacter, 2008; e.g., Buckner & Carroll, 2007; Hassabis & Maguire, 2007; Schacter & Addis, 2007a, 2007b; Schacter et al., 2007, 2008; Suddendorf & Corballis, 2007).

We have put forward one such proposal, which we have termed the *constructive episodic simulation hypothesis* (Schacter & Addis, 2007a, 2007b). By this view, episodic memory provides a source of details for future event simulations, such that past and future events draw on similar information stored in episodic memory and rely on similar cognitive processes during event construction, such as self-referential processing and imagery. Furthermore, we have suggested that the constructive nature of episodic memory supports the flexible recombination of stored details into a coherent simulation of a new event that has not been experienced previously in the same form. This process of flexible recombination is thought to rely on relational processing abilities that are heavily dependent on the hippocampal formation (e.g., Eichenbaum, 2001), with recent evidence implicating the anterior hippocampus specifically in recombining episodic details into novel events (Addis & Schacter, 2008).

Although this view fits well with evidence of similar cognitive and neural processes during past and future event construction and elaboration, the constructive episodic simulation hypothesis may also help to conceptualize one of the intriguing differences that has been documented between past and future events: direct contrasts between past and future tasks in several studies have revealed greater neural activity when imagining future events relative to remembering past events (Addis et al., 2007; Okuda et al., 2003; Szpunar et al., 2007). For example, Addis et al. (2007) reported such future greater than past activity in the hippocampus and frontopolar cortex, with future-specific activity evident only during the early, constructive phase of event generation. Schacter and Addis (2007a) proposed that this finding 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 a common core network. However, only the future task requires that event details extracted from various past events are flexibly recombined into a novel future event. Thus, additional activity supporting these processes, including activity in the hippocampus, is likely engaged by the future event tasks.

In the present article, we address three significant issues that emerge from our own and others' recent studies of past and future events, and are especially relevant to the constructive episodic simulation hypothesis. First, as noted above, this hypothesis places great emphasis on the idea that future event simulations are built by flexibly recombining details from past experiences, likely engaging the relational processes supported by the hippocampus. However, previous studies on imagining future events have not provided any direct evidence that subjects do indeed recombine details from multiple past events into novel future simulations. Although the descriptions of imaginary episodes provided in some future event protocols are consistent with this idea, an alternative possibility is that participants simply recast their memories of individual past

experiences as imagined future events, especially when they are thinking about events that might plausibly occur in the near future. For example, when given the cue "table" and asked to imagine an event that might occur in the next few weeks involving a table, participants might simply recall a recent episode in which they spilled coffee on their kitchen table and imagine that such an incident might occur again in the next few weeks. To the extent that such a recasting process occurred, there would be little or no recombination of details from past events into imagined future scenarios, and the similarity in regions engaged by past and future event tasks would simply reflect the fact that participants are remembering entire episodes in both conditions. A recasting account, however, would not easily explain the finding that several regions show greater activity during imagining the future than remembering the past, which we have suggested results from recombining event details in the future condition. By a recasting account, such activity would be instead attributable to more general cognitive activities associated with the recasting process, such as attaching a new temporal label to an existing memory, rather than to recombination processes specifically.

To address this issue in the present study, we collected from participants, prior to scanning, episodic memories of actual experiences that included details about a *person, object, and place* involved in that event. During the scan, subjects were cued to recall some of the events that had actually occurred. For the conditions in which they imagined events, we randomly recombined details concerning person, object, and place from separate episodes. Participants were thus presented with cues for a person, object and place taken from multiple episodes, and were instructed to imagine them together in a single, novel episode that included the specified details. We will refer to this procedure as *experimental recombination of event details*. If, as suggested by the constructive episodic simulation hypothesis, activity in the hippocampus and other structures in the core network during imagined future events reflects the recombination of details from different episodes, then these structures should show robust activity during experimental recombination. If, on the other hand, core network activity during future imaginings in previous studies is a result of recasting entire past episodes into the future and core network activity occurs only when participants remember entire episodes that have actually happened, then activity in the core network should be reduced significantly during experimental recombination, compared with remembering actual events. Moreover, if future-specific activity reflects general cognitive activities related to recasting rather than recombination, such future > past differences should also diminish in the current study.

A second issue that we address in the present study concerns what can be thought of as an experimental confound in previous studies that have compared remembering the past and imagining the future. While these comparisons are often portrayed as a contrast between past and future events, "past events" and "future events" in previous studies are confounded with a difference between remembering and imagining. For example, activity or characteristics attributed to "future events" could equally well be attributed to "imagined events", irrespective of whether those events refer to the future, the past, or the present. While remembered events, of course, must refer to the past, it is also possible to imagine events that might have occurred in one's personal past.

To date, one study has included a condition which, in part, addresses this issue. Szpunar et al. (2007) had participants not only remember past events and imagine future events, but also imagine events involving Bill Clinton with no specific temporal reference. While this paradigm does help address the confound of prospection and imagining, it is important to note that the Bill Clinton condition does not involve the generation of personal events or the projection of the self over time. Notably, the engagement

of the core network during the generation of Bill Clinton events was lower than the activation associated with imagining future events as well as remembering past events. It is likely that imagining events for an individual, such as Bill Clinton draws more upon semantic information (e.g., what the White House looks like; activities that Presidents of the United States engage in, etc.) rather than details in personal episodic memory (Szpunar & McDermott, 2008; Szpunar et al., 2007). Thus, imagining *personal* events which are not future-oriented, such as imagined past events, may be a more appropriate way to disentangle the effects of prospection and imagining within the realm of projecting the self over time.

The distinction between prospection and imagining is especially important when thinking about conditions that have yielded differences between remembering the past and imagining the future. For example, consider the previously mentioned finding from Addis et al. (2007) that activity in hippocampal and frontopolar regions is greater during the initial construction of imagined future events than remembered past events. Such differences could reflect increased activity related specifically to the prospective aspects of thinking about the future. Alternatively, these differences could reflect increased activity related to the demands of creating a simulation of a novel scenario, irrespective of whether the scenario is imagined to occur in one's personal future or personal past. Our previous discussions of the constructive episodic simulation hypothesis have not explicitly addressed this issue. However, the processes involved in recombining event details into novel scenarios or simulations, heavily emphasized by the constructive episodic simulation hypothesis, should occur regardless of whether an event is imagined to occur in one's past or future. These considerations lead us to suggest that core network activity should be engaged similarly when imagining the future or imagining the past. Indeed, evidence already exists indicating that the core network is engaged when people imagine novel scenarios that are not explicitly tied to a specific time in the future or the past (Hassabis et al., 2007a). To address the issue directly, on some of the trials using experimental recombination of event details, participants imagined events that could plausibly occur in their personal futures, and on other trials imagined events that might have plausibly occurred in their personal pasts.

A final issue is the lack of a consistent neural signature for remembering the past relative to imagining the future. For instance, Addis et al. (2007) and Szpunar et al. (2007) both report that no regions were more engaged by remembering the past than imagining the future, despite finding robust increases of activity throughout the core network associated with future events. However, recalling previously experienced events is thought to involve the recapitulation of sensory-perceptual and contextual details and thus engage the neural regions which originally processed such information (e.g., Johnson, Minton, & Rugg, 2008; Kahn, Davachi, & Wagner, 2004; Wheeler & Buckner, 2004; Woodruff, Johnson, Uncapher, & Rugg, 2005). Moreover, consistent with the reality monitoring framework (Johnson, Foley, Suengas, & Raye, 1988), memories for past events have been found to contain more sensory-perceptual and contextual detail than future events (D'Argembeau & van der Linden, 2004). Given that memories for past episodes contain primarily contextual and visual information (Greenberg & Rubin, 2003), a reasonable expectation is that remembering past events should engage parahippocampal and posterior visual cortices more so than imagining events. Consistent with this perspective, the parahippocampal cortex has been found to be more responsive to real past events than imaginary future events (Addis & Schacter, 2008; Okuda et al., 2003); other studies have reported a similar pattern of neural activity in the hippocampus (Botzung et al., 2008) and medial prefrontal cortex (Botzung et al., 2008;

Hassabis et al., 2007a). However, increased engagement of posterior visual regions such the cuneus and fusiform gyrus has not yet been found during past relative to future events. It is possible that such differences exist but are not evident due to a lack of power and/or differences in timing of associated neural activity. Consistent with this possibility, Conway, Pleydell-Pearce, Whitecross, and Sharpe, (2003) used slow-wave ERP to examine neural differences between recalling memories for experienced past events and recalling previously imagined events. This procedure revealed that while left anterior activity associated with memory for imagined events emerged early in the trial, posterior occipito-temporal signal associated uniquely with memory for experienced past events only emerged later in the trial.

Spatiotemporal partial least squares (PLS) can be used to analyze data where differences in the timing of the neural response may lessen the sensitivity to detect significant differences (Lobaugh, West, & McIntosh, 2001; McIntosh, Bookstein, Haxby, & Grady, 1996; McIntosh, Chau, & Protzner, 2004). Specifically, PLS does not assume the shape of the hemodynamic response function (hrf), and thus enables examination of activity related to different cognitive tasks even if the timing of associated neural activity differs (Addis, McIntosh, Moscovitch, Crawley, & McAndrews, 2004). Moreover, PLS can provide a more sensitive statistical assessment than univariate contrasts in SPM (see Addis et al., 2004 for a comparison); all voxels are analyzed in one single analytic step, thus eliminating the issue of multiple comparisons. Another key advantage of this statistical approach is that PLS identifies distributed whole-brain patterns of activity most related to the experimental conditions and how the activation of such functional networks changes across the duration of the event. Note that even though univariate contrasts may identify a set of regions activated by a certain task, it is not necessary that activity in all of the regions covaries in response to the task. Thus, PLS provides an opportunity to investigate the functional connectivity of the core network that is involved in the imagining and remembering of personal events and the identification of the regions comprising this network.

In the current study, we used an experimental recombination of details procedure to determine whether previous findings of common activation of the core network during remembering and imagining events, as well as increased activation of the core network during the imagining of future events, are still evident when subjects are prevented from recasting past events as future events. We also instructed subjects imagine both future and *past* events in order to disambiguate whether future-event-specific activity related to *prospective* thinking or a more general demand of *imagining* an episodic event in either temporal direction. We also aimed to determine whether greater activation of posterior visual cortices is evident when remembering past experiences relative to imagining novel events. These hypotheses were investigated using a multivariate analytic technique, spatiotemporal PLS, which also enabled us to examine the functional connectivity of the core network and its association with imagining and remembering personal events.

1. Methods

1.1. Participants

Healthy, right-handed young adults with no prior history of neurological or psychiatric impairment were recruited for participation in this study. For any undergraduate students recruited, only those in their second or third year of their 4-year program were permitted to enroll, ensuring that both the last and next 5 years (the temporal interval within which events would be imagined) included both college and non-college years. For the same reason, any college graduates recruited were required to have graduated at least a year prior. Twenty-three healthy, right-handed adults enrolled in the study and gave informed written consent in a

(A) EXAMPLES OF EVENTS & DETAILS RETRIEVED DURING PRE-SCAN SESSION

TITLE: Ring for Xmas
PERSON: John
LOCATION: John's place
OBJECT: Ring

TITLE: Fall outside library
PERSON: Katie
LOCATION: Widener Lib.
OBJECT: Hat

TITLE: Graduation Day
PERSON: Mom
LOCATION: Harvard Yard
OBJECT: Gown

TITLE: Didn't finish exam
PERSON: Prof. Smith
LOCATION: William James Hall
OBJECT: Clock

TITLE: Signing lease
PERSON: Broker
LOCATION: Broker's Office
OBJECT: Contract

TITLE: Buying new TV
PERSON: John
LOCATION: Best Buy
OBJECT: Flat screen TV

TITLE: $100 on lottery
PERSON: Jess
LOCATION: Convenience store
OBJECT: Lottery Ticket

TITLE: Fight with Maggie
PERSON: Maggie
LOCATION: Starbucks
OBJECT: Scarf

TITLE: Meeting Cathy
PERSON: Cathy
LOCATION: Border's Café
OBJECT: Chicken fajita

(B) EXAMPLES OF CUEING SCREENS FROM fMRI SESSION

IMAGINE FUTURE EVENT that involves:

Cathy: Meeting Cathy
Harvard Yard: Graduation Day
Ring: Ring for Xmas

(i) future-imagine

IMAGINE PAST EVENT that involves:

Broker: Signing lease
Best Buy: Buying new TV
Hat: Fall outside library

(ii) past-imagine

RECALL MEMORIES that involved:

Jess: $100 on lottery
Starbucks: Fight with Maggie
Clock: Didn't finish exam

(iii) past-recall

CREATE SENTENCE start with smallest:

Bulb: Include bulb in sentence
Ice: Include ice in sentence
Tree: Include tree in sentence

(iv) control task

Fig. 1. (A) Examples of event titles and details collected from participants during the pre-scan session are shown. Participants retrieved memories of 170 events that occurred within the past 5 years. For each event, a person, place and object featuring in the memory were identified. An event title for each memory was also devised. (B) An example of a cueing screen from each condition is shown. Color-coding shows how event details generated during the pre-scan session (see A) were experimentally recombined for the (i) future-imagine and (ii) future-past events; participants were required to imagine an event involving the person, place and object specified. Titles of the events from which the event details came from originally were given to provide a context for each detail. (iii) For the past-recall task, participants had to recall the event detail and the corresponding original memory for all details shown. (iv) The control task involved the creation of a sentence in the form "X is smaller than Y is smaller than Z", where the object words were slotted into the sentence in order of physical size.

manner approved by the Harvard and Massachusetts General Hospital Institutional Review Boards. Two subjects did not complete the fMRI portion of the study, and fMRI data from another three participants were excluded due to excessively fast reactions times, excessive movement or the presence of an anatomical abnormality. Thus, data from eighteen participants (ten male, eight female; mean age, 21.9 years; range, 18–28 years) were analyzed.

