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Brains creating stories of selves: the neural basis of autobiographical reasoning

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Personal identity critically depends on the creation of stories about the self and one's life. The present study investigates the neural substrates of autobiographical reasoning, a process central to the construction of such narratives. During functional magnetic resonance imaging scanning, participants approached a set of personally significant memories in two different ways: in some trials, they remembered the concrete content of the events (autobiographical remembering), whereas in other trials they reflected on the broader meaning and implications of their memories (autobiographical reasoning). Relative to remembering, autobiographical reasoning recruited a left-lateralized network involved in conceptual processing [including the dorsal medial prefrontal cortex (MPFC), inferior frontal gyrus, middle temporal gyrus and angular gyrus]. The ventral MPFC—an area that may function to generate personal/affective meaning—was not consistently engaged during autobiographical reasoning across participants but, interestingly, the activity of this region was modulated by individual differences in interest and willingness to engage in self-reflection. These findings support the notion that autobiographical reasoning and the construction of personal narratives go beyond mere remembering in that they require deriving meaning and value from past experiences.

Keywords: autobiographical memory; autobiographical reasoning; self-defining memories; self-reflection; fMRI

INTRODUCTION

Humans are storytellers and are especially prone to create stories about themselves and their life. Through personal narratives, we find meaning and purpose in the multiplicity of our experiences and we come to see ourselves as unique individuals endowed with a protracted existence across time (Gallagher, 2000; McAdams, 2001; McLean et al., 2007). The construction of such narratives critically depends on autobiographical reasoning, a process of reflective thinking through which we form links between disparate elements of our life and the self (Habermas and Bluck, 2000). Autobiographical reasoning helps establishing personal identity and continuity across change, and research has shown the importance of this process for identity development, maturity and well-being (King et al., 2000; McLean and Pratt, 2006; Singer et al., 2007; Raffard et al., 2010; Lilgendahl and McAdams, 2011). The aim of this study is to shed light on the neural basis of this process so critical to the construction of a narrative self.

Over the past two decades, important progress has been made in identifying the brain regions that support various facets of self-knowledge (Damasio, 1999; Northoff et al., 2006; Lieberman, 2007; Klein and Gangi, 2010; D'Argembeau and Salmon, 2012; Wagner et al., 2012). The neural basis of autobiographical memory in particular has been much investigated and is now well characterized, with neuroimaging studies consistently showing that the retrieval of autobiographical information recruits a specific set of frontal, parietal and temporal regions (for recent reviews and meta-analyses, see Gilboa, 2004; Svoboda et al., 2006; Cabeza and St Jacques, 2007; McDermott et al., 2009; Spreng et al., 2009; Kim, 2012; Martinelli et al., 2013). The tasks used in these studies typically consist of remembering specific events or retrieving semantic knowledge of facts about one's life (Martinelli et al., 2013). Although it is likely that

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people sometimes engage in autobiographical reasoning while performing such tasks (i.e. reflect on the personal meaning and implications of retrieved information), the brain regions that are specifically involved in this process have not been examined. Thus, while the neural substrates of autobiographical memory are now well known, the brain regions that contribute to deriving a sense of self and identity from personal memories remain to be elucidated.

In the current study, we address this question by contrasting the neural activity associated with two different ways of considering the same autobiographical memories. A few days before the scanning session, participants selected a set of memories that have been important in developing and sustaining their sense of self and identity (i.e. self-defining memories; Blagov and Singer, 2004; Conway et al., 2004; Thorne et al., 2004; Lardi et al., 2010). During scanning, we instructed participants to approach each of their memories in two different ways: in some trials, they had to remember the concrete content of the event in order to mentally re-experience the situation in its original context (autobiographical remembering), whereas in other trials they were asked to reflect on the broader meaning and implications of their memory (autobiographical reasoning). Contrasting the neural activity associated with these two ways of approaching the same self-defining memories allowed us to identify the brain regions specifically involved in the autobiographical reasoning process.

