Temporal Organization of Episodic and Experience-near Semantic Autobiographical Memories: Neural Correlates and Context-dependent Connectivity

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Abstract

■ Autobiographical memory includes a representation of personal life events with a unique spatiotemporal context (episodic autobiographical memory) and factual self-knowledge (personal semantics). Whereas "experience-far" personal semantics have undergone complete abstraction, "experience-near" personal semantics are still linked to a spatiotemporal context. The representation of one's own past involves an autobiographical knowledge base, in the form of a personal timeline, along which autobiographical information is temporally organized into different lifetime periods. Commonalities and differences between brain networks supporting this temporal organization for autobiographical information with different contextual specificity, however, have not been investigated to date. Here, we used task-based fMRI to assess neural substrates of temporal ordering along the personal timeline for real autobiographical episodic and experience-near personal semantic memories. Within a distributed network, the left calcarine cortex was more strongly activated for episodic autobiographical memory than personal semantics, whereas the left ventromedial pFC and right posterior cingulate cortex (PCC), angular gyrus (AG), and anterior middle temporal gyrus (aMTG) showed stronger activation for personal semantics than episodic autobiographical memory. Findings were confirmed by analyses in independently derived ROIs. Generalized psychophysiological interaction analyses between the same regions showed that, during personal semantics compared with episodic autobiographical memory, memory category modulated activity in the left PCC and right PCC, AG, and aMTG. Findings provide insights on how personal events and facts are represented in the timescale of years, suggesting that the temporal organization of autobiographical memory exploits properties of situation models developed within posteromedial, lateral parietal, and medial prefrontal regions. ■

INTRODUCTION

Autobiographical memory, including memory for personal life events and factual knowledge about oneself (Palombo, Sheldon, & Levine, 2018; Renoult, Davidson, Palombo, Moscovitch, & Levine, 2012), plays a key role in the construction and maintenance of a stable and coherent representation of the self across time (Prebble, Addis, & Tippett, 2013; Wilson & Ross, 2003). In line with the seminal distinction proposed by Tulving (1972), an episodic and a semantic component can be identified within the autobiographical memory domain (Renoult et al., 2016; Klein & Gangi, 2010; Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002). Episodic autobiographical memory (EAM) involves a representation of specific events from one's own past, which occurred at a particular time and place and are thus linked to a unique spatiotemporal context. Semantic components of autobiographical memory (often referred to as "personal semantics" [PS]) involve factual knowledge related to the self; this kind of memory includes autobiographical facts (names of relatives and friends, information such as the address of one's first house), self-knowledge (knowledge of personality traits, roles, e.g. "I am a researcher" or "I am shy", and personal beliefs), and repeated events (Grilli & Verfaellie, 2014; Renoult et al., 2012). The most influential cognitive models on the organization of autobiographical memory propose that the representation of the personal past involves an autobiographical knowledge base, corresponding to an organizing representation of the content and structure of one's own life (D'Argembeau, 2020; Conway & Pleydell-Pearce, 2000). The autobiographical knowledge base thus provides a sort of personal timeline, along which autobiographical information is temporally organized in spatial terms (D'Argembeau, 2020; Arzy, Adi-Japha, & Blanke, 2009; Arzy, Molnar-Szakacs, & Blanke, 2008). The autobiographical knowledge base allows the representation of personal past information at different levels of specificity, from lifetime periods to general events to specific events, thus supporting the representation of both episodic autobiographical and personal

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semantic information (D'Argembeau, 2020; Conway & Pleydell-Pearce, 2000).

Previous research has shown that different types of PS may be conceived as more episodic or semantic in nature, depending on the degree to which they are linked to specific episodes (Renoult et al., 2012; Cabeza & St Jacques, 2007). Pieces of information such as "I go to my brother's for dinner every Thursday" involve conceptual knowledge about the self that is derived from repeated individual episodes; conversely, pieces of PS knowledge such as "I have a brother" are more abstract in nature, as they are not related to specific time or place information (Sheldon, Peters, & Renoult, 2020). Specific categories of PS, such as autobiographical facts, are thus considered particularly "experience-near" because they are more strongly linked to a spatiotemporal context compared with general semantic knowledge that is devoid of contextual features (Grilli & Verfaellie, 2016, 2014). Supporting this distinction, lesions to medial temporal regions impair the retrieval of not only specific personal episodes but also experience-near autobiographical facts (Grilli & Verfaellie, 2014).

Neuroimaging studies have provided evidence that autobiographical memory relies overall on a broad neural network, involving the posterior cingulate cortex (PCC), medial and lateral temporal regions, the posterior–inferior parietal cortex, and the anterior cingulate/ventromedial pFC (vmPFC; Teghil, Bonavita, Guariglia, & Boccia, 2021; Svoboda, McKinnon, & Levine, 2006). Brain networks specifically supporting the temporal organization of autobiographical memories along the personal timeline, however, have not been systematically investigated.

St Jacques, Rubin, LaBar, and Cabeza (2008) reported stronger activation of the left dorsolateral pFC, the right parahippocampal gyrus, the posterior midline cortex, and the cuneus when participants discriminated the order of real-life events close in time; temporal order discrimination of events more distant in time, instead, activated the right dorsolateral pFC and the fusiform gyrus (St Jacques et al., 2008). Also, when participants were asked to decide which of two personal life events came before the other, or which of two hypothetic future life events would happen before the other, activation was found in the bilateral intraparietal sulcus, dorsolateral pFC, anterior insula, ACC, and precuneus (pCu) and visual cortex (D'Argembeau, Jeunehomme, Majerus, Bastin, & Salmon, 2015). Both studies investigated temporal order processing of autobiographical information in the range of 1 week (D'Argembeau et al., 2015) or a single day (St Jacques et al., 2008) and thus do not allow to draw inference on whether the same brain networks may also support the organization of autobiographical knowledge in different lifetime periods along one's own personal timeline.

Notably, along a somewhat different line of research, a few studies assessed brain correlates of individuals' ability to "project" themselves at different time points (now, 8 years in the past, or 8 years in the future) along a spatialized representation of their life (a "mental timeline") and to judge whether past- or future-related stimuli occurred/should occur before or after the imagined self-location in time (Arzy, Collette, Ionta, Fornari, & Blanke, 2009; Arzy et al., 2008). Stimuli presented in these studies were either pictures of the participant's face and of a famous person's face modified to demonstrate different ages (Arzy, Collette, et al., 2009), or labels referring to common personal life events (e.g., "first child") or nonpersonal events (e.g., "hurricane Katrina"; Arzy, Collette, et al., 2009; Arzy et al., 2008).

Overall, which brain networks support the ordinal organization of autobiographical information along different lifetime periods on one's own personal timeline is still unknown. Moreover, previous studies assessed mental travel across common personal life events, nonpersonal events, or famous people (Arzy, Collette, et al., 2009; Arzy et al., 2008) or asked participants to discriminate the order of personal episodes (D'Argembeau et al., 2015; St Jacques et al., 2008), whereas possible differences and similarities between brain networks and neural dynamics involved in the temporal organization of different types of personal memory (EAM vs. PS) have not been tested to date.

