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The retrosplenial complex as an integration zone between self- and map-based components of spatial navigation and declarative memory: An activation likelihood estimation metanalysis

Agustina Fragueiro[a,b,*], Annalisa Tosoni[a,b], Federica Santacroce[a,b], Rosalia Di Matteo[a], Ana Raposo[c], Carlo Sestieri[b,d], Giorgia Committeri[a,b]

[a] *Dipartimento di Psicologia, Università G. d'Annunzio di Chieti-Pescara, Italy*
[b] *Istituto di Tecnologie Avanzate Biomediche, Università G. d'Annunzio di Chieti-Pescara, Italy*
[c] *Faculdade de Psicologia, Universidade de Lisboa, Portugal*
[d] *Dipartimento di Neuroscienze, Imaging e Scienze Cliniche, Università G. d'Annunzio di Chieti-Pescara, Italy*

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ABSTRACT

Although spatial navigation and declarative memory share overlapping neural mechanisms, they have traditionally been investigated as largely non-overlapping research domains. Recent theories suggest an evolutionary continuity, proposing that systems for navigating physical and mental spaces are linked through shared transformations between self-based (egocentric) and map-based (allocentric) reference frames. Yet, the extent to which these processes rely on common substrates remains unclear. This metanalysis used Activation Likelihood Estimation (ALE) to quantitatively compare fMRI studies on spatial navigation (egocentric or allocentric) and declarative memory (episodic or semantic), assessing convergence across domains. Results revealed extensive overlap, particularly in the retrosplenial complex (posterior cingulate cortex/retrosplenial cortex), which was consistently activated across all four conditions, highlighting its role in integrating and transforming reference frames. Episodic memory overlapped with egocentric navigation in the occipital place area (OPA), the angular gyrus (AG) and the parahippocampal place area (PPA), and with allocentric navigation in the PPA and hippocampus, suggesting flexible recruitment rather than strict mapping. The dorsal anterior cingulate cortex (dACC) emerged as a domain-general hub across memory and allocentric navigation, possibly supporting the regulation of internally vs. externally driven processing. These findings support a shared, large-scale network involving medial temporal, parietal, and cingulo-retrosplenial regions. The retrosplenial complex, anatomically positioned between the hippocampus and the posterior parietal cortex, appears crucial for converting information between egocentric and allocentric coordinates across domains. Future neuroimaging research could clarify how these transformations generalize across spatial and conceptual domains, and how the default mode and salience networks support adaptive cognition.

1. Introduction

Spatial navigation and declarative memory are two core cognitive functions. Navigation has been traditionally divided in two main components (i.e. egocentric, allocentric) depending on the implemented frame of reference (i.e. self-based, map-based) (Boccia et al., 2014; Ekstrom and Isham, 2017), while declarative memory has been classically decomposed into episodic and semantic components (Tulving and Markowitsch, 1998). However, the storage of ordered sequences of elements appears to be a key aspect of both self-based egocentric navigation and episodic memory (Eichenbaum and Cohen, 2014). Location sequences are indeed linked together by a neural path integrator along one-dimensional space with no need for a map-like representation, as sequentially occurring items are assembled into a coherent contextualized memory episode (Eichenbaum et al., 1999). In contrast, allocentric maps define a location inside a two-dimensional space independently of the navigator's position or the paths performed, in the same way as semantic memory defines concepts inside associative maps

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* Correspondence to: Dipartimento di Psicologia, Istituto di Tecnologie Avanzate Biomediche (ITAB), Università degli Studi G. d'Annunzio di Chieti-Pescara, Via dei Vestini 33, Chieti 66100, Italy.
E-mail address: agustina.fragueiro@unich.it (A. Fragueiro).

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independently of a particular temporal or spatial context, in both cases stablishing omni-directional distance relationships found between landmarks or concepts (Bellmund et al., 2018).

At the neural level, navigation and declarative memory have traditionally been associated with the medial temporal lobe (MTL), and in particular with the hippocampal formation (HF), but largely within distinct research traditions. Foundational evidence came from classical animal neurophysiological studies on spatial navigation mechanisms (Hafting et al., 2005; O'Keefe and Nadel, 1978; Tolman, 1948) on one hand, and from neuropsychological assessments of amnesic patients on the other (Grossi et al., 1988; Levine et al., 1998; Scoville and Milner, 1957). However, MTL/HF damage has been associated with both non-spatial memory deficits (e.g. serial reaction time task, delayed non-match to sample task) (Ergorul and Eichenbaum, 2006; Otto and Eichenbaum, 1992) in studies with behaving animals, and, at least partially, with spatial deficits in amnesic patients (Bartsch et al., 2010; Bohbot et al., 1998; Herdman et al., 2015; Kolarik et al., 2018).

In recent years, several proposals have attempted to reconcile the hippocampal involvement in both spatial navigation and declarative memory, based on evidence that the hippocampus encodes both locations in space and moments in time (Eichenbaum and Cohen, 2014; Ekstrom and Ranganath, 2018; Epstein et al., 2017). This convergence has inspired a range of perspectives that collectively conceptualize hippocampal function in terms of Tolman's notion of "cognitive map" - a mental organization of experience in spatial dimensions that guides behavior. For instance, Buzsáki and Moser (2013) proposed an evolutionary continuity model in which a neural recycling mechanism links navigation in physical and mental (i.e. mnestic) space. Beyond this evolutionary perspective, Milivojevic and Doeller (2013) emphasized the notion of memory as a network of interconnected representations, whereas Maguire and Mullally (2013) focused on the role of the hippocampal-enthorinal region in the reconstruction of spatially coherent scenes during both navigation and memory retrieval. Alternatively, Eichenbaum and Cohen (2014) modeled the hippocampus as encoding a "memory space", wherein events and episodes are integrated within relational networks (Eichenbaum et al., 1999). Finally, Bellmund and Doeller (Bellmund et al., 2018) proposed that spatial navigation mechanisms provide the basic coding principles for navigating non-spatial knowledge, suggesting that a spatial metric guides the representation and manipulation of conceptual (semantic) knowledge. In this framework, a hippocampal-parietal network is assumed to support the organization and retrieval of knowledge across egocentric and allocentric reference frames (Bottini and Doeller, 2020). Similarly to the dual navigational system comprising world-centered (primarily associated with the hippocampal formation) and self-centered (primarily associated with the parietal cortex) representations, conceptual knowledge would be supported by the complementary activity of "cognitive maps" (low-dimensional geometries that are analogs of world-centered environmental representations) and "image spaces" (analogs of self-centered spatial relationships).

The fundamental hypothesized mechanism underlying the common neural coding for spatial navigation and memory is the generalization of experiences. In particular, just like the formation of allocentric maps is based on repeated exploration of the environment (Siegel and White, 1975) , semantic knowledge derives from the extraction of statistical regularities across multiple episodic events (Eichenbaum et al., 1999; Moscovitch et al., 2016). Within this framework, the general notion of "cognitive maps" or "cognitive spaces" for spatial navigation and memory is assumed to depend on a shared transformation process, whereby self-based (egocentric) inputs are converted into a map-based (allocentric) representation. According to Buzsaki and Moser (2013), the neural machinery underlying this generalization process can be identified in the neurophysiological properties of medial temporal neurons of rats and other non-human species. For instance, physiological support for the mental travel model and the sequential encoding of items in the physical and mental space has been found in theta-phase coding and modulation of gamma power by theta rhythm (Bragin et al., 1995; Colgin et al., 2009). Thus, the neural machinery underlying the generalization of experience is assumed to be implemented in the hippocampal formation (Buzsáki and Moser, 2013), where spatial, temporal, or semantic distances are coded by theta oscillations (Solomon et al., 2019).

Behavioral evidence supporting the continuity between self- and map-based coding across spatial navigation and memory domains comes from studies examining the association between performance on various navigational and memory tasks in humans. In particular, across-domain relationships have been observed between path integration/route (self-based) navigation and episodic memory performance (Committeri et al., 2020; Fragueiro et al., 2021, 2022), as well as between survey (map--based) navigation and semantic memory performance (Fragueiro et al., 2023). Moreover, egocentric navigational training has been shown to improve performance on episodic memory tasks (Fragueiro et al., 2022), suggesting the positive causal influence of self-based spatial processing on memory retrieval. Additionally, a significant correlation has been reported between performance on self-based and higher-level, map--based tasks within each domain (Fragueiro et al., 2023), in line with the idea that a transformative process from self- to map-based representations operates similarly across domains.

