



# Knowing me, knowing you: Resting-state functional connectivity of ventromedial prefrontal cortex dissociates memory related to self from a familiar other



Irene de Caso<sup>a,\*</sup>, Theodoros Karapanagiotidis<sup>a</sup>, Elena Aggius-Vella<sup>b</sup>, Mahiko Konishi<sup>a</sup>, Daniel S. Margulies<sup>c</sup>, Elizabeth Jefferies<sup>a</sup>, Jonathan Smallwood<sup>a</sup>

<sup>a</sup> Department of Psychology/York Neuroimaging Centre, University of York, Heslington, York, United Kingdom

<sup>b</sup> Unit for Visually Impaired People, Istituto Italiano di Tecnologia, Genova, Italy

<sup>c</sup> Max Planck Research Group: Neuroanatomy & Connectivity, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

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## ABSTRACT

Material related to the self, as well as to significant others, often displays mnemonic superiority through its associations with highly organised and elaborate representations. Neuroimaging studies suggest this effect is related to activation in regions of medial prefrontal cortex (mPFC). Incidental memory scores for trait adjectives, processed in relation to the self, a good friend and David Cameron were collected. Scores for each referent were used as regressors in seed-based analyses of resting state fMRI data performed in ventral, middle and dorsal mPFC seeds, as well as hippocampal formation. Stronger memory for self-processed items was predicted by functional connectivity between ventral mPFC, angular gyrus and middle temporal gyri. These regions are within the default mode network, linked to relatively automatic aspects of memory retrieval. In contrast, memory for items processed in relation to best friends, was better in individuals whose ventral mPFC showed relatively weak connectivity with paracingulate gyrus as well as positive connectivity with lateral prefrontal and parietal regions associated with controlled retrieval. These results suggest that mechanisms responsible for memory related to ourselves and personally-familiar people are partially dissociable and reflect connections between ventral mPFC, implicated in schema-based memory, and regions implicated in more automatic and controlled aspects of retrieval.

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## 1. Introduction

A fundamental aspect of the brain is its ability to encode, update and retrieve information, processes that can occur in an automatic manner or through the application of conscious effort. Both encoding and retrieval are more likely when the information is personally relevant. Strong automatic effects on memory are illustrated by the *self reference effect* when incidental memory for material that is related to the self tends to be higher than for other types of material, such as items related to others (Kelley et al., 2002;

Kuiper & Rogers, 1979) or semantically judged material (Rogers, Kuiper, & Kirker, 1977). The strong automatic encoding that occurs during self-reference is thought to reflect the rich associative structure of knowledge about who we are (Symons & Johnson, 1997). Knowledge of oneself provides a powerful schema through which information can be organised during encoding and retrieval. In contrast, memory for information with a less rich associative structure is more difficult to encode and retrieve.

There is a growing body of evidence that memories with a rich associative structure depend upon the default mode network (DMN), a large-scale network anchored by medial regions in the medial prefrontal cortex and the posterior cingulate cortex (Andrews-Hanna, 2012). The DMN, and in particular the mPFC, show high levels of activation during tasks that require self-reference (D'Argembeau et al., 2005; Johnson et al., 2002; Kelley et al., 2002; Macrae, Moran, Heatherton, Banfield, & Kelley, 2004; Northoff et al., 2006) as well as for personally familiar referents, such as a close friend (Mitchell, Banaji, & Macrae, 2005), and when

Abbreviations: a, anterior; AG, angular gyrus; ATL, anterior temporal pole; d, dorsal; DAN, dorsal attention network; DMN, default mode network; FC, functional connectivity; HF+, hippocampal formation; Occ, occipital; Paracing, paracingulate gyrus; l, left; mPFC, medial prefrontal cortex; MTG, medial temporal gyrus; r, right; SMG, supramarginal gyrus; v, ventral.

\* Corresponding author at: Department of Psychology, University of York, Heslington, York YO10 5DD, United Kingdom.

E-mail address: [idx508@york.ac.uk](mailto:idx508@york.ac.uk) (I. de Caso).

retrieving dominant semantic associations of words that come to mind relatively automatically (Binder, Desai, Graves, & Conant, 2009; Davey et al., 2015). In all these cases memory encoding and retrieval are aided by the presence of previously formed schemas which are thought to be supported by, at least in part, the vmPFC (Ghosh, Moscovitch, Colella, & Gilboa, 2014; van Kesteren, Rijpkema, Ruiter, & Fernández, 2010). The notion that the DMN has an important role in the retrieval of information is also supported by studies that show strong coupling between the DMN and the hippocampus during successful retrieval (Huijbers, Pennartz, Cabeza, & Daselaar, 2011; van Kesteren, Fernández, Norris, & Hermans, 2010; van Kesteren, Ruiter, Fernández, & Henson, 2012) as well as by studies that show that activity in the mPFC during the encoding phase of a self-reference paradigm predicts subsequent memory scores for items encoded during self-reference (Macrae et al., 2004). Moreover a related literature has shown stronger responses within the DMN during spontaneous retrieval states such as mind-wandering (Mason et al., 2007; Christoff, Gordon, Smallwood, Smith, & Schooler, 2009) in which internally generated information is processed. Activity in the DMN often leads to errors during tasks that depend on a detailed processing of perceptual input (Weissman, Roberts, Visscher, & Woldorff, 2006; Li, Yan, Bergquist & Sinha 2007) and shows patterns of anticorrelation with regions involved in tasks involving controlled external attention at rest (Fox et al., 2005). These converging literatures are often taken as evidence that DMN can support spontaneous and undirected retrieval that interferes with ongoing processes requiring cognitive control (Anticevic et al., 2012). Together these parallel literatures implicate the DMN in the encoding and retrieval of personally relevant information into and from memory. However, recent research has also indicated that DMN sites can couple with regions implicated in executive control in situations that require memory retrieval to be controlled to suit the current demands (Spreng et al., 2014). These and other findings (e.g. Konishi, McLaren, Engen, & Smallwood, 2015; Krieger-Redwood et al., 2016; Vatansever, Menon, Manktelow, Sahakian, & Stamatakis, 2015) suggest the DMN plays a more flexible role in memory processing than may have been recognised in the past.

