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Neural Substrates of the Self-Memory System: New Insights from a Meta-Analysis

Pénélope Martinelli,[1,2] Marco Sperduti,[1,2] and Pascale Piolino[1,2]*

[1] *CNRS FRE 3292, Laboratoire de Psychologie et de Neuropsychologie Cognitives, Boulogne-Billancourt, France*
[2] *Université Paris Descartes, Paris, France*

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Abstract: The self has been the topic of philosophical inquiry for centuries. Neuropsychological data suggest that the declarative self can be fractionated into three functionally independent systems processing personal information at several levels of abstraction, including episodic memories of one's own life (episodic autobiographical memory, EAM), semantic knowledge of facts about one's own life (semantic autobiographical memory, SAM), and semantic summary representations of one's personal identity (conceptual self, CS). Our proposal here was to present a comprehensive description of the neural networks underpinning self-representations. To this aim, we performed three meta-analyses, one each for EAM, SAM, and CS, using the activation likelihood estimation (ALE) method. We expected a shift from posterior to anterior structures associated with the incrementally increasing level of abstraction of self-representations. The key finding was that EAM predominantly activates posterior and limbic regions including hippocampus. SAM is associated with anterior activations and also posterior and limbic activations in a lesser degree than EAM. CS mainly recruits medial prefrontal structures. Interestingly, medial prefrontal cortex is activated irrespective of the level of abstraction, but a more caudal part is recruited during CS, while SAM and EAM activate more rostral portions. To conclude, in line with the previous proposals, our results corroborate the idea that the declarative self is not monolithic but a multidimensional construct comprising distinct representations at different levels of abstraction. *Hum Brain Mapp 34:1515–1529, 2013.* © 2012 **Wiley Periodicals, Inc.**

Key words: self; autobiographical memory; episodic memory; semantic memory; neuroimaging; meta-analysis; MPFC

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INTRODUCTION

The study of the neural bases of the self has attracted increasing attention in the last decades. One of the challenges for the scientific study of this topic is to give a coherent and operational definition of the self. The concept of self is indeed very complex and has been the topic of philosophy for centuries. Its representation encompasses different aspects ranging from low-level bodily perception to highly cognitive processes and social values such as the body schema, body ownership, agency, self-traits, expectancies and values [Klein, 2010]. These processes of self-representation can be practically divided into implicit and declarative aspects of the self. Although implicit processes such as body ownership and agency are linked to proprioception and action planning and remain outside of awareness most of the time, other aspects of the self are tightly connected with explicit memory processes and require high-level cognitive and metacognitive functions [Klein, 2010].

Additional Supporting Information may be found in the online version of this article.

Pénélope Martinelli and Marco Sperduti are co-first authors.

*Correspondence to: Pascale Piolino, LPNCog CNRS FRE 3292, Memory and Language Research Group 71, Avenue Edouard Vaillant 92774 Boulogne-Billancourt, France.
E-mail: pascale.piolino@parisdescartes.fr

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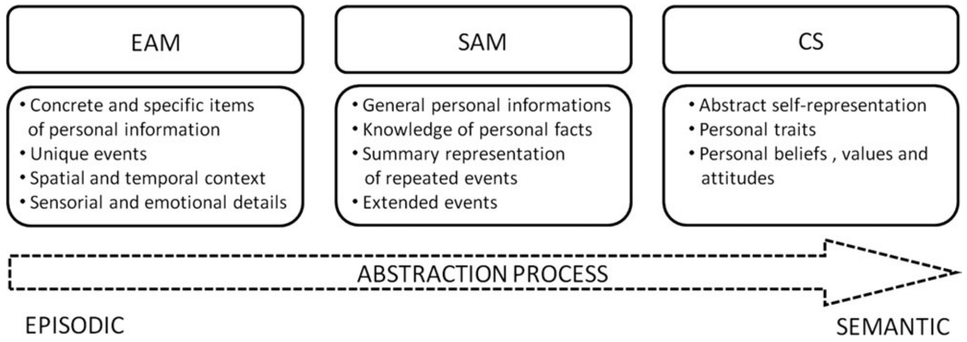

Figure 1.
Schematic representation of the three levels of abstraction of the self with the corresponding cognitive processes.

This "declarative self" can be further analyzed as a set of three functionally independent but highly connected systems: episodic memories of one's own life, semantic knowledge of facts about one's own life, and semantic summary representations of one's personal identity. This proposal has been confirmed and developed by several authors based on experimental and neuropsychological studies [Conway, 2005; Haslam et al., 2010; Klein, 2010], although their terminology differs slightly (e.g., episodic memories in Conway's model versus episodic self-knowledge in Klein and Haslam's models). All these authors consider that one's sense of self fundamentally depends on memories of one's past experiences. Klein [2010] for example argued that episodic memories and semantic self-knowledge have an essential role in accounting for a person's knowledge that he or she possesses some traits but not others. For clarity, we will refer to this distinction using the following terminology: episodic autobiographical memory (EAM), semantic autobiographical memory (SAM) [Addis et al., 2004; Levine et al., 2004; Murphy et al., 2008], and the conceptual self (CS) [Conway, 2005; Duval et al., 2007; Fitts and Warren, 1996]. EAM consists of concrete and specific items of personal information that are closely related to unique autobiographical events situated in a specific time and place [Piolino et al., 2009; Tulving, 2002], which refer to the individual in relation to a specific episodic context (e.g., "The first time I kissed my beloved in a wonderful small village in Italy, it was a warm evening in August . . . "). SAM contains semantic personal information, comprising general knowledge of personal facts (e.g. "My name is X," information about friends and common locations), but also general events encompassing both repeated and extended events, (e.g., "first job", "weekends at the country house," and "that holiday in Italy"). SAM is associated with noetic consciousness involving the awareness of general facts about personal events accompanied by a sense of simply "knowing" without contextual details, while EAM is associated with autonoetic consciousness that gives rise to the sense of phenomenal recollection in the mental re-enactment of previous personal events [Tulving et al., 1988, 2002]. CS is stored in semantic memory in the form of summaries of personal beliefs, values, and attitudes [Conway, 2005], self-knowledge of personality traits [Klein, 2010], and judgments on a number of categories of self-identity [Haslam et al., 2010] that represent our personal identity. We will focus our investigation on the semantic summaries of self-knowledge of personality traits. The reason for this choice is explained in more detail in the following. For a schematic illustration of the three levels of self-representation, see Figure 1.