At the level of the whole-brain functional architecture, however, the correspondence between the neural mechanisms underlying self-based and map-based coding of information in each domain has remained somewhat elusive. As highlighted by Eichenbaum and Cohen (2014), while the hippocampal formation is thought to support allocentric spatial maps acquired through repeated exploration, evidence for its involvement in self-based navigation or path integration is limited. Similarly, although growing evidence points to a crucial role of the hippocampal-entorhinal region in encoding and retrieval of first-person (self-based) experiences, such as spatial and temporal context in episodic memory, semantic knowledge is traditionally considered a form of hippocampal-independent memory, relying instead on neocortical structures (Ranganath and Ritchey, 2012; Renoult et al., 2019; but see Duff et al., 2020). While the hippocampal formation and parahippocampal cortex (PHC) are implicated in associative memory for contextual information (Eichenbaum et al., 2007), self-based components of navigation have been consistently associated with posterior midline regions including the posterior cingulate (PCC)/restrosplenial cortex (RSC), as well as regions of the lateral parietal and medial prefrontal cortex (Bird and Burgess, 2008; Galati et al., 2010; Ranganath and Ritchey, 2012; Sestieri et al., 2017). On the other hand, allocentric coding of environmental information has been linked to both the hippocampal formation and PHC, as well as the RSC (Hartley and Harlow, 2012; Iaria et al., 2003; Jung and Dilks, 2025). Finally, although a recent metanalysis reported a partial overlap between the networks involved in autobiographical episodic memory and egocentric navigation, no systematic correspondence has been found between brain regions subserving autobiographical semantic memory (i.e. personal semantic) and map-based allocentric navigation (Teghil et al., 2021). This challenges the notion of shared neural mechanisms within reference frames across spatial navigation and memory domains (see also Ekstrom and Hill, 2023, for a critical position on this issue).

In summary, while numerous theoretical models and empirical findings have identified the hippocampal complex as a core hub for both spatial navigation and memory, results appear more inconsistent when considering the specific reference frames involved (i.e. self-based vs. map-based). Although there is growing consensus regarding the hippocampus's role in cognitive mapping of both spatial and non-spatial dimensions of experiences (Bellmund et al., 2018; Constantinescu et al., 2016; Viganò and Piazza, 2020), the precise neural correspondence between self-based (i.e. egocentric navigation and episodic memory) and map-based (i.e. allocentric navigation and semantic memory) components of spatial navigation and declarative memory remains largely unclear. Moreover, understanding the complex interplay between memory and spatial navigation likely requires large-scale models that extend beyond the hippocampal formation (Ekstrom and Hill, 2023), incorporating widespread cortical networks. For example, according to prominent neural models of human spatial and non-spatial memory (Bicanski and Burgess, 2018; Miller et al., 2014), a large-scale cortical network – including parietal, retrosplenial and medial temporal areas – support the integration of egocentric representations in first-person perspective with view-independent allocentric representations for long-term storage. Within this framework, the transformation between egocentric (parietal) and allocentric (MTL) reference frames is thought to be mediated by a bidirectional transformation mechanism in the retrosplenial cortex.

In the present meta-analysis, we aimed to explore the relationship between spatial navigation and declarative memory by comparing neuroimaging evidence on the neural systems supporting these functions across different reference frames. Specifically, we assessed the degree of overlap between the neural systems associated with these two functions, based on the implemented reference frame (i.e., self-based or map-based). To this aim, we conducted an Activation Likelihood Estimation (ALE) meta-analysis of functional magnetic resonance imaging (fMRI) studies reporting whole-brain activations during spatial navigation (i.e., egocentric or allocentric) or declarative memory (i.e., episodic or semantic) tasks. Based on the above-reported literature, we expected a broad anatomical overlap between navigation and memory functions, extending beyond the hippocampal formation to include neocortical parietal and frontal regions. Concerning the subdivision into two main reference frames, we expected a larger overlap between the neural mechanisms supporting self-based (i.e., episodic memory and egocentric navigation) vs. map-based (i.e., semantic memory and allocentric navigation) components of navigation and memory. At the same time, we also expected a substantial overlap of activations for different reference frames, reflecting their strong and dynamic interlink through transformation processes, within each cognitive domain.

2. Methods

2.1. Inclusion criteria for research articles

Research articles matching the following a priori inclusion criteria were included: 1) studies reporting whole-brain analyses of functional magnetic resonance imaging (fMRI) (i.e. positron emission tomography, electrophysiology studies, and articles reporting only results from region of interest (ROI) analyses were excluded); 2) studies providing the coordinates of activation foci either in Montreal Neurological Institute (MNI) or in Talairach reference space; 3) studies conducted on a young-adult population (age range: 19–24) (aging studies were excluded); 4) studies not involving any kind of manipulation of the participant's psychophysiological condition (e.g. pharmacological manipulations); 5) single fMRI experiments and contrasts including a control condition; 6) group studies (i.e. single cases were excluded); 7) studies including a task on either (i) the recall of a real or virtual newly learned environment (spatial navigation), or (ii) the retrieval of newly encoded episodic memory or old crystalized as well as new semantic knowledge (declarative memory). Importantly, tasks assessing specifically autobiographical episodic or semantic memory (i.e. personal semantics) were not included, to stress the distinction between self-based episodic memory and map-based semantic memory.

On the 10th of February 2021, two searches, one for spatial navigation and the other for declarative memory, were conducted on Pubmed for publications from the previous 10 years using the filters: humans, English, and young adult (19–24 years).

The following string of words was used for the spatial navigation research: *((allocentric[Title/Abstract]) OR (map-based[Title/Abstract]) OR (egocentric[Title/Abstract]) OR (self-based[Title/Abstract]) OR (route-based[Title/Abstract]) OR (survey-based[Title/Abstract]) OR (path integration[Title/Abstract]) OR (spatial[Title/Abstract]) OR (topographical [Title/Abstract])) AND (navigation[Title/Abstract]) AND ((fMRI[Title/Abstract]) OR (functional neuroimaging[Title/Abstract]) OR (BOLD[Title/Abstract]))*. We obtained 95 results.

The following string of words was used for the declarative memory search: *((declarative[Title/Abstract]) OR (episodic[Title/Abstract]) OR (semantic[Title/Abstract]) OR (recognition[Title/Abstract]) OR (recall [Title/Abstract])) AND (memory[Title/Abstract]) AND ((fMRI[Title/Abstract]) OR (functional neuroimaging[Title/Abstract]) OR (BOLD[Title/Abstract]))*. We obtained 1011 results.

For both datasets, a two-step exclusion process was conducted and double-checked by three experimenters (see flowchart on Fig. 1). First, from an inspection of the title and abstract, we excluded studies: 1) conceived as reviews, 2) including a non-healthy population, 3) focused on aging, 4) without fMRI, 5) with a task performed only outside the fMRI, 6) without a focus on declarative memory or spatial navigation (e.g., focus on language), 7) without a visual task (e.g., auditory tasks), 8) with only resting state fMRI acquisitions. On a second step, the remaining papers were fully inspected with the following exclusion criteria: 1) ROI analysis, 2) no coordinates available, 3) no control condition, 4) lack of clarity about the component being assessed (egocentric navigation [EGO] vs. allocentric navigation [ALLO] – episodic memory [EPI] vs. semantic memory [SEM]). Furthermore, by the end of this inspection, the specific component/s (i.e., EGO, ALLO, EPI, SEM) being assessed in each paper was/were identified. We obtained: 36 papers for EPI, 13 for SEM, 10 for EGO, and 6 for ALLO.

Existing metanalysis conducted on the topics of interest were inspected for older papers not previously identified by the Pubmed search conducted which had focused on the lasts ten years only. First, we checked for not already included studies regarding spatial navigation on the metanalysis of Boccia et al. (2014), and 21 additional papers were included (Brown et al., 2010; Burgess et al., 2001; ; Grön et al., 2000; Iaria et al., 2008; Ino et al., 2002; Latini-Corazzini et al., 2010; Rosenbaum et al., 2004, 2007; Spiers and Maguire, 2006; Wolbers et al., 2007; Xu et al., 2010). In a second step, the metanalysis of Teghil et al. (2021) was checked and 2 new additions, not identified by the previous search, were made (Gomez et al., 2014; Zhang et al., 2012). To increment the number of studies on semantic memory, we additionally inspected the metanalyses conducted by Kim (2016) and by Binder et al. (2009). From Kim (2016), only studies for the semantic/phonological paradigm (which involves semantic and phonological processing tasks for words) were considered, and after checking for the exclusion criteria, 8 new papers were included (Booth et al., 2006; Daselaar et al., 2002; Devlin et al., 2003; Gitelman et al., 2005; Guo and Burgund, 2010; Miceli et al., 2002; Otten and Rugg, 2001; Snyder et al., 2007). From Binder et al. (2009), 10 new papers were included (Assaf et al., 2006; Bedny and Thompson-Schill, 2006; Boronat et al., 2005; Copland et al., 2007; Devlin et al., 2002, 2003; Ebisch et al., 2007; Pilgrim et al., 2002; Raposo et al., 2006; Stringaris et al., 2007; Tyler et al., 2003).