To elucidate a more nuanced view of the role of the DMN in memory retrieval the current study explored whether different patterns of functional connectivity (FC) could predict incidental memory scores and in particular, whether these differ for material with different levels of personal relevance. We asked participants who had already participated in a neuroimaging session in which we recorded resting state activity to return to the laboratory to perform an incidental memory task. They made decisions about whether trait adjectives applied to three different referents: themselves, their best friend or David Cameron (UK Prime Minister). These referents differ on their strength of personal associations which should result in higher incidental memory scores for items related to the self than their best friend and the lowest retrieval for David Cameron. In addition, since memory for similar others are known to elicit similar DMN activation and may be organised using similar or overlapping schema (Mitchell, Macrae, & Banaji, 2006), accurately retrieving information about a best friend may require that competition from self-processed items may be overcome, which have been encoded in a similar way. In contrast, items processed in relation to David Cameron will be more distinct and experience less interference. Individual variations in these scores were used to predict the FC in three sub-regions of the mPFC (ventral, middle, dorsal) taken from a decomposition of the DMN (Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010). Given evidence that the hippocampal formation is important in retrieval of information from memory, and this region is also a member of a subsystem of the DMN (Andrews-Hanna et al.,

2010) this region was also selected as a seed region. In the decomposition of Andrews-Hanna et al. (2010), the hippocampal formation showed stronger connectivity to ventral mPFC than the other seed locations, and ventral mPFC has also been implicated in schema-based memory (Spalding, Jones, Duff, Tranel, & Warren, 2015; van Kesteren et al., 2012), giving rise to the prediction that this site may be particularly critical for self and best friend memory. In addition, we measured executive control via the stop signal response time task (SSRT, (Logan & Cowan, 1984; Verbruggen & Logan, 2009)) to explore whether strong automatic retrieval underpinning the self-reference effect was associated with problems in executive control.

## 2. Methods

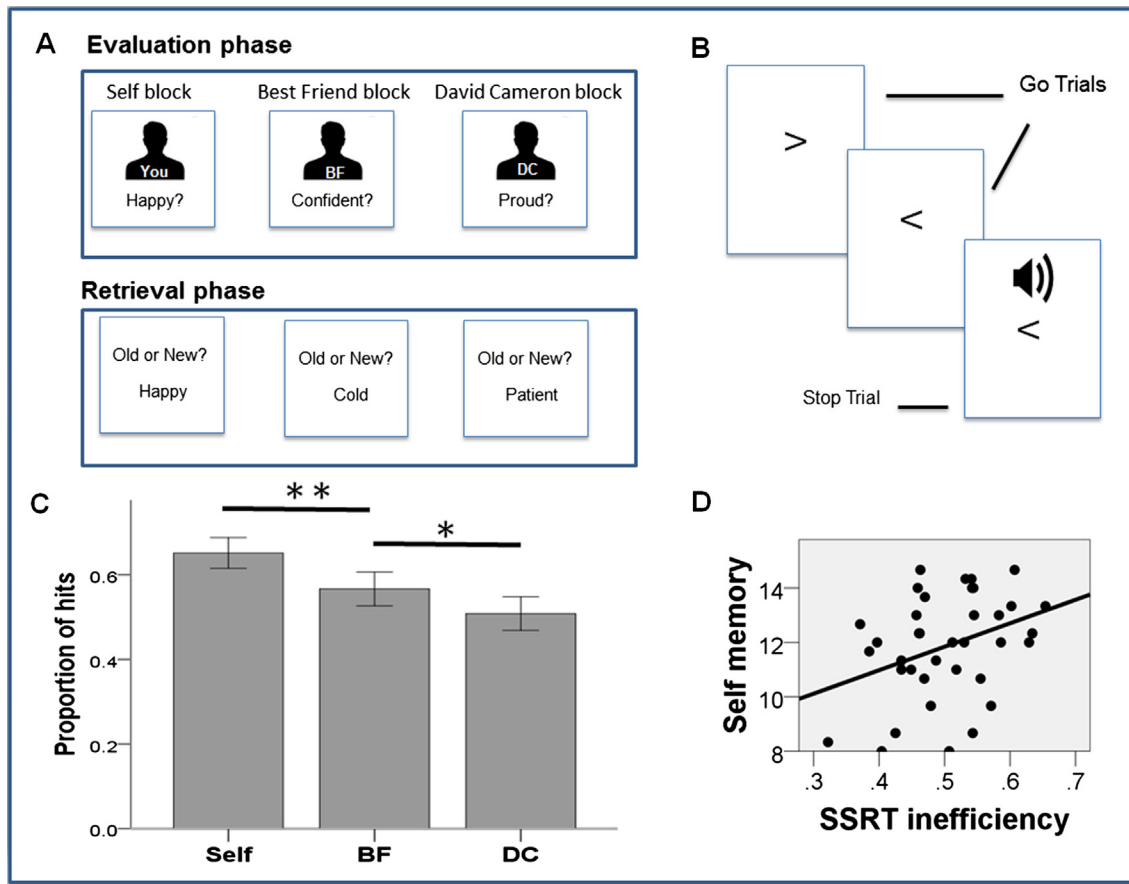
### 2.1. Participants

Forty healthy right-handed participants were recruited through advert and either received a monetary reward of £20 or course credits. One participant had to be excluded from all analyses due to irregularities observed during fMRI scanning. Two further participants were excluded due to poor task performance, one from each task. Separate FC maps for each task were calculated with a total of 38 participants (21 males) with an average age of 22.5 (SD = 2.9) years. Approval for this project was granted by the York Neuroimaging Centre (YNiC) Ethics Committee and was in accordance with the ethical standards of the responsible committee on human experimentation (institutional and national) and with the Helsinki Declaration of 1975, as revised in 2008.

### 2.2. Procedure

#### 2.2.1. Self-reference paradigm

This laboratory task involved an evaluation and a retrieval phase. During the evaluation phase (Fig. 1A, top) participants were asked to make decisions about the association between adjectives and one of three referents ('Self', 'Best Friend' and 'David Cameron'). Adjectives were presented sequentially on-screen and participants were required to indicate whether each adjective applied to a particular referent by pressing 'Y' with the index finger of the right hand for 'yes' or 'N' with the index finger of the left hand for 'no'. For each category, participants were presented with a list of 18 unique adjectives presented in separate blocks and the order in which each category was presented was counterbalanced across participants. Each of the 18-item lists was also rotated across the different referents and the order of item presentation within each block was randomised. Stimuli were separated by an inter-stimulus interval of 2500 ms during which participants were shown a blank screen with a fixation cross. Following the evaluation phase, subjects were presented with a surprise retrieval test in which they were sequentially shown words and asked whether or not that particular item had been presented in the previous phase. This retrieval phase (Fig. 1A, bottom) contained all the words from the previous stage of the experiment, plus an equal number of new words. Items were presented in a random order and participants had to either press 'Y' if they thought the word had appeared before or 'N' if they thought it was a new word. All words were selected from a pool of normalized personality trait adjectives with meaningfulness and likeability ratings (Anderson, 1968). Positive, negative and neutral adjectives with the highest meaningfulness rating were selected for this experiment. Correct memory for each referent was calculated by subtracting the relative number of false alarms from the total number of correctly retrieved items.



**Fig. 1.** Behavioural results. (A) Schematic representation of the self-reference task. Top row: Evaluation phase. Bottom row: Retrieval phase. (B) Schematic representation of the stop signal response time task. (C) Proportion of hits for each referent and error bars. Asterisks represent significant differences in memory performance across referents. (D) Scatterplot reflecting the positive correlation between memory for self items and SSRT inefficiency. Acronyms: BF – Best friend, DC – David Cameron.