The present study had thus two main goals. First, we investigated brain regions supporting the temporal (ordinal) organization of autobiographical knowledge into different lifetime periods along the personal timeline, both for EAMs and experience-near PS (autobiographical facts) hereafter called "enPS". To this purpose, we developed a novel fMRI paradigm, in which participants were presented with labels corresponding to unique events from their own lives (EAMs) or names of personally known individuals (enPS) belonging to different lifetime periods and were asked to judge their relative chronological order. In a previous behavioral study assessing temporal ordering of autobiographical memories, a spatiotemporal interference effect was reported, for which participants were more accurate in judging the order of EAMs when the response direction was compatible with a sagittal mental timeline (i.e., future in front; Teghil, Marc, & Boccia, 2021). Thus, as a secondary aim, we also tested possible brain networks supporting such a spatiotemporal compatibility effect. Second, we assessed context-dependent connectivity within the autobiographical memory network during temporal ordering of EAMs and enPS using generalized psychophysiological interaction (gPPI). To assess the convergent validity of our procedure, we further correlated differences in brain activation associated with temporal ordering of EAMs and enPS within regions of the autobiographical memory network with scores on the Survey of Autobiographical Memory (SAM; Palombo, Williams, Abdi, & Levine, 2013), a previously validated measure of trait mnemonics in everyday life, administered outside the scanner.

Based on previous literature, we hypothesized that a common network could support overall the temporal organization of autobiographical information along

lifetime periods. This network should involve not only the medial temporal lobe and anterior temporal and medial prefrontal regions but also posterior and sensory regions that have been overall proposed to support the representation of the personal past at multiple levels of specificity (D'Argembeau, 2020). Within this network, however, we expected differences in brain activation supporting the temporal ordering of autobiographical memories with different degrees of specificity, and thus, we hypothesized that distinct nodes may play a different contribution to the representation of the temporal order of EAMs and enPS. On the one hand, sensory regions such as the striate and extrastriate cortex, as well as the hippocampus (HC; D'Argembeau et al., 2015; St Jacques et al., 2008), may be more strongly involved in supporting the chronological order of EAMs, which entail the integration of fine-grained sensory details. On the other hand, multimodal integration brain regions such as the anterior temporal lobe, which have been associated to higher-order features of the representation of the personal timeline (D'Argembeau, 2020), may be more strongly involved in enPS. Moreover, we expected that judging the relative order of EAM versus enPS should be associated to specific context-dependent connectivity patterns within the autobiographical memory network. Previous studies on effective connectivity between brain regions supporting autobiographical memory (McCormick, Barry, Jafarian, Barnes, & Maguire, 2020; Nawa & Ando, 2020) highlighted a key role of the vmPFC in driving memory retrieval, and this region has been implicated in the integration of, as well as in the switching between, different levels of autobiographical knowledge (D'Argembeau, 2020). We thus speculated that connectivity patterns of the vmPFC may discriminate between the EAM and enPS conditions.

METHODS

Participants

Thirty-one healthy young volunteers (mean age = 26.87 years, *SD* = 2.63; 20 women) took part in the study. All participants were right-handed and had normal or corrected-to-normal vision.

Sample size was defined a priori using G*Power (Version 3.1.9.6; Faul, Erdfelder, Lang, & Buchner, 2007) to achieve a statistical power higher than 95%, considering an alpha of .05. The effect size ($\eta_p^2 = .23$) was derived from a previous study (Teghil, Marc, & Boccia, 2021). The total sample size resulting from the power analysis was 29; considering possible dropouts, we finally enrolled 31 individuals. This sample is in line with previous fMRI studies investigating memory for realistic materials (Bromis, Raykov, Wickens, Roseboom, & Bird, 2022; Raykov, Keidel, Oakhill, & Bird, 2021). None of the participants had a current or previous history of neurological or psychiatric disorders, nor alcohol or drug abuse, as assessed during an informal interview before testing. The study was designed in accordance with the principles of the Declaration of Helsinki and was approved by the Ethical Committee of IRCCS Fondazione Santa Lucia, Rome (Prot. CE/PROG.824). Written informed consent was obtained from all individual participants included in the study.

Stimuli Collection

Stimuli to be presented during fMRI were collected outside the scanner (mean distance between stimuli collection and scanning was 5.29 days, *SD* = 6.50), using an adapted version of the Autobiographical Fluency Task by Dritschel, Williams, Baddeley, and Nimmo-Smith (1992). For each of five life periods (5–11 years, 11–14 years, 14–19 years, >19 years excluding the last 12 months, and last year), we asked participants to report personal events (EAMs) and names of friends, teachers, schoolmates, or colleagues (enPS) corresponding to those periods, as many as possible. Participants were asked to provide a personalized label that was meaningful to them and that allowed them to unambiguously identify the specific EAM or enPS. They were instructed to report only events that occurred at a specific time and place and to provide names of persons that were not associated to more than one life period (e.g., they were asked to avoid reporting names of siblings or other life-long family members). Ninety seconds were given for each combination of period and memory category (EAM or enPS; Dritschel et al., 1992). After task completion, participants were asked to report when the events occurred (for EAMs) and when they first met the persons they named (for enPS). The whole procedure lasted ~30 min.

On average, participants reported a total number of 35.63 (*SD* = 7.75) EAMs and 50.13 (*SD* = 12.53) enPS. The first two items reported for each period and memory category were used in the fMRI task, assigning them randomly to the compatible and noncompatible conditions (see below). Different labels were presented across conditions (compatible and noncompatible) to avoid spurious effects because of item repetition. However, items from the same periods were presented in different conditions, thus allowing to control for effects of age/remoteness between EAMs and enPS.

fMRI Task

We used a factorial 2 × 2 design, with the factors memory category (EAM vs. enPS) and task condition (compatible vs. noncompatible with the mental timeline). Because of the multifactorial design, which was aimed to test the effect of the main conditions rather than the effect of one condition upon the other (i.e., cross-domain interactions), the fMRI task was developed as a block design. During fMRI, labels corresponding to EAMs and enPS collected before scanning (see above) were presented one at a time, in an unbroken sequential manner, in four serially balanced sequences (one for each memory category

and task condition), in which each stimulus preceded and followed every other stimulus the same number of times (Aguirre, 2007; Nonyane & Theobald, 2007).

In each trial, participants were instructed to decide whether the currently presented stimulus preceded or followed the previously shown stimulus in chronological order (i.e., along their personal timeline; Figure 1). Responses were provided using a two-button MRI-compatible keypad. In the compatible condition, participants were asked to press the "backward" button if the current stimulus temporally preceded the previous one and the "forward" button if it followed the previous one; this mapping was reversed in the noncompatible condition (backward/forward responses for EAMs/enPS following/preceding the previous one; Teghil, Marc, & Boccia, 2021).

Four runs were acquired for each participant. To ensure that instructions were properly understood at the beginning of each scan, task conditions (compatible and noncompatible) were presented across runs; written instructions were presented at the beginning of each run. The order of the four runs was counterbalanced across participants. Within each run, labels referring to EAMs and enPS were presented in different blocks, following an ABBA order. Ten blocks were presented in each run. Each block lasted 25,000 msec. In each block, 10 labels were presented for 2000 msec, followed by a fixation point (500 msec). A fixation point was also presented during interblock intervals, lasting 15,000 msec. Stimuli were generated using E-Prime 3.0 (Psychology Software Tools) and projected on a translucent screen that participants saw through a mirror; accuracy and RTs were collected.

Immediately before fMRI, outside the scanner, participants performed a short familiarization session with the same structure of the experimental task (labels referring to standard EAMs and enPS, e.g., "first job" and "workmate", were presented during this phase, for a total number of 10 trials for each memory category and task condition).