1.2. Pre-scan stimulus collection session

At least 4 days (M = 5 days and 17 h; range = 4–13 days) prior to the scanning session, participants completed a pre-scan stimulus collection session. The procedure required subjects to complete a spreadsheet detailing 170 memories of personal events experienced in the past 5 years. All events had to be specific in time and place, lasting no longer than 1 day. Participants were provided with an extensive list of event cues to facilitate retrieval, but memories were not limited to these cues. For each specific event retrieved, participants dated the event and typed a brief description. Participants also devised a brief 'title' for the event and specified three details from each memory: a person (other than themselves), an object featuring in the memory, and the location at which the event occurred (see Fig. 1A).

1.3. Stimuli

Using the event titles and details provided during the pre-scan session, sixty trial-stimulus-sets for the autobiographical event tasks were created. Each trial-stimulus-set contained a person, location and object event detail, and the cor-responding title of the memory from which this detail was gleaned (see Fig. 1B). Details were randomly extracted from different memories and combined into trial-stimulus-sets. Note that for half of trial-stimulus-sets, details were extracted from two memories and, for the other half, from three memories. In cases where two details were extracted from the same event, whether the details were person-location, person-object or location-person was balanced across conditions. This manipulation was included to enable examination of possible effects of the number of memories drawn upon in a simulation. However, the manipulation had no significant effect, and because it was not the focus of the current paper, the analyses presented here collapse across the two- and three-detail conditions. Importantly, once a detail/event title (or pair of details and event title, in the case where details came from two memories) was included in a trial-stimulus-set, neither those details nor any of the remaining details from that memory were used in any other trial-stimulus-set (see Fig. 1).

For the control task, each trial-stimulus-set contained three cue words—nouns taken from the Clark and Paivio extended norms (Clark & Paivio, 2004). Ninety nouns were selected for use in this study. We selected words that were highly familiar (M = 1.671, sd = .291), imageable (M = 5.86, sd = .326) and concrete (M = 6.846, sd = .323) given that the control task involved imagining objects.

1.4. Experimental tasks

During the scanning session, subjects completed four experimental tasks: imagining future events ("future-imagine"); imagining past events ("past-imagine"); remembering past events ("past-recall") and a semantic/visual imagery control task ("control").

1.4.1. Autobiographical event tasks

Twenty future-imagine, twenty past-imagine and twenty past-recall event trials, each 35 s in length, were presented randomly across the entire scanning session. Each trial began with a 24 s construction-and-elaboration phase. A four-line cueing slide was displayed for the duration of this phase. The first line described the task instructions (i.e., "imagine future event that involves" or "imagine past event that involves" or "recall memories that involved"). Lines two through four contained the trial-stimulus-set, such that each line contained a detail followed by the corresponding memory title (i.e., "[detail]: [event title]"; note that within the square brackets, the relevant personal event stimuli were inserted; see Fig. 1B). Note further that line two contained the person detail, line three contained the location detail and line four contained the object detail.

For the imagine-future and imagine-past tasks, participants were required to imagine a plausible personal experience that might occur in the next 5 years or have might have occurred in the last 5 years, respectively. It was stressed that both of these tasks involved *imagining* events, and thus even when thinking back to the past, the generated event must not have actually happened. The imagined event had to involve the person, location and object details specified on the cueing slide. Note that the participant only has to include the person/place/object details from those original events not the whole events themselves. Given that these details were randomly extracted from various memories (as described above), this procedure constitutes an *experimental recombination of details*. It was explained that the corresponding event title was given for each detail to provide the context for that detail so the subject would know exactly which person, location or object was being referred (e.g., the object "coat" might differ depending on whether it is from a skiing event versus an interview event; presenting the corresponding event title for each detail aided participants in making such distinctions). All events were 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., imagining one's future child versus imagining the birth of one's future child).

For the recall-past task, participants were required to remember the experiences referred to by the event titles on the cueing slide. Specifically, they were required to remember how the person, location and object detail featured in the corresponding memory indicated by the event title. Note that as with the imagining events, the three details may have been drawn from two or three events; even so, participants were instructed that even when two details came from the same event, they were to go through *each* detail and remember how it featured in the event.

Once participants had either imagined an event using the specified details, or had remembered how the specified details featured in the corresponding memories, 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 on the imagined event or the remembered events, i.e., to expand the event representation by generating or retrieving as much detail as possible until the end of the phase (i.e., until the rating task appears). For the past-recall task, where subjects retrieved two or three memories, they were instructed to re-experience as fully as possible the two or three events during the time provided, thus ensuring that subjects were remembering real past events for the duration of elaboration. Participants were instructed to experience all 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). The cueing slide remained onscreen for the entire 24 s duration, irrespective of when the response was made. If no response was made within the 24 s, the next phase of the trial (rating tasks) began. Note that all elaboration of detail was completed silently.

Immediately following elaboration, participants rated the contents of the event. Two rating scales were presented, each for five seconds: (1) a five-point scale concerning the amount of detail they retrieved or imagined (1 = vague with no/few details; 5 = vivid and highly detailed); and (2) 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.

1.4.2. Control task

Twenty control task trials were presented randomly across the entire scanning session. This task followed the same sequence as the autobiographical event tasks and thus began with a 24-s construction-and-elaboration phase, during which a cueing slide was presented. This slide comprised four lines: the first line described the task (i.e., "create sentence, start with smallest"), and lines two through four specified the noun to be used in the sentence (i.e., "[noun]: include [noun] in sentence"; note that within the square brackets, the relevant noun was inserted; see Fig. 1B). Participants were required to order the three objects, as named by the three nouns, by physical size (i.e., a size-discrimination task), and insert them into the following sentence: "X is smaller than Y is smaller than Z". Once subjects had silently said the sentence to themselves, they made a button-press, marking the end of construction and the beginning of elaboration. For the remainder of the 24-s cue presentation, participants elaborated on the representation of the nouns, generating as much detail about the meaning on the noun (including visually imagining the

object). As such, the control task is similar in structure to the autobiographical event tasks given that it requires the integration of information (into a sentence), a button press and generation of semantic and visuospatial details during elaboration.

During the rating phase, two scales were presented (each for 5 s) to control for the rating scales used in the autobiographical event tasks. First, subjects rated the amount of detail generated during elaboration on a five-point scale (1 = vague with no/few details; 5 = vivid and highly detailed). Next, subjects made a binary decision regarding task difficulty (1 = easy; 5 = difficult).

1.5. Scanning session

Immediately prior to scanning, the experimental tasks were explained to participants and examples of appropriate responses were provided. Participants were familiarized with the rating scales and completed ten practice trials (3 × future-imagine; 3 × past-imagine; 2 × past-recall; and 2 × control tasks). These trials were completed aloud to confirm that participants understood the instructions (i.e., that events generated were specific in time and place and imagined events included the three details specified). Participants were aware that during the scan the tasks were to be completed silently and that following the scan they would be required to describe the events generated in response to each cue word presented during scanning.

In the scanning environment, participants completed five runs of functional neuroimaging, each ten minutes in duration. Within each run, 16 trials were randomly presented; this number comprised four trials from each condition (future-imagine, past-imagine, past-recall and control). Each trial consisted of a construction-and-elaboration phase (24 s) and two rating scales (5 s each). Trials were separated by a rest period during which a fixation cross was presented for a mean duration of 3.5 s (jittered between 2 and 5 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.

1.5.1. fMRI data acquisition

Images were acquired on a 1.5 T 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. Post-scan interview

Immediately following scanning, participants completed an interview in which they were prompted with each cueing slide shown in autobiographical event tasks. They were required to think back to the events they retrieved or generated in the scanner, and to briefly describe the event to the experimenter. All the events in the past-recall condition were known to be specific in time and place (i.e., meeting the criteria of an episodic event) from the descriptions provided during the pre-scan stimulus collection session. For the imagined events, the episodic specificity of the event was determined by the experimenter according to a 3-point episodic specificity scale (Williams, Healy, & Ellis, 1999): an event specific in both time and place received a score of 3; events specific in time or place received a score of 2; and events general in both time and place (e.g., personal semantics) received a score of 1. Only those events receiving an episodic specificity score of 3 were included in analyses. Using a 5-point scale, participants rated the intensity of emotion experienced upon imagining or remembering the event (1 = detachment; 5 = highly emotional) and the personal significance of the event (1 = insignificant, did not change my life; 5 = personally significant and life-changing event). For the imagined events, participants rated how similar the event was to (1) previous thoughts/imaginings and (2) previous experiences (1 = I have never imagined/experienced anything similar; 5 = I have imagined/experienced this exact event). Additionally, the age that subjects assigned to an imagined event was collected; these data had been collected previously for past-recall events during the pre-scan stimulus collection session.

1.7. Analysis of behavioral data

Repeated-measures analysis of variance (RM-ANOVA), related-samples *t*-tests and Chi square tests were used to determine whether there were any effects of condition on the reaction times, temporal distance (i.e., years from the present) and phenomenological ratings of the events. Note that if the assumption of sphericity was violated (as indicated by a Greenhouse–Geisser estimate of sphericity, epsilon, of less than .90), the degrees of freedom were adjusted using Greenhouse–Geisser epsilon (Geisser & Greenhouse, 1958). To examine whether frequencies of field and observer ratings differed across the conditions, a 3 × 2 Chi-square test was computed (Preacher, 2001). Finally, ratings of the similarity of imagined future and past events to previous thoughts and experiences were compared using related-sample *t*-tests.

1.8. Data processing

All pre-processing 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 $4\,mm \times 4\,mm \times 4\,mm$ voxels) and spatial smoothing (using an 8 mm full-width half maximum isotropic Gaussian kernel).

1.9. PLS analyses

Spatiotemporal PLS is a multivariate technique that analyses the covariance of brain voxels and the experimental design (i.e., conditions) across the length of an event (Addis et al., 2004; Lin et al., 2003; Lobaugh et al., 2001; McIntosh et al., 2004). Note that unlike univariate event-related analyses, spatiotemporal PLS is not dependent upon assumptions about the shape and time course of the hrf, and thus enables investigation of changes in task-related activity at different lags along the entire course of the event. For these analyses, a 12-s temporal window was specified for each event (i.e., 6 TRs), and the onset of trials was specified at 2 s after stimulus onset, as described above. An additional analysis of the data at elaboration, as per our previous study (Addis et al., 2007), was not conducted here for a number of reasons: (1) we were most interested in teasing apart functional connectivity differences between imagining and remembering events and our previous results suggest that if such differences exist, they should be most apparent during construction (Addis et al., 2007); and (2) conducting a spatio-*temporal* analysis part-way through the trials was not considered appropriate.

The first step of the mean-centered PLS analysis was to compute the cross-covariance between a matrix of vectors coding for the tasks (i.e., design matrix) and a matrix containing all of the voxels across each event, in each image, across all subjects and tasks (i.e., data matrix). Note that in a mean-centered PLS, no *a priori* contrasts are specified. The resulting matrix was then decomposed using singular value decomposition. In doing so, a new set of orthogonal variables (latent variables; LVs) that provide the optimal relation between these data sets is identified. Contributing to each latent variable is a linear contrast, or set of contrasts, between the experimental tasks. The accompanying image displays the brain regions exhibiting the greatest covariance with the contrasts within each time lag or TR. The amount of covariance for which the latent variable accounts is known as the singular value. Further, each brain voxel has a weight or salience that is proportional to these covariances. As this was a mean-centered PLS analysis, each extracted latent variable successively accounted for a smaller portion of the covariance pattern (as indicated by the singular value). In this way, the LVs derived from a mean-centered PLS analysis are determined by the strength of effects in the dataset; the set of LVs explaining the most covariance are identified (and note, the number of LVs is constrained by the degrees of freedom; here we had 4 conditions and 3 degrees of freedom). We also had an *a priori* hypothesis that an LV would be identified that contrasted all three autobiographical event tasks relative to the control task, and associated these tasks with the core network (Addis et al., 2007). However, such an LV did not result from this mean-centered PLS analysis (see Section 2.2). In order to investigate this issue further, we conducted a "non-rotated" PLS analysis that allows the user to specify an *a priori* contrast (McIntosh & Lobaugh, 2004). Here, the *a priori* contrast was a conjunction of the three autobiographical event tasks relative to the control task.

In all PLS analyses, the statistical significance of each LV was determined using permutation tests, that is, randomly re-ordering the data matrix rows and calculating a new set of latent variables (using singular value decomposition) for each

re-ordering. At each permutation, the singular value of each latent variable was compared to the singular value of the original latent variable. The initial value was assigned a probability based on the number of times a statistic from the permuted data exceeds this original value (McIntosh et al., 1996). In the present study, 500 permutations were computed. The reliability of the saliences for the brain voxels within a latent variable was determined using bootstrap estimation of the standard errors. This procedure involves randomly resampling subjects with replacement, and computing the standard error of the saliences after a number of bootstrap samples (McIntosh et al., 1996). In the present study, this sampling and analysis procedure was carried out 300 times. Note that unlike univariate analyses, saliences are identified in one single analytic step and thus a correction for multiple comparisons is not necessary. Clusters of 5 or more voxels ($4\,mm \times 4\,mm \times 4\,mm$) in which the salience-to-standard-error ratio of was greater than 3.2 (roughly equal to a z-score, and a p-value of $p < .001$), were considered to represent reliable voxels. Note that the effects reported here were robust; although the figures show activity at a threshold of $p < .001$, all but two peak voxels survived a more conservative threshold of 4.0 ($p < .0001$).