### 2.2.2. Stop signal response time task (SSRT)

We developed a version of a stop-signal task (Logan & Cowan, 1984; Verbruggen & Logan, 2009) using PsychoPy (Peirce, 2007). Fig. 1B presents a schematic representation of the trial sequence for the task. The task featured arrowheads pointing either to the left (<) or to the right (>) staying on the screen for 1000 ms independently of RT and interleaved by a 500 ms fixation cross. Participants were instructed to respond as quickly as they could, using the left and right arrow keys for the left and right arrowheads, respectively. Participants were also instructed to withhold their respond when they heard a beeping sound (the stop signal) accompanying the arrowhead stimuli, which occurred in 20% of the trials (stop signal trials); the latency between the beep and the arrowhead presentation (stop signal delay or SSD) was initially set at 250 ms and was then varied with a staircase tracking procedure: when inhibition was successful and participants correctly withheld response in stop signal trials, SSD was increased by 50 ms; when inhibition was unsuccessful, SSD was decreased by 50 ms. Participants initially received on-screen instructions, followed by a brief practice session (20 trials) and then moved on to the experimental session, which was composed of 150 trials divided in two equal blocks, allowing participants a quick break in between. The whole task lasted approximately 7 min.

For each participant, a Stop Signal Response Time (SSRT) score was calculated by subtracting mean SSD from the untrimmed mean RT (Logan, Schachar, & Tannock, 1997). Given the wide variance of error percentage in participants a Stop Signal Efficiency score was also calculated by dividing the SSRT score by the proportion of correct stop-signal trial responses. One participant with a

stop-signal trial error percentage higher than 33% was excluded from the analysis.

### 2.3. Resting state

#### 2.3.1. Scan acquisition

Functional MRI data was acquired independent of task stimulus on a 3 T GE scanner. Participants observed a fixation cross for a scan that lasted 7 min. The scan had a repetition time of 2 s, resulting in 210 volumes. We used interleaved slice-timing and isotropic voxel dimensions of 3 mm<sup>3</sup> (matrix size of 64 × 64, 192 mm field of view, and 32 slices) with a 0.5 mm gap between slices.

#### 2.3.2. Pre-processing

All fMRI preprocessing and analysis was performed using FSL. We extracted the brain from the skull using the BET toolbox for both the flair and the structural T1 weighted images and these scans were registered to standard MNI152 (2 mm) space using FLIRT (Jenkinson & Smith, 2001). Prior to conducting the functional connectivity analysis, the following pre-statistics processing was applied to the resting state data; motion correction using MCFLIRT (Jenkinson, Bannister, Brady, & Smith, 2002); slice-timing correction using Fourier-space time-series phase-shifting; non-brain removal using BET (Smith, 2002); spatial smoothing using a Gaussian kernel of FWHM 6 mm; grand-mean intensity normalisation of the entire 4D dataset by a single multiplicative factor; highpass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 100 s; Gaussian lowpass temporal filtering, with sigma = 2.8 s.)

### 2.3.3. First level analysis

Following these steps, the time series of 4 regions of interest (ROI) were extracted. The seed regions corresponded to 3 mm radius spheres centred around the following MNI coordinates: ventromedial Prefrontal Cortex (vmPFC 0, 26, –18), anteriomedial Prefrontal Cortex (amPFC, –6, 52, –2), dorsomedial Prefrontal Cortex (dmPFC 0, 52, 26) and the hippocampal formation (HF+, –22, –20, –26). These locations were selected based on previous literature (Andrews-Hanna et al., 2010) that decomposes the DMN into three subsystems, each mPFC location belonging to a different subsystem. The time series for each location were averaged and used as an explanatory variable in a subject-level FC analysis, which also included the following nuisance regressors: the first five principal time-series components extracted from white matter (WM) and cerebrospinal fluid (CSF) masks in accordance with the CompCor method (Behzadi, Restom, Liu, & Liu, 2007) and six motion parameters. WM and CSF masks were generated by segmenting each individual's high-resolution structural image (using FAST in FSL). The default tissue probability maps, referred to as Prior Probability Maps (PPM), were registered to each individual's high-resolution structural image (T1 space) and the overlap between these PPM and the corresponding CSF and WM maps was identified. Finally, these maps were thresholded (40% for the CSF and 66% for the WM), binarized and combined. The six motion parameters were calculated in the motion-correction step during pre-processing. Linear displacements in each of the three Cartesian directions (x, y, z) and rotations around three axes (pitch, yaw, roll) were included for each individual. No global signal regression was performed (Murphy, Birn, Handwerker, Jones, & Bandettini, 2009).

### 2.3.4. Second-level analysis

To understand how our psychological measures varied with the connectivity of the DMN seed regions, we used FSL to conduct a group-level regression of the connectivity matrices of each seed region. In this analysis we included the mean centred scores for the retrieval of items recalled for each item type as regressors of interest, and the mean movement during the scanning was included as a covariate of no interest. This procedure was repeated in an independent analysis using the SSRT scores instead of the self-other reference task scores. In these analyses the data were processed using FEAT version 5.98 part of FSL (FMRIB's Software Library, [www.fmrib.ox.ac.uk/fsl](http://www.fmrib.ox.ac.uk/fsl)) and the analyses were carried out using FMRIB's Local Analysis of Mixed Effects (FLAME). A grey matter mask with a probability threshold of 40% was used as a pre-thresholding mask and the cluster-forming threshold was set as z-score of 2.3. For these analyses we controlled for Type I errors by controlling for the number of voxels in the brain (Worsley, 2001), as well as the number of ROIs and the two tailed nature of our comparisons yielding an alpha value of  $P < 0.005$  FWE. The unthresholded maps from the contrasts reported in this paper are available at Neurovault at the following link: <http://neurovault.org/collections/1373/>.

### 2.4. Neurosynth meta-analyses

In order to study how the patterns of functional connectivity predictive of memory obtained in the current study were related to previous neuroimaging investigations, we performed a meta-analysis using the online Neurosynth database (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011). We performed a meta-analytic decoding of the unthresholded maps produced in this study by uploading them onto Neurosynth. This allows the identification of the cognitive terms that are most likely to be associated with the specific image. We display the results of these terms in the form of word clouds in the relevant figures. We also performed a specific meta-analysis of the relationship between

the maps produced by our experiment, and the spatial maps that are generated by studies exploring the self. We performed a meta-analysis (903 studies) of the term “self” (<http://neurosynth.org/analyses/terms/self/>) and compared the corresponding map to the connectivity maps predictive of self memory obtained in the current study.

