NeuroImage 57 (2011) 608–616

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Dynamic neural networks supporting memory retrieval

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ARTICLE INFO

Article history:
Received 7 June 2010
Revised 14 April 2011
Accepted 19 April 2011
Available online 30 April 2011

Keywords:
Episodic memory
Autobiographical memory
Retrieval
Large-scale brain network
fMRI
Functional neuroimaging

ABSTRACT

How do separate neural networks interact to support complex cognitive processes such as remembrance of the personal past? Autobiographical memory (AM) retrieval recruits a consistent pattern of activation that potentially comprises multiple neural networks. However, it is unclear how such large-scale neural networks interact and are modulated by properties of the memory retrieval process. In the present functional MRI (fMRI) study, we combined independent component analysis (ICA) and dynamic causal modeling (DCM) to understand the neural networks supporting AM retrieval. ICA revealed four task-related components consistent with the previous literature: 1) medial prefrontal cortex (PFC) network, associated with self-referential processes, 2) medial temporal lobe (MTL) network, associated with memory, 3) frontoparietal network, associated with strategic search, and 4) cinguloopercululum network, associated with goal maintenance. DCM analysis revealed that the medial PFC network drove activation within the system, consistent with the importance of this network to AM retrieval. Additionally, memory accessibility and recollection uniquely altered connectivity between these neural networks. Recollection modulated the influence of the medial PFC on the MTL network during elaboration, suggesting that greater connectivity among subsystems of the default network supports greater re-experience. In contrast, memory accessibility modulated the influence of frontoparietal and MTL networks on the medial PFC network, suggesting that ease of retrieval involves greater fluency among the multiple networks contributing to AM. These results show the integration between neural networks supporting AM retrieval and the modulation of network connectivity by behavior.

Introduction

The brain is intrinsically organized into multiple neural networks that contribute to higher-order cognitive processes through their interaction (Bressler and Menon, 2010; Fuster, 2009; Rubin, 2006). How large-scale brain networks interact to support complex cognitive processes such as autobiographical memory (AM) retrieval is largely unknown. AM retrieval involves strategic search processes that are guided by knowledge about one's self and by current goals, the recovery of memory traces involving a rich sense of re-experience, and monitoring and other control processes (Conway and Pleydell-Pearce, 2000; Norman and Bobrow, 1976). Thus, it is not surprising that recalling memories from our personal past involves a distributed set of brain regions (Cabeza and St. Jacques, 2007; Svoboda et al., 2006) that encompass separate systems, such as those supporting self-reference, memory consolidation and storage, search and goal-related processes (Greenberg and Rubin, 2003; Rubin, 2005, 2006). In the present functional MRI (fMRI) study we investigate the integration between neural networks supporting AM retrieval and the relationship between behavior and neural network dynamics.

Functional neuroimaging studies of AM studies have identified a number of typical regions involved during memory retrieval, including the medial and lateral prefrontal cortices (PFC), lateral and medial temporal lobes (MTL; hippocampus, parahippocampus), ventral parietal cortex, and posterior cingulate cortex (Cabeza and St. Jacques, 2007; McDermott et al., 2009; Spreng et al., 2009; Svoboda et al., 2006). Several studies have also examined the interaction among the brain regions supporting AM retrieval (Addis et al., 2004; Burianova and Grady, 2007; Greenberg et al., 2005; Levine et al., 2004; Maguire et al., 2000; St. Jacques et al., 2011b), with some studies observing that lesions alter these interactions (Addis et al., 2007; Maguire et al., 2001). However, one limitation of previous approaches relying on subtraction paradigms, and task or behavior based multivariate approaches, is that they do not distinguish the coactivation of distinct networks (Friston et al., 1996). Thus, less is known whether the "core network" recruited during AM retrieval actually involves the contribution of multiple networks and their interaction (although see Andrews-Hanna et al., 2010; also see Hassabis et al., 2007).

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doi:10.1016/j.neuroimage.2011.04.039

Functional connectivity analysis of spontaneous blood oxygen level dependent fluctuations during passive resting states has revealed a number of correlated brain regions comprising neural networks (e.g., Damoiseaux et al., 2006; Greicius et al., 2003; Raichle et al., 2001; for reviews see Buckner et al., 2008; Fox and Raichle, 2007) and these networks overlap with structural connections (for a review see Damoiseaux and Greicius, 2009). In particular, four networks have been identified that may contribute to the self-reference, memory, search and goal-related processes important for AM retrieval. First, the medial PFC network comprises dorsal medial PFC, posterior cingulate, and ventral parietal cortices, and is linked to the construction of self-referential simulations (Andrews-Hanna et al., 2010; for a review see Buckner et al., 2008). Second, the MTL network comprises hippocampal, ventral medial PFC, retrosplenial, and ventral parietal cortices, which support memory processes and the construction of mental scenes (Andrews-Hanna et al., 2010; Kahn et al., 2008; Vincent et al., 2006). Together, the medial PFC and MTL networks comprise the default network, the set of brain regions that are coactive during passive resting states (Andrews-Hanna et al., 2010; Buckner et al., 2008), and commonly engaged during AM retrieval, future thinking and theory of mind (e.g., Spreng and Grady, 2010; Spreng et al., 2009). Third, the frontoparietal network, which is similar to the central executive network, comprises lateral PFC, anterior cingulate and inferior parietal regions, and is linked to adaptive cognitive control processes (Dosenbach et al., 2007; Seeley et al., 2007; Vincent et al., 2008), which may support strategic search processes. Fourth, the cinguloopercular network, which is similar to the salience network, comprises frontopolar, anterior insular/frontal operculum, and dorsal anterior cingulate cortices, and is linked to the maintenance of goals (Dosenbach et al., 2007) and the processing of salient events in the environment (Menon and Uddin, 2010; Seeley et al., 2007). Neural networks, however, are not completely segregated from one another but contribute to cognition through the interaction of sparse connections potentially mediated by cortical hubs (Achard et al., 2006; Buckner et al., 2009). Few studies, however, have examined effective connectivity between networks, or the influence of one network on another, and how the connections between these networks are modulated by behavior (although see Spreng et al., 2010; Stevens et al., 2007). In addition, similar analytic techniques applied to task related, as opposed to resting state tasks, find comparable networks and others that correspond to additional cognitive functions involved in AM including visual and auditory processing (Botzung et al., 2010). In the current study we identified multiple networks contributing to AM and we examined how the interaction between these networks was modulated by characteristics of memory retrieval.