Local maxima for the brain areas with reliable saliences on each latent variable were considered to be the voxel with a salience to standard error ratio higher than any other voxel in a 10 mm cube centered on that voxel. MNI co-ordinates were converted to Talairach space and regions of activations were localized in reference to a standard stereotaxic atlas (Talairach & Tournoux, 1988).

2. Results

2.1. Behavioral results

Only successfully completed trials were included in the analyses. For autobiographical events, this included trials on which participants: (1) successfully imagined or retrieved a specific event as instructed *and* (2) described the event during the post-scan interview, resulting in the loss of an average of 3.19% (sd = 6.41%) and 1.94% (sd = 4.42%) of trials, respectively. Additionally, trials for which the reaction time was missing or excessively fast (i.e., before the trial onset of 2 s used in the analysis) were also excluded from analysis. For three participants, fMRI data from a number of trials (6, 10 and 27 events out of a total of 80) were lost due to a scanner malfunction. Thus, individual participants contributed an average of 19.06 future-imagine (sd = 1.92), 18.39 past-imagine (sd = 2.89), 18.83 past-recall (sd = 1.98) and 19.22 control (sd = 1.56) trials (out of a maximum of 20 of each event type) to the analyses. The final number of trials in each condition did not differ significantly, as confirmed by a RM-ANOVA, $F(2.09, 35.49) = 1.97$, $p = .153$.

Average reaction times, temporal distance, phenomenological ratings and frequencies of field and observer ratings for the autobiographical events included in our analyses are presented in Table 1. A RM-ANOVA of reaction time data indicated there was a main effect of condition, $F(1.65, 28.09) = 6.02$, $p = .010$, reflecting a small (approximately 1 s) but significant decrease in reaction times for the control task relative to the future-imagine ($p = .009$),

Table 1
Mean reaction time data, temporal distance and phenomenological ratings of autobiographical events.

Measure	Mean (standard deviation)		
	Future-imagine	Past-imagine	Past-recall
Reaction time (ms)	7503.11 (2695.55)	7530.98 (2485.62)	7145.36 (1616.65)
Temporal distance (yrs)	1.82 (.805)	1.63 (.462)	1.97 (.499)
Detail	3.91 (.431)	3.81 (.481)	4.12 (.493)[*]
Emotionality	3.25 (.620)	3.10 (.641)	3.78 (.683)[**]
Personal significance	2.76 (.588)	2.72 (.676)	3.15 (.646)[*]
Field/observer perspective[a]	.927/.073	.902/.098	.959/.041
Similarity to thoughts	2.35 (.351)	2.35 (.330)	n/a
Similarity to events	2.73 (.536)	3.10 (.423)[*]	n/a

Note: Significant main effects of event condition are indicated by an asterisk on the condition mean that is significantly higher than all other condition means for that measure. ms = milliseconds; yrs = years.

[a] Mean proportion of events in each category.

[*] $p < .01$.

[**] $p < .001$.

past-imagine ($p = .004$) and past-recall ($p = .007$) tasks. Importantly, there were no significant differences in reaction time between the autobiographical event tasks (p-values ranged from .275 to .861). This pattern of results is consistent with the results from our previous neuroimaging study on past and future events (Addis et al., 2007).

In accordance with instructions, participants retrieved or generated significantly more autobiographical events from a field ($M = 53.06$, sd = 9.64) rather than an observer ($M = 3.44$, sd = 4.93) perspective, as confirmed by a related-samples t-test, $t = 15.02$, $p < .001$. A 3×2 Chi-square test (Preacher, 2001) indicated that the frequencies of field and observer ratings did not significantly

differ across the autobiographical event conditions ($\chi^2 = 4.08$, $p = .130$). There were also no significant differences between the autobiographical event tasks with respect to the temporal distance of events (i.e., the number of years from the present), $F(1.42,24.06) = 2.52$, $p = .116$. The phenomenology of autobiographical events differed across autobiographical event type (detail, $F(1.50,25.48) = 7.37$, $p = .006$; emotionality, $F(2,34) = 22.81$, $p < .001$; personal significance, $F(1.60,27.21) = 8.47$, $p = .003$). Specifically, past-recall events were rated as more detailed, emotional and personally significant than both future-imagine (detail, $p = .023$, emotionality, $p < .001$; personal significance, $p = .007$) and past-imagine (detail, $p = .007$; emotionality, $p < .001$; personal sig-
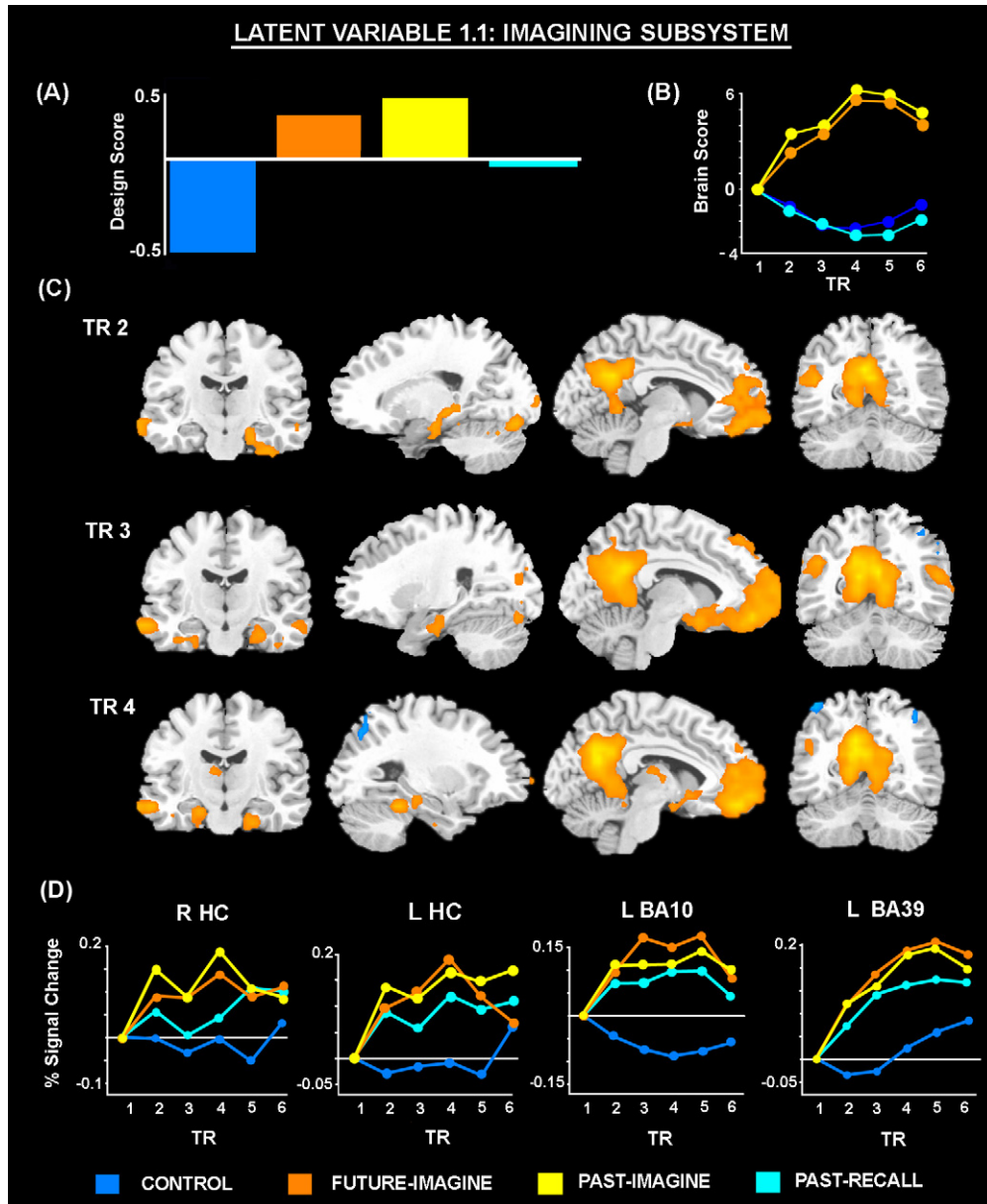

Fig. 2. *Latent variable 1.1* ($p < .001$) describes the *imagining subsystem*. (A) A plot of design scores, indicating the amount of correlation between each task and the associated pattern of brain activity. Here, the future-imagine and past-imagine tasks are associated with brain regions shown in warm colors, while the control and past-recall tasks are associated with brain regions shown in cool colors. (B) This graph illustrates the weighted average of activation across all voxels in all subjects across the length of the experimental tasks (divided into 2 s TRs). Overall, the imagining tasks result in more activity than the other tasks, and activation of the imagining subsystem peaks during the fourth TR. (C) The brain regions in which activation was associated with imagine tasks (warm colors; the imagining subsystem) or the control and past-recall tasks (cool colors) are shown for TRs 2-4, superimposed over a standard MRI template. All regions are shown at a threshold of $p < .001$. (D) Plots of the hemodynamic responses of peak voxels in the right hippocampus ($xyz = 23\ -13\ -26$), left hippocampus ($xyz = -20\ -13\ -20$), left BA 10 ($xyz = -8\ 46\ -16$), and left BA 39 ($xyz = -51\ 68\ 29$) are displayed. BA = Brodmann Area, LHC = left hippocampus, RHC = right hippocampus.

nificance, $p = .004$) events. Imagined-past events were rated as more similar to past experiences than imagined future events ($t = -2.72, p = .014$), though note the difference was small (.363 units on a 5-point scale). There was no significant difference between past- and future-imagined events with respect to the similarity of events to previous thoughts or imaginings ($t = .154, p = .879$).

2.2. Mean-centered PLS of AM and control tasks

2.2.1. Latent variable 1.1

The mean-centered PLS analysis identified two significant patterns of brain activity across tasks (i.e., LVs). The first LV ($p < .001$;

singular value = 25.55) differentiated between the imagining tasks (future-imagine and past-imagine) and the control task, but did not correlate strongly with past-recall (see Fig. 2A, where the "design score" indicates degree of correlation between each task and its corresponding pattern of whole-brain activity, and the degree of anti-correlation with the other pattern of whole-brain activity). Additionally, this LV indicated the presence of neural overlap between the future-imagine and past-imagine tasks, given that both tasks are associated with the same network of regions. The positive saliences listed in Table 2 and shown in warm colors in Fig. 2 correspond to greater activity during the imagining tasks (i.e., the "imagining subsystem"). Interestingly, the subsys-
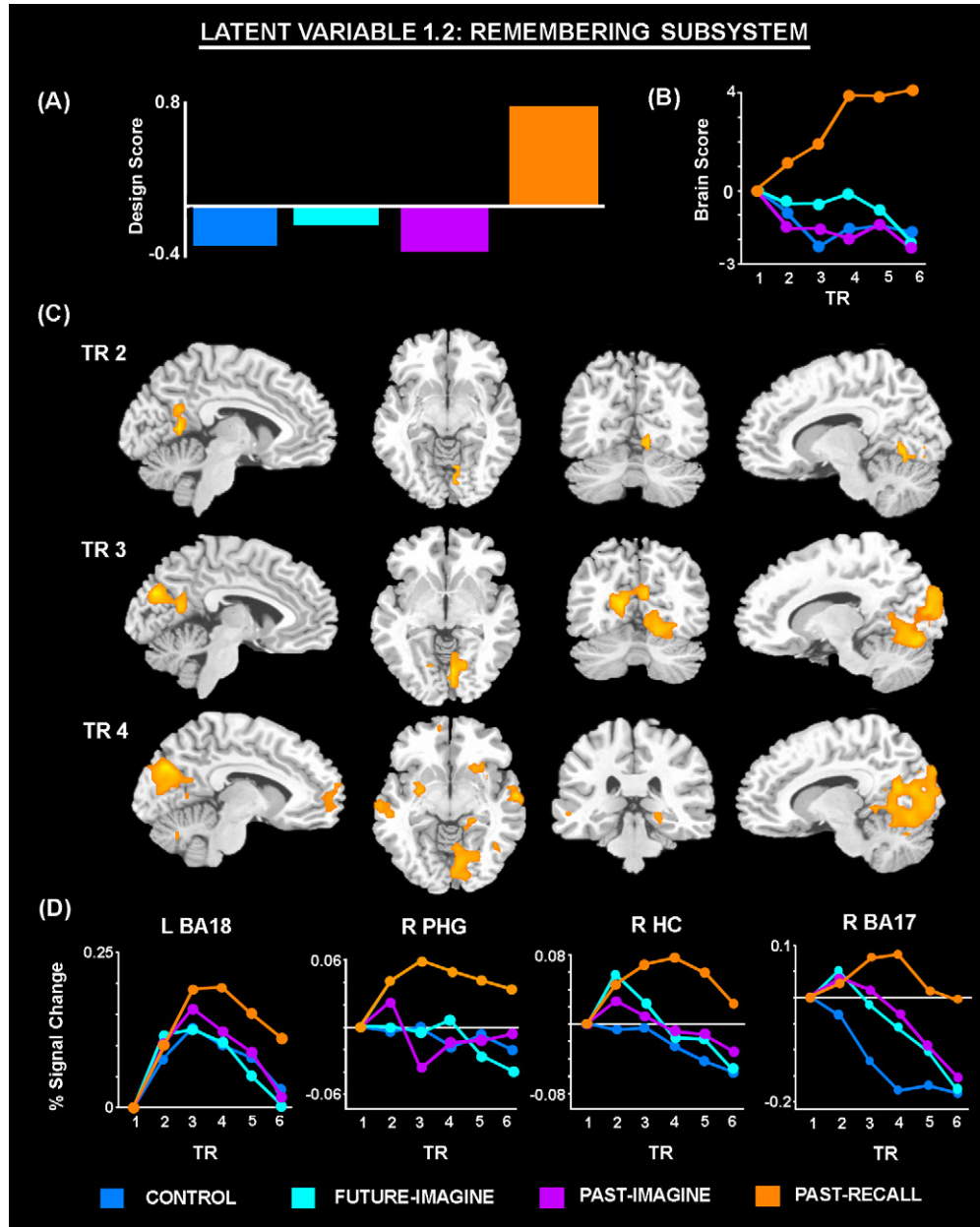

