

Watching My Mind Unfold versus Yours: An fMRI Study Using a Novel Camera Technology to Examine Neural Differences in Self-projection of Self versus Other Perspectives

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Abstract

■ Self-projection, the capacity to re-experience the personal past and to mentally infer another person's perspective, has been linked to medial prefrontal cortex (mPFC). In particular, ventral mPFC is associated with inferences about one's own self, whereas dorsal mPFC is associated with inferences about another individual. In the present fMRI study, we examined self-projection using a novel camera technology, which employs a sensor and timer to automatically take hundreds of photographs when worn, in order to create dynamic visuospatial cues taken from a first-person perspective. This allowed us to ask participants to self-project into the personal past or into the life of another person. We predicted that self-projection to the personal past would elicit greater activity in ventral mPFC, whereas self-projection of another perspective would rely on dorsal mPFC.

There were three main findings supporting this prediction. First, we found that self-projection to the personal past recruited greater ventral mPFC, whereas observing another person's perspective recruited dorsal mPFC. Second, activity in ventral versus dorsal mPFC was sensitive to parametric modulation on each trial by the ability to relive the personal past or to understand another's perspective, respectively. Third, task-related functional connectivity analysis revealed that ventral mPFC contributed to the medial temporal lobe network linked to memory processes, whereas dorsal mPFC contributed to the fronto-parietal network linked to controlled processes. In sum, these results suggest that ventral-dorsal subregions of the anterior midline are functionally dissociable and may differentially contribute to self-projection of self versus other. ■

INTRODUCTION

Self-projection is the capacity that allows us to shift our perspective from the present moment to alternative temporal and mental locations (Mitchell, 2009; Buckner & Carroll, 2007; Suddendorf & Corballis, 2007). The neural correlates supporting temporal simulations of the personal past during autobiographical memory (AM) retrieval overlap with those supporting mental simulations of another person's perspective during Theory of Mind (ToM) tasks (for meta-analysis, see Spreng, Mar, & Kim, 2009). However, few functional neuroimaging studies have manipulated self-projection within the same individual (although see Rabin, Gilboa, Stuss, Mar, & Rosenbaum, 2010; Spreng & Grady, 2010) while also using naturalistic stimuli. In the present fMRI study, we examined temporal and mental forms of self-projection using a novel camera technology to create dynamic visuospatial cues which provided the opportunity to step into the personal past or another individual's perspective.

Functional neuroimaging studies have linked self-projection to medial prefrontal cortex (mPFC; Mitchell, 2009). Medial PFC is involved in abstract forms of mentalizing (Amodio & Frith, 2006; Gallagher & Frith, 2003) such as integrating social information about the stable dispositions of others and the self across time (Van Overwalle, 2009). Subregions within mPFC, however, may differentially contribute to self-projection. Ventral mPFC is sensitive to the ability to re-experience the self in time during AM (Levine et al., 2004; Maguire & Mummery, 1999), and focal lesions that overlap here impair the subjective experience of re-experiencing the personal past (Wheeler & Stuss, 2003). Moreover, resting-state functional connectivity has shown that subregions of mPFC comprise separable networks. Ventral mPFC is linked to the hippocampus and other regions associated with the medial temporal lobe (MTL) network (Kahn, Andrews-Hanna, Vincent, Snyder, & Buckner, 2008; Vincent et al., 2007), a system of brain regions important for internally directed processes, such as memory. In contrast, dorsal mPFC is linked to dorso-lateral PFC and lateral parietal cortices associated with the fronto-parietal network (Vincent, Kahn, Snyder, Raichle, & Buckner, 2008), a system of brain regions associated with

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controlled processes. Ventral mPFC has been associated with inferences about one’s own self, whereas dorsal mPFC has been associated with inferences about another individual (Krueger, Barbey, & Grafman, 2009; Mitchell, 2009; Van Overwalle, 2009). However, there is considerable debate regarding the functional specialization of mPFC with respect to self versus other processing (Northoff et al., 2006).

The goal of the present fMRI study was to examine self-projection of self versus other elicited by naturalistic stimuli within the same individuals by employing a novel camera technology. We tested three main predictions regarding the role of mPFC, which were based on the evidence regarding ventral and dorsal subregions in self versus other processing (Krueger et al., 2009; Mitchell, 2009; Van Overwalle, 2009). First, ventral mPFC will be preferentially recruited during self-projection of self, whereas dorsal mPFC will be recruited to a greater extent for self-projection of other. Second, ventral versus dorsal mPFC will be sensitive to variability in the ability to re-experience the personal past and to understand another’s perspective. Third, ventral versus dorsal mPFC will be functionally con-

nected to separable neural networks contributing to self-projection of self versus other.

METHODS

Participants

The study recruited 23 participants (12 women; mean age = 23.7, *SD* = 3.6) who were healthy, right-handed, and without history of neurological or psychiatric episodes. Participants gave written informed consent for a protocol approved by the Duke University Institutional Review Board.

Procedure

SenseCam

SenseCam (<http://research.microsoft.com/en-us/um/cambridge/projects/sensecam/>) is a small wearable digital camera that has electronic sensors (e.g., light, heat, motion) which can automatically and silently trigger thousands of photographs in a single day (see Figure 1A). This differs