## 3. Results

### 3.1. Behavioural results

A one-way analysis of variance (ANOVA) indicated a significant effect of referent on incidental memory performance ( $F(2, 76) = 21.58, p < 0.001$ , see Fig. 1C), as measured during the retrieval phase of the self-other reference paradigm. Post-hoc Bonferroni corrected comparisons indicated that words referred to the Self were recalled better than best friend words ( $p < 0.01$ ), and these were better recalled than David Cameron ( $p = 0.05$ ) items. In addition, examination of the confidence intervals for memory for David Cameron suggested it was at chance (95% CI [0.46, 0.54]), whereas memory for best friend (95% CI [0.52, 0.60]) and self (95% CI [0.61, 0.68]) were both above chance. Next we examined how the process of self-reference was associated with a participant's tendency for behavioural inhibition as measured by their efficiency on the SSRT. A linear regression with incidental memory for items processed in relation to the Self, Best Friend and David Cameron as independent variables and the SSRT inefficiency as the dependent variable, revealed a model that accounted for a 22% of the variance in behavioural inhibition scores [ $F(3, 36) = 3.14, p < 0.05, r^2 = 0.22$ ]. Higher memory for the Self was associated with less efficiency on the SSRT (standardized  $\beta = 0.47, t(33) = 2.7, p < 0.01$ ) (Fig. 1D). Memory scores for best friend and David Cameron items were not a reliable predictor (standardized  $\beta = 0.153, t(33) = 0.9, p = 0.35$ ; standardized  $\beta = -0.34, t(33) = -1.9, p = 0.58$ , respectively).

### 3.2. RS fMRI analyses

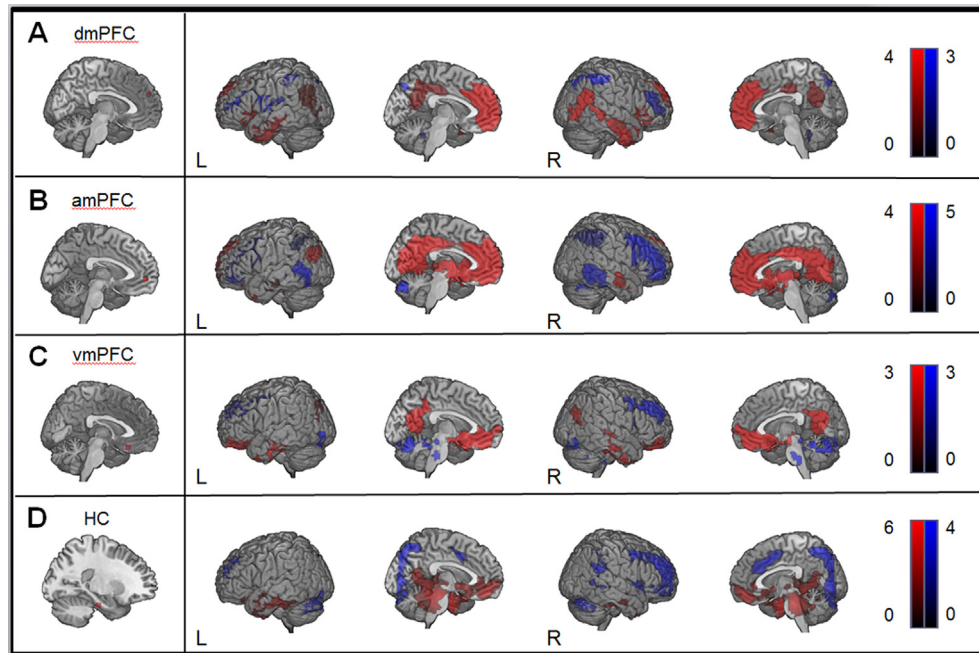
We conducted a series of multiple regressions in which the functional connectivity map of each region was the dependent variable. For each seed region we entered a measure of retrieval performance for each referent type (Self, Best Friend, David Cameron) as an explanatory variable. Independently we performed the same analysis using the SSRT efficiency scores instead of the memory scores. This SSRT measure did not reveal any patterns of functional connectivity predictive of inhibitory control for any of the seeded locations.

Fig. 2 displays the FC group maps for each seed location and Table 1 summarises the clusters that were predictive of memory performance and that passed correction for multiple comparisons, including correction for whole-brain analysis, two-tailed tests and the number of seeded locations. Clusters that passed the first two corrections but did not pass correction for the number of seeded locations are still included in the results but are presented separately (in yellow in Figs. 3 and 4).

#### 3.2.1. vmPFC

The FC of the vmPFC seed region predicted memory for self and best friend items. In particular, memory performance for self items was related to the FC between vmPFC and 3 clusters: right middle temporal lobe (rMTG) (Fig. 3A, first row), left superior angular gyrus (IAG) (Fig. 3B, first row), and left medial and anterior temporal lobe (IMTG cluster) (Fig. 3C, first row). In all cases, stronger FC between the vmPFC and these clusters predicted better memory for self-related items as seen in the corresponding scatterplots in





**Fig. 2.** Seed regions (left column) and associated functional connectivity (FC) group maps (right column). (A) Dorsal medial Prefrontal Cortex (dmPFC) 0, 52, 26. (B) Anterior medial Prefrontal Cortex (amPFC) -6, -52, -2. (C) Ventral medial Prefrontal Cortex (vmPFC) 0, 26, -18. (D) Hippocampal formation (HF+) -22, -20, -26.

**Table 1**

Regions that exhibited stronger functional coupling with the ROI dependent upon memory for either the self or other.

| Seed  | MNI coordinates | Contrast | Cluster              | Regions   | Peak         | Size | p-value     |
|-------|-----------------|----------|----------------------|---|--------------|------|-------------|
| vmPFC | 0, 26, -18      | Self up  | rMTG<br>IAG          | Right medial temporal gyrus   | 62, -30, -12 | 641  | 0.0202      |
|       |                 |          |                      | Left superior angular gyrus   | -46, -54, 26 | 1119 | 0.00071     |
|       |                 |          |                      | Left superior lateral occipital cortex  |              |      |             |
|       |                 |          | IMTG                 | Left medial temporal gyrus  | -62, -28, -4 | 1951 | 5.6 * 10e-6 |
|       |                 | BF up    | IMFG<br>rSMG<br>rMFG | Left medial frontal gyrus   | -46, 20, 30  | 717  | 0.0114      |
|       |                 |          |                      | Right superior supramarginal gyrus  | 22, -76, 54  | 1029 | 0.00128     |
|       |                 |          |                      | Right medial frontal gyrus  | 46, 8, 16    | 1111 | 0.000751    |
|       |                 | BF down  | Paracingulate gyrus  | Right inferior frontal gyrus  |              |      |             |
|       |                 |          |                      | Paracingulate gyrus   | 2, 56, -2    | 1722 | 1.9 * 10e-5 |
| dmPFC | 0, 52, 26       | Self up  | rOcc                 | Right lingual gyrus<br>Right supracalcarine gyrus<br>Right lateral occipital cortex | 30, -70, -16 | 1453 | 0.000242    |
| HF+   | -22, -20, -26   | Self up  | lvATL                | Left ventral anterior temporal lobe   | -16, 6, -20  | 1215 | 0.0006      |

Note: Coordinates are based on the Montreal Neurological Institute coordinate system.