Recollection, the ability to retrieve contextual details and to re-experience or relive a past event, is a central feature of AM that distinguishes episodic (e.g., unique) from semantic types of personal memories (e.g., repeated events; Brewer, 1986; Rubin et al., 2003; Tulving, 1983). The ability to mentally time travel or re-experience the personal past is linked to the frontal lobes (Wheeler et al., 1997), and is supported by the recovery of contextual details via posterior brain regions such as the MTL, retrosplenial cortex and lateral parietal cortices (Cabeza and St. Jacques, 2007; St. Jacques and Cabeza, in press; Svoboda et al., 2006). AMs that are richly recollected also tend to be voluntarily retrieved more quickly often via direct or associative retrieval processes (Conway and Pleydell-Pearce, 2000), although longer retrieval times involving qualitatively different generative retrieval processes can elicit recollection (St. Jacques and Cabeza, in press; Svoboda et al., 2006). Thus, it is important to consider the contribution of both recollection and memory accessibility to understand the neural correlates supporting AM retrieval.

To investigate the dynamic interaction between neural networks during AM retrieval and the modulation of network connectivity by recollection and memory accessibility, we used a generic cue method to elicit unprepared memories during fMRI scanning. Participants searched for and constructed AMs, indicated once a memory was formed by a self-paced button press, elaborated on the retrieved memory, and made online ratings including recollection (e.g., Daselaar et al., 2008). The goal of the current study was to examine how spatially extensive whole-brain networks interact. Thus, we employed independent component analysis (ICA; Calhoun et al., 2001b) to distinguish the coactivation of spatially distinct networks contributing to AM retrieval from activation within a single "core network." We then combined the output of the ICA (i.e., the network time-courses) and dynamic causal modeling (DCM; Friston et al., 2003), a method developed by Stevens et al. (2007), to identify interactions between the large-scale neural networks contributing to AM retrieval and the modulation of these connections by both recollection and memory accessibility.

Materials and methods

Participants

There were seventeen (18–35 years of age) participants who were healthy, right-handed and without history of neurological or psychiatric episodes. All participants reported that they were not taking medication known to affect cognitive function. Participants gave written informed consent for a protocol approved by the Duke University Institutional Review Board. One participant was excluded due to symptoms of depression as indicated by scores >13 on the Beck Depression Inventory (Beck et al., 1996). Furthermore, two participants were excluded from the analyses because of problems with completing the task as instructed. Thus, the reported results are based on data from fourteen (7 females; mean age = 24.43, $SD = 3.73$) participants.

Materials

Memory cues consisted of 60 emotionally arousing words selected from the affective norms for English words database (Bradley and Lang, 1999), such that there were 30 positive (valence mean = 7.93, $SD = 0.45$; arousal mean = 5.96; $SD = 0.83$) and 30 negative (valence mean = 2.17, $SD = 0.52$; arousal mean = 6.00; $SD = 1.03$) words that were equally arousing. In order to create auditory cues the words were recorded in a female voice and constrained to an equal duration of 1 s.

Procedure

The procedure was based on Daselaar et al. (2008). During scanning participants were asked to search for and construct autobiographical memories (AMs) triggered by the auditory cue words. Participants were instructed to retrieve an AM with specific spatiotemporal coordinates. They indicated when a specific AM was found by making a response on the button-box and then continued to elaborate on the retrieved event in as much detail as possible for the rest of the trial. Thirty seconds following the onset of the auditory cue participants were given auditory instructions to rate reliving (low to high) associated with the memory and the amount of emotion (negatively arousing to positively arousing) on an 8-point scale. Emotion ratings were included for a separate analysis (St. Jacques et al., 2011a). The order of the ratings was counterbalanced between participants. Rating responses were self-paced (up to 6 s) and separated by at least 0.5 s. Since the ratings were self-paced up to 6 s any remaining time after pressing the button was added to the fixation to ensure that the next trial began on the TR. There were 6 functional runs, with 10 memory cues in each run (5 positive words and 5 negative words), and an inter-trial interval of at least 1.5 to 7.5 s. Participants were instructed to keep their eyes closed for the duration of each run.