Two main predictions were tested in the present study. First, because autobiographical reasoning involves linking a remembered event to more general (semantic) knowledge about one's life and the self-concept (Habermas and Bluck, 2000; McLean and Fournier, 2008), we expected this process to engage brain regions that support the storage, retrieval and manipulation of semantic knowledge, such as the lateral temporal cortex, posterior inferior parietal lobe, inferior frontal gyrus and dorsomedial prefrontal cortex, especially in the left hemisphere (Binder *et al.*, 2009). On the other hand, when participants focus on remembering the content of their self-defining memories (compared with when they engage in autobiographical reasoning), they should preferentially recruit regions involved in mentally

re-experiencing past events, such as the posterior cingulate/retrosplenial cortex, regions of the medial temporal lobe (hippocampus and parahippocampal gyrus) and, due to the emotions that may be evoked, the amydgala (Addis *et al.*, 2004a,b; Gilboa *et al.*, 2004; Daselaar *et al.*, 2008).

Our second prediction was that autobiographical reasoning would engage brain structures mediating the processing of personal/affective significance. The product of autobiographical reasoning is that we come to realize the importance of our past experiences (e.g. by considering the role these experiences have played in shaping us into our present selves), which provides us with a sense of meaning and purpose in our life (Habermas and Bluck, 2000; Lilgendahl and McAdams, 2011). We predicted that this increased meaning and sense of value in relation to one's personal past would be reflected in higher activation of the ventral medial prefrontal cortex (MPFC). Indeed, the ventral MPFC may function to assign value to self-relevant information (D'Argembeau et al., 2012) and, more generally, to generate affective meaning from various sources of information (Roy et al., 2012). It is important to recognize, however, that people differ in the extent to which they reflect on the meaning and implications of their past experiences (Blagov and Singer, 2004; McLean and Fournier, 2008; Lilgendahl and McAdams, 2011), and for this reason we also sought to investigate whether individual differences in self-reflection would modulate the neural correlates of autobiographical reasoning. People who are more inclined to introspect about their personal attributes and experiences may derive more meaning and value from reflecting on their self-defining memories (Trapnell and Campbell, 1999). Therefore, we expected individual differences in self-reflection to be associated with differential activation of brain regions involved in generating personal significance, in particular the ventral MPFC.

Finally, another purpose of this study was to investigate possible differences between the remembrance of self-defining experiences and the recall autobiographical memories that have been elicited in response to cue words, which is one of the most commonly used method to investigate the neural correlates of autobiographical memory (Cabeza and St Jacques, 2007). On the one hand, one could expect that the recall of self-defining memories may automatically generate a higher sense of meaning and value compared with the recall of word-cued memories (because the latter would presumably refer to more mundane events), which may be associated with increased activity in brain regions implicated in the generation of personal significance (such as the ventral MPFC). On the other hand, focusing on remembering the content of events (rather than reflecting on their meaning and implications) may reduce, and perhaps even eliminate, differences in value signals associated with self-defining vs word-cued memories. Here, we examined these possibilities by contrasting the neural activity associated with remembering these two kinds of autobiographical memories.

METHODS

Participants

Participants were 24 right-handed young adults (16 women; mean age = 22.7 years, range = 19–26 years), with no history of neurological or psychiatric disorder. They all gave their written informed consent to take part in the study, which was approved by the Ethics Committee of the Medical School of the University of Liège.

Task description and procedures

Pre-scan interview

Between 1 and 3 days before the functional magnetic resonance imaging (fMRI) session, participants were asked to generate five memories for personally significant events; the instructions for eliciting these

memories were adapted from the self-defining memory task (Singer and Moffitt, 1991–1992; Blagov and Singer, 2004). Five memories generated in response to cue words (e.g. restaurant) and matched with the self-defining memories with regard to temporal distance were also selected (see the Supplementary Materials for further details).

fMRI session

During the fMRI session, participants were asked to approach the previously selected self-defining memories in two different ways. In some trials, they were instructed to remember the content of the event in as much detail as possible, in order to mentally re-experience the situation in its original context (i.e. to remember where they were, with whom, what happened, how they felt and so on). In other trials, participants were instructed to reflect on the broader meaning of the event and to think about the importance and implications of this event in relation to the self (i.e. to think about what the event says about their personality, how they have changed following this event, what they have learned and to consider the links between this event and other significant life experiences). The instructions emphasized that in the 'content condition', participants should exclusively focus on the concrete content of the event (i.e. what they saw, heard, felt and so on), without reflecting on the larger meaning of this event. Participants also performed the content condition for the word-cued memories that were selected from the pre-scan interview (i.e. they tried to remember each event in as much detail as possible, in order to mentally re-experience the situation). The autobiographical reasoning task was not performed for word-cued memories because pre-tests revealed that this task was quite artificial in this case, as the memories were not particularly meaningful and had few (if any) implications for the self.