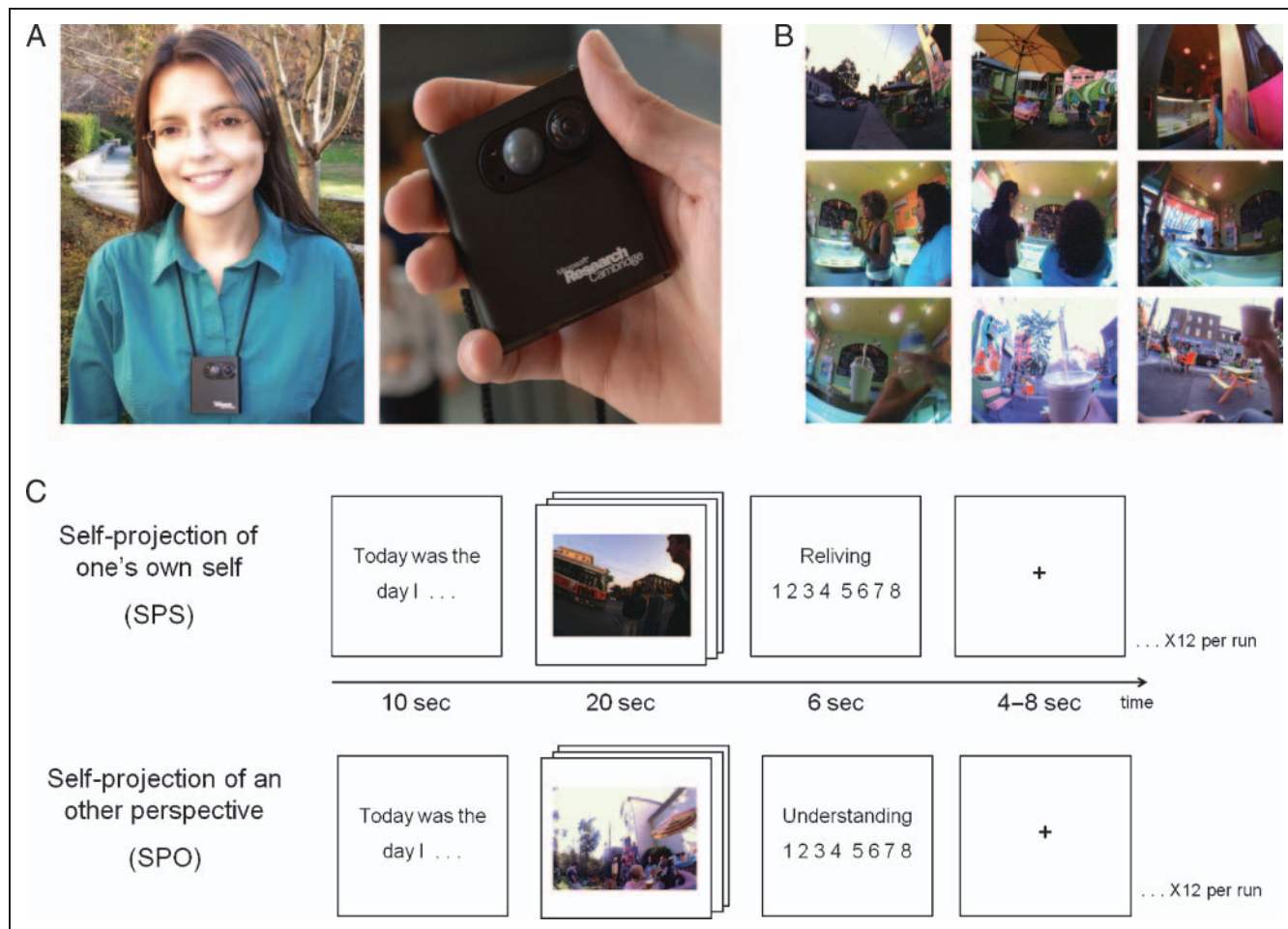


Figure 1. SenseCam. (A) The SenseCam is a small wearable device that takes photographs automatically, without input from the user. (B) SenseCam images acquired during a trip to the ice-cream shop. (C) The experimental design depicting the study conditions.

considerably from the normal way in which we can use a camera to generate retrieval cues (St. Jacques, Rubin, Labar, & Cabeza, 2008; Cabeza et al., 2004) because it does not disrupt the ongoing experience of events through the act of taking a photograph (also see Levine et al., 2004). Several photographs taken from a particular event (e.g., eating ice-cream; see Figure 1B) can be consecutively viewed to create a dynamic visuospatial cue (www.youtube.com/watch?v=sr1i-sICaf8). The SenseCam lens also maximizes the field of view to better capture the perspective of the wearer by incorporating a wide-angle (fish-eye) lens. In sum, the SenseCam captures dynamic images taken from the first-person perspective, which provide highly effective cues for self-projection to alternative self versus other perspectives.

Prospective Collection

Retrieval cues were prospectively collected, such that participants were asked to keep a record of their lives prior to the scanning session by wearing the SenseCam. Participants wore the SenseCam for 6 days and kept a schedule of each day's activities to be used to parse the SenseCam images into events. The daily schedule was recorded at the end of each day, along with a unique identifier to distinguish that particular day from others (e.g., "Today was the day I had lunch with Ben"). Participants were instructed to write about 10 to 15 brief sentences, one for each major event during the day (e.g., "Had breakfast," "went to the grocery store") which were used to segregate the images into events.

Cue Selection

Three days were randomly assigned to elicit self-projection of one's own self (SPS). The content of the remaining 3 days was used for an analysis that was not the main focus of the present investigation (St. Jacques, Conway, & Cabeza, under review). For each day, 12 events were selected to be tested in the scanner. To elicit self-projection of other perspectives (SPO), images were collected by three volunteers who wore a SenseCam in locations at least 100 miles away from Duke University and whose lifestyles differed from the participants. Images in the SPO condition depicted events that would have been familiar to the participants (e.g., going to the grocery store, eating at a restaurant), but which were not self-relevant, thus minimizing the likelihood that the other-perspective condition would include pictures of self-relevant people, places, and activities, which might inadvertently trigger AMs. Debriefing following the scanning session indicated that the SPO images were familiar to many of the participants, but did not trigger personal memories. The SPO images were also carefully selected to be similar to the SPS images (indoor/outdoor, time of day, etc.). Images in both conditions were selected to ensure good picture quality.

fMRI Scanning

The scanning session took place one week following the last day the SenseCam was worn (mean length of delay = 8 days, $SD = 1.2$). There were a total of nine fMRI runs blocked by condition and presented in an alternating order (i.e., ABCABCABC), counterbalanced across participants based on a Latin square design. Three of the separate runs consisted of another condition, which was included for a separate analysis. The structure of the remaining six runs was similar in each condition (see Figure 1C). Each of these runs began with a 10-sec title screen (i.e., "Today was the day I...") and consisted of 12 cues presented in chronological order from that day, for a total of 36 events per condition across 3 runs. Cues were presented for 20 sec, and participants were instructed to recall the events depicted from their own perspective (SCS) or to understand the events being depicted from another person's perspective (SCO). The cues in each condition consisted of 40 SenseCam pictures depicting a single event and presented at a rate of two pictures per second.

