Patterns of Brain Activity Supporting Autobiographical Memory, Prospection, and Theory of Mind, and Their Relationship to the Default Mode Network

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Abstract

■ The ability to rise above the present environment and reflect upon the past, the future, and the minds of others is a fundamentally defining human feature. It has been proposed that these three self-referential processes involve a highly interconnected core set of brain structures known as the default mode network (DMN). The DMN appears to be active when individuals are engaged in stimulus-independent thought. This network is a likely candidate for supporting multiple processes, but this idea has not been tested directly. We used fMRI to examine brain activity during autobiographical remembering, prospection, and theory-of-mind reasoning. Using multivariate analyses, we found a common pattern of neural activation underlying all three processes in the DMN. In addition, autobiographical remembering and prospection engaged midline DMN structures to a greater degree and theory-of-mind reasoning engaged lateral DMN areas. A functional connectivity analysis revealed that activity of a critical node in the DMN, medial prefrontal cortex, was correlated with activity in other regions in the DMN during all three tasks. We conclude that the DMN supports common aspects of these cognitive behaviors involved in simulating an internalized experience. ■

INTRODUCTION

Remembering one's past (autobiographical memory), imagining one's future (prospection), and imagining the thoughts and feelings of others (theory of mind) are similar in that they all involve simulating an experience that is distinct from stimulus-driven behavior (Buckner & Carroll, 2007). Two domains, autobiographical memory and prospection, have shown substantial behavioral and neural overlap. They are correlated in their phenomenological detail (D'Argembeau & Van der Linden, 2004) and temporal distribution (Spreng & Levine, 2006). Furthermore, they appear to share a common set of active brain areas (Addis, Wong, & Schacter, 2007; Szpunar, Watson, & McDermott, 2007; Okuda et al., 2003). Focal lesions to the medial-temporal lobes have resulted in co-occurring deficits in memory and imagining novel scenarios (Hassabis, Kumaran, Vann, & Maguire, 2007; Tulving, 1985).

Autobiographical memory, prospection, and theory of mind are also interrelated (Perner, 2000; Suddendorf & Corballis, 1997). Simulation-based accounts of theory-of-mind resemble the process of remembering one's past and imagining one's future. Theory-of-mind reasoning can involve imagining the mindset of others and simulating their experience in order to understand their internal states (Blakemore & Decety, 2001). In all three instances, the individual must recreate an experience outside of their personal present moment (Buckner & Carroll,

2007). This trio of abilities emerges at the same time developmentally, at about 3.5 years of age (Perner, Kloo, & Gornik, 2007; Suddendorf, 1999). Autobiographical memory and theory of mind are not necessarily mutually dependent in adults, however, as shown in two patients with retrograde amnesia who performed well on theory-of-mind tasks (Rosenbaum, Stuss, Levine, & Tulving, 2007). Nevertheless, a quantitative summary of multiple independent observations has found substantial neural overlap between these three cognitive domains (Spreng, Mar, & Kim, 2009). To date, no study has directly tested the idea of common neural underpinnings for autobiographical memory, prospection, and theory-of-mind reasoning within the same individuals.

There is evidence of overlap between the functional neuroanatomy of these domains and that of the default mode network (DMN; Spreng et al., 2009; Buckner & Carroll, 2007). The DMN is an intrinsically organized core set of brain regions observed to be more metabolically active at "rest." The network includes midline frontal and parietal structures, medial and lateral temporal lobes, and lateral parietal cortex (Buckner, Andrews-Hanna, & Schacter, 2008; Mazoyer et al., 2001; Raichle et al., 2001; Shulman et al., 1997). Behaviorally, the DMN may underlie stimulus-independent thought (McGuire, Paulesu, Frackowiak, & Frith, 1996). Self- and other-attribution judgments have been associated with medial prefrontal cortex (MPFC) activity (Mitchell, Banaji, & Macrae, 2005; Gusnard, Akbudak, Shulman, & Raichle, 2001), a reliable node of the DMN. Therefore, the process of projecting the self into the past,

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the future, or into the minds of others may all rely on the DMN (Buckner et al., 2008; Buckner & Carroll, 2007). A separate network of regions that is "anticorrelated" to the DMN appears to be related to stimulus-driven attention that is common with many cognitive tasks. This network is typically referred to as the task-positive network (Fox et al., 2005). These two networks account for large-scale patterns of covariance across hundreds of neuroimaging studies (Toro, Fox, & Paus, 2008).

In the present study, we tested the hypothesis that adults who are engaged in autobiographical remembering, prospection, and theory-of-mind reasoning would activate the same set of brain regions across all three conditions. This hypothesis is consistent with the idea that the DMN mediates these processes. We used a multivariate method of analysis known as partial least squares (PLS) to identify where activity covaried across the three experimental conditions in the entire brain, and to see if this pattern was consistent with the DMN. To provide additional evidence that the DMN, and not the task-positive network, was engaged across the task conditions, we conducted a functional connectivity analysis of brain regions known to be part of these networks (Fox et al., 2005). We did so by examining the correlations of the DMN and task-positive seed regions across the three experimental conditions and the rest of the brain.

METHODS

Participants

fMRI scans of 16 healthy participants (mean age = 25.9 years, SD = 4.0; 5 men; 1 left-handed) were acquired while they engaged in cued autobiographical remembering, prospection, and theory-of-mind reasoning. Participants had normal or corrected-to-normal vision and no history of neurological or psychiatric illness. Years of education averaged 18.0 years (SD = 1.8). Participants gave written informed consent before inclusion in the study, which was approved by the ethics committee of Baycrest Centre.

Stimuli and Procedure

The study comprised three experimental conditions and a sensorimotor control condition. In the experimental conditions, participants engaged in cued autobiographical remembering, prospection, and theory-of-mind reasoning. Four 10-min runs, each consisting of 8 trials of each condition, for a total of 32 trials per condition, were presented and counterbalanced across participants. The study paradigm was designed to match visual input but vary the task demands.

In all experimental trials, a photograph and associated word were used as cues and were presented on the same screen for 4 sec. The 96 photographs were selected from the International Affective Picture System (IAPS: Lang, Bradley, & Cuthbert, 2005). Image valence ranged from positive to neutral to negative while depicting people in various situations. By IAPS standards, the range of images was moderate (without graphic depictions of sex or mutilation): pleasure mean = 5.35 (SD = 1.8), arousal mean = 5.29 (SD = 1.5), and dominance mean = 5.36 (SD = 2.0). Matched for valence, arousal, and dominance, the stimuli were randomized within and unique to each run and were counterbalanced across conditions.