Fig. 3. *Latent variable 1.2* ($p = .006$) describes the *remembering subsystem*. (A) This plot illustrates the design scores, indicating the amount of correlation between each task and the associated pattern of brain activity. Here, the past-recall tasks are associated with brain regions shown in warm colors, while the control, past-future and past-imagine tasks are associated with brain regions shown in cool colors. (B) This graph illustrates the weighted average of activation across all voxels in all subjects across the length of the experimental tasks (divided into 2 s TRs). Overall, the recall tasks result in more activity than the other tasks, and activation of this subsystem peaks during the fourth TR. (C) The brain regions in which activation was associated with the past-recall task (yellow-red) or the imagine and control tasks (blue) are shown for TRs 2–4, superimposed over a standard MRI template. All regions are shown at a threshold of $p < .001$. (D) Plots of the hemodynamic responses of peak voxels in the left BA 18 ($xyz = -36 -90 -6$), right parahippocampal gyrus ($xyz = 20 -43 2$), right hippocampus ($xyz = 20 -35 -2$) and right BA 17 ($xyz = -8 -81 11$) are displayed. BA = Brodmann area, RHC = right hippocampus.

tem associated with the imagining tasks shows a clear neural differentiation from the remembering and control tasks as early as the second TR (2–4 s after stimulus onset), with activity peaking fourth TR (6–8 s after stimulus onset; see Fig. 2B and D). The pattern of brain activity found to characterize the future- and past-imagine tasks was extensive, comprising the major components of the core network including bilateral medial prefrontal cortex (BA 10/11), inferior frontal gyrus (BA 47), temporal pole (BA 21/38), posterior temporal cortex (21/22/39), hippocampus, parahippocampal gyrus, medial parietal cortex (23/31/7) and cerebellum (Fig. 2C).

The laterality of some components of this neural subsystem changed across the duration of the trial. For instance, the hippocampus was activated on the right during the early TRs (2–4) and on the left during later TRs (4 and 5). This pattern is clearly evident in the signal extracted from these regions (see Fig. 2D), where, for instance, activity associated with imagined events in the right hippocampus is clearly differentiated from activity associated with past-recall during TRs 2–4, but is indistinguishable during TRs 5 and 6. The activity in the left hippocampus later in the trial appears to be driven primarily by the past-imagine task; activity associated with the future-imagine task peaks at TR 4 and then begins to drop.
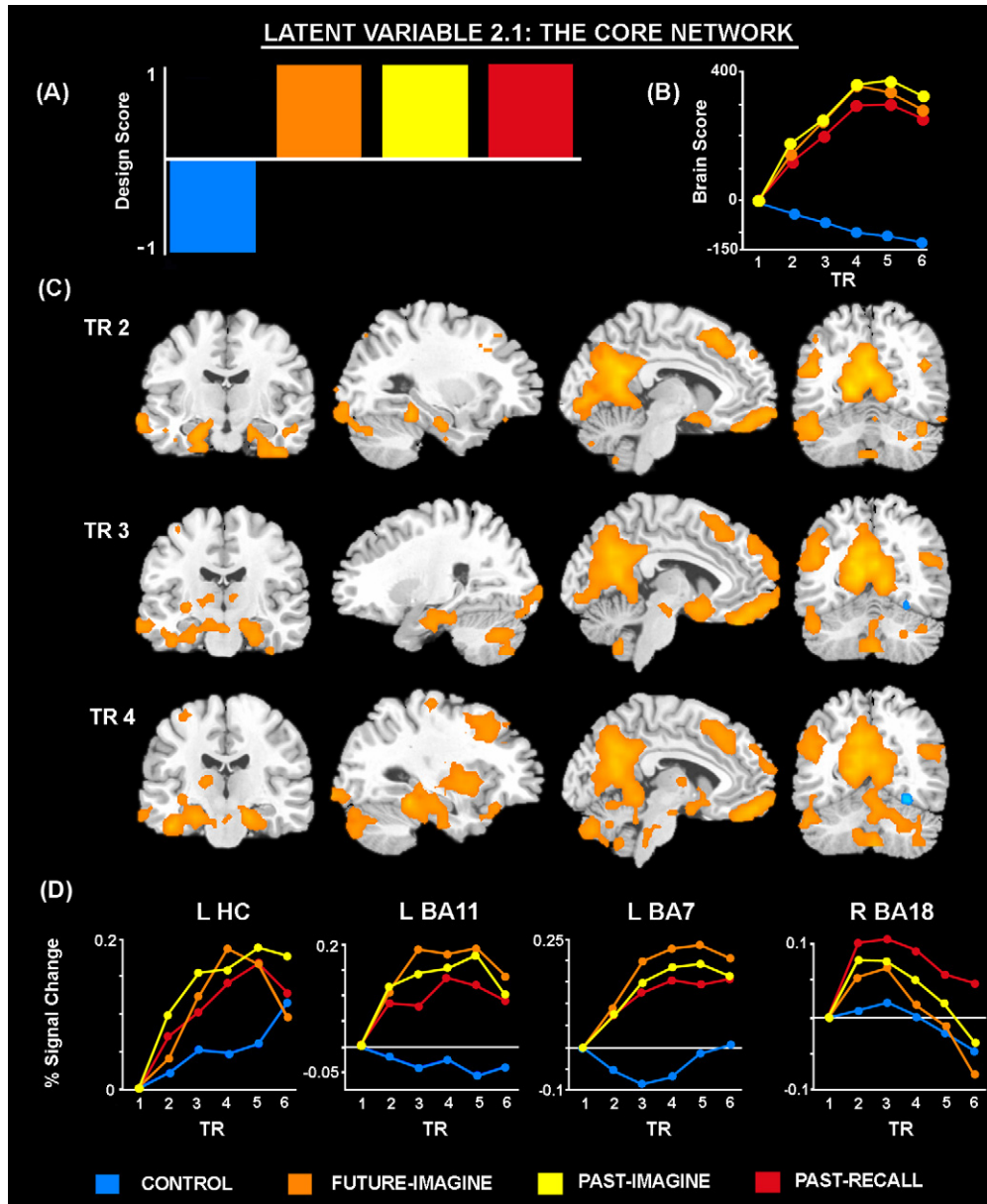

Fig. 4. *Latent variable 2.1* ($p < .001$) describes the *core network*. (A) This plot illustrates the design scores for the a priori conjunction contrast, and indicates the amount of correlation between each task and the associated pattern of brain activity. Here, the autobiographical event tasks (past-imagine, future-imaging and past-recall) are associated with brain regions shown in warm colors, while the control task is associated with brain regions shown in cool colors. (B) This graph illustrates the weighted average of activation across all voxels in all subjects across the length of the experimental tasks (divided into 2 s TRs). Overall, the autobiographical event tasks result in more activity than the control task, and activation of the core network peaks during TRs 4 and 5. (C) The brain regions in which activation was associated with the autobiographical event tasks (yellow-red) or the control task (blue) are shown for TRs 2–4, superimposed over a standard MRI template. All regions are shown at a threshold of $p < .001$. (D) Plots of the hemodynamic responses of peak voxels in the left hippocampus ($xyz = -24\ -20\ -16$), left BA 11 ($xyz = -8\ 42\ -19$), left BA 7 ($xyz = -8\ -53\ 32$), right BA 18 ($xyz = 24\ -86\ -6$) are displayed. BA = Brodmann area, LHC = left hippocampus.

Table 2
Co-ordinates of regions associated with imagined future and imagined past events from *latent variable 1.1* of the mean-centered PLS analysis.

Brain region	Co-ordinates			Bootstrap ratio[a]
	x	y	z	
TR 2 (2–4 s after stimulus onset)				
L Medial prefrontal cortex (BA 10)[b]	−12	50	−9	7.507
L Superior/middle frontal gyrus (BA 9)	−20	37	31	5.485
R Superior frontal gyrus (BA 8)	24	29	43	5.117
L Inferior frontal gyrus (BA 47)	−32	30	−18	5.100
R Inferior frontal gyrus (BA 47)	59	23	−1	4.889
L Thalamus (medial dorsal nucleus)	−4	−11	12	4.138
R Hippocampus/parahippocampal gyrus (BA 28)	24	−20	−19	5.076
L Parahippocampal gyrus (BA 35)	−16	−13	−26	4.358
L Parahippocampal gyrus (BA 30)	−24	−43	−5	4.825
R Superior temporal gyrus (BA 39)	44	−53	25	4.516
L Middle temporal gyrus (BA 21)	−67	−12	−13	6.819
L Middle temporal gyrus (BA 21)	−55	−43	−1	4.461
R Middle temporal gyrus (BA 21)	51	−9	−16	7.000
L Posterior cingulate (BA 31)[c]	−4	−53	28	10.650
L Angular gyrus (BA 39)	−48	−65	29	6.463
L Lingual gyrus (BA 18)	−16	−78	−6	6.660
R Lingual gyrus (BA 18)	16	−82	−9	6.527
R Cerebellum	36	−48	−21	6.713
TR 3 (4–8 s after stimulus onset)				
L Medial prefrontal cortex (BA 11)[b]	−4	50	−16	9.825
L Middle frontal gyrus	−32	25	43	6.390
L Caudate body	−16	16	10	4.719
R Hippocampus	28	−16	−16	4.986
L Middle temporal gyrus (BA 21)	−63	−1	−13	9.834
R Middle temporal gyrus (BA 21)	63	−12	−13	5.340
R Superior temporal/angular gyrus (BA 22/39)	51	−49	21	6.993
R Posterior cingulate (BA 23)[c]	4	−53	21	13.157
L Angular gyrus (BA 39)	−48	−64	33	7.652
R Cerebellum	4	−52	−34	4.5673
TR 4 (6–8 s after stimulus onset)				
L Medial prefrontal cortex (BA 11)[b]	−8	46	−16	10.863
L Inferior frontal gyrus (BA 47)	−51	35	−8	4.834
R Inferior frontal gyrus (BA 47)	48	34	−12	5.521
L Hippocampus	−20	−13	−20	5.529
R hippocampus/parahippocampal gyrus (BA 35)	24	−13	−26	5.515
L Parahippocampal/fusiform gyrus (BA 20)	−28	−40	−15	7.614
R Parahippocampal gyrus (BA 36)	32	−32	−15	7.226
R Superior temporal gyrus (BA 38)	40	26	−25	4.950
R Middle temporal gyrus (BA 21/20)	55	−20	−12	4.338
L Middle temporal gyrus (BA 39)	−51	−68	29	5.1619
R Middle temporal gyrus (BA 39)	51	−61	29	4.017
L Inferior temporal gyrus (BA 21)	−59	−8	−13	10.675
L Posterior cingulate/precuneus (BA 31)[c]	−8	−57	25	11.849
R Inferior occipital gyrus (BA 19)	48	−86	−6	5.294
R Cerebellum	20	−71	−13	4.704
TR 5 (8–10 s after stimulus onset)				
L Medial prefrontal cortex (BA 10/11)[a]	−4	62	−10	9.881
L Superior frontal gyrus (BA 8)	−8	52	38	5.384
L Inferior frontal gyrus (BA 47)	−36	30	−22	4.251
L Middle frontal gyrus (BA 8)	−28	33	43	5.995
R Medial globus pallidus	8	0	−7	6.580
L Thalamus (dorsal medial nucleus)	−4	−7	8	4.581
L Hippocampus	−36	−24	−12	3.732
L Parahippocampal gyrus (BA 37)	−28	−36	−12	5.784
R Parahippocampal gyrus (BA 37)	28	−36	−12	4.826
R Parahippocampal gyrus (BA 35/36)	24	−13	−26	4.025
L Middle temporal gyrus (BA 39)	−48	−61	25	5.193
R Middle temporal/angular gyrus (BA 39)	48	−57	25	5.597
L Inferior temporal gyrus (BA 21)	−59	−5	−13	6.205
L Precuneus (BA 7)[b]	−12	−53	32	11.338
L Cerebellum	−28	−40	−15	7.017

Table 2 (*Continued*)

Brain region	Co-ordinates			Bootstrap ratio[a]
	x	y	z	
R Cerebellum	4	−53	−41	6.012
TR 6 (10–12 s after stimulus onset)				
L Medial prefrontal cortex (BA 11)[a]	−1	65	−13	6.778
L Superior frontal gyrus (BA 8)	−24	37	46	4.955
L Inferior frontal gyrus (BA 47)	−40	19	−18	4.603
R Thalamus (lateral dorsal nucleus)	8	−19	16	4.470
L Superior temporal gyrus (BA 39)	−44	−57	21	4.115
L Middle temporal gyrus (BA 21)	−63	−1	−20	5.289
R Middle temporal gyrus (BA 21)	48	6	−27	4.841
R Middle temporal/angular gyrus (BA 39)	51	−65	25	5.605
L Precuneus (BA 7)[b]	−4	−53	32	7.877
L Superior occipital gyrus (BA 19)	−44	−80	37	6.240
L Cerebellum	−24	−75	−33	3.811
R Cerebellum	4	−52	−34	5.075

Note: Activations are reported for each 2 s TR. All activations reported survive a threshold of $p < .0002$ (bootstrap ratio of 3.7) and an extent threshold of 5 voxels (4 mm × 4 mm × 4 mm). For brevity, only the Talairach co-ordinates of the maximally activated voxel within a cluster is reported (with the exception of the MTL), as indicated by the highest bootstrap ratio. BA = Brodmann area; L = left; R = right.