As detailed in Supplementary Table 1, the spatial navigation studies included in this metanalysis implemented mainly wayfinding tasks, and some of them used heading or pointing tasks. Among tasks emphasizing an egocentric strategy, we also included path integration or route-based tasks, while among tasks emphasizing an allocentric strategy, we included map-based and positioning tasks. On the other side, for the declarative memory dataset, among the studies investigating the episodic component, we mainly included item (words or pictures) recognition and remember/know/new paradigms. Among the studies emphasizing the semantic component, we mainly included semantic association judgements and categorization tasks (using words, sentences or pictures as materials).

Following the rules postulated by Müller et al. (2018), we controlled for multiple contrasts inside a same study by only including few experiments from the same paper. Only in the cases of more than one contrast strictly assessing the function of interest or using different tasks, more than one contrast was included. The metanalysis on episodic memory was conducted on 49 experiments from 37 papers with a total of

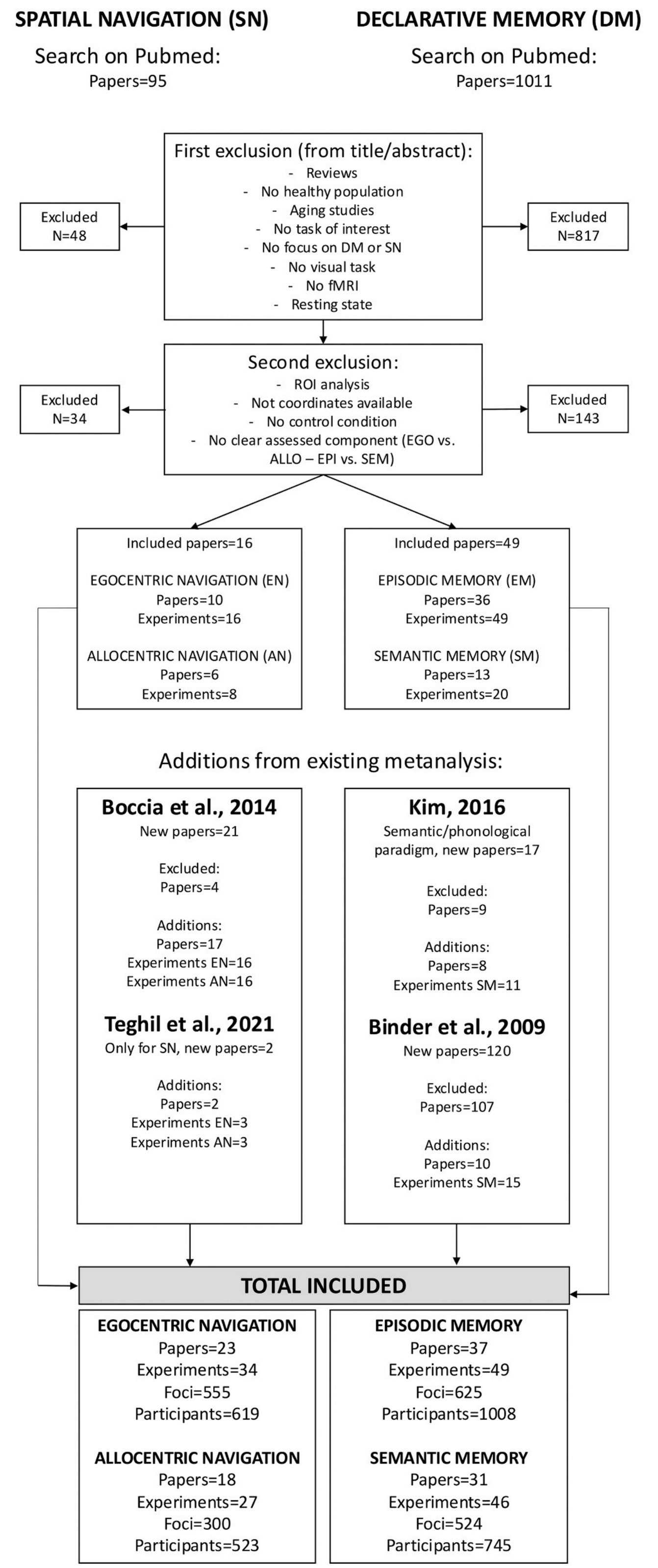

Fig. 1. Flow chart of dataset construction for all four components: egocentric navigation, allocentric navigation, episodic memory and semantic memory.

1008 participants, and the metanalysis on semantic memory was performed on 46 experiments from 31 papers with a total of 745 participants. The metanalysis on egocentric navigation was conducted on 34 experiments from 23 papers with a total of 619 participants, while the metanalysis on allocentric navigation was performed on 27 experiments from 18 papers with a total of 523 participants. The complete list of papers, experiments and participants is available in the Supplementary Table 1, and the complete dataset of coordinates included in our study are stored in the public repository Figshare (https://doi.org/10.6084/m9.figshare.30365065.v1).

2.2. *Activation Likelihood Estimation (ALE)*

An Activation Likelihood Estimation (ALE) metanalysis was performed using GingerALE 3.0.2 (brainmap.org) with MNI coordinates. Talairach coordinates were converted automatically into MNI coordinates using the same software. ALE calculations created the 3D image for each foci group using the small (more conservative) mask set, the foci and a Gaussian blur with a FWHM empirically derived from the subject's group size. These Modeled Activation (MA) maps (Eickhoff et al., 2009) were computed following the non-additive procedure proposed by Turkeltaub et al. (2012) by finding the maximum across each focus's Gaussian as it limits the effect of an experiment with multiple foci very near one to another. Thus, the MA maps reflect the spatial distribution of activation likelihoods associated with the reported foci, without multiple foci from a single experiment to jointly influence the individual map value of a single voxel. The ALE image is the union of all the MA maps. The ALE values of each voxel in the brain were computed using the standard procedure (Eickhoff et al., 2009), and the null distribution of the ALE statistic was calculated for each voxel. The Full-Width Half-Maximum (FWHM) value was automatically calculated by the number of subjects in each experiment (Eickhoff et al., 2009). All the thresholded ALE maps were computed using p values from the previous step, a cluster-level inference at the 0.05 level of significance with 1000 threshold permutations, and a cluster-forming threshold at $p < 0.005$ (uncorrected) (Eickhoff et al., 2016).

First, six single dataset analyses were conducted, one for spatial navigation (i.e. egocentric and allocentric navigation pooled together), one for declarative memory (i.e. episodic and semantic memory pooled together), and one for each specific function of interest independently (i.e., egocentric navigation, allocentric navigation, episodic memory, semantic memory). In a second moment, we performed conjunction and contrast analyses. Contrast analyses highlight the regions significantly more activated for one component comparing to the other, while conjunction analyses allowed us to investigate which brain regions are commonly activated by both components. To the purpose of this study, we only report here conjunction analyses. We first compared within-domain components: 1) egocentric (EGO) and allocentric (ALLO) navigation; and 2) episodic (EPI) and semantic (SEM) memory. In a second moment, we studied general across-domain conjunction, thus, between 3) spatial navigation and declarative memory functions. Finally, we studied specific across-domain conjunctions based on the frame of reference implemented: 4) self-based components (i.e., EPI and EGO), and 5) map-based components (i.e., SEM and ALLO). The remaining across-domain conjunctions were also investigated: 6) first control condition (i.e., EPI and ALLO), and 7) second control condition (i.e., SEM and EGO). We expected broader across-domain overlaps between the components implementing the same reference frame (i.e. self-based conjunctions vs. map-based conjunctions) comparing to the "control conjunctions" (between the components implementing different reference frames).

3. Results

3.1. *Single analyses*

Detailed output for each single metanalyses conducted for spatial navigation and declarative memory are reported in Supplementary Tables 5 and 6, respectively.