Each photograph contained one or more persons, such as a family around a dinner table. Below the photograph, a related cue word, such as "Family" was displayed. After the 4-sec viewing period, participants were presented with the instruction screen for 10 sec. On the instruction screen, participants were directed to use the photograph and the word as a cue to remember an event, imagine a future event or imagine the thoughts and feelings of someone in the photograph. For example: (A) "Remember a time when you went out with your family" (remembering), (B) "Imagine a time you will go out with your family" (prospection), or (C) "Imagine what the father in the picture was thinking and feeling" (theory-of-mind reasoning). To ensure sufficient time for autobiographical memory retrieval, a 10-sec interval was selected based on electrophysiological evidence (c.f. Conway, Pleydell-Pearce, Whitecross, & Sharpe, 2003). Next, participants rated how clearly they engaged in the recollection or imagining (1 = Very clearly, 2 = Somewhat clearly, 3 = Not clearly at all; see Figure 1).

In the control condition, participants viewed 32 scrambled photographs that were meaningless but matched the experimental photographs for perceptual input. The words "Control Stimulus" were displayed underneath each image (cf. Burianova & Grady, 2007). This was followed by a button press instruction (e.g., "Press the key that corresponds to the letter 'P'."). As in the experimental conditions, responses were made by pressing 1, 2, or 3 on a keypad (e.g., "1 = N, 2 = B, 3 = P"). Responses were recorded using a fiber-optic response pad placed in the participants' right hand. One participant's responses were not recorded.

All participants went through a three-step training session prior to scanning that included instruction, practice, and discussion. Training included an instructional conversation about autobiographical events being unique to time and place, envisaging future scenarios, and imagining the thoughts and feelings of others. After completing five practice trials for each condition, participant compliance was assessed. This included discussing the ability to engage the task for 8 to 10 sec, ease of engagement, and making a clarity judgment at the end of the 10-sec interval. Six participants requested to complete another practice run to clarify what was expected of them. All participants found the task to be easy and a majority spontaneously reported it to be enjoyable after the scanning session.

Image Preprocessing and Analysis

Brain imaging data were acquired with a 3.0-T Siemens scanner with a standard head coil. Anatomical scans

Figure 1. Example of an experimental trial. Participants viewed a photograph for 4 sec. Next, a condition-specific instruction with three clarity ratings was displayed for 10 sec. The intertrial interval (fixation) was 2 sec. In the example, the question relates to the future condition. Other participants may have seen the photograph paired in the autobiographical memory condition with the instruction, "Remember a time you had an intimate moment"; or, the theory-of-mind condition with the instruction, "Imagine what the woman was thinking and feeling." Each photograph was presented only once per participant. Photographs were presented in their original color.
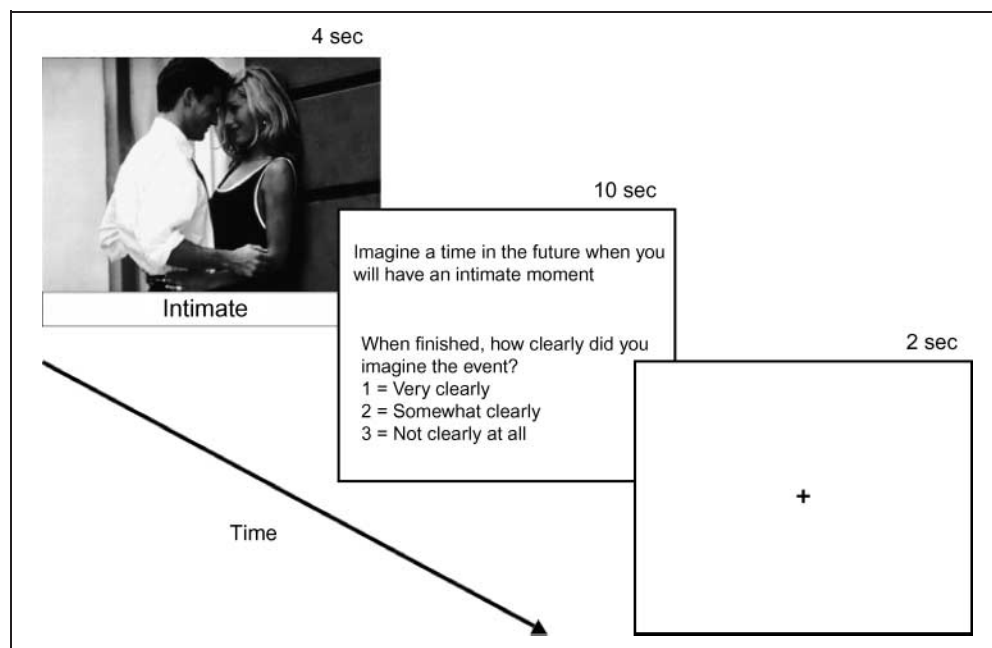
were acquired using a T1-weighted volumetric MRI (TR = 2000 msec, TE = 2.63 msec, 160 axial slices, 1.0 mm thick, FOV = 256 mm). Four runs of BOLD functional scans were acquired with a T2*-weighted EPI pulse sequence (TR = 2000 msec, TE = 30 msec, flip angle = 70°, FOV = 200 mm, 64 × 64 acquisition matrix), consisting of 30 contiguous, 5-mm-thick axial slices.

Images were reconstructed in AFNI (Cox, 1996), where they were first corrected for respiration and heart rate. Slice-timing was corrected to the first slice; next, motion was corrected using a 3-D Fourier transform interpolation using a functional volume that minimized the amount of motion to less than 2 mm. Finally, participants' images were spatially normalized to MNI space and smoothed using a 6-mm FWHM Gaussian filter in SPM5. The resulting voxel size was 4 × 4 × 4 mm.

To analyze the fMRI data, we used spatio-temporal PLS, a multivariate functional neuroimaging analysis tool designed to identify whole-brain patterns of activity that are correlated with task (McIntosh, Chau, & Protzner, 2004). PLS assessed the covariance between brain voxels (BOLD signal) and the experimental design to identify a limited number of components (latent variables, LVs) that optimally relate the two data matrices. This data-driven approach was similar to a principal component analysis and determined whole-brain patterns of activity. Unlike the standard univariate analysis that examines the independent activity of any single voxel, PLS is capable of detecting brain-wide systems that covary with the experimental design. With PLS, the hemodynamic response is not modeled explicitly, in the sense of defining a canonical response; instead, the algorithm determines the response that best characterizes the conditions of interest.