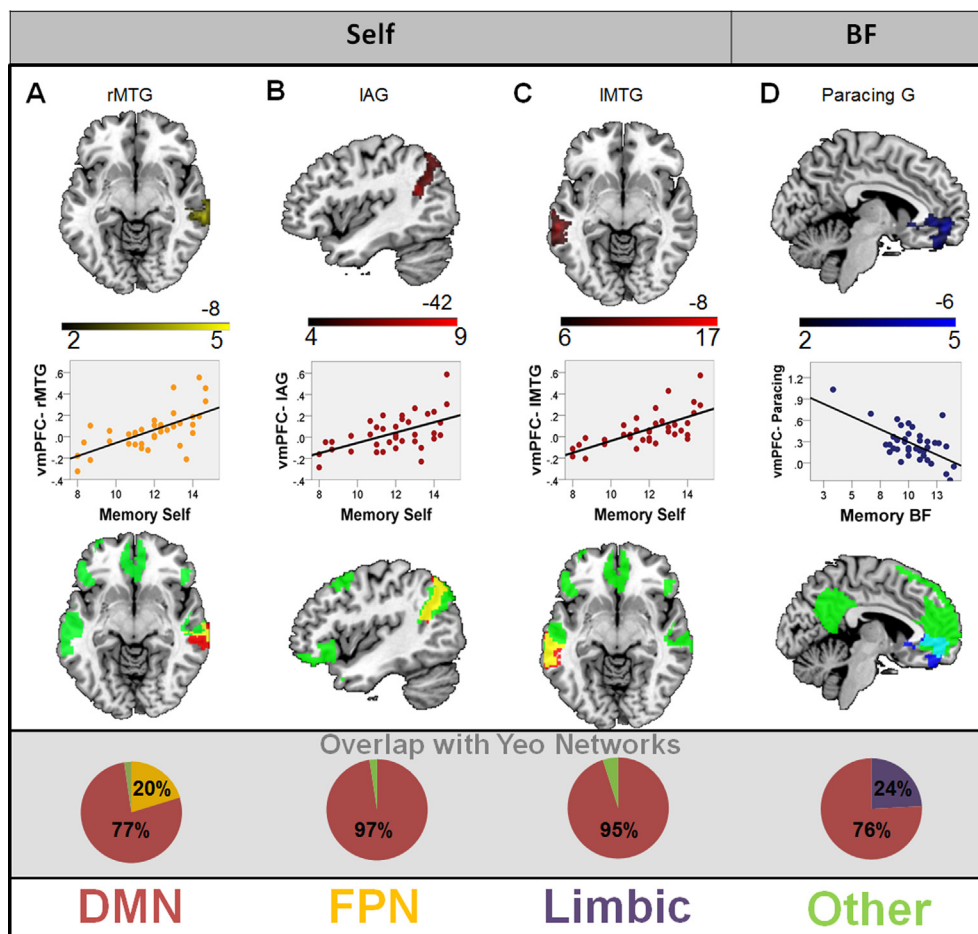
BF: Best Friend HF+: hippocampal formation; IAG: left angular gyrus; IMFG: left medial frontal gyrus; IMTG: left medial temporal gyrus; lvATL: left ventral anterior temporal lobe; rMFG: right medial frontal gyrus; rMTG: right medial temporal gyrus; rOcc: right occipital; rSMG: right supramarginal gyrus; vmPFC: ventromedial prefrontal cortex.

**Fig. 3.** The rMTG cluster did not pass correction for the number of seeded locations (and is therefore shown in yellow).

In order to study the association between the clusters found and resting state networks, these clusters were overlaid with the Yeo networks (Yeo et al., 2011). The pie charts presented in the grey panel in Fig. 3 illustrate the overlap with the DMN (Network 7), Frontoparietal Control (FPN) (Network 6) and Limbic Network (Network 5) as defined by Yeo and colleagues (2011). These show the greatest overlap with the DMN (indicated in red) suggesting that functional coupling within the DMN is associated with increased memory for self-related items. In addition, the region in the rMTG shows overlaps with the FPN (indicated in orange).

FC between vmPFC and the paracingulate gyrus predicted relatively poor memory for best friend items (Fig. 3D, first row). Overlay of this cluster with the Yeo networks revealed a strong overlap with the DMN and with the Limbic Network (indicated in purple in the corresponding pie chart in Fig. 3). Therefore, stronger connectivity within DMN was associated with poorer memory for best friend related items, a result that stands in contrast to the findings associated with the self.

In contrast, memory for best friend items was predicted by high levels of connectivity between the vmPFC and three clusters on lateral regions of cortex. In particular, stronger FC between vmPFC and left middle frontal gyrus (IMFG) (Fig. 4A, first row), right supe-



**Fig. 3.** Association between ventromedial prefrontal cortex (vmPFC) connectivity and better self memory (Panel A, B & C) and worse Best Friend (BF) memory (Panel D). (A) A region in Right Middle Temporal Gyrus (rMTG) was more coupled to vmPFC for individuals with better memory for self-related items. This cluster does not pass correction for the number of seeded locations. (B) A Region of Left Angular Gyrus (IAG) showed stronger FC to vmPFC in individuals with stronger memory for self-related items. (C) A Region of Left Middle Temporal Gyrus showed stronger FC to vmPFC for individuals with better memory for self-related items. (D) A region of Paracingulate gyrus showed stronger FC to the vmPFC for individuals with reduced memory for BF items. Second Row: Scatterplots reflecting relationship between memory performance and FC between ROI and cluster. Third row: Overlap (yellow) between clusters and Default Mode Network (green). Grey panel: Pie charts and legend reflecting the percentage of the cluster that overlaps with each one the Yeo networks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

rior supramarginal gyrus (rSMG) (Fig. 4B, first row) and right middle and inferior frontal gyrus (rMFG) (Fig. 4C, first row) predicted stronger memory for best friend items. The IMFG cluster did not pass correction for the number of seeded locations. These clusters were again overlaid with the 7 Yeo resting state networks. The overlapping proportion of each cluster and the Yeo networks is displayed in the pie charts in Fig. 4. These clusters generally overlap with regions that are important in tasks that demand externally oriented attention such as the FPN and the dorsal attention network (DAN). This overlap can be observed in the third row of Fig. 4, in which the DAN and FPN have been displayed with the same colour (green) for visualization purposes. Unlike a heightened memory for self, better retrieval of trait adjectives related to a best friend was associated with coupling in regions involved in executive control that largely fall outside the DMN.

### 3.2.2. amPFC

The FC of this brain location did not predict individual differences in memory for any of the three referents.

