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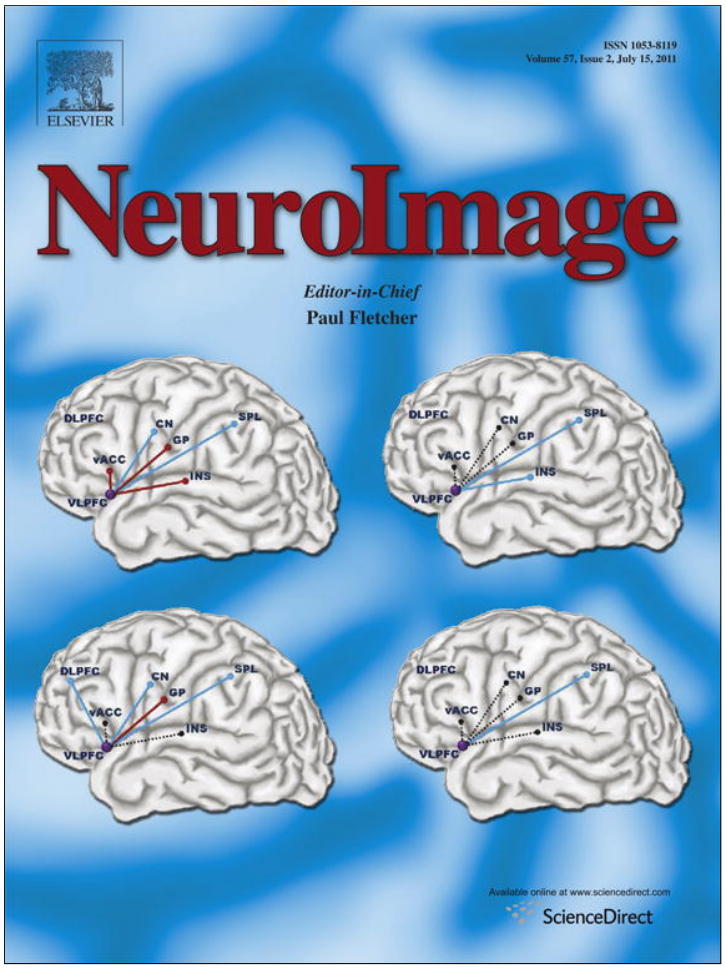

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Dynamic neural networks supporting memory retrieval

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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) cinguloopercular 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.

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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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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.

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fMRI methods

Image acquisition

Scanning was conducted using a 4T GE magnet. Auditory stimuli were presented using headphones and behavioral responses were recorded using an eight-button fiber optic response box (Resonance Technology, Northridge, CA). Head motion was minimized using foam pads and a headband. Anatomical scanning started with a T1-weighted sagittal localizer series, and then 3D fast spoiled gradient echo recalled (SPGR) structural images were acquired in the coronal plane (256^2 matrix, TR = 12.3 ms, TE = 5.4 ms, flip angle = 20°, FOV = 240, 68 slices, 1.9 mm slice thickness). Coplanar functional images were subsequently acquired using an inverse spiral sequence (64^2 image matrix, TR = 2000 ms, TE = 6 ms, FOV = 240, flip angle = 60°, 34 slices, 3.8 mm slice thickness).

Image processing

Image processing and analyses were performed using Statistical Parametric Mapping software in MATLAB (SPM5; Wellcome Department of Imaging Neuroscience). Functional images were corrected for slice acquisition order, realigned to correct for motion artifacts, and then spatially normalized to a standard stereotactic space, using the template implemented in SPM5. Subsequently, the functional images were spatially smoothed using an 8 mm FWHM isotropic Gaussian kernel.

Independent component analysis

ICA was used to determine spatially distinct networks contributing to AM retrieval unbiased with respect to an underlying temporal model (for conventional analysis using a general linear model see St. Jacques et al., 2011a). These spatially independent networks were identified with ICA as implemented in the Group ICA of fMRI Toolbox (GIFT; Calhoun et al., 2001a; Stephan et al., 2010). This method involves performing ICA on functional data concatenated over every participant, creating a series of spatial maps and associated time courses for the group. Back reconstruction is then used to create individual time courses and spatial maps from each participant's functional data. The number of components was estimated to be 30 using the minimum description length criteria. The amplitude of individual time courses and spatial maps were calibrated to percent signal change for comparison across participants. Percent signal change was calculated by regressing component time courses onto the original data at maximal voxels for a component, scaling to reflect percent change from the mean, and then applying additional scaling so that the maximal component voxel contains the maximal percent signal change value. Spatial variability of components across subjects was examined by performing one sample t-tests on these scaled component maps. For subsequent DCM analysis, component time courses were high pass filtered with a cutoff of 128 s and adjusted for confounds (session mean and motion parameters).