When applying PLS analysis to event-related data, the results provide a set of brain regions that are reliably related to the task conditions at eight poststimulus TRs (16 sec) for each LV (McIntosh et al., 2004). Activity at each time point for each event was normalized to activity in the first TR of the trial, defined here as the onset of the instructions. As we were primarily interested in activity related to the conditions, and not in stimulus-related activity to the cue photographs/words per se, we examined those neuroimages beginning with the instructions to engage in autobiographical remembering, prospection, theory-of-mind reasoning, or the control task. The TRs sampling brain activity during the interval of time spent viewing the photographs were not included in the analysis (see Discussion for potential carryover effects of picture viewing). In PLS, each brain voxel is given a weight, known as a salience (akin to a component loading). This salience is proportional to the covariance of activity with the task contrast at each time point on each LV. Multiplying the salience by the BOLD signal value in that voxel and summing the product across all voxels gives a brain score for each participant for each time point on a given LV (like a component score). These scores can be used to examine differences in brain activity across conditions, as greater activity in brain areas with positive (or negative) saliences on an LV will yield positive (or negative) mean scores for a given condition over each time point. The plots of mean brain scores show the pattern of activity across the brain, expressed over the 16-sec period, and are analogous to hemodynamic response functions typically plotted for individual brain regions.

The significance of each LV was determined by permutation testing (McIntosh, Bookstein, Haxby, & Grady,

1996), using 500 permutations. In a second, independent step, the reliability of the saliences for the brain voxels, characterizing each pattern identified by an LV, was determined by bootstrap resampling to estimate the standard errors for each voxel (Efron & Tibshirani, 1985). For each voxel at each TR, the salience/standard error ratio, or bootstrap ratio (BSR), was calculated and is roughly equivalent to a Z-score. Peak voxels with a BSR greater than four were considered reliable and approximates a p value of 10^{-4}. Clusters containing at least 10 reliable voxels were extracted, and a local maximum for each cluster was defined as the voxel with a BSR higher than any other voxel in a 2-cm cube centered on that voxel. Although most regions showed reliable activations across multiple time points, results are reported from the bootstrap ratios for the fourth and fifth TR (i.e., at 8–12 sec after instruction onset) as a representative index of brain activity in time. In focusing on these early and middle time points, brain activity associated with clarity judgments, made at approximately 9 sec after instruction onset (see Results), would be minimized. Locations of the maxima are reported in the stereotaxic coordinates of MNI space.

In order to directly examine task covariance in neural activity at the voxel level, changes in BOLD signal intensity for each TR were extracted for peak voxels from the task PLS analysis from the first LV in DMN regions (locations specified by Buckner et al., 2008, Table 1).

A common way of assessing activity in the DMN and in the task-positive network is to measure resting state functional connectivity using MPFC and inferior parietal sulcus (IPS) seed regions, respectively (Fox et al., 2005). In order to test the hypothesis that the three experimental conditions are associated with the DMN, and not the task-positive network, we sought to identify functionally connected networks of brain regions associated with the experimental conditions using "seed" PLS (McIntosh, 1999). Seed PLS correlates activity in a given region of interest with activity in all other brain voxels to assess the functional connectivity of this region and then examines how these correlation patterns differ across experimental conditions (McIntosh, 1999). We evaluated whether seeds in MPFC (0, 52, −16) and IPS (24, −64, 48) could reinstate the intrinsically organized default and task-positive networks in a *task-related* functional connectivity analysis. The coordinates from Fox et al. (2005) were transformed from Talairach to MNI using the Lancaster transformation (Lancaster et al., 2007). These seeds were selected because the regions are reliably engaged across conditions (Spreng et al., 2009; Toro et al., 2008) and functionally connected to the respective networks at rest (Fox et al., 2005). In seed PLS, correlation values represent the relationship between activity in a voxel and the whole-brain pattern identified in the analysis. We considered any region to be part of either the DMN or the task-positive network if it was within 2 cm of the average coordinate from a resting state functional

Table 1. Peak Regions Associated with LV1

Location	Hemis	BA	x	y	z	Ratio
Past, Future, Other > Control						
STS/MTG	L	21	−68	−36	−4	9.4
Pre-SMA	LR	8	−4	20	52	8.6
ACC	L	32	−12	32	20	8.0
RSC	L	29	−8	−44	4	7.8
MPFC	L	9	−12	56	44	7.8
MFG	L	6	−44	16	52	7.7
IFG (orbitalis)	L	47	−44	36	−12	7.4
Cerebellum	R	NA	20	−88	−36	7.1
PHC	R	30	32	−60	4	7.1
Putamen	R	NA	20	8	12	6.9
Putamen	L	NA	−20	4	8	6.7
IFG (triangularis)	L	45	−48	28	4	6.6
PCC	LR	23	−4	−48	24	6.4
MFG	L	8	−52	24	36	6.3
MTG	L	21	−64	−12	−16	6.2
ITG	L	20	−60	−12	−28	6.1
IPL	L	39	−40	−76	40	5.9
Frontal pole	L	10	−12	64	24	5.9
Control > Past, Future, Other						
MT+	R	19	28	−60	−16	−15.3
MT+	L	19	−48	−80	8	−12.5
Insula	L	13	−48	0	−4	−11.2
Thalamus	R	NA	20	−28	0	−9.3
Paracentral lobule	L	31	−16	−40	48	−6.5
Cerebellum	L	NA	−8	−72	−44	−6.3
Precentral gyrus	R	4	52	0	28	−6.0
Postcentral gyrus	L	1	−32	−32	72	−5.7

Clusters reported at TR5 with a minimum of 10 voxels with a BSR greater than 4. Hemis = hemisphere; L = left; R = right; BA = Brodmann's area; ACC = anterior cingulate cortex; HC = hippocampus; IFG = inferior frontal gyrus; IPL = inferior parietal lobule; ITG = inferior temporal gyrus; MCC = middle cingulate cortex; MFG = middle frontal gyrus; MOG = middle occipital gyrus; MPFC = medial prefrontal cortex; MT+ = ventral occipital cortex; MTG = middle temporal gyrus; PCC = posterior cingulate cortex; PCu = precuneus; PHC = parahippocampal gyrus; RSC = retrosplenial cortex; SOG = superior occipital gyrus; SMA = supplementary motor area; SMG = supramarginal gyrus; STS = superior temporal sulcus. Coordinates are in MNI space.

connectivity study (Fox et al., 2005) and a large-scale meta-analysis of coactivation patterns from 792 neuroimaging papers (Toro et al., 2008) and within the same neuroanatomical structure (e.g., posterior cingulate cortex).

