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

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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 connnectivity 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.

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.

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retrieving dominant semantic associations of words that come to mind relatively automatically (Binder, Desai, Graves, & Conant, 2009; Davey et al., 2015). In all this 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.