

# Functional Dissociation of Ventral Frontal and Dorsomedial Default Mode Network Components During Resting State and Emotional Autobiographical Recall

Patricia Bado,<sup>1,2</sup> Annerose Engel,<sup>1,3</sup> Ricardo de Oliveira-Souza,<sup>1,4</sup>  
Ivanei E. Bramati,<sup>1,2</sup> Fernando F. Paiva,<sup>1,5</sup> Rodrigo Basilio,<sup>1</sup> João R. Sato,<sup>1,6</sup>  
Fernanda Tovar-Moll,<sup>1,2</sup> and Jorge Moll<sup>1\*</sup>

<sup>1</sup>Cognitive and Behavioral Neuroscience Unit, D'Or Institute for Research and Education (IDOR), Rio de Janeiro, Brazil

<sup>2</sup>Instituto de Ciências Biomédicas (ICB), Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

<sup>3</sup>Music Cognition and Action Group, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

<sup>4</sup>Gaffrée e Guinle University Hospital, Federal University of the State of Rio de Janeiro, Rio de Janeiro, Brazil

<sup>5</sup>Centro de Imagens e Espectroscopia In Vivo por Ressonância Magnética (CIERMAG), Instituto de Física de São Carlos, Universidade de São Paulo, São Carlos, Brazil

<sup>6</sup>Center for Mathematics, Computation, and Cognition, Universidade Federal do ABC, Santo André, Brazil



**Abstract:** Humans spend a substantial share of their lives mind-wandering. This spontaneous thinking activity usually comprises autobiographical recall, emotional, and self-referential components. While neuroimaging studies have demonstrated that a specific brain “default mode network” (DMN) is consistently engaged by the “resting state” of the mind, the relative contribution of key cognitive components to DMN activity is still poorly understood. Here we used fMRI to investigate whether activity in neural components of the DMN can be differentially explained by active recall of relevant emotional autobiographical memories as compared with the resting state. Our study design combined emotional autobiographical memory, neutral memory and resting state conditions, separated by a serial subtraction control task. Shared patterns of activation in the DMN were observed in both emotional autobiographical and resting conditions, when compared with serial subtraction. Directly contrasting autobiographical and resting conditions demonstrated a striking dissociation within the DMN in that emotional autobiographical retrieval led to stronger activation of the dorsomedial core regions (medial prefrontal cortex, posterior cingulate cortex), whereas the resting state condition engaged a ventral frontal network (ventral striatum, subgenual and ventral anterior cingulate cortices) in addition to the IPL. Our results reveal an as yet

---

Contract grant sponsors: FAPERJ (Pronex and INNT grants) (to J.R.S.), CAPES, CNPq, and IDOR, Brazil.

\*Correspondence to: Jorge Moll, Cognitive and Behavioral Neuroscience Unit, D'Or Institute for Research and Education, Rua Diniz Cordeiro, 30/3° andar, Rio de Janeiro 22281-100, Brazil. E-mail: jorge.moll@idor.org

Received for publication 27 March 2013; Revised 9 August 2013; Accepted 4 September 2013.

DOI 10.1002/hbm.22403

Published online 6 November 2013 in Wiley Online Library (wileyonlinelibrary.com).

© 2013 The Authors Human Brain Mapping Published by Wiley Periodicals, Inc.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

unreported dissociation within the DMN. Whereas the dorsomedial component can be explained by emotional autobiographical memory, the ventral frontal one is predominantly associated with the resting state proper, possibly underlying fundamental motivational mechanisms engaged during spontaneous unconstrained ideation. *Hum Brain Mapp* 35:3302–3313, 2014. © 2013 The Authors Human Brain Mapping Published by Wiley Periodicals, Inc.

**Key words:** fMRI; default mode; autobiographical memory; emotion; functional dissociation

---

## INTRODUCTION

The idle state of the human mind has long been acknowledged by philosophers and artists. Mind-wandering is an ubiquitous psychological state, occurring not only during mental idleness but also during breaches of attention in a variety of contexts [Singer, 1975].

A seminal functional imaging study demonstrating that a specific brain network is engaged when individuals are lying quietly in the scanner without performing any specific cognitive task marked the beginning of the current investigation of the neural and psychological mechanisms underpinning this “resting state” of the brain [Raichle et al., 2001]. The brain “default mode network” (DMN) integrates functionally and anatomically diverse regions including the posterior cingulate cortex (PCC)/precuneus (Prec), the ventral anterior cingulate cortex (vACC), medial prefrontal cortex (mPFC), bilateral inferior parietal lobules (IPL), and the middle temporal gyri (MTG) [Buckner et al., 2008; Fox and Raichle, 2007; Greicius et al., 2003; Gusnard and Raichle, 2001; Raichle et al., 2001; for meta-analyses, see Laird et al., 2009; Schilbach et al., 2008, 2012]. The DMN shows ongoing intrinsic activity during resting wakefulness [Greicius et al., 2003], sleep [Fukunaga et al., 2006; Horowitz et al., 2008], and superficial anesthesia [Greicius et al., 2008]. Despite important advances, the functional role of different brain networks implicated in the DMN and their specific underlying cognitive mechanisms remains poorly understood.

Functional imaging studies have suggested that internally driven functions, such as episodic or autobiographical memory [Spreng and Grady, 2010], emotional experience [Harrison et al., 2008b; Pitroda et al., 2008], and self-projection [Buckner and Carroll, 2007] may each be involved in DMN activity. Consistent with this assumption, a large overlap between regions implicated in emotional processing, social and moral cognition and those activated during resting state has been reported [Bzdok et al., 2012; Harrison et al., 2008a; Schilbach et al., 2008, 2012]. Moreover, spontaneous autobiographical recall, when social-emotional memories are pervasive [Conway and Pleydell-Pearce, 2000], has been consistently reported during the resting state [Fransson, 2005; Mazoyer et al., 2001]. Although other studies have described a degree of fractionation of DMN components [e.g., Andrews-Hanna et al., 2010], no study has so far directly contrasted emotional autobiographical memory with resting state conditions in order to investigate whether brain activity elicited by emotional autobiographical memory

explains the engagement of DMN components beyond unconstrained stimulus-independent ideation.

Here we asked whether the activity in DMN core regions could be explained by emotional autobiographical recall of personally salient life events, using an explicit autobiographical recall task. We also explored whether other DMN subcomponents would still be more strongly engaged during resting state as compared with emotional autobiographical recall. For this purpose, we used functional magnetic resonance imaging (fMRI) at 3 T to investigate 15 healthy adults while they engaged in a resting state, emotional or neutral autobiographical recall, and in a cognitively demanding serial subtraction task. Our findings provide strong support for a functional dissociation in dorsomedial and ventral frontal sectors of the DMN: whereas “core” DMN regions (medial PFC and PCC/Prec) were more strongly recruited by explicit emotional autobiographical recall than during rest, the ventral frontal sectors of the DMN (ventral striatum, vACC, and subgenual cortex) were more robustly engaged by the resting condition.

## MATERIALS AND METHODS

### Participants

Eighteen adult healthy volunteers participated in the fMRI study. Data from three participants were discarded due to signal dropouts in basal forebrain extending beyond its ventral-posterior area or excessive movement, beyond 2 mm translation or 2°. The final dataset included 15 participants (seven women; age =  $26 \pm 3.5$  years). All participants were right-handed according to the Edinburgh handedness inventory [Oldfield, 1971], native Portuguese speakers and had normal or corrected-to-normal vision. Participants had no history of psychiatric or neurological disorders, and were not taking centrally active medications. Written informed consent was obtained from all participants. The study was conducted in accordance with ethical standards compliant with the declaration of Helsinki and approved by the D’Or Institute Ethics and Scientific Committees.