These multiple systems and their functional independence have been reported in numerous neuropsychological studies of patients with memory disorders [Klein and Gangi, 2010]. In most of these neuropsychological cases, EAM is deficient while SAM and trait-knowledge are preserved. Tulving showed that K.C., an amnesic patient, possessed accurate and detailed knowledge about his postaccident facts and personality traits despite having no conscious access to any episodic memories from which he could infer that knowledge [Tulving et al., 1988, 1993]. Studies on semantic dementia, a pathological state characterized by a gradual breakdown in general semantic knowledge in which patients gradually lose their knowledge of objects, concepts, famous people, and public events [Hodges and Patterson, 2007], showed the reverse pattern (i.e., deficits of SAM and spared EAM [Piolino et al., 2003]). In the same vein, CS seems to be partially independent from SAM and EAM. In a recent case study, Klein and Lax [2010] presented results supporting the idea that personality trait-knowledge is a specific type of semantic knowledge that can be preserved even when EAM and SAM are altered (see also Duval et al. [revision]). Additionally, studies on Alzheimer's disease have shown that the progressive loss of SAM in addition to EAM deficits leads to an inability to upgrade one's trait self-concept and impacts the integrity of identity [Addis and Tippet, 2004; Klein et al., 2003]. Klein and Lax [2010] suggested that EAM and SAM may constitute a potential source for CS but that judgments about one's own personality may be immediately available and precomputed summaries of the dispositions that one has manifested in various behavioral episodes. All these neuropsychological cases favor the view that the self is composed of multiple systems—i.e., EAM, SAM, and CS—which, while functionally isolable in neuropsychological patients, normally operate in interconnection.

According to Conway's model [2005, 2009], these systems are organized hierarchically from highly abstract self-concepts such as personal beliefs, attitudes, and self-images (CS) through semantic self-knowledge (SAM) to specific and experience-near knowledge on unique events (EAM). During AM retrieval, most EAM are indirectly accessed via a chain of activation from CS and SAM. Moreover, most semantic self-representations (SAM and CS) emerge from the summary of episodes that yield abstracted scripts and concepts (see also Klein and Gangi [2010] and Haslam et al. [2010]). For example, general events knowledge is supposed to be generated by the repetition of similar events producing a shift from knowledge about specific to general events, that is, from episodic memory to semantic knowledge [Cermak, 1982; Conway et al., 1997; Piolino et al., 2006]. Also, according to this model, information about one's own personality traits is abstracted from episodes and behaviors [Klein and Lax, 2010]. Therefore, AM plays a fundamental role in the formation of self-identity and the experience of personhood, as AM retrieval can sustain or change aspects of the self [Conway and Pleydell-Pearce, 2000; Klein and Lax, 2010].

Although the interconnection of the self and memory systems is behaviorally well established [Rogers et al., 1977; Symons and Johnson, 1997] and theoretically described [Conway, 2005; Haslam et al., 2010; Klein, 2010], at present, little is known about their interconnections at the neural level. Work on the neural correlates of the self has generally studied mainly self-referential processing, involving the more abstract level of self-representation, while the more concrete levels of the self have been quite exclusively considered within the scope of AM research itself. Neural correlates of the different levels of self-representations, from episodic memories to the CS, are briefly summarized in the following.

The conceptual proximity of AM and self-referential processing is often evoked but rarely examined, especially at the neural level. Svoboda et al. [2006] proposed in their meta-analysis that AM is supported by a predominantly left-lateralized network comprising the medial and ventrolateral prefrontal cortices, medial and lateral temporal cortex, posterior cingulate cortex (PCC), temporo-parietal junction, and the cerebellum. Beyond this core network, activations have also been reported, albeit less frequently, in dorsolateral prefrontal cortex (dLPFC), superior medial and lateral frontal cortex (Ba 6), anterior cingulate cortex (ACC), medial orbitofrontal cortex, polar temporal cortex, the occipital cortices, the thalamus, and the amygdala [Daselaar et al., 2008; Maguire, 2001; Maguire and Frith, 2003b; Svoboda et al., 2006]. Differences in activations between studies may be principally explained by the type of control task and the nature of autobiographical representations retrieved (i.e., semantic or episodic).

Based on a neurophysiological study, Conway et al. [2003] suggested that when searching for EAM, left fronto-temporal activations reflect the initial strategic and generative process via SAM and CS while reliving specific EAM preferentially engages the right hemisphere, especially the posterior cortical regions (see also Cabeza and St Jacques [2007]). More recently, Conway [2009] suggested that fronto-temporal and temporo-occipital regions are responsible for personal knowledge and episodic details, respectively. Indeed, left prefrontal and middle temporal activations seem to be associated with the initial search for semantic information at the beginning of the AM retrieval process [Svoboda et al., 2006], while reliving episodic experience seems to be directly linked to posterior structures and hippocampal formations, apparently regardless of the age of memories [Nadel and Moscovitch, 1997; Moscovitch et al., 2005; Piolino et al., 2009; Viard et al., 2007, 2010]. The network underpinning SAM encompasses the right inferior temporal gyrus, medial frontal cortex, and left thalamus [Addis et al., 2004]. Several experiments have reported that the neural network that sustains the processing of the familiarity of general personal information is linked to ACC, PCC, and retrosplenial cortex [Donix et al., 2010a; Gobbini et al., 2004]. In a study distinguishing between EAM and SAM activations, Levine et al. [2004] found that both EAM and SAM engage left anteromedial prefrontal cortex associated with self-reference processes, but EAM retrieval did so to a greater extent and specifically engaged medial temporal, posterior cingulate, and diencephalic regions. Moreover, Addis et al. [2004] showed that EAM was more strongly associated with the activation of regions involved in imagery, including the left precuneus, left superior parietal lobule, and right cuneus, while SAM was linked to the activation of the right inferior temporal gyrus, right medial frontal cortex, and left thalamus. In a recent study, Holland et al. [2011] showed that prefrontal cortex and the lateral temporal lobe were mainly engaged by EAM during the initial search process and by SAM during the elaboration process.

The neural correlates of CS are frequently investigated by asking participants to judge whether a trait adjective describes their personality: the operations required are referred to as self-referential processing. Self-referential processing involves a complex set of cognitive functions involved in the processing of stimuli that are experienced as strongly related to one's own person [Northoff et al., 2006]. However, given its broad definition, CS could also be recruited in virtually any aspect of real life such as decision making, feeling, or attribution of social emotions as guilt, shame or pride, and mental state attribution as belief. Each of these aspects constitutes a well-defined and independent research topic in neuroimaging literature. Here, it is important to distinguish between the content and the process of self-reference. The former refers to representations concerning the self stored in memory, and the latter involves the very process of experiencing and interacting with the world in first person and is intrinsic to all the processes listed earlier. For example, basic emotions, but also social emotions [Shin et al., 2000; Takahashi et al., 2008], are studied by inducing different moods by means of pictures, faces, videos, or scripts presentation depicting different emotions (for a recent review, see [Vytal and Hamann, 2010]). Usually, the crucial difference between conditions in these studies is the emotionality (e.g., positive vs. neutral situation) and not the self-referential aspect (e.g., me vs. others). This is mainly due to the process of interest, emotion, but it is also the consequence of the very nature of this process, which is intrinsically self-referential and for which it is quite difficult to disentangle a self from a non-self emotional processing. This is in line with the findings on the neural correlates of empathy showing a common network for personal feeling and seeing emotions in others (for a recent meta-analysis, see Fan et al. [2011]). For these reasons, in this work, we focused on self-referential processes based on self-trait judgment as a paradigm to study the abstracted representational content of one's personal identity (CS), because this paradigm allows, compared to non-self judgment using similar material, to isolate the self-dimension per se. Converging evidence suggests an essential role for the medial prefrontal cortex (MPFC) [D'Argembeau et al., 2007; Kelley et al., 2002] and other medial posterior regions (PCC and the precuneus) [Fossati et al., 2003; Johnson et al., 2002; Kircher et al., 2002; Schmitz et al., 2004]. However, only ventromedial prefrontal cortex (vMPFC) seems to be specifically involved in self-referential processing (for a recent meta-analysis, see van der Meer et al. [2010]), while other midline cortical regions seem to be involved in reflective processes more generally [Legrand and Ruby, 2009]. Van der Meer et al. [2010] argued that the vMPFC may be specifically linked to the affective processing of self-relevant information, the dorsal MPFC (dMPFC) involved in evaluation, decision-making related to determining whether a certain stimulus is applicable to the self or to another person, and the posterior cingulate involved in the access to AM. To summarize, on this view, MPFC, and particularly its ventral component, plays a pivotal role in processing information related to the CS. Moreover, several studies have especially pointed to the role of left-hemispheric superior and inferior prefrontal cortex and lateral temporal cortex in semantic memory when people are required to judge trait adjectives for self-descriptiveness [Craik et al., 1999; Kelley et al., 2002; D'Argembeau et al., 2007].

