Running title: neural correlates of investments in self-views

Valuing one's self: medial prefrontal involvement in epistemic and emotive investments in self-views

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Abstract

Recent neuroimaging research has revealed that the medial prefrontal cortex (MPFC) is consistently engaged when people form mental representations of themselves. However, the precise function of this region in self-representation is not yet fully understood. Here, we investigate whether the MPFC contributes to epistemic and emotive investments in selfviews, which are essential components of the self-concept that stabilize self-views and shape how one feels about oneself. Using fMRI, we show that the level of activity in the MPFC when people think about their personal traits (by judging trait adjectives for selfdescriptiveness) depends on their investments in the particular self-view under consideration, as assessed by post-scan rating scales. Furthermore, different forms of investments are associated with partly distinct medial prefrontal areas: a region of the dorsal MPFC is uniquely related to the degree of certainty with which a particular self-view is held (one's epistemic investment), whereas a region of the ventral MPFC responds specifically to the importance attached to this self-view (one's emotive investment). These findings provide new insight into the role of the MPFC in self-representation and suggest that the ventral MPFC confers degrees of value upon the particular conception of the self that people construct at a given moment.

<u>Keywords:</u> fMRI; medial prefrontal cortex; self; value

The ability to form mental representations of the self is a central, perhaps distinguishing, feature of the human mind. Certain other species—and even some robots (Bongard et al. 2006)—possess rudimentary self-models that allow them to distinguish themselves from their environment, but there is no certainty that they think about themselves in abstract and symbolic ways as humans routinely do (Sedikides and Skowronski 1997; Leary and Buttermore 2003). We possess many different ideas and beliefs about who we are and what we are like—our traits, abilities, preferences, and goals—and how we feel and behave is strongly influenced by these self-conceptions, for better and worse (Leary 2004).

Substantial progress has recently been made in understanding how self-conceptions are represented and processed in the human brain. Neuroimaging studies have revealed that the medial prefrontal cortex (MPFC) and other cortical midline structures (CMS) are consistently engaged when people think about their own personal characteristics, such as their traits (e.g. Johnson et al. 2002; Kelley et al. 2002; Lieberman et al. 2004; D'Argembeau et al. 2005; Moran et al. 2006) and goals (e.g. Johnson et al. 2006; Packer and Cunningham 2009; D'Argembeau et al. 2010a). A recent review (Lieberman 2010) indicates that the ventral portion of the MPFC¹ is most frequently involved (94% of studies), followed by the posterior cingulate cortex/precuneus (63% of studies) and dorsal MPFC (53% of studies) (see also the meta-analyses of Northoff et al. 2006; Van Overwalle 2009; van der Meer et al. 2010). These findings demonstrate that CMS somehow contribute to self-representation, but the precise function of these regions remains unclear and debated (for different perspectives, see Northoff and Bermpohl 2004; Schmitz and Johnson 2007; Legrand and Ruby 2009; Mitchell 2009; D'Argembeau and Salmon in press).

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¹ The designation of different portions of MPFC varies somewhat across authors. In this article, the term ventral MPFC is used to describe a large portion of the medial prefrontal cortex that includes parts of the medial area 10, medial orbitofrontal cortex, and anterior cingulate cortex (z coordinate \leq 10 mm), whereas the term dorsal MPFC is used to refer to the higher portion of the medial prefrontal cortex (z coordinate \geq 10 mm).