### Autobiographical Interview and Stimulus Customization

Before scanning participants provided detailed contextual information on the to-be-remembered episodes in an autobiographical interview and chose a cue word to be

presented during the fMRI experiment as a trigger for the retrieval of the corresponding episode. Participants were required to remember different autobiographical episodes that included a second person. Emotional valence was controlled by having participants generate six neutral, six pleasant (positive valence) and six unpleasant (negative valence) autobiographical episodes of their lives.

### fMRI Protocol

All stimuli were orally presented via scanner-compatible headphones (Philips Medical Systems, The Netherlands). Functional scanning was completed in approximately 60 min. The fMRI paradigm used a slow event-related design with data acquisition done in two runs, each consisting of nine autobiographical trials (three positive, three negative, and three neutral events, length of condition each 132 s), three resting trials (132 s), and 12 serial subtraction trials (33 s). During scanning, participants retrieved the pre-defined autobiographical episodes in the autobiographical conditions. In the resting state, they were instructed to relax and stay awake while not engaging in any specific task or memory. The autobiographical and resting trials were presented in a pseudo-random order and were each followed by the serial subtraction task, in which participants performed serial subtractions of 7's from an arbitrary number. Each trial started with an auditory instruction presenting either the autobiographical cue, the Portuguese equivalent for the word "rest" for resting trials, or a randomly chosen start number higher than 99 for the serial 7's subtractions (Fig. 1).

After scanning, participants rated each of the 18 autobiographical episodes on a computer according to (a) degree of affiliative emotions ("care/tenderness"; 10-point rating scales with anchor points 0 = "absent" and 9 = "very intense"), (b) emotional valence (15-point rating scales with anchor points 7 = "very unpleasant" and 7 = "very pleasant", 0 = "neutral"), (c) arousal (10-point rating scales with anchor points 0 = "absent" and 9 = "very intense") and (d) vividness of visual imagery (VVIQ Questionnaire; 5-point rating scale ranging from 4 = "perfectly clear and as vivid as normal vision" and 0 = "no image at all, you only "know" that you are thinking of an object").

### Statistical Analysis of Behavioral Data

Results are expressed as means and standard deviations. The behavioral effects of the age of autobiographical episodes and emotional arousal ratings were assessed with *t*-tests for pairwise comparisons. VVIQ ratings among autobiographical conditions were assessed with one-way analysis of variance. A significance threshold ( $\alpha$ ) of .05, two-tailed, was adopted for all statistical tests.

### Image Acquisition and Analysis

For each run, 1,200 functional images were acquired with a 3 T Achieva scanner (Philips Medical Systems, The

Netherlands) using an eight-channel SENSE head coil and a single-shot T2\*-weighted fast-field echo (FFE) echo-planar imaging (EPI) sequence (TR = 1,650 ms, TE = 22 ms, matrix = 80 × 80, FOV = 240 mm, flip angle = 90°, 3 mm isotropic voxel size, 29 slices with no gap in ascending acquisition order). Before each run, five dummy volumes were collected for T1 equilibration purposes. A SENSE factor of 2 and "dynamic stabilization" were additionally employed. These parameters were based on careful sequence parameter optimization in order to maximize temporal signal-to-noise [Bellgowan et al., 2006; Bodurka et al., 2007] in brain regions that normally suffer from magnetic susceptibility effects, including the basal forebrain areas and ventromedial regions of the prefrontal cortex. Reference anatomical images were acquired using a T1-weighted three-dimensional magnetization-prepared, rapidly acquired gradient echo (MP-RAGE) sequence (TR/TE = 7.2/3.4s, matrix/FOV = 240/240 mm, flip angle = 90°, 1 mm isotropic voxel size, 170 sagittal slices). Head motion was restricted with foam padding and straps over the forehead and under the chin (estimated translation and rotation parameters were inspected and never exceeded 2 mm or 2°). Statistical Parametric Mapping (SPM8; available at: [www.fil.ion.ucl.ac.uk/spm/software/spm8](http://www.fil.ion.ucl.ac.uk/spm/software/spm8)) implemented in Matlab R 2009b (The Mathworks Inc.; available at: <http://www.mathworks.com>) was used for image

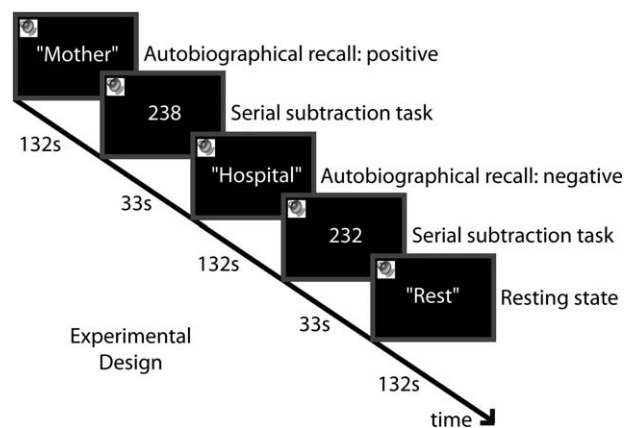


Figure 1.

Experimental design. Schematic representation of the time course during fMRI scanning in which each participant was presented with auditory cues indicating different experimental conditions. For the three autobiographical conditions (positive, negative and neutral), words predefined by each participant were presented to indicate specific memories. Numbers cued the starting point for performing serial subtractions. The Portuguese equivalent to the word "rest" was presented to cue the beginning of resting blocks. The length of each block was 132 s for the autobiographical and resting conditions and 33 s for the serial subtraction condition. Blocks of the autobiographical and resting conditions were presented pseudo-randomly and separated from each other by serial subtraction blocks.

analysis [Friston, 1995; Worsley and Friston, 1995]. Functional datasets were preprocessed by realigning all volumes of each subject to the mean image generated for each run, and by applying slice time correction. Functional images were co-registered and normalized to the standard MNI EPI template (Montreal Neurological Institute brain template), using 12-parameter affine normalization. The voxel dimensions of each reconstructed functional scan were  $3 \text{ mm} \times 3 \text{ mm} \times 3 \text{ mm}$ . Functional images were also spatially smoothed using an 8 mm full-width half-maximum (FWHM) Gaussian spatial kernel. Unwanted low frequencies in the fMRI time series were removed with high-pass filtering (384 s) and cubic detrending [Macey et al., 2004].

In the first level analysis, pre-processed images of each participant were analyzed with a General Linear Model comprising five predictors: (1) episodes for positive autobiographical memory (POS); (2) episodes for negative autobiographical memory (NEG); (3) episodes for neutral autobiographical memory (NEUTR); (4) resting (REST); (5) serial subtraction task (SUBTR). All predictors were modeled as a boxcar function with a length of 132 s for predictors (1–4) and a length of 33 s for predictor (5) and convolved with the canonical hemodynamic response function [Zarahn et al., 1997]. In the first level analyses, categorical contrasts were generated for POS versus SUBTR, NEG vs. SUBTR, NEUTR versus SUBTR, REST versus SUBTR. The four resulting contrast images of each subject were submitted to a second level one-way analysis of variance (ANOVA) in order to calculate a logical AND conjunction [Nichols et al., 2005] to identify brain areas activated commonly in all four contrasts. Further contrasts generated in the first level comprised [(POS + NEG) vs. REST], [REST vs. (POS + NEG)], [NEUTR vs. REST], [REST vs. NEUTR] and the resulting contrast images of each subject were each entered into a second level one sample *t*-test.