Here, we wanted to give a unitary account of the neural bases of these three different levels of self-representation using a meta-analytic procedure. To this end, we searched for neuroimaging studies investigating the functions of interest—EAM, SAM, and CS—and included only studies that compared these functions with high-level processes that differ in terms of self-relevance. Previous meta-analyses have been conducted separately on CS and AM material.

Previous quantitative meta-analyses concerning EAM have focused on the neural substrates of episodic memories formed in the laboratory context [Spaniol et al., 2009] or on the differences between EAM and laboratory episodic memory [McDermott et al., 2009]. Although the latter study included experiments using several types of control condition including either low- or high-level cognitive tasks, we selected only studies that compared EAM with a control condition that required memory processes. Although various meta-analyses explore the neural substrate of several aspects of AM processes, no study to date has fully addressed the brain correlates of SAM [Svoboda et al., 2006]. Here, we pooled together studies requiring subjects to access memories for general personal information (e.g., familiar people, places, names, and faces) and generalized events (e.g., information about extended and repeated events).

Legrand and Ruby [2009] offered a qualitative synthesis of major results on self-representation, other-representation, and recall. Northoff et al. [2006] compared neural correlates during processing of stimuli related to the self with those of non-self-referential stimuli with a special focus on cortical midline structures. In another recent study, van der Meer et al. [2010] used a quantitative method to shed light on self-reflective processes, focusing uniquely on self-referential processing. In our meta-analysis of the CS condition, because we were interested in structures engaged in the treatment of strictly self-related material, we reproduced the part of this meta-analysis comparing self versus other trait judgments, excluding studies that did not fit the purpose and inclusion criteria of this work as listed earlier (e.g., we excluded studies requiring episodic retrieval of information learned in the laboratory).

To examine the functional independence of the three levels of representation [Conway, 2009; Haslam et al., 2010; Klein and Gangi, 2010], we performed three separate meta-analyses using the activation likelihood estimation (ALE) method [Laird et al., 2005; Turkeltaub et al., 2002] for EAM, SAM, and CS (see Fig. 1). We also tested statistical differences in brain activations between each condition, using meta-analytic subtraction to explore the distinct structures involved in each of these processes. Our main hypothesis was a distinct pattern of activation for each type of self-content, with a shift from posterior to anterior structures associated to the gradually increasing abstraction of the relevant level of representation (from EAM to CS). In sum, the main goal of this work was to study common and distinct substrates of self-representations from experience-grounded events (EAM) to semantic self information (SAM) to completely abstract representation (CS), filling a gap in the literature between self-referential processing and AM.

MATERIALS AND METHODS

Studies Selection

Articles included in the present meta-analysis were identified by a literature search using specific terms, depending on the condition, in the PubMed database and recent meta-analyses published up to March 2011. For the EAM condition, the query terms used were "(autobiographical memory) AND Episodic AND (fMRI OR PET)." Articles for the SAM were identified using a PubMed search with "(autobiographical memory) AND (Semantic OR personal information) AND (fMRI OR PET)" as keywords. For the CS condition, articles were identified through two recent meta-analyses [Northoff et al., 2006; van der Meer et al., 2010] and a PubMed search "(Personal Traits) AND (fMRI OR PET)." For all three categories, we identified additional studies by searching through the reference lists of studies obtained through the initial search.

General Inclusion Criteria

1. Studies measuring regional cerebral blood flow (PET), glucose metabolism (PET), or blood oxygenation (fMRI). Studies including whole brain statistics were included, while studies reporting only region-of-interest analyses were excluded.
2. Articles reporting results as coordinates in a standard reference frame (Talairach and Tournoux or MNI).
3. Studies including healthy subjects with no neurological, medical, or psychiatric disorders or substance abuse. Articles including patients were also selected if they reported results for the control group separately.
4. Studies including young adults (mean range, 18–59 years) were included to avoid effects due to aging in self-memory processes [Gutchess et al., 2007; Levine et al., 2002; Piolino et al., 2002].
5. Experiments using both auditory and visual cues for memory retrieval (e.g., words, sentences, pictures, photographs, or faces) were included.
6. Studies were included independently of the emotional valence of the memory retrieved or of the cue (positive, negative, or neutral).
7. If several instances of the same dataset were encountered, only one was used in the meta-analysis.

Specific Inclusion Criteria

EAM criteria

1. Studies that measured brain activity during the retrieval of a personal past event recollected in the context of a particular time and place and with some reference to oneself as a participant in the episode.
2. Studies assessing brain correlates of the retrieval of both remote and recent memories were included (from childhood to recent past events).

SAM criteria

1. Studies assessing brain correlates of the retrieval of general personal events (both extended in time and repeated) or personal information (including familiar people, objects, places, names, voices, and autobiographical facts).

CS criteria

1. Studies measuring brain activity during the judgment of the self- and other-applicability of personal trait descriptions (word or sentence).

Contrast Selection

Thirty-eight studies (EAM = 13, SAM = 13, and CS = 12) met our criteria, comprising a total of 575 subjects (EAM = 171, SAM = 186, and CS = 210) and reporting 444 foci of activation (EAM = 190, SAM = 184, and CS = 83). All foci were accepted when reported as significant according to the criteria designated in each individual study. Coordinates originally published in MNI space were converted to Talairach space using the Lancaster transformation [Lancaster et al., 2007]. Only activation data were included, while deactivations were not considered. Separate ALE meta-analyses were conducted to investigate the brain activations related to each condition. An overview of studies and contrasts included is provided in Table I.

In the EAM condition, autobiographical retrieval had to be compared to a control task that was a memory task (e.g., semantic knowledge, laboratory episodic memory, famous face recognition, retrieval of public events, and general semantic memory including category generation and sentence completion). Contrasts between EAM and a low-level task were excluded (e.g., rest, perception task, and mental reading). In the SAM condition, contrasts identified had to compare personal general events or personal information with nonpersonal general information (e.g., laboratory episodic memory, general semantic knowledge, unfamiliar faces, names, voices, places, and objects). For the CS meta-analysis, we selected only contrasts directly comparing self versus other judgment for an adjectival trait.