[a] The bootstrap ratio is the parameter estimate for that voxel over its standard error and is proportional to a z score.

[b] This medial prefrontal cluster is bilateral.

[c] This medial parietal cluster is bilateral and encompasses the posterior cingulate, retrosplenial cortex and precuneus.

A laterality change was also evident in the inferior frontal gyrus and cerebellum, where initial right lateralized activity during TRs 2–4 became bilateral later in the trial (TRs 5 and 6). The lingual gyrus (BA 18) was only active early in the trial (TR 2, 3), while in contrast, left inferior temporal gyrus (BA 21), right medial globus pallidus and occipital gyrus (BA 19) were only active during TRs 4–6.

The negative saliences correspond to greater activity during the control task but not the imagined tasks or the remembered events (the correlation between the past-recall task and this pattern of brain activity is less than .01; see Fig. 2A). Activity for this subsystem also peaks during the fourth TR (6–8 s after stimulus onset; see Fig. 2B; for brevity, these results are not included in Table 3). Throughout the trial, enhanced activity related to the control task was evident primarily in bilateral inferior parietal lobule (BA 40; as evident in Fig. 2C), inferior frontal gyrus (BA 44) and middle/superior frontal gyrus (BA 6) and right superior temporal gyrus (BA 21/22); from the fourth TR, bilateral activation of the precentral gyrus was evident; and from the fifth TR, left superior temporal gyrus (BA 22/38) and bilateral precuneus (BA 7) activity was evident.

2.2.2. Latent variable 1.2

The second significant LV ($p = .006$; singular value = 19.21) to emerge from this PLS analysis differentiated the remembering task from the future-imagine, past-imagine and control tasks (Fig. 3A). The activation associated with remembering reached a peak during TR 4, but by TR 6 it had still not begun to subside (Fig. 3B). The positive saliences listed in Table 3 and shown in warm colors in Fig. 3C correspond to greater activity during the past-recall task (i.e., the "remembering subsystem"). This subsystem was predominated by posterior regions known to support visuospatial processing, including right parahippocampal gyrus and bilateral lingual gyrus, cuneus and superior, middle and inferior occipital gyri (BA 17/18/19; though more extensively on the right). Interestingly, activity associated with the past-remember is not clearly differentiated from the other tasks until around TR 3 or 4—later in the trial than the differentiation evident in LV1.1 (see Figs. 2D and 3D). At the 4th TR, there was a distinct increase in whole-brain

Table 3
Co-ordinates of regions associated with recalled past events from *latent variable 1.2* of the mean-centered PLS analysis.

Brain region	Co-ordinates			Bootstrap ratio[a]
	x	y	z	
TR 2 (2–4 s after stimulus onset)				
L Retrosplenial cortex (BA 23)[b]	−4	−53	25	5.188
R Lingual gyrus (BA 18)	12	−58	3	4.288
R Cuneus (BA 19)	12	−88	34	4.454
TR 3 (4–8 s after stimulus onset)				
R Medial prefrontal cortex (BA 11)	8	46	−19	4.147
R Precentral gyrus (BA 6)	59	−10	37	4.080
R Parahippocampal gyrus (BA 30)	20	−43	2	4.939
L Superior temporal gyrus (BA 21)	−71	−43	2	4.293
L Superior temporal gyrus (BA 38)	−63	11	−11	4.194
R Superior temporal gyrus (BA 22)	59	−54	14	3.826
R Lingual gyrus (BA 18)	12	−74	−6	7.414
L Cuneus (BA 18)[b]	−20	−88	30	5.583
L Cerebellum	−40	−40	−22	7.251
TR 4 (6–8 s after stimulus onset)				
L Medial prefrontal cortex (BA 10)	−8	58	1	5.047
R Medial prefrontal cortex (BA 10)	12	59	12	4.680
R Inferior frontal gyrus (BA 44)	48	9	22	5.895
L Precentral gyrus (BA 3)	−63	−17	41	4.511
R Precentral gyrus (BA 4)	24	−24	68	4.806
R Precentral gyrus (BA 4/6)	44	−9	52	4.581
L Cingulate gyrus (BA 31)	−12	−13	45	4.459
L Putamen	−28	−4	−7	6.020
R Hippocampus	20	−35	−2	5.759
L Middle temporal gyrus (BA 21)	−55	−27	−2	5.987
R Middle temporal gyrus (BA 21)	63	−8	−6	8.228
L Postcentral lobule (BA 40)	−51	−36	61	4.213
L Paracentral lobule (BA 5)	−1	−29	46	4.213
L Posterior cingulate (BA 31)[c]	−12	−65	22	6.581
R Inferior parietal lobule (BA 40)	44	−36	57	3.876
R Cuneus (BA 17)	8	−81	11	8.477
L Cerebellum	−36	−44	−18	5.561
R Cerebellum	36	−48	−21	6.809
TR 5 (8–10 s after stimulus onset)				
R Anterior cingulate gyrus (BA 24)	4	2	40	5.211
L Hippocampus	−32	−17	−19	4.492
L Paracentral lobule (BA 5)	−12	−25	49	4.073
R Precuneus (BA 7)[c]	20	−71	51	7.402
R Fusiform gyrus (BA 20)	40	−32	−15	4.651
L Lingual gyrus (BA 17)	−12	−85	4	3.852
R Lingual gyrus (BA 19)	20	−39	−1	5.188
R Middle occipital gyrus (BA 19)	55	−73	7	5.068
L Cerebellum	−40	−40	−22	4.153
R Cerebellum	16	−56	−38	5.394
TR 6 (10–12 s after stimulus onset)				
R Middle frontal gyrus (BA 6)	28	6	44	4.545
R Anterior cingulate gyrus (BA 24)	4	2	40	4.533
R Putamen	16	11	−4	3.944
R Amygdala	28	−8	−13	4.182
R Parahippocampal gyrus (BA 27)	20	−35	−2	4.681
R Middle temporal gyrus (BA 22)	55	−31	5	4.253
L Cingulate (BA 31)	−4	−29	42	5.852
L Precuneus (BA 7/31)[b]	−20	−57	29	5.273
L Inferior parietal lobule (BA 40)	−40	−36	50	4.103
R Inferior parietal lobule (BA 40)	59	−37	42	4.999
L Fusiform gyrus (BA 19)	−44	−74	−10	4.234
R Fusiform gyrus (BA 37)	48	−63	−10	4.925
R Lingual gyrus (BA 19)	20	−66	0	3.837
R Cuneus (BA 17)	8	−85	8	8.916
R Superior occipital gyrus (BA 19)	32	−84	23	5.753
L Middle occipital gyrus (BA 18)	−28	−89	−2	4.751
R Middle occipital gyrus	36	−81	8	4.144
R Inferior occipital gyrus (BA 19)	36	−82	−6	3.683
L Cerebellum	−8	−67	−10	5.270
R Cerebellum	32	−55	−7	6.226

Note: Activations are reported for each 2 s TR. All activations reported survive a threshold of $p < .0002$ (bootstrap ratio of 3.7) and an extent threshold of 5 voxels ($4 \times 4 \times 4\,mm^3$). For each cluster of activation, the Talairach co-ordinates of the maximally activated voxel is reported (with the exception of the MTL), as indicated by the highest bootstrap ratio. BA = Brodmann area; L = left; R = right.

[a] The bootstrap ratio is the parameter estimate for that voxel over its standard error and is proportional to a *z* score.

[b] This cluster is bilateral and also encompasses bilateral retrosplenial cortex, precuneus and cuneus.

[c] This cluster bilateral and also encompasses bilateral posterior cingulate, retrosplenial cortex, precuneus and cuneus.

Table 4
Co-ordinates of regions associated with all three autobiographical event tasks from *latent variable 2.1* of the non-rotated PLS analysis.

Brain region	Co-ordinates			Bootstrap ratio[a]
	x	y	z	
TR 2 (2–4 s after stimulus onset)				
L Medial prefrontal cortex (BA 11/10)[b]	−8	46	−19	7.748
L Superior frontal gyrus (BA 10)	−12	67	11	5.557
L Middle frontal gyrus (BA 46)	−48	20	21	8.962
L Middle frontal gyrus (BA 11)	−32	34	−19	7.089
R Middle frontal gyrus (BA 11)	32	34	−19	4.867
L Precentral gyrus (BA 4)	−32	−13	49	4.099
L Putamen	−28	−12	1	4.485
R Caudate	16	16	10	4.372
L Red nucleus/thalamus (medial dorsal nucleus)	−8	−23	−2	5.261
R Thalamus (anterior medial nucleus)	4	−8	4	4.118
L Hippocampus	−24	−13	−20	6.193
R Hippocampus/parahippocampal gyrus (BA 28)	24	−20	−19	7.699
L Middle temporal gyrus (BA 21)	−63	−1	−17	7.673
R Middle temporal gyrus (BA 21)	51	−9	−16	6.530
L Middle temporal gyrus (BA 21)	−63	−39	−1	6.970
L Middle temporal gyrus (BA 39)	−48	−65	29	9.216
R Middle temporal gyrus/angular gyrus (BA 39)	44	−57	25	5.926
R Posterior cingulate (BA 23)[c]	1	−53	21	12.103
L Inferior parietal lobule (BA 40)	−44	−64	44	9.364
L Fusiform gyrus (BA 20)	−32	−40	−15	6.725
L Lingual gyrus (BA 18)	−12	−54	6	12.973
R Lingual gyrus (BA18)	12	−50	3	12.035
L Cuneus (BA 17)	−16	−89	4	5.180
R Middle occipital gyrus/cuneus (BA 18)	24	−86	−6	5.075
L Cerebellum	−4	−51	−18	4.035
R Cerebellum	36	−44	−21	6.178
TR 3 (4–8 s after stimulus onset)				
L Medial prefrontal cortex (BA 11)[c]	−8	50	−16	11.034
L Superior frontal gyrus (BA 8)	−40	18	51	11.522
R Middle frontal gyrus (BA 11)	32	38	−15	5.616
R Middle frontal gyrus (BA 9)	36	17	36	4.360
L Inferior frontal gyrus (BA 47)	−51	35	−8	7.682
R Inferior frontal gyrus (BA 46)	59	32	13	4.640
L Caudate	−16	16	10	7.174
R Caudate	16	8	11	7.165
L Thalamus (medial dorsal nucleus)	−8	−15	4	4.774
L Hippocampus	−24	−13	−20	5.807
R Hippocampus/parahippocampal gyrus (BA 28)	24	−17	−19	5.722
L Parahippocampal gyrus (BA 37)	−32	−39	−11	8.890
L Middle temporal gyrus (BA 21)	−63	−1	−17	8.306
R Middle temporal gyrus (BA 21)	63	−12	−13	4.857
L Middle temporal gyrus (BA 20)	−59	−43	−11	6.183
R Middle temporal/angular gyrus (BA 39)	44	−61	25	7.386
L Precuneus (BA 31)[c]	−16	−53	28	15.216
R Retrosplenial Cortex (BA 29)[c]	8	−50	6	17.072
L Angular gyrus (BA 39)	−48	−64	33	13.666
L Cerebellum	−20	−45	−38	7.157
R Cerebellum	40	−40	−25	5.670
TR 4 (6–8 s after stimulus onset)				
L Medial prefrontal cortex (BA 10/11)[b]	−8	42	−19	11.690
R Superior frontal gyrus (BA 9)	8	52	31	4.227
L Middle frontal gyrus (BA 8)	−40	18	43	8.545
R Middle frontal gyrus (BA 21)	28	10	36	5.296
L Inferior frontal gyrus (BA 47)	−51	31	−8	9.666
R Inferior frontal gyrus (BA 47)	55	27	−1	7.622
L Precentral gyrus (BA 4)	−32	−20	60	6.084
L Lateral globus pallidus	−20	−4	8	8.882
R Putamen	16	8	7	6.870
R Thalamus (pulvinar)	24	−35	5	4.103
L Hippocampus	−24	−20	−16	8.608
R Hippocampus	20	−20	−16	9.110