Spatial navigation: As displayed in Fig. 2 (blue navy + yellow color), spatial navigation clusters were located bilaterally in large swaths of

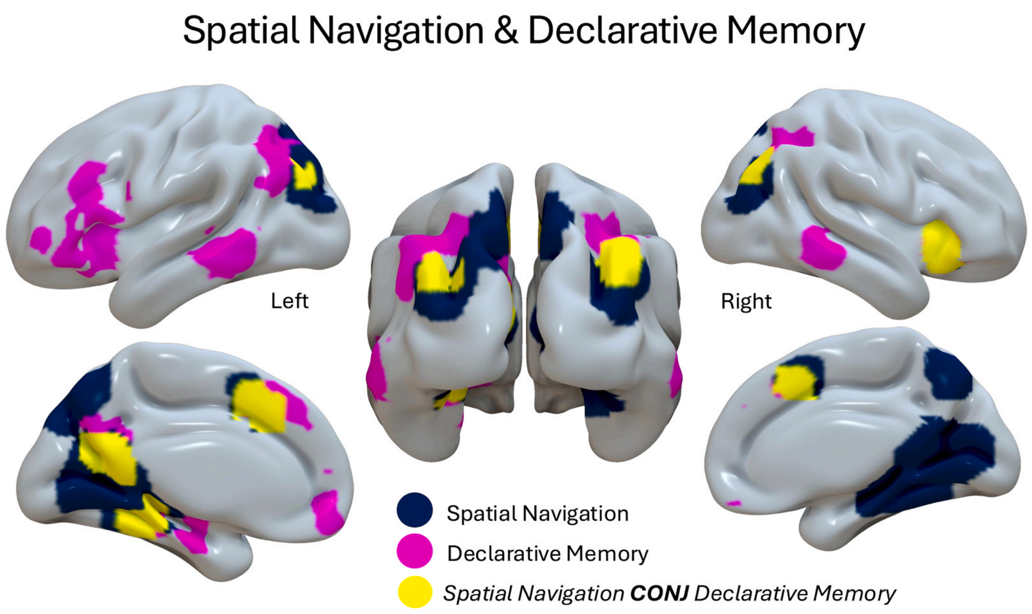

Fig. 2. Single metanalyses on spatial navigation (blue navy) and declarative memory (magenta) domains, and conjunctions between them (yellow).

cortex extending from the medial occipito-temporal to the retrosplenial and medial parietal cortex. Activation clusters also extended to lateral regions in the superior occipital and inferior parietal cortex and included isolated foci in the frontal cingulate cortex and the right insula.

Egocentric navigation: Bilateral clusters were located in the parahippocampal gyrus (PHG), posterior cingulate cortex (PCC)/retrosplenial cortex (RSC), precuneus and superior occipital gyrus (SOG), extending to the angular gyrus (AG) in the right hemisphere (Fig. 3, cyan + yellow).

Allocentric navigation: Bilateral clusters were located in the PHG, extending to the hippocampus (HIP) in the left hemisphere, PCC/RSC, and dorsal anterior cingulate cortex (dACC) (Fig. 3, green + yellow).

Declarative memory: As displayed in Fig. 2 (magenta + yellow color), activation clusters for declarative memory were mainly located in leftward regions within the medial temporal lobe (MTL), the retrosplenial cortex, the inferior parietal cortex and the lateral prefrontal cortex. Bilateral activation clusters included the lateral temporal and intraparietal cortex, as well as the frontal cingulate cortex. A right lateralized cluster was also located in the insula.

Episodic memory: Clusters of activation (Fig. 4, blue + yellow) were mainly bilateral and were localized laterally in the middle temporal gyrus and the superior and inferior (AG) parietal cortex (extending to the SOG), while medially in the PCC/RSC and the dACC. Further clusters were left-lateralized and included the PHG/HIP and the middle and inferior frontal gyri, while a right-lateralized cluster was located in the insula.

Semantic memory: Clusters of activation (Fig. 4, orange + yellow) were mainly localized in the left hemisphere and included the middle, inferior and fusiform gyri of the temporal lobe, the PCC/RSC, the AG and the lateral (inferior and middle frontal gyri) and ventromedial prefrontal cortex (vmPFC). A single bilateral cluster was observed in the dACC.

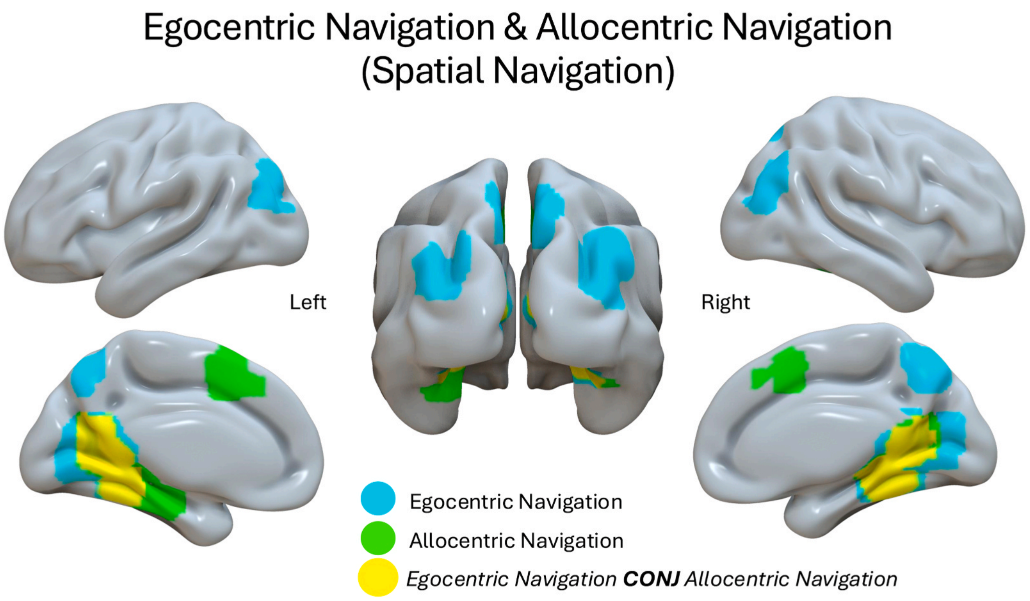

Fig. 3. Single metanalyses and conjunction analysis on spatial navigation. Egocentric navigation (cyan), allocentric navigation (green), and conjunction between them (yellow).

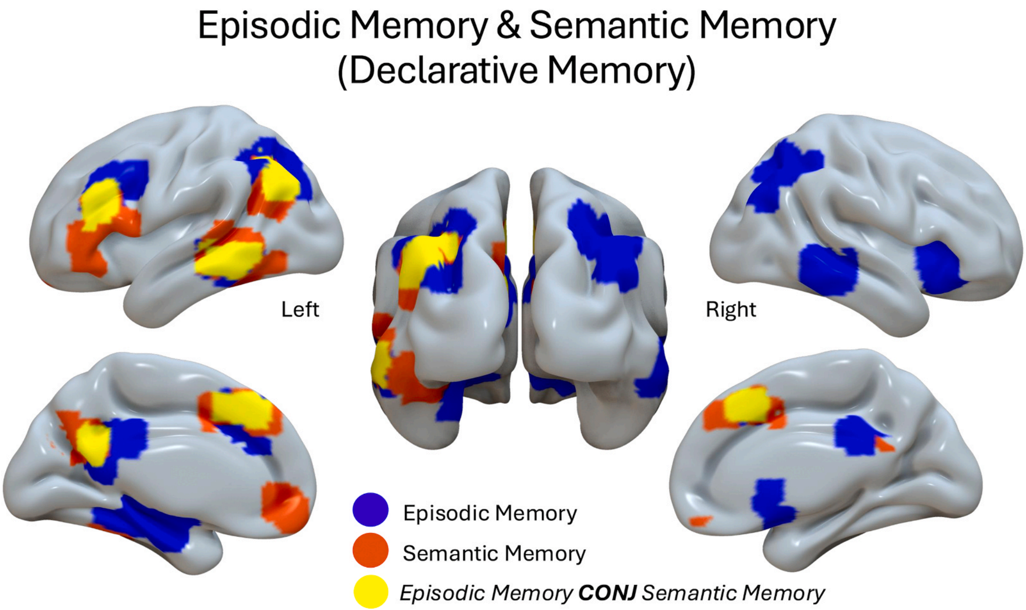

Fig. 4. Single metanalyses on episodic (blue) and semantic (orange) components of declarative memory, and conjunctions between them (yellow).

3.2. Conjunction analyses

Navigation CONJ Memory: As depicted in Fig. 2 (yellow), conjunctions between navigation and memory were observed bilaterally in the SOG (extending to the AG in the right hemisphere) and dACC, in the left PCC/RSC, the left PHG and fusiform gyrus, as well as in the right insula. Table 1 details the output of the conjunction analyses on navigation and memory (see also Supplementary Figure 1 and Supplementary Table 7 for consistent results obtained from a merged single metanalysis between spatial navigation and declarative memory).

Egocentric navigation CONJ allocentric navigation: As displayed in Fig. 3 (yellow), conjunctions were observed bilaterally in the PCC/RSC and in the PHG and fusiform gyrus (Table 2).