Statistical Analysis

The technique of ALE meta-analysis has been recently described [Laird et al., 2005; Turkeltaub et al., 2002]. The original ALE algorithm was modified for the current version (GingerALE 2.0, http://brainmap.org) [Eickhoff et al., 2009]. In short, all reported foci (coordinates of maximum activation) for a given study are modeled as the peaks of a 3D Gaussian probability distribution. A "modeled activation" (MA) map is computed, representing a summary of the results of that specific study. ALE scores are then calculated on a voxel-by-voxel basis by taking the union of these individual MA maps. This revised analysis tests for convergence between studies (random effects) rather than foci (fixed effects). Statistical significance was assessed using the analytic solution implemented in the new version of GingerALE [Eickhoff et al., 2009]. To assess statistical significance, a P threshold corrected for multiple comparisons using the false discovery rate was fixed at 0.05 [Genovese et al., 2002; Laird et al., 2005], and a minimum cluster size of 200 mm^3 was used. To assess brain

TABLE I. Overview of studies included in the three meta-analyses

Articles	Category	Method	Subjects	Mean age	Exp Cond, Cont	Contrast
Addis et al., 2004	EAM	fMRI	14	28	EAM, SAM, Cont, GS	EAM > SAM
Cabeza et al., 2004	EAM	fMRI	13	20.8	EAM,LEM	EAM > LEM
Conway et al., 1999	EAM	PET	6	34.3	EAM, LEM, Cont	EAM > LEM
Denkova et al., 2006	EAM	fMRI	10	40.6	EAM, Cont	EAM > FF
Donix et al., 2010b	EAM	fMRI	15	28	EAM, SAM	EAM > SAM
Gilboa et al., 2004	EAM	fMRI	9	50.7	EAM, Cont	vivid > nonvivid
Greenberg et al., 2005	EAM	fMRI	11	18–25	EAM, Cont	EAM > GS
Levine et al., 2004	EAM	fMRI	5	26–37	EAM, SAM, GS, other events	EAM > SAM + GS + other events
Mayes et al., 2004	EAM	fMRI	9	22	EAM, GS	EAM > GS
Oddo et al., 2010	EAM	fMRI	15	20.8	EAM, PE	EAM > PE
Okuda et al., 2003	EAM	fMRI	12	20.7	EAM, Future Events, GS	EAM > Cont
Summerfield et al., 2008	EAM	fMRI	18	25.1	EAM, LEM, IE, Cont	EAM-Cont > IE-Cont
Vandekerckhove et al., 2005	EAM	fMRI	16	21–32	EAM, Cont	EAM > Cont
Addis et al., 2004	SAM	fMRI	14	28	EAM, SAM, Cont, GS	SAM > EAM
Donix et al., 2010a	SAM	fMRI	12	30.4	FF, FP, UF, UP	FF + FP > UF + UP
Gobbini et al., 2004	SAM	fMRI	10	26.8	FF, UF, FamF	FF > UF
Leibenluft et al., 2004	SAM	fMRI	7	20–40	FF, UF	FF > UF
Levine et al., 2004	SAM	fMRI	5	26–37	EAM, SAM, GS, other events	SAM > EAM
Maddock et al., 2001	SAM	fMRI	8	22–45	FN, UN	FN > UN
Maguire et al., 2003a	SAM	fMRI	12	32.4	EAM, SAM, PE, GS, Cont	SAM > Cont
Nakamura et al., 2000	SAM	PET	7	23–29	FF, FP, Cont	(FF-Cont) + (FP-Cont)
Shah et al., 2001	SAM	fMRI	10	28.5	FV, FF, UV, UF	FF + FV > UF + UV
Sugiura et al., 2005	SAM	fMRI	25	18–31	FP, FO, UP, UO	FO + FP > UF + UO
Sugiura et al., 2006	SAM	fMRI	24	18–25	FN, UN, FamN	FN > UN
Sugiura et al., 2009	SAM	fMRI	28	18–32	FN, UN, FamN	FN > UN
Sugiura et al., 2011	SAM	fMRI	24	19–31	FF, UF, FamF	FF > UF
D’Argembeau et al., 2008	CS	fMRI	16	21	STJ, OTJ	STJ > OTJ
Gutchess et al., 2007	CS	fMRI	19	23.11	STJ, OTJ, PT	STJ > OTJ
Heatherton et al., 2006	CS	fMRI	30	24	STJ, OTJ, PT	STJ > OTJ
Jenkins et al., 2008	CS	fMRI	13	20.7	Sop, Oop	Sop > Oop
Kelley et al., 2002	CS	fMRI	24	20	STJ, OTJ, PT	STJ > OTJ
Kjaer et al., 2002	CS	PET	7	22–27	STJ,OTJ	STJ > OTJ
Modinos et al., 2009	CS	fMRI	16	20.8	STJ,OTJ	STJ > OTJ
Ochsner et al., 2005	CS	fMRI	16	29.95	STJ, OTJ, PT	STJ > OTJ
Pfeifer et al., 2007	CS	fMRI	12	26.1	STJ, OTJ	STJ > OTJ
Schmitz et al., 2004	CS	fMRI	19	24	STJ, OTJ, VJ	STJ > OTJ
Seger et al., 2004	CS	fMRI	12	20–32	STJ, OTJ	STJ > OTJ
Zhu et al., 2007	CS	fMRI	26	22.3	STJ, OTJ	STJ > OTJ

EAM, episodic autobiographical memory; SAM, semantic autobiographical memory; CS, conceptual self; Cont, control; GS, general semantic; LEM, laboratory episodic memory; PE, public events; IE, imagined events; FF, famous faces; FP, familiar places; UP, unfamiliar places; FO, familiar objects; UO, unfamiliar objects; FN, familiar names; UF, unfamiliar names; FF, familiar faces; UF, unfamiliar faces; FamF, famous faces; FV, familiar voices; UV, unfamiliar voices; STJ, self traits judgment; OTJ, other traits judgment; PT, perception task; VJ, valence judgment; Sop, self-opinion; Oop, other opinion.

correlates for EAM, SAM, and CS, we ran three separate meta-analyses and overlaid the corresponding ALE map onto an anatomical template generated by spatially normalizing the International Consortium for Brain Mapping template to the Talairach space [Kochunov et al., 2002]. To estimate statistical differences in brain activations between conditions, we used the meta-analytic subtraction procedure implemented in a previous version of GingerALE (GingerALE 1.2) that uses the permutation technique described in Laird et al. [2005]. The number of spatial permutations was set to 5,000, as generally reported in previous studies (e.g. [Fusar-Poli et al., 2009; Vytal and Hamann, 2010]). Statistical threshold and cluster size were the same used in the three separate meta-analyses for each condition.