Thinking about the self involves more than the dispassionate contemplation of one's personal attributes. As William James put it more than a century ago, "the altogether unique kind of interest which each human mind feels in those parts of creation which it can call me or mine may be a moral riddle, but it is a fundamental psychological fact" (James 1890, p. 289). The interest and affective value we place on our conceptions of ourselves is an essential constituent of the self-concept that stabilizes self-views and shapes how we feel about ourselves (Pelham 1991). Interestingly, the brain region that is most consistently recruited when people think about themselves—the ventral MPFC—is also well-known for its role in emotion (Phan et al. 2002; Schaefer et al. 2003) and valuation processes (Wallis 2007; Peters and Buchel 2010; Rangel and Hare 2010). Notably, there is evidence that activity in the ventral MPFC tracks the subjective value of various kinds of stimuli, including food, monetary rewards, and attractive faces (O'Doherty et al. 2003; Kable and Glimcher 2007; Chib et al. 2009; Hare et al. 2009), and some studies have shown that the degree of selfrelatedness assigned to the stimuli correlates with activity in value-related regions, including the ventral MPFC (Phan et al. 2004; de Greck et al. 2008). Together, these findings suggest that the ventral MPFC represents the personal value of information from diverse sources, ranging from primary rewards to complex social information (Montague et al. 2006; Peters and Buchel 2010). Although these studies focused on the subjective value assigned to external environmental stimuli, the ventral MPFC could play a similar putative role for mental representations of the self (e.g., people's beliefs about their personal traits). An intriguing possibility is thus that activity in the ventral MPFC when people think about themselves represents the value they attach to the particular self-conception that is displayed in their minds at a given moment.

Here, we specifically set out to test this hypothesis by investigating the neural correlates of people's investments in their self-views. Furthermore, we sought to examine

whether different forms of investment in self-views are supported by dissociable brain regions. Research has revealed that people possess at least two different forms of investment in their self-conceptions: they can place more or less importance and value on particular self-views, and can hold these self-views with more or less confidence (Pelham 1991). These two forms of investment—referred to as emotive and epistemic—involve distinct processes: the extent to which a self-view is valued and considered important (emotive investment) is related to one's personal goals and motives, whereas the degree of certainty with which a self-view is held (epistemic investment) depends on the amount and consistency of information one has about this aspect of the self (Pelham 1991). For example, someone might be certain that she is generally punctual (high epistemic investment), yet consider that punctuality is not a particularly important trait for her to possess (low emotive investment). On the other hand, this person might invest much importance in being attractive (high emotive investment) but might still feel uncertain about whether or not she truly possesses this attribute (low epistemic investment).

Although the neural substrates of epistemic and emotive investments in self-views have not yet been investigated, there are reasons to suspect that they may involve at least partly distinct brain areas. There is substantial functional specialization within the MPFC (Gilbert et al. 2006) and valuation processes primarily engage the ventral portion of MPFC (Wallis 2007; Peters and Buchel 2010; Rangel and Hare 2010). We thus expected that the ventral MPFC would mainly encode emotive investments in self-views. The dorsal MPFC, on the other hand, has been related to cognitive aspects of self-referential processing (e.g., introspective or evaluation processes) (Gusnard et al. 2001; Northoff and Bermpohl 2004; Schmitz and Johnson 2007), and might thus respond preferentially to epistemic investments in self-views.

We thus hypothesized that (1) activity in the MPFC when people think about their personal characteristics would track their investments in self-views and (2) at least partly distinct portions of MPFC (ventral versus dorsal) would be associated with emotive and epistemic investments in self-views. To test these hypotheses, we measured blood oxygenation level-dependent (BOLD) signals using whole brain fMRI while participants rated the self-descriptiveness of a series of trait adjectives (e.g., sincere, lazy, punctual). In line with previous research (Moran et al. 2006), we expected that activity in CMS would show a linear relationship with ratings of self-descriptiveness. More importantly for our purpose, we also obtained estimates of participants' epistemic and emotive investments in self-views by having them rate, immediately after scanning, their degree of certainty in each self-view and the importance they attach to each self-view. We then correlated participants' BOLD signal obtained during the self-descriptiveness judgments with their own subsequent evaluations of certainty and importance, which allowed us to identify the brain regions that responded to epistemic and emotive investments in self-views on a trial-by-trial basis.

Materials and Methods

Participants

Participants were 23 healthy, right-handed young adults (12 women; mean age = 21.5 years, range = 18-25), 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

During scanning, participants judged the self-descriptiveness of 240 trait adjectives selected from a published database (Anderson 1968) and translated into French (Le Barbenchon et al.