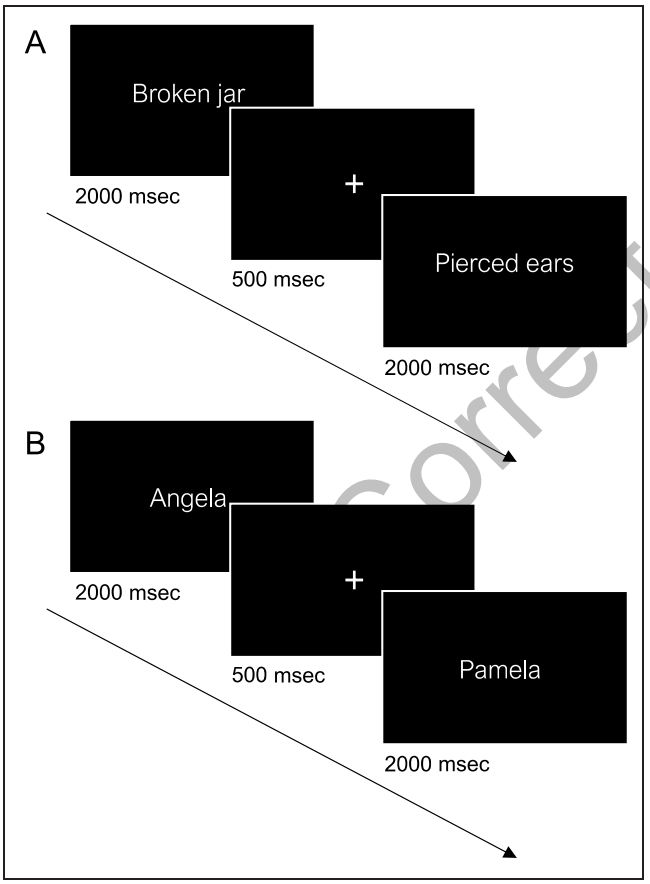

Figure 1. Example of stimuli presented during the fMRI task. The task was conceived as a 1-back task; in each trial, participants had to decide whether the currently presented personal event (episodic autobiographical memory condition; (A) or personally known person (experience-near personal semantics condition; (B) followed or preceded the previously presented one in chronological order along one's own personal timeline (stimuli showed in (A) corresponds to actual labels provided by one of the authors during preliminary testing of the fMRI paradigm).

SAM (Palombo et al., 2013)

The SAM is a self-report questionnaire, assessing episodic autobiographical (eight items), personal and general semantic memory (six items), spatial memory (six items), and future thinking (six items). Items are rated on a 5-point Likert scale (from 1 = *strongly disagree* to 5 = *strongly agree*). The SAM has been validated and used in different behavioral and neuroimaging studies on autobiographical memory (e.g., Fan, Abdi, & Levine, 2021; Petrican, Palombo, Sheldon, & Levine, 2020; Sheldon, Farb, Palombo, & Levine, 2016; Palombo et al., 2013). Scoring was performed for each participant according to the procedure by Palombo et al. (2013).

Image Acquisition

MR images were collected using a high-performance 3 T scanner (Siemens MAGNETOM Prisma) equipped with a 32-channel head coil. Functional, whole-brain MR images were acquired with a T_2 -weighted gradient-echo EPI sequence, a multiband factor of 4, and an isotropic voxel size of 2.4 mm^3 (60 slices, field of view = 208 × 208 mm^2, repetition time [TR] = 1100 msec, echo time [TE] = 30 msec, flip angle = 65°, no in-plane acceleration; Xu et al., 2013; Feinberg et al., 2010; Moeller et al., 2010). In each run, we acquired 370 fMRI volumes, including six dummy scans before each run, which were discarded.

Two spin-echo EPI volumes with phase encoding in opposite direction, no multiband acceleration, and the same geometrical and sampling properties of functional runs were acquired for field mapping (TE = 80 msec, TR = 7000 msec).

T_1-weighted structural images were acquired on each subject using an MPRAGE (magnetization-prepared rapid gradient-echo) sequence with perspective motion

correction and selective reacquisition of data corrupted by motion based on interleaved 3-D EPI navigators (Tisdall et al., 2012; Hess, Tisdall, Andronesi, Meintjes, & van der Kouwe, 2011). Volumetric imaging included 176 slices, isotropic resolution = 1 mm^3, TR = 2500 msec, TE = 2 msec, inversion time = 1070 msec, flip angle = 8°.

The MRI acquisition included other scans not used for the present study.

Behavioral Analyses

Behavioral data were analyzed using SPSS (IBM SPSS Statistics 20). First, 2 × 2 within-subject ANOVAs were performed on accuracy and RTs in the temporal ordering task, with the factors Memory Category (EAM vs. enPS) and Task Condition (compatible vs. noncompatible). Also, we tested whether the temporal distance between presented items differently affected temporal ordering of EAMs and enPS. We categorized each stimulus as coming from the same lifetime period of the previous one, or as being separated from the previous one by one, two, three, or four lifetime periods. Because two stimuli from each period were presented in each carryover sequence and the first stimulus of the sequence could not be judged (see the fMRI task description reported above), the maximum number of correct responses was different between levels of the factor temporal distance (zero, one, two, three, or four lifetime periods). Thus, for each level of temporal distance, we calculated an accuracy score as the proportion of correct responses. We then performed a 2 × 5 within-subject ANOVA on accuracy in the task with the factors Memory Category (EAM vs. enPS) and Temporal Distance (whether the to-be-judged stimulus belonged to the same lifetime period of the previous one, or it was separated from the previous one by one, two, three, or four lifetime periods).

Analysis of Imaging Data

Image preprocessing and analysis were performed using SPM12 (https://www.fil.ion.ucl.Ac.uk/spm). A field map was computed from the spin-echo EPI images acquired with opposite encoding polarity (Holland, Kuperman, & Dale, 2010). All fMRI images were simultaneously corrected for head movements and B_0 distortion, including motion × field interaction (realignment and unwarping; Andersson, Hutton, Ashburner, Turner, & Friston, 2001) using the first volume as reference. After slice-timing correction, the images of each participant were coregistered onto the respective T_1-weighted image and normalized to the standard MNI-152 template using the T_1 image as a source (voxel size: 2.4 × 2.4 × 2.4 mm^3). Images were finally smoothed using a 6-mm FWHM isotropic Gaussian kernel.

Functional images were analyzed for each participant separately on a voxel-by-voxel basis, according to the general linear model. Neural responses during EAM and enPS blocks were modeled as boxcar functions, convolved with a canonical hemodynamic response function, and used as separate predictors in the general linear model (one for each experimental condition). Interblock intervals were also modeled in relation to the nature of the previous block (EAM-rest or enPS-rest) and treated as baseline.

Whole-brain Analyses

To identify brain regions generally supporting the temporal organization of autobiographical information, without considering the specific memory category or task condition, we first computed an omnibus *F*-contrast comparing all experimental conditions against the baseline; only positive activations were tested (the *t*-contrast map was used as an inclusive mask thresholded at $p < .5$). The resulting statistical parametric map was thresholded using $p < .05$ family-wise error (FWE) and a cluster size $k > 30$ voxels. For each subject and region, a regional estimate of the amplitude of the hemodynamic response in each experimental condition was calculated entering a spatial average (across all voxels in the region) of the preprocessed time series into the individual general linear models. Then, regional hemodynamic responses were analyzed using 2 × 2 ANOVAs, with Memory Category and Task Condition as independent variables. Following Bonferroni's procedure, alpha level for these ANOVAs was set at $p < .002$.