RESULTS

In the EAM meta-analysis, we found evidence for activations encompassing anterior and posterior cortical regions and subcortical structures. More precisely, we found activation in limbic structures (left hippocampus and bilateral parahippocampal formation), midline cortical structures (MPFC, precuneus, and PCC), and left middle

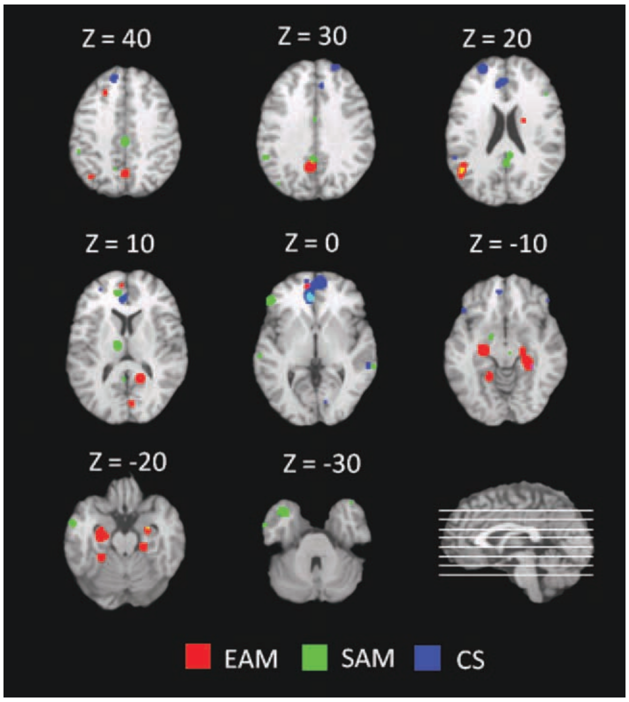

Figure 2.
Results of the separate meta-analyses for EAM, SAM and CS superimposed to axial slices. All activations are significant at $P < 0.05$ corrected for multiple comparisons using the false discovery rate (FDR). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

temporal gyrus. The activations revealed by the ALE for SAM tasks fall within ACC and PCC, MPFC, left middle and inferior frontal gyrus, left superior and middle temporal gyrus, left thalamus, left fusiform gyrus, and parahippocampus. The meta-analysis for CS revealed activations in vMPFC and dMPFC, lateral frontal cortex in both hemispheres, and ACC. The results of the three meta-analyses are summarized in Figures 2 and 3 and Table II.

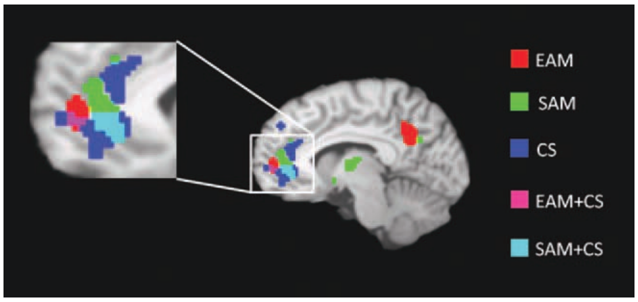

Figure 3.
Sagittal view of differential and common MPFC activations for the three levels of self-representation (EAM, SAM, and CS). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

MPFC activations were shared by all conditions, but in slightly different locations along a rostrocaudal gradient from EAM to SAM to CS (Fig. 3).

With regard to activations specific to each condition, our meta-analytic subtraction revealed greater activations in left temporo-parietal junction, bilateral parahippocampus, precuneus, and PCC in EAM than in the other two conditions (SAM and CS). SAM showed greater activation in MPFC, bilateral middle frontal gyrus, left middle and superior

TABLE II. Peaks of activation for EAM, SAM, and CS

Region	Brodmann area	Volume (mm^3)	Talairach coordinates		
			x	*y*	*z*
EAM					
R parahippocampal gyrus	BA 36	2776	26	−36	−10
R parahippocampal gyrus	BA 35		20	−22	−14
R culmen			22	−30	−18
L hippocampus		2512	−26	−20	−16
L precuneus	BA 31	2080	−6	−58	26
R precuneus	BA 7		2	−64	40
L middle temporal gyrus	BA 39	1352	−48	−64	22
L middle temporal gyrus	BA 19		−48	−62	18
L parahippocampal gyrus	BA 19	760	−16	−42	−4
L culmen			−16	−50	−10
R posterior cingulate	BA 30	672	16	−52	8
L medial frontal gyrus	BA 10	432	−6	50	6
L cerebellum		328	−24	−42	−20
SAM					
R posterior cingulate	BA 23	1520	6	−50	26
R posterior cingulate	BA 23		2	−50	24
R posterior cingulate	BA 29		6	−42	20
L anterior cingulate	BA 32	1096	−6	40	4
L medial frontal gyrus	BA 10		−10	44	14
Thalamus		856	−6	−10	4
L superior temporal gyrus	BA 38	784	−32	10	−28
L middle temporal gyrus	BA 21		−44	6	−26
L superior temporal gyrus	BA 38		−38	18	−26
L middle frontal gyrus	BA 47	776	−48	36	−2
L inferior frontal gyrus	BA 47		−54	26	−6
L fusiform gyrus	BA 20	712	−56	−4	−24
L middle temporal gyrus	BA 21	520	−60	−26	−4
R cingulate gyrus	BA 31	400	2	−28	38
R parahippocampal gyrus		392	26	−10	−16
R middle frontal gyrus	BA 46	368	46	24	24
L parahippocampal gyrus		208	−22	−8	−16
CS					
R medial frontal gyrus	BA 10	3288	6	54	2
L anterior cingulate	BA 32		−6	40	−2
L medial frontal gyrus	BA 10		−10	56	4
L middle frontal gyrus	BA 10	1280	−24	52	20
L anterior cingulate	BA 32	1128	−8	28	4
L anterior cingulate	BA 32		−2	38	16
L medial frontal gyrus	BA 8	832	−12	40	36
R superior frontal gyrus	BA 9	432	22	52	30
R superior frontal gyrus	BA 9		28	52	36
R anterior cingulate	BA 32	368	6	30	26

L = Left, R = Right, BA = Brodmann Area

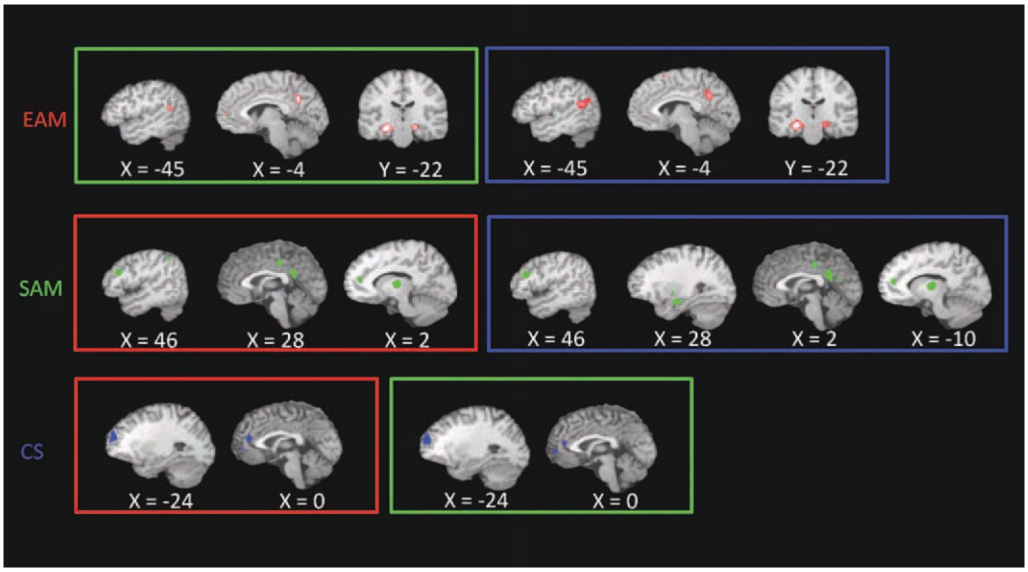

Figure 4.