### 3.2.3. dmPFC

The FC of the dmPFC ROI predicted individuals' memory for self-related items. Stronger FC between dmPFC and a cluster located in the right occipital lobe was correlated with better memory for self-

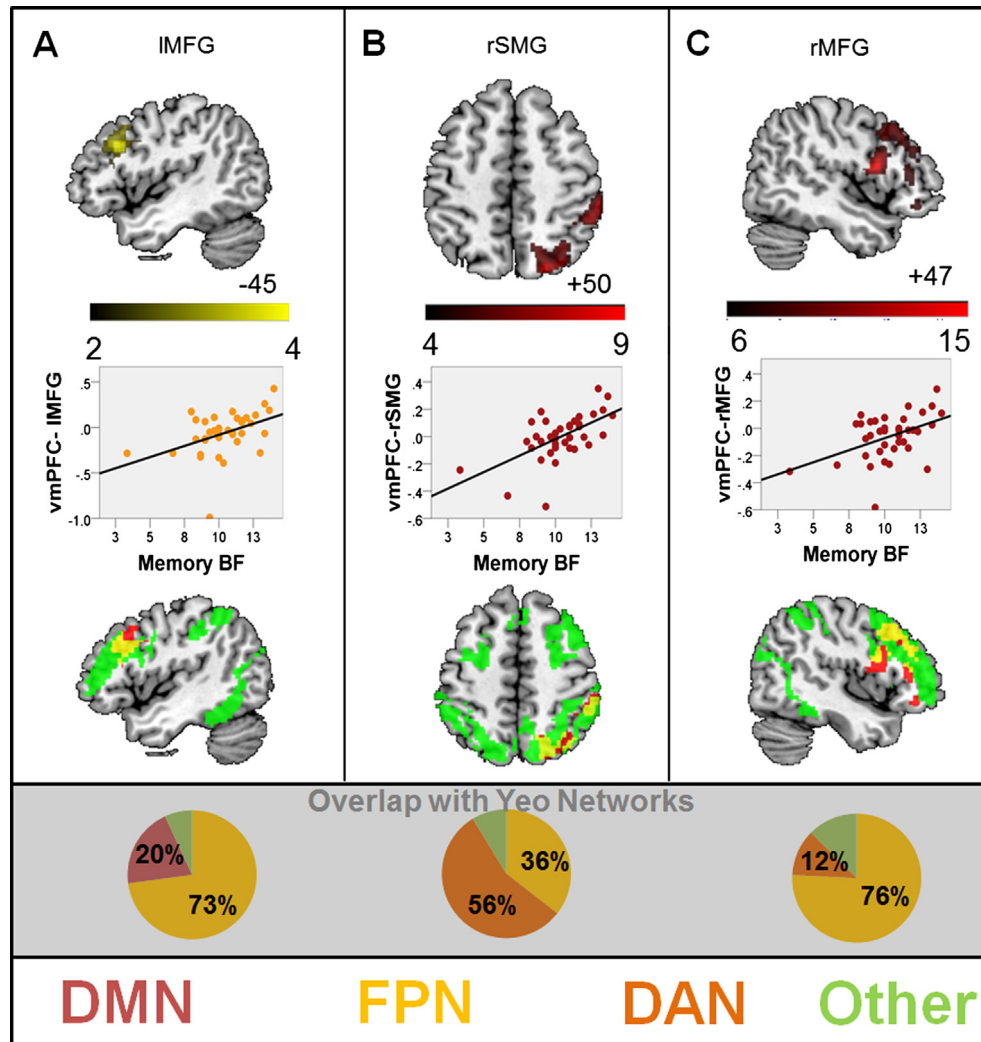
referent items (Fig. 5A, first row). This cluster overlapped with the visual network as defined by Yeo et al.'s (2011) resting state network analysis (see Fig. 5).

### 3.2.4. Hippocampal formation

The regression analyses performed on the HF+ seed revealed effects for self-related items: in particular stronger FC between the seed region and a cluster in left ventral anterior temporal lobe (lvATL) (Fig. 5B, first row) resulted in a better memory for self-related items. This cluster showed strong overlap with the Limbic Yeo Network (see right pie chart in Fig. 5). Visualization of this overlap can be observed in the third row of Fig. 5B.

### 3.3. Neurosynth decoding meta-analysis

To provide a quantitative inference of our experimental data, the connectivity maps obtained for each ROI and for each regressor was decoded using NeuroSynth's dataset (<http://www.neurosynth.org/decode/>). Fig. 6 displays all the functional terms from which the corresponding neuroimaging data from the database had correlation values bigger than 0.1 for each contrast in our data. From this meta-analytic decoding it can be seen that the functional connectivity map obtained for stronger memory for self-related items was associated with studies from the database containing terms



**Fig. 4.** Regions showing increased coupling with the ventro medial prefrontal cortex (vmPFC) showing increased memory for Best Friend (BF). (A) A region of left Middle Frontal Gyrus showing stronger FC with vmPFC for individuals with better memory for BF-related items. This cluster does not pass correction for the number of seeded locations. (B) A region of right Super Marginal Gyrus showing stronger FC to the vmPFC in individuals with stronger memory for BF-related items. (C) rMFG cluster with stronger FC to ROI in individuals with better memory for BF-related items (MNI:  $x = 47$ ). First row: Cluster corrected maps illustrating regions of the FC map that correlate with behaviour. Second row: Scatterplots reflecting relationship between memory performance and FC between ROI and cluster. Third row: Overlap (yellow) between clusters and the Dorsal Attention and Frontal Parietal Control Yeo networks (green). Grey panel: Pie charts and legend reflecting the percentage of the cluster that overlaps with each one the Yeo networks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

such as retrieval, autobiographical, emotion, mentalizing, semantics and theory of mind. In contrast, connectivity maps obtained for better memory for best friend were associated with terms such as working memory, working and task. Importantly the term self-referential was positively associated with the maps obtained for self memory and negatively associated with those obtained for best friend memory. These patterns of associations are consistent with the proposal that the map associated with self-related memory is associated with relatively automatic processes, and ones that are characteristic of the DMN, while the map associated with memory for a best friend is associated with relatively controlled processes.

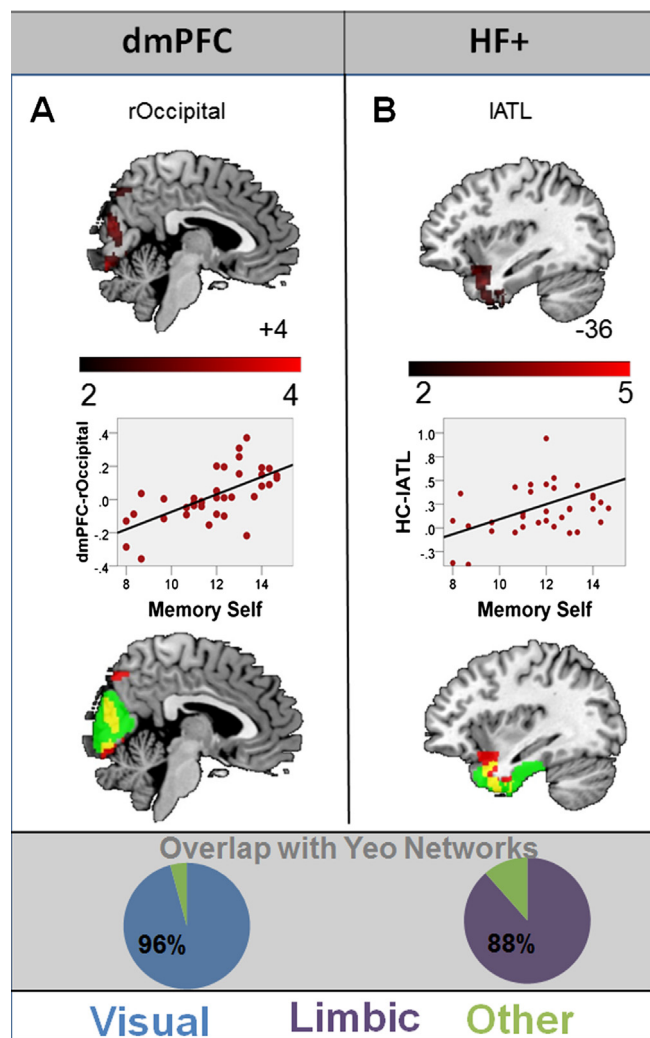
#### 3.4. Neurosynth “self” map activations

