# Neural correlates of context-independent and context-dependent selfknowledge

Charlotte Martial<sup>a</sup>, David Stawarczyk<sup>b</sup>, Arnaud D'Argembeau<sup>b,c</sup>

<sup>*a*</sup> Coma Science Group, GIGA Research Center and Neurology Department, University and University Hospital of Liège, Liège, Belgium

<sup>b</sup> Psychology and Neuroscience of Cognition Research Unit, Department of Psychology, University of Liège, Liège, Belgium

<sup>c</sup> GIGA-CRC In Vivo Imaging, University of Liège, Liège, Belgium.

## **Postal addresses**:

Arnaud D'Argembeau & David Stawarczyk Psychology and Neuroscience of Cognition Research Unit Place des Orateurs 1 (B33) 4000 Liège Belgium Tel: 0032/4.366.46.57 Fax: 0032/4.366.28.08

# **Corresponding author:**

Charlotte Martial GIGA-Research Coma Science Group and Neurology Department University and University Hospital of Liège Avenue de l'Hôpital, 11 4000 Liège Belgium cmartial@uliege.be Tel: 0032/4.366.24.44 Fax: 0032/4.366.84.49

#### Abstract

The self-concept consists of both a general (context-independent) self-representation and a set of context-dependent selves that represent personal attributes in particular contexts (e.g., as a student, as a daughter). To date, however, neuroimaging studies have focused on general selfrepresentations, such that little is known about the neural correlates of context-dependent selfknowledge. The present study aimed at investigating this issue by examining the neural correlates of both kinds of self-knowledge. Participants judged the extent to which trait adjectives described their own personality or the personality of a close friend, either in a specific context (i.e., as a student) or in general. We found that both kinds of self-judgments were associated with common activation in the medial prefrontal cortex (MPFC), as compared to judgments about others. Interestingly, however, there were also notable differences between self-judgments, with context-independent judgments being associated with higher activity in the MPFC, whereas context-dependent judgments were associated with greater activation in posterior brain regions (i.e., the posterior cingulate/retrosplenial cortex). These findings show that context-independent and context-dependent self-referential judgments recruit both common and distinct brain regions, thereby supporting the view that the selfconcept is a multi-dimensional knowledge structure that includes a general self-representation and a set of context-specific selves.

Keywords: self; fMRI; trait judgment; self-representation; medial prefrontal cortex

## 1. Introduction

The notion of self is a complex, multi-dimensional construct that has been much discussed and investigated in philosophy, psychology and, more recently, neuroscience (Conway, 2005; Damasio, 1999; Gallagher, 2000; Klein & Gangi, 2010; Leary & Tangney, 2003; Neisser, 1988; Northoff & Bermpohl, 2004). One particular aspect of the self that has attracted growing theoretical and empirical attention is the self-concept or self-schema, which refers to the collection of representations that an individual has about his or her personal characteristics and attributes (Brewer, 1988; Markus, 1977; Renoult et al., 2012).

The self-concept is most frequently investigated using trait judgment paradigms in which participants are asked to decide whether a given trait describes their personality (e.g., Kelley et al., 2002; Rogers et al., 1977). Recent neuroimaging studies have shown that this kind of self-referential judgment activates cortical midline structures (CMS), including the medial prefrontal cortex (MPFC) and posteromedial cortices (for meta-analyses, see Araujo et al., 2013; Murray et al., 2012; van der Meer et al., 2010; Van Overwalle, 2009). It remains unclear, however, whether these brain regions are specialized in self-related cognition or play a broader role in person knowledge (Wagner et al., 2012; Welborn & Lieberman, 2015). Furthermore, the role of CMS in representing different facets of the self-concept remains to be investigated in detail.

The self-concept is both stable, in the sense that diverse self-aspects are integrated in a coherent long-term representation, and variable, in the sense that self-representations can vary across time and contexts (Baumeister, 2011; Markus & Wurf, 1987; McConnell et al., 2012; Prebble et al., 2012). To account for this unity and multiplicity of self-views, it has been suggested that the self-concept consists of both a general self-representation and a set of context-dependent selves (Schell et al., 1996). This view holds that self-knowledge is organized in memory in a hierarchical fashion: the top of the hierarchy includes a general

(context-independent) representation of the self, which branches into more specific selfaspects that represent personal attributes in particular contexts (e.g., as a student, as a daughter, when meeting new people, and so on). General self-knowledge consists of abstract summary representations of one's personal attributes that have emerged, but are represented independently, from past experiences in multiple contexts (Klein & Lax, 2010; Schell et al., 1996). By contrast, context-dependent self-views are more specific representations of one's personal attributes that serve to guide one's behavior in particular contexts (McConnell, 2011). These self-representations are thus more likely to include knowledge of specific behaviors one has performed in particular settings (Schell et al., 1996), although they typically describe attributes (e.g., traits) that have been derived from multiple personal experiences in a given context (e.g., "As a student, I am conscientious"; McConnell, 2011). While behavioral data provides support for this hierarchical model of self-knowledge (Schell et al., 1996), little is known about the neural correlates of context-dependent self-knowledge.

A recent meta-analysis by Martinelli et al. (2013) has revealed that the retrieval of selfknowledge is associated with a shift from posterior to anterior structures with increasing abstraction of self-representations. More specifically, these authors found that abstract selfrepresentations (i.e., trait self-knowledge and semantic knowledge of facts about one's life) mainly recruited medial prefrontal structures, whereas memories for specific past experiences were associated with additional activations in posterior regions (including the medial temporal lobes). According to the authors, this may be due to the involvement of posterior regions in recollection processes, whereas medial prefrontal regions are involved in self-referential assessment (Martinelli et al., 2013).

Previous neuroimaging studies thus suggest that abstract self-knowledge and memories for specific experiences are associated with different patterns of activation along anterior/posterior brain structures. It remains unknown, however, whether different levels of abstraction within the self-concept (i.e., general versus context-specific self-knowledge) are associated with a similar shift in the recruitment of anterior and posterior structures. One possibility is that context-dependent self-knowledge relies on specific event representations (e.g., memories of one's behavior in specific situations) to a greater extent than contextindependent self-knowledge (Schell et al., 1996), thus recruiting posterior brain regions involved in episodic memory retrieval. Another possibility would be that both kinds of selfknowledge rely on an abstract knowledge base that is independent of memories for specific past events. On this latter view, context-independent and context-dependent self-knowledge would both depend on semantic memory representations (i.e., context-dependent selfknowledge would involve descriptive attributes that have been abstracted from a number of specific episodes within a given context; McConnell, 2011), and thus should not recruit posterior structures involved in episodic remembering.

To test these hypotheses, we conducted an fMRI study in which participants were instructed to reflect on their own traits and those of a close friend, either in general or in a specific context; a control condition, in which participants judged the valence of traits, was also included. This allowed us (1) to identify brain regions that are activated by each of the four trait judgment conditions compared to the control condition; (2) to determine what brain regions are involved in making self- versus other-referential judgments in general and in a specific context; and (3) to investigate whether context-independent and context-dependent self-judgments are associated with differential brain activation, notably in posterior structures supporting episodic memory.