2005). The stimuli encompassed a wide range of social desirability values (range = 1.44-6.31, on a 7-point rating scale; M = 4.01, SD = 1.38). The 240 adjectives and 60 null events consisting of a fixation cross were presented in random order for 3500 msec, followed by a fixation cross of variable duration (random normal distribution with a mean duration of 1000 msec and standard deviation of 250 msec). Participants were instructed to rate each trait for self-descriptiveness (i.e., "to what extent does this trait describe you?"), using a Likert-type 4-point rating scale (pressing button 1 for "not at all," to button 4 for "completely"). Before the scanning session participants went through a series of practice trials (with a different set of adjectives) in order to familiarize them with the task.

Immediately after the scanning session, participants were presented with the same set of 240 trait adjectives and were instructed to make three kinds of judgments for each trait: (1) self-descriptiveness (i.e., "to what extent does this trait describe you?"; 1 = not at all, 4 = completely), (2) certainty in the self-view (i.e., "how certain are you that you possess or do not possess this trait?"; 1 = not at all, 4 = completely), and (3) importance of the self-view (i.e., "how important is it for you to possess or not possess this trait?"; 1 = not at all important, 4 = very important). The three kinds of judgments were self-paced, and participants were encouraged to use the four response possibilities in order to refine their judgments.

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² It is worth mentioning that the constructs of epistemic and emotive investments in self-views are distinct from the cognitive and affective components of self as defined by Moran et al. (2006). The cognitive component of self in Moran et al. referred to the brain areas that responded to degrees of self-descriptiveness (a dimension that is simply referred to here as self-descriptiveness). The affective component of self referred to brain areas that were more active for positive compared to negative traits that were judged self-descriptive. On the other hand, the construct of emotive investment that is investigated here refers to the importance/value attached to a self-view, whatever the valence of the trait under consideration. In the present sample, the average correlation between ratings of importance and the normative values for trait valence was .09 (i.e., they shared less than 1% of their variance).

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 = 192x192 mm², voxel size 3x3x3 mm³, 25% interslice gap, matrix size 64x64x34, TR = 2040 ms, TE = 30 ms, $FA = 90^{\circ}$). Six hundred and seventy functional volumes were acquired, and the first three volumes were discarded to avoid T₁ saturation effects. 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 = 230x230 mm², 64x64 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 EPI data. 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 x 173 mm², matrix size 256 X 192 X 176, voxel size 0.9 X 0.9 X 0.9 mm³). Head movement was minimized by restraining the subject's head using a vacuum cushion. Stimuli were displayed on a screen positioned at the rear of the scanner, which the participant could comfortably see through a mirror mounted on the standard head coil.

fMRI data analyses

fMRI data were preprocessed and analyzed using SPM8 (Wellcome Department of Imaging Neuroscience, http://www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB (Mathworks Inc., Sherborn, MA). 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) in SPM8. 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 X 2 X 2 mm³) 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.

Data were analyzed using the general linear model (GLM) as implemented in SPM8. First, we sought to replicate previous research demonstrating that activity in CMS shows a linear relationship with ratings of self-descriptiveness (Moran et al. 2006). To do so, we estimated a GLM that included a regressor for the presentation of the stimuli, a parametric regressor (the participant's ratings for self-descriptiveness), and the realignment parameters to account for any residual movement-related effect. Next, our main interest was to identify the brain areas that responded to epistemic and emotive investments in self-views. To do so, we estimated a GLM that included a regressor for the presentation of the stimuli, two parametric regressors (the participant's ratings for certainty and importance of self-views), and the realignment parameters. The two parametric regressors were entered simultaneously in the GLM because there was a small positive correlation between ratings of certainty and importance (see the 'Behavioral results' section) and we wanted to examine the effect of one dimension after the effect of the other dimension had been accounted for. The canonical heamodynamic response function was used and a high pass filter was implemented using a cut-off period of 128 s 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). Contrast images coding for each parametric regressor were constructed for each participant and were then entered into second-level random-effects analyses using one-sample *t*-tests.