Episodic CONJ semantic memory: As displayed in Fig. 4 (yellow), conjunctions were observed in the left middle temporal and inferior/middle frontal gyri, AG and PCC/RSC, as well as bilaterally in the dACC (Table 3).

Episodic memory CONJ egocentric navigation (self-based components): As displayed in Fig. 5 (yellow), the conjunction analysis on self-based components of memory and navigation highlighted common foci in the bilateral SOG, extending to the AG in the right hemisphere, as well as in the left PHG and PCC/RSC (Table 4).

Table 1
Conjunction analysis on declarative memory and spatial navigation. For each cluster, labels, hemisphere, cluster size (mm^3) and MNI coordinates of the maximum peaks are provided. PCC/RSC = posterior cingulate cortex/retrosplenial cortex; pCu = precuneus; dACC = dorsal anterior cingulate cortex; PHG = parahippocampal gyrus; SOG/AG = superior occipital gyrus/angular gyrus, Cu = cuneus; LH = left hemisphere; RH = right hemisphere.

Cluster	*Region*	*Hemisphere*	*Volume (mm^3)*	*x*	*y*	*z*
1	Insula	RH	1192	34	24	−6
2	PCC/RSC	LH	1192	−8	−54	14
	pCu	LH		−12	−60	22
3	dACC	LH	808	−2	14	46
		RH		4	18	46
		LH		−6	22	38
		LH		−4	22	42
4	PHG	LH	576	−24	−36	−10
		LH		−30	−40	−6
5	SOG/AG	RH	536	38	−78	36
		RH		38	−74	40
6	SOG	LH	368	−34	−84	32
7	Cu	LH	16	−30	−76	34

Table 2
Conjunction analysis on egocentric and allocentric navigation. For each cluster, labels, hemisphere, cluster size (mm^3) and MNI coordinates of the maximum peaks are provided. PCC/RSC = posterior cingulate cortex/ retrosplenial cortex; PHG = parahippocampal gyrus; LH = left hemisphere; RH = right hemisphere.

Cluster	*Region*	*Hemisphere*	*Volume (mm^3)*	*x*	*y*	*z*
1	PCC/RSC	LH	3256	−14	−58	12
2	PHG	RH	2352	26	−38	−8
3	PCC/RSC	RH	1872	16	−54	14
4	PHG	LH	1304	−22	−44	−12

Table 3
Conjunction analysis on episodic and semantic memory. For each cluster, labels, hemisphere, cluster size (mm^3) and MNI coordinates of the maximum peaks are provided. MTG = middle temporal gyrus; dACC = dorsal anterior cingulate cortex; MFC = middle frontal gyrus; AG = angular gyrus; PCC/RSC = posterior cingulate cortex/retrosplenial cortex; LH = left hemisphere; RH = right hemisphere.

Cluster	*Region*	*Hemisphere*	*Volume (mm^3)*	*x*	*y*	*z*
1	MTG	LH	1208	−60	−36	−6
		LH		−62	−44	−8
2	dACC	LH	1040	−4	26	46
		LH		−2	16	44
		LH		−4	34	42
3	MFG	LH	992	−52	26	28
		LH		−52	30	20
4	AG	LH	576	−44	−68	34
5	PCC/RSC	LH	392	−4	−50	28
		LH		−6	−54	22
6	AG	LH	200	−34	−60	42
		LH		−38	−64	46
7	MFG	LH	16	−52	36	14
8	AG	LH	8	−36	−58	40

Semantic memory CONJ Allocentric navigation (map-based components): As displayed in Fig. 6 (yellow), conjunction analysis on map-based components of memory and navigation identified a a left-lateralized cluster in the PCC/RSC and a bilateral cluster in the dACC (Table 5).

Control conjunctions: A set of conjunction maps were also conducted

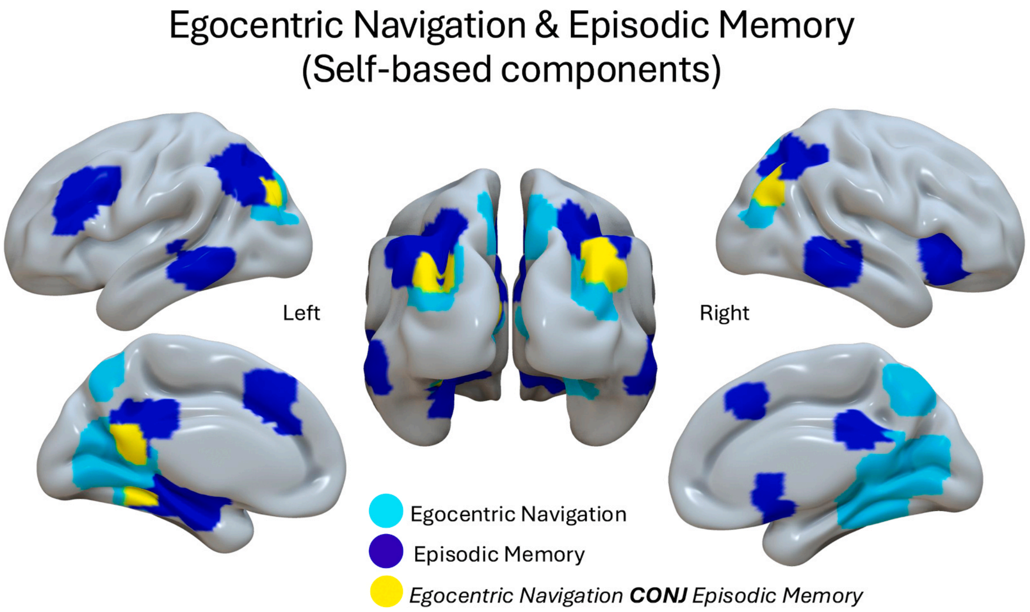

Fig. 5. Single metanalyses on egocentric navigation (cyan) and episodic memory (blue), and conjunctions between them (yellow).

Table 4
Conjunction analyses on episodic memory and egocentric navigation (self-based components). For each cluster, labels, hemisphere, cluster size (mm^3) and MNI coordinates of the maximum peaks are provided. PCC/RSC = posterior cingulate cortex/retrosplenial cortex; SOG/AG = superior occipital gyrus/angular gyrus; MTG = medial temporal gyrus; PHG = parahippocampal gyrus; LH = left hemisphere; RH = right hemisphere.

Cluster	*Region*	*Hemisphere*	*Volume (mm^3)*	*x*	*y*	*z*
1	PCC/RSC	LH	488	−8	−52	12
2	SOG/AG	RH	416	38	−78	36
				38	−76	42
	MTG			42	−72	30
3	SOG	LH	272	−32	−84	32
4	PHG	LH	72	−28	−44	−12

Table 5
Conjunction analyses on semantic memory and allocentric navigation (map-based components). For each cluster, labels, hemisphere, cluster size (mm^3) and MNI coordinates of the maximum peaks are provided. dACC = dorsal anterior cingulate cortex; PCC/RSC = posterior cingulate cortex/retrosplenial cortex; LH = left hemisphere; RH = right hemisphere.

Cluster	*Region*	*Hemisphere*	*Volume (mm^3)*	*x*	*y*	*z*
1	dACC	LH	688	−2	12	44
				−2	22	44
		LH/RH		0	28	44
2	PCC/RSC	LH	200	−16	−60	22
				−14	−58	18
3	RSC	LH	8	−10	−56	20

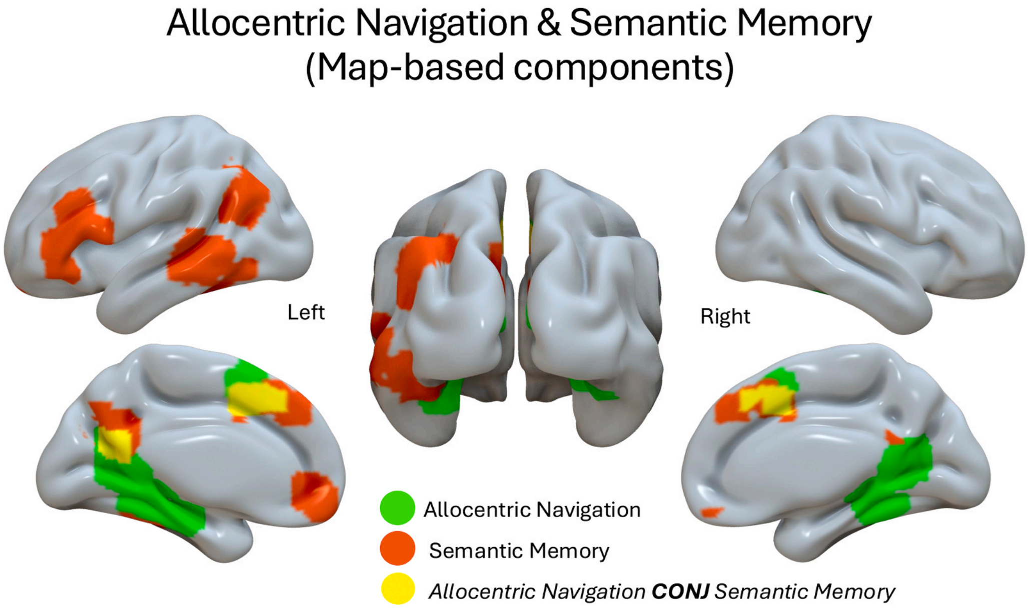

Fig. 6. Single metanalyses on allocentric navigation (green) and semantic memory (orange), and conjunctions between them (yellow).