Component identification

Components with time courses related to the experimental design were identified using multiple regression using the temporal sorting feature of the GIFT toolbox. AM retrieval operations were modeled by convolving stimuli functions with the canonical haemodynamic response. This model, implemented in SPM5, had separate regressors for the Cue, Construction, Response, Elaboration, and the Ratings in the task. Stimuli functions varied between regressors as either zero duration Dirac delta functions (Cue, Response, and Ratings) or as variable duration box-car functions (Construction and Elaboration) that depend on the time of the motor response. The primary interest of the present study was to determine components associated with construction and elaboration phases of AM retrieval. We conducted a regression analysis to determine β weights associating the components with construction and elaboration phases separately in each participant. One sample t-tests on these β weights showed four components that were significantly related ($p < .001$) to construction and elaboration phases, which were subject to further examination.

Dynamic causal model

To examine the interaction among the spatially distinct networks identified by ICA, the effective connectivity of the four task related components was analyzed using bilinear DCM (Friston et al., 2003) as implemented in SPM5. Unlike other measures of effective connectivity, DCM examines the strength of causal connections by accounting for both the bilinear and dynamic nature of neuronal interactions and the perturbation of this system by experimental manipulation (i.e., driving or modulatory inputs). Utilizing ICA as a feature selection tool for DCM differs significantly from the more commonly utilized volume of interest approach. Typically, several regions related to a process of interest are selected and representative time courses are created by taking the first principal component over all voxels in the volume of interest. Due to current practical constraints a maximum of eight regions can be selected in a DCM. Because of this, it is not possible to model all regions or sub-networks that may interact with key regions of interest, and the occurrence of unmodeled indirect connections is a possibility. As an alternative, ICA can be used to separate functional data into spatially independent networks with corresponding time courses and has the potential to account for what would be unmodeled regions (for a similar method see Stevens et al., 2007).

As there was no a priori hypothesis about the relationship between the components, we created a large model space (for the full model space please see Supplemental Fig. 1) and used Bayesian Model Selection (BMS) as implemented in SPM8 to select an optimal model (Stephan et al., 2009). Components and corresponding timecourses related to the Construction and Elaboration phases were used as inputs, creating a network comprised of four components. Because two of the task-related components were additionally associated with the presentation of the Cue, we included the Cue phase as a possible input in the creation of the model space. Memory retrieval involves external sources that drive activity (i.e., auditory cue), as well as internal sources (i.e., memory retrieval that prompts further recovery of memory during construction and elaboration phases); thus, we considered both external and internal sources as driving inputs in the DCM. Different models were created for all possible permutations of component-phase pairings (e.g., Construction phase as driving input on the medial prefrontal cortex component, etc.), so long as every task phase (i.e., Cue, Construction, Elaboration) had at least one input in the model. Each model tested included all possible intrinsic connections. Further, we used a bilinear interaction term to determine how the context of re-experience and ease of retrieval modulated connectivity for all connections in each model, separately for each phase. We note that modulation here refers to alteration of connectivity between networks. Accessibility was determined by the response time to retrieve an AM as indicated by the button press, and operationalized as those trials that were less than the median response time as calculated separately for each subject. Recollection was determined by participant ratings that followed each trial, and was operationalized as trials that were greater than the median reliving rating as calculated separately within each subject. In the model space, we allowed ease of retrieval to potentially modulate both phases because it could impact both how a memory is constructed and elaborated. For example, a memory that is more accessible may involve less effortful initial construction processes, as well as greater elaboration of the recovered memory. We adopted a similar unbiased approach when examining the impact of reliving by allowing it to modulate both Construction and Elaboration phases. The final model space included 36 models that were estimated for each participant and replicated over the six sessions. The estimated models were included in a random effects BMS procedure to determine the most likely model. We conducted one