Each trial started with the presentation of a cue slide that indicated the kind of task to perform (i.e. remembering the content or reflecting on the importance), as well as a short sentence summarizing one event that was reported during the pre-scan session. Once they had identified the task and corresponding event, participants were instructed to close their eyes and to press a button to indicate that they start performing the task; this phase was self-paced and could take up to 5 s. Participants then either remembered the content of the event or reflected on its importance and meaning with eyes closed for 20 s. After 20 s, participants heard a beep indicating that they should open their eyes and a fixation cross was presented on the screen (jittered between 4 and 8 s); participants were instructed to try to empty their mind before the next trial began.

Three functional runs were acquired and, in each run, participants had to perform each task (i.e. remembering the content of self-defining memories, reflecting on the importance of self-defining memories and remembering the content of word-cued memories) for each of the memories that had been selected during the pre-scan session. Thus, in total, there were 15 trials per condition (i.e. participants performed each task three times for each of the five memories). Within each run, trials were presented in pseudo-random order, such that a particular condition could not be repeated immediately and could not be separated by more than three trials of a different condition.

Individual differences in self-reflection

Individual differences in the disposition to engage in self-reflection were assessed using the Rumination-Reflection Questionnaire (RRQ) (Trapnell and Campbell, 1999; we here used the French version of the RRQ constructed by Jermann *et al.*, 2010). The RRQ was designed to distinguish intellectual curiosity or epistemic interest in the self (reflection) from maladaptive forms of self-focus (rumination). Here, we were particularly interested in the reflection scale, although the entire questionnaire was administered. In the reflection scale,

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respondents have to assess their curiosity and interest in reflecting or introspecting about the self and about their life (e.g. 'I love exploring my "inner" self', 'I often love to look at my life in philosophical way'), using a rating scale ranging from 1 (strongly disagree) to 5 (strongly agree). In the rumination scale, respondents have to assess their tendency to experience recurrent thoughts or ruminations about the self and past events (e.g. 'Often I am playing back over in my mind how I acted in a past situation'). In the present sample, both scales had good internal reliability ($\alpha = 0.93$ and 0.87, for the rumination and reflection scales, respectively) and the two scales were not significantly correlated (r = -0.02).

fMRI data acquisition

Functional MRI time series were acquired on a 3T head-only scanner (Magnetom Allegra, Siemens Medical Solutions, Erlangen, Germany) operated with the standard transmit-receive quadrature head coil. Multislice T2*-weighted functional images were acquired with a gradient-echo echo-planar imaging (EPI) sequence using axial slice orientation and covering the whole brain (34 slices, FoV = $192 \times$ 192 mm^2 , voxel size = $3 \times 3 \times 3 \text{ mm}^3$, 25% interslice gap, matrix size = $64 \times 64 \times 34$, TR = 2040 ms, TE = 30 ms, FA = 90°). For each run, around 225 functional volumes were acquired, and the first three volumes were discarded to avoid T1 saturation effects. After the third run, a gradient-recalled sequence was applied to acquire two complex images with different echo times (TE = 4.92 and 7.38 ms, respectively; TR = 367 ms, $FoV = 230 \times 230 \text{ mm}^2$, $64 \times 64 \text{ matrix}$, 34 transverse slices with 3 mm thickness and 25% interslice gap, FA = 90°, bandwidth = 260 Hz/pixel) and generate field maps for distortion correction of the EPI images. A structural MR scan was obtained at the end of the session (T₁-weighted 3D MP-RAGE sequence, TR = 1960 ms, TE = 4.4 ms, $FoV = 230 \times 173 \text{ mm}^2$, matrix size = $256 \times 192 \times 176$, voxel size = $0.9 \times 0.9 \times 0.9 \text{ mm}^3$).