RESULTS

There were no differences in the proportion of clarity ratings between the experimental conditions (all *ps* > .05). The majority of responses were rated as "very clearly" (75–78%) followed by "somewhat clearly" (16–22%). Participants rated a small proportion of responses (2–5%) as "not clearly at all." The pattern of brain activity remained unchanged when the data from responses that were rated as "not clearly at all" were excluded from the analysis. Therefore, we included all trials for each condition in the fMRI analysis. Response times were significantly faster for the control condition (mean = 2.9 sec, SD = 3.0 sec) than the autobiographical memory (mean = 9.0 sec, SD = 1.4 sec), prospection (mean = 9.4 sec, SD = 1.1 sec), and theory-of-mind (mean = 8.4 sec, SD = 1.5 sec). The experimental conditions did not differ [$F(3, 60) = 66.41$, $p < .001$, post hoc Tukey's HSD $p < .05$].

Autobiographical memory, prospection, and theory-of-mind shared a common pattern of neural activity that accounted for 81.42% of the covariance in the data and was reliably differentiated from the control condition (LV1; $p = .002$; Figure 2). This common pattern included activation of the midline structures in frontal and parietal lobes; left-lateralized activation of inferior frontal gyrus, temporal pole, middle temporal gyrus, superior temporal sulcus and inferior parietal lobule; and activation

of right medial-temporal lobe (Table 1). In contrast, the control task was associated with increased bilateral activity in lateral parietal (including IPS) and occipital cortex (Table 1). Burianova and Grady (2007) observed a similar pattern of activation with the same control task, which is similar to the task-positive network revealed by resting state functional connectivity (Fox et al., 2005), only without dorsolateral prefrontal cortex. A second significant pattern of brain activity dissociated autobiographical memory and prospection from theory-of-mind, accounting for 13.75% of the covariance in the data (LV2; $p = .056$; Figure 3). Autobiographical memory and prospection demonstrated relatively greater frontal and parietal midline activity, along with substantial involvement of the hippocampal formation (Table 2). Theory-of-mind, in contrast, engaged the lateral temporal regions and right temporo-parietal junction (Table 2).

A critical question is whether these brain regions involved in autobiographical memory, prospection, and theory-of-mind are part of the DMN. The pattern of activity associated with LV1 and autobiographical memory, prospection, and theory of mind closely resembles the DMN, although the spatial extent of MPFC is smaller and the overall pattern is less bilateral than previous characterizations of the DMN (e.g., Buckner et al., 2008; Figure 2). Indeed, many areas of activity associated with LV1 and LV2 were located within 2 cm of published values

Figure 2. LV1 shows a functional differentiation between autobiographical memory (Past), prospection (Future), and theory-of-mind (Other) conditions (represented as warm colors) and control (cool colors) at TR4. Left medial and lateral views are on the left. The temporal brain score chart (bottom) conveys changes in brain activity related to task over time. For each LV, mean brain scores (summed scores of activity across the entire brain of each participants and averaged across participants) show the divergence between experimental and control conditions over time (eight 2-sec TRs), and are analogous to hemodynamic response functions typically plotted for individual brain regions.
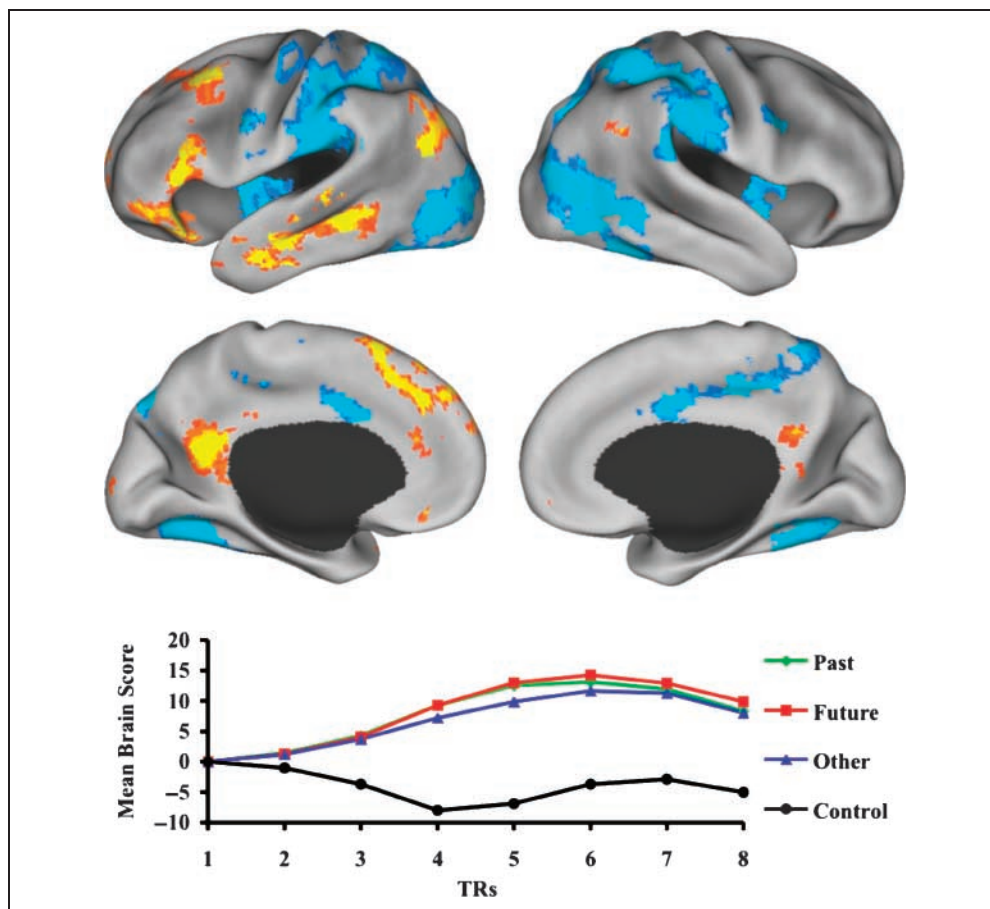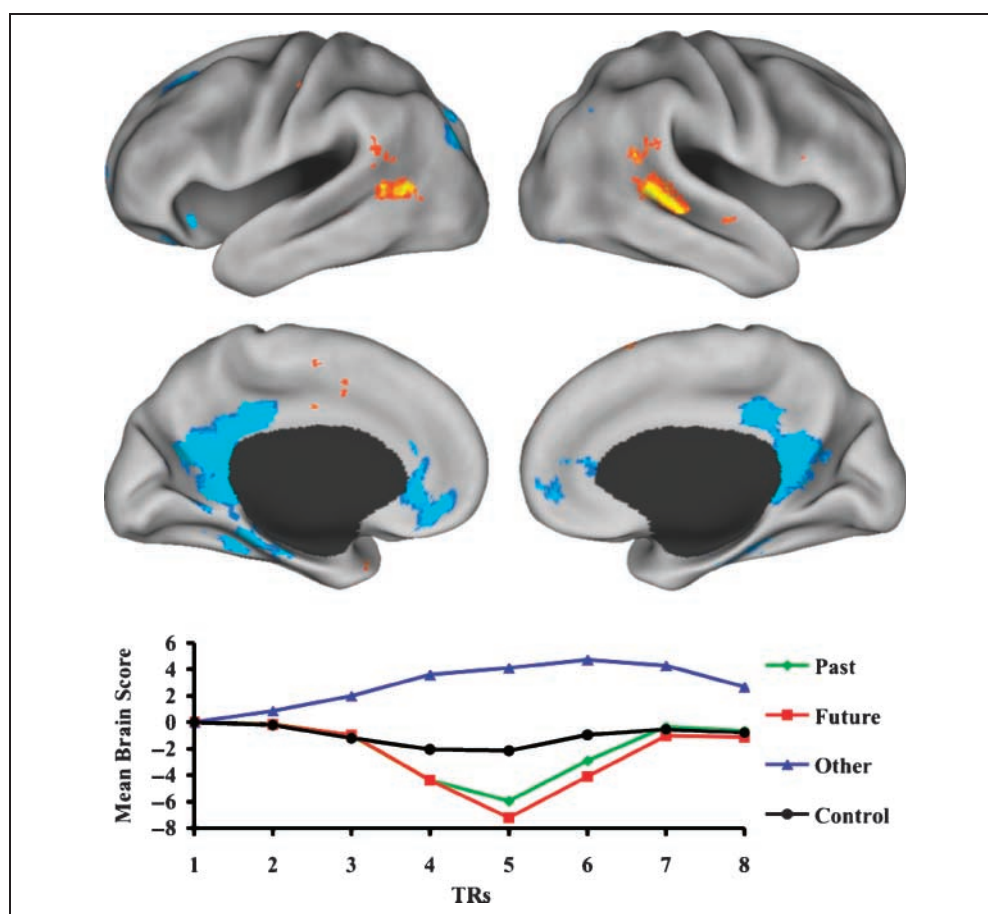
Figure 3. LV2 differentiates autobiographical memory (Past) and prospection (Future) (represented as cool colors) from theory-of-mind (Other) (warm colors), where control is roughly at zero at TR5. Temporal brain scores (bottom) demonstrated maximal differentiation at the fifth TR. Left medial and lateral views are on the left.