Following each cue presentation, participants indicated their subjective experience. In the SPS condition, participants rated the subjective experience of recollection, *reliving*, which refers to how much they were able to re-experience the event depicted as if it were happening right now or as if they were mentally traveling back to the time when the event occurred. It is important to note that reliving is similar to other subjective measures of recollection, such as the remember/know paradigm (for a review, see Yonelinas, 2002). For example, in the remember/know paradigm, participants are asked to use introspection to classify items as recollected (vivid re-experiencing of the original event and its context) or merely familiar. Although introspection has its limitations, the results of hundreds of remember/know studies are highly consistent with findings of hundreds of studies using objective measures of recollection, such as source memory (Yonelinas, 2002). However, there are some critical differences between the reliving scale and the remember/know paradigm, which make the reliving scale a better measure for AM. First, the reliving scale could be considered a better subjective measure of recollection in AM than the remember/know paradigm because it does not require the assumption of a dual-process model (Wixted, 2007; Yonelinas, 2002). Second, reliving is a better predictor of recollection in AMs compared to the remember/know scale, which is a better predictor of confidence in AMs (Rubin, Schrauf, & Greenberg, 2004; Rubin, Burt, & Fifield, 2003). In the SPO condition, participants were asked to indicate the amount of *understanding* of the other person's perspective. While taking another person's perspective, participants were instructed to try to understand what was happening, where the event was taking place, and why the event was occurring. Ratings were conducted on an 8-point scale from low to high, and were self-paced (up to 6 sec). Following a response, a fixation cross was presented

for a jittered interval between 4 and 8 sec plus any remaining time from the response period.

fMRI Methods

Image Acquisition

Scanning was conducted using a 4-T GE magnet. Anatomical scanning included a T1-weighted sagittal localizer series and 3-D fast spoiled gradient-echo recalled (SPGR) structural images were acquired in the coronal plane (256² matrix, TR = 12.3 msec, TE = 5.4 msec, flip angle = 20°, FOV = 240, 68 slices, 1.9 mm slice thickness). Coplanar functional images were acquired using an inverse spiral sequence (64² image matrix, TR = 2000 msec, TE = 6 msec, FOV = 240, flip angle = 60°, 34 slices, 3.8 mm slice thickness).

fMRI Analyses

Image processing and analyses were performed using Statistical Parametric Mapping software in Matlab (SPM5; Wellcome Department of Imaging Neuroscience). Functional images were corrected for slice acquisition order, realigned to correct for motion artifacts, spatially normalized to a standard stereotactic space, and spatially smoothed using an 8-mm isotropic Gaussian kernel. Coordinates are reported in Talairach space using a transformation from the Montreal Neurological Institute coordinates (Brett, Christoff, Cusack, & Lancaster, 2001).

Self-projection of Self versus Other

To examine activation differences between self versus other self-projection during the presentation of the SenseCam images, we used a Finite Impulse Response (FIR) basis function. The FIR approach allowed us to examine potential activation differences without assuming a particular canonical hemodynamic response function, and thus, was appropriate for the complex and temporally protracted processes elicited in the present study. The FIR model included 16 regressors of peristimulus time bins of 2 sec duration (equal to the TR) for each condition, yielding estimates of fMRI signal change across the entire trial period (SenseCam presentation and rating).

We conducted a Condition (SPS, SPO) × Time (0 to 20 sec) ANOVA implemented in SPM5 in order to isolate activation differences in the self versus other conditions across the FIR timepoints associated with the presentation of the SenseCam images. We examined the main effect of condition at an FDR-corrected threshold of $p = .05$ using a two-voxel extent threshold, and inclusively masked with the effect of interest (SPS > SPO or SPO > SPS) at $p = .05$ to determine the direction of the effect. An extent threshold of 2 voxels was chosen here because the ROI approach combined with a corrected threshold was considered very conservative. Further, we took an ROI approach to examine brain regions associated with self versus other

self-projection in the present study based on a previous quantitative meta-analysis which generated activation likelihood estimation maps corresponding to statistically significant concordance of activated voxels in 19 AM and 50 ToM studies (Spreng et al., 2009).

Parametric Modulation by Behavior

To examine the neural correlates associated with self versus other self-projection that was sensitive to on-line behavioral responses, we employed a parametric approach. To identify increases in activity as a function of increasing behavioral responses on each trial, we created a GLM in which temporal versus mental self-projection was modulated by reliving and understanding using the first-order

Table 1. Self-projection of Self vs. Other

Region	BA	x	y	z	F	Voxels
<i>SPO > SPS</i>						
Dorsal mPFC	9	-7	38	33	14.17	12
	9	-11	56	25	13.67	5
Dorsolateral PFC	9	19	49	33	30.51	12
Ventral parietal cortex	39	-45	-67	38	15.26	5
	40	-56	-57	27	12.59	7
	40	52	-53	34	10.93	5
<i>SPS > SPO</i>						
Ventral mPFC	10	-7	54	-3	53.56	51
Fronto-polar cortex	10	-37	48	12	80.47	18
Ventrolateral PFC	45	-41	23	16	17.94	9
	47	-45	14	-7	6.79	2
	47	-41	29	-8	6.73	3
	47	52	29	-5	17.06	3
Anterior cingulate	24	-7	30	20	32.01	7
Supplemental motor area	6	4	10	52	16.61	7
Thalamus	-	4	-7	0	42.34	8
Temporo-polar cortex	38	-37	17	-26	24.59	12
Middle temporal cortex	21	-52	-15	-12	27.71	17
	21	41	-8	-9	17.46	5
Superior temporal cortex	22	-45	-57	17	25.61	22
Hippocampus	-	-22	-12	-15	28.68	71
Retrosplenial cortex	29	0	-51	6	20.00	10
Posterior cingulate	31	-7	-31	33	19.20	2
Ventral parietal cortex	39	-37	-75	25	14.31	11

Talairach coordinates reported. BA = Brodmann's area; PFC = prefrontal cortex; mPFC = medial prefrontal cortex.

parametric modulation option integrated in SPM5. Subsequently, random effects analyses were performed on the parameter estimate of the parametric regressor for the behavioral response. We used the results of the one-sample t test ($p = .05$) reflecting activity modulated by reliving or understanding as an inclusive mask to determine whether the regions showing activation differences in self versus other self-projection were also sensitive to behavior.