Significance was determined by combining an uncorrected voxel-level threshold of  $P < 0.005$  (minimum cluster size of 5 voxels) in a whole brain analysis and small volume correction (SVC) for multiple comparisons in a priori defined regions of interest (ROI). Only clusters of activation with a threshold of  $P < 0.05$ , family wise error (FWE) corrected for multiple comparisons on a cluster level were considered. The single ROI comprised 13 brain areas known to be involved in the DMN. Respective MNI coordinates (*x*, *y*, *z*) were derived from a previous meta-analysis [Laird et al., 2009; PCC:  $-3$ ,  $-52$ ,  $25$ ; Prec:  $-2$ ,  $-56$ ,  $50$ ; vACC:  $3$ ,  $35$ ,  $-17$ ; mPFC:  $-1$ ,  $57$ ,  $10$ ; left middle frontal gyrus:  $-27$ ,  $23$ ,  $43$ ; left IPL:  $-59$ ,  $-34$ ,  $31$ ; right IPL:  $58$ ,  $-26$ ,  $24$ ; left middle temporal gyrus:  $-44$ ,  $-67$ ,  $23$ ; right middle temporal gyrus:  $51$ ,  $-67$ ,  $19$ ) and three other independent studies for the basal regions ([Di Martino et al., 2008]; left ventral striatum:  $-9$ ,  $9$ ,  $-8$ , and right ventral striatum:  $9$ ,  $9$ ,  $-8$ ); [Zahn et al., 2009] (SGC:  $0$ ,  $26$ ,  $-5$ ); [Moll et al., 2012; anterior hypothalamus/septal area:  $-3$ ,  $2$ ,  $-14$ ]. We included the SGC, bilateral striatum and ante-

rior hypothalamus/septal area as a priori ROIs since the vACC cluster often encompasses the neighboring medial and ventral portions of the striatum, extending into the septal area, in several studies [for a meta-analysis see Schilbach et al., 2012], including the present study.

For each single brain area, a ROI was created by drawing a sphere with a radius of 10 mm around the peak coordinates. These single ROIs were combined in a second step to one ROI and used for SVC. Displays of activations were created by means of the software package MRICron (available at: <http://www.sph.sc.edu/comd/rorden/mri-cron/>) by superimposing SPM *t*-maps resulting from the second level analysis maps on an MNI standard brain ( $P < 0.005$  uncorrected, cluster size  $\geq 5$  voxel).

Finally, a functional connectivity analysis was carried out by extracting the time courses of the a priori DMN regions [Laird et al., 2009] and also from ventral frontal regions (bilateral vSTR, SGC) [Di Martino et al., 2008; Zahn et al., 2009] using Marsbar SPM toolbox (available at: <http://marsbar.sourceforge.net/>). The mean BOLD signal (from preprocessed images) of each ROI was extracted and filtered with a Butterworth high-pass filter with a cut-off of 50 s. Pearson's correlation coefficients between these signals at each experimental condition were calculated in order to obtain a measure of functional connectivity (pairwise). The significance of contrasts between different conditions across subjects was then assessed with paired *t*-tests of these correlation coefficients. The functional connectivity analysis was performed with the R software (available at: <http://www.r-project.org>).

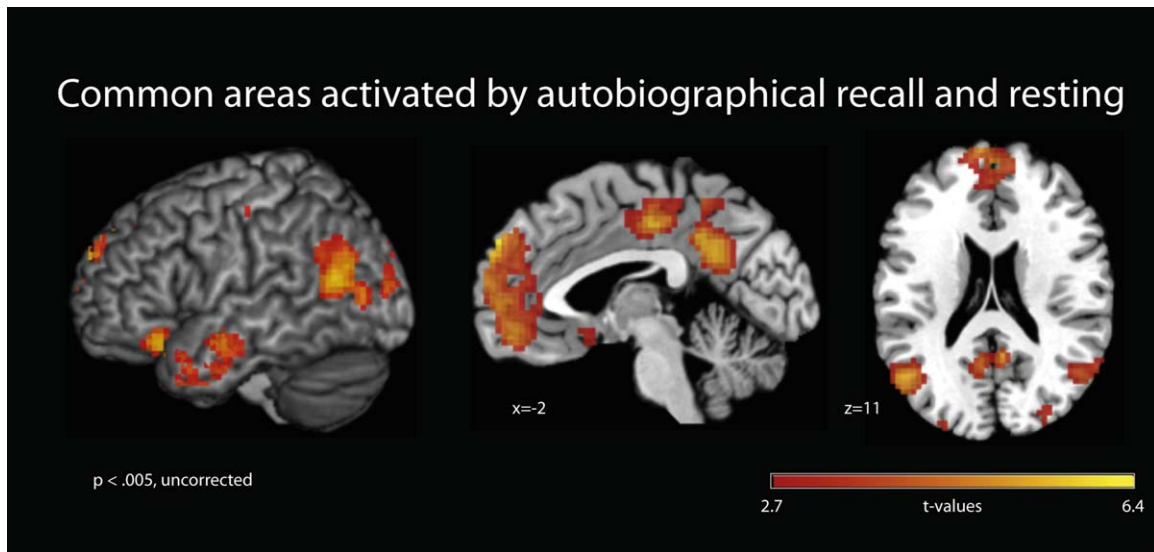
## RESULTS

### Behavioral results

Autobiographical conditions did not differ in age of emotional episodes (positive:  $3.5 \pm 2.2$  years; negative:  $4.3 \pm 2.6$  years,  $t_{(14)} = 0.96$ ,  $P = 0.34$ ), but neutral episodes were in general more recent in age of occurrence than positive and negative ones ( $0.1 \pm 0.2$  years;  $t_{(28)} = 8.86$ ;  $P < 0.001$ ). Emotional arousal ratings had a trend towards significance between the positive ( $6.8 \pm 1.4$ ) and negative conditions ( $5.9 \pm 1.18$ ,  $t_{(28)} = 2.01$ ;  $P = 0.05$ ), and were higher for the emotional episodes when compared with the neutral ones ( $6.39 \pm 1.24$  vs.  $3.40 \pm 2.67$ ;  $t_{(28)} = 3.94$ ;  $P < 0.001$ ). Finally, the vividness of the recalled episodes did not differ among the autobiographical conditions (positive:  $2.9 \pm 0.45$ ; negative:  $2.6 \pm 0.58$ ; neutral:  $2.7 \pm 0.8$ ;  $F_{(2,14)} = 1.25$ ;  $P = 0.30$ ).

### Functional Imaging Results

To explore brain areas shared by emotional (positive and negative) and neutral autobiographical recall, and resting conditions, we performed a conjunction analysis that included the contrasts of each of these four conditions



**Figure 2.**

Common default mode regions. Extent of activations in regions of the default mode network for the three autobiographical and resting conditions, compared with the serial subtraction task (conjunction analysis). Statistical parametric maps are overlaid on an MNI standard brain using a threshold of uncorrected  $P =$

0.005 and a minimum cluster extent of  $k = 5$  voxels (for display purposes). Colorbars indicate t-values. MNI: Montreal Neurological Institute. [Color figure can be viewed in the online issue, which is available at [wileyonlinelibrary.com](http://wileyonlinelibrary.com).]

compared with the serial subtraction condition. The analysis revealed robust effects ( $P < 0.05$ , corrected for multiple comparisons using family wise error [FWE] correction at cluster level) in the PCC/Prec, mPFC, and the bilateral IPL reaching into posterior superior temporal sulcus (STS) and temporal parietal junction (TPJ; Table I; Fig. 2). All these regions were previously described as belonging to the DMN [Greicius et al., 2003; Laird et al., 2009; Raichle et al., 2001].

To assess the effect of emotional recall on the DMN, the emotional autobiographical conditions were contrasted with the resting state condition. A robust activation ( $P < 0.05$ , FWE corrected at cluster level) of the mPFC and PCC/Prec was observed within our ROI (Table II), in addition to dorsomedial thalamus among other areas when considering the whole brain (see Fig. 3a). No activation in the mPFC and PCC/Prec or in other brain areas were found for the neutral autobiographical memory condition versus rest (Table II; Fig. 3b) at the same significance level ( $P < 0.05$ , FWE corrected at cluster level). To further explore the spatial consistency of these effects in the mPFC and PCC/Prec in the context of previous studies, we extracted the parameter estimates (beta values) for a priori selected coordinates of these anatomical regions based on a recent meta-analysis [Laird et al., 2009]; Figure 3(c,d). This confirmed that activations in the mPFC and PCC/Prec were stronger in the emotional autobiographical conditions, but not in the neutral condition, as compared with rest.