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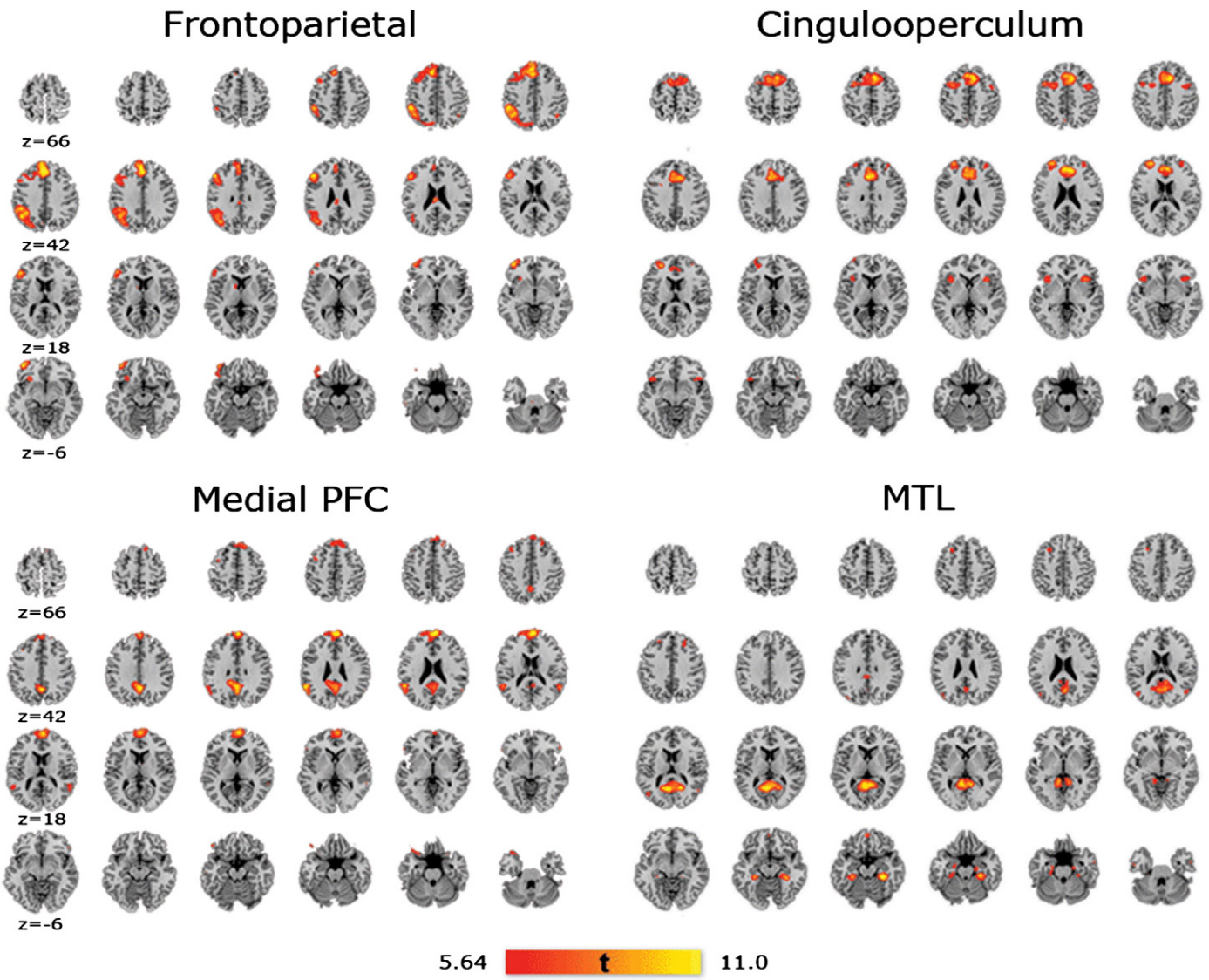

Fig. 1. The task-related independent components supporting AM retrieval. Activation is displayed at FDR corrected $p<.001$, 5 voxels.

sample t-tests ($p<.001$) on each parameter coefficient (intrinsic connectivity, modulatory inputs, and driving inputs) separately on the chosen model for further inference.

Results

Behavioral results

Participants recalled a memory elicited by the cue on 99% of the trials ($SD=.02$), which were associated with an average retrieval speed of 6.55 s ($SD=2.11$) and average reliving ratings of 5.03 ($SD=1.07$). Additionally, retrieval speed and reliving were negatively correlated on each trial within participants (Mean $R=-.29$, $SD=0.18$; $t(13)=5.47$, $p<.001$), showing that AMs associated with reliving were also retrieved more quickly.

fMRI results

Independent component analysis

We used ICA to identify neural networks contributing to construction and elaboration during AM retrieval. ICA revealed four task-related networks ($ps<.001$; see Table 1, Fig. 1; all activations are reported at FDR corrected $p<.001$) corresponding to large-scale networks that have previously been found (Damoiseaux et al., 2006) and which overlap with structural connectivity (Skudlarski et al., 2008). The first component showed a pattern of integrated left-lateralized frontal and parietal cortices, including dorsal mPFC and striatum, which overlaps with the frontoparietal network and similar central executive network (Dosenbach et al., 2007; Seeley et al., 2007; also see Vincent et al., 2008). Interestingly, the frontoparietal network we observed here was left-lateralized, consistent with evidence that this network sometimes splits into left and right hemispheres (Damoiseaux et al., 2006) and is lateralized (Vincent et al., 2008). The second component showed an integrated pattern of bilateral frontopolar cortex and left insula, along with dorsal anterior cingulate, which is consistent with the cinguloopercular network and related salience network (Dosenbach et al., 2007; Seeley et al., 2007; also see Vincent et al., 2008). The third component showed an integrated pattern along the midline consisting primarily of dorsal medial PFC and posterior cingulate, along with bilateral VPC, which is consistent with the medial PFC network (Buckner et al., 2008). Finally, the fourth component showed an integrated pattern of medial temporal lobe (MTL), ventromedial PFC, retrosplenial cortex, and bilateral VPC, which is consistent with the MTL network that supports declarative memory (Vincent et al., 2006).