In a separate voxel-wise analysis, we investigated brain regions more strongly involved in supporting the temporal ordering of autobiographical information depending on the memory category (EAM or enPS). Thus, contrast maps resulting from the contrasts EAM–enPS and enPS–EAM at the first-level analysis were entered into second-level random effects analyses, and statistical inference for each contrast was derived using a one-sample *t* test. The resulting statistical parametrical maps were thresholded using $p < .05$ FWE at the peak level and a cluster size $k > 30$ voxels.

ROI Analyses

We further investigated activation specifically related to the temporal sequencing of EAM and enPS in relation to one another within the brain network generally supporting autobiographical memory. The same steps described above for voxel-wise analyses comparing EAM and enPS were performed in a series of independent and theoretically motivated ROIs. Ten spherical ROIs (10-mm radius) were centered on peak coordinates derived from a previous activation likelihood estimation meta-analysis on autobiographical memory (Teghil, Bonavita, et al., 2021). The following ROIs were derived: left and right angular gyrus (AG), left and right anterior middle temporal gyrus (aMTG), left and right HC, left and right PCC, right posterior cerebellum (pCer), and left vmPFC (center coordinates of each ROI are reported in Table 1). One-sample *t* tests in these ROIs were performed for

Table 1. ROIs

Region	*x*	*y*	*z*
AGl	−46	−68	32
AGr	52	−68	32
aMTGl	−58	−4	−22
aMTGr	58	−4	−18
HCl	−24	−26	−16
HCr	26	−14	−18
PCCl	−8	−54	14
PCCr	10	−50	32
pCer	26	−80	−34
vmPFCl	−4	50	−6

For each ROI, center MNI coordinates are reported.

the *t*-contrast comparing the two memory categories (EAM and enPS) by applying a Bonferroni-corrected threshold of $p < .005$ (0.05/10). ROI analyses were performed using the MarsBaR toolbox (https://marsbar.sourceforge.net). Finally, two-tailed Pearson correlation coefficients were calculated between BOLD signal change between the two memory categories, which reflects neural activity unique of ordering enPS compared with ordering EAMs, within the ROIs and participants' scores on the SAM, entering total SAM score and scores on the Episodic, Semantic, Spatial, and Future Thinking subscales in the correlation matrix (since SAM scores were not available for six participants, correlation analyses were performed on $n = 25$).

gPPI Analysis

Context-dependent interactions between brain regions involved in the autobiographical memory network were assessed using a gPPI approach (McLaren, Ries, Xu, & Johnson, 2012), as implemented in the CONN Toolbox (v. 20b; www.nitrc.org/projects/conn, RRID:SCR_009550; Whitfield-Gabrieli & Nieto-Castanon, 2012). PPI is one of the more simple and intuitive methods to test the interaction between a physiological variable and an experimental factor (Friston, 2011), allowing to assess whether and how brain regions interact depending on the specific experimental condition. In brief, neural responses in a target region are modeled in terms of the interaction between a psychological process and the neural signal from a source region, thus allowing to assess whether the functional connectivity between a source and a target region is modulated by the experimental condition. In PPI, the interaction can be interpreted as a change, following an experimental manipulation, in the effective connectivity between a brain region, expressing a significant interaction, and a seed region (Friston, 2011). In block designs, the PPI can be interpreted as the difference in the regression slopes when regressing activity in one brain region on another one, under the two experimental contexts; thus, the PPI corresponds to the change in effective connectivity, given the experimental condition (Di, Zhang, & Biswal, 2021).

BOLD signal in each target region was modeled as a combination of (1) the effect of the two experimental conditions (EAM and enPS), (2) the time course in the source region, and (3) PPI terms corresponding to the product of the first two regressors, expressing the interaction between activation in each experimental condition and the neural signal in the source region, according to McLaren et al. (2012). gPPI analyses were performed between the 10 theoretically motivated ROIs described in the previous step. All of these regions have been found to be intrinsically connected (default mode network [DMN]) and have been recently hypothesized to be key nodes of a larger brain network involved in transmodal high-level processes (e.g., declarative memory, autobiographical memory, verbal semantics, and cognitive control; Margulies et al., 2016). Also, the pCer is functionally connected to the autobiographical memory network both

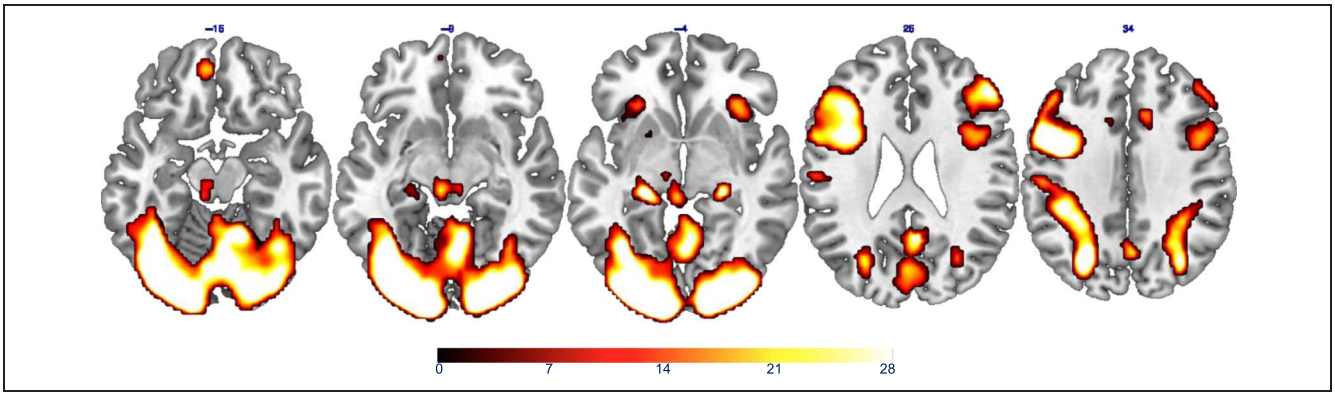

Figure 2. Regions involved in temporal sequencing of autobiographical information without considering memory category and compatibility with the mental timeline (see Table 2 for labels and results).

Table 2. Results of the 2 × 2 ANOVAs Performed in Brain Regions Generally Supporting the Temporal Sequencing of Autobiographical Information along the Autobiographical Knowledge Base