Table 4 (*Continued*)

Brain region	Co-ordinates			Bootstrap ratio[a]
	x	y	z	
R Parahippocampal gyrus (BA 36)	24	−32	−15	6.843
L Middle temporal gyrus (BA 21)	−59	−5	−17	8.695
R Middle temporal gyrus (BA 21)	55	−9	−16	5.092
R Inferior temporal gyrus (BA 20)	40	−13	−33	5.718
L Middle temporal gyrus/angular gyrus (BA 39)	−48	−65	29	9.609
R Middle temporal gyrus/angular gyrus (BA 39)	48	−61	29	7.510
L Postcentral gyrus (BA 3)	−51	−21	38	4.905
L Precuneus (BA 7)[c]	−8	−53	32	11.253
R Posterior Cingulate (BA 29)[c]	8	−50	6	18.499
L Fusiform gyrus (BA 20)	−44	−21	−23	11.779
R Cuneus (BA 18)	20	−101	5	4.791
L Lingual gyrus	−28	−97	−5	6.934
TR 5 (8–10 s after stimulus onset)				
L Superior frontal gyrus (BA 8)	−40	18	47	14.306
R Inferior frontal gyrus (BA 45)	51	27	2	5.993
R Anterior cingulate (BA 24)	8	2	40	4.228
L Precentral gyrus (BA 4)	−32	−20	60	4.548
L Lateral globus pallidus	−20	−4	−3	7.776
R Lateral globus pallidus	16	4	−7	5.817
L Hippocampus	−24	−16	−16	5.290
R Hippocampus/parahippocampal gyrus (BA 28)	20	−17	−19	5.086
R Parahippocampus gyrus (BA 36)	28	−32	−15	5.496
L Middle temporal gyrus (BA 21)	−63	−5	−17	6.099
R Inferior temporal gyrus (BA 20)	40	−13	−33	4.310
L Middle temporal/angular gyrus (BA 39)	−48	−61	25	8.712
R Middle temporal/angular gyrus (BA 39)	48	−61	25	8.531
R Retrosplenial cortex (BA 29)[c]	8	−50	6	12.869
L Fusiform gyrus (BA 37)	−28	−40	−15	9.067
L Cerebellum	−28	−52	−21	4.023
R Cerebellum	12	−87	−29	8.511
TR 6 (10–12 s after stimulus onset)				
L Medial prefrontal cortex (BA 11)[c]	−8	38	−22	7.048
L Middle frontal gyrus (BA 9)	−44	29	35	8.241
R Middle frontal gyrus (BA 8)	20	33	39	5.609
L Inferior frontal gyrus (BA 47)	−48	23	−8	4.782
R Inferior frontal gyrus (BA 45)	55	28	10	4.086
R Inferior frontal gyrus (BA 47)	55	34	−15	5.310
L Putamen	−20	8	11	8.812
R Caudate	12	−7	22	10.528
L Hippocampus	−32	−16	−16	4.274
R Hippocampus/parahippocampal gyrus (BA 35)	20	−20	−16	4.977
L Parahippocampal gyrus (BA 20)	−40	−20	−19	5.920
L Uncus (BA 36)	−20	−9	−30	6.718
L Middle temporal gyrus (BA 21)	−67	−5	−17	5.426
R Superior temporal gyrus (BA 21)	32	10	−27	5.067
R Middle temporal/angular gyrus (BA 39)	51	−61	25	9.406
R Inferior occipital gyrus (BA 18)	32	−94	−15	4.567
R Cerebellum	12	−87	−29	9.306

Note: Activations are reported for each 2 s TR. All activations reported survive a threshold of *p* < .0001 (bootstrap ratio of 4.0) and an extent threshold of 5 voxels (4 mm × 4 mm × 4 mm). For brevity, only the Talairach co-ordinates of the maximally activated voxel within a cluster is reported (with the exception of the MTL), as indicated by the highest bootstrap ratio. BA = Brodmann area; L = left; R = right.

[a] The bootstrap ratio is the parameter estimate for that voxel over its standard error and is proportional to a *z* score.

[b] This medial prefrontal cluster is bilateral.

[c] This medial parietal cluster is bilateral and encompasses the posterior cingulate, retrosplenial cortex, precuneus and cuneus.

activity associated with remembering, and accordingly, the number of regions activated by remembering doubled between TRs 3 and 4. This increase included recruitment of other posterior visuospatial regions, such as bilateral fusiform gyrus (BA 19/20/37) and precuneus (BA 7) as well as bilateral medial prefrontal cortex (BA 10/11; though more extensively on the left), superior and middle temporal gyri (BA 21/22/38), medial temporal lobe (bilateral hippocampus and right amygdala), inferior parietal lobule (BA 40) and cerebellum, right middle/inferior frontal gyri (BA 6/44) and anterior cingulate (BA 24).

Additionally, LV1.2 indicated the presence of some neural overlap between the past-imagine, future-imagine and control tasks (see Fig. 3A and B), in contrast to the past-recall task. The past-imagine and control tasks were somewhat more strongly correlated with this pattern of brain activity than future-imagine task (as indicated by stronger "design scores" in Fig. 3A), and such activity was evident in only very few regions: left inferior frontal gyrus (BA 45/46), right inferior parietal lobule (BA 40) and left superior (BA 10) and medial (BA 9) frontal gyrus.

2.3. Non-rotated PLS analysis—conjunction contrast

2.3.1. Latent variable 2.1

This second PLS analysis tested and confirmed our *a priori* hypothesis of a core network of regions common to all three autobiographical event tasks relative to the control task (*LV2.1*, see Fig. 4A; *p* < .001; singular value = 42.39). The activation associated with constructing autobiographical event peaked during TRs 4 and 5 (Fig. 4B). In contrast, the hrf associated with the control task was still rising by TR 6. Also of note is that the brain scores for the past- and future-imagine tasks are very tightly coupled, almost overlaid, while the past-recall brain score were lower across all TRs, albeit only slightly. However, this slight difference may reflect a neural difference, reflecting perhaps the distinct subsystems associated with imagining and remembering, as identified by the mean-centered PLS.

Consistent with this idea, visual inspection of Fig. 4C reveals that the core network identified by the conjunction analysis contains the majority of regions comprising both the imagining and remembering subsystems. The regions of the core network exhibiting greater activity during the autobiographical event tasks relative to the control task are listed in Table 4 (positive saliences) and shown in warm colors in Fig. 4C. This network included bilateral medial prefrontal cortex (BA 10/11), superior and middle frontal gyrus (BA 8/9/11), inferior frontal gyrus (BA 47), temporal pole (BA 21/38), posterior temporal and angular gyri (21/39), hippocampus, parahippocampal gyrus (BA 28/35/36/37), medial parietal cortex (23/31/7) and cerebellum; left cuneus (BA 17), lingual (BA 18) and fusiform (BA 20) gyri; and right cuneus/middle occipital gyrus (BA 18).

Moreover, the hrfs (Fig. 4D) reveal an interesting pattern differentiating regions that were also associated with the imagining and remembering subsystems in the mean-centered PLS analysis. Specifically, in 'imagining' regions (*LV1.1*), such as the left medial PFC (BA 11), hippocampus and precuneus (BA 31), the past- and future-imagine tasks are associated with greater percent signal change than the past-recall task. However, the reverse pattern is evident in regions associated with remembering (*LV1.2*), such as middle occipital gyrus (BA 18), with the past-recall task activating these regions more so than the imagine tasks.

Given the network of regions associated with the conjunction is nearly identical to the two LVs identified in the mean-centered PLS, it is worthwhile considering why this LV was not identified by the mean-centered PLS analysis. One possible explanation is related to the fact that the sum of the singular values of the set of LVs in the mean-centered PLS (*LV1.1* = 25.55; *LV1.2* = 19.21; sum = 44.76)

is slightly greater than the singular value of this *LV2.1* (42.39). Given that mean-centered PLS searches for the set of effects that explain the most covariance, together *LV1.1* and *LV1.2* satisfies this criterion over *LV2.1*. Moreover, it is possible that within the mean-centered PLS analysis, the optimal least-squares solution required the set of contrasts (*LV1.1, LV1.2*) in order to satisfy the orthogonality requirement, suggesting also that *LV2.1* alone did not satisfy this requirement.

2.4. Comparison with SPM

For the sake of comparison, SPM analyses (using SPM2) were also conducted using the contrasts specified in each significant LV (i.e., Imagined events > Remembered events; Remembered events > Imagined events; a conjunction of all autobiographical events > control task). In all cases, the overall pattern of activity identified by SPM was remarkably similar to that of PLS, with clusters evident in the majority of regions identified by the PLS analyses. For instance, the Imagined > Remembered SPM contrast revealed activity in medial PFC, bilateral MTL, retrosplenial cortex, precuneus and thalamus. The Remembered > Imagined SPM contrast identified occipital activation. However, the patterns of activity evident in SPM did not reach statistical significance (only being evident at *p* < .05, uncorrected), reflecting the increased statistical sensitivity of PLS. This informal comparison is consistent with a published comparison of SPM and PLS (McIntosh et al., 2004). These authors attribute the increased power of PLS over SPM to a number of factors, including the multivariate approach (which is typically more sensitive than univariate analyses, especially in situations where the dependent measures are correlated), as well as the conservative nature of random effects analyses (based on Random Field Theory) and the use in SPM of a canonical hrf (sensitivity is reduced if the voxel's response differs from the canonical hrf).

3. Discussion

3.1. Common activation of the core network during imagining and remembering

The present study was designed to address a number of issues arising from recent neuroimaging studies on remembering the past and imagining the future. One issue concerns the underlying basis for the common activation of the core network during past and future event tasks. In our constructive episodic simulation hypothesis (Schacter & Addis, 2007a, 2007b), we proposed that such common activation reflects the reliance of both past and future events on episodic memory: when remembering, an episodic memory of a past event is retrieved; when imagining, relevant details are gleaned from various episodic memories to furnish the future event simulation. However, it is possible that this common activity actually reflects the retrieval of a single episodic memory during both remembering and imagining; when simulating future events, individuals might simply recast a memory of a past experience as an imagined future event. Previous findings of greater activation of the core network when simulating future events (Addis et al., 2007; Szpunar et al., 2007) could be taken to speak against this possibility, suggesting that constructing future events is a more cognitively demanding process requiring the recombination of details. However, it is also possible that the process of 'recasting' a past event as a future event, rather than simply retrieving it as required in the past condition, also results in a higher degree of core network activity.

The results of the current study provide direct evidence against the possibility that the finding of common past-future activity,

and/or increased future-related activity, is related to the process of recasting past events as future events. Here, we induced participants to engage in a recombination process when imagining events by experimentally recombining details that were randomly selected from the participants' own past events. Post-scan descriptions of the imaginary events generated during the scanner confirmed that subjects were able to recombine the specified person, place and object details extracted from different episodic memories into a coherent representation of an imaginary future or past event. Importantly, the non-rotated PLS analysis of all autobiographical events relative to the control task demonstrated that even when subjects are recombining details to create imagined events, extensive neural overlap between imagining and remembering is evident. Specifically, overlap was evident in all the major components of the core network: medial prefrontal and frontopolar cortex, lateral prefrontal regions (e.g., inferior frontal gyrus), hippocampus, parahippocampal gyrus, lateral and anterior temporal cortex, medial parietal cortex (including posterior cingulate, retrosplenial cortex and precuneus), lateral parietal cortex, lingual and fusiform gyri, the cuneus and cerebellum. Thus, the present data indicate clearly that, consistent with the constructive episodic simulation hypothesis, the core network that subserves remembering is also robustly engaged when individuals *recombine* details from past episodes into imaginary event constructions. Note, however, that a full experimental evaluation of the recasting account would ideally include a condition in which subjects are specifically instructed to recast past experiences as possible future events, which should reveal the key differences between recombining and recasting.

In contrast to our previous findings of extensive past-future overlap arising only during the elaboration phase of the autobiographical event tasks (Addis et al., 2007), here we found neural overlap to be extensive during the construction phase. This difference from our previous finding is not entirely surprising. Unlike our previous study where non-personal cues (nouns) were presented, the use of an experimental recombination procedure in the current study required the use of personal event details as cues. Such personalized cues provide more direct access to episodic information than do the non-personal cues used in our previous study, where participants have to first make the link between a non-personal cue and personal information in episodic memory to even begin the process of retrieving or imagining an event. Therefore, although reaction times are approximately equivalent between the two studies, it is nonetheless likely that in the current paradigm, participants were able to imagine or retrieve personal events more easily than in our previous paradigm. Consistent with this suggestion, other studies using personalized cues have also found activation of the core network early in the trial (Botzung et al., 2008; D'Argembeau, Xue, Lu, van der Linden, & Bechara, 2008). Additionally, we also showed that the neural overlap between these tasks withstands differences in the phenomenological qualities of remembered and imagined events. While previously we found strong neural overlap when past and future events were matched for the level of detail, emotionality and personal significance (not by design but rather chance), we show that the same network is engaged even when remembered events are more detailed, emotional and personally significant than imagined events.

Although all three autobiographical event tasks engaged the core network more than the control task, the responses of regions within the core network to these tasks were not uniform. The hrfs indicated that some regions of the core network responded more strongly to imagining than remembering, while other regions showed the reverse pattern. Consistent with this finding, the mean-centered PLS analysis identified two distinct networks of regions within the core network: the imagining subsystem and the remembering subsystem.