for nodes within the DMN (Toro et al., 2008; Fox et al., 2005). The conditions differentially activated DMN for LV2 (Figure 3). Remembering the past or thinking about the future preferentially activated midline and medial temporal lobe structures, whereas theory-of-mind reasoning preferentially activated lateral temporal and parietal regions. Thus, brain activity across the conditions showed overlap, as well as some functional specialization, within the DMN.

Hemodynamic response function plots of peak voxels in DMN regions from LV1 (Figure 4A–I) demonstrated a nearly uniform pattern of covariance, dissociating autobiographical memory, prospection, and theory of mind from control in dorsal and ventral MPFC, bilateral lateral temporal cortex, bilateral inferior parietal lobule, and right parahippocampus. The theory-of-mind condition was not dissociated from control in left parahippocampus (Figure 4G). The contribution of theory of mind to the pattern of activity in posterior cingulate also was less robust (Figure 4I). A recently published formal graph-analytic network analysis of resting state functional connectivity correlations revealed five distinct yet highly interconnected hubs: MPFC, bilateral IPL, and two in posterior cingulate, one rostral (-2, $-38, 36$) and one caudal ($-1, -53, 32$) (Buckner et al., 2009; coordinates in MNI space). Response function plots of these two hubs within posterior cingulate cortex (Figure 4K, L) demonstrated theory of mind covarying with autobiographical memory and prospection in only the caudal region of

posterior cingulate. Both regions reliably contributed to the pattern of activity observed in LV1. However, only the rostral portion was reliably involved in the pattern identified by LV2 (BSR $= -10.3$) and was associated with autobiographical memory and prospection. The caudal region was not (BSR $= -2.4$).

Both seed PLS analyses revealed a significant pattern of functional connectivity ($p = .002$) that was reliable for MPFC (a key node in the DMN) and IPS (a key node in the task-positive network) based on a 99% confidence interval, for all three experimental conditions. In each experimental condition, measures of overall brain activity were significantly correlated with activity in the seed voxel across subjects: in the MPFC seed analysis, $r = .87$ for autobiographical memory, $r = .88$ for prospection, and $r = .74$ for theory-of-mind; in the IPS seed analysis, $r = .81$ for autobiographical memory, $r = .95$ for prospection, and $r = .85$ for theory of mind. The hemodynamic response function plots for the two seed voxels are shown in Figure 4B and J.

If thinking about the past, future, or the thoughts and feelings of others was associated with the DMN then the MPFC seed should be correlated with core regions of the DMN (Buckner et al., 2008) in these three conditions. This was indeed the case—the MPFC seed was correlated with activity in the left frontal pole, left inferior parietal lobule, medial parietal cortex, bilateral medial temporal