		Memory Category			*Task Condition*			*Memory Category × Task Condition*		
Label	*Hemisphere*	*F(1, 30)*	*p*	η_p^2	*F(1, 30)*	*p*	η_p^2	*F(1, 30)*	*p*	η_p^2
LPC	R	2.74	.11	.08	0.01	.96	<.001	0.01	.92	<.001
	L	8.33	.007 (EAM > enPS)	.22	0.21	.65	.01	0.08	.78	.003
pHC	R	8.22	.008 (EAM > enPS)	.22	2.50	.12	.08	0.31	.58	.01
	L	5.34	.028 (EAM > enPS)	.15	0.01	.94	<.001	0.04	.85	.001
PCC	R	**94.72**	**<.001 (enPS > EAM)**	**.76**	0.64	.43	.02	0.01	.92	<.001
	L	**22.64**	**<.001 (enPS > EAM)**	**.43**	0.40	.53	.01	0.51	.48	.02
vmPFC	L	**65.09**	**<.001 (enPS > EAM)**	**.68**	2.72	.11	.08	0.10	.76	.003
aIns	R	2.10	.16	.07	3.82	.06	.11	0.16	.69	.01
	L	2.29	.14	.07	4.40	.045 (NC > C)	.13	<0.001	.99	<.001
IFG	R	8.94	.006 (enPS > EAM)	.23	2.25	.14	.07	1.72	.20	.05
SMA	R	4.70	.038 (enPS > EAM)	.14	4.42	.044 (NC > C)	.13	0.03	.86	.001
	L	5.27	.029 (enPS > EAM)	.15	4.27	.048 (NC > C)	.12	0.22	.65	.01
midFG	R	3.62	.067	.11	1.93	.18	.06	0.19	.66	.01
LFC	R	4.30	.047 (enPS > EAM)	.13	2.77	.11	.08	0.01	.94	<.001
preCG	L	0.49	.49	.02	2.60	.12	.08	0.88	.36	.03
CC	R	6.34	.017 (EAM > enPS)	.17	<0.001	.98	<.001	0.08	.78	.003
	L	**17.11**	**<.001 (EAM > enPS)**	**.36**	0.08	.78	.003	0.12	.73	.004
BG	L	6.91	.013 (enPS > EAM)	.19	0.76	.39	.02	0.16	.69	.01
Cerebellum	R	0.09	.76	.003	1.06	.31	.03	0.06	.81	.002
	L	0.73	.40	.02	0.39	.54	.01	0.01	.93	<.001
Vermis	L	6.20	.019 (enPS > EAM)	.17	0.91	.35	.03	0.02	.90	.001

Results surviving Bonferroni correction ($p < .002$) are reported in **bold**, together with the direction of the observed effect. R = right; L = left; LPC = lateral parietal cortex; pHC = posterior portion of the HC; aINS = anterior insula; IFG = inferior frontal gyrus; midFG = middle frontal gyrus; LFC = lateral frontal cortex; preCG = precentral gyrus.

during rest and autobiographical memory retrieval (Addis, Moloney, Tippett, Roberts, & Hach, 2016). ROI-to-ROI parametric maps were thresholded using threshold-free cluster enhancement analyses (Smith & Nichols, 2009) with an FWE-corrected threshold of $p < .05$ at the connection level.

RESULTS

Behavioral Results

The 2 × 2 ANOVA on accuracy showed a trend toward a main effect of Memory Category (EAM: $M = 73.16$, $SD = 2.19$; enPS: $M = 74.93$, $SD = 2.33$) $F(1, 30) = 4.03$, $p = .054$, $\eta_p^2 = .12$, whereas the effect of Task Condition was significant (compatible: $M = 76.89$, $SD = 2.70$; noncompatible: $M = 71.21$, $SD = 2.27$), $F(1, 30) = 6.25$, $p = .018$, $\eta_p^2 = .17$. There was no significant interaction effect, $F(1, 30) = 0.32$, $p = .57$, $\eta_p^2 = .01$. Concerning RTs, there was a significant main effect of Memory Category, with participants being faster to respond to enPS ($M = 1079.76$, $SD = 130.55$) than to EAMs ($M = 1131.58$, $SD = 148.72$), $F(1, 30) = 18.96$, $p < .001$, $\eta_p^2 = .39$. The effect of Task Condition was also significant, $F(1, 30) = 8.16$, $p = .008$, $\eta_p^2 = .21$, with faster responses in the compatible ($M = 1077.93$, $SD = 27.09$) than in the noncompatible condition ($M = 1133.41$, $SD = 26.82$). The interaction effect was not significant, $F(1, 30) < .001$, $p = .1$, $\eta_p^2 < .001$.

Concerning the effects of the temporal separation between presented EAMs and enPS, we found a trend toward a significant main effect of Memory Category,

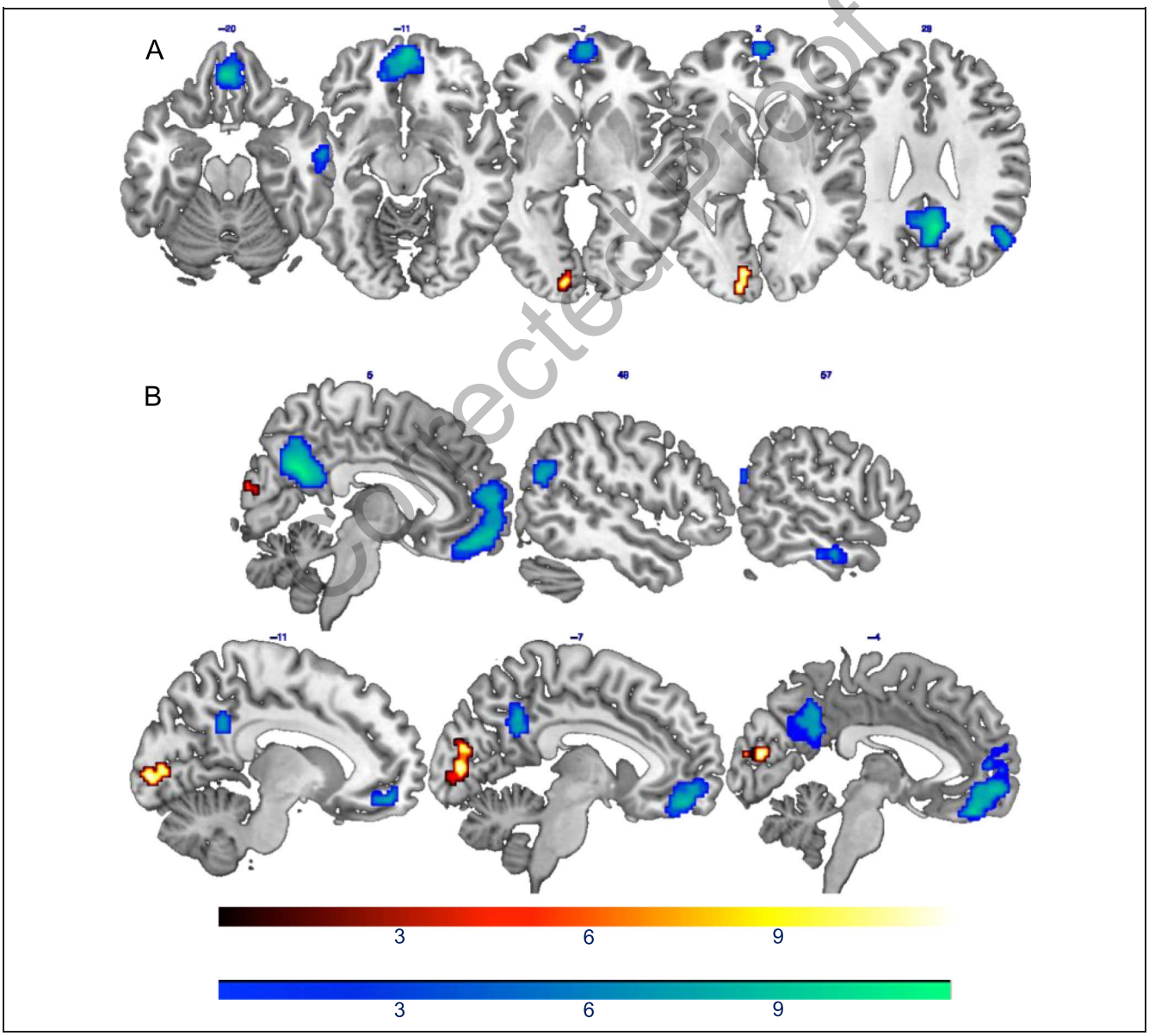

Figure 3. Brain activations more strongly associated with temporal ordering along lifetime periods for EAM compared with enPS (shown in red to yellow) and for enPS compared with EAM (shown in blue to green). (A) Axial view. (B) Sagittal view.