3.2. The imagining subsystem

The *imagining subsystem* comprised regions that were preferentially associated with imagining events in the past or the future. This functional network included extensive aspects of bilateral medial prefrontal cortex, inferior frontal gyrus, medial temporal lobe, polar and posterior temporal cortex, medial parietal cortex and cerebellum. These results show that even when details for participants' imagined events are experimentally recombined, there was greater activation in many regions on the core network for imagining versus remembering. We therefore suggest that this pattern of results reflects the increased cognitive demands related to *recombining episodic details* into an imaginary scenario, as opposed to the *recasting* of an entire past event as a future event.

Interestingly, the findings of this analysis converge with recent work by Kahn and colleagues (Kahn, Andrews-Hanna, Vincent, Snyder, & Buckner, 2008) examining the anatomical networks associated with the hippocampus by analyzing intrinsic functional connectivity (Vincent et al., 2006). They found that different medial temporal regions were associated with two distinct networks, both of which we found active during imagining. First, the body of the hippocampus and the parahippocampal gyrus were part of a network that included medial prefrontal, medial parietal and lateral parietal regions. Interestingly, we found similar regions engaged as part of the imagining subsystem that were also associated with activity in the body of the right hippocampus during TR 2, and the parahippocampal cortex throughout the trial. Second, Kahn et al. report that the anterior hippocampus was connected primarily with the temporopolar cortex, regions that we also found to comprise the imagining events here. Notably, these two regions were not preferentially associated with the remembering subsystem (for further discussion of subsystems within the core network, see Buckner et al., 2008).

The medial temporal lobe components of the imagining subsystem primarily included the anterior right hippocampus, which we previously found to be uniquely active during the construction of future events (Addis et al., 2007). Moreover, in a parametric modulation study, we also found that the anterior hippocampus was responsive to the level of detail in future but not past events (Addis & Schacter, 2008). This pattern is consistent with the idea that the anterior hippocampal region supports relational processing (Chua, Schacter, Rand-Giovannetti, & Sperling, 2007; Davachi, Mitchell, & Wagner, 2003; Jackson & Schacter, 2004; Kirwan & Stark, 2004; Schacter & Wagner, 1999), including the flexible recombination of elements extracted from previously learned associations (Preston, Shrager, Dudukovic, & Gabrieli, 2004). Thus, the present finding of more anterior hippocampal activity during the imagining of scenarios when the flexible use of details extracted from previously encoded memories of past events was experimentally induced further supports the idea that recombination is an important process of simulating events.

3.3. Imagining future versus past events

The second aim of this study was to determine whether regions previously reported as preferentially activated by imagining future events, such as the right frontopolar cortex and hippocampus (Addis et al., 2007), are related mainly to the prospective nature of imagining future events (that is, the requirement to mentally "look ahead" to an event that might occur in one's personal future), or to the imagining process inherent in the future event task. An issue with most previous studies is that these factors have been confounded: the past and future event tasks that have been used differ both with respect to temporal direction (past, future) and process (imagining, remembering). Although one previous study included a

task requiring one to imagine Bill Clinton events, the core network was less activated by this task than by imagining one's personal past or imagining one's personal future (Szpunar et al., 2007). Here, participants imagined past events that had not previously occurred in addition to remembering real past events and imagining future events. The results of the mean-centered PLS analyses indicated that activity we had previously found to be associated with future events appears to reflect the imagining component of the future event task rather than the prospective component. Specifically, here we found that imagining both past and future events relied on the same subsystem—the imagining subsystem. With respect to the hippocampus, these data are consistent with the idea that recombining event details into an imaginary event would be engaged regardless of the temporal direction of the event, consistent with findings from recent research revealing hippocampal engagement when individuals imagine novel but 'atemporal' events that are not located specifically in the past or future (Hassabis et al., 2007a, 2007b).

In the context of these findings, it is interesting to consider, or to reconsider, the role of the anterior medial prefrontal cortex (including the frontal poles) during event simulation. Originally we proposed that activity in this region may support the prospective aspect of future events, such as the representation of intentions (Addis et al., 2007). Okuda et al. (2003) had found frontopolar cortex to be responsive to the amount of intentional information comprising the future events, in addition to a number of lesion and neuroimaging studies linking this region with prospective memory (Okuda et al., 1998; Burgess, Quayle, & Frith, 2001; Burgess, Veitch, de Lacy Costello, & Shallice, 2000) and anticipation of future consequences in decision making (Bechara, Damasio, & Damasio, 2000; Bechara, Damasio, Damasio, & Anderson, 1994). However, our current results indicate that frontopolar cortex was engaged when imagining the future *and* the past. Therefore, this region likely supports a function related to the process of imagining rather than the content or temporal direction of the event per se. One candidate function we have suggested previously is the overall integration of multimodal information from diverse systems, supported by a capacity known as the *episodic buffer* (Schacter & Addis, 2007c). Baddeley (2000) updated his well-known tripartite model of working memory, consisting of a central executive, phonological loop, and visuo-spatial sketchpad, to include a fourth component, the episodic buffer. In the updated model, the central executive is associated with strategic control of processing, whereas the episodic buffer is "a limited capacity system that provides temporary storage of information held in a multimodal code, which is capable of binding information from the subsidiary systems, and from long-term memory, into a unitary episodic representation" (Baddeley, 2000, p. 417). Neuroimaging data indicate that the maintenance of integrated spatial and verbal information in working memory task engages medial prefrontal cortex more so than the maintenance of non-integrated information (Prabhakaran, Narayanan, Zhao, & Gabrieli, 2000). Thus we have suggested that this region may provide the "stage" (see also, Suddendorf & Corballis, 2007) for simulations of imaginary events, holding together the diverse elements compromising such representations. As revealed by the current PLS analysis, anterior medial prefrontal cortex is an integral part of the imagining subsystem, along with other regions involved in the integration of multimodal episodic details, such as the anterior hippocampus. Future work exploring the interactions between the medial prefrontal cortex and hippocampus will enable a better understanding of recombining process integral to imagining episodic events.

Although the second latent variable from the mean-centered PLS analysis primarily described the remembering subsystem, it also revealed a limited number of regions that were associated with the

imagining and control tasks in contrast to remembering task. One such region was the left inferior frontal gyrus, a region previously found to be associated with imagining future events relative to remembering past events (Addis et al., 2007). This region is thought to support semantic generation (Fletcher, Shallice, & Dolan, 2000; Poldrack et al., 1999), including the cue-specification strategies and retrieval of semantic information regarding life events which may be engaged when imagining personal events (Conway et al., 2003). While such processes are likely recruited when imagining both the past and the future, our results also suggest that imagining past events is somewhat more correlated with activity in these regions than imagining future events. It is possible that imagining a past event that never actually happened requires more intensive generative processing; one has to be more imaginative to come up with a unique past event that can fit plausibly into one's past. Moreover, the random experimental recombination of details may have demanded more imaginative work on those past-imagine trials when the participant had to integrate people and places that were not known simultaneously in the past. For example, some trials may have required a participant to imagine a plausible past event that involved their high school auditorium and a friend they later met in college. In contrast, generating an imaginary future event is not subject to the constraints—as the future has not yet happened, one does not have to "fit" their imagined events into a prescribed time course of life events.

Regardless of how such issues are resolved, the present results suggests that in addition to further exploration of the imagining subsystem in simulating future events, investigators should also examine its role in counterfactual thinking, which involves constructing mental representations of alternative versions of past events (e.g., Byrne, 2005; Knight & Grabowecky, 1995; Roese, 1997; Schacter, 2001). People tend to construct counterfactual representations of past events involving negative outcomes and emotions, such as regret or disappointment, imagining how an event could have or should have turned out differently than it did. We suspect that some of the same regions that are important for simulating possible future outcomes also play role in simulating alternative outcomes to actual past events.

3.4. The remembering subsystem

The third aim of this study was to determine whether remembering past events is associated with a distinct pattern of neural activity. Specifically, we predicted that remembering the past should engage the parahippocampal and posterior visual cortices more so than imagining, in line with the fact that memories contain rich contextual and visual information (Greenberg & Rubin, 2003; Rubin & Greenberg, 1998) and often to a greater degree than imagined events (e.g., D'Argembeau & van der Linden, 2004). The finding of a neural signature associated with past and not future events has been inconsistent: some studies report no unique activity (e.g., Addis et al., 2007; Szpunar et al., 2007), while others have identified the medial prefrontal cortex (Botzung et al., 2008; Hassabis et al., 2007a), hippocampus (Botzung et al., 2008) and parahippocampal cortex (Addis & Schacter, 2008; Okuda et al., 2003). The present study, however, is the first of such studies to report that remembering past events is associated with greater recruitment of a *remembering subsystem* than is imagining events. As predicted, this subsystem included posterior visual cortices, such as fusiform, lingual and occipital gyri and cuneus, in addition to regions previously associated with remembering past events (i.e., medial prefrontal, hippocampus and parahippocampal gyrus). The association of posterior visual regions with remembering past events is consistent with the idea of *recapitulation*—that the reactivation of sensory-perceptual and contextual details during retrieval

recruits the neural regions which originally processed such information (e.g., Johnson et al., 2008; Kahn et al., 2004; Wheeler & Buckner, 2004; Woodruff et al., 2005). Moreover, the regions comprising the remembering subsystem found here are consistent with the functional network identified by Kahn et al. (2008) as associated with the posterior medial temporal lobe.

Why might this pattern of activity be evident in the current but not other studies? First, it may be related to the level of detail associated with remembered events. In the fMRI studies by Addis et al. (2007) and Hassabis et al. (2007a), the level of detail was indistinguishable for remembered and imagined events. Moreover, in other studies phenomenological data were not collected, so it is not clear if detail was equated across event types (Botzung et al., 2008; Okuda et al., 2003; Szpunar et al., 2007). However, in the current study, remembered events were rated as significantly more detailed than imagined events, in line with previous behavioral studies (e.g., D'Argembeau & van der Linden, 2004) and the reality monitoring framework (Johnson et al., 1988). Reality monitoring is the process of determining whether retrieved information which was originally internally or externally generated. Johnson and colleagues theorize that the level of perceptual detail comprising an event can indicate whether an event was experienced or imagined, such that more perceptually detailed events are thought to have been previously experienced, and thus externally generated. Rubin (1998) argues that these types of detail can lead individuals to assess memories of past events as accurate and believable. Recent neuroimaging evidence indicates that activity in visual processing regions is associated with attributing a remembered item to previously perceiving an item versus imagining it (Kensinger & Schacter, 2006). While this strategy is concordant with the fact that experienced events tend to be more detailed, it can break down when imagined events are highly detailed (Johnson et al., 1988). However, in the present study, where remembered events were more detailed than imagined events, regions, such as posterior visual and parahippocampal cortices were preferentially engaged during remembering, supporting the retrieval of contextual and visuospatial detail, respectively. This observation implies that if detail were equated across event conditions as in previous studies, or included as a covariate to statistically match event conditions, this effect would be diminished, if not eliminated.

It is also likely that such differences may have not been evident in previous studies because of an inability to detect the effect due to insufficient power and/or differences in the timing of neural activity, as suggested by the findings of Conway et al. (2003). Although their slow-wave ERP study examined *memory* for previously imagined events (rather than the imagining of events) and memory for previously experienced events, they observed timing differences in activity related to their tasks. Specifically, left prefrontal activity associated with imagined events emerged early in the trial during the construction phase (i.e., prior to a button press indicating the subjects had a memory in mind). However, posterior activity in temporal, parietal and occipital electrodes associated with memory for experienced events only emerged later in the trial, around the time of the button press and throughout the 7.5 s elaboration phase. To address these kinds of issues, we specifically employed spatiotemporal PLS, a multivariate analytic approach for neuroimaging data (a) is more powerful than univariate analyses and (b) does not assume a canonical hrf, thus allowing for differences in timing of functional networks (Addis et al., 2004).

In the current study, we found that the imagining and remembering subsystems had somewhat different temporal characteristics. Although we think that these findings should be treated cautiously pending confirmation from other studies, a couple of points seem worth noting. First, the percent signal change data extracted from regions comprising the imagining

subsystem demonstrate that as early as TR 2 (i.e., two to four seconds after stimulus onset) the imagining and remembering tasks were differentiated. In contrast, activity in regions comprising the remembering subsystem is not clearly distinct across the tasks until TR 3. Second, plots of the weighted average of whole-brain activity suggest that while activity in the imagining subsystem peaks at TR 4 and then subsides, the engagement of the remembering subsystem is at a peak throughout TRs 4–6. While these temporal differences are small, they may have resulted in difficulty teasing apart the subsystems with univariate analyses using a canonical hrf.

In summary, by using a novel paradigm in which details from participants' own personal experiences were experimentally recombined for the purpose of imagining past and future events, we were able to address and resolve a number of issues arising from recent work on past and future events. First, even when subjects were required to recombine details, we replicated findings of core network activity common to both remembering and imagining events, and increased activity related to imagining events. These observations provide evidence against the possibility that these results reflect an 'imagining' process whereby participants simply recast past events as future events. Second, we found evidence of distinct subsystems within the core network that are engaged by imagining and remembering. The imagining subsystem, including the anterior hippocampus and extensive medial prefrontal and parietal regions, was engaged both when imagining the future and the past. These data suggest that regions previously found to be associated with future events, including anterior hippocampus, medial prefrontal cortex and inferior frontal gyrus, support processes general to imagining events that are not related specifically to prospection. In contrast, the remembering subsystem included extensive regions of posterior visual cortex, consistent with the rich contextual and visuospatial detail comprising memories of events experienced in the past.