As indicated by the regression analysis (see Table 2), the frontoparietal and cinguloopercular network were associated with the

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Table 1
Networks supporting autobiographical memory.

Region	BA	x	y	z	Z	Voxels
Medial PFC network						
Dorsal mPFC	9	4	56	23	6.05	446
Ventrolateral PFC	47	−49	34	−15	4.70	40
	45	−56	26	4	4.64	7
	45/47	56	30	−4	5.17	9
Supplementary motor cortex	6	−38	0	57	4.52	13
Premotor cortex	8	−38	23	46	4.49	13
Middle temporal cortex	21	49	8	−38	4.89	10
Posterior cingulate	31	4	−56	38	5.72	203
Lateral parietal cortex	39	−53	−53	30	5.63	74
	39	56	−56	23	5.12	33
MTL network						
Premotor cortex	8	−26	19	49	4.59	14
	8	23	26	42	4.37	6
Ventral mPFC	11	0	53	−15	5.11	12
Hippocampus	–	−23	−15	−19	4.72	7
Posterior parahippocampus	–	−30	−38	−11	5.36	40
	–	30	−38	−15	5.99	68
Retrosplenial cortex	30	−8	−64	15	5.93	345
Posterior cingulate	31	0	−41	34	4.81	6
Lateral parietal cortex	39	−45	−79	23	4.51	22
	39	53	−68	19	4.37	8
Frontoparietal network						
Dorsal mPFC	8/9	0	34	38	6.37	562
Frontopolar cortex	10	−41	49	−4	5.79	152
Dorsolateral PFC	9	−49	23	30	5.76	562
Posterior cingulate	23	−4	−26	27	5.60	18
Lateral parietal cortex	40	−53	−45	49	5.58	433
	39	41	−60	46	5.14	8
Caudate	–	−11	0	11	4.87	8
Cerebellum	–	−8	−30	−30	4.86	8
Cinguloopercular network						
Anterior cingulate	32	8	34	27	6.12	811
Frontopolar cortex	10	−26	49	23	5.54	112
	10	34	41	30	4.70	35
Insula/frontal operculum	13	−38	15	8	4.82	78
Claustrum	–	34	15	4	5.20	64
	6	41	−4	49	4.66	49
Precuneus	7	−4	−75	53	4.61	5

MNI coordinates reported. BA, Brodmann's area.
PFC = prefontal cortex; mPFC = medial prefontal cortex; MTL = medial temporal lobe.

construction phase, whereas medial PFC and MTL networks were associated with both phases (for visualization see Fig. 2). Further, we note that the strength of the association of both the frontoparietal and cinguloopercular networks was greater for the construction phase when compared to the elaboration phase, but there were no differences between these two phases in the other components.

Dynamic causal model

To determine how the neural networks identified by ICA interacted during AM retrieval we employed DCM and a Bayesian Model Selection (BMS) procedure to find the most likely model within a large model space (Stevens et al., 2007). Model selection showed that the most likely model within the model space had an exceeded probability of 0.17, which was on average 7.36 times more likely than other models (see Supplemental Fig. 2). The DCM (see Fig. 3) revealed that construction and elaboration phases of AM retrieval were driving inputs (i.e., produced evoked responses) in the medial PFC network (for coefficient values see Table 3). In contrast, presentation of the generic memory cue evoked activity in the system via the frontoparietal and cinguloopercular networks. The cue coefficient is negative because inhibitory activity originating in frontoparietal and cinguloopercular networks cascades to the neural networks contributing to AM retrieval during processing associated with the cue (i.e., auditory analysis; also see Fig. 2). These results suggest that the medial PFC network drives the construction and elaboration of AMs. There were reciprocal direct connections between some, but not all of the neural networks contributing to AM retrieval. There was a reciprocal positive influence between the frontoparietal and cinguloopercular networks, the frontoparietal and medial PFC networks, and the medial PFC and MTL networks.