$F(1, 30) = 3.96, p = .056, \eta_p^2 = .12$, with participants more accurate in ordering enPS ($M = .84, SD = .025$) than EAMs ($M = .823$, $SD = .024$). There was a significant effect of Temporal Distance, $F(1, 1.7) = 43.03$, Greenhouse–Geisser corrected, $p < .001$, $\eta_p^2 = .59$. Post hoc analyses applying Bonferroni's correction showed that all comparisons were significant, with the proportion of correct responses increasing with increasing temporal distance between consecutive stimuli (same lifetime period: $M = .72$, $SD = .02$; 1 lifetime period distance: $M = .79$, $SD = .03$; 2 lifetime periods distance: $M = .85$, $SD = .03$; 3 lifetime periods distance: $M = .88$, $SD = .03$; 4 lifetime periods distance: $M = .91$, $SD = .3$). The interaction between Memory Category and Temporal Distance was not significant, $F(1, 2.73) = 0.41$, Greenhouse–Geisser corrected, $p = .73$, $\eta_p^2 = .01$.

Whole-brain Analyses

As a first step, we investigated brain networks generally supporting the temporal sequencing of autobiographical information along the autobiographical knowledge base. We thus performed an omnibus *F*-contrast comparing all experimental conditions versus the baseline, identifying brain regions generally involved in ordinal processing of autobiographical information independently from the memory category or task condition. A broad network was highlighted, spanning both hemispheres (Figure 2). Specifically, in the occipital lobe, we found activation spanning the bilateral calcarine cortex (CC); the posteromedial cortex (pCu) was also activated. Activation was also found in the bilateral HC (posterior portion), in lateral parietal regions, in both hemispheres, and in the left precentral gyrus. The bilateral anterior insula was also activated, spanning the inferior frontal gyrus in the right hemisphere. In the frontal lobes, further activations were found corresponding to the right middle frontal gyrus, bilateral SMA, and left vmPFC. The bilateral cerebellum and the BG in the left hemisphere were also activated. Results of the 2 × 2 ANOVAs with the factors Memory Category and Task Condition in each region showed that the bilateral pCu and the left vmPFC were more activated during the ordering of enPS compared with EAMs, whereas the left CC was more strongly involved in the EAM than in the enPS condition. No other significant effect was detected. Results are summarized in Table 2.

Next, we investigated brain networks more strongly involved in the temporal organization of EAMs and enPS. Because no significant interaction effect between memory category and task condition was found either at the behavioral or neural level in the analyses mentioned above, only the factor memory category was considered in following analyses.

The contrast EAM > enPS highlighted a cluster in the left CC that was more strongly activated during ordering of EAMs than of enPS (see Figure 3 and Table 3). Concerning the reverse contrast (enPS > EAM), results of the whole-brain analyses showed stronger activation during ordering of enPS than EAMs in a set of brain regions including the right pCu/PCC and the left vmPFC on the medial brain surface and the AG and aMTG of the right hemisphere on the lateral surface (see Figure 3 and Table 3).

ROI Analyses

Further analyses were performed to investigate differences in brain activation for temporal ordering of EAM and enPS within the core brain network supporting

Table 3. Brain Regions More Strongly Activated during Temporal Ordering of EAM and enPS Compared with the Other Condition

Region	*Hemisphere*	*x*	*y*	*z*	*T*	*p-FWE*	*Voxels*
EAM > enPS							
CC	L	−8	−86	4	7.16	.003	113
		−4	−83	14	7.09	.004	
		−11	−93	0	7.03	.005	
enPS > EAM							
pCu/PCC	R	6	−54	26	11.72	.000	494
		−6	−52	38	7.90	.000	
vmPFC		−1	44	−20	9.99	.000	623
		1	58	−8	9.84	.000	
		1	51	−15	9.62	.000	
AG	R	52	−66	24	8.46	.000	81
aMTG	R	61	−9	−22	7.66	.001	46

L = Left hemisphere; R = Right hemisphere.

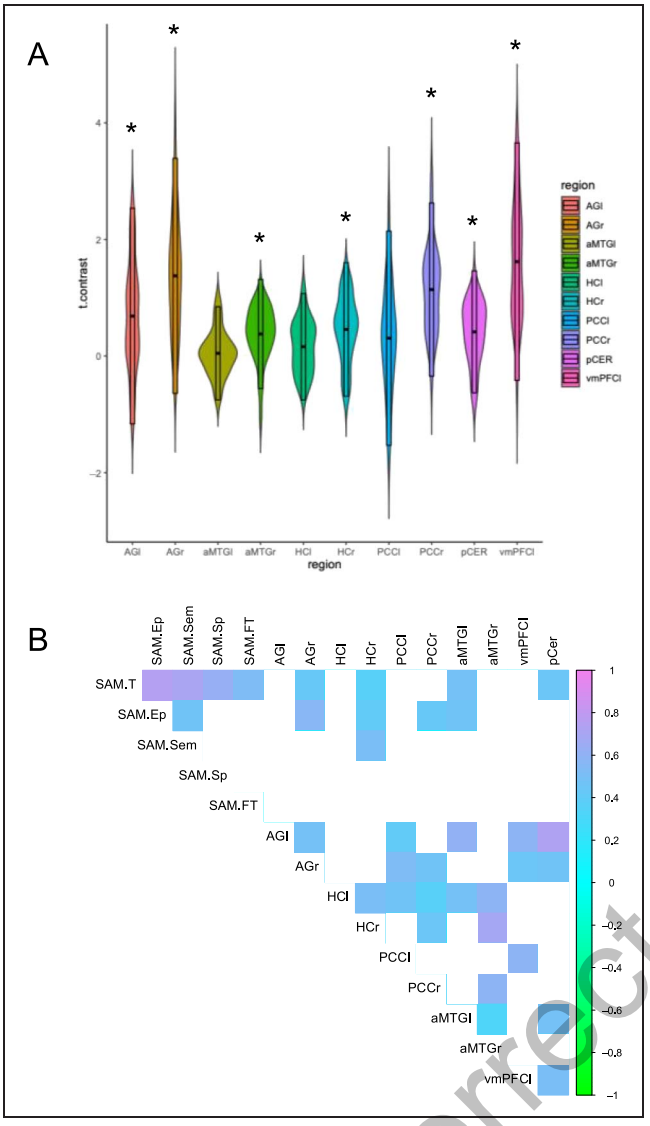

Figure 4. (A) Violin plots of *t* statistics for the contrast enPS > EAM for the 10 ROIs. Significant results of the one-sample *t* tests are marked with an asterisk ($p < .005$; the results of the one-sample *t* tests on the reverse contrast are not shown because they yield to symmetrical results). (B) Correlation plot showing the association between participants' scores on the SAM and activation difference between enPS and EAM in the ROIs. Only significant correlations are shown ($p < .05$, two-tailed). l = left hemisphere; r = right hemisphere; SAM.T = SAM total; SAM.Ep = SAM Episodic Memory subscale; SAM.Sem = SAM Semantic Memory subscale; SAM.Sp = SAM Spatial Memory subscale; SAM.FT = SAM Future Thinking subscale.

autobiographical memory (bilateral AG, aMTG, HC, and PCC; right pCer; left vmPFC; Teghil, Bonavita, et al., 2021). A significant stronger activation in enPS compared with EAM was found in the left and right AG, right HC, right PCC, right aMTG, left vmPFC, and pCer (Figure 4a).