Results of meta-analytic subtractions between each pair of conditions. First row EAM versus SAM (green) and CS (blue). Second row SAM versus EAM (red) and CS (blue). Third row CS versus EAM (red) and SAM (green). All activations are significant at $P < 0.05$ corrected for multiple comparisons using the false discovery rate (FDR). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

temporal gyrus, left inferior parietal lobe, PCC, and left thalamus compared to CS and EAM. Moreover, in SAM, left parahippocampus was more activated in comparison with CS only. Finally, CS compared to the other two conditions recruited vMPFC and dMPFC, ACC, and left lateral prefrontal cortex to a larger extent than the other two conditions. Activations for each comparison are reported in Figure 4, and the local maxima of activation clusters are detailed in Table III.

DISCUSSION

In this study, we conducted a quantitative meta-analysis of 38 studies for a total of 575 subjects to investigate the neural correlates of different levels of declarative self-representation. In particular, we carried out three separate analyses to study differences and commonalities in brain activity between EAM, SAM, and CS. The existence of these three interdependent systems that support self-representation was proposed by Conway [2005] and recently integrated into Klein [2010]'s and Haslam et al. [2010]'s theoretical models of the self as a multiplicity of related contents comprising both personal identity and AM. Our main hypotheses, based on neuropsychological and neuroimaging studies were (1) dissociable activations for the three categories, suggesting some functional independence of the three systems and (2) a posterior-to-anterior gradient of activations with the movement from experience-near to abstract personal information.

The main findings confirmed our hypotheses, showing that each category uniquely activated specific cortical regions as evidenced by meta-analytic subtractions, with a shift from posterior to anterior structures associated with gradually increasing abstraction of representation from EAM to CS. Indeed, EAM predominantly activated posterior and limbic structures, including hippocampus, whereas CS recruited medial prefrontal structures. SAM was associated with anterior, posterior, and limbic activations, although in a lesser degree than EAM. Moreover, we found differential recruitment of medial prefrontal areas. MPFC was indeed activated irrespective of the abstraction of the self-representation, but in slightly different locations.

In what follows, we will first discuss the functional role of the specific structures activated in each condition as evidenced by meta-analytic subtractions. Thereafter, we will focus on MPFC as a core system for self-representation, as indicated by its engagement in all three conditions, and we will propose a tentative interpretation of the different MPFC activations associated with each condition. We will then describe the postero-anterior shift in cortical activation associated with the abstraction level of representation. Finally, we will briefly describe the contribution of our results to the understanding of neuropsychological diseases in which different aspects of personal information are dysfunctional.

Functional Independence and Commonality Within the Self-Memory System

Neural correlates of EAM

In our EAM meta-analysis, we reported activations encompassing anterior and posterior cortical regions and

TABLE III. Peaks of activation of meta-analytic subtractions between EAM, SAM, and CS

Region	Brodmann area	Volume (mm^3)	Talairach coordinates		
			x	*y*	*z*
EAM-SAM					
R parahippocampal gyrus	BA 36	3064	26	−36	−10
R culmen			22	−30	−18
R parahippocampal gyrus	BA 35		20	−22	−14
L hippocampus		1840	−26	−20	−16
L precuneus	BA 31	1344	−6	−58	28
R precuneus	BA 7		2	−64	40
L culmen		872	−16	−50	−10
L parahippocampal gyrus	BA 19		−16	−42	−4
R posterior cingulate	BA 30	808	16	−52	8
L superior temporal gyrus	BA 22	584	−44	−54	16
L middle temporal gyrus	BA 19		−48	−62	14
L fusiform gyrus	BA 20	488	−30	−38	−18
EAM-CS					
R parahippocampal gyrus	BA 36	3392	24	−34	−12
Culmen			20	−30	−18
R parahippocampal gyrus	BA 35		20	−22	−14
R hippocampus			26	−12	−20
L hippocampus		3160	−26	−20	−16
L middle temporal gyrus	BA 19	2080	−48	−62	18
L superior temporal gyrus	BA 22		−46	−56 18	18
L precuneus	BA 31	2056	−6	−58	28
R precuneus	BA 7		2	−64	−40
L culmen		912	−26	−42	−20
L culmen		888	−16	−50	−10
L parahippocampal gyrus	BA 19		−16	−42	−4
R posterior cingulate	BA 30	760	16	−52	8
R precuneus	BA 31	320	12	−60	24
L precuneus	BA 19	224	−38	−68	38
L superior frontal gyrus	BA 6		−6	12	60
R superior frontal gyrus	BA 6		2	6	−56
R caudate		208	20	−4	20
SAM-EAM					
Thalamus		1176	−10	−14	6
R middle frontal gyrus	BA 46	608	46	24	24
L middle frontal gyrus	BA 47	560	−48	36	−2
L superior temporal gyrus	BA 38	552	−32	8	−28
L anterior cingulate	BA 24	504	−6	38	2
L medial frontal gyrus	BA 9		−10	42	14
L posterior cingulate	BA 23	496	0	−50	24
L fusiform gyrus	BA 20	384	−58	−4	−24
L middle temporal gyrus	BA 21		−60	−26	−4
L superior frontal gyrus	BA 8	368	−26	26	54
L inferior parietal lobule	BA 40	312	−50	−40	42
L supramarginal gyrus	BA 40		−52	−46	32
R cingulate gyrus	BA 31	304	2	−28	38
L medial frontal gyrus	BA 11	280	−2	56	−14
L lentiform nucleus		248	−14	−4	−8
R superior frontal gyrus	BA 6	224	12	12	62
SAM-CS					
R posterior cingulate	BA 23	1776	2	−50	24
L posterior cingulate	BA 30		−4	−56	6
Thalamus		1312	−10	−14	6
L middle frontal gyrus	BA 47	888	−48	34	−2
L fusiform gyrus	BA 20	784	−56	−4	−24
R middle frontal gyrus	BA 46	712	46	24	24
L middle temporal gyrus	BA 21	560	−60	−26	−4
L middle temporal gyrus	BA 39	552	−52	−68	26
L middle temporal gyrus	BA 39		−46	−28	
L lentiform nucleus		536	−14	−4	−8
L parahippocampal gyrus			−22	−6	−16
R hippocampus		528	26	−10	−16
L superior temporal gyrus	BA 38	416	−36	10	−30
L inferior parietal lobule	BA 40	376	−50	−40	42
L supramarginal gyrus	BA 40		−50	−48	34
R cingulate gyrus	BA 31	336	2	−28	38
L medial frontal gyrus	BA 10	248	−10	44	14
R middle temporal gyrus	BA 21	240	54	4	−26
L superior parietal lobule	BA 7		−40	−60	52
R lentiform nucleus		232	24	−6	−2
L medial frontal gyrus	BA 11	200	−2	58	−14
CS-EAM					
R medial frontal gyrus	BA 10	880	6	56	4
L anterior cingulate	BA 32	672	−2	38	16
L medial frontal gyrus	BA 8	592	−12	40	36
L middle frontal gyrus	BA 10	568	−24	52	20
L anterior cingulate	BA 24	280	−6	38	0
CS-SAM					
R medial frontal gyrus	BA 10	1344	6	54	2
L middle frontal gyrus	BA 10	920	−24	52	20
L medial frontal gyrus	BA 38	456	−10	42	36
R superior frontal gyrus	BA 39	256	22	52	30
L anterior cingulate	BA 32	216	0	38	16