fMRI data analysis

Data were preprocessed and analyzed using SPM8 (Wellcome Department of Imaging Neuroscience, http://www.fil.ion.ucl.ac.uk/spm). EPI time series were corrected for motion and distortion using Realign and Unwarp (Andersson *et al.*, 2001) together with the Fieldmap Toolbox (Hutton *et al.*, 2002). The high-resolution T_1 image was then coregistered to the functional images and segmented into gray matter, white matter and cerebrospinal fluid. Functional images were spatially normalized to MNI space (voxel size: $2 \times 2 \times 2 \,\mathrm{mm}^3$) using the normalization parameters obtained from the segmentation procedure, and subsequently smoothed with a Gaussian kernel with full-width at half maximum of 8 mm.

Preprocessed fMRI data were analyzed using the general linear model. For each participant, the task phase was modeled separately for each condition (i.e. remembering the content of self-defining memories, reflecting on the importance of self-defining memories, and remembering the content of word-cued memories) as epochs of 20 s duration. The design matrix also included one epoch regressor corresponding to the presentation of the cue slide and the realignment parameters to account for any residual movement-related effect. The canonical hemodynamic response function was used and a high-pass filter was implemented using a cutoff period of 128s in order to remove the low-frequency drifts from the time series. Serial autocorrelations were estimated with a restricted maximum likelihood algorithm with an autoregressive model of order 1 (+ white noise). For each participant, contrasts were calculated to identify differential activity associated with (i) remembering the content of self-defining memories vs reflecting on the meaning of self-defining memories and (ii) remembering the content of self-defining memories vs

remembering the content of word-cued memories. The individual contrast images were then entered into second-level random-effects analyses using one-sample t-tests. We also examined whether neural activity associated with reflecting on the meaning of self-defining memories was modulated by individual differences in self-reflection. In order to do so, the contrast images corresponding to the difference between reflecting on the meaning of self-defining memories νs remembering the content of these memories were entered in a whole-brain regression analysis using the scores on the reflection and rumination scales of the RRQ as predictors.

For all analyses, statistical parametric maps (SPMs) were thresholded at P < 0.001, uncorrected, and statistical inferences were corrected for multiple comparisons (P < 0.05, FWE-corrected) using Gaussian random field theory at the voxel level in a small spherical volume (radius, $10\,\mathrm{mm}$) around a priori locations of structures of interest (see Supplementary Materials). Regions outside a priori areas of interest are reported if they survived a threshold of P < 0.05, corrected for multiple comparisons (FWE) over the entire volume.

RESULTS

Autobiographical remembering vs autobiographical reasoning

Our main interest in this study was to identify the brain regions that show differential activity depending on the way people approach memories for significant personal experiences. First, we examined the regions that were more active when participants focused on the concrete content of their self-defining memories in order to mentally re-experience the events (autobiographical remembering) compared with when they reflected on the importance and meaning of these events (autobiographical reasoning). This contrast was associated with a large cluster of activation that included the ventral posterior cingulate/retrosplenial cortex and extended bilaterally to the parahippocampal gyrus, fusiform gyrus and posterior thalamus (Figure 1A and Table 1). Further foci of activation were found in the precuneus, the right angular gyrus, the lateral temporal cortex, the occipito-parietal junction, the dorsolateral prefrontal cortex, the amygdala (extending to the anterior hippocampus) and the medial orbitofrontal cortex (Figure 1A and Table 1).

Next, we examined the brain regions that were more active when participants engaged in autobiographical reasoning compared with when they remembered the concrete content of their self-defining memories. This contrast showed that reflecting on the importance and meaning of self-defining memories induced activation in the left dorsal MPFC, in a region that extended from the posterior upper part of the MPFC to the frontal pole [thus including medial Brodmann areas (BA) 8, 9 and 10; Figure 1B and Table 2]; another cluster of activation was also detected in the left pre-supplementary motor area. Besides these dorsomedial prefrontal areas, autobiographical reasoning was associated with greater activation in the left inferior frontal gyrus, the left middle temporal gyrus and the left angular gyrus (Figure 1B and Table 2).