Task-related Functional Connectivity Analysis

Seed voxels in ventral versus dorsal mPFC that were identified in our previous analysis on self versus other self-projection were further interrogated to examine the task-related network of brain regions functionally connected with dissociable mPFC regions. We should note that in the present article we refer to dorsal mPFC (z -axis on Talairach atlas: >20 mm) and ventral mPFC (z -axis on Talairach atlas: <20 mm to >-15 mm; e.g., Krueger et al., 2009; Van Overwalle, 2009), however, the particular naming convention may differ among authors (e.g., Buckner, Andrews-Hanna, & Schacter, 2008; Northoff & Bermpohl, 2004). To find these functional connectivity maps, we employed a second analysis based on individual trial activity (Rissman,

Gazzaley, & D'Esposito, 2004). Specifically, we first created a GLM in which each individual trial was modeled by a separate covariate, thus yielding different parameter estimates for each individual trial and for each individual subject. The resulting correlation maps were Fisher transformed to allow for statistical comparison. Then, to examine differences in functional connectivity of ventral versus dorsal mPFC regions associated with temporal versus mental self-projection, we conducted a two-sample t test in SPM5 using an FDR-corrected threshold of $p = .05$, and a two-voxel extent threshold.

RESULTS

Behavioral

SPS was associated with a mean reliving rating of 5.04 ($SD = 0.56$; $RT = 1.42$ sec, $SD = 0.67$), and SPO was associated with a mean understanding rating of 4.50 ($SD = 0.86$; $RT = 1.35$ sec, $SD = 0.61$). There were no significant differences in the reaction time across the two conditions (Cohen's $d = 0.11$). The behavioral results suggest that the SenseCam images evoked a strong ability to re-experience the personal past and to comprehend another individual's perspective.

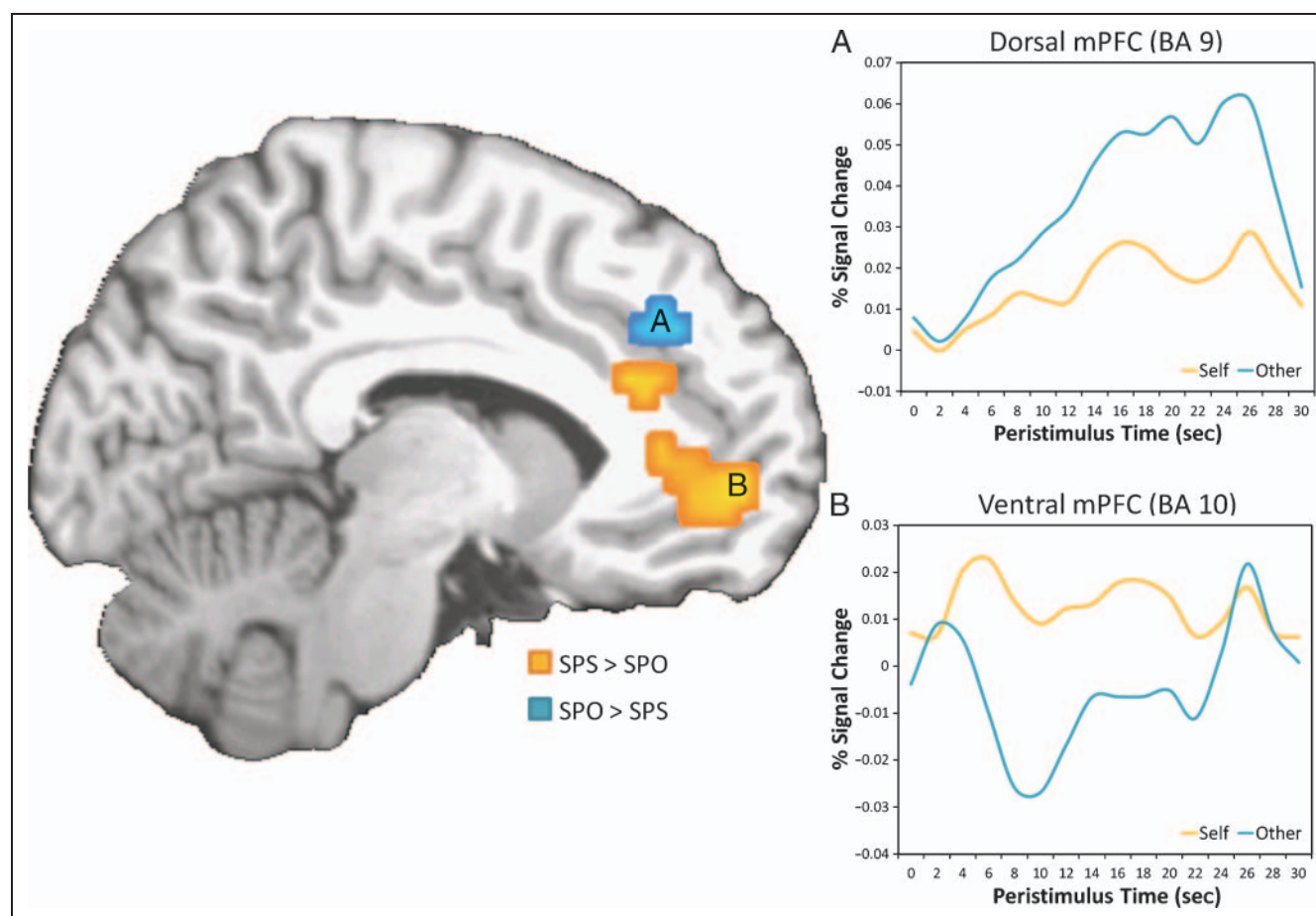


Figure 2. Self-projection of self versus other. There was a dorsal (A) versus ventral (B) distinction in the recruitment of mPFC during self versus other self-projection. BA = Brodmann's area.

Table 2. Parametric Modulation by Behavior

Region	BA	x	y	z	F	Voxels
<i>SPS: Understanding</i>						
Dorsal mPFC	9	-7	38	33	14.17	6
	9	19	49	36	26.63	4
Ventral parietal cortex	39	-45	-67	42	13.38	4
<i>SPO: Reliving</i>						
Ventral mPFC	10	-7	47	-6	21.66	8
Anterior cingulate	24	-4	34	16	31.90	6
	24	0	37	5	24.70	12
Supplemental motor area	6	4	10	52	16.61	5
Thalamus	-	4	-7	0	42.34	6
Temporo-polar cortex	38	-37	17	-26	24.59	7
Middle temporal cortex	21	-56	-15	-15	22.29	6
Superior temporal cortex	22	-45	-57	17	25.61	22
Hippocampus	-	-22	-12	-15	28.68	33
Retrosplenial cortex	29	0	-51	6	20.00	9

Talairach coordinates reported. BA = Brodmann's area; PFC = prefrontal cortex; mPFC = medial prefrontal cortex.