Finally, to identify whether any components of the DMN showed increased hemodynamic responses during the rest condition, the reverse contrasts were investigated. Contrasting the rest condition against either the emotional or neutral autobiographical conditions revealed robust activation ( $P < 0.05$ , FWE corrected at cluster level) in the regions comprising the medial aspect of the ventral striatum (vSTR), extending dorsally into the septal region,

**TABLE I. Common brain activation during positive, negative and neutral autobiographical recall conditions and resting state when contrasted with the serial subtraction condition (conjunction analysis)**

Anatomical region	Cluster size	MNI coordinates			Z-score
		x	y	z	
Posterior cingulate cortex	127	3	-52	28	5.35
Medial prefrontal cortex	138	0	59	16	4.71
Left IPL/STS/TPJ	87	-45	-70	22	4.99
Right IPL/STS/TPJ	66	54	-67	13	4.18

The values shown are Montreal Neurological Institute (MNI) coordinates for significant activation maxima of clusters in the random effects analyses ( $P < 0.05$ , family-wise error corrected for multiple comparisons on the cluster level).

IPL, inferior parietal lobe; STS, superior temporal sulcus; TPJ, temporal parietal junction.

**TABLE II. Brain Activations During Emotional Autobiographical Recall Versus Resting Condition**

Anatomical region	Cluster size	MNI coordinates			Z-score
		x	y	z	
Medial prefrontal cortex	44	-3	62	10	4.69
Posterior cingulate cortex	107	-3	-58	25	4.34

Values represent Montreal Neurological Institute (MNI) coordinates for significant activation maxima of clusters in the random effects analyses ( $P < 0.05$ , family-wise error corrected for multiple comparisons on the cluster level).

subgenual cortex (SGC) and vACC (Table III; Fig. 4a,b). Additionally, significant activations at the same significance level were found in the bilateral IPL's in the rest versus autobiographical emotional recall contrast. To better illustrate this result, we extracted the parameter estimates using a priori coordinates for the vSTR bilaterally [Di Martino et al., 2008], the SGC [Zahn et al., 2009] and the vACC from the same meta-analysis on resting state studies [Laird et al., 2009]; Figure 4(c,d,e,f). All these regions showed stronger activation in the rest condition when compared with each of the memory retrieval conditions.

### Functional Connectivity Results

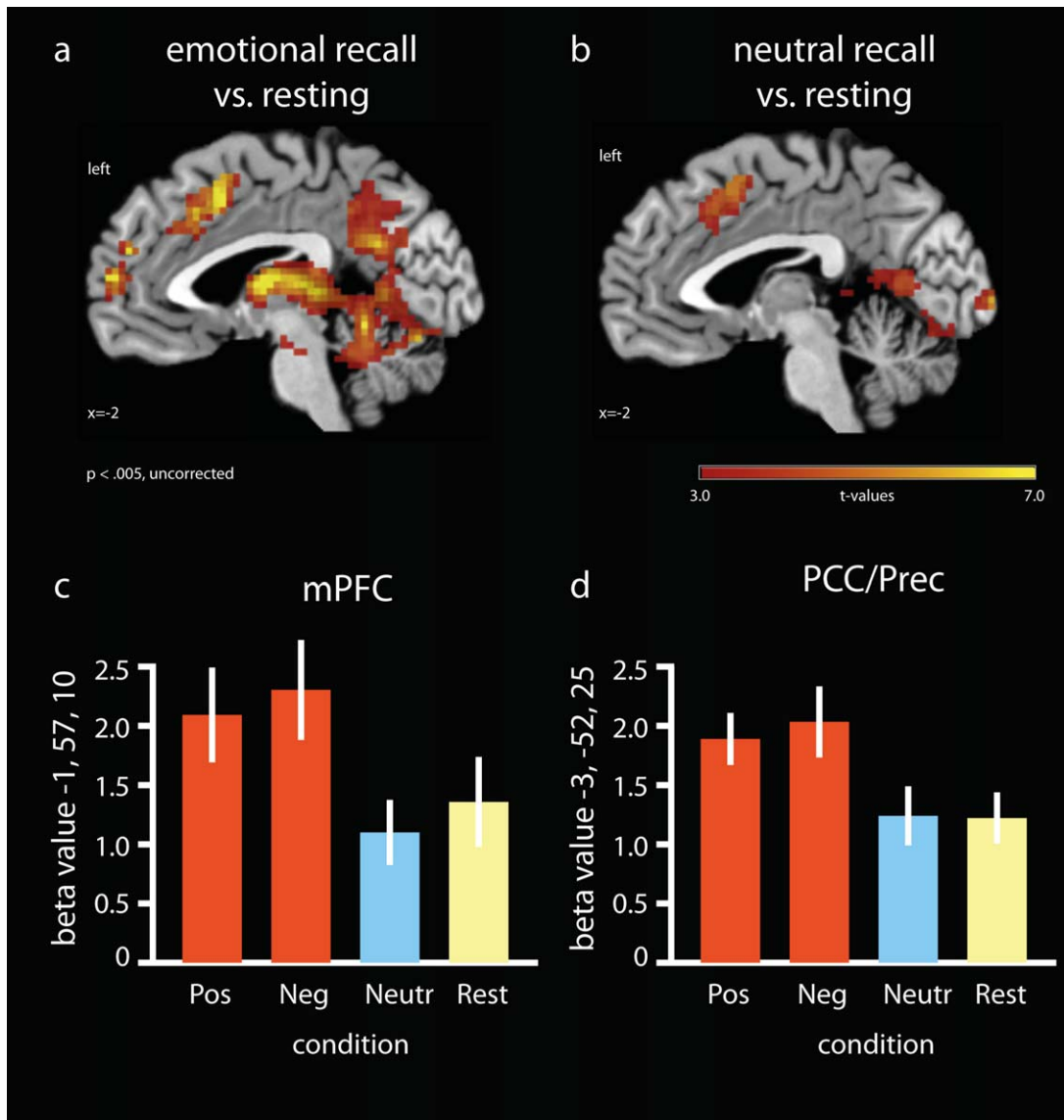
Considering that the mPFC and the PCC/Prec showed increased BOLD responses to the emotional autobiographical recall conditions when compared with rest, we investigated whether BOLD effects were associated with changes in functional connectivity. To this aim, we correlated the time-series of the hemodynamic response observed in these two core regions of the DMN (mPFC and PCC/Prec). Functional connectivity between mPFC and PCC was higher in emotional autobiographical recall conditions as compared with rest (Table IV). A similar analysis performed on the time series of the ventral frontal regions showing higher BOLD responses in the resting versus autobiographical conditions (vACC/SGC and bilateral vSTR) revealed neither significant nor even trend differences in the connectivity strength among these regions when comparing autobiographical and rest conditions (see correlation coefficients in Table IV).

### DISCUSSION

The main finding of our study was the observation of a dorsoventral dissociation in which activation of dorso-medial regions of the DMN (mPFC and PCC/Prec) were more strongly associated with emotional autobiographical recall, whereas activity in ventral frontal regions (ACC, vACC, and vSTR), along with the IPLs, were more robustly engaged during rest. We investigated whether

activity in components of the DMN could be better accounted for by the explicit engagement in emotional autobiographical recall or, alternatively, for unconstrained thoughts during the resting state. To allow for direct comparisons between conditions, our design employed relatively long, interspersed blocks of autobiographical memory and rest. As expected, shared activation in the core regions of the DMN (mPFC and PCC/Prec) was observed when comparing the autobiographical or resting conditions with the serial subtraction task.

