The Common Neural Basis of Autobiographical Memory, Prospection, Navigation, Theory of Mind and the Default Mode: A Quantitative Meta-analysis

R. Nathan Spreng[1,2], Raymond A. Mar[3], and Alice S. N. Kim[1,2]

Abstract

■ A core brain network has been proposed to underlie a number of different processes, including remembering, prospection, navigation, and theory of mind [Buckner, R. L., & Carroll, D. C. Self-projection and the brain. *Trends in Cognitive Sciences, 11,* 49–57, 2007]. This purported network—medial prefrontal, medial-temporal, and medial and lateral parietal regions—is similar to that observed during default-mode processing and has been argued to represent self-projection [Buckner, R. L., & Carroll, D. C. Self-projection and the brain. *Trends in Cognitive Sciences, 11,* 49–57, 2007] or scene-construction [Hassabis, D., & Maguire, E. A. Deconstructing episodic memory with construction. *Trends in Cognitive Sciences, 11,* 299–306, 2007]. To date, no systematic and quantitative demonstration of evidence for this common network has been presented. Using the activation likelihood estimation (ALE) approach, we conducted four separate quantitative meta-analyses of neuroimaging studies on: (a) autobiographical memory, (b) navigation, (c) theory of mind, and (d) default mode. A conjunction analysis between these domains demonstrated a high degree of correspondence. We compared these findings to a separate ALE analysis of prospection studies and found additional correspondence. Across all domains, and consistent with the proposed network, correspondence was found within the medial-temporal lobe, precuneus, posterior cingulate, retrosplenial cortex, and the temporo-parietal junction. Additionally, this study revealed that the core network extends to lateral prefrontal and occipital cortices. Autobiographical memory, prospection, theory of mind, and default mode demonstrated further reliable involvement of the medial prefrontal cortex and lateral temporal cortices. Autobiographical memory and theory of mind, previously studied as distinct, exhibited the most extensive functional overlap. These findings represent quantitative evidence for a core network underlying a variety of cognitive domains. ■

INTRODUCTION

A single core network has recently been proposed to underlie a number of cognitive domains previously seen as distinct, specifically: (a) remembering, (b) prospection, (c) spatial navigation, and (d) theory of mind (Buckner & Carroll, 2007). The network of brain regions hypothesized to be common to these domains comprise the fronto-polar and anterior midline structures in addition to the medial-temporal lobe, medial parietal, and a lateral posterior parietal region, the temporo-parietal junction. These authors believe that the core network may support self-projection: the ability to mentally project oneself from the present moment into a simulation of another time, place, or perspective. Additionally, the default-mode network (Mazoyer et al., 2001; Raichle et al., 2001; Schulman et al., 1997)—the set of brain areas typically found to be associated with stimulus-independent thought (Mason et al., 2007; McGuire, Paulesu, Frackowiak, & Frith, 1996)—may be similar

in composition, perhaps indicating that this activation pattern signals a shift from the processing of external stimuli to internal and imagined situations (Buckner & Carroll, 2007).

This intriguing proposal has generated a great deal of interest, evidenced, in part, by a prompt response arguing that scene construction, and not self-projection, provides a more specific and empirically supported account of the core network (Hassabis & Maguire, 2007). Constructing a complex and coherent scene involves the retrieval and integration of information toward the visualization of a spatial context that can be maintained and manipulated. The position of Hassabis and Maguire (2007) is supported by the observation that the pattern identified by Buckner and Carroll (2007) is also observed when individuals imagine fictitious circumstances that may have no relation to the self or time (Hassabis, Kumaran, & Maguire, 2007; Hassabis & Maguire, 2007).

Missing from both proposals is concrete evidence that a reliable pattern of brain activity is observed across these domains. Both groups (Buckner & Carroll, 2007; Hassabis & Maguire, 2007) rely upon a narrative-based

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[1]Rotman Research Institute, Baycrest Centre, [2]University of Toronto, [3]York University

review to present evidence, citing studies suggestive of a similar network rather than employing a systematic and quantitative approach. Before any debate regarding the explanatory depth of self-projection or scene construction can take place, it is necessary to demonstrate that a core network truly is common to all these domains. Applying a systematic, extensive, and quantitative meta-analytic approach that can properly evaluate the evidence for this hypothesized neural system is a necessary undertaking. The domains thought to reflect this common system are described in brief below along with their possible relation to self-projection or scene construction.

Remembering

Remembering the past appears to be related to both self-projection and scene construction, especially upon consideration of the theory of autonoetic awareness (Wheeler, Stuss, & Tulving, 1997; Tulving, 1985). According to this theory, declarative memory is based on two systems that correspond to distinct subjective states of awareness: noetic and autonoetic. Noetic awareness involves the recall of knowledge or facts, and supports semantic memory. Autonoetic awareness supports the remembering of contextual and subjective associations from the original experience or episodic memory. Episodic recollection of personal events from one's own life is referred to as autobiographical memory. During autobiographical recall, spatially and temporally bound information is retrieved and the relevant scene vividly reconstructed. This is accompanied by a feeling of reminiscence, where the self being remembered is the same self engaged in recollection, and the re-experiencing of these memories may elicit strong emotions. Remembering thus involves a process of projecting the self back through time, as well as constructing a past scene and experience. Autonoetic awareness, however, may also be applied in a more flexible fashion to other domains such as imagining the future.

Prospection

Imagining ourselves in the future, or prospection, plays an integral role in planning, allowing one to plot strategic behavior in order to engage in successful goal pursuit (Levine, Freedman, Dawson, Black, & Stuss, 1999). Through the mental simulation of possible futures and their outcomes, we can avoid negative ends and maximize positive ones. A number of theorists have hypothesized that remembering and future-oriented thinking may reflect a single underlying process (Atance & O'Neill, 2001; Suddendorf & Corballis, 1997; Wheeler et al., 1997). This idea has only recently been supported by empirical data. In one study, for example, the temporal distribution of self-generated, probable future events (the ''intention function'') maps almost identi-

cally onto the distribution of recalled past events (the ''retention function''); this close similarity replicates across individuals at different points in their lifespan (Spreng & Levine, 2006). Other researchers have shown that the descriptions of both past and future events show decreasing phenomenological richness with increasing time from the present (D'Argembeau & Van der Linden, 2004), and that the episodic specificity of past and future events declines with age in an equivalent fashion (Addis, Wong, & Schacter, 2008). It is thus likely that a shared mechanism for remembering and prospection exists, and reflects a shared neural substrate.

Navigation

Topographical orientation involves the capacity to navigate spatial environments (Maguire, 1997), largely by imagining one's current position, the desired endpoint, and possible routes using both egocentric and allocentric perspectives. The latter perspective involves considering the relation between landmarks irrespective of an individual's viewpoint (Aguirre, Zarahn, & D'Esposito, 1998). This may involve either projecting the ''mind's eye'' into a perspective separate from the immediate environment, or the construction of a scene or map of our environs.

Theory of Mind

A key aspect of successful social navigation involves our possession of a theory of mind, that is, an understanding that the behavior of others is motivated by internal states such as thoughts, emotions, and beliefs (a.k.a. mentalizing; Carruthers & Smith, 1996). Understanding others, in part, involves the taking of another's perspective in order to predict their actions and reactions (Garfield, Peterson, & Perry, 2001). Simulation-based accounts of theory of mind are broadly consistent with the idea that self-projection is an important aspect of mentalizing, proposing that we take on the mindset of others and use our self to simulate their experience in order to understand them (Blakemore & Decety, 2001; Carruthers & Smith, 1996; cf. Stich & Nichols, 1992 for a propositional account). In constructing simulations of actors' potential actions and reactions, we may employ self-projection or perhaps construct imaginary scenes of potential situations.

Default Mode

The pattern of brain activation observed in participants during rest conditions (Mazoyer et al., 2001; Schulman et al., 1997) has been called the default mode of brain function (Raichle et al., 2001) and may represent stimulus-independent thought or mind-wandering (Mason et al., 2007). Driven not by attention to the external environ-

ment, but an internal mode of cognition, the default mode may set the stage for self-projection or scene construction by enabling a switch in perspective from the external to the internal (Gusnard, Akbudak, Shulman, & Raichle, 2001, see also Raichle & Gusnard, 2005).