Table 2. Peak Regions Associated with LV2

Location	Hemis	BA	x	y	z	Ratio
Other > Past, Future						
STS/MTG	R	21/22	48	−36	−4	8.0
Temporo-parietal junction	R	39	48	−48	20	7.2
STS	L	22	−52	−48	12	6.6
Past, Future > Other						
PCC	LR	31	−4	−36	40	−14.5
PCC	LR	31	−8	−60	24	−12.0
RSC	L	29	−8	−44	8	−11.5
PHC	L	36	−24	−40	−20	−10.7
Fusiform gyrus	L	19	−32	−80	44	−10.1
PHC	R	30	8	−40	4	−9.6
HC	L	NA	−20	−20	−24	−8.1
ACC	LR	32	−4	40	4	−8.1
Frontal pole	L	10	−16	64	12	−7.8
Cerebellum	R	NA	16	−44	−52	−7.3
MFG	L	6	−24	16	52	−7.0
Thalamus	R	NA	4	−8	12	−6.8
Cerebellum	R	NA	44	−72	−44	−6.8
IFG (orbitalis)	L	47	−32	24	−8	−6.6
PHC	R	36	28	−40	−12	−6.4
Head of caudate	L	NA	−12	12	−4	−6.0
Brainstem	L	NA	−4	−20	−28	−5.4

lobes, and bilateral inferior temporal gyri (Table 3). The only DMN regions not included in this pattern of connectivity were the right lateral parietal cortex and right frontal pole. Alternatively, if thinking about the past, future, or the thoughts and feelings of others was associated with the task-positive network, functional connectivity would be expected within the core regions of this network, such as anterior insula, frontal eye fields, supplementary motor area, dorsolateral prefrontal and ventral occipital cortex. However, within the task-positive network, activity in the IPS voxel was only correlated with contralateral IPS region and left ventral occipital cortex (Table 3). No other core regions of this network were significantly correlated. Instead, the IPS seed was functionally associated with some DMN regions, including medial parietal cortex, as well as medial and lateral temporal cortex (Table 3). Both seeds demonstrated functional correlations with regions outside of the networks as well, such as cerebellum, cuneus, and occipital cortex (Table 3). Overall, the seed PLS analyses indicated more engagement of the DMN than the task-positive network during the experimental conditions.

DISCUSSION

In this study, we investigated the neural mechanisms underlying autobiographical memory, prospection, and theory of mind, and determined whether these domains rely upon a pattern of brain activity operating within the DMN. We used PLS analysis of fMRI data to examine whole-brain patterns of activity associated with thinking about the past, the future, and the thoughts and feelings of others. We then used seed PLS to examine the functional connectivity of brain regions that have previously been shown to be functionally associated with the DMN and the task-positive network while participants are at rest (Fox et al., 2005).

Autobiographical memory, prospection, and theory of mind shared a common pattern of brain activity, including midline structures in the frontal and parietal lobes. This is consistent with brain activity related to self- and other-referential thought (D'Argembeau et al., 2008; Johnson et al., 2006; Northoff & Bermpohl, 2004). Additionally, activation was observed in right medial temporal lobe and left-lateralized activation in inferior frontal gyrus, middle frontal gyrus, temporal pole, lateral temporal lobe, and inferior parietal lobule. Notably, we found activation of these DMN regions in the experimental conditions, relative to the control condition, despite the fact that our participants may have reverted back to the default mode after completing the easy and rapidly performed sensorimotor control task. Thus, autobiographical memory, prospection, and theory-of-mind tasks may activate DMN regions over and above spontaneous default activity. The observed regions may support the generative processing related to each of the experimental conditions, including semantic retrieval (Binder, Desai, Graves, & Conant, in press; Martin & Chao, 2001); the recollection of generic scripts that frame the remembered or imagined scene; and the integration of sensorimotor modalities comprising these scenes. Overall, the functional coordination of these heteromodal regions may be sufficient for producing self-relevant stimulus-independent thought.

Autobiographical memory and prospection demonstrated greater frontal and parietal midline activity, relative to theory-of-mind. Notably, there was also substantial involvement of the hippocampal formation for autobiographical memory and prospection: This may be due to the temporal extension of the self and greater recombination of contextualized event details involved in remembering and prospection (Hassabis, Kumaran, & Maguire, 2007; Schacter & Addis, 2007; Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006). In contrast, theory-of-mind reasoning uniquely activated superior temporal sulcus and right temporo-parietal junction, which may be preferentially engaged in mental and biological inferencing more specific to this domain (Gallagher & Frith, 2003; Saxe & Kanwisher, 2003). Alternately, the medial/lateral dissociation may be due to the allocation of attention to internal representations versus external stimuli (Buckner

Figure 4. BOLD signal response function plots. The magnitude of hemodynamic response function change is on the *y*-axis; TRs are on the *x*-axis. Bootstrap ratios (BSR) are from LV1 at TR4. A and C–I are peak LV1 voxels in default mode regions. B is the DMN seed region, contiguous to the peak ventral MPFC voxel (−4, 48, −16), not pictured. As indicated by the BSR, all voxels were highly reliable and remain so over multiple time points; however, some of these regions (B, E, F, G) did not meet the 10-voxel cluster size cutoff for reporting in Table 1. J is the task-positive seed region. K and L are discrete cortical network hubs in rostral posterior cingulate cortex (rosPCC) and caudal posterior cingulate cortex (cauPCC) identified by graph analysis (Buckner et al., 2009). Please refer to Table 1 note for abbreviations.
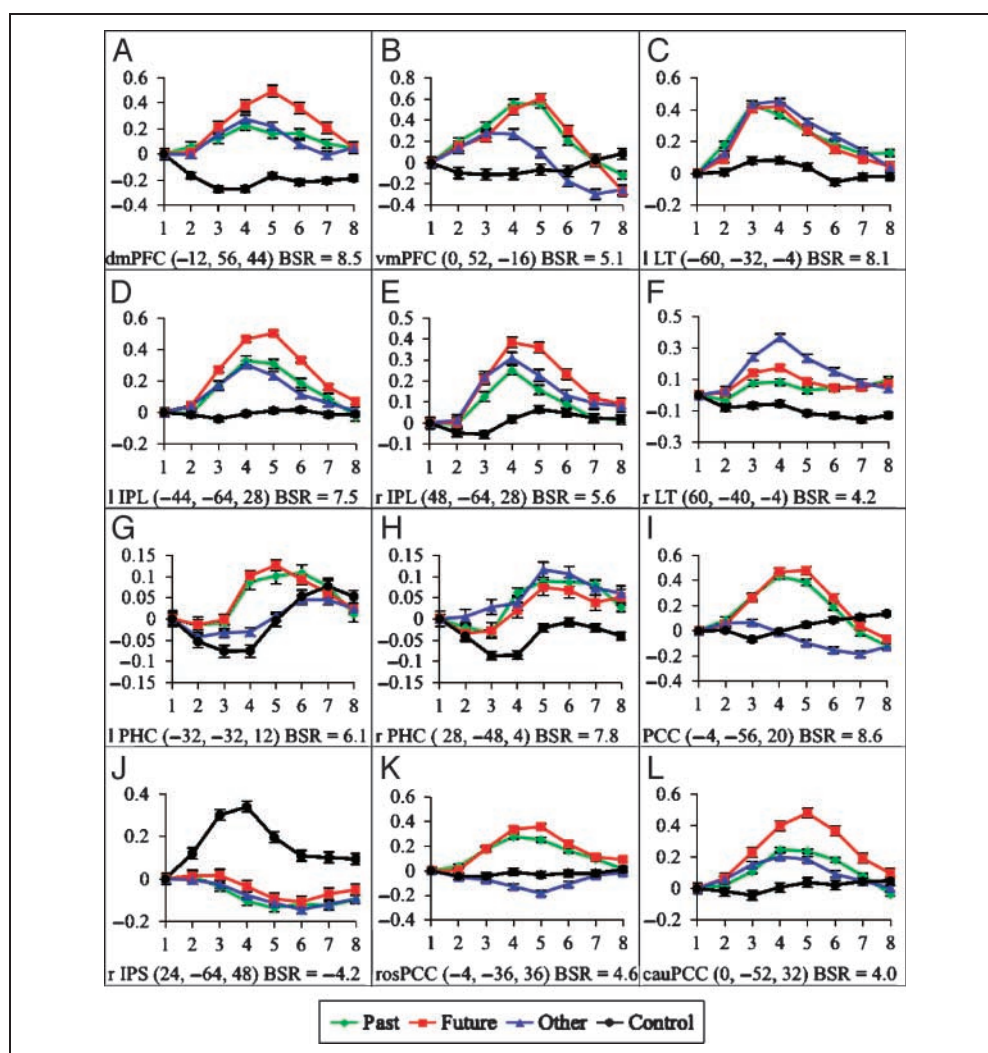
et al., 2008). That is, participants engaged in memory and prospection may have used the cue to access internal representations, whereas in the theory-of-mind condition, participants may have needed to retrieve more information about the photographs in order to imagine the mental states of the depicted people.