Shared DMN regions between the autobiographical recall and resting state have been previously reported [Spreng and Grady, 2010; Spreng et al., 2009]. However, these studies did not directly compare rest with other conditions, such that potential differences between these processes remained unexplored. Using an experimental design in which the resting condition was embedded within the same functional run as the other conditions allowed us to directly contrast these cognitive states, and quantitatively explore both their similarities and distinctions. The stronger hemodynamic responses in the mPFC and PPC/Prec in the emotional autobiographical versus rest contrasts, but not in the neutral autobiographical versus rest comparison, suggest a key role of these two core components of the DMN for emotional episodic recall. This finding is corroborated by the results of the functional connectivity analysis, which showed increased coupling between the mPFC and the PPC/Prec in the emotional autobiographical memory conditions when compared with rest, but not for the neutral autobiographical memory condition (compared with rest). These results are consistent with previous research that implicated the mPFC and the PPC/Prec in autobiographical memory [Cabeza and St Jacques, 2007; Svoboda et al., 2006] and emotional processing [Maddock, 1999; Phan et al., 2002], including affiliative emotion [Moll et al., 2012]. In addition, a recent electrophysiological study [Foster et al., 2012] demonstrated an increase in the human posteromedial cortex activity during autobiographical episodic memory retrieval that was proportional to the activity suppression in the same region during arithmetic calculation. This associated response was observed during autobiographical memory condition only, and not during self-semantic nor self-judgment conditions. Moreover, the mPFC has been implicated in self-referential mechanisms [Kelley et al., 2002; Whitfield-Gabrieli et al., 2011] and functional connectivity between mPFC and PPC was related to constrained psychological functioning and world experiences [Carhart-Harris et al., 2012]. The first fMRI study comparing a resting condition with a cognitive-emotional one [Harrison et al., 2008a), namely a moral dilemma condition, also demonstrated an overlap of DMN regions across conditions, as well as a higher activity of the medial frontal cortex and ventral PCC in the moral dilemma condition compared with resting state. This study [Harrison et al., 2008a) also demonstrated higher functional connectivity in PCC and mPFC for the moral dilemma condition



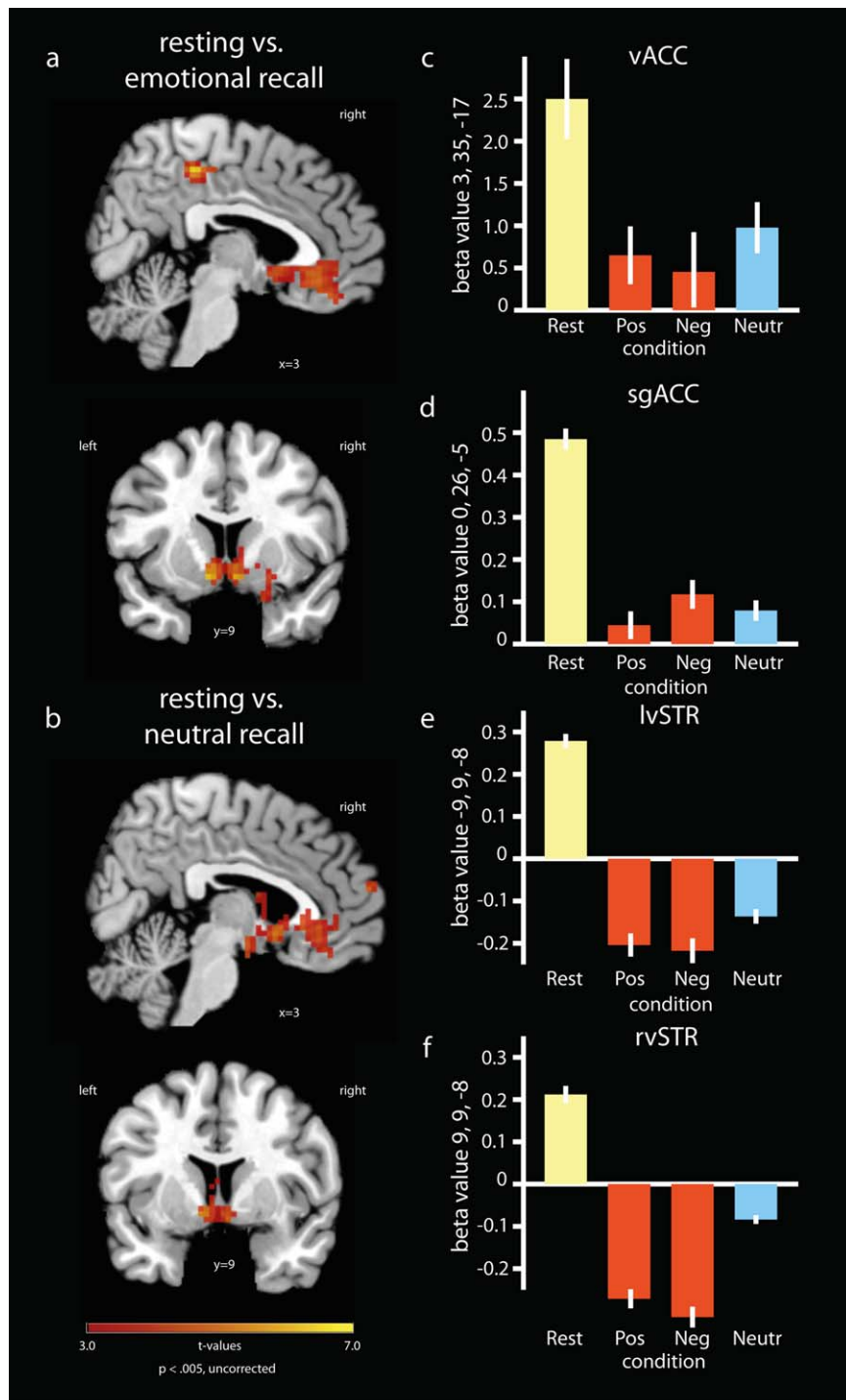
**Figure 3.**

Regions associated with autobiographical recall. Activation clusters for the contrasts (a) emotional autobiographical recall versus resting and (b) neutral autobiographical recall versus resting. Statistical parametric maps are overlaid on an MNI standard brain and thresholded at uncorrected  $P = 0.005$ , minimum cluster extent of  $k = 5$  voxels for display purposes. Bar plots show averaged beta values (in arbitrary units) for the autobiographical recall and resting conditions obtained from the same MNI coord-

inates reported in Laird et al. [2009] for (c) the medial prefrontal cortex (mPFC) and (d) the posterior cingulate cortex (PCC). Error bars show the standard error of the mean. MNI: Montreal Neurological Institute. Pos, Neg, Neutr: positive, negative, and neutral autobiographical conditions, respectively; Rest: resting state condition. [Color figure can be viewed in the online issue, which is available at [wileyonlinelibrary.com](http://wileyonlinelibrary.com).]

compared with rest. Relating these findings with the results of our study, it might be suggested that the dorso-medial components of the DMN (PCC/Prec and mPFC) may have a more specific role in task-related, emotionally-relevant self-referential cognition. Furthermore, in our study, participants were requested to imagine social scenar-

ios that generally involved “close others” (e.g. family and friends) in the emotional autobiographical memory condition. This is in line with the fact that processing personally relevant information related to close others engages sectors of the mPFC and the PPC/Prec [Buckner et al., 2008; Krienen et al., 2010].