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References

Addis, D. R., McIntosh, A. R., Moscovitch, M., Crawley, A. P., & McAndrews, M. P. (2004). Characterizing spatial and temporal features of autobiographical memory retrieval networks: A partial least squares approach. *Neuroimage, 23*, 1460–1471.

Addis, D. R., & Schacter, D. L. (2008). Effects of detail and temporal distance of past and future events on the engagement of a common neural network. *Hippocampus, 18*, 227–237.

Addis, D. R., Wong, A. T., & Schacter, D. L. (2007). Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. *Neuropsychologia, 45*, 1363–1377.

Addis, D. R., Wong, A. T., & Schacter, D. L. (2008). Age-related changes in the episodic simulation of future events. *Psychological Science, 19*, 33–41.

Baddeley, A. D. (2000). The episodic buffer: A new component of working memory? *Trends in Cognitive Sciences, 4*, 417–423.

Bechara, A., Damasio, H., & Damasio, A. R. (2000). Emotion, decision making and the orbitofrontal cortex. *Cerebral Cortex, 10*, 295–307.

Bechara, A., Damasio, A. R., Damasio, H., & Anderson, S. W. (1994). Insensitivity to future consequences following damage to human prefrontal cortex. *Cognition, 50*, 7–15.

Botzung, A., Dankova, E., & Manning, L. (2008). Experiencing past and future personal events: Functional neuroimaging evidence on the neural bases of mental time travel. *Brain and Cognition*, 66, 202–212.

Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: Anatomy, function, and relevance to disease. The Year in Cognitive Neuroscience. *Annals of the New York Academy of Sciences, 1124*, 1–38.

Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences*, 11, 49–57.

Burgess, P. W., Quayle, A., & Frith, C. D. (2001). Brain regions involved in prospective memory as determined by positron emission tomography. *Neuropsychologia*, 39, 545–555.

Burgess, P. W., Veitch, E., de Lacy Costello, A., & Shallice, T. (2000). The cognitive and neuroanatomical correlates of multitasking. *Neuropsychologia*, 38, 848–863.

Byrne, R. M. J. (2005). *The rational imagination*. Cambridge, MA: MIT Press.

Chua, E., Schacter, D. L., Rand-Giovannetti, E., & Sperling, R. A. (2007). Evidence for a specific role of the anterior hippocampal region in successful associative encoding. *Hippocampus*, 17, 1071–1080.

Clark, J. M., & Paivio, A. (2004). Extensions of the Paivio, Yuille, and Madigan (1968) norms. *Behavior Research Methods, Instruments and Computers*, 36, 371–383.

Clayton, N. S., Bussey, T. J., & Dickinson, A. (2003). Can animals recall the past and plan for the future? *Nature Reviews Neuroscience*, 4, 685–691.

Conway, M. A., Pleydell-Pearce, C. W., Whitecross, S. E., & Sharpe, H. (2003). Neurophysiological correlates of memory for experienced and imagined events. *Neuropsychologia*, 41, 334–340.

D'Argembeau, A., Raffard, S., & van der Linden, M. (2008). Remembering the past and imagining the future in schizophrenia. *Journal of Abnormal Psychology*, 117, 247–251.

D'Argembeau, A., & van der Linden, M. (2004). Phenomenal characteristics associated with projecting oneself back into the past and forward into the future: Influence of valence and temporal distance. *Consciousness & Cognition*, 13, 844–858.

D'Argembeau, A., & van der Linden, M. (2006). Individuals differences in the phenomenology of mental time travel: The effects of vivid visual imagery and emotion regulation strategies. *Consciousness and Cognition*, 15, 342–350.

D'Argembeau, A., Xue, G., Lu, Z. L., van der Linden, M., & Bechara, A. (2008). Neural correlates of envisioning emotional events in the near and far future. *Neuroimage*, 40, 398–407.

Davachi, L., Mitchell, J. P., & Wagner, A. D. (2003). Multiple routes to memory: Distinct medial temporal lobe processes build item and source memories. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 2157–2162.

Dickson, J. M., & Bates, G. W. (2005). Influence of repression on autobiographical memories and expectations of the future. *Australian Journal of Psychology*, 57, 20–27.

Eichenbaum, H. (2001). The hippocampus and declarative memory: Cognitive mechanisms and neural codes. *Behavioural Brain Research*, 127, 199–207.

Fletcher, P., Shallice, T., & Dolan, R. J. (2000). Sculpting the response space—An account of left prefrontal activation at encoding. *Neuroimage*, 12, 404–417.

Geisser, S., & Greenhouse, S. W. (1958). An extension of box's results on the use of the F distribution in multivariate analysis. *The Annals of Mathematical Statistics*, 29, 885–891.

Greenberg, D. L., & Rubin, D. C. (2003). The neuropsychology of autobiographical memory. *Cortex*, 39, 687–728.

Hassabis, D., Kumaran, D., & Maguire, E. A. (2007). Using imagination to understand the neural basis of episodic memory. *The Journal of Neuroscience*, 27, 14365–14374.

Hassabis, D., Kumaran, D., Vann, S. D., & Maguire, E. A. (2007). Patients with hippocampal amnesia cannot imagine new experiences. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 1726–1731.

Hassabis, D., & Maguire, E. A. (2007). Deconstructing episodic memory with construction. *Trends in Cognitive Sciences*, 11, 299–306.

Jackson, O., 3rd, & Schacter, D. L. (2004). Encoding activity in anterior medial temporal lobe supports subsequent associative recognition. *Neuroimage*, 21, 456–462.

Johnson, M. K., Foley, M. A., Suengas, A. G., & Raye, C. L. (1988). Phenomenal characteristics of memories for perceived and imagined autobiographical events. *Journal of Experimental Psychology: General*, 117, 371–376.

Johnson, J. D., Minton, B. R., & Rugg, M. D. (2008). Content dependence of the electrophysiological correlates of recollection. *Neuroimage*, 39, 406–416.

Kahn, I., Andrews-Hanna, J. R., Vincent, J. L., Snyder, A. Z., & Buckner, R. L. (2008). Distinct cortical anatomy linked to subregions of the medial temporal lobe revealed by intrinsic functional connectivity. *Journal of Neurophysiology*, 100, 129–139.

Kahn, I., Davachi, L., & Wagner, A. D. (2004). Functional-neuroanatomic correlates of recollection: Implications for models of recognition memory. *The Journal of Neuroscience*, 24, 4172–4180.

Kensinger, E. A., & Schacter, D. L. (2006). Neural processes underlying memory attribution on a reality-monitoring task. *Cerebral Cortex*, 16, 1123–1126.

Kirwan, C. B., & Stark, C. E. (2004). Medial temporal lobe activation during encoding and retrieval of novel face-name pairs. *Hippocampus*, 14, 919–930.

Klein, S. B., Loftus, J., & Kihlstrom, J. F. (2002). Memory and temporal experience: The effects of episodic memory loss on an amnesic patient's ability to remember the past and imagine the future. *Social Cognition*, 20, 353–379.

Knight, R. T., & Grabowecky, M. (1995). Escape from linear time: Prefrontal cortex and conscious experience. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 1357–1371). Cambrdige, MA: Cambridge University Press.

Lin, F. H., McIntosh, A. R., Agnew, J. A., Eden, G. F., Zeffiro, T. A., & Belliveau, J. W. (2003). Multivariate analysis of neuronal interactions in the generalized partial least squares framework: Simulations and empirical studies. *Neuroimage*, 20, 625–642.

Lobaugh, N. J., West, R., & McIntosh, A. R. (2001). Spatiotemporal analysis of experimental differences in event-related potential data with partial least squares. *Psychophysiology*, 38, 517–530.

McIntosh, A. R., Bookstein, F. L., Haxby, J. V., & Grady, C. L. (1996). Spatial pattern analysis of functional brain images using partial least squares. *Neuroimage*, 3, 143–157.

McIntosh, A. R., Chau, W. K., & Protzner, A. B. (2004). Spatiotemporal analysis of event-related fMRI data using partial least squares. *Neuroimage*, 23, 764–775.

McIntosh, A. R., & Lobaugh, N. J. (2004). Partial least squares analysis of neuroimaging data: Applications and advances. *Neuroimage*, 23(Suppl. 1), S250–263.

Okuda, J., Fujii, T., Yamadori, A., Kawashima, R., Tsukiura, T., Fukatsu, R., et al. (1998). Participation of the prefrontal cortices in prospective memory: Evidence from a PET study in humans. *Neuroscience Letters*, 253, 127–130.

Okuda, J., Fujii, T., Ohtake, H., Tsukiura, T., Tanji, K., Suzuki, K., et al. (2003). Thinking of the future and the past: The roles of the frontal pole and the medial temporal lobes. *Neuroimage*, 19, 1369–1380.

Poldrack, R., Wagner, A. D., Prull, M. W., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1999). Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *Neuroimage*, 10, 15–35.

Prabhakaran, V., Narayanan, K., Zhao, Z., & Gabrieli, J. D. (2000). Integration of diverse information in working memory within the frontal lobe. *Nature Neuroscience*, 3, 85–90.

Preacher, K. J. (2001). Calculation for the chi-square test: An interactive calculation tool for Chi-square tests of goodness of fit and independence [Computer software]. Available from http://www.quantpsy.org.

Preston, A. R., Shrager, Y., Dudukovic, N. M., & Gabrieli, J. D. (2004). Hippocampal contribution to the novel use of relational information in declarative memory. *Hippocampus*, 14, 148–152.

Roese, N. J. (1997). Counterfactual thinking. *Psychological Bulletin*, 121, 133–148.

Rubin, D. C. (1998). Beginnings of a theory of autobiographical remembering. In C. P. Thompson, & D. J. Herrmann (Eds.), *Autobiographical memory: Theoretical and applied perspectives* (pp. 47–67). Mahwah, N.J: Lawrence Erlbaum Associates, Publishers.

Rubin, D. C., & Greenberg, D. L. (1998). Visual memory-deficit amnesia: A distinct amnesic presentation and etiology. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 5413–5416.

Schacter, D. L. (2001). *The seven sins of memory: How the mind forgets and remembers*. Boston and New York: Houghton Mifflin.

Schacter, D. L., & Addis, D. R. (2007a). The cognitive neuroscience of constructive memory: Remembering the past and imagining the future. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 362, 773–786.

Schacter, D. L., & Addis, D. R. (2007b). The ghosts of past and future. *Nature*, 445, 27.

Schacter, D. L., & Addis, D. R. (2007c). On the constructive episodic simulation of past and future events. *Behavioral and Brain Sciences*, 30, 299–351.

Schacter, D. L., Addis, D. R., & Buckner, R. L. (2007). The prospective brain: Remembering the past to imagine the future. *Nature Reviews Neuroscience*, 8, 657–661.

Schacter, D. L., Addis, D. R., & Buckner, R. L. (2008). Episodic simulation of future events: Concepts, data, and applications. The Year in Cognitive Neuroscience. *Annals of the New York Academy of Sciences 1124*, 39–60.

Schacter, D. L., & Wagner, A. D. (1999). Medial temporal lobe activations in fMRI and PET studies of episodic encoding and retrieval. *Hippocampus*, 9, 7–24.

Spreng, R. N., & Levine, B. (2006). The temporal distribution of past and future autobiographical events across the lifespan. *Memory and Cognition*, 34, 1644–1651.

Suddendorf, T., & Corballis, M. C. (1997). Mental time travel and the evolution of the human mind. *Genetic Society General Psychology Monographs*, 123, 133–167.

Suddendorf, T., & Corballis, M. C. (2007). The evolution of foresight: What is mental time travel, and is it unique to humans? *Behavioral and Brain Sciences*, 30, 299–351.

Szpunar, K. K., & McDermott, K. B. (2008). Episodic future thought and its relation to remembering: Evidence from ratings of subjective experience. *Consciousness & Cognition*, 17, 330–334.

Szpunar, K. K., Watson, J. M., & McDermott, K. B. (2007). Neural substrates of envisioning the future. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 642–647.

Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York, NY: Thieme Medical Publishers, Inc.

Tulving, E. (1985). Memory and consciousness. *Canadian Psychologist*, 25, 1–12.

Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review of Psychology*, 53, 1–25.

Vincent, J. L., Snyder, A. Z., Fox, M. D., Shannon, B. J., Andrews, J. R., Raichle, M. E., et al. (2006). Coherent spontaneous activity identifies a hippocampal-parietal memory network. *Journal of Neurophysiology*, 96, 3517–3531.

Wheeler, M., & Buckner, R. L. (2004). Functional-anatomic correlates of remembering and knowing. *Neuroimage*, 21, 1337–1349.

Williams, J. M., Ellis, N. C., Tyers, C., Healy, H., Rose, G., & MacLeod, A. K. (1996). The specificity of autobiographical memory and imageability of the future. *Memory and Cognition*, 24, 116–125.

Williams, J. M., Healy, H. G., & Ellis, N. C. (1999). The effect of imageability and predictability of cues in autobiographical memory. *Quarterly Journal of Experimental Psychology A*, 52, 555–579.

Woodruff, C. C., Johnson, J. D., Uncapher, M. R., & Rugg, M. D. (2005). Content-specificity of the neural correlates of recollection. *Neuropsychologia*, 43, 1022–1032.