Recollection and accessibility of AMs also modulated the connectivity among the neural networks. First, AMs that were more accessible were associated with greater influence of the frontoparietal and MTL networks on the medial PFC network. Accessibility modulated the connectivity between the frontoparietal and medial PFC networks, such that the frontoparietal network influenced activity in the medial PFC network during the construction phase, whereas the medial PFC network influenced the frontoparietal network during elaboration. The latter result suggests that accessibility may also impact how a memory is elaborated, with greater connectivity between medial PFC and frontoparietal networks. However, these effects were not greater for accessibility when compared to recollection. Accessibility was also associated with more bottom-up influence of the MTL on the medial PFC network during construction, and there was a trend showing that this effect was also greater in the context of accessibility vs. recollection, $t\,(14) = -1.37$, $p = .19$. These results suggest that accessibility impacts both construction and elaboration phases of AM. Second, recollection of AMs was associated with greater connectivity between the medial PFC and MTL networks during elaboration, potentially as the result of increased recovery of memory details, and this effect was significantly greater for recollection vs. accessibility, $t\,(14) = 2.04$, $p < .06$.

Post-hoc analysis of nodes common to networks

To identify nodes within each network that were common across the networks identified by the DCM, we employed a conjunction approach to examine the intersection of pairs of networks. An FDR corrected $p < .001$ and a 5 voxel extent threshold for each contrast was used. The results revealed that there was some overlap between the networks (ranging from 0.94% to 8.84% of possible voxels), especially those having a direct influence on one another. Frontoparietal and cinguloopercular networks overlapped in the recruitment of the dorsal anterior cingulate/medial frontal (81 voxels; MNI: 0, 30, 38) near Brodmann Area (BA) 32/9. Medial PFC and frontoparietal networks both recruited lateral parietal cortex (25 voxels; MNI: −53, −53, 30; BA 40), dorsal medial PFC (36 voxels; MNI: −4, 56, 38; BA 9), ventrolateral PFC (5 voxels; MNI: −45, 30, −19; BA 47) and dorsolateral PFC (9 voxels; MNI: −38, 23, 46; BA 9). Finally, medial PFC and MTL networks overlapped in the recruitment of the posterior cingulate (24 voxels; MNI: 0, −68, 34; BA 23/31). In contrast, there was

Table 2
Independent component analysis.

Component	Cue				Construction				Elaboration				Const>Elab	
	M	SD	t (13)	P	M	SD	t (13)	P	M	SD	t (13)	P	t (26)	P
Frontoparietal	−4.46	2.42	−7.15	<.0001	0.37	0.34	4.27	<.001	0.14	0.30	1.77	0.10	2.05	<.05
Cinguloopercular	−2.76	1.37	−7.79	<.0001	0.61	0.47	5.03	<.001	0.19	0.36	2.06	0.06	2.75	0.01
Medial PFC	−0.02	1.66	−0.06	0.96	0.85	0.63	5.19	<.001	0.79	0.32	9.53	<.0001	0.33	0.75
MTL	−1.37	1.50	−3.54	<.01	0.55	0.53	4.08	<.01	0.63	0.31	7.95	<.0001	−0.51	0.62

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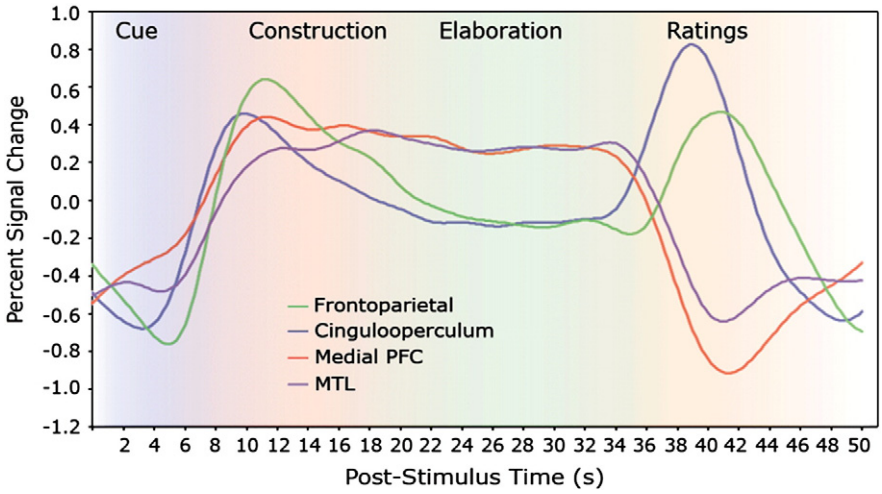

Fig. 2. The time course of each independent component across the AM retrieval task reveals that frontoparietal and cinguloopercular networks contribute to construction, whereas, the medial temporal lobe (MTL) and medial prefrontal cortex (PFC) networks contribute to both construction and elaboration phases.

less overlap among the networks that were not directly connected as identified by the DCM. The MTL and frontoparietal networks showed overlap in a region in the premotor cortex (5 voxels; MNI: −26, 19, 46; BA 8), and the medial PFC and cinguloopercular networks overlapped in premotor (13 voxels; MNI: −38, 0, 57; BA 6) and supplementary motor areas (7 voxels; MNI: 11, 19, 65; BA 6). There was no overlap between the MTL and cinguloopercular networks.