**Figure 4.**

Regions associated with resting state. Activation clusters for the contrasts **(a)** resting versus emotional autobiographical recall and **(b)** resting versus neutral autobiographical recall. Statistical parametric maps are overlaid on an MNI standard brain and thresholded at uncorrected  $P = 0.005$ , minimum cluster extent of  $k = 5$  voxels (for display purposes). Bar plots show averaged beta values (in arbitrary units) for the resting and autobiographical recall conditions obtained from MNI coordinates described

in the Methods section for **(c)** the ventral anterior cingulate cortex (vACC), **(d)** subgenual cortex (SGC), **(e)** left ventral striatum (lvSTR), and **(f)** right ventral striatum (rvSTR). Error bars show the standard error of the mean. MNI: Montreal Neurological Institute. Pos, Neg, Neutr: positive, negative, and neutral autobiographical conditions, respectively. Rest: resting state condition. [Color figure can be viewed in the online issue, which is available at [wileyonlinelibrary.com](http://wileyonlinelibrary.com).]



**TABLE III. Brain Activation During Resting Versus Autobiographical Recall**

Anatomical region	Cluster size	MNI coordinates			Z-score
		x	y	z	
Rest versus emotional autobiographical recall					
Cluster in the frontal medial cortex	253				
lvSTR		-9	14	-11	4.67
rvSTR		9	17	-8	4.43
aHyp/Sept		-6	11	-11	3.99
vACC		12	32	-17	3.96
SGC		9	23	-8	3.59
rIPL	113	57	-25	19	4.61
lIPL	63	-60	-31	40	4.24
Rest versus neutral autobiographical recall					
Cluster in the frontal medial cortex	218				
rvSTR		6	14	-8	4.45
SGC		9	26	-8	3.67
lvSTR		-6	8	-8	3.66
vACC		12	32	-14	3.65

The values shown are Montreal Neurological Institute (MNI) coordinates for significant activation maxima of clusters in the random effects analyses ( $P < 0.05$ , FWE corrected on the cluster level).

lvSTR, left ventral striatum; rvSTR, right ventral striatum; aHyp/Sept, anterior hypothalamus/septal area; vACC, ventral anterior cingulate cortex; SGC, subgenual cingulate cortex; lIPL, left inferior parietal lobe; rIPL, right inferior parietal lobe.

Finally, these results also indicate that an active, explicit, cognitive task (emotional autobiographical recall) engages the mPFC and PPC/Prec more robustly than rest, thus challenging the notion that these DMN regions are more active during rest than during explicit or externally guided tasks [Fox et al., 2005; Gusnard et al., 2001].

A second striking finding of our study was the robustly increased activation in ventral frontal brain regions comprising the vACC, SGC, and vSTR during rest versus autobiographical recall. Although the SGC and bilateral striatum have not been explicitly described as being part of the DMN, the SGC largely corresponds to the vACC, which has been reported in previous studies as a DMN component [Laird et al., 2009; Schilbach et al., 2012]. In addition, previous activation and connectivity studies [Bzdok et al., 2013; Greicius et al., 2003; Raichle et al., 2001; Schilbach et al., 2012] have shown that vACC cluster extends to the ventromedial cortex (including the subgenual/posterior OFC) and bilaterally to the striatum and the neighboring septohypothalamic region.

Activity in these ventral frontal regions (vACC, SGC, and vSTR) may be interpreted as reflecting core functional aspects related to unconstrained thoughts or spontaneous self-evaluation mechanisms occurring more intensely during rest. Interestingly, vACC/SGC activity has been reported in association with individual differences in rumination tendency, a closely related psychological process [Ray et al., 2005]. Furthermore, these regions are intimately involved in fundamental homeostatic, emotional and motivational functions [Alheid and Heimer, 1988; Northoff and Panksepp, 2008; Stellar, 1994] and are anatomically con-

nected with other DMN cortical areas, such as mPFC [Masterson and Cummings, 1997; Rempel-Clower and Barbas, 1998]. Bilateral damage to these areas produces the most telling cases of vigilant akinetic mutism in humans, a condition characterized by a blank state of mind, in which the patient lies inert in bed with the eyes open, but without any evidence of ideation, emotional experience, and motivational drive whatsoever [Fisher, 1983].

The ventral frontal brain regions (vACC, SGC, and vSTR) were more active, but not more functionally interconnected, during rest than during autobiographical recall. The increased BOLD effect in these ventral regions in the absence of increased functional integration among them may correspond to a sort of undirected motivational promptness, a generalized motivational inclination, to engage in goal-directed behavior. When a given task is called for, these motivational networks become selectively and functionally integrated with cortical regions responsible for sophisticated cognitive functions, providing the required motivation without which cognition and behavior cannot take place [Northoff and Panksepp, 2008]. In fact, it has been suggested that mind wandering may be intimately associated with goal-related proneness [Smallwood and Schooler, 2006]. The ventral frontal DMN regions (vACC, SGC, and vSTR) might represent a key implicit or automatic aspect of spontaneous goal-related thoughts and actions. Our findings may therefore contribute to the ongoing debate on automatic and executive control of mind wandering [McVay and Kane, 2010]. These possibilities should be investigated in future studies looking more in depth into activity patterns of these ventral frontal brain networks (e.g. vACC, SGC, and vSTR).

**TABLE IV. Results of functional connectivity analysis**

Connectivity	Rest	Positive	Negative	Neutral
mPFC–PCC	0.344	0.400*	0.398**	0.363
vACC–rvSTR	0.194	0.261	0.260	0.221
vACC–lvSTR	0.233	0.269	0.276	0.248
vACC–SGC	0.201	0.248	0.240	0.212
SGC–rvSTR	0.102	0.174	0.183**	0.116
SGC–lvSTR	0.130	0.169	0.162	0.130
rvSTR–lvSTR	0.436	0.450	0.440	0.420

Correlation coefficient matrix between the time series for each pair of regions of each experimental condition.

\* $P < 0.05$ , \*\* $P = 0.06$ , paired  $t$ -test between rest and autobiographical conditions.

PCC, posterior cingulate cortex; mPFC, medial prefrontal cortex; lvSTR, left ventral striatum; rvSTR, right ventral striatum; vACC, ventral anterior cingulate cortex; SGC, subgenual cingulate cortex.

It is important to point that in addition to the ventral frontal network (vACC, SGC, and vSTR), dorsolateral parietal areas, more specifically the IPLs, were also more strongly activated in the resting state compared with emotional autobiographical memory. The IPL has been consistently reported as a DMN component [Laird et al., 2009]. Although previous studies suggest that the lateral IPL (in connection with the medial parietal areas) might be involved in self-related mechanisms [Lou et al., 2004] and conscious awareness [Gusnard and Raichle, 2001], it is less clear why the IPLs were found to have higher activity during rest compared with emotional autobiographical memory, and needs to be investigated in future studies.

Our finding of a functional dissociation in DMN regions is in line with the results of a recent meta-analysis of task-related social cognition fMRI studies showing a ventral-dorsal dissociation of mPFC networks [Bzdok et al., 2013]. This study provided evidence for a parcellation of mPFC connectivity, in which the ventral mPFC showed strong connection with brain areas associated with reward-related processes and modulation of online approach-avoidance behavior, whereas the dorsal mPFC subnetwork was associated with perspective-taking and episodic memory retrieval tasks, as well as scene construction for past and future events [Bzdok et al., 2013]. The ventral frontal versus dorsomedial functional dissociation of the DMN components reported in the present study is compatible with Bzdok et al.’s findings, in that the ventral frontal regions (vACC, SGC, and vSTR) may be associated with “here and now” aspects while the dorsomedial regions (mPFC and PCC/Prec) may underpin reflective, hypothetical and elaborative emotional processing of self-projecting scenarios (e.g. “another time and place”). Other studies have also noted different dissociations of the DMN in episodic memory recall. A recent meta-analysis on episodic memory retrieval reported a dorsoventral dissociation of frontoparietal regions on a “remember-know” paradigm, in which

ventral regions of the mPFC, PCC, the caudate and anterior insula were more active during strong memories responses, possibly reflecting incentive salience [Kim, 2010]. Another study [Andrews-Hanna et al., 2010] showed a dissociation of DMN regions into temporal and dorsal subsystems related to mnemonic scene reconstruction and affective social processes, respectively. Furthermore, Sestieri et al. proposed an anterior-posterior dissociation in DMN between episodic memories and resting [Sestieri et al., 2011]. In line with our results, these studies support the notion of functional heterogeneity in the DMN, although the exact contribution of distinct functional components is still poorly understood.