# 2. Material and methods

#### 2.1.Participants

Data were acquired from 20 right-handed French-speaking young adults (12 women; mean age = 22 years, SD = 2, range: 19 to 26 years) who were all students at the University of Liège. Five additional participants were excluded from the analysis due to excessive motion in the scanner (two participants), a very low correlation (i.e., < 0.40; two participants) between trait descriptiveness ratings obtained during the scanning and post-scan sessions (suggesting that their judgments were not reliable; all other participants had correlations > 0.60), or felt dizzy in the scanner (one participant). Prior to their inclusion, written informed consent was obtained from all the participants enrolled in the study. None of them had any history of neurological or psychological disorder. This study was approved by the Ethics Committee of the Faculty of Medicine of the University of Liège.

## 2.2. Tasks and procedure

Before the experiment, participants were asked to identify someone they personally know well (a close friend) and whom they see at the university. This person was used when it was requested to judge personality traits in reference to a close friend during the scanning session.

In the scanning session, participants were instructed to make different types of judgments on a series of adjectives describing personality traits. First, as in previous studies about the neural correlates of trait self-knowledge, participants made some general self-referential judgments. In this condition, they were asked to evaluate the extent to which each presented trait describes their personality in general, that is, their usual way of being, thinking and behaving, independently of the specific context or situation in which they find themselves (e.g., "In general, I am courageous"). Similar general judgments were also made in reference to their friend (e.g., "In general, Sarah is courageous"). Second, participants made a series of context-specific self- and other-referential judgments. Given that all participants were university students, the context of the university was considered as an ideal and well-defined setting for making context-specific judgments. Accordingly, for context-specific selfreferential judgments, participants were required to evaluate the extent to which each presented trait describes them at the university, that is, their way of being, thinking and behaving in the specific context of the university (e.g., "At the university, I am courageous"). Similar context-specific judgments were also made in reference to their friend (e.g., "At the university, Sarah is courageous"). Finally, a control condition was included in which participants were invited to judge to what extent each adjective referred to a positive trait. This control condition required to process the semantic meaning of the stimuli without reflecting on the psychological characteristics of a particular individual.

In all five conditions, the same set of 40 trait adjectives was used (20 positive and 20 negative traits selected from Anderson, 1968, and translated into French; e.g., sincere, reliable, lazy). All trials were presented in a single session, using a block design (with 10 blocks per condition) and a different random order for the five conditions was generated for each participant. Each block started with a brief instruction screen informing participants about the type of judgment they had to make (1500 ms). Then, four adjectives were successively presented for 3500 ms each (with a variable inter-stimulus interval of 750-1250 ms). For each adjective, participants were required to make their judgment by pressing one of four buttons (1 = "not at all", 2 = "a little", 3 = "quite well", 4 = "completely"). Between each block, a fixation cross appeared on the screen for a variable duration between 1000 and 3000 ms. Before the scanning session, participants performed practice trials (with different traits) in order to become familiar with the task.

Immediately following the scanning session, participants completed a series of post-scan judgments on a computer in a quiet room. The same trait adjectives were presented and, for each trait, participants were asked to perform the same descriptiveness judgments as in the scanning session (i.e., they were required to evaluate the extent to which each presented trait describes themselves or their close friend, in the context of the university or in general). In addition, they were asked to perform two other kinds of judgments: first, they rated the difficulty they had to make the descriptiveness judgment during the scanning session (1 =

"very easy", 2 = "quite easy", 3 = "quite difficult", 4 = "very difficult"); second, they were asked to indicate whether some specific events came to mind when they made their judgment during the scanning session (1 = "no specific event", 2 = "one specific event", 3 = "several specific events", 4 = "a lot of specific events").

## 2.3.MRI acquisition

MRI data were acquired on a 3-T head-only scanner (Magnetom Allegra, Siemens Medical Solutions, Erlangen, Germany). 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 (TR = 2040 ms, TE = 30 ms, FoV = 192 x 192 mm<sup>2</sup>, matrix size 64 x 64 x 34, voxel size 3 x 3 x 3 mm<sup>3</sup>). Structural images were obtained using a T1-weighted 3-D MP-RAGE sequence (TR = 1960 ms, TE = 4.4 msec, FoV = 230 x 173 mm<sup>2</sup>, matrix size 256 x 192 x 176, voxel size 0.9 x 0.9 x 0.9 mm<sup>3</sup>). Head motion was restricted by placement of comfortable padding around the subject's head.

#### 2.4.MRI analyses

Data were preprocessed and analyzed using Statistical Parametric Mapping (SPM) 12 software (www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB 2015b (Mathworks Inc., Sherborn, MA). Functional scans were preprocessed by realigning all volumes by using iterative rigid body transformations that minimize the residual sum of squares between the first and subsequent images. The first three volumes were discarded to avoid T1 saturation effects. The scans were normalized to the MNI EPI template (voxel size:  $2 \times 2 \times 2 \text{ mm}^3$ ) and spatially smoothed with a Gaussian kernel with full width at half maximum (FWHM) of 8 mm.

Preprocessed fMRI data were analyzed for each subject using a general linear model with epoch regressors. Blocks were modeled separately for the five conditions ("Self General", "Self Specific", "Other General", "Other Specific", and control condition), with each block corresponding to the period starting with the appearance of the first trait on the screen and ending with the disappearance of the fourth (and last) trait. The design matrix also included 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 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). For each participant, contrasts were calculated to identify differential activity associated with (1) each type of trait descriptiveness judgments compared to the control task ("Self General" > control, "Self Specific" > control, "Other General" > control, "Other Specific" > control), (2) general judgments about the self versus a close other ("Self General" > "Other General"), (3) judgments about the self versus a close other in a specific context ("Self Specific" > "Other Specific"), and (4) judgments about the self in general versus in a specific context ("Self General" > "Self Specific", "Self Specific" > "Self General"). Finally, because examination of parameter estimates suggested a gradient of activity in the MPFC across four trait descriptiveness judgements (see Results section), we investigated whether this gradient of activation was reliable by setting up a linear contrast across the four conditions ("Self General" > "Self Specific" > "Other General" > "Other Specific").