The Current Study

The aim of the present study is to assess the correspondence of neural activations across multiple studies for autobiographical memory, prospection, navigation, theory of mind, and default mode using the activation likelihood estimation (ALE) approach to quantitative meta-analysis for neuroimaging data (Laird, Fox, et al., 2005; Turkeltaub, Eden, Jones, & Zeffiro, 2002). We employed the ALE approach to reveal statistically significant concordance of activated voxels across numerous experiments for each domain while controlling for chance clustering. By seeking concordance at the voxel level, ALE tests for statistically reliable clustering of activations in standardized locations, avoiding spatial distinction errors and problematic incongruence of labeling across studies that can befall tabular meta-analytic approaches and narrative-based reviews. A subsequent conjunction analysis can then assess correspondence across domains by identifying where clusters from different domains either directly overlap or converge within brain structures.

To date, six neuroimaging studies have explicitly examined prospection (D'Argembeau, Xue, Lu, Van der Linden, & Bechara, in press; Botzung, Denkova, & Manning, 2008; Addis, Wong, & Schacter, 2007; Sharot, Riccardi, Raio, & Phelps, 2007; Szpunar, Watson, & McDermott, 2007; Okuda et al., 2003). Because of this small number of studies, prospection was not assessed in the conjunction analysis. However, brain regions reliably activated by prospection were compared with the other domains.

METHODS

Selection of Studies

Studies for autobiographical memory, navigation, theory of mind, and default mode were selected using a systematic search process. Peer-reviewed articles published in English between January 1985 and June 2007 were selected from the search results of three separate databases: (1) PsycInfo, (2) Medline, and (3) Science Citation Index. Keyword searches were conducted using the following terms: (1) "neuroimaging" <OR> "fMRI" <OR> "PET," and the domain-specific terms (2i) "autobiographical memory," (2ii) "navigation," (2iii) "theory of mind" <OR> "mentalizing" <OR> "mindreading," and (2iv) "default mode" <OR> "default network" <OR> "default state" <OR> "stimulus-independent thought." As a result, 117 unique papers were found on autobiographical memory, 142 for navigation, 135 for theory of mind, and 118 for default mode. Theoreti-

cal papers and reviews were excluded, as were studies that did not provide data on nonclinical samples (e.g., Castelli, Frith, Happe, & Frith, 2002), studies that did not report activation foci as 3-D coordinates in stereotaxic space (e.g., Berthoz, 1997), or those that used "rest" or "fixation" as a control condition (which effectively controlled for default mode, preventing an examination of overlap with stimulus-independent thought; e.g., Cabeza et al., 2004; Platek, Keenan, Gallup, & Mohamed, 2004). For studies containing multiple independent samples, all appropriate data were included (e.g., Walter et al., 2004). The reference lists of these papers were searched for additional studies that fit these criteria. Domain-specific exclusions are described below.

Autobiographical memory papers that did not directly examine the retrieval of an autobiographical memory were excluded (e.g., episodic or semantic memory tasks; Sugiura et al., 2007), or those that employed another type of autobiographical memory as a contrast condition (e.g., recent vs. remote; Maguire & Frith, 2003; or sad vs. happy, Markowitsch, Vandekerckhove, Lanfermann, & Russ, 2003; see Svoboda, McKinnon, & Levine, 2006 for a meta-analysis examining autobiographical memory). In total, 19 appropriate studies were included (Table 1).

A total of 13 studies were included for the navigation domain once studies that did not involve the retrieval of allocentric or egocentric spatial information were excluded (Table 2). Studies that examined encoding were not included in the present study because the process of encoding necessarily involves attention to the present environment (e.g., spatial exploration; Maguire, Frackowiak, & Frith, 1996). Studies tapping the retrieval of spatial location (e.g., Harrison, Duggins, & Friston, 2006; Parslow et al., 2004) were judged not to reflect navigation from one point to another (i.e., wayfinding) and were therefore excluded.

In the case of theory of mind, studies were excluded if they did not involve a basic theory-of-mind task but reported a more narrow investigation (e.g., examination of the role of self–other similarity; Mitchell, Macrae, & Banaji, 2006), or if the task did not clearly involve inferring the mental state of another (e.g., hearing one's own name; Kampe, Frith, & Frith, 2003). Additionally, papers with emotional stimuli (e.g., emotional faces or disturbing pictures; Dolan & Frith, 2004) were excluded in the interests of drawing a more homogeneous sample. In the end, a total of 50 studies met the criteria for inclusion in the theory-of-mind meta-analysis. Due to the relatively large number of foci (compared to other domains) and potential inflation of cluster size as a result (Laird, Fox, et al., 2005), a randomly determined (via random number generation) subsample of studies was selected that approximately matched the number of foci for this domain with the number of foci in the next most extensive domain (i.e., autobiographical memory). A total of 30 theory-of-mind studies were included (Table 3).

Table 1. Autobiographical Memory Data Sources

Study	Task	Comparison Task	Modality	n	Foci	Comments
Addis et al. (2004). *Hippocampus, 14,* 752–762.	Cued recall from prescan interview	Sentence completion, size discrimination	fMRI	14	16	
Andreasen et al. (1995). *American Journal of Psychiatry, 152,* 1576–1585.	Described personal past events	SMR	PET	13	7	
Denkova et al. (2006). *Neuropsychologia, 44,* 2783–2791.	Cued recall using famous names	SMR	fMRI	12	15	
Denkova et al. (2006). *Brain Research, 1078,* 143–150.	Cued recall using old photos	SMR	fMRI	10	26	
Fink et al. (1996). *Journal of Neuroscience, 16,* 4275–4282.	Listening to AB information	Listening to stranger's information	PET	7	5	
Gilboa et al. (2004). *Cerebral Cortex, 14,* 1214–1225.	Cued recall using photos of self	Imagined event from stranger's photo	fMRI	9	5	
Graham et al. (2003). *Cognitive, Affective, & Behavioral Neuroscience, 3,* 234–254.	Cued recall using concepts (nouns)	SMR	PET	24	10	
Greenberg et al. (2005). *Neuropsychologia, 43,* 659–674.	Cued recall using preassigned cues	SMR	fMRI	11	18	
Levine et al. (2004). *Journal of Cognitive Neuroscience, 16,* 1633–1646.	Cued recall using AB audio recordings	PSK, SMR, other's recordings	fMRI	5	14	
Maddock et al. (2001). *Neuroscience, 104,* 667–676.	Cued recall using familiar names	SMR	fMRI	8	24	
Maguire & Mummery (1999). *Hippocampus, 9,* 54–61.	True/False judgments for AB sentences	Listening to words, syllable counting	PET	8	8	
Maguire et al. (2000). *Hippocampus, 10,* 475–482.	True/False judgments for AB sentences	Listening to words, syllable counting	fMRI	6	9	
Maguire & Frith (2003). *Brain, 126,* 1511–1523.	True/False judgments for AB sentences	SMR	fMRI	12	4	young adults
ibid.	True/False judgments for AB sentences	Listening to words, syllable counting	fMRI	12	5	older adults
Markowitsch et al. (2000). *Behavioural Neurology, 12,* 181–190.	Listening to AB information	Listened to fictitious information	PET	8	8	
Piefke et al. (2003). *Brain, 126,* 650–668.	Cued recall using AB sentences	Reading	fMRI	20	18	
Rekkas & Constable (2005). *Journal of Cognitive Neuroscience, 17,* 1950–1961.	Cued recall for recent past	SMR	fMRI	12	24	
Tsukiura et al. (2003). *NeuroReport, 14,* 658–658.	Cued recall for recent past	SMR	PET	9	8	
Vandekerckhove et al. (2005). *Behavioural Neurology, 16,* 203–210.	Cued recall using AB sentences	Item visualization	fMRI	16	18	
Viard et al. (2007). *Cerebral Cortex, 17,* 2453–2467.	Cued recall using AB sentences	Letter detection	fMRI	12	7	older adults
			total	228	249	

AB = autobiographical; SMR = semantic memory retrieval; PSK = personal semantic knowledge; fMRI = functional magnetic resonance imaging; PET = positron emission tomography; ROI = region of interest.