For all analyses, statistical inferences were corrected for multiple comparisons using Gaussian random field theory at the voxel level in a small spherical volume (radius, 10 mm)

around a priori locations of structures of interest, taken from the literature on self-referential processing. These a priori regions of interest mainly concerned CMS areas, specifically the ventral MPFC (-6, 54, -2; 10, 52, 2) (Kelley et al. 2002; D'Argembeau et al. 2008), dorsal MPFC (-2, 56, 26; 10, 44, 24) (D'Argembeau et al. 2007, 2008), and posterior cingulate cortex (-2, -58, 26) (D'Argembeau et al. 2008). Other brain regions that have been associated with self-referential processing (though less consistently across studies) were also considered, including the inferior parietal lobe (-44, -66, 32; 46, -68, 40; 44, -54, 38) (Lou et al. 2004; D'Argembeau et al. 2010b), lateral temporal cortex (-62, -10, -12; 68, -10, -20) (Benoit et al. 2010; Rameson et al. 2010), insula (-36, 20, 4; 44, -10, 14) (Tsakiris et al. 2007; Modinos et al. 2009), and caudate nucleus (-12, 10, 12) (Enzi et al. 2009). For completeness, all brain regions outside a priori areas of interest that survived a threshold of p < .001 (uncorrected for multiple comparisons) with at least 30 contiguous voxels (i.e., a volume of 240 mm³) are listed in the Supplementary tables, but these regions are not discussed further.

Results

Behavioral results

Due to a defect in the MRI-compatible response box, the response times for the self-descriptiveness judgments made during scanning were not recorded for four participants. For the remaining 19 participants, a repeated-measure analysis of variance (ANOVA) of the median response times revealed that the speed of participants' responses differed as a function of self-descriptiveness ratings, F(3, 54) = 29.28, p < .001 (Figure 1). In line with previous findings (Moran et al. 2006), response times were shorter when a trait was self-descriptive or not self-descriptive (i.e., ratings of 1 and 4) compared to the graded responses (i.e., ratings of 2 and 3), F(1, 18) = 33.42, p < .001.

The response times for self-descriptiveness judgments were also influenced by epistemic and emotive investments in self-views, as measured by the post-scan ratings of certainty and importance. As shown in Figure 1, response times for self-descriptiveness judgments decreased with increasing certainty in self-views, F(3, 54) = 17.29, p < .001. In the same vein, response times decreased with increasing importance of self-views, F(3, 54) = 15.30, p < .001 (Figure 1). Thus, although participants did not explicitly reflect on epistemic and emotive investments in self-views during scanning, their investments can be objectified in terms of their influence on the speed of self-descriptiveness judgments. These data provide support for the validity of our measures of investments in self-views.

In line with previous findings (Pelham 1991), there was a positive correlation between ratings of certainty and ratings of importance. However, this correlation was rather small: the average correlation was .26 (which is comparable to the average correlation reported by Pelham 1991), meaning that the two forms of investments shared only about 7% of their variance in this sample.

fMRI results

We first investigated the brain regions in which neural activity was correlated with ratings of self-descriptiveness. In line with previous observations (Moran et al. 2006), self-descriptiveness was positively correlated with activity in several CMS, including the ventral MPFC, dorsal MPFC, and posterior cingulate cortex (PCC) (Figure 2, Table 1). Figure 2 shows that the signal change in the peak voxel in the MPFC (which was located in the ventral MPFC; see Table 1) took the form of deactivations relative to baseline (with less decreases in activity as a function of increasing self-descriptiveness), which also replicates previous findings (Moran et al. 2006). A positive correlation with self-descriptiveness was also detected in the left inferior parietal lobe, right insula, and left caudate (Table 1).

Having replicated previous findings that CMS activity correlates with self-descriptiveness, our main interest was then to identify the brain areas that responded to epistemic and emotive investments in self-views. To do so, we correlated participants' BOLD signal obtained while they performed the self-descriptiveness judgments with their own subsequent evaluations of the certainty and importance of each self-view. In accord with our prediction that neural activity in the MPFC would track participants' investments in their self-views, we found that ratings of personal importance were positively correlated with activity in a region of the ventral MPFC and a region of the dorsal MPFC; a positive correlation was also detected in the PCC/precuneus, inferior parietal lobe, and right insula (Table 2). Ratings of certainty were also positively correlated with neural activity in the MPFC, in both ventral and dorsal regions; a positive correlation was also detected in the PCC, inferior parietal lobe, and lateral temporal cortex (Table 2).