across non-corresponding reference frames between memory and navigation. As depicted in Fig. 7 (yellow), common activation foci between allocentric navigation and episodic memory as well as between egocentric navigation and semantic memory were identified in the left PCC/RSC. In addition, left-lateralized clusters in the PHG and fusiform gyrus as well as in the dorsal ACC were identified in the conjunction between allocentric navigation and episodic memory (Table 6).

Table 6

Control conjunction analyses between egocentric navigation and semantic memory, and between allocentric navigation and episodic memory. For each cluster, labels, hemisphere, cluster size (mm^3) and MNI coordinates of the maximum peaks are provided. PCC/RSC = posterior cingulate cortex/retrosplenial cortex; dACC = dorsal anterior cingulate cortex; PHG = parahippocampal gyrus; LH = left hemisphere; RH = right hemisphere.

Conjunction between egocentric navigation and semantic memory

Cluster	*Region*	*Hemisphere*	*Volume (mm^3)*	*x*	*y*	*z*
1	PCC/RSC	LH	328	−16	−60	22
				−10	−58	22
				−14	−58	18

Conjunction between allocentric navigation and episodic memory

Cluster	*Region*	*Hemisphere*	*Volume (mm^3)*	*x*	*y*	*z*
1	PHG	LH	208	−26	−38	−12
				−28	−44	−12
2	dACC	LH	176	−2	16	46
				−2	22	44
		LH/RH		0	28	44
3	PHG	LH	104	−30	−18	−16
4	PCC/RSC	LH	72	−12	−54	18
				−10	−54	14
5	PHG	LH	16	−28	−28	−18
6	PHG	LH	8	−30	−30	−18
7	RSC	LH	8	−8	−56	14

4. Discussion

In the present meta-analysis, we investigated the neural convergence between systems supporting spatial navigation and declarative memory across different reference frames. Using an Activation Likelihood Estimation (ALE) approach, we assessed the degree of spatial overlap between brain regions involved in egocentric (self-based) and allocentric (map-based) components of both domains. Guided by recent large-scale models proposing evolutionary continuity between spatial and mnemonic processes, we hypothesized widespread neural commonalities between navigation in physical and mental space. Specifically, we expected greater overlap within than between self-based and map-based components of each domain, reflecting across-domain coding of reference frames. We further predicted that the interplay between egocentric and allocentric processes, known to operate dynamically in both navigation and memory, would be supported by distributed networks extending beyond the medial temporal lobe to include parietal and frontal cortical regions.

The findings partially confirmed our initial predictions, while also offering a more comprehensive account of how memory and navigation relate across reference frames. Rather than revealing strict clustering by domain or reference frame, the results showed shared recruitment of brain regions both within and between domains and frames, pointing to flexible, partially overlapping neural architectures. Strikingly, the retrosplenial complex (PCC/RSC) was the only region consistently activated across all four conditions (egocentric and allocentric navigation, episodic and semantic memory), highlighting its central role in integrating spatial and non-spatial information across reference frames.

In the following, we will first discuss the conjunctions observed within each cognitive domain, then the overlap between the two domains and, finally, the shared patterns within and between the reference frames across the two domains (for a graphical representation of all conjunctions see Fig. 8).

4.1. Neural systems for egocentric and allocentric navigation

In the domain of spatial navigation, both egocentric and allocentric tasks consistently engaged the parahippocampal gyrus, likely corresponding to the Parahippocampal Place Area (PPA; Epstein and Kanwisher, 1998), as well as the posterior cingulate and retrosplenial cortices (PCC/RSC). Alongside the Occipital Place Area (OPA), these regions form part of the core scene-selective network (Dilks et al., 2021). Notably, PPA and RSC are particularly sensitive to landmarks and spatial layout (Committeri et al., 2004; Galati et al., 2010), supporting their role in stable scene recognition and spatial orientation.

In the present context, we use the term retrosplenial complex (Beyh et al., 2022; Burles et al., 2017) to refer to the region encompassing the retrosplenial cortex (BAs 29–30) and posterior cingulate cortex (BAs 23–31) (Leech and Sharp, 2014; Vogt et al., 2006). The retrosplenial complex, through reciprocal connections with the hippocampus, parahippocampus, posterior parietal cortex, and early visual areas, supports spatial representation construction (Boccia et al., 2014; Kravitz et al., 2011). Lesion (Ino et al., 2007) and fMRI studies (Auger and Maguire, 2013) suggest that it encodes stable environmental features and their spatial relationships, contributing to allocentric spatial memory. Importantly, it integrates egocentric and allocentric inputs, enabling reference frame transformation (Clark et al., 2018; Epstein, 2008) and contains both place (Mao et al., 2017) and head-direction cells (Shine et al., 2016), suggesting hippocampal-like computational functions.

Beyond the retrosplenial and parahippocampal regions commonly

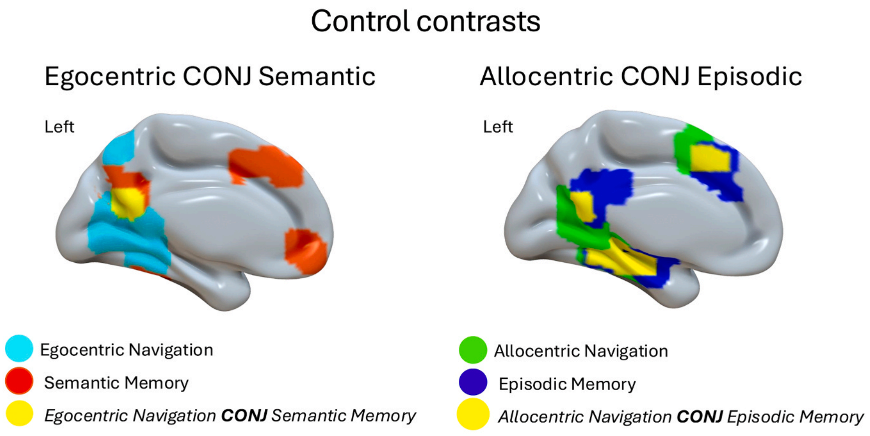

Fig. 7. (A) Single metanalyses on egocentric navigation (cyan) and semantic memory (orange), and conjunctions between them (yellow); (B) single metanalyses on allocentric navigation (green) and episodic memory (blue), and conjunctions between them (yellow).

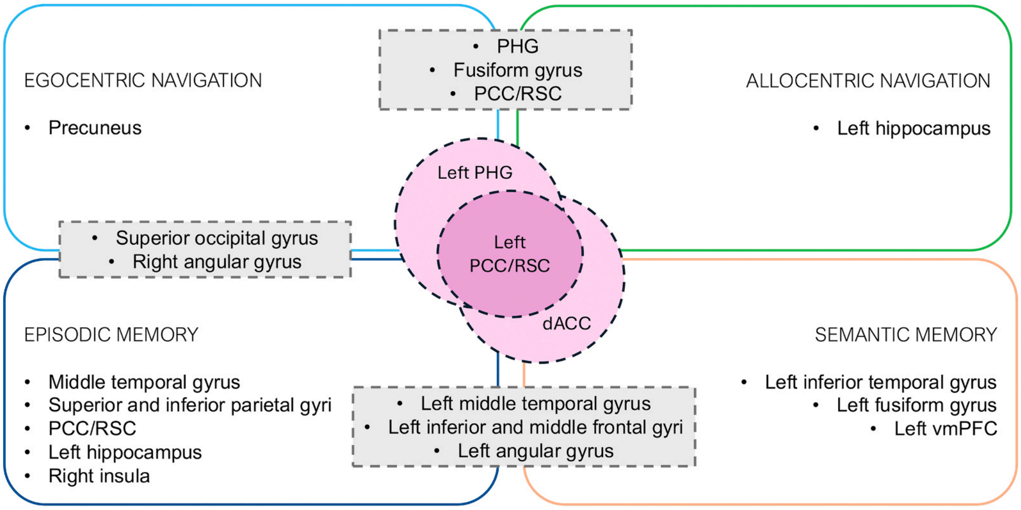

Fig. 8. Graphic overview of all the single (solid lines) and overlapping (dashed lines) activations reported on the manuscript. If no lateralization is provided in the figure, it means that the activation was bilateral. In summary, the left posterior cingulate cortex/retrosplenial complex (PCC/RSC) emerged as the only region activated across all four conditions. The dorsal anterior cingulate cortex (dACC) was activated for episodic and semantic memory, as well as for allocentric navigation; while the left parahippocampal gyrus (PHG) was activated for egocentric and allocentric navigation, as well as for episodic memory. This figure was inspired by Figure 3 of Aggleton and O'Mara (2022).