Table 2. Navigation Data Sources

Study	Task	Comparison Task	Modality	n	Foci	Comments
Avila et al. (2006). *American Journal of Neuroradiology, 27*, 498–503.	Hometown-walking task	Number counting	fMRI	12	11	
Ghaem et al. (1997). *NeuroReport, 8*, 739–744.	Mental simulation of routes	Mental visualization of landmarks	PET	5	3	
Hartley et al. (2003). *Neuron, 37*, 877–888.	Wayfinding in VE	Trail following in VE	fMRI	16	8	
Iaria et al. (2007). *European Journal of Neuroscience, 25*, 890–899.	Wayfinding in VE	Trail following in VE	fMRI	9	19	
Jordan et al. (2004). *NeuroReport, 15*, 135–140.	Wayfinding in VE	PM, cued route, AV in VE	fMRI	8	15	
Kumaran & Maguire (2005). *Journal of Neuroscience, 25*, 7254–7259.	MN between friends' houses	Social relational task	fMRI	18	8	
Maguire et al. (1997). *Journal of Neuroscience, 17*, 7103–7110.	Mental simulation of routes	Number repetition	PET	11	11	
Maguire et al. (1998). *Science, 280*, 921–924.	Wayfinding in VE	Trail following in VE	PET	10	10	
Mayes et al. (2004). *Neuropsychology, 18*, 426–441.	MN of newly learned route	Recall newly learned word definition	fMRI	9	7	
Mellet et al. (2002). *Cerebral Cortex, 12*, 1322–1330.	Mental simulation of routes	Word pair counting	PET	6	12	
Pine et al. (2002). *Neuroimage, 15*, 396–406.	Wayfinding in VE	Trail following in VE	fMRI	20	27	10 adults, 10 adolescents
Rosenbaum et al. (2004). *Hippocampus, 14*, 826–835.	Mental simulation of routes	Vowel counting	fMRI	10	7	
Spiers & Maguire (2006). *Neuroimage, 31*, 1826–1840.	Customer-driven route planning in VE	Coasting	fMRI	20	13	
			total	154	151	

MN = mental navigation; VE = virtual environment; PM = passive movement; AV = attentive viewing.

Table 3. Theory-of-Mind Data Sources

Study	Task	Comparison Task	Modality	n	Foci	Comments
Aichhorn et al. (2006). *Neuroimage, 30,* 1059–1068.	Adopted perspective of other	Perspective of self	fMRI	18	3	
Berthoz et al. (2002). *Brain, 125,* 1696–1708.	Intentional social violation story	Unintentional social violation story	fMRI	12	10	
Bhatt & Camerer (2005). *Games & Economic Behavior, 52,* 424–459.	Second-order belief judgment	Belief judgment	fMRI	16	2	
Brunet et al. (2000). *Neuroimage, 11,* 157–166.	Intention attribution	Physical causality attribution	PET	8	17	
Castelli et al. (2000). *Neuroimage, 12,* 314–325.	ToM animated shapes	Randomly moving shapes	PET	6	10	
Ferstl & von Cramon (2002). *Neuroimage, 17,* 1599–1612.	Take perspective of person in sentences	Judged nonword sentences	fMRI	9	13	
Finger et al. (2006). *Neuroimage, 33,* 414–421.	Moral or social transgression stories	Neutral stories	fMRI	16	2	
Fletcher et al. (1995). *Cognition, 57,* 109–128.	ToM story judgment	Physical causation story judgment	PET	6	4	
Fukui et al. (2006). *Neuroimage, 32,* 913–920.	Competed against other in game	Played game independently	fMRI	16	2	
Gallagher & Frith (2004). *Neuropsychologia, 42,* 1725–1736.	Expressive gestures	Instrumental gestures	fMRI	12	7	
German et al. (2004). *Journal of Cognitive Neuroscience, 16,* 1805–1817.	Viewing pretense actions	Viewing real actions	fMRI	16	18	
Goel et al. (1995). *NeuroReport, 6,* 1741–1746.	Judge if Columbus could classify object	Simple classification of object	PET	10	4	
Grèzes et al. (2004). *Journal of Neuroscience, 24,* 5500–5505.	Judged action as deceptive	Judged action as honest	fMRI	11	11	
Harris et al. (2005). *Neuroimage, 28,* 763–769.	Internal attributions for behavior	Other attributions	fMRI	12	12	
Kobayashi et al. (2006). *Brain and Language, 98,* 210–220.	False belief tasks	Sentence previously presented	fMRI	32	7	16 bilinguals, 16 monolinguals
Mitchell et al. (2005). *Journal of Cognitive Neuroscience, 17,* 1306–1315.	Form impression based on behavior	Remember sequence of information	fMRI	18	13	
Ohnishi et al. (2004). *NeuroReport, 15,* 1483–1487.	ToM animated shapes	Randomly moving shapes	fMRI	10	13	adolescents

Reference	Task 1	Task 2	Method		
Perner et al. (2006). *Social Neuroscience, 1,* 245–258.	False belief stories	False photograph stories	fMRI	19	6
Rilling et al. (2004). *Neuroimage, 22,* 1694–1703.	Competed against putative other in game	Button presses	fMRI	19	10
Ruby & Decety (2003). *European Journal of Neuroscience, 17,* 2475–2480.	Adopted lay perspective	Perspective of self	PET	10	13
Russell et al. (2000). *American Journal of Psychiatry, 157,* 2040–2042.	Judge mental state from face	Judge gender from face	fMRI	7	4
Saxe & Kanwisher (2003). *Neuroimage, 19,* 1835–1842.	ToM story judgment	Physical causality story judgment	fMRI	25	5
Saxe et al. (2006). *Social Neuroscience, 1,* 284–298.	False belief stories	False photograph stories	fMRI	12	8
Saxe & Wexler (2005). *Neuropsychologia, 43,* 1391–1399.	False belief stories	False photograph stories	fMRI	12	4
Schilbach et al. (2006). *Neuropsychologia, 44,* 718–730.	View social interaction with self	View social interaction with other	fMRI	18	3
Spiers & Maguire (2006). *Neuropsychologia, 44,* 1674–1682.	Spontaneous ToM events	Non-ToM events	fMRI	20	1
Vogeley et al. (2001). *Neuroimage, 14,* 170–181.	ToM story judgment	Non-ToM story judgments	fMRI	8	7
Vollm et al. (2006). *Neuroimage, 29,* 90–98.	ToM cartoon judgment	Physical causality cartoon judgment	fMRI	13	13
Walter et al. (2004). *Journal of Cognitive Neuroscience, 16,* 1854–1863.	Communicative intention	Physical causality attribution	fMRI	13	18
ibid	Communicative intention	Physical causality attribution	fMRI	12	15
Wicker et al. (2003). *Neuropsychologia, 41,* 139–146.	Intention attribution to direct gaze	Averted gaze	PET	10	1
			total	416	255

ToM = theory of mind.

Studies on default mode included those reporting foci for either task-related deactivations (e.g., Schulman et al., 1997) or activations (e.g., Mason et al., 2007) associated with rest or fixation. Studies were excluded if they examined brain deactivations associated with cognitively demanding tasks relative to another active task (e.g., covert counting vs. lexical retrieval; Hutchinson et al., 1999), if the baseline or rest condition involved responding to an external stimulus (e.g., flashing screen; Gilbert, Simons, Frith, & Burgess, 2006), or if the study constituted a functional connectivity analysis rather than a typical contrast analysis (e.g., Greicius, Krasnow, Reiss, & Menon, 2003). In total, 16 studies of the default network were included in the analysis (Table 4).

A surge in neuroimaging studies examining prospection has begun to unravel the neural underpinnings of future-oriented thinking. In light of these papers, we have elected to loosen the inclusion criteria and incorporate six papers into a separate ALE analysis (Table 5). Unlike the aforementioned domains, we included studies with baseline conditions equivalent to our other task domains (e.g., theory-of-mind control task, Szpunar et al., 2007; fixation, Sharot et al., 2007) and contacted the authors for information on unpublished contrasts of interest (Future > Control; Addis et al., 2007; Sharot et al., 2007; Szpunar et al., 2007). Due to the small number of studies, collection of papers outside the designated time window, and reliance upon unpublished results, we do not include prospection in the conjunction analysis with the other four domains. Patterns of brain activity identified by the prospection meta-analysis are, however, discussed in light of those identified by the conjunction analysis.

Creation of ALE Maps for Each Domain

The ALE method provides a voxel-based meta-analytic technique for functional neuroimaging data (Turkeltaub et al., 2002). The software (BrainMap Search&View 3.2.1) computes statistically significant concordance in the pattern of brain activity among several independent experiments. ALE maps are derived based on foci of interest, which comprise statistically significant peak activation locations from multiple studies.