To allow the visual comparison of medial prefrontal areas responding to the importance of self-views with those responding to certainty, Figure 3 displays simultaneously the activation maps corresponding to each dimension. As can be seen, the two maps overlapped in a small region of the ventral MPFC. However, Figure 3 shows that certainty and importance were also associated with distinct medial prefrontal areas. Notably, certainty was associated with more extensive activation in the dorsal MPFC, whereas importance was associated with more extensive activation in the ventral MPFC.

To formally investigate the brain regions that were specifically related to each form of investment in self-views, we performed exclusive masking analyses. The contrast images coding for one dimension were exclusively masked by the contrast images coding for the other dimension, and the exclusive masks were thresholded using a liberal significance level (p < .05, uncorrected) in order to increase the confidence with which it can be concluded that the resulting brain activations are specific to each type of investment. These analyses revealed

a region of the dorsal MPFC that responded specifically to the certainty of self-views and a region of the ventral MPFC that responded specifically to the importance of self-views (Figure 4, Table 3). As can be seen in Figure 4, the signal change in the ventral MPFC took the form of deactivations relative to resting baseline, whereas the dorsal MPFC showed signal increases relative to baseline. The exclusive masking analyses also revealed a region of the left lateral temporal cortex that responded specifically to certainty, whereas a region of the right posterior insula and a region of the right inferior parietal lobe responded specifically to importance (Table 3).

Finally, we performed an inclusive masking analysis to formally investigate the brain areas that were associated with both forms of investments in self-views (the inclusive mask was thresholded at p < .001, uncorrected). This analysis revealed that a region of the ventral MPFC (MNI coordinates: -2 50 -2, Z = 4.18, $p_{\rm svc} = .002$), the PCC (MNI coordinates: 0 -54 34, Z = 3.40, $p_{\rm svc} = .027$), and the left inferior parietal lobe (MNI coordinates: -50 -62 38, Z = 4.99, $p_{\rm svc} < .001$) responded to both epistemic and emotive investments in self-views.

Discussion

The value we attach to particular conceptions of ourselves is an important constituent of our self-concept that stabilizes self-views and shapes how we feel about ourselves (James 1890; Pelham 1991). This study provides new evidence for the role of the MPFC in this valuation process. The results demonstrate that the level of activity in the MPFC when people think about their personal traits depends on their investments in the particular self-view under consideration. Furthermore, we show that two different forms of investment in self-views—epistemic and emotive—are associated with partly distinct medial prefrontal areas: a region of the dorsal MPFC is uniquely related to the degree of certainty with which a

particular self-view is held, whereas a region of the ventral MPFC responds specifically to the importance attached to this self-view.

There is growing evidence that activity in the ventral MPFC tracks the subjective value of different kinds of stimuli from the external environment, such as food, monetary rewards, and social information (O'Doherty et al. 2003; Kable and Glimcher 2007; de Greck et al. 2008; Chib et al. 2009; Hare et al. 2009; Smith et al. 2010). The current study add to these findings by showing that neural activity in a region of the ventral MPFC correlates with the importance/value people assign to their conceptions of themselves. This region is similar to the regions reported in several previous studies of valuation (e.g. Chib et al. 2009; Smith et al. 2010), which suggests the intriguing possibility that the same subjective valuation mechanisms could be applied to external stimuli from the environment and internally generated representations of the self. It should be noted, however, that there is some heterogeneity in the precise location of activation peaks across studies (Peters and Buchel 2010) and that the value of different kinds of information could be represented by distinct neurons in the ventral MPFC, which cannot be easily detected with fMRI due to its limited spatial resolution (Grabenhorst and Rolls 2011).