The individual contrast images were then entered into second-level random-effects analyses using one-sample *t*-tests. To examine brain regions that were commonly engaged when making self versus other judgments in general and in a specific context, a conjunction analysis (conjunction null; Friston et al., 2005) was performed with the two contrast images. For all analyses, statistical parametric maps (SPMs) were thresholded at p < .001, uncorrected, and statistical inferences were corrected for multiple comparisons at the voxel level (p < .05, FWE-corrected) using a small volume correction (SVC) within a priori regions of interest. These a priori regions of interest corresponded to brain areas that have been previously related to self-referential processing, as determined by a meta-analysis performed with Neurosynth (Yarkoni et al., 2011; www.neurosynth.org). We searched the Neurosynth database for coordinates linked to the term "self-referential", resulting in the identification of 127 studies. As described in more detail in Yarkoni et al. (2011), whole-brain binary activation images were generated for each published manuscript containing the *a priori* search term at high frequency by setting the intensity of a voxel to "1" if it fell within 4 mm of a fMRI coordinate reported in the manuscript, or "0" otherwise. Statistical analyses were calculated by aggregating the articles using  $\chi^2$  tests of statistical independence, testing the dependency between the presence of the search term and the presence of activation (voxel assigned "1" versus "0"). These statistical maps were then corrected for multiple comparisons by setting the whole-brain false discovery rate (FDR) to p < .05. For the purposes of the present study, we focused on the "reverse inference" map (the posterior probabilities that a search term was used in an article given the presence of activation) because it reveals neural systems that discriminate cognitive functions rather than being non-specifically invoked by many different functions. This map included 68 clusters (including the MPFC, posterior cingulate/precuneus, angular gyrus, and lateral temporal cortex), which were combined into a single mask (total number of voxels: 3566) that was used for the SVC. Regions outside a priori areas of interest are reported if they survived a threshold of p < .05, corrected for multiple comparisons (FWE) over the whole brain.

## 3. Results

#### 3.1.Behavioral data

Response times (RTs) for judgments made in the scanner differed across the five judgment conditions, as revealed by a one-way repeated-measures ANOVA, F(4, 76) = 12.80,

p < .001; post-hoc tests (Bonferroni-corrected) indicated that valence judgments were made faster than trait judgments (all ps < .005), with no significant differences between the four types of trait judgments (see Table 1 for mean RTs).

Correlations between the ratings of trait descriptiveness obtained during the scanning and post-scan sessions were computed for each participant and for each type of trait judgment (i.e., "Self General", "Self Specific", "Other General", "Other Specific"). This showed that participants made reliable judgments in all conditions (see Table 1). To investigate whether the consistency of trait judgments varied across conditions, correlation coefficients were Fisher z-transformed and entered into a one-way repeated-measures ANOVA. This showed that the size of correlations between descriptiveness ratings differed significantly between conditions, F(3, 57) = 7.75, p < .001, and post-hoc tests (Bonferroni-corrected) indicated that descriptiveness judgments were significantly more consistent for general self-judgments compared to general and specific other-judgments (ps < .005); the other comparisons were not statistically significant (ps > .05). To investigate to what extent representations of the self in the specific context of interest (i.e., as a student) overlapped with general self-representations, we also examined the correspondence between specific self-judgments made during scanning and general self-judgments made during the post-scan session. This showed that, on average, specific and general self-judgments were not positively correlated to each other, r = -0.05, 95% CI [-0.09, -0.02], suggesting that the two kinds of judgments relied on distinct selfrepresentations. The comparison of Fisher's z-transformed correlation coefficients confirmed that the correspondence between specific and general self-judgments was significantly lower than the correspondence between general self-judgments across the scanning and post-scan sessions, t(19) = 22.46, p < .001.

The four types of trait judgments did not differ in terms of difficulty (as estimated by the ratings obtained during the post-scan session), F(1.83, 34.69) = 3.25, p = .055 (the

Greenhouse-Geisser correction was applied because the assumption of sphericity was violated; see Table 1 for mean ratings). On the other hand, there was a significant difference between the four trait judgments for ratings of the amount of specific events recalled, F(2.28, 43.27) = 9.46, p < .001. Post-hoc tests (Bonferroni-corrected) indicated that ratings were higher for general self-judgments than for context-specific self- and other-judgments (ps < .05); the other conditions did not differ from each other (see Table 1 for mean ratings). Although statistically significant, it should be noted that these differences were small (the largest difference being 0.12 on the 4-point rating scale) and the average rating was about 2 (indicating the recall of a single event) in all conditions.

 Table 1. Behavioral data.

		Cor	nditions		
	Self General	Self Specific	Other General	Other Specific	Control
Response time (msec)	1746 (288)	1766 (293)	1747 (302)	1804 (320)	1580 (240)
Consistency of trait	0.88 (0.06)	0.85 (0.06)	0.80 (0.14)	0.80 (0.13)	-
descriptiveness (correlation)					
Difficulty	1.67 (0.39)	1.74 (0.47)	1.58 (0.33)	1.71 (0.44)	-
Recall of specific events	2.12 (0.73)	1.87 (0.66)	1.99 (0.62)	1.82 (0.57)	-

Note: SDs are shown in parentheses.

# 3.2.fMRI data

# 3.2.1. Neural correlates of trait descriptiveness judgments

We first examined brain regions that showed higher activity for each of the four descriptiveness judgment conditions ("Self General", "Self Specific", "Other General", "Other Specific") compared with the control task. This showed that the four types of trait descriptiveness judgments activated CMS, including the MPFC and the posterior cingulate cortex/precuneus (see Table 2, Figure 1).

Contrasts	Brain regions	MNI coordinates		K	<i>t</i> -values	
		X	у	Z		
Self General > Control	Precuneus/posterior cingulate cortex	-2	-58	20	638	15.41 <sup>a</sup>
	Medial prefrontal cortex	-6	48	-10	1435	8.95 <sup>a</sup>
	L superior frontal gyrus	-22	32	48	49	7.50 <sup>a</sup>
	L middle temporal gyrus	-58	-2	-24	16	6.44 <sup>a</sup>
	Anterior cingulate cortex	2	34	4	8	5.88 <sup>a</sup>
	Lingual gyrus	8	-86	-6	1347	8.83 <sup>b</sup>
	R angular gyrus	52	-64	34	135	8.58 <sup>b</sup>
	R caudate	12	4	14	417	8.19 <sup>b</sup>
	L inferior frontal gyrus	-44	28	-8	604	7.49 <sup>b</sup>
Self Specific > Control	Precuneus/posterior cingulate cortex	4	-56	16	654	13.44 <sup>a</sup>
	Lingual gyrus	-8	-48	0	77	11.16 <sup>a</sup>
	Medial prefrontal cortex	-8	58	-8	172	6.88 <sup>a</sup>
	L superior frontal gyrus	-20	32	42	41	6.42 <sup>a</sup>
	L angular gyrus	-48	-70	26	37	6.29 <sup>a</sup>
	Medial prefrontal cortex	2	52	20	260	5.75 <sup>a</sup>