Correlation analyses with self-report measures of everyday memory (Palombo et al., 2013) showed that total SAM scores and scores on the Episodic subscale correlated positively with the portion of activation specifically associated to enPS compared with EAM in the right AG (SAM total: $r = .44$, $p = .029$; SAM Episodic: $r = .58$, $p = .003$) and in the left aMTG ROIs (SAM total: $r = .47$, $p = .019$; SAM Episodic: $r = .42$, $p = .035$). Activation difference in the right HC ROI was also significantly positively correlated with the SAM total ($r = .47$, $p = .019$), Episodic ($r = .47$, $p = .018$), and Semantic ($r = .54$, $p = .005$) subscales. A significant positive correlation was also found between differences in BOLD signal in the right PCC ROI and SAM Episodic scores ($r = .43$, $p = .030$; Figures 4B and 5). The full correlation matrix is reported in Table 4. No significant correlation was found between BOLD signal extracted in the ROIs and scores on the Spatial and Future Thinking subscales. This was an exploratory analysis, and findings should be considered with caution, because not all correlations would survive a stringent correction for multiple comparison. Results of the correlations, however, show an association between differences in task-related brain activation in response to the temporal ordering of different categories of autobiographical information in key nodes of the autobiographical memory network (Teghil, Bonavita, et al., 2021) and individual variations in trait mnemonics. Moreover, no correlation was observed between differences in task-related brain activation and scores on the Spatial and Future Thinking subscales, in line with findings from the original article by Palombo et al. (2013) that these subscales could be more reliably separated from those assessing episodic and semantic memory. These results suggest that differences in brain activation between the two memory categories evoked by our paradigm could be reliably associated to autobiographical memory processes.

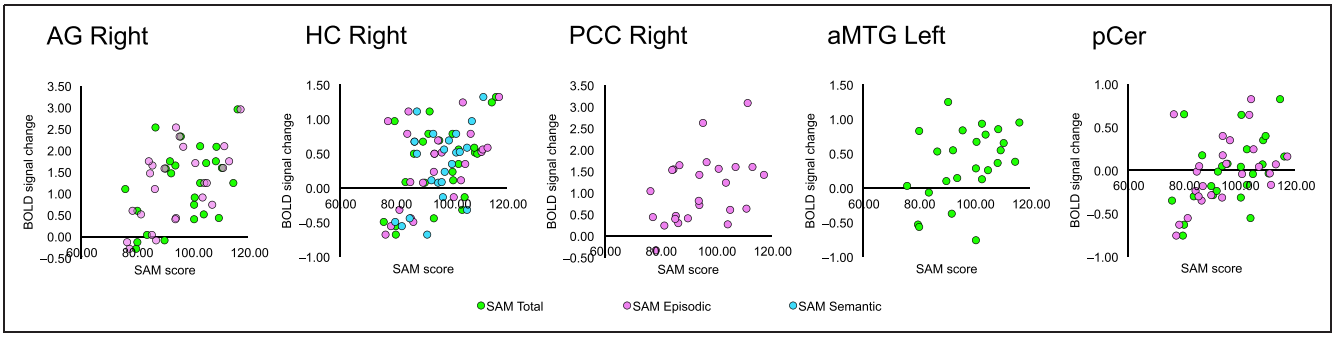

Figure 5. Scatter plot showing significant associations between SAM scores and activation differences between enPS and EAM in the ROIs.

Table 4. Pearson's Correlation Coefficients between Scores on the SAM and Activation Difference between enPS and EAM in the ROIs

	SAM Total	*SAM Ep*	*SAM Sem*	*SAM Sp*	*SAM FT*	*AGl*	*AGr*	*HCl*	*HCr*	*PCCl*	*PCCr*	*aMTGl*	*aMTGr*	*vmPFCl*	*pCer*
SAM total	1	.78***	.72***	.60**	.55**	.30	.44*	.12	.47*	.26	.26	.47*	.28	.05	.40*
SAM Ep	.78***	1	.45*	.38	.14	.28	.58**	.34	.47*	.31	.43*	.42*	.32	.23	.38
SAM Sem	.72***	.45*	1	.38	.22	.21	.03	.08	.54**	.14	−.01	.33	.28	−.05	.22
SAM Sp	.60**	.38	.38	1	.02	.30	.32	.14	.30	.28	.11	.23	.16	.15	.27
SAM FT	.55**	.14	.22	.02	1	.05	.17	−.19	.04	.03	.11	.22	.07	−.23	.18
AGl	.30	.28	.21	.30	.05	1	.51**	.38	.12	.41*	.29	.54**	.29	.47*	.74***
AGr	.44*	.58**	.03	.32	.17	.51**	1	.34	.32	.52**	.49*	.23	.24	.45*	.48*
HCl	.12	.34	.08	.14	−.19	.38	.34	1	.53**	.46*	.50*	.45*	.60**	.21	.35
HCr	.47*	.47*	.54**	.30	.04	.12	.32	.53**	1	.29	.42*	.19	.64**	.13	.10
PCCl	.26	.31	.14	.28	.03	.41*	.52**	.46*	.29	1	.33	.31	.33	.53**	.38
PCCr	.26	.43*	−.01	.11	.11	.29	.49*	.50*	.42*	.33	1	.22	.63**	.35	.39
aMTGl	.47*	.42*	.33	.23	.22	.54**	.23	.45*	.19	.31	.22	1	.45*	.13	.48*
aMTGr	.28	.32	.28	.16	.07	.29	.24	.60**	.64**	.33	.63**	.45*	1	.34	.19
vmPFCl	.05	.23	−.05	.15	−.23	.47*	.45*	.21	.13	.53**	.35	.13	.34	1	.45*
pCer	.40*	.38	.22	.27	.18	.74***	.48*	.35	.10	.38	.39	.48*	.19	.45*	1

SAM Ep = SAM Episodic memory subscale; SAM Sem = SAM Semantic Memory subscale; SAM Sp = SAM Spatial Memory subscale; SAM FT = SAM Future Thinking subscale; l = left hemisphere; r = right hemisphere.

* $p < .05$.