Autobiographical reasoning and individual differences in self-reflection

As reported above, the dorsal MPFC was significantly more active when participants reflected on the importance and meaning of their self-defining memories compared with when they focused on the concrete content of these memories. The portion of MPFC that was detected in this contrast is clearly distinct from (i.e. more dorsal to) the medial prefrontal area that has been most frequently associated with self-reflection in previous studies (which is located in BA 10/32; for meta-analyses, see van der Meer *et al.*, 2010; Qin and Northoff, 2011; Denny *et al.*, 2012; Murray *et al.*, 2012). In the present study, this ventral portion of MPFC was not consistently engaged across participants when they reflected on the importance of their self-defining

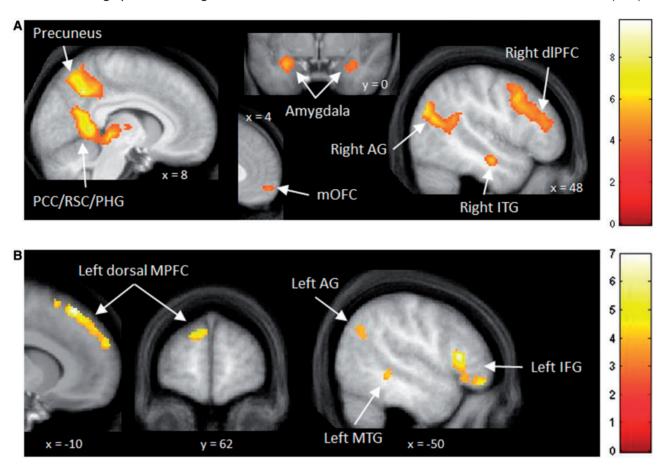


Fig. 1 Brain regions showing differential activity depending on the way of approaching self-defining memories. (**A**) Areas that were more active during autobiographical remembering compared with autobiographical reasoning. (**B**) Areas that were more active during autobiographical reasoning compared with autobiographical remembering. Displayed at P < 0.001 (uncorrected) on the mean structural MRI of all participants. AG: angular gyrus, dIPFC: dorsolateral prefrontal cortex, IFG: inferior frontal gyrus, ITG: inferior temporal gyrus, mOFC: medial orbitofrontal cortex, MPFC: medial prefrontal cortex, PCC: posterior cingulate cortex, PHG: parahippocampal gyrus, RSC: retrosplenial cortex.

memories compared with when they remembered their concrete content (see Figure 2A). Interestingly, however, we found that the recruitment of the ventral MPFC during autobiographical reasoning depended on individual differences in the disposition to engage in self-reflection. Specifically, we performed a whole-brain search for regions that were correlated with scores on the reflection scale of the RRQ within the contrast comparing the two ways of approaching self-defining memoires (i.e. reflecting on their importance vs focusing on their concrete content). This analysis revealed that the differential activation of the ventral MPFC between the two conditions depended on individual differences in self-reflection: participants who had a higher disposition to engage in self-reflection activated the ventral MPFC to a greater extent when reflecting on the importance and meaning of their self-defining memories [Figure 2B; MNI coordinates: -6, 54, 4; k = 205 voxels; Z-score = 3.99, P = 0.005 corrected for multiple comparisons (FWE) at the voxel level over small volume of interest]. No other brain region showed a significant correlation with individual differences in self-reflection and scores on the rumination scale of the RRQ did not correlate significantly with any brain region for the same contrast.

Remembering self-defining memories vs word-cued memories

No brain region showed significantly higher activation when participants focused on the content of their self-defining memories compared with when they remembered the content of word-cued memories. The reverse contrast (recollecting word-cued memories > recollecting self-defining memories) did not reveal any significant activation either.