fMRI

Self-projection of Self versus Other

The results of the self versus other self-projection revealed a dorsal versus ventral distinction in mPFC (see Table 1 and Figure 2). There was greater activity in the dorsal mPFC during SPO compared to SPS (Figure 2A). Additionally, the SPO >

SPS contrast revealed greater recruitment of right dorsolateral PFC and ventral parietal cortices. In contrast, there was greater recruitment of the ventral mPFC during self versus other self-projection (Figure 2B). Additionally, the SPS > SPO contrast revealed greater recruitment in several regions associated with AM retrieval (Cabeza & St. Jacques, 2007), including the left hippocampus, lateral temporal, posterior midline, and bilateral ventrolateral PFC. Interestingly, the difference between SPS versus SPO was reflected by less deactivation in ventral mPFC but greater activity in dorsal mPFC, which is a pattern of findings consistent with others (Gusnard, Akbudak, Shulman, & Raichle, 2001), and linked to a default state of cognitive processing (Gusnard, Raichle, & Raichle, 2001). In sum, these results suggest that ventral versus dorsal subregions of PFC contribute to separable forms of self-projection.

Parametric Modulation of Behavior

In order to directly link activation differences in self-projection to behavior, we examined activity in the above regions that was modulated on each trial by the extent of reliving in the case of SPS, and understanding in the case of SPO (see Table 2 and Figure 3). We found greater modulation of ventral mPFC during highly relived trials for SPS, but no modulation by understanding in this same region for SPO. In contrast, there was greater modulation of dorsal mPFC by better understanding for SPO, but no modulation in this region by reliving for SPS. In sum, these results show that activity in ventral mPFC is sensitive to reliving when taking one's own past perspective during memory retrieval, whereas activity in dorsal mPFC is sensitive to better understanding when projecting one's self onto a different mental perspective.

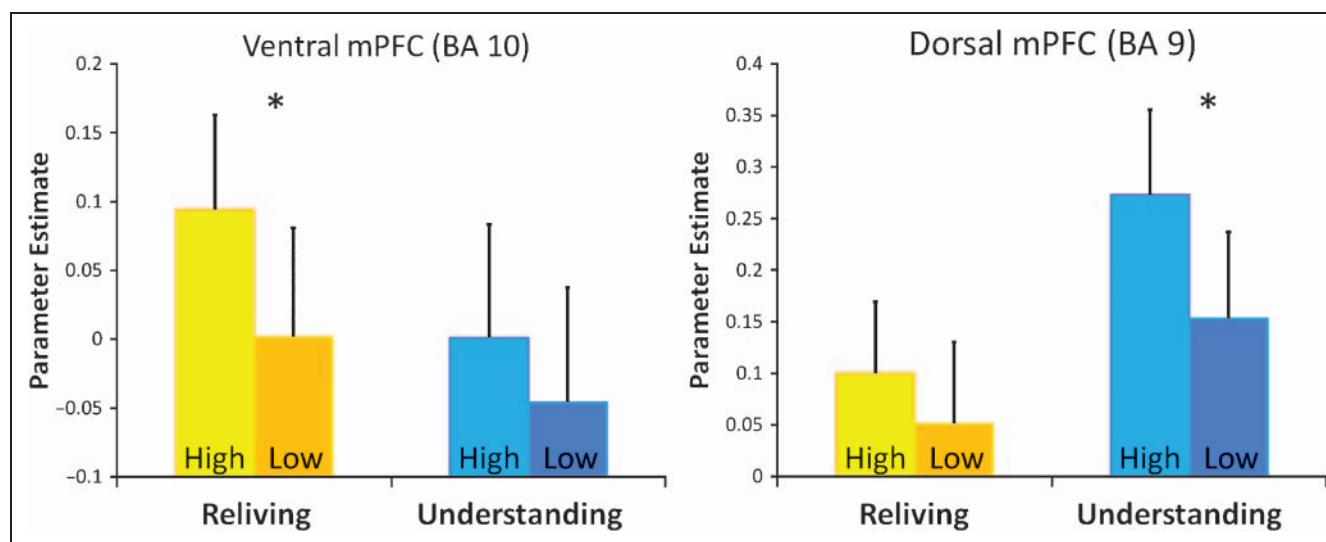


Figure 3. Parametric modulation of behavior. Ventral versus dorsal mPFC modulated the amount of reliving during self-projection of one's own self (SPS) and the amount of understanding during self-projection of another perspective (SPO), respectively. The graphs depict high and low ratings based on a median split; however, the parametric analysis is based on the continuous ratings. BA = Brodmann's area.

Task-related Functional Connectivity Analysis

For examining functional connectivity, we used the peak voxels identified in the ventral and dorsal mPFC regions engaged by self versus other self-projection as seed voxels in individual trial-based analyses. These analyses revealed that ventral versus dorsal mPFC showed task-related functional connectivity with MTL and fronto-parietal networks (see Table 3 and Figure 4). Ventral mPFC showed greater coactivation with the left hippocampus and precuneus, compared to dorsal mPFC. In contrast, dorsal mPFC showed

greater coactivation with bilateral frontal and parietal regions, compared to ventral mPFC. The pattern of functional connectivity of these ventral versus dorsal mPFC regions is consistent with previous studies examining spontaneous patterns of coherent activity during passive resting state, which have revealed an MTL network (Kahn et al., 2008; Vincent et al., 2006) and a fronto-parietal network (Vincent et al., 2008). In sum, the findings from the functional connectivity analysis provide strong support for the dissociable role of dorsal versus ventral mPFC in self versus other self-projection.

Table 3. Task-related Functional Connectivity of Medial Prefrontal Cortex during Self-projection of Self vs. Other

Region	BA	x	y	z	t	Voxels
<i>SPO > SPS</i>						
Dorsal mPFC	9	-7	38	30	17.08	645
Dorsolateral PFC	9	-52	24	34	4.8	132
	9	45	35	37	3.35	2
	46	48	37	16	3.29	4
Ventrolateral PFC	47	-52	36	-2	4.84	29
	47	-52	18	-4	4.19	11
Orbito-frontal cortex	11	-45	43	-18	4.32	30
	11/47	48	43	-9	3.72	5
Fronto-polar cortex	10	26	51	-3	3.61	2
Caudate	-	-22	21	-7	4.55	11
	-	22	21	-7	5.71	48
Middle temporal cortex	21	-56	-30	-11	3.4	4
	21	63	-33	-14	3.46	14
	21	67	-26	-8	3.23	2
Superior temporal cortex	41	41	-33	5	3.66	3
Precuneus	7	15	-78	46	3.82	2
Dorsal parietal cortex	7/40	-45	-48	55	6.04	300
	7/40	48	-49	48	5.02	162
Cerebellum	-	-37	-60	-29	4.54	83
	-	-15	-81	-22	3.79	5
	-	37	-67	-25	4.67	42
<i>SPS > SPO</i>						
Ventral mPFC	10	-7	55	1	17.3	277
Hippocampus	-	26	-22	-12	4.11	2
Precuneus	7	-11	-49	48	5.09	2