Be that as it may, the present results provide new insight into the role of the ventral MPFC in self-representation. It is noteworthy that participants in this study did not explicitly reflect on the importance they attach to their self-views during scanning, such that the observed activity in the ventral MPFC is unlikely to represent the engagement of explicit evaluation processes (see also Moran et al. 2009; Rameson et al. 2010, for recent evidence that the ventral MPFC increases its activity in response to self-relevant information in the absence of explicit self-referential judgments). Instead, the ventral MPFC might automatically confer degrees of value to the conceptions of the self that people form in their minds when they think about themselves. The value assigned to self-conceptions might in turn determine

their impact on people's emotions, thoughts, and behaviors (Pelham 1991). For example, a person who considers herself shy and unattractive will feel all the more anxious when meeting new people if she considers it important to make a good impression to others and, consequently, she will avoid going to big parties (Rapee and Heimberg 1997). By conferring degrees of value to self-conceptions, the ventral MPFC may thus play a central role in mediating the emotional and motivational impact of the self-concept. Disturbances of such valuation process may play an important role in various psychopathological states in which self-views impact emotions and behavior negatively, such as depression (Beck et al. 1979) and social anxiety disorder (Rapee and Heimberg 1997).

While emotive investments in self-views correlated specifically with activity in a region of the ventral MPFC, epistemic investments were uniquely related to a more dorsal area of the MPFC. These two areas were also dissociable in terms of their patterns of responses relative to resting baseline: in line with previous findings (Gusnard et al. 2001), the ventral MPFC showed decreased activity relative to baseline, whereas the dorsal MPFC increased its activity. These findings provide support for the idea that the dorsal MPFC mediates cognitive rather than affective aspects of self-referential processing (Gusnard et al. 2001; Schmitz and Johnson 2007). A recent meta-analysis (van der Meer et al. 2010) indicates that contrary to the ventral MPFC, the involvement of the dorsal MPFC is not unique to selfrepresentation, but is also apparent when thinking about others (see also Lieberman 2010). The dorsal MPFC might mediate general purpose cognitive processes that contribute to selfrepresentation, such as memory retrieval and evaluation processes (Legrand and Ruby 2009). People's degree of confidence in a particular self-view depends on the amount and consistency of information they have about this aspect of themselves (Pelham 1991). The increased activity in the dorsal MPFC that was observed in this study for more certain selfviews could therefore reflect the engagement of processes that support the retrieval,

evaluation, and/or integration of self-related information in order to construct coherent self-views.

The current findings could shed light on a number of previous observations that have been made regarding the neural correlates of self-representation. Although the majority of neuroimaging studies have found that the degree of activity in the ventral MPFC is higher when thinking about the self than when thinking about other persons (see the meta-analysis of van der Meer et al. 2010), the studies that have compared the self with close others have yielded more inconsistent results (Ochsner et al. 2005; Heatherton et al. 2006; D'Argembeau et al. 2007; Vanderwal et al. 2008). These divergent findings could, in part, stem from differences in the value attached to the other person. To some extent, people treat the resources, perspectives and identities of close others as their own, but this inclusion of the other in the self can be more or less pronounced (for review, see Aron et al. 2004). Whether or not one finds differences in ventral MPFC activity when people think about themselves versus another person might depend on the extent to which the other is included in (and thus valued as much as) the self. In a similar vein, previous studies have shown that the level of activity in the ventral MPFC is lower when thinking about past and future selves than when thinking about the present self (D'Argembeau et al. 2008; Ersner-Hershfield et al. 2009; D'Argembeau et al. 2010b; Mitchell et al. 2011). These findings could also be explained in terms of the value attributed to different self-conceptions. People tend to distance themselves from psychologically remote selves, such that these are devalued and, in some ways, regarded as other persons (Wilson and Ross 2003; Pronin and Ross 2006). The reduced activity in ventral MPFC when thinking about temporally distant selves could thus reflect the diminished value that is assigned to these self-conceptions. Our findings may also be relevant for interpreting previous results concerning the neural correlates of self-referential processing in major depression. There is evidence that depressed patients display abnormal activations in the

MPFC during self-referential processing (Grimm et al. 2009; Johnson et al. 2009; Lemogne et al. 2009; Yoshimura et al. 2010), but the pattern of functional abnormalities seems to differ for ventral and dorsal portions of the MPFC (for review, see Lemogne et al. in press). This could in part be due to dissociable effects of depression on epistemic and emotive investments in self-views, although this awaits further investigation (see also Lemogne et al. in press, for other possible accounts).