The original studies contributing these foci for each domain are presented in Tables 1–5. Coordinates reported in MNI were converted to Talairach using the Brett (1999) transformation. In the approach taken by ALE, localization probability distributions for the foci are modeled at the center of 3-D Gaussian functions, where the Gaussian distributions are summed across the experiments to generate a map of interstudy consistencies that estimate the likelihood of activation for each voxel, the ALE statistic, as determined by the entire set of studies. Voxel sizes were determined at full-width half-maximum of 10 mm. The ALE values are computed using the same full-width half-maximum value and for each domain, randomly generated foci (identical in number to those being tested) were employed as the null set across 5000 permutations. The false discovery rate method was employed to correct for multiple comparisons at a significance threshold of $p < .05$ (Laird, Fox, et al., 2005). For each of the five domains, ALE maps and cluster reports were generated. Anatomical labels were then applied to the resultant clusters using the Talairach Daemon and visual inspection (for greater detail on the ALE method, see Laird, Fox, et al., 2005; Turkeltaub et al., 2002; for a discussion of meta-analytic approaches to neuroimaging data, see Wager, Lindquist, & Kaplan, 2007).

Conjunction Analysis

The ALE maps were imported into AFNI (Cox, 1996), and a conjunction analysis was undertaken to examine the correspondence of consistently activated regions across autobiographical memory, navigation, theory of mind, and default mode. Conjunction was determined by creating a mask, using 3dcalc, and overlaying the resultant ALE maps for each domain onto an anatomical template in Talairach space (Talairach & Tournoux, 1988) to visualize cluster overlay (N.B. this does not constitute a statistical test). The location of overlapping clusters is reported in Talairach coordinates.

RESULTS

Domain-specific ALE results are presented in Figure 1 and Tables 6–10. Discussion of the individual meta-analyses performed for each domain is unfortunately outside the scope of this article (see Buckner, Andrews-Hanna, & Schacter, in press; Schacter, Addis, & Buckner, in press; Cabeza & St Jacques, 2007; Spiers & Maguire, 2007; Gallagher & Frith, 2003, for reviews on these topics). The results of the conjunction reveal correspondence of ALE clusters across four or three cognitive domains in a number of locations and are described below (also Table 11 and Figure 2) along with their consistency with prospection findings (Table 11). Correspondence across domains is said to occur if, (a) ALE clusters directly overlapped within 3-D space or, (b) if clusters converge within the same brain structure. Clusters are said to converge if they fall within 10 mm of each other, and are within the same Brodmann's area (BA) or unlabeled region (e.g., hippocampus). Prospection is reported to be consistent with the conjunction analysis if the ALE output demonstrates a similar cluster in the same brain region. This method of determining convergence across domains with prospection is similar to the determination of coactivation using a tabular method.

The conjunction analysis was also utilized to determine differences in cluster location among the domains.

Table 4. Default-mode Data Sources

Study	Task	Comparison Task	Modality	n	Foci	Comments
Andreasen et al. (1995). *American Journal of Psychiatry, 152,* 1576–1585.	Rest	Semantic memory retrieval	PET	13	7	
Binder et al. (1999). *Journal of Cognitive Neuroscience, 11,* 80–93.	Rest	Active listening	fMRI	30	8	
Christoff et al. (2004). *Cortex, 40,* 623–630.	Rest	Arrow cued button press	fMRI	12	15	
D'Argembeau et al. (2005). *Neuroimage, 25,* 616–624.	Rest	Reflecting on self, other and society	PET	12	9	
Fransson (2006). *Neuropsychologia, 44,* 2836–2845.	Rest	Working memory	fMRI	14	21	
Greicius et al. (2004). *Proceedings of the National Academy of Sciences, 101,* 4637–4642.	Rest	Button press to flashing screen	fMRI	14	8	young adults
ibid.	Rest	Button press to flashing screen	fMRI	14	17	young adults
ibid.	Rest	Button press to flashing screen	fMRI	13	22	older adults
Gould et al. (2006). *Neuroimage, 31,* 818–831.	Rest	Paired associate retrieval and encoding	fMRI	24	18	12 young, 12 older adults
Kennedy et al. (2006). *Proceedings of the National Academy of Sciences, 103,* 8275–8280.	Fixation	Counting Stroop task	fMRI	14	8	
Mason et al. (2007). *Science, 315,* 393–395.	Rest	Working memory	fMRI	19	20	
Mazoyer et al. (2001). *Brain Research Bulletin, 54,* 287–298.	Rest	Multiple Experimental Conditions A	PET	63	24	MA (9 studies)
McGuire et al. (1996). *NeuroReport, 7,* 2095–2099.	SITF	Articulation	PET	5	5	
ibid.	SITF	Reading	PET	6	1	ROI
McKiernan et al. (2003). *Journal of Cognitive Neuroscience, 15,* 394–408.	Rest	Target detection	fMRI	30	20	
Persson et al. (2007). *Journal of Cognitive Neuroscience, 19,* 1021–1032.	Fixation	Verb generation	fMRI	60	11	32 young, 28 older adults
Raichle et al. (2001). *Proceedings of the National Academy of Sciences, 98,* 676–682.	Rest	ROI regional/global brain oxygen flow	PET	19	6	ROI
ibid.	Rest	ROI regional/global brain oxygen flow	PET	19	7	ROI
Shulman et al. (1997). *Journal of Cognitive Neuroscience, 9,* 648–663.	Fixation	Visual information processing	PET	132	14	MA (9 studies)
Wicker et al. (2003). *Brain Research Reviews, 43,* 224–230.	Rest	Multiple Experimental Conditions B	PET	42	6	MA (5 studies)
			total	555	247	

SIT = stimulus independent thought. Multiple Experimental Conditions A include visual, calculation, imagery, language, and perception processing. Multiple Experimental Conditions B comprises spatial, intentional, pleasantness and belief judgments, and perception of gaze. MA = meta-analysis.

Table 5. Prospection Data Sources

Study	Task	Comparison Task	Modality	n	Foci	Comments
Addis et al. (2007). *Neuropsychologia, 45,* 1363–1377.	Cued future event elaboration	Imagery and semantic elaboration	fMRI	14	14	Coordinates provided by author
Botzung et al. (2008). *Brain and Cognition, 66,* 202–212.	Cued "pre-experiencing" of previously determined event	Judgment of semantic relatedness	fMRI	10	12	
D'Argembeau et al. (in press). *Neuroimage,* doi:10.1016/j.neuroimage.2007.11.025.	Cued "pre-experiencing" of previously determined event	Imagining routine activity	fMRI	12	6	
Okuda et al. (2003). *Neuroimage, 19,* 1369–1380.	Talking about personal distant future	Talking about the meaning of words	PET	12	14	
Sharot et al. (2007). *Nature, 450,* 102–105.	Cued future event from short description	Fixation	fMRI	15	24	Coordinates provided by author
Szpunar et al. (2007). *Proceedings of the National Academy of Sciences, 104,* 642–647.	Cued future event of common life experience	Cued imagining of Bill Clinton	fMRI	21	16	Coordinates provided by author
			total	84	86	

Domain-specific clusters that are unshared and unique to a particular domain are noted in Tables 6–9. Unique clusters are defined as occurring at a distance greater than 10 mm from any other cluster. Additionally, a cluster that converges with another in one BA may extend to an additional region in isolation. These are noted in Tables 6–9 as well.

All four domains demonstrated correspondence within the medial-temporal lobe, medial parietal regions, the temporo-parietal junction, the occipital lobe, and the lateral prefrontal cortex. When considering all domains except for navigation, two additional areas showed correspondence: the medial prefrontal and lateral temporal regions. Prospection was associated with all of these areas except for the occipital lobe. The extent of convergence and overlap within each region is reviewed below.

Medial-Temporal Lobe

All four domains converged within the left medial-temporal lobe. Direct overlap was observed within the left parahippocampal gyrus (BA 36) [−28, −35, −10] and all domains except default mode converged within the left hippocampus. Differences in the pattern of medial-temporal clusters were also observed. Autobiographical memory demonstrated far more expansive left medial-temporal clusters compared with the other domains (Table 5). Navigation engaged the medial-temporal lobes bilaterally and extended more posteriorly compared with autobiographical memory (Table 6). Prospection also engaged the parahippocampus and the hippocampus bilaterally.

