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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

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