**Table 2.** fMRI activations associated with each type of trait descriptiveness judgment.

	L middle temporal gyrus	-58	-6	-22	8	5.35 <sup>a</sup>
	Lingual gyrus	-4	-86	-8	731	5.83 <sup>b</sup>
	R superior frontal gyrus	22	26	46	129	7.12 <sup>b</sup>
Other General > Control	Precuneus/posterior cingulate cortex	-2	-58	20	661	14.58 <sup>a</sup>
	Lingual gyrus	-8	-48	0	70	8.02 <sup>a</sup>
	Medial prefrontal cortex	-4	56	30	284	8.01 <sup>a</sup>
	Medial prefrontal cortex	0	58	-12	133	7.11 <sup>a</sup>
	L superior frontal gyrus	-20	32	42	38	7.11 <sup>a</sup>
	L middle temporal gyrus	-60	-4	-22	15	6.47 <sup>a</sup>
	R middle temporal gyrus	56	-10	-22	56	5.92 ª
	Lingual gyrus	-6	-86	-6	1694	13.41 <sup>b</sup>
Other Specific > Control	Lingual gyrus Precuneus/posterior cingulate cortex	-6 -2	-86 -58	-6 22	1694 688	13.41 <sup>b</sup> 13.02 <sup>a</sup>
Other Specific > Control	Lingual gyrus Precuneus/posterior cingulate cortex L middle temporal gyrus	-6 -2 -58	-86 -58 -10	-6 22 -18	1694 688 19	13.41 <sup>b</sup> 13.02 <sup>a</sup> 8.23 <sup>a</sup>
Other Specific > Control	Lingual gyrus Precuneus/posterior cingulate cortex L middle temporal gyrus L angular gyrus	-6 -2 -58 -44	-86 -58 -10 -64	-6 22 -18 26	1694 688 19 37	13.41 <sup>b</sup> 13.02 <sup>a</sup> 8.23 <sup>a</sup> 6.18 <sup>a</sup>
Other Specific > Control	Lingual gyrus Precuneus/posterior cingulate cortex L middle temporal gyrus L angular gyrus L superior frontal gyrus	-6 -2 -58 -44 -20	-86 -58 -10 -64 32	-6 22 -18 26 42	1694 688 19 37 40	13.41 <sup>b</sup> 13.02 <sup>a</sup> 8.23 <sup>a</sup> 6.18 <sup>a</sup> 4.45 <sup>a</sup>
Other Specific > Control	Lingual gyrus Precuneus/posterior cingulate cortex L middle temporal gyrus L angular gyrus L superior frontal gyrus Medial prefrontal cortex	-6 -2 -58 -44 -20 -2	-86 -58 -10 -64 32 58	-6 22 -18 26 42 -12	1694 688 19 37 40 47	13.41 <sup>b</sup> 13.02 <sup>a</sup> 8.23 <sup>a</sup> 6.18 <sup>a</sup> 4.45 <sup>a</sup> 5.67 <sup>a</sup>
Other Specific > Control	Lingual gyrus Precuneus/posterior cingulate cortex L middle temporal gyrus L angular gyrus L superior frontal gyrus Medial prefrontal cortex R middle temporal gyrus	-6 -2 -58 -44 -20 -2 56	-86 -58 -10 -64 32 58 -10	-6 22 -18 26 42 -12 -22	1694 688 19 37 40 47 57	13.41 <sup>b</sup> 13.02 <sup>a</sup> 8.23 <sup>a</sup> 6.18 <sup>a</sup> 4.45 <sup>a</sup> 5.67 <sup>a</sup> 5.59 <sup>a</sup>
Other Specific > Control	Lingual gyrus Precuneus/posterior cingulate cortex L middle temporal gyrus L angular gyrus L superior frontal gyrus Medial prefrontal cortex R middle temporal gyrus R angular gyrus	-6 -2 -58 -44 -20 -2 56 48	-86 -58 -10 -64 32 58 -10 -62	-6 22 -18 26 42 -12 -22 28	1694 688 19 37 40 47 57 93	13.41 <sup>b</sup> 13.02 <sup>a</sup> 8.23 <sup>a</sup> 6.18 <sup>a</sup> 4.45 <sup>a</sup> 5.67 <sup>a</sup> 5.59 <sup>a</sup> 5.40 <sup>a</sup>
Other Specific > Control	Lingual gyrus Precuneus/posterior cingulate cortex L middle temporal gyrus L angular gyrus L superior frontal gyrus Medial prefrontal cortex R middle temporal gyrus R angular gyrus Lingual gyrus	-6 -2 -58 -44 -20 -2 56 48 -4	-86 -58 -10 -64 32 58 -10 -62 -86	-6 22 -18 26 42 -12 -22 28 -6	1694 688 19 37 40 47 57 93 846	13.41 <sup>b</sup> 13.02 <sup>a</sup> 8.23 <sup>a</sup> 6.18 <sup>a</sup> 4.45 <sup>a</sup> 5.67 <sup>a</sup> 5.59 <sup>a</sup> 5.40 <sup>a</sup> 11.70 <sup>b</sup>

L = left hemisphere; R = right hemisphere; <sup>a</sup> Significant at p < .05 corrected for multiple comparisons at the voxel level over a priori regions of interest (see Method and material section for details); <sup>b</sup> Significant at p < .05 corrected for multiple comparisons at the voxel level over the entire volume.



**Figure 1.** Brain activity involved in each descriptiveness judgment condition compared to the control task (SG = Self General; SS = Self Specific; OG = Other General; OS = Other Specific; C = Control). Displayed at p < .001 (uncorrected and inclusively masked with a priori regions of interest from the Neurosynth meta-analysis) on an inflated surface map (population average landmark surface: PALS-B12) using CARET software (Van Essen, 2005).

## 3.2.2. Self- versus other-referential judgments in general and in a specific context

We next investigated brain regions that were involved in making self- versus otherreferential judgments, in general and in a specific context. We found that the MPFC was more activated when making judgments about the self compared to judgments about the other person, both when judgments referred to the person in general (MNI coordinates of peak voxel: -2, 42, 0; k = 134; *t*-value = 4.12,  $p_{svc}$  = .037) and when judgments referred to the person in a specific context (MNI coordinates of peak voxel: -2, 48, -8; k = 145; *t*-value = 6.80,  $p_{svc}$  = .002). A conjunction analysis between these two independent contrasts confirmed that both types of self-referential judgments were associated with common activation in the MPFC (MNI coordinates of peak voxel: -4, 48, -6; k = 58; *t*-value = 4.54,  $p_{svc}$  = .04) (Figure 2A). Examination of parameter estimates for each trait judgment condition suggested a gradient of activation in this medial prefrontal region across the four conditions (Figure 2B). To investigate whether this gradient of activation was reliable, we set up a linear contrast across the four conditions (see Material and methods). This analysis yielded a significant cluster in the MPFC (MNI coordinates of peak voxel: 8, 42, -2; k = 393; *t*-value = 7.60,  $p_{svc}$  = .001), thus providing more direct evidence for a gradient of medial prefrontal activity across the four conditions.



**Figure 2.** (A) Medial prefrontal region commonly activated when making self-referential judgments in general and in a specific context (relative to corresponding other-referential judgments), as revealed by the conjunction analysis between the contrasts Self General > Other General and Self Specific > Other Specific. Displayed at p < .001 (uncorrected and inclusively masked with a priori regions of interest from the Neurosynth meta-analysis) on the mean structural image of the participants. The color bar represents T-values. (B) Mean parameter estimates for each trait judgment condition (relative to baseline) for the peak voxel (coordinates: -4, 48, -6) identified in the conjunction analysis (error bars represent the standard error of the mean).