DISCUSSION

Our results demonstrate that a number of brain regions within the autobiographical memory network (Gilboa, 2004; Svoboda et al., 2006; Cabeza and St Jacques, 2007; McDermott et al., 2009; Spreng et al., 2009; Kim, 2012; Martinelli et al., 2013) show differential activity depending on the way people approach the same self-defining memories. Specifically, a left-lateralized network composed of the dorsal MPFC, inferior frontal gyrus, middle temporal gyrus and angular gyrus was more active when participants reflected on the personal significance and implications of their memories (autobiographical reasoning), while other brain regions commonly engaged in autobiographical memory retrieval (i.e. posterior cingulate/retrosplenial cortex, precuneus, amygdala/hippocampus, parahippocampal gyrus, dorsolateral prefrontal cortex and medial orbitofrontal cortex) showed higher activation when participants focused on the concrete content of the events and attempted to re-experience them in their original context (autobiographical remembering).

Although it is likely that participants in previous neuroimaging studies of autobiographical memory sometimes engaged in autobiographical reasoning when retrieving personal memories, the specific neural substrates of this self-reflective process remained to be elucidated. The present results are therefore important in showing that a specific set of brain regions within the autobiographical memory network is preferentially engaged when people reflect on the meaning and implications of their memories. As predicted, these brain regions are part of a left-lateralized network that has been consistently implicated in semantic processing (Vigneau *et al.*, 2006; Binder *et al.*, 2009; Price,

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Table 1 Brain regions that were more active for autobiographical remembering than for autobiographical reasoning

		MNI coordinates				
Brain region	BA	Х	у	Z	k	Z-score
Ventral PCC/RSC/PHG	29/30	8	-48	4	4051	5.50*
Left fusiform gyrus	37	-28	-44	-16	Same	6.08*
Right fusiform gyrus	37	30	-42	-14	Same	4.88*
Precuneus	7	6	-54	40	4290	6.07*
Right angular gyrus	39	46	-64	20	Same	4.66**
Left inferior temporal gyrus	37	-56	-56	-8	351	5.77*
Right inferior temporal gyrus	20	52	-14	-18	276	5.14*
Left occipito-parietal junction	39/19	-38	-80	28	753	5.83*
Left dorsolateral PFC	6/8	-24	10	58	966	4.47**
Right dorsolateral PFC	6/9/46	34	6	54	2832	4.86*
Right amygdala/anterior hippocampus	28/35	24	-8	-18	241	4.35**
Left amygdala/anterior hippocampus	28/35	-28	0	-20	208	4.18**
Medial orbitofrontal cortex	11	4	58	—12	61	3.69**

^{*}Significant at P < 0.05 corrected for multiple comparisons (FWE) at the voxel level over the entire volume. **Significant at P < 0.05 corrected for multiple comparisons (FWE) at the voxel level over small volumes of interest.

Table 2 Brain regions that were more active for autobiographical reasoning than for autobiographical remembering

		MNI coo	rdinates			
Brain region	BA	X	у	Z	k	Z-score
Left dorsal MPFC	8/9	-10	34	56	494	5.05*
	10	-8	62	28	Same	4.04**
Left inferior frontal gyrus	45	-50	20	10	502	4.80*
	47	-44	38	-14	Same	4.31**
Left pre-SMA	6	-6	18	64	102	4.23**
Left middle temporal gyrus	21	-56	-34	-4	166	3.48**
Left angular gyrus	39	-48	-62	30	51	3.46**

^{*}Significant at P < 0.05 corrected for multiple comparisons (FWE) at the voxel level over the entire volume. **Significant at P < 0.05 corrected for multiple comparisons (FWE) at the voxel level over small volumes of interest.

2010). Most previous studies of semantic memory involved the processing of simple and non-personal stimuli (e.g. accessing the meaning of words). The present results thus extend previous findings by showing that many of the same brain regions are also recruited for processing the meaning of more complex and personal information, such as autobiographical memories (for further discussion of the notion of personal semantics and its relationship to general semantic memory, see Renoult *et al.*, 2012). Furthermore, our findings support the idea that autobiographical reasoning goes beyond mere remembering in that it involves extracting the deeper meaning of one's past experiences and integrating them with conceptual knowledge about the self and one's life (Habermas and Bluck, 2000; McLean and Fournier, 2008).