Finally, we formally compared the data produced through the individual difference analysis of resting state functional connectivity approaches with a spatial meta-analysis of peak activations performed by Neurosynth (search term: “self”; 903 contributing studies; <http://neurosynth.org/analyses/terms/self/>). The overlap

between the meta-analytical map and the patterns of functional connectivity can be observed in Fig. 7. It can be seen that there is overlap in several regions, most clearly in the left angular gyrus, and bilaterally in the lateral temporal lobe.

#### 4. Discussion

The current study set out to understand whether the functional architecture of the mPFC and the HF+ at rest predicted the strength of incidental memories produced when personality adjectives were related in terms of their applicability to different agents. Consistent with previous studies (Kelley et al., 2002; Kuiper & Rogers, 1979), the magnitude of incidental memory effects was related to the personal relevance of the individual to which a trait adjective was rated: Stronger memories were formed for words related to the self than a best friend and the weakest memories were produced when words were rated with respect to David Cameron (a non-familiar control), the latter not surpassing chance performance. Using the scores for each referent as regressors in an individual difference analysis of resting state FC, we found that stronger memories fol-



**Fig. 5.** Functional connectivity of dorsal medial prefrontal cortex (dmPFC) and the hippocampal formation (HF+) associated with stronger memory for the self. (A) A region of the right occipital (rOcc) cortex that showed stronger FC with the dmPFC for individuals with better memory for self-related items. (B) A region of left ventral Anterior Temporal Lobe (lvATL) that showed stronger coupling with the HF+ for participants with a better memory for items related to the self. First row: Cluster corrected maps illustrating regions of the FC map that correlate with behaviour. Second row: Scatterplot reflecting relationship between memory performance and FC between ROI and cluster. Third row: (A) Overlap (yellow) between limbic Yeo network (green) and rOcc cluster (red). (B) Overlap (yellow) between Yeo visual network (green) and lvATL cluster. Grey panel: Pie charts and legend reflecting the percentage of the clusters that overlap with each of the Yeo networks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

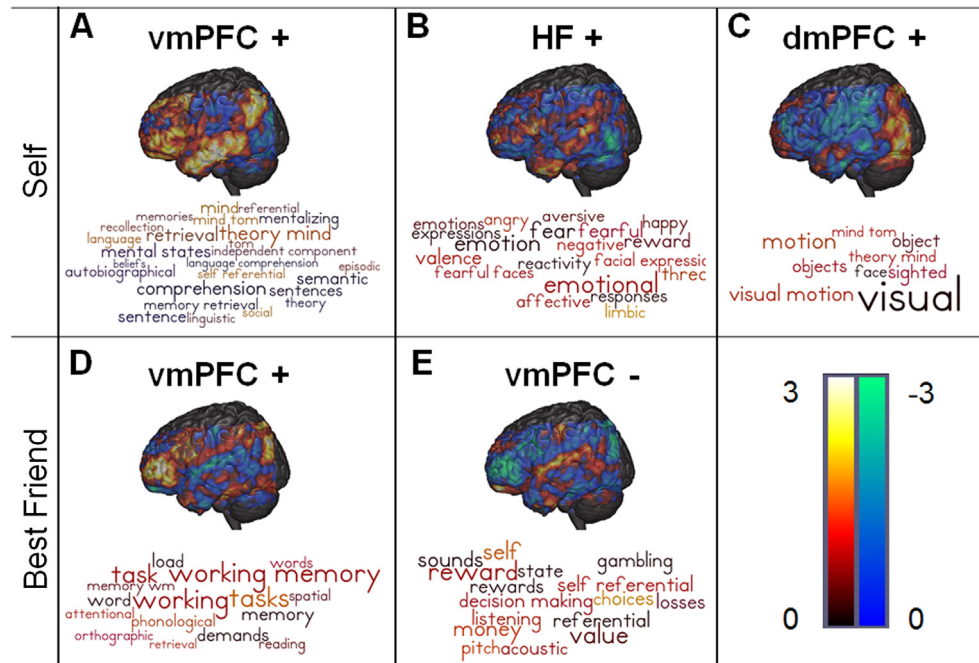
lowing self-related processing were related to stronger functional coupling between the vmPFC and bilateral mid temporal lobe, and left angular gyrus, as well as coupling between HF+ and regions of lvATL. We also found that stronger memory for self related items was linked to coupling between the dmPFC seed and a region of medial visual cortex, a region that falls at the boundary of the DMN and the visual cortex. In contrast, successful retrieval of words encoded with respect to the best friend was linked to decoupling between the ventral prefrontal cortex and the paracingulate gyrus, plus coupling with lateral parietal and prefrontal regions. No patterns of FC predicted memory scores for items related to David Cameron possibly due to retrieval for these items being at chance. Finally, a meta-analytic decoding of the connectivity maps predictive of self and best friend memory

supported our distinction between individuals who excel at memory for themselves, rather than their best friends: Memory for self was associated with terms such as theory of mind, autobiographical or self-referential whereas enhanced memory for best friend was associated with terms like working memory.