A previous study also aiming at isolating DMN autobiographical components [Ino et al., 2011] demonstrated that a distributed pattern of brain areas, including PCC/Prec and mPFC, were more active during autobiographical recall than in resting condition. In addition, the IPL was found more active during resting than during autobiographical recall. In contrast to our study, these authors did not make use of social or emotional stimuli, and allowed only a very short time for recollection and resting state conditions (16 s). Our study employed much longer blocks (132 s) for rest and autobiographical retrieval, allowing appropriate time for both a better recollection of specific autobiographical episodes and a deeper immersion in the state of mind associated with the “typical” resting state.

It might be claimed that participants were not engaged in the autobiographical task. However, ratings on vividness for single imagined autobiographical episodes obtained after scanning indicate that autobiographical episodes were clearly and vividly imagined while participants were in the scan, making this hypothesis unlikely. Furthermore, it is difficult to ascertain what exactly subjects were thinking of, and how their minds wandered freely across different topics and psychological states during the rest periods. This is, in fact, a difficult question that has stubbornly resisted inquiry across studies. Consistent with previous resting state studies tasks [Brewer et al., 2011; Fransson, 2005; Greicius et al., 2003; Mazoyer et al., 2001], we instructed our participants to relax and to refrain from any particular mental task during resting periods. It should be noted that this type of instruction, although commonly used in resting state studies, is somewhat problematic because (a) instructing someone “not to engage” in a specific task may sound paradoxical and (b) experimenters lack strict control of what participants are actually doing during such kind of free mind wandering.

Here we used an approach to identify common and distinct brain responses by using both a conjunction analysis and direct contrasts of emotional autobiographical memory and resting state conditions. While these analyses cannot warrant the presence of one given cognitive process (emotional autobiographical memory) in another condition [resting state; Poldrack, 2006], previous studies in the field have indicated that autobiographical memory is

indeed highly prevalent during the idling state of the “resting” condition [Fransson, 2005; Mazoyer et al., 2001].

In conclusion, our study is the first to show that the ventral frontal subnetwork (vACC, SGC and vSTR) of the resting-state DMN is functionally dissociated from its dorsomedial counterpart, which is more strongly engaged by explicit emotional autobiographical recall. Our findings point to novel venues for the exploration of subcomponents of the DMN, with possible implications for neuropsychiatric conditions associated with dysfunctions in the ventral frontal subcomponent (vACC, SGC, and vSTR), such as mood and personality disorders.

## ACKNOWLEDGMENTS

J.M., R.O.S., F.T.M., and R.B. designed the research. P.B., F.F.P., I.B., J.R.S., R.B., A.E., and J.M. performed fMRI data acquisition and/or analyses. P.B., A.E., J.M., R.O.S., and F.T.M. wrote the article. The authors are thankful to Fernanda Meirelles and Debora Lima for helping with scanning procedures and study coordination.

## REFERENCES

- Alheid GF, Heimer L (1988): New perspectives in basal forebrain organization of special relevance for neuropsychiatric disorders: The striatopallidal, amygdaloid, and corticopetal components of *substantia innominata*. *Neuroscience* 27:1–39.
- Andrews-Hanna JR, Reidler JS, Sepulcre J, Poulin R, Buckner RL (2010): Functional-anatomic fractionation of the brain’s default network. *Neuron* 65:550–562.
- Bellgowan PSF, Bandettini PA, Van Gelderen P, Martin A, Bodurka J (2006): Improved BOLD detection in the medial temporal region using parallel imaging and voxel volume reduction. *NeuroImage* 29:1244–1251.
- Bodurka J, Ye F, Petridou N, Murphy K, Bandettini PA (2007): Mapping the MRI voxel volume in which thermal noise matches physiological noise-implications for fMRI. *NeuroImage* 34:542–549.
- Brewer JA, Worhunsky PD, Gray JR, Tang YY, Weber J, Kober H (2011): Meditation experience is associated with differences in default mode network activity and connectivity. *Proc Natl Acad Sci USA* 108:20254–20259.
- Buckner RL, Andrews-Hanna JR, Schacter DL (2008): The brain’s default network: anatomy, function, and relevance to disease. *Ann NY Acad Sci* 1124:1–38.
- Buckner RL, Carroll DC (2007): Self-projection and the brain. *Trends Cogn Sci* 11:49–57.
- Bzdok D, Langner R, Schilbach L, Engemann DA, Laird AR, Fox PT, Eickhoff SB (2013): Segregation of the human medial prefrontal cortex in social cognition. *Front Hum Neurosci* 7:1–17.
- Bzdok D, Schilbach L, Vogeley K, Schneider K, Laird AR, Langner R, Eickhoff SB (2012): Parsing the neural correlates of moral cognition: ALE meta-analysis on morality, theory of mind, and empathy. *Brain Struct Funct* 217:783–796.
- Cabeza R, St Jacques P (2007): Functional neuroimaging of autobiographical memory. *Trends Cogn Sci* 11:219–227.
- Carhart-Harris RL, Erritzoe D, Williams T, Stone JM, Reed LJ, Colasanti A, Tyacke RJ, Leech R, Malizia AL, Murphy K, Hobden P, Evans J, Feilding A, Wise RG, Nutt DJ (2012): Neural correlates of the psychedelic state as determined by fMRI studies with psilocybin. *Proc Natl Acad Sci USA* 109:2138–2143.
- Conway MA, Pleydell-Pearce CW (2000): The construction of autobiographical memories in the self-memory system. *Psychol Rev* 107:261–288.
- Di Martino A, Scheres A, Margulies DS, Kelly AMC, Uddin LQ, Shehzad Z, Biswal B, Walters JR, Castellanos FX, Milham MP (2008): Functional connectivity of human striatum: a resting state fMRI study. *Cereb Cortex* 18:2735–2747.
- Fisher CM (1983): Honored guest presentation: *abulia minor* vs. agitated behavior. *Clin Neurosurg* 31:9–31.
- Foster BL, Dastjerdi M, Parvizi J (2012): Neural populations in human posteromedial cortex display opposing responses during memory and numerical processing. *Proc Natl Acad Sci USA* 109:15514–15519.
- Fox MD, Raichle ME (2007): Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. *Nat Rev Neurosci* 8:700–711.
- Fox MD, Snyder AZ, Vincent JL, Corbetta M, Van Essen DC, Raichle ME (2005): The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proc Natl Acad Sci USA* 102:9673–9678.
- Fransson P (2005): Spontaneous low-frequency BOLD signal fluctuations: an fMRI investigation of the resting-state default mode of brain function hypothesis. *Hum Brain Mapp* 26:15–29.
- Friston K (1995): Characterizing Evoked Hemodynamics with fMRI. *NeuroImage* 2:157–165.
- Fukunaga M, Horovitz SG, Van Gelderen P, De Zwart JA, Jansma JM, Ikonomidou VN, Chu R, Deckers RHR, Leopold DA, Duyn JH (2006): Large-amplitude, spatially correlated fluctuations in BOLD fMRI signals during extended rest and early sleep stages. *Magn Reson Imaging* 24:979–992.
- Greicius MD, Kiviniemi V, Tervonen O, Vainionpää V, Alahuhta S, Reiss AL, Menon V (2008): Persistent default-mode network connectivity during light sedation. *Hum Brain Mapp* 29:839–847.
- Greicius MD, Krasnow B, Reiss AL, Menon V (2003): Functional connectivity in the resting brain: A network analysis of the default mode hypothesis. *Proc Natl Acad Sci USA* 100:253–258.
- Gusnard DA, Akbudak E, Shulman GL, Raichle ME (2001): Medial prefrontal cortex and self-referential mental activity: relation to a default mode of brain function. *Proc Natl Acad Sci USA* 98:4259–4264.
- Gusnard DA, Raichle ME (2001): Searching for a baseline: functional imaging and the resting human brain. *Nature Rev Neurosci* 2:685–694.
- Harrison BJ, Pujol J, López-Solà M, Hernández-Ribas R, Deus J, Ortiz H, Soriano-Mas C, Yücel M, Pantelis C, Cardoner N (2008a): Consistency and functional specialization in the default mode brain network. *Proc Natl Acad Sci USA* 105:9781–9786.
- Harrison BJ, Pujol J, Ortiz H, Fornito A, Pantelis C, Yücel M (2008b): Modulation of brain resting-state networks by sad mood induction. *PLoS One* 3:e1794.
- Horovitz SG, Fukunaga M, De Zwart JA, Van Gelderen P, Fulton SC, Balkin TJ, Duyn JH (2008): Low frequency BOLD fluctuations during resting wakefulness and light sleep: A simultaneous EEG-fMRI study. *Hum Brain Mapp* 29:671–682.
- Ino T, Nakai R, Azuma T, Kimura T, Fukuyama H (2011): Brain activation during autobiographical memory retrieval with special reference to default mode network. *Open Neuroimaging J* 5:14–23.