#### 3.2.3. Context-independent versus context-dependent self-judgments

The preceding analyses indicated that general and context-specific self-referential judgments were associated with common brain activations. Next, we sought to identify possible differences in the neural correlates of these two kinds of self-referential judgments by directly comparing them to each other. This analysis revealed that general judgments about the self were associated with increased activation in the MPFC (MNI coordinates of peak voxel: 6, 50, 20; k = 56; t-value = 5.48,  $p_{svc}$  = .024; and 2, 40, 2; k = 71; t-value = 5.43,  $p_{svc}$  = .027; Figure 3). On the other hand, context-specific judgments about the self were associated with greater activations in some posterior regions, including the posterior cingulate/retrosplenial cortex (MNI coordinates of peak voxel: -8, -48, 2; k = 43; t-value = 5.91,  $p_{svc} = .011$ ; and -8, -60, 10; k = 63; t-value = 5.50,  $p_{svc} = .024$ ; Figure 3). However, we did not find differential activation in the medial temporal lobes, even at a lower statistical threshold (p < .005, uncorrected).

### 3.2.4. Between-conditions differences in activity are independent of RTs

Finally, to investigate whether the differences in activity between the two self conditions observed in the preceding analyses reflect differences in neural engagement or differences in effortful memory search processes during retrieval, we performed additional analyses using RTs (Taylor, Rastle, & Davis, 2014). Specifically, rather than using block regressors at the first level, trials of the two self conditions were modelled using epochs of 3500 ms (corresponding to the presentation of each trait on the screen) and two parametric modulators were added: one coding RT (in ms), and the other coding the type of judgments (1 for context-independent or 0 for context-dependent). In this model, the RT (first) parametric modulator captures neural response differences that are due to processing effort, whereas the task (second) parametric modulator captures differential engagement for context-independent versus context-dependent self-judgments, independent of RT differences (Taylor et al., 2014).

In other words, the task regressor was orthogonalized with respect to RT (because SPM automatically orthogonalizes a parametric regressor with respect to the ones preceding it; Mumford, Poline, & Poldrack, 2015).

The results confirmed that context-independent self-judgments recruited the MPFC to a greater extent than context-dependent self-judgments (MNI coordinates of peak voxel: 2, 40, 2; k = 44; *t*-value = 5.16,  $p_{svc}$  = .044; and 6, 50, 20; k = 24; *t*-value = 5.18,  $p_{svc}$  = .043), whereas context-dependent self-judgments were associated with higher activation in the posterior cingulate/retrosplenial cortex (MNI coordinates of peak voxel: -10, -48, 4; k = 44; *t*-value = 6.20,  $p_{svc}$  = .006; and -8, -60, 10; k = 100; *t*-value = 5.75,  $p_{svc}$  = .015). These additional analyses suggest that the effect of task condition reflects differences in neural engagement between the two types of self-judgments and not differences in retrieval effort.



**Figure 3.** Brain regions associated with differential activation for general versus contextspecific self-judgments. Regions showing increased activation for general judgments are shown in blue and regions showing increased activation for context-specific judgments are shown in red. Displayed at p < .001 (uncorrected and inclusively masked with a priori regions of interest from the Neurosynth meta-analysis) on the mean structural image of the participants. SG = Self General; SS = Self Specific.

#### 4. Discussion

With the advent of neuroimaging techniques, important progress has been made in identifying the neural correlates of the self-concept (Araujo et al., 2013; Murray et al., 2012; van der Meer et al., 2010; Van Overwalle, 2009; Wagner et al., 2012). However, most studies to date have focused on general, context-independent self-representations, such that little is known about the neural basis of more specific, context-dependent self-knowledge. The aim of this study was to investigate the neural correlates of both types of self-representations. To this end, we asked participants to make self- and other-referential judgments in general and in reference to a specific context (i.e., as a student). In line with earlier research, we found that self- and other-judgments were associated with increased activity in CMS (i.e., medial prefrontal and posteromedial cortices) compared to a semantic control condition. More importantly, we also observed that context-independent and context-dependent self-judgments were associated with both common and distinct neural correlates. Both kinds of selfjudgments were associated with greater activation in the MPFC compared to corresponding judgments about a close other. However, context-independent self-judgments recruited the MPFC to a greater extent than context-dependent self-judgments, whereas the latter were associated with higher activation in some posterior brain regions (i.e., the posterior cingulate/retrosplenial cortex).

Compared to control semantic memory judgments, evaluating the extent to which traits applied to the self or another individual was associated with activation in CMS, in line with the idea that these regions play a central role in self-related cognition and person knowledge (Van Overwalle, 2009; Wagner et al., 2012). Importantly, however, the results also showed that the MPFC was more activated when making self-related judgments than when making judgments about a close other (see also Benoit et al., 2010; D'Argembeau et al., 2007, 2008; Heatherton et al., 2006; Krienen et al., 2010; but see Ochsner et al., 2005, Vanderwal et al., 2008, for divergent findings), and this difference was observed for both context-independent and context-dependent judgments. Furthermore, the same region of the MPFC was more activated for context-independent than for context-dependent self-judgments. Taken together, these findings show a gradient of activation in the MPFC, with increasing activity from otherrelated judgments to context-specific self-judgments to general self-judgments (see Figure 2B). This gradient was located in a ventral region of the MPFC that is typically activated when making judgments about the self and close/similar others (whereas judgments about non-close/similar other are associated with more dorsal MPFC activations; e.g., Mitchell et al., 2006; Murray et al., 2012) and the present results thus demonstrate that the involvement of the ventral MPFC depends on the specificity of trait judgments.

Although the MPFC is undoubtedly the brain region that has been most consistently associated with thinking about the self and others (for meta-analyses, see Araujo et al., 2013; Denny et al., 2012; Martinelli et al., 2013; Murray et al., 2012; Northoff et al., 2006; van der Meer et al., 2010), its exact function remains unclear (for different views, see e.g., D'Argembeau, 2013; Flagan & Beer, 2013; Moran et al., 2013; Welborn & Lieberman, 2015). One possibility is that the MPFC supports the processing of pre-existing knowledge, such as schemas (Gilboa & Marlatte, 2017), that people use for making self- and other-referential judgments. Schemas are superordinate knowledge structures that represent abstracted commonalities across multiple experiences, and neuroimaging studies have indeed shown that the MPFC plays a central role in schema processing (for reviews, see Brod et al., 2013; Gilboa & Marlatt, 2017; Van Kesteren et al., 2012). In particular, recent findings have demonstrated that the MPFC is implicated in the retrieval of schema-congruent information (Brod et al, 2015; Berkers et al., 2017). People not only possess abstract, summary representations of their own personal attributes (i.e., self-schemata; Markus, 1977) but also general representations about well-known others. However, these two forms of trait

knowledge are functionally independent (Klein & Lax, 2010), and there is evidence that general self-representations form a particularly elaborated and organized knowledge structure (Symons & Johnson, 1997). The present result showing that general self-descriptiveness judgments were the most consistent between the scanning and post-scan sessions is in line with this view. Therefore, our fMRI data showing higher activation of the MPFC when making context-independent self-judgments might be related to the greater amount or richness of information contained within general self-knowledge (e.g., more elaborated schemas), as compared to context-dependent self-knowledge and knowledge about other individuals (see also Welborn & Lieberman, 2015, for evidence that the MPFC shows greater activity when evaluating persons about whom one has more knowledge). The exact processing operations at play remain to be determined, however. Possible explanations of the observed activity include that the MPFC represents summary "trait codes" (Ma et al., 2014), acts as an integrative hub for self-representations (Moran et al., 2013; Sui & Humphreys, 2015), or plays a role in schema instantiation and schema-mediated retrieval processes (Brod et al., 2015; Gilboa & Marlatte, 2017).