Although we focused here on the MPFC, investments in self-views were correlated with activity in other brain regions as well. First, activity in the PCC was positively correlated with both epistemic and emotive investments in self-views. The PCC has been associated with self-referential processing in several previous studies (e.g. Johnson et al. 2002; Johnson et al. 2006; Moran et al. 2006; D'Argembeau et al. 2008) and has also been linked to value assignment (e.g. O'Doherty et al. 2003; Kable and Glimcher 2007; Schiller et al. 2009). This region could thus contribute to the valuation of self-views, in association with the ventral MPFC. Alternatively, the increased PCC activity that was detected in this study might reflect the retrieval and integration of autobiographical information (Svoboda et al. 2006) to support self-views that are valued more. Investments in self-views were also associated with increased activity in the inferior parietal lobe. This region is known for its role in attentional shifts to salient information (Corbetta and Shulman 2002), including retrieved memory contents (Cabeza et al. 2008). The increased activity in the inferior parietal lobe that was detected in this study could (tentatively) reflect an increased attention to self-conceptions on which people place more investments.

We also detected increased activity in the lateral temporal cortex in relation to epistemic investments in self-views. This might reflect the retrieval of semantic autobiographical knowledge (Svoboda et al. 2006), considering that the degree of confidence with which a particular self-view is held depends on the amount of information people have to

support this aspect of themselves (Pelham 1991). Another notable finding was that emotive investments in self-views were associated with increased activity in the right posterior insula. This region is involved in representing primary interoceptive signals that provide the basis for the sense of the physiological condition of the body (Craig 2002). Lesion and functional neuroimaging studies suggest that the right posterior insula also contributes to the genesis of the sense of body ownership and sense of agency (Karnath and Baier 2010). For example, Tsakiris et al. found that activity in the right posterior insula (in the same region as the one detected in this study) correlated positively with the subjective feeling of owning the rubber hand in the rubber hand illusion paradigm (Tsakiris et al. 2007). The present results thus suggest the intriguing possibility that the value we attach to high-level, conceptual representations of ourselves is, in part, grounded in a more "primitive" bodily sense of self (Damasio 1999).

Finally, it should be noted that although epistemic and emotive investments are quite distinct, they are nonetheless slightly positively correlated (Pelham 1991). The present study replicated this finding and further showed that epistemic and emotive investments influenced the speed of self-descriptiveness judgments in similar ways. Moreover, although each form of investment was associated with specific neural substrates, the two forms of investment overlapped to some extent, notably in a small region of the ventral MPFC and in the PCC. These areas thus seem to constitute "core regions" for the self-concept, responding to those self-views for which one is most certain and to which one attaches most importance. It is noteworthy that these ventral MPFC and PCC regions correspond to the "hubs" of the default network, a network of brain regions that is engaged during rest and low demand task conditions (Gusnard and Raichle 2001; Buckner et al. 2008). People experience various kinds of thoughts during so-called resting states (D'Argembeau et al. 2005) or when their mind wanders (Smallwood and Schooler 2006), and there is evidence that the default network

contributes to such internally generated thoughts (Buckner et al. 2008; Spreng et al. 2009; Stawarczyk et al. 2011). Recent findings further indicate that the default network comprises multiple, dissociated components and that the ventral MPFC and PCC represent a core set of "hubs" within this network (Andrews-Hanna et al. 2010). These core regions may contribute to a set of processes that evaluate, select, and organize mental representations on the basis of their personal relevance (Andrews-Hanna et al. 2010; D'Argembeau et al. 2010a). The present results provide support for this view and further suggest that these processes are sensitive to both epistemic and emotive aspects of self-relevance.

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Table 1. Brain regions in which activity correlated with self-descriptiveness

	M	NI coordina			
Brain region	X	у	z	Z-score	$p_{ m svc}$
Ventral MPFC	-8	50	-10	5.37	< .001
Dorsal MPFC	-10	60	22	3.26	.044
Posterior cingulate cortex	-4	-52	28	5.10	< .001
Left inferior parietal lobe	-44	-74	38	4.86	< .001
Right insula	44	-2	10	3.86	.008
Left caudate	-10	14	8	4.20	.002

Note: MPFC = medial prefrontal cortex. Ventral MPFC refers to z coordinate ≤ 10 mm and dorsal MPFC to z coordinate > 10 mm. $p_{\text{SVC}} = p$ -value corrected for multiple comparisons at the voxel level over small volumes of interest (see Materials and Methods for details).