Discussion

The brain is organized into multiple neural networks and higher-order cognitive processes, such as AM, are constructed through their interaction (Fuster, 2009; Rubin, 2005, 2006). Understanding how networks interact to support complex cognitive processes is critical for AM retrieval, because it relies on a distributed set of brain regions (Cabeza and St. Jacques, 2007; Maguire, 2001; Svoboda et al., 2006) that may encompass separate networks. Previous functional neuroimaging studies have identified the brain regions supporting AM (for review see Cabeza and St. Jacques, 2007; St. Jacques and Cabeza, in press; St. Jacques, in press) and have examined the interaction among coactive regions (Addis et al., 2009; Burianova and Grady, 2007; Burianova et al., 2010; Spreng and Grady, 2010; for meta-analysis see Svoboda et al., 2006), but they do not distinguish the co-activation of multiple neural networks supporting AM retrieval. Here we used a

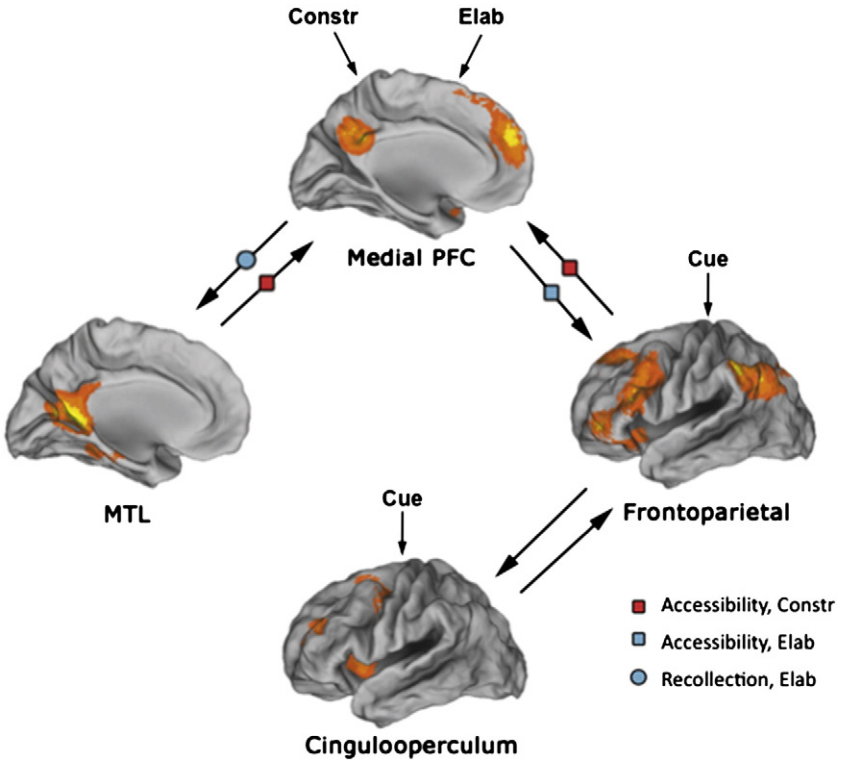

Fig. 3. The dynamic causal model of the integration between neural networks supporting autobiographical memory retrieval. Red square = modulation by accessibility during construction (constr), blue square = modulation by accessibility during elaboration (elab), blue circle = modulation by recollection during elaboration.

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Table 3
Coefficients in the dynamic causal model.

Name	M	SD	t (13)	P
Driving input				
Construction on medial PFC	0.030	0.033	3.36	0.005
Elaboration on medial PFC	0.042	0.024	6.47	<.0001
Cue on frontoparietal	−0.170	0.156	4.08	0.001
Cue on cinguloopercular	−0.230	0.119	7.25	<.0001
Intrinsic connection				
Medial PFC on MTL	0.272	0.142	7.18	<.00001
Medial PFC on frontoparietal	0.096	0.123	2.93	0.012
MTL on medial PFC	0.461	0.191	3.74	<.0001
Frontoparietal on medial PFC	0.108	0.133	3.03	0.010
Frontoparietal on cinguloopercular	0.191	0.112	6.41	<.0001
Cinguloopercular on frontoparietal	0.122	0.125	3.66	0.003
Modulatory input				
Accessibility, construction: MTL on medial PFC	0.019	0.031	2.32	0.035
Accessibility, construction: frontoparietal on medial PFC	0.045	0.063	2.68	0.019
Accessibility, elaboration: medial PFC on frontoparietal	0.049	0.054	3.42	0.004
Recollection, elaboration: MTL on medial PFC	0.117	0.089	4.93	<0.001