Although autobiographical memory, prospection, and theory-of-mind are types of stimulus-independent thought, and appear to engage the DMN, there is little consensus on whether the DMN is actually responsible for these kinds of processing. To further complicate the issue, monkeys show DMN activity (Vincent et al., 2007) but may have little concept of time (Roberts, 2002); in contrast, children with rudimentary autobiographical memory, prospection, and theory-of-mind skills do not have a fully developed DMN (Fair et al., 2008). Studying evolutionary changes to the frontal poles and lateral parietal cortex, and investigating developmental maturation of brain characteristics such as frontal white matter myelination, could resolve these issues eventually. Nevertheless, current functional neuroimaging methods are sufficient for examining the hypothesis that stimulus-independent thought, such as autobiographical memory, prospection, and theory-of-mind, share a common neural basis in humans within the DMN. Our task-related functional connectivity analysis was capable of recapitulating most of the DMN, thereby supporting this hypothesis. Absent was right lateral parietal cortex, which is hypothesized to be involved in heteromodal integration between external salience and internal representations (Corbetta, Patel, & Shulman, 2008), a task demand predominant in only the theory-of-mind condition (LV2). The right frontal pole was also absent from the connectivity pattern, which is surprising considering that damage to this region can result in impaired perspective taking (Stuss, Gallup, & Alexander, 2001) and episodic memory (Wheeler, Stuss, & Tulving, 1997). The task-positive network, however, was not associated with autobiographical memory, prospection, or theory-of-mind. Instead, the results from the seed PLS analyses suggest that IPS, a key node of the task-positive network, can in fact be correlated with areas of the DMN when engaged in structured introspective behaviors, even though the two networks are "anticorrelated" when functional connectivity is assessed during the resting state (Fox et al., 2005). This disparity

Table 3. Functional Connectivity of the MPFC and rIPS Associated with Autobiographical Memory, Prospection, and Theory-of-Mind

	MPFC Seed							IPS Seed					
fc-Region	Hemis	BA	x	y	z	Ratio	fc-Region	Hemis	BA	x	y	z	Ratio
Default Mode Regions													
PCu	LR	7	0	−68	36	7.8	PCu	LR	7	0	−60	44	7.2
PCC	L	31/23	−8	−40	28	12.1							
HC	L	NA	−36	−28	−12	6.6	PHC	L	28	−20	−28	−12	6.9
HC	R	NA	36	−20	−16	8.3	PHC	R	34	32	0	−20	5.8
ITG/MTG	L	20/21	−64	−16	−20	6.3							
ITG	R	20	48	−16	−28	4.9	MTG	R	21	60	−28	−12	9.4
Frontal pole	L	10	−8	56	8	6.4							
IPL	L	39	−48	−60	24	5.3							
Task-positive Regions													
							IPS	L	7	−20	−64	48	14.7
							MT+	L	37	−48	−60	4	6.6
Other Regions													
Cerebellum	L	NA	−16	−60	−16	6.2	Cerebellum	L	NA	−28	−48	−24	6.6
							Cerebellum	R	NA	36	−48	−28	8.3
SOG	LR	17	4	−88	0	7.1	MOG	L	19	−36	−76	20	12.0
Cuneus	LR	18	−4	−84	12	5.5	Cuneus	LR	17	−4	−72	8	8.7
							Cuneus	R	18	24	−60	8	6.5
Precentral gyrus	R	6	52	0	28	8.1	IFG	R	44	36	4	28	7.8
Precentral gyrus	R	6	52	−12	28	6.9	Brainstem	L	NA	−12	−28	−28	6.4
MCC	R	24	8	−16	40	7.8	SMG	L	40	−60	−24	36	5.1
							Lingual gyrus	L	18	−28	−76	−8	5.1

fc-Regions are functionally connected regions in the network. Regions labeled as DMN or task-positive are within 2 cm of published coordinates for this network and within the same brain structure.

suggests that regions comprising the default mode and task-positive networks may not be mutually inhibitory, or may be a consequence of the functional connectivity methodology (such as regressing out global mean signal; Murphy, Birn, Handwerker, Jones, & Bandettini, 2009). However, the absence of a positive association between IPS and the experimental conditions in the task PLS analysis limits strong conclusions.