activated by the two reference frames, allocentric navigation additionally recruited more anterior and ventromedial temporal regions, including the left hippocampus and bilateral dorsal anterior cingulate cortex (dACC). Egocentric navigation instead activated more dorsal-posterior regions such as the precuneus and the lateral occipital cortex (extending to the angular gyrus in the right hemisphere), the latter corresponding to OPA (Dilks et al., 2013), which encodes navigation-relevant cues like direction and distance (Kang and Park, 2024). According to our meta-analysis, therefore, navigational tasks emphasizing the use of self-based information activate more posterior and dorsal regions compared to tasks stressing the use of map-based information, which recruit anterior and ventral regions of the medial temporal lobe.

Overall, the present findings support a gradient of egocentric-to-allocentric information processing from parietal to medial temporal cortex, and viceversa, via the retrosplenial complex (Bicanski and Burgess, 2018; Clark et al., 2018; Miller et al., 2014). In line with this, the specific deficits reported in patients with topographical disorientation differ depending on lesion location, with parahippocampal and parietal damage impairing allocentric and egocentric representations of the environment, respectively (for a review, see Miller et al., 2014).

4.2. Neural systems for episodic and semantic memory

In the domain of declarative memory, the conjunction analysis revealed a predominantly left-lateralized network shared by episodic and semantic memory, including the middle temporal gyrus, the inferior and middle frontal gyri, the angular gyrus, and the retrosplenial complex, along with a bilateral involvement of the dorsal anterior cingulate cortex. These overlapping regions align closely with those reported by Renoult et al. (2019) and support the view of a declarative memory continuum, in which different memory types engage a common set of regions with varying relative contributions (Tanguay et al., 2023).

Beyond these shared areas, episodic memory additionally recruited right-hemisphere homologues of the middle temporal and inferior parietal cortices (extending into the intraparietal sulcus and superior parietal lobule), a left medial temporal lobe (MTL) cluster, and a right-lateralized insular region. In contrast, semantic memory did not engage the MTL but showed additional activation in the left ventromedial and ventrolateral prefrontal cortex. The activation in the ventromedial prefrontal cortex (vmPFC) for semantic memory aligns with its proposed role in memory consolidation and schema-based retrieval. The vmPFC supports the integration of temporally distributed experiences into abstract, generalized memory schemas, which facilitate retrieval by linking new information to prior knowledge (Gilboa and Marlatte, 2017; Moscovitch et al., 2016). This process may eventually enable hippocampus-independent access to neocortical traces.

Our findings are consistent with prominent models of memory organization, such as the Multiple Trace Theory and the Trace Transformation Theory. Both frameworks posit that the hippocampus is essential for memory retrieval as long as memories retain their episodic, context-rich nature, whereas semantic, decontextualized representations become increasingly supported by neocortical regions. According to the Trace Transformation Theory (Moscovitch et al., 2016; Sekeres et al., 2018), all memories are initially encoded as episodic traces, but over time, some undergo a transformation process, known as semantization, through which specific spatial and temporal details are gradually lost. As a result, richly detailed episodic memories continue to depend on the hippocampus, while transformed semantic memories become hippocampus-independent. Semantic memory, particularly when consolidated over time, as in the case of the tasks included in our meta-analysis, is indeed supported by a distributed neocortical network (Nadel and Moscovitch, 1997), with the specific cortical areas engaged depending on the type of information being retained (Renoult et al., 2019).

In line with this, a previous meta-analysis by Binder et al. (2009) identified three major cortical systems supporting semantic memory: (1) posterior association areas (including angular gyrus, middle temporal gyrus, and fusiform gyrus), (2) prefrontal regions (dorsal, ventromedial, and inferior frontal cortex), and (3) posterior midline structures (parahippocampal and posterior cingulate/retrosplenial cortices). The activation patterns observed in our meta-analysis closely correspond to these systems. Moreover, many of these regions overlap with the Default Mode Network (DMN), supporting the idea that semantic memory is tightly linked to intrinsic, internally directed modes of cognition (see next paragraph).

Unlike in the spatial navigation domain, no clear functional gradient emerged between self-based and map-based components of declarative memory. One possibility is that early stages of semantic knowledge formation depend on hippocampal and parahippocampal structures, akin to the role these regions play in building spatial maps. However, crystallized semantic memory appears to involve an additional layer of abstraction and language mediation, making it increasingly content-general and hippocampus-independent. This could account for the marked left-lateralization observed in semantic memory activations.

4.3. Conjunctions between memory and navigation domains

When examining the conjunctions between spatial navigation and declarative memory, independently of reference frame, we found overlapping activations in bilateral dorsal anterior cingulate cortex and the superior occipital region corresponding to OPA (extending to the angular gyrus on the right), in the left retrosplenial and parahippocampal cortices (including the PPA), and in the right insula. Notably, many of these regions overlap with the Default Mode Network (DMN) (Supplementary Figures 2, 3 and 4; Yeo et al., 2011), a system consistently associated with internally directed cognition, particularly memory-related processes (Buckner et al., 2008; Mason et al., 2007; Spreng and Schacter, 2012). DMN activity emerges when attention shifts away from the external world and toward self-generated processes such as autobiographical recall, episodic simulation, future thinking, and scene construction (Buckner and Carroll, 2007; De Brigard et al., 2015; Hassabis and Maguire, 2007; Schacter et al., 2008; Spreng et al., 2009). These functions are also central to declarative memory and often recruit the same brain regions engaged in spatial navigation, suggesting a shared functional architecture (Menon, 2023).

This convergence supports the idea that spatial navigation and declarative memory may rely on shared computational principles, consistent with the hypothesis that neural mechanisms originally evolved for navigating physical space have been repurposed, or "recycled", for navigating mental space (Buzsáki and Moser, 2013). In this context, Bottini and Doeller (2020) propose that cognitive maps reflect a domain-general strategy for structuring information within low-dimensional internal models defined by a few meaningful axes. Building on this framework, they describe two interacting systems: cognitive maps, associated with stable, allocentric (world-centered) representations, and image spaces, supporting egocentric (self-centered) perspectives. These systems jointly support the flexible manipulation of both spatial and conceptual knowledge.

Similarly, Peer et al. (2021) propose that cognitive graphs, networks of nodes and links, underlie navigation across both physical and conceptual spaces. They suggest that scene-selective regions such as OPA, PPA, and RSC support this process by respectively encoding local environmental geometry, contextual identity, and the integration of local information within the global environment, i.e. the transition from egocentric to allocentric representations. Consistent with this view, our results revealed overlap between navigation and memory in all three regions, supporting shared mechanisms for spatial and non-spatial cognitive mapping.

4.4. Neural systems within/between reference frames

Based on the phylogenetic continuity hypothesis (Buzsáki and Moser, 2013), we examined domain-general overlaps between navigation and declarative memory as a function of the employed reference frame.

When focusing on the self-based components (egocentric navigation and episodic memory), we observed overlapping activations in bilateral occipito-parietal cortex, including the OPA (extending to the angular gyrus in the right hemisphere), in line with the meta-analysis by Teghil et al. (2021), which also reported a right-lateralized convergence in this region. Additional conjunctions emerged in the retrosplenial complex and caudal parahippocampal cortex, consistent with Teghil's findings and with the posterior medial system proposed by Ranganath and Ritchey (2012), a network reliably implicated in episodic memory (Brown and Aggleton, 2001; Eichenbaum et al., 2007; Spaniol et al., 2009) and included in the navigational parieto-medial temporal pathway described by Kravitz et al. (2011).