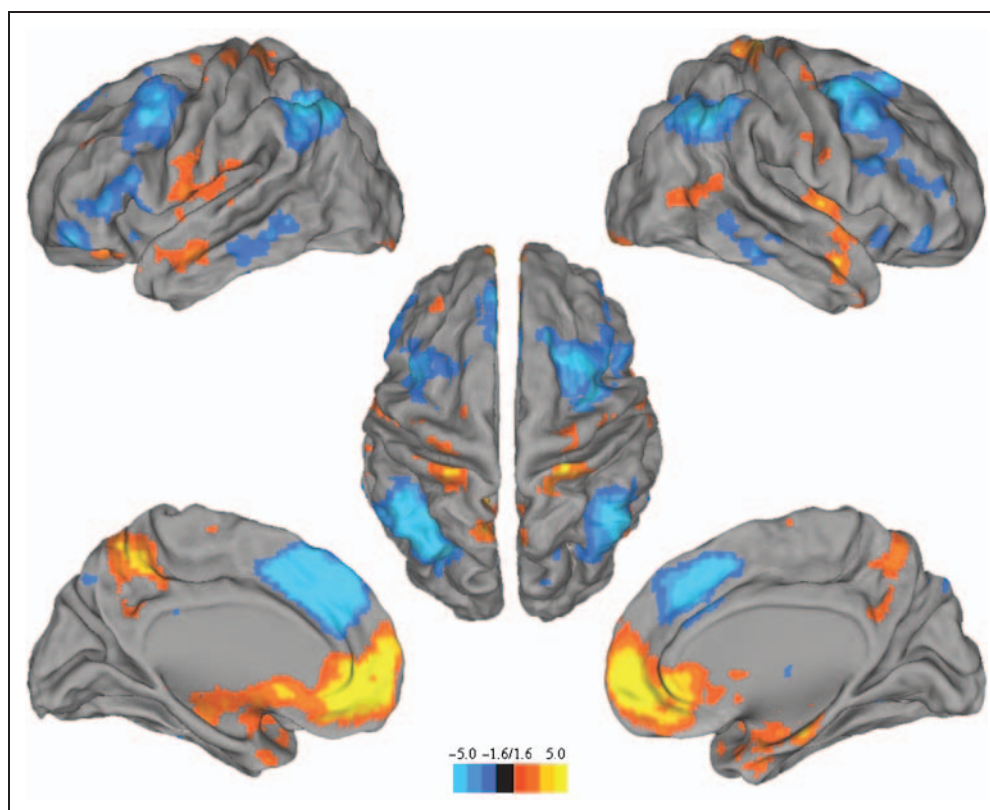
Talairach coordinates reported. BA = Brodmann's area; PFC = prefrontal cortex; mPFC = medial prefrontal cortex.

DISCUSSION

The present fMRI study investigated the neural mechanisms underlying self-projection to the personal past and into the life of another person within the same individuals via naturalistic stimuli that were prospectively generated using a novel camera technology. Our data indicate that there is a ventral versus dorsal distinction in mPFC during self-projection relying on shifts in perspective from one's own self versus another individual. There were three main findings supporting this result. First, we found that temporal self-projection into the personal past recruited greater ventral mPFC, whereas mental self-projection into another person's perspective recruited greater dorsal mPFC. Second, activity in ventral versus dorsal mPFC was sensitive to parametric modulation on each trial by the ability to relive the personal past or to understand another's perspective. Third, task-related functional connectivity analysis revealed that ventral mPFC contributed to the medial temporal lobe network linked to memory processes, whereas dorsal mPFC contributed to the fronto-parietal network linked to controlled processes.

mPFC is a critical node in the network of regions supporting tasks relying on self-projection such as AM retrieval (Mitchell, 2009; Spreng et al., 2009; Buckner & Carroll, 2007) and ToM (Mitchell, 2009; Spreng et al., 2009; Buckner & Carroll, 2007). Here we show that ventral versus dorsal mPFC may differentially support self versus other forms of self-projection during these tasks. The mPFC coordinates reported here also overlap with those found by a previous meta-analysis on social cognition (Van Overwalle, 2009) and one on self-referential processing (Northoff et al., 2006). The exact role of particular subregions within mPFC has been a matter of considerable debate, with some studies observing recruitment of ventral mPFC when making inferences about one's own self and dorsal mPFC when mentalizing about others (Krueger et al., 2009; Van Overwalle, 2009; also see Spreng et al., 2009), and other studies observing that both dorsal and ventral mPFC recruited during self-referential processes (Northoff et al., 2006). The recruitment of particular subregions of mPFC during self-projection may vary according to the degree of personal relevance. Consistent with this idea, in a series of studies, Mitchell and colleagues (Ames, Jenkins, Banaji, & Mitchell, 2008; Jenkins, Macrae, & Mitchell, 2008; Mitchell,

Figure 4. Task-related functional connectivity analysis. Ventral versus dorsal mPFC were functionally connected to separate neural networks during self-projection of one's own self (SPS; orange/red activation) versus self-projection of another perspective (SPO; blue activation). The activation in showing the results of the functional connectivity in each condition was projected to the cortical surface using CARET.



Macrae, & Banaji, 2006; Mitchell, Banaji, & Macrae, 2005) found that ventral mPFC was recruited to a greater extent when mentalizing about similar others (e.g., people with the same political beliefs), presumably because they could rely more on the retrieval of information from their own life. In contrast, dorsal mPFC was recruited more when making inferences about dissimilar others. In the case of the current study, we found dorsal mPFC for a dissimilar other and ventral mPFC for a very similar other—one's own past self. Two previous studies investigating self-projection within the same individuals also found greater recruitment of ventral mPFC for AM versus ToM, but they did not observe differences in the recruitment of dorsal mPFC (Rabin et al., 2010; Spreng & Grady, 2010). Control over the use of the first-person perspective during self-projection (e.g., D'Argembeau et al., 2007), employment of naturalistic dynamic visuospatial cues, and other methodological differences may potentially account for the observed difference between the current and previous studies.