No previous experiment has directly examined the relations among autobiographical memory, prospection, and theory-of-mind. One study compared cued autobiographical recollection from personal photos against a theory-of-mind type control task where participants imagined scenarios from stranger's photographs, including the thoughts and feelings of people in the photos (Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004). The results from their univariate analysis of autobio-

graphical memory closely resembled the midline and medial-temporal regions found here in LV2.[1] Univariate analysis, however, does not detect the optimal relationship between brain activity and conditions unlike the multivariate analysis that was used in this study. Consistent with studies comparing autobiographical memory and prospection, a common pattern of neural activity is observed (Schacter & Addis, 2007), although some subsystems may differ (Addis, Pan, Vu, Laiser, & Schacter, 2009). Notably, the present work demonstrated common and differential recruitment between autobiographical, prospection, and theory-of-mind. Multivariate methods are not only more sensitive than the standard General Linear Model in detecting distributed patterns of brain activity (McIntosh et al., 2004), but are capable of quantifying the amount of covariance associated with neural events that can be explained by the tasks. We found that the amount of variance in brain

activity shared by the experimental conditions actually was greater than that which differentiated them, relative to the sensorimotor control condition. The shared pattern of neural activity in LV1 and the MPFC seed PLS analyses support the hypothesis that the same network is responsible for the core processing of the experimental tasks. Further, LV2, which accounts for less variance in neural activity, may reveal functional specialization of regions within DMN subsystems. Resting state functional connectivity analysis supports this view. Seed activity in posterior cingulate, medial prefrontal, or lateral parietal cortex are correlated with the entire default mode network (Fox et al., 2005; Buckner et al., 2008). Autobiographical memory and prospection, however, are associated with the hippocampal formation subsystem (Vincent et al., 2006). Further, connectivity with a dorsal MPFC seed region is associated with the theory-of-mind regions (Buckner et al., 2008). Core regions common to autobiographical memory, prospection, and theory-of-mind may support the construction and integration of personally salient information. Subsystems may provide specialized information to the core DMN. This may include information from prior experiences via input from the medial-temporal lobes, as well as elaborated representations of other people's actions and intentions with input from posterior STS and temporo-parietal junction.

The common brain activity across the experimental conditions might simply reflect neural processes driven by the carryover effect of viewing complex photographs and/or making a manual rating in response to a mental event; however, this is unlikely for several reasons. First, we limited the time points included in the analysis to those where self-projection was taking place and not when photos were being viewed. In addition, activity was normalized to the first TR after the photographs were viewed, reducing the impact of the BOLD signal related to prior perception. With spatio-temporal PLS, the progression of BOLD signal change over time is analyzed. In focusing our interpretation on the fourth and fifth TR, the impact of BOLD signal associated with photograph viewing was further reduced, although may still account for some covariance. Second, the shared pattern of brain activation is also unlikely to be related to the clarity ratings to any great extent. Most studies of autobiographical memory include a behavioral rating, such as amount of detail, immediately following the recollective interval. Participant awareness of an impending rating is unlikely to confound the phenomenological experience and associated neural activity of these processes prior to ratings actually being made, although these processes undoubtedly influence the rating itself. The absence of ratings, however, would eliminate a means to assess compliance. Furthermore, in this study, ratings occurred, on average, 9 sec after the participants were instructed to begin recollecting, planning, or thinking about the thoughts and feelings of others. As a result, BOLD signals related to clarity ratings fell outside the interpreted analysis.

Third, Burianova and Grady (2007) used a similar paradigm and found the first LV dissociated experimental conditions (autobiographical, episodic, and semantic memory retrieval) from a sensorimotor control condition identical to the one used here. In their experiment, complex photographs were also viewed and a behavioral rating was made in the experimental conditions. In the control condition, scrambled images were also presented and a manual response was made. Importantly, the regions identified by Burianova and Grady as common across retrieval conditions showed little overlap with the regions identified here as common to autobiographical memory, prospection, and theory of mind. However, both experiments found increased activity across experimental conditions in left lateral inferior and middle frontal gyri (Brodmann's areas 47, 8). These regions are involved in cognitive control (Vincent, Kahn, Snyder, Raichle, & Buckner, 2008; Brass, Derrfuss, Forstmann, & von Cramon, 2005), and thus, are likely to be involved across multiple cognitive domains. Taken together, the evidence from both studies, as well as the high rates of participant compliance (as indicated by the clarity ratings), makes it likely that the shared pattern of covariance (seen after the instructions are presented but before the clarity ratings are made) is related to the shared processes of the experimental conditions themselves.

The current set of analyses provides converging evidence that DMN regions are engaged with specific cognitive behaviors. These behaviors may not be limited to those observed here, but may also include related processes such as moral decision-making (Greene, Sommerville, Nystrom, Darley, & Cohen, 2001), fictional narrative simulation (Mar & Oatley, 2008; Mar, 2004), or mind-wandering (Christoff, Gordon, Smallwood, Smith, & Schooler, 2009; Mason et al., 2007). In order to determine the neural (in)dependence of these processes, however, neuropsychological investigations into co-occurring autobiographical and interpersonal deficits with compromised functional integrity of the midline, and lateral parietal and lateral temporal cortex are also necessary.

Our analyses were designed to investigate the neural mechanisms underlying autobiographical memory, prospection, and theory-of-mind, and to determine if these domains rely upon a pattern of brain activity operating within the DMN. The results provide the first direct evidence to support previous independent observations that projection of the self into the past, the future, or the minds of others engages a common set of brain regions largely overlapping with the DMN (Spreng et al., 2009; Buckner & Carroll, 2007). Task-related functional connectivity analysis revealed reliable correlations within the core regions of the DMN, and only two nodes in the task-positive network, suggesting that the DMN was engaged during our experimental conditions, but not the task-positive network. The present study does not directly compare the experimental tasks with "rest." Although pre- and postscan questionnaires have helped clarify resting state cognition (e.g., Andrews-Hanna, Huang, Reidler, &

Buckner, 2008; Mason et al., 2007), we remain unsure what people do while resting. In order to circumvent this issue, novel techniques and analyses are needed to assess default cognition and its neural associations. For example, one study assessed the overlap between episodic memory and theory-of-mind tasks, and then determined peak activity's relationship with the DMN using resting state functional connectivity analysis (Andrews-Hanna, Saxe, Poulin, & Buckner, 2007). The present set of analyses provides converging evidence that the neuroanatomical correlates of autobiographical memory, prospection, and theory-of-mind are shared and that the DMN is involved in the processing necessary to carry out these specific cognitive behaviors. This sharing of neural resources may allow remembering the past and imagining the future to provide a "long view" in decision-making, over and above stimulus–reward driven behavior, thereby facilitating theory-of-mind and promoting social cooperation (Boyer, 2008).

Acknowledgments

Note

1. During the preparation of this article, we learned of a highly relevant paper by Rabin, Gilboa, Stuss, Mar, and Rosenbaum (2010) who used a very similar paradigm as Gilboa et al., (2004), but included a common baseline to assess conjunction as well as differences between autobiographical memory and theory of mind. Despite different methods, the authors report a striking consistency with the present findings.

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