L, left; R, right; BA, Brodmann area.

subcortical structures. More precisely, we found activation in the limbic system (hippocampus and bilateral parahippocampal formation), midline cortical structures (MPFC, precuneus, and PCC), and left middle temporal gyrus. Our results are congruent with the proposal in Maguire [2001]'s meta-analysis that left hippocampus is more highly activated during EAM retrieval than in SAM, retrieval of public events, or general semantic knowledge [Maguire, 2001; Maguire and Mummery, 1999; Maguire et al., 2000]. It is important to note that hippocampus was specifically activated in EAM compared to the other two conditions. This is coherent with its role as a pointer to sensory and perceptual details as well as temporal context [Holland et al., 2011].

Voluntary retrieval of EAM, like SAM, depends on self-referential processing involving MPFC for the construction of personal memory as well as control processes [Cabeza and St Jacques, 2007]. During EAM retrieval, monitoring processes are commonly associated with vMPFC [Moscovitch et al., 2005]. The activations of vMPFC during EAM that our results suggest are consistent with Graham et al. [2003] who found vMPFC activations in EAM retrieval compared to general semantic memory. Gilboa et al. [2004] confirmed these results, showing that BA 10 activations were greater with retrieval of episodic autobiographical memories than episodic memories related to laboratory material. Moscovitch and Winocur [2002] suggested the interpretation of BA 10 activations during EAM as the sign of a typical intuitive and preconscious form of monitoring called "feeling of rightness," very different from the monitoring associated with episodic retrieval of laboratory material (see also Cabeza and St Jacques [2007]). EAM remembering also includes specific vividness and visuospatial processes linked to the uniqueness of past event evocation. These processes are usually associated to the activation of more posterior regions such as precuneus, PCC, and hippocampal formations [Addis et al., 2004; Gardini et al., 2006; Gilboa et al., 2004], as reported in this study. On the other hand, we did not find activations in dLPFC, which is often reported for memory search and controlled retrieval [Cabeza and St Jacques, 2007]. This could be due to our choice of contrasts of interest, whose aim was to isolate the "selfness" of the episodic memory processing and that may thus have excluded other processes commonly engaged in episodic memory retrieval more generally.

Neural correlates of SAM

Our meta-analysis revealed an association between SAM and activations in ACC and PCC, MPFC, bilateral ventrolateral prefrontal cortex (vLPFC), left superior and middle temporal gyrus, left thalamus, left fusiform gyrus, and parahippocampus. SAM engaged left anteromedial prefrontal cortex associated with self-reference [Levine et al., 2004] and more posterior regions such as temporo-parietal and parieto-frontal systems that are known to be involved in spatial egocentric processing and top-down attentional control, respectively [Levine et al., 2004] and activations in the PCC related to the processing of personal familiarity [Donix et al., 2010a; Epstein et al., 2007; Shah et al., 2001; Sugiura et al., 2005]. Interestingly, our results specifically linked SAM to thalamic activation, compared to EAM and CS. The involvement of the thalamus in SAM, although frequently reported, has seldom been debated. The thalamus is frequently reported to be activated in studies that test general semantic or linguistic processes (i.e., verbal fluency [Senhorini et al., 2011]) and frequency effect [Vannest et al., 2011]); thalamic activation was also reported in a recent study on chronesthesia [Nyberg et al., 2010]. Nyberg et al. [2010] asked trained participants to imagine themselves in a familiar place, varying the moment of imagined time (past, present, and future). Their results demonstrated the implication of bilateral thalamus in the past and future conditions of familiar scene imagination. Indeed, these results may suggest that the thalamus is involved in the evocation of general events. This tempting interpretation is consistent with our results, but it must be taken with caution, and further research is needed before drawing a firm conclusion.

Neural correlates of CS

In neuroimaging studies of CS based on self-referential processes, activations are frequently reported in medial cortical structures, lateral prefrontal cortex, lateral parietal cortex, bilateral temporal poles, insula, and subcortical regions [D'Argembeau et al., 2007; Northoff et al., 2006; van der Meer et al., 2010]. In our meta-analysis, we found activations only in MPFC, including both ventral and dorsal prefrontal regions, and in ACC. This was probably due to our choice of contrasts of interest, because we were specifically interested in self-referential processes and not in reflection processes more generally, we included only conditions contrasting self- versus other-referential processing. The role of the ventral and dorsal parts of the MPFC during self-referential processing is still under debate. On the one hand, vMPFC has been implicated in emotional processes such as the specific affective processing of self-referential stimuli [van der Meer et al., 2010], the assessment of the salience of a stimuli [Gusnard et al., 2001], the coupling of emotional and cognitive processes in decision-making [Bechara et al., 1997], the detection of the self-relevance of a perceived stimulus [Schmitz and Johnson, 2006], and the processing of the emotional component inherent to self-processing [Northoff and Bermpohl, 2004]. On the other hand, dMPFC has been implicated in multiple cognitive processes, including the evaluation of self-referential stimuli [Northoff and Bermpohl, 2004], introspection processes [Schmitz and Johnson, 2007], as well as reflection processes per se, such as in evaluation and decision-making on whether a stimulus is applicable to the self or to another person [van der Meer et al., 2010]. Schmitz and Johnson [2007] showed that vMPFC is consistently activated only during the presentation of stimuli requiring appraisal (e.g., affective or arousing) of informational features that convey implications for one's own survival, well-being, and potential goals. In line with these results, Schmitz and Johnson [2007] proposed to distinguish between two top-down systems involved in the processing of self-relevant stimuli: the vMPFC-vACC system, responsible for an automatic preattentive biasing for salient or explicitly self-relevant information, and the dMPFC, engaged in introspective processes (e.g., self-reflection, evaluation, and recollection). The presence of both vMPFC and dMPFC activation in our meta-analysis fits with this proposal, taking vMPFC and dMPFC, respectively, as the emotional and cognitive counterparts of self-referential processes.