In contrast, the map-based components (allocentric navigation and semantic memory) showed overlapping activity in the left dorsal anterior cingulate cortex (dACC) and retrosplenial complex. These findings diverge from those reported by Teghil et al. (2021), who found no conjunction for map-based components. This discrepancy may reflect methodological differences: whereas Teghil et al. focused on autobiographical memory, we excluded such studies to avoid conflating episodic and semantic elements (Irish et al., 2010; Levine et al., 2002, 2004; Renoult et al., 2012), and instead selected classical episodic and semantic paradigms allowing a clearer functional dissociation.

The dACC is involved in conflict monitoring (Botvinick, 2007) and may exert top-down inhibitory control over the hippocampus (Crespo-García et al., 2022), guiding goal-directed retrieval by suppressing irrelevant traces (Barry and Maguire, 2019; Brod et al., 2015). Notably, the dACC was consistently engaged across all functions except egocentric navigation. As a key node of the salience network (Menon, 2023; Seeley et al., 2007), the dACC is thought to support the integration of internal models with external cues and goals, facilitating adaptive, goal-directed behavior. Its engagement across memory and allocentric tasks may reflect the externally anchored nature of these paradigms, which typically require attentional shifts toward salient environmental information. In contrast, egocentric navigation relies more heavily on self-referenced processing and internal sensorimotor cues, especially in cue-deprived contexts, potentially explaining the absence of dACC activation. These findings highlight the role of the dACC not merely as an attentional node, but as a regulatory interface between internally and externally driven processing.

Converging activations between allocentric navigation and episodic memory were observed in the hippocampus and parahippocampal regions, consistent with their role in spatial mapping and memory consolidation. Notably, a topographical gradient emerged: episodic memory overlapped with allocentric navigation in more anterior portions of the parahippocampal formation and hippocampus, whereas overlap with egocentric navigation was restricted to posterior parahippocampal areas. This dissociation suggests that episodic memory does not align exclusively with either spatial strategy but flexibly recruits components from both systems depending on task demands and representational context.

These findings resonate with critical perspectives on the memory-navigation analogy (Eichenbaum and Cohen, 2014; Ekstrom and Hill, 2023), which argue that while shared computational principles exist, the underlying neural architectures are only partially overlapping. In particular, the transformations across reference frames, the network-level dynamics, and the nature of spatial versus conceptual cues, all influence the degree of convergence between memory and navigation processes.

Finally, an overlap in the retrosplenial complex (PCC/RSC) was observed for all the conjunction analyses conducted (see next paragraph).

4.5. The retrosplenial complex as an integration hub

As introduced above, all conjunction analyses in our study overlapped in the retrosplenial complex (PCC/RSC) (Fig. 9, black line), highlighting its role as a key integration hub for reference frames transformation across navigation and declarative memory. The retrosplenial complex anatomically sits at the intersection of limbic and cortical systems, where it integrates sensory, motor and visual information (Clark et al., 2018; Miller et al., 2014). It receives dense inputs from the hippocampus, anterior thalamic nuclei and visual cortices, and maintains reciprocal connections with the posterior parietal cortex, forming a retrosplenial-parietal network (Clark et al., 2018). Functionally, it enables conjunctive coding of spatial and contextual cues, supporting translation between self-based (egocentric) and map-based (allocentric) reference frames (Miller et al., 2014).

Our findings are consistent with recent metanalyses investigating the neural substrates of autobiographical episodic memory (Daviddi et al.,

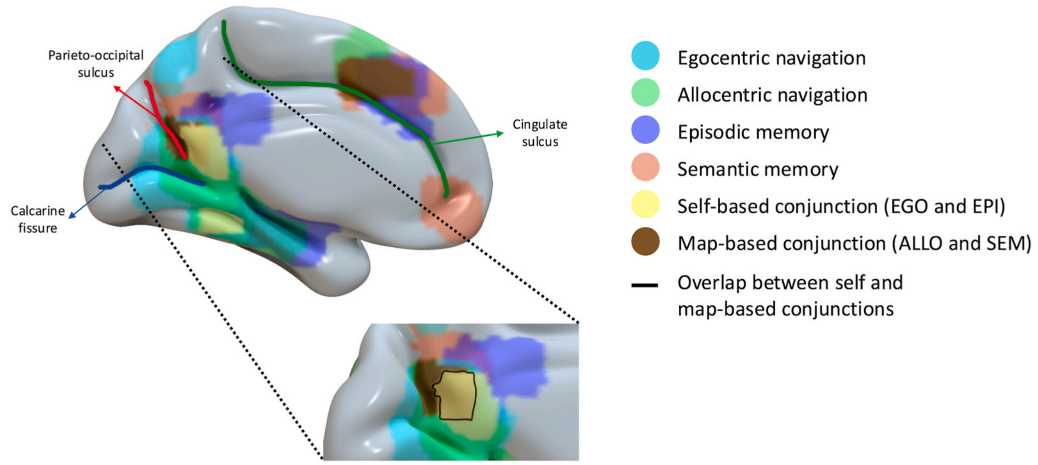

Fig. 9. Single metanalyses on egocentric navigation (cyan), allocentric navigation (green), episodic memory (blue) and semantic memory (orange). Conjunctions analyses between self-based components (i.e. egocentric navigation and episodic memory; yellow) and between map-based components (i.e. allocentric navigation and semantic memory; brown). Overlap between both self-based and map-based conjunctions (delineated with the black line).

2023, 2024). These studies identified the retrosplenial complex as a central hub that, beyond supporting the reliving of personal events, integrates memory details into coherent, self-related narratives. Together with the hippocampus, this region forms a network that enables autobiographical memories to be retrieved with vividness, coherence, and personal significance, reflecting the broader function of the retrosplenial complex in integrating self-based episodic retrieval with overarching semantic knowledge about the self.

Consistent with the idea that core components of spatial navigation, such as landmark anchoring, spatial coding, and route planning, generalize to abstract domains like memory and reasoning (Buzsáki and Moser, 2013; Epstein et al., 2017), the retrosplenial complex emerges as a key structure for integrating and transforming reference frames across domains. Anatomically situated at the intersection of medial temporal and parietal regions, the retrosplenial complex is well-suited to convert information between world-centered and self-centered coordinates.

Crucially, Epstein et al. (2017) have suggested that two fundamental operations in spatial cognition, context retrieval and orientation, may generalize across domains. In the spatial domain, context retrieval refers to the selection of an appropriate map for a given environment, while orientation involves determining one’s position and heading direction within that map. Analogously, in non-spatial domains such as semantic or episodic memory, context retrieval may involve accessing a relevant conceptual space, whereas orientation entails aligning current information to salient prototypes or axes within that space.

Our findings align with this view, highlighting the retrosplenial complex as a central hub in both spatial and non-spatial domains. Rather than encoding content *per se*, the retrosplenial complex may support dynamic mapping functions that allow individuals to anchor themselves within retrieved cognitive spaces, whether navigating a physical environment, recalling an episode, or reasoning about abstract concepts. Its role in mediating between reference frames suggests that it supports a general-purpose mechanism for situating experience within structured models (either cognitive maps or graphs), enabling flexible cognition across domains.

4.6. Limitations

Metanalyses are subject to inherent limitations that should be considered when interpreting the findings and generalizing conclusions. First, meta-analytic results are constrained by the pool of available studies. Publication bias may skew results, as studies reporting significant or positive findings are more likely to be published, whereas null or negative results tend to be underrepresented. Thus, in general, biases in literature are reproduced in metanalyses. Secondly, heterogeneity across studies, for example, differences in populations, experimental designs and tasks, may limit the comparability of findings and reduce confidence in estimates. To cope with this limitation, we specifically restricted our analysis to studies involving young adult participants and excluded studies that performed any form of intervention. Further research should examine the generalizability of these results to other age groups and populations.

5. Conclusions

Our findings partially confirmed the initial hypotheses, while offering a more comprehensive account of how memory and navigation relate across reference frames. Rather than strict domain- or frame-specific clustering, we observed flexible neural recruitment. The retrosplenial complex consistently emerged across all conditions, supporting its role as a key hub for integrating egocentric and allocentric information across spatial and non-spatial domains. This aligns with models of phylogenetic continuity and suggests a conserved mechanism repurposed for abstract cognition. Together, these findings highlight the dynamic, integrative nature of reference frame transformations across memory and navigation systems.

Future research could use fine-grained techniques such as multivoxel pattern and representational similarity analysis to clarify how different frames of reference are instantiated across spatial and non-spatial domains, and how structured knowledge is organized within shared neural architectures. Experimental paradigms that manipulate task demands across domains could help identify common computational principles and their network-level implementation. This, in turn, may shed light on how large-scale systems, such as the default mode and salience networks, support self-referenced mapping and internal model updating across diverse forms of content.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neubiorev.2025.106470.

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