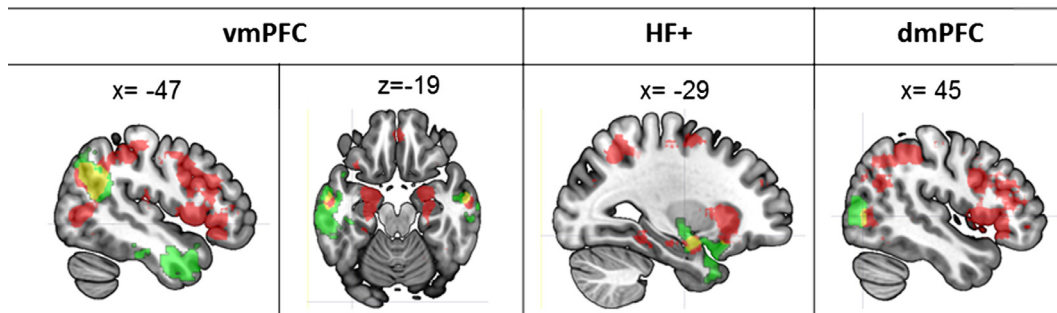
It is often assumed that the reason why items that are referred to the self form strong memories is because of the rich associative structure that is associated with our knowledge of who we are (Symons & Johnson, 1997): this self-knowledge provides a strong schema to support memory encoding and retrieval allowing it to be retrieved efficiently and automatically. Prior work has shown that schema-based memory engages vmPFC (Ghosh et al., 2014; McKenzie et al., 2014; Spalding et al., 2015; van Kesteren, Rijpkema, et al., 2010; van Kesteren et al., 2012) and our study suggests that a strong bias to remembering information rated to ourselves depends on forming a network between this region and lateral and anterior regions of the temporal lobe and the angular gyrus – regions that together make up the DMN (Raichle & Snyder, 2007; Raichle et al., 2001). Functional studies often implicate the DMN in situations when information from memory is often retrieved effortlessly, such as making global semantic associations (Bar, Aminoff, Mason, & Fenske, 2007) periods of spontaneous thought (Mason et al., 2007) and the process of self-reference itself (Gusnard, Akbudak, Shulman, & Raichle, 2001; Macrae et al., 2004; Northoff et al., 2006). These are all states that can involve the automatic retrieval of information from memory. Behaviourally we observed that self-memory was correlated with relatively poor performance on the SSRT. The SSRT is a measure of inhibitory control and previous studies have shown that errors in response inhibition are linked to a lack of DMN deactivation (Li et al., 2007). Moreover SSRT can be used to distinguish subjects with ADHD from normal controls (Senderecka, Grabowska, Szewczyk, Gerc, & Chmylak, 2012) and previous research on ADHD has revealed reduced DMN deactivations during complex tasks (Fassbender et al., 2009) supporting the notion that successful executive control requires DMN deactivation. In addition, high activity in the DMN precedes lapses in cognitively demanding tasks (Weissman et al., 2006). Altogether our results therefore are consistent with the idea that self-relevant memories are supported by integrated activity within the DMN, a state that promotes the automatic and elaborated processing of associative information from memory that can at times be hard to inhibit.

Information related to best friends was retrieved more effectively than for the David Cameron control items. However, this type of memory was associated with a different network of regions than those observed for strong memories of the self. Better memory for a best friend involved a network that spanned the lateral surface of parietal and frontal cortex, including middle frontal and inferior frontal gyrus and supramarginal gyrus. Overlap with the Yeo networks, revealed that although this network was anchored in the vmPFC, these regions are a part of the dorsal attention and frontoparietal control networks, large-scale systems that are often activated by attention-demanding tasks (Collette et al., 1999; Corbetta & Shulman, 2002; Duncan, 2010). Thus unlike a strong memory for the self, a tendency to remember items related to one's best friend was linked to a coupling between ventral regions of the mPFC and regions beyond the broader DMN that are involved in goal-directed attention. Studies have shown that the lateral prefrontal cortex, particularly the inferior frontal gyrus, often activates when participants make semantic decisions that are more difficult either because the meaning is ambiguous or because participants must make links between stimuli that are only weakly related together (Noonan, Jefferies, Garrard, Eshan, & Lambon Ralph, 2013). More generally, co-activation between the DMN and the lateral prefrontal cortex occurs when novel or complicated decisions have to be made based on memory such as during cre-





**Fig. 6.** Neurosynth meta-analysis of the unthresholded images obtained for each significant contrast. (A) Ventral Medial Prefrontal Cortex (vmPFC) map. (B) Hippocampal formation (HF+) and (C) Dorsal Medial Prefrontal Cortex (dmPFC) maps associated with better memory for self-related items. (D) vmPFC map associated with better memory for Best Friend related items. (E) vmPFC map associated with worse memory for Best Friend related items.



**Fig. 7.** Overlap (yellow) between Neurosynth meta-analytic map for term self (red) and clusters predictive of memory for self items (green). First row represents the seed region from where the clusters in green were originated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

activity (Beatty et al., 2014) or when we plan the future (Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010). Together the enhanced retrieval for best friend relative to the David Cameron control, as well as a functional connectivity network anchored in the vmPFC seed, suggest that memory for the best friend is likely to also benefit from an elaborate schema, perhaps one that is similar to that of the self (e.g. Mitchell et al., 2005). Importantly, this similarity with the self may mean that an accurate memory for close personal acquaintances is not only hampered by the weaker traces formed at encoding but may also depend on overcoming interference from associations with self memories and requires regions outside of the DMN that may function to guide retrieval in the face of interference. This possibility is supported by previous research which has commonly found inferior and dorsolateral prefrontal gyri, regions predictive of best friend memory in this study, to be involved in working memory processes (Curtis & D'Esposito, 2003). This hypothesis should be examined in future studies.

One general implication of our results is that vmPFC may act as a hub whose FC determines how schematic information is represented in the cortex. As well as connections to other regions of

the mPFC, it can be seen from Fig. 2 that this region of cortex is connected to medial aspects of the temporal lobe, as well as other limbic regions. In topographical terms this region is therefore well placed to integrate affective and episodic information into the broader prefrontal cortex. Consistent with this view, our data shows that, across people, the nature of the patterns of connectivity it exhibits at rest has implications for aspects of social memory: A strong memory for self-relevant information was associated with greater integration within the DMN, whereas a stronger memory for best friend required integration with regions important for executive control. One implication of this view is that the vmPFC exhibits modes of cortical processing that reflect how different aspects of mnemonic and affective information dominate cognition. Although our current data are consistent with this hypothesis, it is impossible to infer whether these patterns exert their effect on memory during encoding or retrieval since the current study explored individual differences in resting state FC rather than measuring online neural activity. Future studies exploring different patterns of FC during different types of social and non social memory retrieval will help to address this question.

It is worth considering certain limitations with the current data. Our study shows that better memory for different referents is associated with distinct patterns of functional connectivity however, the current study is unable to decipher whether the different patterns of functional connectivity predictive of memory for self and best friend items are indeed capturing the processing differences in referents per se, or whether instead they are reflecting differences in general memory strength. Future studies using a control memory task matched in accuracy to the reference task but instead employing a different memory manipulation such as elaborative semantic encoding will be able to address this issue.

Regardless of these issues, our results suggest that information related to the self and to one's best friend is supported by different patterns of FC with the vmPFC. Whereas information exclusively related to the self relies on integration between these region and the DMN, remembering information about a similar other, benefits from integration between the vmPFC and executive control regions. We argue that this occurs because there are different strengths of association for the different types of memory. Memories associated with a best friend have weaker associations than do self-related. Consequently, remembering information about a personally significant other will require additional executive control directed either to retrieve the weaker memory trace, or to correctly select the appropriate memory despite interference from the stronger, and often associated, memories about the self.

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