Medial Parietal Regions

Convergence in the precuneus, the posterior cingulate, and the retrosplenial cortex was extensive for all four domains. Within the precuneus and the posterior cingulate, direct overlap was observed in the right hemisphere [6, −59, 17] and left hemisphere [−5, −50, 30] for all domains except navigation. On the left, an additional point of convergence was observed with all domains except theory of mind [−10, −57, 24]. Retrosplenial cortex clusters were observed bilaterally for autobiographical memory and navigation, on the right for theory of mind and on the left for default mode. All three medial parietal areas were reliably involved in prospection, bilaterally.

Temporo-parietal Junction and Occipital Lobe

All domains engaged the temporo-parietal junction. Within the right hemisphere, all domains converged in the temporo-parietal junction. In the left hemisphere, direct overlap was observed for all domains except for
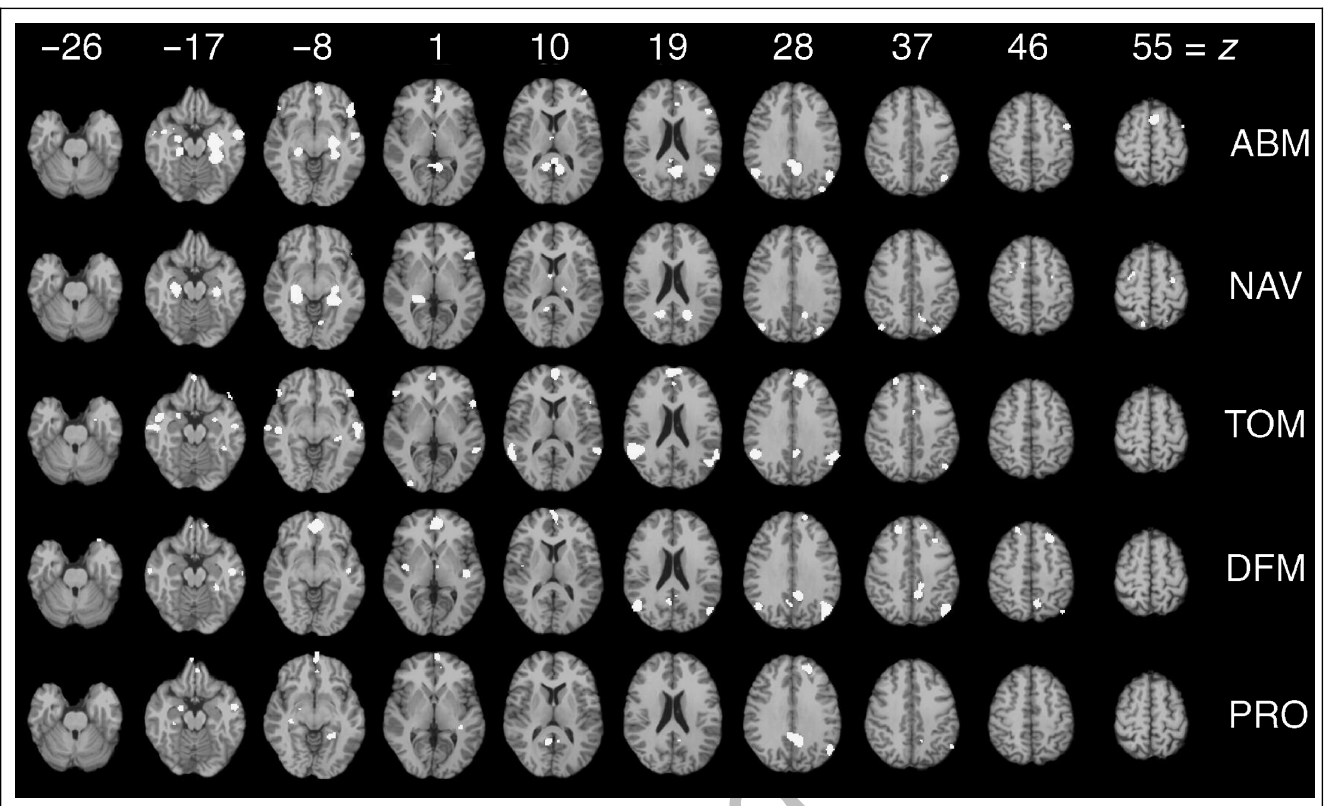
Figure 1. ALE meta-analysis maps for individual domains demonstrating significant concordance across studies ($p < .05$, corrected for multiple comparisons). ABM = autobiographical memory; NAV = navigation; TOM = theory of mind; DFM = default mode; PRO = prospection. Images follow radiological convention: Left side of the brain is right.

navigation [−42, −68, 37], with navigation converging in close proximity. For theory of mind, temporo-parietal clusters extended anteriorly into BA 40, whereas the other domain clusters extended posteriorly from the temporo-parietal junction to the occipital cortex (BA 19), where they overlapped in the left hemisphere [−38, −80, 31]. Prospection also involved the left temporo-parietal junction but not the occipital lobe.

Lateral Prefrontal Cortex

All four domains reliably involved the left lateral prefrontal cortex. Convergence occurred in the left ventrolateral prefrontal cortex (inferior frontal gyrus; BA 47) between all domains save default mode. Prospection also engaged the left ventrolateral prefrontal cortex.

Medial Prefrontal Cortex

Autobiographical memory, theory of mind, and default mode, but not navigation, demonstrated additional correspondence in the medial prefrontal cortex. Convergence extended throughout the medial prefrontal cortex and the rostral anterior cingulate (BA 32) with direct overlap observed within the frontal pole (BA 10) [0, 51, 2]. Prospection clusters were also observed throughout the frontal pole and frontal midline structures.

Lateral Temporal Lobe

Convergence was observed for autobiographical memory, theory of mind, and default mode throughout the left and right lateral temporal lobe (BAs 21, 22). Prospection also engaged these regions within the left hemisphere.

DISCUSSION

The strength of evidence for the presence of a core network that underlies multiple cognitive domains was assessed through quantitative ALE meta-analyses. By examining conjunction across autobiographical memory, navigation, theory of mind, and default mode, correspondence was found in the predicted regions (Buckner & Carroll, 2007) and areas not originally proposed. A high degree of agreement was also observed between the output of this conjunction and prospection. The results provide evidence in favor of a core set of brain regions within the default network that underlie remembering, prospection, navigation, and theory of mind. These results also lend support to both the self-projection and scene construction account of a core network by providing extensive, quantitative evidence of a common set of functional neural correlates. The pattern of activation across domains demonstrates that far more is shared than unique. Shared clusters had higher ALE

Table 6. Autobiographical Memory Results

	Extent of Cluster		Coordinates				
Laterality	Anatomic Region(s)	Brodmann's Area(s)	x	y	z	ALE (10^{-3})	Vol (mm^3)
L and R	PCu, PCC	7, 31, 23	−2	−53	18	26.4	9256
L	HC, PHC, AMG	35, 36, 28[a]	−25	−26	−14	27.0	7776
L	TPJ	39, 22	−47	−61	26	19.6	3632
L	Medial prefrontal cortex, rACC (bilateral)	10, 24, 32	−3	47	−1	20.8	2456
L	STS, MTG, inferior temporal sulcus	20, 21	−56	−8	−14	22.8	2192
L	Ventrolateral prefrontal cortex, temporal pole	47, 38	−47	25	−5	14.0	1664
R	HC, PHC	36, 35, 28	23	−31	−12	20.8	1640
L and R[b]	Middle frontal gyrus	6	−3	12	57	24.0	1448
R	TPJ	39	49	−59	27	14.3	1136
L[b]	Posterior lateral prefrontal cortex	6	−45	3	45	14.6	704
L[b]	Frontal pole (lateral)	10	−40	47	14	16.8	672
R	HC, PHC	28	23	−13	−15	15.2	640
R	Temporal pole, STS, MTG	38[a], 21	49	−5	−13	11.8	608
L	Temporal pole	38	−37	14	−32	14.2	584
L	Occ	19	−37	−81	30	12.8	568
L[b]	Dorsolateral prefrontal cortex	46[a], 45	−46	24	21	13.8	456
R	Ventrolateral prefrontal cortex	47	50	27	−5	8.9	240
L	Frontal pole (medial)	10	−11	55	17	9.8	184
R	Thalamus	n/a	3	−9	5	9.3	184
L	rACC	32	−5	33	22	10.7	168
L	PCC	31	−6	−37	33	10.9	152
L	Superior frontal sulcus	6	−28	9	51	9.6	144
R	AMG	n/a	28	1	−19	10.1	104

ALE meta-analysis results demonstrating significant concordance across studies ($p < .05$, corrected for multiple comparisons). Higher ALE value indicates greater concordance. Coordinates are reported according to the Talairach and Tournoux (1988) atlas. ALE = activation likelihood estimation; Vol = cluster volume; L = left; R = right.