- Kelley WM, Macrae CN, Wyland CL, Caglar S, Inati S, Heatherton TF (2002): Finding the self? An event-related fMRI study. *J Cogn Neurosci* 14:785–794.
- Kim H (2010): Dissociating the roles of the default-mode, dorsal, and ventral networks in episodic memory retrieval. *NeuroImage* 50:1648–1657.
- Krienen FM, Tu P-C, Buckner RL (2010): Clan mentality: evidence that the medial prefrontal cortex responds to close others. *J Neurosci* 30:13906–13915.
- Laird AR, Eickhoff SB, Li K, Robin DA, Glahn DC, Fox PT (2009): Investigating the functional heterogeneity of the default mode network using coordinate-based meta-analytic modeling. *J Neurosci* 29:14496–14505.
- Lou HC, Luber B, Crupain M, Keenan JP, Nowak M, Kjaer TW, Sackeim HA, Lisanby SH (2004): Parietal cortex and representation of the mental self. *Proc Natl Acad Sci USA* 101:6827–6832.
- Macey PM, Macey KE, Kumar R, Harper RM (2004): A method for removal of global effects from fMRI time series. *NeuroImage* 22:360–366.
- Maddock RJ (1999): The retrosplenial cortex and emotion: new insights from functional neuroimaging of the human brain. *Trends Neurosci* 22:310–316.
- Masterman DL, Cummings JL (1997): Frontal-subcortical circuits: The anatomic basis of executive, social and motivated behaviors. *J Psychopharmacol* 11:107–114.
- Mazoyer B, Zago L, Mellet E, Bricogne S, Etard O, Houdé O, Crivello F, Joliot M, Petit L, Tzourio-Mazoyer N (2001): Cortical networks for working memory and executive functions sustain the conscious resting state in man. *Brain Res Bull* 54:287–298.
- McVay JC, Kane MJ (2010): Does mind wandering reflect executive function or executive failure? Comment on Smallwood and Schooler (2006) and Watkins (2008). *Psychol Bull* 2010;136: 188–197; discussion 198–207.
- Moll J, Bado P, De Oliveira-Souza R, Bramati IE, Lima DO, Paiva FF, Sato JR, Tovar-Moll F, Zahn R (2012): A Neural Signature of Affiliative Emotion in the Human Septohypothalamic Area. *J Neurosci* 32:12499–12505.
- Nichols T, Brett M, Andersson J, Wager T, Poline J-IB (2005): Valid conjunction inference with the minimum statistic. *NeuroImage* 25:653–660.
- Northoff G, Panksepp J (2008): The trans-species concept of self and the subcortical-cortical midline system. *Trends Cogn Sci* 12:259–264.
- Oldfield RC (1971): The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia* 9:97–113.
- Phan KL, Wager T, Taylor SF, Liberzon I (2002): Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. *NeuroImage* 16:331–348.
- Pitroda S, Angstadt M, McCloskey MS, Coccaro EF, Phan KL (2008): Emotional experience modulates brain activity during fixation periods between tasks. *Neurosci Lett* 443:72–76.
- Poldrack RA (2006): Can cognitive processes be inferred from neuroimaging data? *Trends Cogn Sci* 10:59–63.
- Raichle ME, MacLeod AM, Snyder AZ, Powers WJ, Gusnard DA, Shulman GL (2001): A default mode of brain function. *Proc Natl Acad Sci USA* 98:676–682.
- Ray RD, Ochsner KN, Cooper JC, Robertson ER, Gabrieli JDE, Gross JJ (2005): Individual differences in trait rumination and the neural systems supporting cognitive reappraisal. *Cogn Affect Behav Neurosci* 5:156–168.
- Rempel-Clower NL, Barbas H (1998): Topographic organization of connections between the hypothalamus and prefrontal cortex in the rhesus monkey. *J Comp Neurol* 398:393–419.
- Schilbach L, Bzdok D, Timmermans B, Fox PT, Laird AR, Vogeley K, Eickhoff SB (2012): Introspective minds: Using ALE meta-analyses to study commonalities in the neural correlates of emotional processing, social & unconstrained cognition. *PLoS One* 7:e30920.
- Schilbach L, Eickhoff SB, Rotarska-Jagiela A, Fink GR, Vogeley K (2008): Minds at rest? Social cognition as the default mode of cognizing and its putative relationship to the “default system” of the brain. *Conscious Cogn* 17:457–467.
- Sestieri C, Corbetta M, Romani GL, Shulman GL (2011): Episodic memory retrieval, parietal cortex, and the default mode network: Functional and topographic analyses. *J Neurosci* 31: 4407–4420.
- Singer (1975): Navigating the stream of consciousness: Research in daydreaming and related inner experience. *Am Psychol* 30: 727–738.
- Smallwood J, Schooler JW (2006): The restless mind. *Psychol Bull* 132:946–958.
- Spreng RN, Grady CL (2010): Patterns of brain activity supporting autobiographical memory, prospection, and theory of mind, and their relationship to the default mode network. *J Cogn Neurosci* 22:1112–1123.
- Spreng RN, Mar RA, Kim ASN (2009): The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. *J Cogn Neurosci* 21:489–510.
- Stellar (1994): The physiology of motivation. *Psychol Rev* 101:301–311.
- Svoboda E, McKinnon MC, Levine B (2006): The functional neuroanatomy of autobiographical memory: A meta-analysis. *Neuropsychologia* 44:2189–2208.
- Whitfield-Gabrieli S, Moran JM, Nieto-Castañón A, Triantafyllou C, Saxe R, Gabrieli JDE (2011): Associations and dissociations between default and self-reference networks in the human brain. *NeuroImage* 55:225–232.
- Worsley KJ, Friston KJ (1995): Analysis of fMRI time-series revisited- again. *NeuroImage* 2:173–181.
- Zahn R, De Oliveira-Souza R, Bramati I, Garrido G, Moll J (2009): Subgenual cingulate activity reflects individual differences in empathic concern. *Neurosci Lett* 457:107–110.
- Zarahn E, Aguirre GK, D’Esposito M (1997): Empirical analyses of BOLD fMRI statistics. *NeuroImage* 5:179–197.