PFC = prefontal cortex, MTL = medial temporal lobe.

novel approach to understand these issues (e.g., Stevens et al., 2007) by combining ICA and DCM to examine the interaction among large-scale neural supporting AM retrieval, and the modulation of network connections by behavior. The results of the ICA revealed four task-related components: 1) a left-lateralized frontoparietal network, 2) the cinguolooperculum network, 3) the medial PFC network, and 4) the MTL network. DCM on these neural networks, represented by ICA time courses, revealed two main findings demonstrating the importance of the medial PFC network. First, the medial PFC network drove neuronal activation among the other networks, confirming the integral contribution of this subsystem of the default network to AM construction. Second, connectivity with the medial PFC network and other networks increased when AMs were recollected and accessible, suggesting that this network has a substantial influence on AM retrieval. We discuss these findings below.

Neural networks supporting AM retrieval

Previous functional neuroimaging studies of AM have observed a "core network" of regions that are typically coactive and interact during AM retrieval (Cabeza and St. Jacques, 2007; McDermott et al., 2009; Spreng et al., 2009; Svoboda et al., 2006). The current results suggest that the regions recruited during AM retrieval comprise functionally dissociable networks including the frontoparietal network, cinguolooperculum network, MTL network and medial PFC network.

Two of the networks identified by ICA contributed primarily to the construction phase during AM retrieval. First, we found a frontoparietal network, which is linked to adaptive controlled processes (Dosenbach et al., 2008, 2007; Vincent et al., 2008). Controlled operations that act on memory are associated with the engagement of frontal and parietal cortices (Cabeza et al., 2008; Moscovitch and Winocur, 2002). The predominantly left-lateralized recruitment of the frontoparietal network during construction is consistent with previous functional neuroimaging studies of AM (for a meta-analysis see Svoboda et al., 2006), which observed recruitment of left-lateralized brain regions overlapping with those found here. Moreover, the left-lateralized pattern of the frontoparietal network suggests that it may contribute more specifically to strategic verbal retrieval processes relying on semantic information that guide the construction of a specific AM (Cabeza and St. Jacques, 2007), perhaps as the retrieval cue is processed and elaborated upon. Second, we observed the cinguloopercular network linked to goal-maintenance (Dosenbach et al., 2008, 2007) and to salience processing (Seeley et al., 2007). The finding that frontoparietal and cinguloopercular components were associated with construction rather than elaboration suggests that the initial processes involved in AM elicited by generic cues relies upon additional control and goal-related processes. Conjointly the frontoparietal and cinguloopercular networks may potentially contribute to retrieval mode, cue specification or monitoring and verification operations (for a review see Rugg and Wilding, 2000) that lead to the recovery and validation of memory.

The remaining two components were associated with both construction and elaboration phases during AM retrieval, and included the medial PFC network, which previous research has suggested may support self-referential simulations (for a review see Buckner et al., 2008), and the MTL network associated with declarative memory (Kahn et al., 2008; Vincent et al., 2006) and scene construction (Andrews-Hanna et al., 2010; also see Hassabis et al., 2007). The finding that the medial PFC and MTL networks were sustained across the Construction and Elaboration phases is consistent with the iterative nature of AM retrieval, which would involve multiple construction-memory mappings. The MTL and medial PFC networks overlap with the set of regions engaged by the default network (Greicius et al., 2003; Raichle et al., 2001) and compose separate subsystems (Andrews-Hanna et al., 2010). For example, Andrews-Hanna et al. (2010) identified subsystems of the default network and their relationship to cognitive functions. They found that an MTL subsystem contributed to the construction of mental scenes, whereas a dorsal medial PFC subsystem contributed to self-referential functions. Understanding the role of separable networks contributing to AM retrieval may be particularly important for understanding the component processes of memory and for distinguishing memory from other tasks relying on the same core network (Spreng and Grady, 2010).

Neural network dynamics during AM retrieval and modulation by behavior

The medial PFC network drove neuronal activation within the system during both construction and elaboration of AM. In contrast, the frontoparietal and cinguloopercular networks drove activity during the presentation of the cue. It is interesting that the medial PFC network associated with self-referential processes (Gusnard et al., 2001; Kelley et al., 2002), rather than other networks associated with memory related or controlled processes, was found to initiate and maintain AM retrieval. Self-reference is a critical and defining component of AM, which may importantly modulate the construction of AMs (Cabeza and St. Jacques, 2007; Conway, 2005; Conway and Pleydell-Pearce, 2000; St. Jacques, in press). Consistent with this idea, in a previous fMRI study (Daselaar et al., 2008) we found that medial PFC region were activated to a greater extent during the initial construction of AM. Similarly, Muscatell et al. (2010) directly modulated the extent of self-involvement and found increased effective connectivity with the medial PFC during AM retrieval. Future studies should examine the potential interactions between both self-referential and memory processes on the networks supporting AM retrieval.