Table 2. Brain regions in which activity correlated with the certainty and the importance of self-views

	MNI coordinates				
Brain region	X	у	z	Z-score	$p_{ m svc}$
Certainty					
Dorsal MPFC	-6	54	22	4.63	< .001
Ventral MPFC	-6	54	0	4.51	.001
Posterior cingulate cortex	0	-54	34	3.40	.027
Left inferior parietal lobe	-50	-62	38	4.99	< .001
Right inferior parietal lobe	50	-56	44	3.62	.014
Left middle temporal gyrus	-56	-16	-16	4.05	.003
Right middle temporal gyrus	64	-16	-14	3.53	.018
Importance					
Ventral MPFC	4	52	-6	4.36	.001
Dorsal MPFC	8	44	26	3.60	.015
Posterior cingulate	-2	-66	32	3.98	.004
cortex/precuneus					
Left inferior parietal lobe	-48	-64	40	5.30	< .001
Right inferior parietal lobe	54	-50	34	3.69	.011
Right insula	40	-12	6	3.65	.013

Note: MPFC = medial prefrontal cortex. Ventral MPFC refers to z coordinate ≤ 10 mm and dorsal MPFC to z coordinate > 10 mm. $p_{\text{SVC}} = p$ -value corrected for multiple comparisons at the voxel level over small volumes of interest (see Materials and Methods for details).

Table 3. Brain regions that were specifically related to either the certainty or importance of self-views

	MNI coordinates				
Brain region	X	у	Z	Z-score	$p_{ m svc}$
Regions specifically related to certa	inty (certain	ty exclusive	ly masked l	by importanc	ce)
Dorsal MPFC	-6	54	22	4.63	< .001
Left middle temporal gyrus	-56	-16	-16	4.05	.003
Regions specifically related to impo	rtance (impo	rtance excli	usively mas	sked by certa	inty)
Ventral MPFC	6	48	-6	4.05	.003
Right insula	40	-12	6	3.65	.013
Right inferior parietal lobe	52	-52	34	3.57	.016

Note: MPFC = medial prefrontal cortex. Ventral MPFC refers to z coordinate ≤ 10 mm and dorsal MPFC to z coordinate > 10 mm. $p_{\text{SVC}} = p$ -value corrected for multiple comparisons at the voxel level over small volumes of interest (see Materials and Methods for details).

Figure captions

Figure 1. Response times for the self-descriptiveness judgments as a function of degrees of self-descriptiveness (left panel), certainty in self-views (middle panel), and importance of self-views (right panel). Error bars represent the standard error of the mean.

Figure 2. Brain regions in which neural activity was positively correlated with ratings of self-descriptiveness. Displayed at p < .001 (uncorrected) on the mean structural MRI of all participants. The right panel shows the signal change in the peak voxel in the ventral MPFC.

Figure 3. Brain regions that responded to epistemic and emotive investments in self-views. The brain areas in which activity was correlated with the certainty of self-views (epistemic investments) are displayed in blue, whereas the brain areas in which activity was correlated with the importance of self-views (emotive investments) are displayed in red; the overlap between the two activation maps is shown in purple. Displayed at p < .001 (uncorrected) on the mean structural MRI of all participants.

Figure 4. Medial prefrontal areas that were specifically related to epistemic and emotive investments in self-views (exclusive masking analyses). (A) A region of the ventral MPFC responded specifically to the importance of self-views (emotive investments). As can be seen from the right panel, the signal change in this area took the form of deactivations relative to resting baseline. (B) The dorsal MPFC responded specifically to the certainty of self-views (epistemic investments). This area showed signal increases relative to baseline (right panel). The maps are displayed at p < .001 (uncorrected) on the mean structural MRI of all participants.