Some unique clusters ([b]) were within 10 mm of another domain's cluster, but never within the same BA. Some brain regions with no ipsilateral convergence ([a]) fell within 10 mm of another domain's clusters but never within the same BA.

AMG = amygdala; dACC = dorsal anterior cingulate cortex; HC = hippocampus; MTG = middle temporal gyrus, Occ = occipital lobe; PHC = parahippocampal cortex; PCC = posterior cingulate cortex; PCu = precuneus; rACC = rostral anterior cingulate cortex; RSC = retrosplenial cortex; STS = superior temporal sulcus; TPJ = temporo-parietal junction.

[a]Brain region (BA) showed no ipsilateral correspondence with any other domain.

[b]Clusters greater than 10 mm away from any other domain's clusters.

values and far outweighed the number of unique clusters, which tended toward lower ALE values. Less than a quarter of clusters were domain-specific. Autobiographical memory, prospection, navigation, and theory of mind engage the default network in the medial-temporal lobes, medial parietal regions, and the temporo-parietal junction, as predicted by Buckner and Carroll (2007). However, these domains also engage the lateral prefrontal cortex and the occipital cortex, regions not initially predicted to be part of the core network. This finding illustrates the advantages of the ALE approach over narrative reviews. The lateral prefrontal cortex potentially serves to maintain and manipulate information held online (D'Esposito, Postle, Ballard, & Lease, 1999), possibly sustaining a mental simulation or scene. Occipital cortex involvement likely supports mental imagery processes (Farah, 1989), useful for visual simulation or imagining scenes.

Autobiographical memory, prospection, and theory of mind demonstrate further functional correspondence,

activating the remaining areas of the default network: medial prefrontal cortex and lateral temporal regions (e.g., Buckner et al., in press; Schulman et al., 1997). Although not predicted by Buckner and Carroll (2007), lateral temporal regions have been previously noted to be involved in autobiographical memory (Svoboda et al., 2006), theory of mind (Gallagher & Frith, 2003), default mode (i.e., task-related deactivations; Schulman et al., 1997), and has been implicated in prospection as well (Schacter, Addis, & Buckner, 2007).

Why is less correspondence observed for navigation? Although navigation primarily involves the retrieval of a detailed visuospatial context, this context does not necessarily involve the self or semantic information. Self-related processes engage the medial prefrontal cortex (D'Argembeau et al., 2007; Mitchell, Banaji, & Macrae, 2005; Ochsner et al., 2005; Northoff & Bermpohl, 2004; Johnson et al., 2002; Craik et al., 1999) and appear likely to be involved in autobiographical memory, prospection, theory of mind, and default-mode processing. Likewise, navigation appears less likely to involve the recollection of semantic information than the other domains, a process tied to the lateral temporal cortices (Martin & Choa, 2001). Medial prefrontal and lateral temporal involvement may add to the richness of a scene, bringing a range of personal, interpersonal, temporal, and semantic detail on-line.

This core network may be involved in more processes than presently reviewed. One potential additional domain is engagement with narrative fiction. A review of story-processing studies found that the associated brain areas are similar to those involved in autobiographical memory and theory of mind (Mar, 2004). This correspondence was interpreted as evidence that theory-of-mind reasoning and autobiographical recollection are engaged during story processing. A number of theorists and researchers have argued for a close link between

Table 7. Navigation Results

Laterality	Extent of Cluster Anatomic Region(s)	Brodmann's Area(s)	x	y	z	ALE (10^{-3})	Vol (mm^3)
R	HC, PHC	28, 27[a], 35, 36	25	−30	−8	24.3	5928
L	HC, PHC	27, 35, 36	−25	−34	−8	17.3	4440
L	RSC, PCC	30, 31	−17	−58	21	20.2	1800
L	TPJ, Occ	39, 19	−34	−78	34	13.9	1584
R	RSC, PCC	30, 31	16	−54	17	13.4	1400
R	TPJ, Occ	39, 19	42	−74	32	13.3	1168
L	Ventrolateral prefrontal cortex	47, 45	−47	22	1	12.8	1104
R[b]	Superior frontal sulcus	6	27	−3	53	8.8	616
L[b]	Superior frontal sulcus	6	−27	−11	55	9.5	448
R[b]	Superior parietal lobule	7	13	−68	54	8.8	304
L[b]	Cerebellar vermis	n/a[a]	−6	−69	−10	9.0	296
L	PCu	7	−12	−62	39	8.4	264
R	Thalamus	n/a	7	−6	7	8.8	264
L[b]	Ventral temporal lobe	20	−37	−8	−35	9.4	256
R[b]	Posterior medial prefrontal cortex, dACC	6, 32	13	11	47	7.9	224
L	Superior parietal lobule	7	−20	−67	52	8.4	216
L	Thalamus	n/a	−13	−24	8	9.0	208

ALE meta-analysis results demonstrating significant concordance across studies ($p < .05$ corrected for multiple comparisons). Higher ALE value indicates greater concordance. Coordinates are reported according to the Talairach and Tournoux (1988) atlas. ALE = activation likelihood estimation; Vol = cluster volume; L = left; R = right.

Some unique clusters ([b]) were within 10 mm of another domain's cluster, but never within the same BA. Some brain regions with no ipsilateral convergence ([a]) fell within 10 mm of another domain's clusters but never within the same BA.

AMG = amygdala; dACC = dorsal anterior cingulate cortex; HC = hippocampus; MTG = middle temporal gyrus; Occ = occipital lobe; PHC = parahippocampal cortex; PCC = posterior cingulate cortex; PCu = precuneus; rACC = rostral anterior cingulate cortex; RSC = retrosplenial cortex; STS = superior temporal sulcus; TPJ = temporo-parietal junction.

[a]Brain region (BA) showed no ipsilateral correspondence with any other domain.

[b]Clusters greater than 10 mm away from any other domain's clusters.

Table 8. Theory-of-mind Results

Laterality	Extent of Cluster Anatomic Region(s)	Brodmann's Area(s)	x	y	z	ALE (10^{-3})	Vol (mm^3)
L and R	Anterior medial prefrontal cortex, rACC	10, 9, 32	−3	52	20	20.9	7704
R	TPJ	39, 40[a], 22	54	−49	19	22.9	6944
L	TPJ	39, 40[a], 22	−54	−54	18	16.4	4168
R	Temporal pole, STS, MTG	38, 21, 20	54	−13	−13	17.1	3024
L	STS, MTG	21	−55	−17	−10	18.2	1752
L and R	PCu, PCC	7, 31	−4	−52	31	12.7	1000
L	Temporal pole, ventrolateral prefrontal cortex,	38, 47	−46	29	−11	20.3	888
R	Ventrolateral prefrontal cortex	45, 47	50	30	−3	12.1	824
L	Ventrolateral prefrontal cortex	45, 44, 47	−50	15	3	14.0	616
L	AMG	n/a	−25	−6	−20	15.4	592
R[b]	Occ	18[a]	34	−92	1	14.1	568
R	Dorsolateral prefrontal cortex	9, 8	23	46	39	13.9	472
R	AMG	n/a	24	1	−18	13.0	352
L and R	Ventromedial prefrontal cortex	11	3	50	−16	11.7	320
R	PCC, RSC	23, 29, 30	6	−57	15	12.5	312
L	Fusiform gyrus	37	−37	−44	−14	11.4	248
L	TPJ	39	−43	−68	39	12.1	248
L	HC, PHC	36	−30	−31	−9	10.2	224
R[b]	Occ	19	26	−97	14	9.2	176
R[b]	Insula	13	46	8	−4	10.8	160
L and R[b]	dACC	24	−1	4	37	10.3	112
L	PCu	7	−9	−51	42	9.7	112

ALE meta-analysis results demonstrating significant concordance across studies ($p < .05$ corrected for multiple comparisons). Higher ALE value indicates greater concordance. Coordinates are reported according to the Talairach and Tournoux (1988) atlas. ALE = activation likelihood estimation; Vol = cluster volume; L = left; R = right.