The different areas of the semantic processing network that were recruited in this study may mediate specific representational systems and component processes involved in autobiographical reasoning. The left lateral temporal cortex and angular gyrus may function as multimodal convergence zones that represent conceptual knowledge, while the dorsomedial and inferior prefrontal cortices may control the top-down activation and selection of the information stored in these temporoparietal areas (Binder and Desai, 2011). The left dorsomedial

prefrontal region that was active in the present study extended further to the frontal pole, an area that may support the integration of retrieved knowledge (Green *et al.*, 2012). Previous neuroimaging studies have shown that the left inferior frontal gyrus plays an important role in inner speech (Jones and Fernyhough, 2007; Geva *et al.*, 2011); this region is frequently activated during self-referential thinking and may mediate the use of inner speech as a cognitive tool for processing self-related information (Morin and Michaud, 2007; Morin, 2011). Together, these areas may support the retrieval, manipulation and integration of conceptual knowledge about the self and one's life, in an effort to derive meaning from one's past experiences.

The dorsal MPFC area that showed higher activity during autobiographical reasoning has been associated with social cognition and, in particular, with tasks that involve thinking about other individuals (Van Overwalle, 2009; Denny et al., 2012). Previous studies have shown that self-defining memories frequently feature relationship themes (Lardi et al., 2010; Thorne et al., 2004; Singer et al., 2007), and a content analysis shows that 40% of the memories collected in the present study were indeed centered on relationships with others (see Supplementary Materials). Given this, it could be that the dorsal MPFC was active during autobiographical reasoning because reflecting on one's past experiences often involved thinking about others (e.g. inferring their mental states and reflecting on what the event meant for them). It would be interesting in future studies to select, in a systematic way, self-defining memories that feature different thematic contents (e.g. relationship vs achievement themes) to test this hypothesis further.

Despite the fact that the ventral MPFC is the area most commonly activated during self-reflection tasks (van der Meer et al., 2010; Qin and Northoff, 2011; Denny et al., 2012; Murray et al., 2012; Martinelli et al., 2013), we did not find consistent activation in this region across participants when they reflected on the meaning of their past experiences compared with when they remembered their concrete content. Of particular interest, however, we found that the activity of the ventral MPFC during autobiographical reasoning was modulated by individual differences in self-reflection: the ventral MPFC showed higher activity during autobiographical reasoning only in participants who have greater interest and willingness to introspect about their personal attributes and experiences. People who are more inclined to self-reflect have more extensive self-knowledge and may derive more meaning from their memories, hence providing them with a higher sense of value and purpose in their life (Trapnell and Campbell, 1999). The activation of the ventral MPFC in these individuals may reflect this sense of value and meaning derived from one's past experiences. This interpretation fits well with evidence that the ventral MPFC tracks the personal value placed on self-related information (D'Argembeau et al., 2012) and, more generally, functions to generate affective meaning from various sources of information (Roy et al., 2012). More speculatively, such value signals generated by the ventral MPFC during autobiographical reasoning might play some role in determining the integration of past experiences in personal narratives (i.e. experiences that receive higher value might be those that are given center stage in an individuals' life story), and in shaping the impact of these experiences on personal traits, goals and behavior patterns.

Another set of regions within the autobiographical memory network was preferentially activated when participants focused on the concrete content of their self-defining memories compared with when they reflected on the broader meaning of these memories. These regions included posterior and limbic structures (i.e. the posterior cingulate/retrosplenial cortex, precuneus, amydgala/hippocampus and parahippocampal gyrus) that have been associated with the episodic aspect of autobiographical memory and likely mediate the mental re-experience of past events (Addis *et al.*, 2004a; Gilboa *et al.*, 2004; Martinelli *et al.*, 2013). Furthermore, autobiographical remembering activated the

¹The specific function of the angular gyrus is still debated (for a review of different views, see Seghier, 2012) and another possibility would be that this region supports the bottom-up capture of attention by information that is retrieved during the autobiographical reasoning process (Cabeza *et al.*, 2012).