While context-independent self-judgments were associated with higher activity in the MPFC compared to context-dependent self-judgments, the reverse contrast revealed higher activity in the posterior cingulate/retrosplenial cortex. Activations in these posterior regions have been associated with the retrieval of specific events (Martinelli et al., 2013; McDermott et al., 2009; Spreng et al., 2009), and thus one could argue that they might reflect the contribution of episodic memories to context-dependent self-judgments. However, our results do not provide clear evidence for a special role of episodic memory in context-dependent self-knowledge. Indeed, participants did not estimate that they recalled more episodic memories when making context-dependent judgments than context-independent self-judgments; if anything, the difference was in the opposite direction, although it was small and, on average,

participants indicated that they recalled only about one specific event for each type of judgments.<sup>1</sup> Furthermore, we did not find differential activation in other regions that are typically associated with the retrieval of specific memories, such as medial temporal lobe structures (Martinelli et al., 2013; McDermott et al., 2009; Spreng et al., 2009). Overall, then, the present results do not provide conclusive evidence that context-dependent self-judgments rely on episodic memory to a greater extent than context-independent self-judgments. Another possibility is that the activation of posterior regions when making context-dependent self-judgments self-judgments reflects the retrieval of more general contextual associations or situation models (e.g., typical places, objects, people or activities that are associated with a given trait; see e.g. Bar & Aminoff, 2003; Ranganath & Ritchey, 2012). This interpretation should be taken with caution, however, as it relies on reverse inference (Poldrack, 2006). Further studies need to be conducted to better understand the mechanisms underlying context-dependent self-judgments.

Although the present results seem in contradiction to the study of Schell and colleagues (1996) showing that context-dependent self-judgments rely on specific memories to a greater extent than general self-judgments, this might be related to differences in the methods used to assess the contribution of episodic memories. Indeed, as noted above (see also footnote 1), the ratings made by participants in the present study might not only reflect the retrieval of trait-consistent memories but also the retrieval of trait-inconsistent memories, whereas the priming paradigm used by Schell et al. (1996) specifically measured the retrieval of trait-consistent and

<sup>&</sup>lt;sup>1</sup> The fact that participants indicated that they recalled, on average, about one specific event when making a general self-judgment requires further discussion. Indeed, previous studies have shown that making general trait judgments about the self does not facilitate the retrieval of specific memories in which one displayed behavior relevant to the trait in question, thus providing evidence that trait self-judgments do not involve episodic memories but instead rely on pre-existing summary representations that are stored in semantic memory (for review, see Klein & Lax, 2010). While the present results may at first sight seem in contradiction with these findings, a possible explanation is that the memories recalled in the present study when making general self-judgments referred to trait-inconsistent rather than trait-consistent episodes. Indeed, there is evidence that the activation of trait summaries can prime the retrieval of trait-inconsistent episodic memories, which serve to delimit the scope of general self-knowledge (e.g., "I am usually calm, except the last time I talked about politics with David"; Klein et al., 2001). The post-scan ratings obtained in the present study might thus indicate the retrieval of such trait-inconsistent memories when making general self-judgments.

trait-consistent memories to context-independent and context-dependent self-knowledge. Whatever it may be, the present fMRI data showing that context-dependent and contextindependent self-judgments were not positively correlated and were associated with distinguishable patterns of brain activation are in line with the view that the self-concept is not a unitary structure, but includes both a general self-representation and a set of context-specific selves.

A number of limitations of the present study need to be considered. First, the same trait adjectives were presented in the five rating conditions. This was done in order to ensure that variations in brain activity across conditions are not due to particular properties of the presented adjectives. It should be acknowledged, however, that this might have led to some "contaminations" between the different kinds of judgments (e.g., when making a particular judgment, a participant might remember how he or she judged the same adjective in another condition). This potential issue was limited by randomizing the order of presentation of traits, but it would be valuable in future studies to replicate the present results with different sets of traits for each condition. Second, the activation of episodic memories when making self- and other-referential judgments was assessed retrospectively (during the post-scan session), so it is possible that these evaluations were biased to some extent (e.g., due to forgetting). However, it should be noted that post-scan judgments were administrated immediately following the scanning session and we found that descriptiveness judgments were highly consistent between the scanning and post-scan session; thus, we are inclined to believe that the post-scan ratings were reliable. Finally, the present study involved only one contextdependent self (i.e., the self-as-student). For our participants who were all college students, being a student is probably an important part of their self-concept for which they have quite elaborate knowledge. It would be interesting in future studies to assess other types of contextdependent selves and to investigate whether the neural correlates of context-dependent selfjudgments vary according to the amount of knowledge and personal importance of the context-specific self under consideration.

In conclusion, our results show that context-independent and context-dependent selfreferential judgments are associated with both common and distinct patterns of brain activations, thus providing evidence that the self-concept is not a unitary structure, but instead a multidimensional construct that includes a general self-representation and a set of contextspecific selves. Furthermore, our findings indicate a gradient of activation in the MPFC, with increasing activity from other-related judgments to context-specific self-judgments to general self-judgments. This modulation of MPFC activity might reflect the amount or richness of pre-existing knowledge associated with self- and other-representations. Acknowledgments: C. Martial, D. Stawarczyk, and A. D'Argembeau are, respectively, Research fellow, Postdoctoral Researcher, and Senior Research Associate of the Fonds de la Recherche Scientifique (F.R.S.-FNRS).

**Funding:** This work was supported by the University of Liège (Fonds spéciaux – Crédit classique n° 2251).

Conflicts of interest: None.