The recruitment of mPFC also modulated the extent of self-projection to the personal past or into the life of another person. Ventral mPFC was recruited to a greater extent when temporal self-projection involved greater re-experience of the personal past as measured by subjective ratings of the amount of reliving. These results are consistent with prior functional neuroimaging studies showing that ventral mPFC is sensitive to the ability to re-experience the self in time during AM (Levine et al., 2004; Maguire & Mummery, 1999), and with patient studies

showing that lesions with overlap here impair the subjective experience of re-experiencing the personal past (Wheeler & Stuss, 2003). In contrast, dorsal mPFC was recruited to a greater extent when mental self-projection involved better understanding of another person's perspective. Dorsal mPFC is recruited during tasks that rely on evaluation (Northoff et al., 2006) such as during impression formation of another individual (Mitchell, Neil Macrae, & Banaji, 2005). The sensitivity of dorsal mPFC to better understand a dissimilar other may reflect increased reliance on rule-based strategies to infer an alternative perspective.

Ventral versus dorsal mPFC were functionally connected to separate neural networks, which differentially contributed to self-projection. Ventral mPFC showed greater functional connectivity with the hippocampus and precuneus, a pattern of results consistent with the MTL network supporting memory (Kahn et al., 2008; Vincent et al., 2006), whereas dorsal mPFC showed greater functional connectivity with lateral frontal, fronto-polar, and dorsal parietal cortices, a pattern of functional connectivity which is consistent with the fronto-parietal network supporting controlled processes (Vincent et al., 2008). The MTL network is a subsystem of the default network, the set of brain regions that are coactive during passive resting states and associated with internally directed processes such as memory (Buckner et al., 2008). Greater involvement of the MTL network during self-projection to the personal past is consistent with the idea that the ability to take one's own perspective may rely upon the recovery of memory details. In

contrast, the fronto-parietal network supports the initiation and flexible adjustment of controlled processes (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008). Vincent et al. (2008) suggested that the fronto-parietal network may contribute to the integration between externally directed attention and internally directed thought, given that it is anatomically juxtaposed between the dorsal attention and default networks. These types of controlled processing may be particularly important during self-projection into the life of another person, which potentially involves greater integration between an externally presented perspective and internally directed processes. The functional dissociation between the neural networks supporting self-projection observed in the present study is also consistent with evidence that AM and ToM are independent (Rosenbaum, Stuss, Levine, & Tulving, 2007).

Although mPFC is frequently observed in tasks relying on self-projection (Spreng et al., 2009), it is also one of the most frequent regions observed during emotional tasks (Phan, Wager, Taylor, & Liberzon, 2002). Very few studies have controlled for both self-reference and emotion within the same individuals, thus it is difficult to definitively distinguish these processes (for a meta-analysis, see Gilbert et al., 2006). However, one study found that ventral mPFC was sensitive to the self-relevance of stimuli irrespective of emotion (Moran, Macrae, Heatherton, Wyland, & Kelley, 2006). In the present study, the elicitation of emotional responses during self-projection was minimized because the SenseCam images depicted very recent, everyday events (attending class, studying, etc.). Moreover, the dorsal versus ventral distinction observed in the current study would be difficult to explain based on the role of these mPFC subregions in emotion (e.g., Dolcos, LaBar, & Cabeza, 2004). Thus, the pattern of results observed in the present study is more consistent with the suggestion that the ventral versus dorsal distinction in mPFC is related to differences in the nature of self-projection rather than emotion. Future studies, however, should directly manipulate the elicitation of emotion during self-projection for self versus other.

Conclusions

The dynamic visuospatial cues employed in the current study provided a novel way to investigate self-projection of one's own life or the life of another individual. We found a ventral versus dorsal distinction in the recruitment of mPFC for self versus other shifts in perspective. Further, ventral mPFC modulated the extent to which one's own perspective was re-experienced, whereas dorsal mPFC modulated the ability to understand an alternative perspective. Supporting the dissociable role of these mPFC subregions during different forms of self-projection, task-related functional connectivity analysis revealed that ventral versus dorsal mPFC were nodes in different neural networks. Ventral mPFC contributed to the MTL network linked to memory processes, whereas dorsal mPFC contributed to the fronto-parietal network linked to controlled processes.

In sum, the results of the current study suggest that mPFC contributes to shifts from the present moment to alternative self and other perspectives.

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REFERENCES

- Ames, D. L., Jenkins, A. C., Banaji, M. R., & Mitchell, J. P. (2008). Taking another person's perspective increases self-referential neural processing. *Psychological Science, 19*, 642–644.
- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience, 7*, 268–277.
- Brett, M., Christoff, K., Cusack, R., & Lancaster, J. L. (2001). Using the Talairach atlas with the MNI template. *Neuroimage, 13*, S85.
- Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Science, 1124*, 1–38.
- Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences, 11*, 49–57.
- Cabeza, R., Prince, S. E., Daselaar, S. M., Greenberg, D. L., Budde, M., Dolcos, F., et al. (2004). Brain activity during episodic retrieval of autobiographical and laboratory events: An fMRI study using a novel photo paradigm. *Journal of Cognitive Neuroscience, 16*, 1583–1594.
- Cabeza, R., & St. Jacques, P. L. (2007). Functional neuroimaging of autobiographical memory. *Trends in Cognitive Sciences, 11*, 219–227.
- D'Argembeau, A., Ruby, P., Collette, F., Degueldre, C., Baetens, E., Luxen, A., et al. (2007). Distinct regions of the medial prefrontal cortex are associated with self-referential processing and perspective taking. *Journal of Cognitive Neuroscience, 19*, 935–944.
- Dolcos, F., LaBar, K. S., & Cabeza, R. (2004). Dissociable effects of arousal and valence on prefrontal activity indexing emotional evaluation and subsequent memory: An event-related fMRI study. *Neuroimage, 23*, 64–74.
- Dosenbach, N. U., Fair, D. A., Cohen, A. L., Schlaggar, B. L., & Petersen, S. E. (2008). A dual-network architecture of top-down control. *Trends in Cognitive Sciences, 12*, 99–105.
- Gallagher, H. L., & Frith, C. D. (2003). Functional imaging of "theory of mind". *Trends in Cognitive Sciences, 7*, 77–83.
- Gilbert, S. J., Spengler, S., Simons, J. S., Steele, J. D., Lawrie, S. M., Frith, C. D., et al. (2006). Functional specialization within rostral prefrontal cortex (area 10): A meta-analysis. *Journal of Cognitive Neuroscience, 18*, 932–948.
- Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. *Proceedings of the National Academy of Sciences, U.S.A., 98*, 4259–4264.