Some unique clusters ([b]) were within 10 mm of another domain's cluster, but never within the same BA. Some brain regions with no ipsilateral convergence ([a]) fell within 10 mm of another domain's clusters but never within the same BA.

AMG = amygdala; dACC = dorsal anterior cingulate cortex; HC = hippocampus; MTG = middle temporal gyrus; Occ = occipital lobe; PHC = parahippocampal cortex; PCC = posterior cingulate cortex; PCu = precuneus; rACC = rostral anterior cingulate cortex; RSC = retrosplenial cortex; STS = superior temporal sulcus; TPJ = temporo-parietal junction.

[a]Brain region (BA) showed no ipsilateral correspondence with any other domain.

[b]Clusters greater than 10 mm away from any other domain's clusters.

social cognition and narrative processing (e.g., Mar & Oatley, in press; Keen, 2007; Mar, Oatley, Hirsh, dela Paz, & Peterson, 2006; Zunshine, 2006; Palmer, 2004; Peskin & Astington, 2004; Oatley, 1999; Bruner, 1986). A core network involved in simulating different times, different spaces, and other minds (Buckner & Carroll, 2007) or constructing complex coherent scenes (Hassabis & Maguire, 2007) could thus also play a role in narrative processing as well.

Beyond exploring the role of a core network that contributes to a broad number of domains, a narrower investigation of the parallel between theory of mind and autobiographical memory could prove informative. These two domains displayed the greatest degree of overlap in the conjunction analysis. Autobiographical memory and theory of mind demonstrated similar patterns of activity from the ventrolateral and medial prefrontal cortex, to the precuneus, posterior cingulate, and retrosplenial cortex; into the medial-temporal region and amygdalae; and from the temporo-parietal junction, down the superior temporal sulcus and middle temporal gyrus to the temporal poles. Both autobiographical

memory and theory of mind require meta-representational ability (Perner, 2000), where there must be an awareness of the relation between knowledge sources and present knowledge states; one must possess a theory of mind for oneself in order to acknowledge the past self in relation to the present rememberer. Moreover, there are evolutionary reasons to believe that autobiographical memory and theory of mind should be functionally bound.

It has been argued that hominid brain evolution was driven by social selection pressures (Humphrey, 1976). These pressures gave rise to complex social processes such as deception, perspective taking, and alliance build-

ing (Dunbar, 1993; Byrne & Whiten, 1988). A likely component to the evolution of these attributes is the ability to remember specific social encounters and the changing social conditions among group members. Stimulus-bound actions and semantic memory would not be sufficient to adaptively inform cooperative/competitive decision-making and accommodate rapidly changing social dynamics. This may explain why many autobiographical memories and plans are characterized by social events (Larocque & Oatley, 2006; de Vries & Watt, 1996). The contents of memory and prospection may be necessarily and adaptively tied to things social in nature, potentially the most behaviorally relevant stimuli. As such,

Table 9. Default-mode Results

| | Extent of Cluster | | Coordinates | | | | |
Laterality	Anatomic Region(s)	Brodmann's Area(s)	x	y	z	ALE (10^{-3})	Vol (mm^3)
L and R	Medial prefrontal cortex, rACC	10, 11, 32	−1	47	−1	27.4	5976
L	TPJ, Occ	39, 19	−43	−69	32	28.4	4888
L	PCu, PCC, RSC	7, 31, 23, 30, 29	−7	−48	31	19.3	3152
R	TPJ, STS	39, 22	49	−63	20	22.2	2464
L	Insula, superior temporal gyrus, STS	13[a], 22	−43	−19	−2	18.7	1464
L	Dorsal prefrontal cortex	9, 8[a]	−24	27	45	16.5	1408
R	Dorsal prefrontal cortex	9, 8	20	38	40	18.1	1240
L	Dorsal prefrontal cortex	8[a]	−12	42	39	12.0	784
L	PHC	36, 37, 35, 20	−26	−36	−13	12.4	776
L	Inferior temporal sulcus	20	−49	−18	−18	17.4	760
L	PCu	7	−6	−61	48	15.6	720
R	PCu, PCC	7, 31	6	−59	24	11.5	696
R[b]	Insula	13	40	−11	4	14.3	608
L	Ventral prefrontal cortex, temporal pole	47, 38	−29	24	−21	11.9	464
L	Frontal pole, dorsolateral prefrontal cortex	10, 9	−15	55	26	12.6	288
L	Thalamus	n/a	−3	−12	5	12.6	272
L	Inferior temporal sulcus, MTG	20, 21	−60	−15	−19	9.7	240
R	Inferior temporal sulcus, MTG	20, 21	62	−16	−17	11.0	240
R[b]	Cerebellum, pyramis	n/a[a]	41	−76	−33	10.5	232
L[b]	Cerebellum, inferior semilunar lobule	n/a[a]	−6	−58	−40	11.8	184
L	Superior lateral prefrontal cortex	8[a]	−35	20	50	10.1	128

ALE meta-analysis results demonstrating significant concordance across studies ($p < .05$ corrected for multiple comparisons). Higher ALE value indicates greater concordance. Coordinates are reported according to the Talairach and Tournoux (1988) atlas. ALE = activation likelihood estimation; Vol = cluster volume; L = left; R = right.

Some unique clusters ([b]) were within 10 mm of another domain's cluster, but never within the same BA. Some brain regions with no ipsilateral convergence ([a]) fell within 10 mm of another domain's clusters but never within the same BA.

AMG = amygdala; dACC = dorsal anterior cingulate cortex; HC = hippocampus; MTG = middle temporal gyrus; Occ = occipital lobe; PHC = parahippocampal cortex; PCC = posterior cingulate cortex; PCu = precuneus; rACC = rostral anterior cingulate cortex; RSC = retrosplenial cortex; STS = superior temporal sulcus; TPJ = temporo-parietal junction.

[a]Brain region (BA) showed no ipsilateral correspondence with any other domain.

[b]Clusters greater than 10 mm away from any other domain's clusters.

Table 10. Prospection Results

Laterality	Anatomic Region(s)	Brodmann's Area(s)	x	y	z	ALE (10^{-3})	Vol (mm^3)
L and R	PCC, PCu	31, 23	−5	−51	29	16.8	2944
L and R	Anterior medial prefrontal cortex	10, 11	−1	59	−4	9.9	1536
L	TPJ	39	−49	−64	29	13.2	1136
L	HC, PHC, tail of caudate	37	−28	−41	−5	9.0	1024
L	Dorsolateral prefrontal cortex	9	−17	45	30	9.7	968
L and R	rACC, ventromedial prefrontal cortex (left only)	32, 11	−1	41	−12	7.7	608
L	STS, MTG	21, 20	−52	−7	−14	10.8	600
R	AMG, PHC	34, 28	21	−9	−13	11.6	600
R	RSC	30, 29	9	−54	9	9.0	496
R	HC, PHC	36	32	−28	−11	8.3	392
L	RSC	30, 29	−5	−53	12	7.0	112
L	rACC	32	−7	46	1	7.0	104

ALE meta-analysis results demonstrating significant concordance across studies ($p < .05$ corrected for multiple comparisons). Higher ALE value indicates greater concordance. Coordinates are reported according to the Talairach and Tournoux (1988) atlas. ALE = activation likelihood estimation; Vol = cluster volume; L = left; R = right.

AMG = amygdala; dACC = dorsal anterior cingulate cortex; HC = hippocampus; MTG = middle temporal gyrus; Occ = occipital lobe; PHC = parahippocampal cortex; PCC = posterior cingulate cortex; PCu = precuneus; rACC = rostral anterior cingulate cortex; RSC = retrosplenial cortex; STS = superior temporal sulcus; TPJ = temporo-parietal junction.

the evolutionary advancement of autonoetic awareness would correspond to the neural processes of theory of mind. The utilization of prospection is arguably of greatest strategic importance, particularly in the securing of mates, protection, and resources (Suddendorf & Corballis, 2007; Flinn, Geary, & Ward, 2005).