## References

- Anderson, N.H., 1968. *Likableness ratings of 555 personality-trait words*. J Pers Soc Psychol. 9(3), 272–279. doi:10.1037/h0025907.
- Araujo, H.F., Kaplan, J., Damasio, A., 2013. Cortical midline structures and autobiographical-self processes: an activation-likelihood estimation meta-analysis.
   Front Hum Neurosci. 7(548), 1–10. doi:10.3389/fnhum.2013.00548.
- Bar, M., Aminoff, E., 2003. Cortical analysis of visual context. Neuron. 38(2), 347–358. doi:10.1016/S0896-6273(03)00167-3.
- Baumeister, R.F., 2011. *The Unity of Self at the Interface of the Animal Body and the Cultural System*. Psychol Stud. 56(1), 5–11. doi:10.1007/s12646-011-0062-5.
- Berkers, R., van der Linden, M., de Almeida, R., Muller, N., Bovy, L., Dresler, M., Morris,
  R., Fernandez, G., 2017. *Transient medial prefrontal perturbation reduces false memory formation*. Cortex. 88, 42–52. doi: 10.1016/j.cortex.2016.12.015.
- Benoit, R.G., Gilbert, S.J., Volle, E., Burgess, P.W., 2010. When I think about me and simulate you: Medial rostral prefrontal cortex and self-referential processes. Neuroimage. 50(3), 1340–1349. doi: 10.1016/j.neuroimage.2009.12.091.
- Brewer, M., 1988. A dual process model of impression formation, in: Wyer, R.S., Srull, T.K.(Eds.), Advances in Social Cognition. Erlbaum, Hillsdale, pp. 1–36.
- Brod, G., Werkle-Bergner, M., Shing, Y., 2013. The influence of prior knowledge on memory: a developmental cognitive neuroscience perspective. Front Behav Neurosci. 7, 139. doi: 10.3389/fnbeh.2013.00139.
- Brod, G., Lindenberger, U., Werkle-Bergner, M., Shing, Y., 2015. Differences in the neural signature of remembering schema-congruent and schema-incongruent events.

NeuroImage 117, 358-366. doi: 10.1016/j.neuroimage.2015.05.086.

- Conway, M.A., 2005. *Memory and the self*. J Mem Lang. 53, 594–628. doi:10.1016/j.jml.2005.08.005.
- Conway, M.A., 2009. *Episodic memories*. Neuropsychologia. 47(11), 2305–2313. doi: 10.1016/j.neuropsychologia.2009.02.003.
- Damasio, A.R., 1999. The Feeling of What Happens: Body and Emotion in the Making of Consciousness. Harcourt Brace, New York.
- D'Argembeau, A., 2013. On the role of the ventromedial prefrontal cortex in self-processing: the valuation hypothesis. Front Hum Neurosci. 7, 372. doi: 10.3389/fnhum.2013.00372.
- D'Argembeau, A., Feyers, D., Majerus, S., Collette, F., Van der Linden, M., Maquet, P., Salmon, E., 2008. Self-reflection across time: cortical midline structures differentiate between present and past selves. Soc Cogn Affect Neurosci. 3, 244–252. doi:10.1093/scan/nsn020.
- D'Argembeau, A., Ruby, P., Collette, F., Degueldre, C., Balteau, E., Luxen, A., Maquet, P., Salmon, E., 2007. Distinct regions of the medial prefrontal cortex are associated with self-referential processing and perspective taking. J Cogn Neurosci. 19(6), 935–944. doi:10.1162/jocn.2007.19.6.935.
- Denny, B.T., Kober, H., Wager, T.D., Ochsner, K.N., 2012. A meta-analysis of functional neuroimaging studies of self and other judgments reveals a spatial gradient for mentalizing in medial prefrontal cortex. J Cogn Neurosci. 24, 1742–1752. doi:10.1162/jocn\_a\_00233.
- Flagan, T., Beer, J.S., 2013. Three ways in which midline regions contribute to self-

evaluation. Front Hum Neurosci. 7, 450. doi: 10.3389/fnhum.2013.00450.

- Friston, K.J., Penny, W.D., Glaser, D.E., 2005. *Conjunction revisited*. Neuroimage. 25(3), 661–7. doi:10.1016/j.neuroimage.2005.01.013.
- Gallagher, S., 2000. *Philosophical conceptions of the self: Implications for cognitive sciences*. Trends Cogn Sci. 4(1), 14–21. doi:10.1016/S1364- 6613(99)01417-5.
- Gilboa, A., Marlatte, H., 2017. *Neurobiology of Schemas and Schema-Mediated Memory*. Trends Cogn Sci. 21(8), 618–631. doi: 10.1016/j.tics.2017.04.013.
- Heatherton, T.F., Wyland, C.L., Macrae, C.N., Demos, K.E., Denny, B.T., Kelley, W.M., 2006. *Medial prefrontal activity differentiates self from close others*. Soc Cogn Affect Neurosci. 1(1), 18–25. doi:10.1093/scan/nsl001.
- Kelley, W.M., Macrae, C.N., Wyland, C.L., Caglar, S., Inati, S., Heatherton, T.F., 2002. Finding the self? An event-related fMRI study. J Cogn Neurosci. 14(5), 785–794. doi/10.1162/08989290260138672.
- Klein, S.B., Cosmides, L., Tooby, J., Chance, S., 2001. Priming Exceptions: A Test of the Scope Hypothesis in Naturalistic Trait Judgments. Soc Cogn. 19(4), 443–468.
- Klein, S. B., Gangi, C.E., 2010. The multiplicity of self: Neuropsychological evidence and its implications for the self as a construct in psychological research. Ann N Y Acad Sci. 1191, 1–15. doi:10.1111/j.1749- 6632.2010.05441.x.
- Klein, S.B., Lax, M.L., 2010. *The unanticipated resilience of trait self-knowledge in the face of neural damage*. Memory. 18(8), 918–948. doi:10.1080/09658211.2010.524651.
- Krienen, F.M., Tu, P.-C., Buckner, R.L., 2010. Clan mentality: evidence that the medial prefrontal cortex responds to close others. J Neurosci. 30(41), 13906–13915. doi:10.1523/JNEUROSCI.2180-10.2010.

- Leary, M.R., Tangney, J.P., 2003. The self as an organizing construct in the behavioral and social sciences, in: Leary, M.R., Tangney, J.P. (Eds.), Handbook of Self and Identity.
  Guilford Press, New York, pp. 3–14.
- Ma, N., Baetens, K., Vandekerckhove, M., Kestemont, J., Fias, W., Van Overwalle, F., 2014.
   *Traits are represented in the medial prefrontal cortex: An fMRI adaptation study.* Soc
   Cogn Affect Neurosci. 9(8), 1185–1192. doi: 10.1093/scan/nst098.
- Markus, H., 1977. Self-schemata and processing information about the self. J Pers Soc Psychol. 35(2), 63–78. doi:10.1037/0022-3514.35.2.63.
- Markus, H., Wurf, E. 1987. *The dynamic self concept: A social psychological perspective*. Ann Rev Psychol. 38, 299–337. doi:10.1146/annurev.ps.38.020187.001503.
- Martinelli, P., Sperduti, M., Piolino, P., 2013. Neural substrates of the self-memory system: New insights from a meta-analysis. Hum Brain Mapp. 34(7), 1515–1529. doi:10.1002/hbm.22008.
- McConnell, A.R., 2011. The Multiple Self-Aspects Framework: Self-Concept Representation and Its Implications. Pers Soc Psychol Rev. 15(1), 3–27. doi:10.1177/1088868310371101.
- McConnell, A.R., Shoda, T.M., Skulborstad, H.M., 2012. *The Self As a Collection of Multiple Self-Aspects; Structure, Development, Operation, and Implications*. Soc Cogn. 30(4), 380–395.
- McDermott, K.B., Szpunar, K.K., Christ, S.E., 2009. Laboratory-based and autobiographical retrieval tasks differ substantially in their neural substrates. Neuropsychologia. 47(11), 2290–2298. doi: 10.1016/j.neuropsychologia.2008.12.025.