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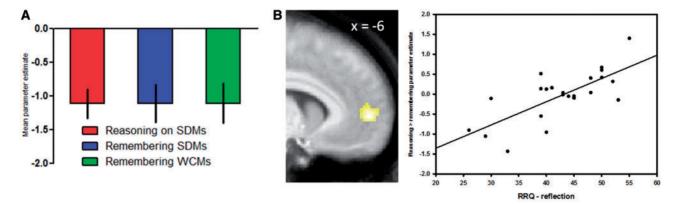


Fig. 2 Ventromedial prefrontal activity. (A) Mean parameter estimates within an a priori region of the ventral MPFC (6 mm radius sphere centered at -6, 50, 4), as a function of the task condition (error bars represent s.e.m.). Consistent with previous findings (Buckner et al., 2008), the signal change in this region took the form of deactivations relative to fixation baseline, but there was no significant difference between the three conditions across participants. (B) Ventromedial prefrontal area showing differential activity during autobiographical reasoning vs autobiographical remembering as a function of individual differences in self-reflection. Displayed at P < 0.001 (uncorrected) on the mean structural MRI of all participants. SDMs: self-defining memories, WCMs: word-cued memories, RRQ: Rumination-Reflection Ouestionnaire

dorsolateral prefrontal cortex, which likely reflects the engagement of memory search and controlled retrieval processes to reconstruct the past events (Cabeza and St Jacques, 2007). Increased activity was also found in the medial orbitofrontal cortex, a region that may support quick intuitive processes that monitor the veracity and cohesiveness of retrieved memories (Gilboa, 2004). Collectively, these brain areas may mediate the reconstruction of the details of past episodes in order to mentally re-experience the situations in their original context.

The autobiographical memory network overlaps substantially with the default mode network (DMN), a set of interacting brain areas that may support spontaneous cognition during wakeful rest (Gusnard and Raichle, 2001; Buckner et al., 2008; Spreng et al., 2009). Results from anatomical and functional connectivity studies suggest that the DMN is intrinsically organized into distinct subsystems that support different functions (reviewed in Buckner et al., 2008). Two such subsystems-the so-called 'medial temporal lobe (MTL)' and 'dorsal MPFC' subsystems (Andrews-Hanna et al., 2010)—are remarkably similar to the two sets of brain regions that were associated, respectively, with autobiographical remembering and autobiographical reasoning in the present study. In line with our findings, there is evidence that the MTL subsystem supports the construction of specific event representations, whereas the dorsal MPFC plays a broad role in introspective processes (Andrews-Hanna, 2012). It would be interesting to investigate further whether and how the spontaneous activation of these subsystems during wakeful rest serves an identity function. An intriguing possibility, suggested by the present findings, is that the spontaneous engagement of the dorsal MPFC subsystem at rest might play some role in integrating novel experiences in the autobiographical database and associated self-concept (Conway, 2005), thereby contributing to maintaining a sense of personal unity and continuity across time and change.

Another purpose of this study was to investigate possible differences between remembering the content of self-defining memories and remembering the content of autobiographical memories that have been elicited in response to cue words. Although self-defining memories were rated as more personally significant than word-cued memories, the two kinds of memories were not associated with differential brain activation. Related findings have been previously reported in a study by Addis et al. (2009), who showed that the same core network was engaged when representing the content of different kinds of events (real past events, imagined past events and imagined future events) despite significant differences in their personal importance. Although these findings may at first sight seem surprising, a plausible explanation is that instructions to focus on the concrete content of the events might supersede the effect of personal significance, such that participants only recruit brain areas involved in constructing and mentally experiencing the events. Another possibility would be that the lack of differences between the two kinds of memories in the present study is due, in whole or in part, to the fact that participants had to remember the same memories multiple times during the scanning session. Repeatedly remembering the content of the same memories might have reduced associated neural activation (Svoboda and Levine, 2009), thus wiping out differences between self-defining and word-cued memories.

In conclusion, the present study shows that autobiographical reasoning relies on a specific set of regions within the autobiographical memory network, which may mediate the retrieval, manipulation and integration of conceptual knowledge about the self and one's life in order to derive meaning and value from past experiences. These regions may play a key role in the creation of personal narratives, thereby contributing to sustaining a coherent and stable sense of self and identity. The present study thus opens new perspectives for investigating the neural basis of disturbances in narrative identity that characterize some psychopathological conditions such as schizophrenia (Raffard et al., 2010).

SUPPLEMENTARY DATA

Supplementary data are available at SCAN online.

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