A Core System: MPFC Activation

MPFC was the only region activated in all conditions. This result confirms the pivotal role of MPFC in self-representation as discussed in the previous sections. Nevertheless, differential activations were revealed in MPFC, corresponding to the level of abstraction of the material involved. The results suggested that EAM only activates a rostral region of MPFC, SAM a more caudal part, and CS both rostral and caudal MPFC. These results were confirmed by subtractions between conditions. MPFC activations entirely disappeared when CS or SAM was subtracted from EAM. SAM activated a rostral subregion of MPFC (BA 10) when compared with EAM and CS. Finally, CS, compared to EAM and SAM, led to greater activation in a more caudal part of MPFC (BA 10) at the border with ACC. MPFC is one of the least understood regions of the human brain [Christoff et al., 2003; Gilbert et al., 2006; Ramnani and Owen, 2004]. Ramnani and Owen [2004] argued that rostral MPFC is a functionally homogeneous region involved in the "processing of internal states," "memory retrieval models," "prospective memory," "branching and reallocation of attention," and "relational integration." On the other hand, there is evidence for a functional differentiation within MPFC [Bush et al., 2000; Steele and Lawrie, 2004] with emotional and cognitive tasks represented in more rostral and more caudal parts, respectively. Moreover, Gilbert et al. [2006] reported a functional distinction within medial rostral MPFC (BA10), with the more caudal portion, at the border with the paracingulate cortex, being activated for mentalizing emotional tasks, while a more rostral part was more highly activated when coordination between different tasks was required. Our results are in line with these findings and corroborate the hypothesis of a functional differentiation within MPFC. In particular, a more caudal part seems to be recruited during CS, while SAM and EAM seem to activate progressively more rostral portions. We think that the investigation of functional differentiation within MPFC is of great interest and hope that our findings will stimulate experimental research on this topic in relation to self-representation.

To summarize, our results show a core region for self-representations in MPFC, as evidenced by the activation of this region in all conditions, and they are also in line with a functional differentiation between the three levels of representation, as evidenced by the specific activation for each condition reported in our meta-analytic subtractions. Specifically, EAM seems to activate regions linked to memory retrieval, scene construction, and reviviscence, probably supporting continuity in subjective time. SAM seems to recruit basically the same structures (to a lesser extent), excluding the hippocampus and precuneus, which are specifically linked to the re-experiencing of a particular moment. This data shows that SAM is supported by memory processes that do not attain the specificity of EAM. Finally, CS only recruits MPFC, suggesting that at this level of abstraction, a memory query is not necessary and that this region may subserve crystallized and ready-to-use self-representations.

The Postero-Anterior Distinction

We hold that the shift from posterior to anterior structures associated with gradually increasing abstraction of representation is due to the involvement of posterior regions in reviviscence processes and access to autobiographical information, whereas prefrontal cortical regions are involved in self-referential assessment. Indeed, our results showed a clear shift from posterior parieto-temporal regions for EAM to anterior MPFC structures for CS. However, we did not find that CS specifically engages regions underpinning storage or access to semantic knowledge, as might have been expected [Craik et al., 1999; Kelley et al., 2002; D'Argembeau et al., 2007]. This point could be explained by the lack in this meta-analysis of neuroimaging experiments concerning the retrieval of highly abstract conceptual knowledge, more abstract than the knowledge involved in self-referential processing (see below).

This result is also in line with previous work on the precise timing of activations during AM retrieval. Conway et al. [2003] demonstrated a pattern of activation in PFC during the first seconds of retrieval followed later by additional temporo-occipital activation once a memory was formed. This was interpreted as resulting from the activation of PFC during initial access to CS and SAM in the construction of AM, and, once a memory was formed, the activation of posterior regions was related to the sensory and perceptual features of EAM. On this view, PFC activity is characteristic of the generative phase of retrieval, during which CS and SAM are accessed, reflecting the operation of control processes related to the elaboration of cues, the probing of the personal knowledge base, and the evaluation of the relevance of accessed knowledge [Conway et al., 2003]. In Conway's model, the most abstract and conceptual knowledge (goals, attitudes, desires, and life summary or life-story) is represented in frontal and anterior temporal regions involved in semantic processes, whereas sensory perceptual details of specific events are associated with more posterior structures. In this meta-analysis, we confirm and extend Conway et al. [2003]'s results showing a gradual shift of the pattern of activation from frontal to posterior and limbic structures depending on the level of specificity of self-related memory retrieval.

Our findings may offer further insights about neuropsychological reports (for review, see Conway and Fthenaki [2003], Klein and Gangi [2010], and Kopelman and Kapur [2001]). Klein and Lax [2010] proposed the existence of a subsystem within semantic memory that they called "trait self-knowledge" (which corresponds to CS) that is functionally specialized. On one hand, they suggest that this CS system is stored independently of episodic memory [Klein and Lax, 2010], and this could explain why CS information is rapidly accessible with no systematic consultation of each pertinent EAM to determine personality traits. Tulving [1993] showed that the amnesic patient K.C. presented accurate and detailed knowledge about his post-accident personality despite the fact that he had no conscious access to any EAM from which he could infer that knowledge. Our results are in line with these neuropsychological data, because we found CS activations to be relatively independent of EAM activations. On the other hand, CS as personality trait-knowledge may be a specific type of semantic knowledge that is partly independent of other forms of semantic memory [Klein and Lax, 2010]. Klein and Lax [2010] tested amnesic patients and suggest that within semantic memory, SAM can be impacted by cognitive or neural damage in patients with a preserved CS. These authors presented the case of patient D.B., who had preserved CS but whose SAM appeared to be only partially intact (42 vs. 92% of correct responses in control subjects on the modified Autobiographical Memory Interview [Klein and Lax, 2010]). Our results are in line with these neuropsychological findings, which go beyond the traditional episodic/semantic distinction to suggest that there are content-specific dissociations within semantic self-knowledge [Klein and Lax, 2010]. These results demonstrate the existence of a subsystem within semantic memory that processes specifically self-related information based on trait-knowledge and seems to be associated with specific regions of MPFC. Further studies should extend these findings to other kinds of information within the CS and explore the distinction from general semantic memory.

LIMITATIONS AND CONCLUSION

As pointed out in the "Introduction" section, research included in the CS category of our study did not cover the broader theoretical definition of CS, because we were only able to include experiments investigating self-referential processes by means of personality traits, opinion, or tastes. This is due to the lack of published neuroimaging experiments suiting our inclusion criteria on CS-knowledge, such as beliefs, goals, and desires. In the same vein, due to the restricted number of studies, we included experiments using different materials (visual, acoustic, verbal, picture, etc.). Thus, we cannot rule out that different kinds of stimuli differently affect brain activity. We tentatively performed three new separate meta-analyses for each category comprising only verbal stimuli, as this condition was the most represented across the three categories. Results for CS and EAM were close to those presented earlier, while results for SAM slightly differed (MPFC, left thalamic, and right parahippocampal activations were no longer found). These differences could be explained, however, by low-statistical power for SAM, as only 7 of the 13 originally included studies on SAM were included in this supplementary analysis. A summary of these results is reported in Supporting Information Table I.

To conclude, in line with the previous reports, our results corroborate that the "self" is not monolithic, but rather a multidimensional construct comprising representations at different levels of abstraction that are supported by different neural correlates. MPFC seems to play a crucial role in self-representation independently of the level of abstraction, with different areas within this region differentially activated at different levels, while other structures such as the limbic system and posterior medial regions appear to be gradually recruited when specific information has to be retrieved in order to build a more experience-near representation.

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