Mitchell, J.P., Macrae, C.N., Banaji, M.R., 2006. Dissociable medial prefrontal contributions

to judgments of similar and dissimilar others. *Neuron*, 50(4), 655–663. doi: 10.1016/j.neuron.2006.03.040

- Moran, J.M., Kelley, W.M., Heatherton, T.F., 2013. *What can the organization of the brain's default mode network tell us about self-knowledge?* Front Hum Neurosi. 7, 391. doi: 10.3389/fnhum.2013.00391.
- Mumford, J.A., Poline, J.B., Poldtrack, R.A., (2015). Orthogonalization of regressors in *FMRI models*. PLoS ONE, 10(4), e0126255. doi: 10.1371/journal.pone.0126255
- Murray, R.J., Schaer, M., Debbané, M., 2012. Degrees of separation: A quantitative neuroimaging meta-analysis investigating self-specificity and shared neural activation between self- and other-reflection. Neurosci Biobehav Rev. 36(3), 1043–1059. doi:10. 1016/j.neubiorev.2011.12.013.
- Neisser, U., 1988. *Five kinds of self knowledge*. Philos Psychol. 1, 35–59. doi.org/10.1080/09515088808572924.
- Northoff, G., Bermpohl, F., 2004. *Cortical midline structures and the self*. Trends Cogn Sci. 8(3), 102–107. doi:10.1016/j.tics.2004.01.004.
- Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., Panksepp, J., 2006. Self-referential processing in our brain: A meta-analysis of imaging studies on the self. Neuroimage. 31(1), 440–457. doi: 10.1016/j.neuroimage.2005.12.002.
- Ochsner, K.N., Beer, J.S., Robertson, E.R., Cooper, J.C., Gabrieli, J.D.E., Kihsltrom, J.F., et al., 2005. *The neural correlates of direct and reflected self-knowledge*. Neuroimage. 28(4), 797–814. doi:10.1016/j.neuroimage.2005.06.069.
- Pearson, J., Naselaris, T., Holmes, E.A., Kosslyn, S.M., 2015. Mental Imagery: Functional Mechanisms and Clinical Applications. Trends Cogn Sci. 19(10), 590-602. doi:

10.1016/j.tics.2015.08.003.

- Poldrack, R.A., 2006. *Can cognitive processes be inferred from neuroimaging data?* Trends Cogn Sci. 10(2), 59–63.
- Prebble, S.C., Addis, D.R., Tippett, L.J., 2013. Autobiographical memory and sense of self. Psychol Bull. 139, 815–840. doi:10.1037/a0030146.
- Ranganath, C., Ritchey, M., 2012. *Two cortical systems for memory-guided behaviour*. Nat Rev Neurosci, 13, 713–726. doi: 10.1038/nrn3338.
- Renoult, L., Davidson, P.S.R., Palombo, D.J., Moscovitch, M., Levine, B., 2012. Personal semantics: At the crossroads of semantic and episodic memory. Trends Cogn Sci. 16(11), 550–558. doi:10.1016/j.tics.2012.09.003.
- Rogers, T.B., Kuiper, N.A., Kirker, W.S., 1977. Self-reference and the encoding of personal information. J Pers Soc Psychol. 35(9), 677–688. doi:10.1080/09658211.2011.626429.
- Rubin, D.C., 2014. *Model of The Basic-Systems Episodic Memory*. Perspect Psychol Sci. 1(4), 277–311. doi: 10.1111/j.1745-6916.2006.00017.
- Schell, T.L., Klein, S.B., Babey, S.H., 1996. *Testing a hierarchical model of self-knowledge*. Psychol Sci. 7(3), 170–173.
- Spreng, R.N., Mar, R.A., Kim, A.S., 2009. The common neural basis of autobiographical memory, prospection, naviation, theory of mind, and the default mode: A quantitative meta-analysis. J Cogn Neurosi. 21(3), 489–510. doi:10.1162/jocn.2008.21029.
- Sui, J., Humphreys, G.W., 2015. The Integrative Self: How Self-Reference Integrates Perception and Memory. Trends Cogn Sci. 19(12), 719–728. doi: 10.1016/j.tics.2015.08.015.

- Symons, C.S., Johnson, B.T., 1997. *The Self-Reference Effect in Memory: A Meta-Analysis*. Psychol Bull. 121(3), 371–394.
- Taylor, J.S.H., Rastle, K., Davis, M.H., 2014. Interpreting response time effects in functional imaging studies. NeuroImage. 99, 419–433. doi: 10.1016/j.neuroimage.2014.05.073.
- van Buuren, M., Gladwin, T.E., Zandbelt, B.B., Kahn, R.S., Vink, M., 2010. Reduced functional coupling in the default-mode network during self-referential processing. Hum Brain Mapp. 31(8), 1117–27. doi:10.1002/hbm.20920.
- van der Meer, L., Costafreda, S., Aleman, A., David, A.S., 2010. Self-reflection and the brain: A theoretical review and meta-analysis of neuroimaging studies with implications for schizophrenia. Neurosci Biobehav Rev. 34(6), 935–946. doi:10.1016/j.neubiorev. 2009.12.004.
- Vanderwal, T., Hunyadi, E., Grupe, D. W., Connors, C.M., Schultz, T., 2008. Self, mother and abstract other: an fMRI study of reflective social processing. Neuroimage. 41, 1437–1446. doi:10.1016/j.neuroimage.2008.03.058.
- Van Essen, D.C., 2005. A Population-Average, Landmark- and Surface-based (PALS) atlas of human cerebral cortex. Neuroimage. 28(3), 635–662. doi:10.1016/j.neuroimage.2005.06.058.
- Van Kesteren, M.T.R., Ruiter, D.J., Fernandez, G., Henson, R.N., 2012. How schema and novelty augment memory formation. Trends Neurosci. 35(4), 211–219. doi:10.1016/j.tins.2012.02.001.
- Van Overwalle, F., 2009. Social cognition and the brain: A meta-analysis. Hum Brain Mapp. 30, 829–858. doi:10.1002/hbm.20547.
- Wagner, D.D., Haxby, J.V., Heatherton, T.F., 2012. The representation of self and person

*knowledge in the medial prefrontal cortex*. Wiley Interdiscip Rev Cogn Sci. 3(4), 451–470. doi:10.1002/wcs.1183.

- Welborn, B.L., Lieberman, M.D., 2015. Person-specific Theory of Mind in medial prefrontal cortex. J Cogn Neurosci. 27, 1–12. doi:10.1162/jocn\_a\_00700.
- Yarkoni, T., Poldrack, R.A., Nichols, T.E., Van Essen, D.C., Wager, T.D., 2011. Large-scale automated synthesis of human functional neuroimaging data. Nat Methods. 8(8), 665– 670. doi:10.1038/nmeth.1635.