- Gusnard, D. A., Raichle, M. E., & Raichle, M. E. (2001). Searching for a baseline: Functional imaging and the resting human brain. *Nature Reviews Neuroscience*, *2*, 685–694.
- Jenkins, A. C., Macrae, C. N., & Mitchell, J. P. (2008). Repetition suppression of ventromedial prefrontal activity during judgments of self and others. *Proceedings of the National Academy of Sciences, U.S.A.*, *105*, 4507–4512.
- Kahn, I., Andrews-Hanna, J. R., Vincent, J. L., Snyder, A. Z., & Buckner, R. L. (2008). Distinct cortical anatomy linked to subregions of the medial temporal lobe revealed by intrinsic functional connectivity. *Journal of Neurophysiology*, *100*, 129–139.
- Krueger, F., Barbey, A. K., & Grafman, J. (2009). The medial prefrontal cortex mediates social event knowledge. *Trends in Cognitive Sciences*, *13*, 103–109.
- Levine, B., Turner, G. R., Tisserand, D., Hevenor, S. J., Graham, S. J., & McIntosh, A. R. (2004). The functional neuroanatomy of episodic and semantic autobiographical remembering: A prospective functional MRI study. *Journal of Cognitive Neuroscience*, *16*, 1633–1646.
- Maguire, E. A., & Mummery, C. J. (1999). Differential modulation of a common memory retrieval network revealed by positron emission tomography. *Hippocampus*, *9*, 54–61.
- Mitchell, J. P. (2009). Inferences about mental states. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences*, *364*, 1309–1316.
- Mitchell, J. P., Banaji, M. R., & Macrae, C. N. (2005). The link between social cognition and self-referential thought in the medial prefrontal cortex. *Journal of Cognitive Neuroscience*, *17*, 1306–1315.
- Mitchell, J. P., Macrae, C. N., & Banaji, M. R. (2006). Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. *Neuron*, *50*, 655–663.
- Mitchell, J. P., Neil Macrae, C., & Banaji, M. R. (2005). Forming impressions of people versus inanimate objects: Social-cognitive processing in the medial prefrontal cortex. *Neuroimage*, *26*, 251–257.
- Moran, J. M., Macrae, C. N., Heatherton, T. F., Wyland, C. L., & Kelley, W. M. (2006). Neuroanatomical evidence for distinct cognitive and affective components of self. *Journal of Cognitive Neuroscience*, *18*, 1586–1594.
- Northoff, G., & Bermpohl, F. (2004). Cortical midline structures and the self. *Trends in Cognitive Sciences*, *8*, 102–107.
- Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., & Panksepp, J. (2006). Self-referential processing in our brain: A meta-analysis of imaging studies on the self. *Neuroimage*, *31*, 440–457.
- Phan, K. L., Wager, T., Taylor, S. F., & Liberzon, I. (2002). Functional neuroanatomy of emotion: A meta-analysis of emotion activation studies in PET and fMRI. *Neuroimage*, *16*, 331–348.
- Rabin, J. S., Gilboa, A., Stuss, D. T., Mar, R. A., & Rosenbaum, R. S. (2010). Common and unique neural correlates of autobiographical memory and theory of mind. *Journal of Cognitive Neuroscience*, *22*, 1095–1111.
- Rissman, J., Gazzaley, A., & D'Esposito, M. (2004). Measuring functional connectivity during distinct stages of a cognitive task. *Neuroimage*, *23*, 752–763.
- Rosenbaum, R. S., Stuss, D. T., Levine, B., & Tulving, E. (2007). Theory of mind is independent of episodic memory. *Science*, *318*, 1257.
- Rubin, D. C., Burt, C. D., & Fifield, S. J. (2003). Experimental manipulations of the phenomenology of memory. *Memory & Cognition*, *31*, 877–886.
- Rubin, D. C., Schrauf, R. W., & Greenberg, D. L. (2004). Stability in autobiographical memories. *Memory*, *12*, 715–721.
- Spreng, R. N., & Grady, C. L. (2010). Patterns of brain activity supporting autobiographical memory, prospection, and theory-of-mind and their relationship to the default mode network. *Journal of Cognitive Neuroscience*, *22*, 1112–1123.
- Spreng, R. N., Mar, R. A., & Kim, A. S. (2009). The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: A quantitative meta-analysis. *Journal of Cognitive Neuroscience*, *21*, 489–510.
- St. Jacques, P. L., Conway, M. A., & Cabeza, R. (under review). Gender differences in autobiographical memory for everyday events: Retrieval elicited by SenseCam images vs. verbal cues.
- St. Jacques, P. L., Rubin, D. C., Labar, K. S., & Cabeza, R. (2008). The short and long of it: Neural correlates of temporal-order memory for autobiographical events. *Journal of Cognitive Neuroscience*, *20*, 1327–1341.
- Suddendorf, T., & Corballis, M. C. (2007). The evolution of foresight: What is mental time travel, and is it unique to humans? *Behavioral and Brain Sciences*, *30*, 299–313; discussion 313–351.
- Van Overwalle, F. (2009). Social cognition and the brain: A meta-analysis. *Human Brain Mapping*, *30*, 829–858.
- Vincent, J. L., Kahn, I., Snyder, A. Z., Raichle, M. E., & Buckner, R. L. (2008). Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. *Journal of Neurophysiology*, *100*, 3328–3342.
- Vincent, J. L., Patel, G. H., Fox, M. D., Snyder, A. Z., Baker, J. T., Van Essen, D. C., et al. (2007). Intrinsic functional architecture in the anaesthetized monkey brain. *Nature*, *447*, 83–86.
- Vincent, J. L., Snyder, A. Z., Fox, M. D., Shannon, B. J., Andrews, J. R., Raichle, M. E., et al. (2006). Coherent spontaneous activity identifies a hippocampal–parietal memory network. *Journal of Neurophysiology*, *96*, 3517–3531.
- Wheeler, M. A., & Stuss, D. T. (2003). Remembering and knowing in patients with frontal lobe injuries. *Cortex*, *39*, 827–846.
- Wixted, J. T. (2007). Dual-process theory and signal-detection theory of recognition memory. *Psychological Review*, *114*, 152–176.
- Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, *46*, 441–517.