Both theories of self-projection and scene construction emphasize the role of the medial-temporal lobes (Buckner & Carroll, 2007; Hassabis & Maguire, 2007). Medial-temporal lobe involvement in the core network may reflect a common reliance on mnemonic or relational processes (Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006; Eichenbaum, 2000; Squire & Zola-Morgan, 1991). The function of the medial-temporal lobe may also apply more broadly toward the construction of coherent scenes, events (Hassabis & Maguire, 2007), and mental models (Schacter & Addis, 2007). Rich memories allow one to find commonalities between current events and the past. Pattern matching, paired with the flexible reconstruction of information, allows for the application of recollection to social problem-solving. Not all theory-of-mind tasks, however, necessarily require this mnemonic component. The hippocampus may not be necessary to support theory of mind as it does autobiographical memory and other aspects of scene construction (Hassabis & Maguire, 2007; Moscovitch et al., 2006; Maguire, 1997; e.g., Hassabis, Kumaran, Vann, & Maguire, 2007; Rosenbaum et al., 2000)

Table 11. Correspondence across Domains

Domain	Prefrontal			Medial Temporal			Medial Parietal		Lateral		
	Pole	rACC	Lateral	HC	PHC	AMG	PCu/PCC	RSC	TPJ	STS/MTG	Occ
Autobiographical memory	L	LR	LR	LR	LR	LR	LR	LR	LR	LR	L
Navigation	–	–	L	LR	LR	–	LR	LR	LR	–	LR
Theory of mind	LR	LR	LR	L	L	LR	LR	R	LR	LR	R
Default mode	LR	LR	L	–	L	–	LR	L	LR	LR	L
Prospection	LR	LR	L	LR	LR	R	LR	LR	L	L	–

L = left hemisphere cluster; R = right hemisphere cluster; rACC = rostral anterior cingulate gyrus; HC = hippocampus; PHC = parahippocampal cortex; AMG = amygdala; PCu/PCC = precuneus and posterior cingulate cortex; RSC = retrosplenial cortex; STS/MTG = superior temporal sulcus and middle temporal gyrus; Occ = occipital lobe.

Figure 2. Conjunction between ALE maps of four domains. Red and yellow demarcate conjunction between two and three domains, respectively. The encapsulated black voxel (1 cm^2) indicates overlap across all four domains. Coronal coordinates for the panel slices are: (A) $y = 51$; (B) $y = -64$. Images follow radiological convention: Left is right. Sagittal coordinates of the left hemisphere panel slices are: (C) $x = -4$; (D) $x = -27$; (E) $x = -48$.
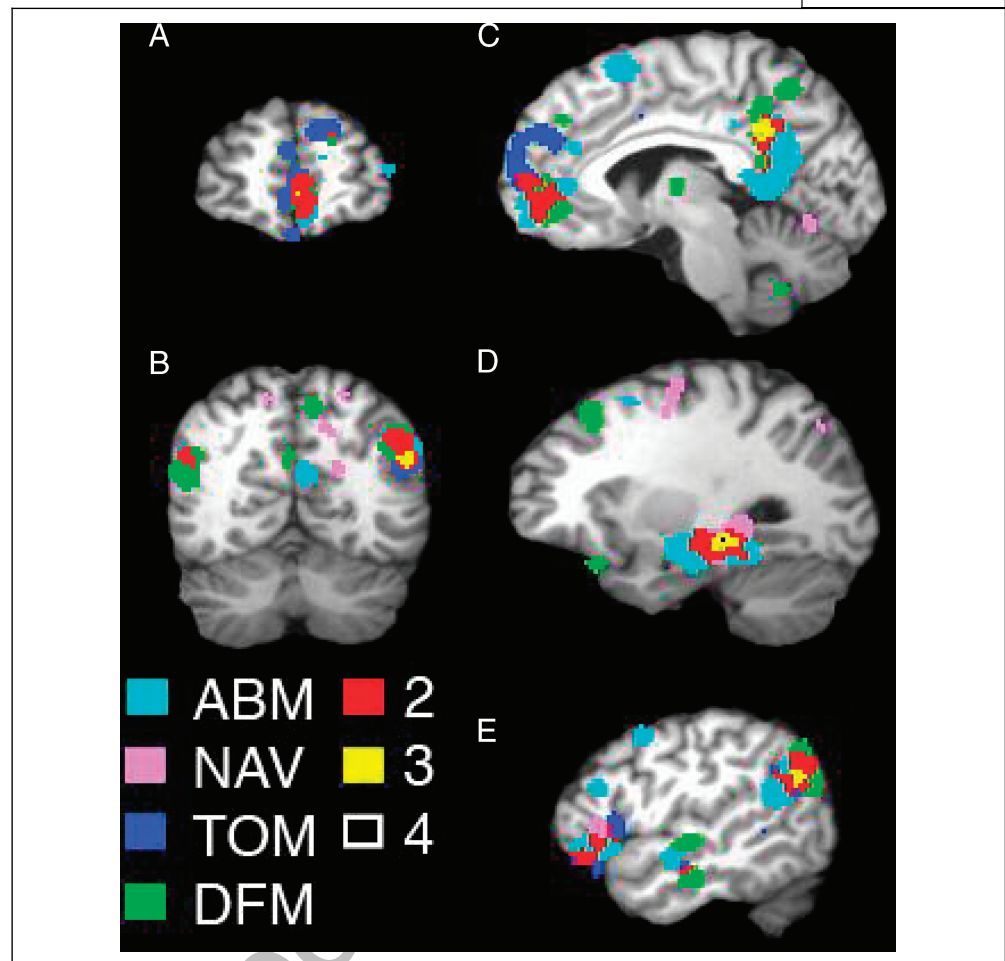
as evidenced in part by two patients with episodic memory impairment who have been shown to perform well on theory-of-mind tasks (Rosenbaum, Stuss, Levine, & Tulving, 2007). Further work will be required to delineate the neural relationship between the interpersonal and the autobiographical.

Although we believe that our approach has many strengths, particularly over tabular meta-analyses and narrative reviews, our method does have some limitations. Lack of direct overlap across all of the domains studied may be due to the relative paucity of published neuroimaging investigations of relevant aspects of navigation (i.e., allocentric recall) and prospection. The small number of available foci for inclusion in these ALE analyses may reduce the probability of identifying reliable clusters. Additionally, because foci are pooled across studies and treated as fixed effects, individual studies may exert undue influence (Wager et al., 2007). Some limitations are tempered by the quantification of cluster coherence provided by the ALE statistic (e.g., few theory-of-mind studies report activity in the medial-temporal region as compared to the medial frontal cortex and the values of the ALE statistic reflects this; see Table 8). Despite its limitations, the ALE technique has demonstrated convergent validity with other approaches to meta-analysis (e.g.,

tabular methods in the case of autobiographical memory; Svoboda et al., 2006; Gilboa, 2004; see also Laird, McMillan, et al., 2005) while contributing more sophisticated statistical threshold calculations (Laird, Fox, et al., 2005). Additionally, the correspondence we observed between autobiographical memory and default mode is consistent with previous observations (Buckner et al., 2005; Raichle et al., 2001; Andreasen et al., 1995) and validates our approach to determining correspondence of functional neuroanatomy across domains. Causal inferences with respect to the relation between brain region and brain function, however, cannot be made without convergent neuropsychological evidence. Evidence of co-occurring functional deficits across domains due to neurological insult within the core network is less well characterized (for exceptions, see Hassabis, Kumaran, Vann, et al., 2007; Rosenbaum et al., 2000, 2007).

One alternative explanation for our data is that functional similarities between tasks may reflect the coincident activation of multimodal regions, not a core network. Also, neural demands from different domains may recruit similar and overlapping brain areas, but not be functionally dependent upon the same neurons. One other concern is that our analysis relies on group data for each data point, which means that small differences in anatomic locali-

zation between individuals are necessarily obscured. In light of this fact, it must be acknowledged that this is a somewhat broad approach and there are likely subtle distinctions that have not been captured. Despite a correspondence of data across more than 1000 participants, correspondence at the individual level remains unknown and certainly worth further investigation.

In this study, we empirically demonstrated reliable patterns of brain activity common across a number of cognitive tasks. In addition to medial prefrontal, medial-temporal, and parietal regions (Buckner & Carroll, 2007), our analysis has revealed evidence of an extended core network that includes the lateral prefrontal cortex, lateral temporal cortex and the occipital lobe. The correspondence of functional neuroanatomy across domains suggests that a core network may be involved in the execution of a broad set of domains. This core network may support a set of processes that promote self-projection (Buckner & Carroll, 2007), scene construction (Hassabis & Maguire, 2007), or some other as yet unidentified cognitive account. Although this meta-analytic study does not allow for a verdict to be delivered regarding these differing theories, it contributes toward the overall endeavor of an exciting, integrative, cross-disciplinary approach to cognitive neuroscience.

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Acknowledgments

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