We found direct intrinsic connections between some but all of the networks supporting AM. First, there was a reciprocal positive influence between the frontoparietal and cinguloopercular networks, suggesting that these networks directly influence one another during AM retrieval. These results are in line with previous studies suggesting interregional interactions between these top-down control networks, with the frontoparietal network initiating and flexibly adjusting controlled processes that are maintained by the cinguloopercular network (Dosenbach et al., 2008, 2007). Second, there was a reciprocal connection between the frontoparietal and medial PFC networks. Frontoparietal cortex may contribute to the integration

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between externally directed attention and internally directed thought, given that it is anatomically juxtaposed between the dorsal attention and default networks (Spreng et al., 2010; Vincent et al., 2008). Third, there was reciprocal connectivity between the medial PFC and MTL networks, which suggests that AM retrieval relies on the connectivity between these subsystems of the default network (Andrews-Hanna et al., 2010; Buckner et al., 2008).

Neural networks are thought to interact with one another through sparse connections potentially mediated by cortical hubs, which are regions that demonstrate high levels of cortical functional connectivity (Achard et al., 2006; Buckner et al., 2009). Supporting this suggestion, we found greater overlap among the networks with reciprocal connections. For example, there was overlap in the regions comprising the MTL and medial PFC networks, but no overlap between the indirectly connected MTL and cinguloopercular networks. Interestingly, the regions of overlap observed here were generally located in heteromodal association areas that are ideally situated for integrating divergent information across brain systems (Mesulam, 1998), and which have previously been identified as cortical hubs (Achard et al., 2006; Buckner et al., 2009; Hagmann et al., 2008). In particular, we found that the medial PFC and MTL networks overlapped in the recruitment of the posterior cingulate, a region that is part of a midline core interspersed between dorsal medial PFC and MTL subsystems of the default network (Andrews-Hanna et al., 2010; Buckner et al., 2008). Cinguloopercular and frontoparietal networks both engaged the dorsal anterior cingulate/medial PFC, a region that also has been shown to overlap in the salience and executive control networks (Seeley et al., 2007). Further, there was overlap in lateral parietal cortex and dorsal medial PFC between the medial PFC and frontoparietal networks. It will be important for future work to determine how these overlapping nodes potentially contribute to the mechanisms of connectivity between networks.

Memory accessibility and recollection modulated the intrinsic connections among the neural networks, particular with the medial PFC network. AM retrieval occurs via effortful processes that engage top-down control processes or directly through associative retrieval processes involving bottom-up recovery of the memory trace (Conway and Pleydell-Pearce, 2000; Moscovitch, 1992). Here we show that when AMs are more easily retrieved both the top-down and bottom-up processes impinge on the medial PFC network that drives activity within the system during construction. In contrast, the influence of recollection was observed during elaboration via the modulation of the medial PFC network on the MTL network. These results are consistent with evidence that recollection depends upon activation that occurs later during retrieval once a memory is found and can be elaborated upon (Daselaar et al., 2008; for review see St. Jacques and Cabeza, in press). Increased interaction between the MTL network and medial PFC network during elaboration of recollected memories may be associated with additional visualization of the constructed scene as participants were asked to recall additional details during this phase. Interestingly, a direct comparison of modulation by accessibility versus recollection revealed that the connectivity between MTL and medial PFC networks also tended to show context specific effects. The bottom-up influence of the MTL network on the medial PFC network tended to increase for memory accessibility more than the recollective outcome of retrieval, whereas the top-down influence of the medial PFC on the MTL network increased to a greater extent for recollection than memory accessibility. In sum, recollection and memory accessibility uniquely modulated connectivity among some of the networks contributing to AM retrieval.

Conclusions

The findings support the proposal that AM retrieval is supported by the interaction among separable neural networks which have been associated with self-referential, memory, search and goal-directed processes (Rubin, 2006). DCM of the neural networks supporting AM retrieval revealed that the medial PFC network drives neuronal activation, and that reciprocal connectivity with this network increased when memories were accessible and recollected. In sum, the data suggest that the medial PFC network importantly contributes to AM retrieval.

Elucidating neural network dynamics has important implications for understanding and potentially distinguishing higher-order cognitive functions (Spreng et al., 2010). The neural networks identified in the current study during AM retrieval may also support tasks relying on similar component processes, such as envisioning the future and taking another person's perspective (i.e., Theory of Mind; Hassabis and Maguire, 2007; Schacter et al., 2007). Examination of the recruitment of particular neural networks, their interaction, and modulation of behavior may help to further distinguish these tasks. Our findings highlight the important role of large-scale neural networks in the generation of complex cognitive processes.

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