** $p < .01$.

*** $p < .001$

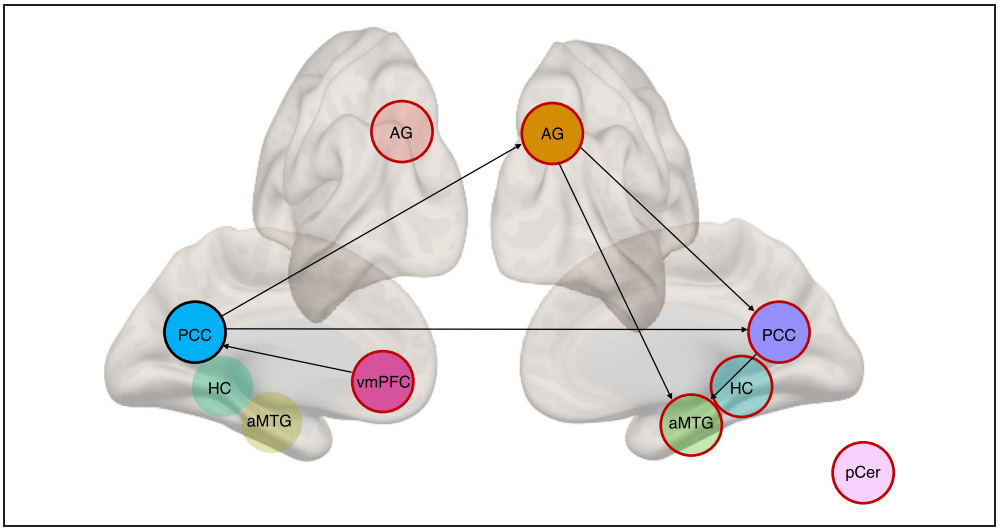

Figure 6. Schematic illustration of the results of the gPPI analyses. Significant effects are represented by arrows, identifying seed-to-target direction. Seeds showing significant PPIs with target regions are identified by darker colors. ROIs showing a stronger activation during enPS compared with EAM are highlighted by red edges.

Table 5. Results of the gPPI Analysis for the Contrast enPS > EAM

Analysis Unit	*Statistic*	*p-unc*	*p-FWE*
Cluster 1/1	TFCE = 27.13	.001829	.004000
Connection PCCl–PCCr	$T(30) = 4.20$		
Connection PCCl–AGr	$T(30) = 1.99$		
Connection PCCr–aMTGr	$T(30) = 0.79$		
Connection vmPFCl–PCCl	$T(30) = 0.75$		
Connection AGr–PCCr	$T(30) = 0.71$		
Connection AGr–aMTGr	$T(30) = 0.01$		

TFCE = threshold-free cluster enhancement; l = left hemisphere; r = right hemisphere.

gPPI Analysis

Context-dependent connectivity between the 10 ROIs described above was investigated using gPPI. Thus, we assessed whether the functional connectivity between each couple of regions within the brain network involved in autobiographical memory from previous literature (Teghil, Bonavita, et al., 2021) was affected by the experimental condition (temporal ordering of EAMs or enPS). For all seeds, functional connectivity was stronger during the enPS than the EAM condition. In detail, we found that, during enPS compared with EAM, the BOLD time course in the right PCC and in the right AG was predicted by the PPI in the left PCC. In turn, activity in the right PCC and in the right aMTG was predicted by the interaction between the experimental condition and the time course in the right AG. Activity in the right PCC was also significantly predicted by the PPI in the aMTG. Finally, neural activity in the left PCC was predicted by the interaction between the experimental condition and the time course in the left vmPFC (see Figure 6 and Table 5).

DISCUSSION

The present study investigated neural substrates of the ordinal representation of different formats of autobiographical information along one's own personal timeline. Both local regional effects and network-level interactions were assessed.

First, voxel-wise analyses highlighted a distributed network commonly involved in supporting the chronological organization of autobiographical knowledge. Within this network, different brain regions were preferentially involved in ordering EAMs and enPS along one's own personal timeline. Concerning EAMs, we found a single cluster in the left CC that was significantly more activated in this condition. Different fMRI studies have reported activation of occipital areas during tasks relying on EAM (Viard et al., 2011; Daselaar et al., 2008; Cabeza et al., 2004). Such an activation has been associated with the construction of a visual scene in service of episodic autobiographical remembering (Cabeza & St Jacques, 2007), also in line with neuropsychological evidence that lesions to the

visual cortex may lead to autobiographical memory impairments (Cabeza & St Jacques, 2007; Greenberg & Rubin, 2003). It has been proposed that the construction of a visual scene, including its spatial layout, is an integral part of reliving and characterizes specifically episodic remembering (Rubin & Umanath, 2015). The recollection of complex episodic details, however, involves both a memory construction and a memory elaboration phase and extends across several seconds (Daselaar et al., 2008; Conway & Pleydell-Pearce, 2000). Stronger activation of the left CC during EAM in the present study could thus reflect a partial reactivation of visual features of EAMs during the temporal ordering task. Activation of occipital areas, together with that of lateral parietal regions and the pCu, has been also reported when participants decided which of two recently experienced events preceded the other, suggesting that these regions may support EAM sequencing through a spatialized representation of time (D'Argembeau et al., 2015). Although the present study does not allow to disentangle between these two possibilities, our results suggest that activation of regions of the ventral visual stream may specifically characterize temporal sequencing along lifetime periods of specific events, compared with that of PS information that, although experience-near, do not possess the same level of contextual specificity (Grilli & Verfaellie, 2014). Further studies will be needed to understand the specific role of visual areas in supporting the temporal organization of EAMs along lifetime periods, as well as the role of factors such as the vividness of these memories.

Voxel-wise analyses also highlighted a set of brain regions more strongly activated during temporal sequencing of enPS compared with EAM and involving the left vmPFC, the right pCu/posterior cingulate, and the right AG and aMTG.

Medial prefrontal regions interact with lateral temporal and posterior parietal structures during the organization of personal past experiences in thematically related clusters (Demblon, Bahri, & D'Argembeau, 2016) and thus have been proposed to be pivotal for the integration of specific autobiographical elements within higher-order autobiographical knowledge (D'Argembeau, 2020). Also, the vmPFC represents temporal positions within schematic sequences (Hsieh & Ranganath, 2015) and is sensitive to the temporal organization of narratives segments within familiar scripts, over the order of multiple minutes (Baldassano, Hasson, & Norman, 2018). Further supporting a possible role of this region in orientation in time, activation of the vmPFC was found in a previous study when participants judged which of two common life events was temporally closer to them (Peer, Salomon, Goldberg, Blanke, & Arzy, 2015). These findings have been recently extended to the domain of autobiographical memory because, in individuals with highly superior autobiographical memory, the left vmPFC shows increased pattern distinctness for memories more distant in time (Santangelo, Pedale, Macrì, & Campolongo, 2020), supporting the possibility that this region contributes to the representation of the temporal structure of one's own past.

Concerning the cluster of activation found in the pCu/posterior cingulate, lesions to the right PCC impair the ability to establish the relation between one's own position and a larger spatial context (Aguirre & D'Esposito, 1999). Indeed, the retrosplenial complex has been shown to code for imagined facing direction and location during memory retrieval, allowing to situate one's own imagined position and heading direction with respect to a representation of the local environment based on memory (Marchette, Vass, Ryan, & Epstein, 2014). Moreover, in a recent fMRI study in which participants compared the time elapsed between personal events at different timescales (hour, day, week, month), the PCC/pCu showed a sensitivity for the temporal timescale, with a maximum preference for longer timescales (i.e., months; Monsa, Peer, & Arzy, 2020). Because of its preference for longer timescales, it is not surprising that the PCC/pCu was more activated during temporal sequencing along lifetime periods for enPS than for EAMs; indeed, memories for personally known persons span across timescales inevitably longer than those of memories for specific events (which span a few hours).

The AG has been implicated in egocentric spatial computations (Boccia, Nemmi, & Guariglia, 2014), and disruption of neural activity in this region reduces the tendency to report personal memories in a first-person perspective (Bonnici, Cheke, Green, FitzGerald, & Simons, 2018). Notably, activation of the right pCu, together with the ipsilateral AG, has been recently shown to carry information about the temporal distance between previously experienced movie frames and their context (Foudil, Kwok, & Macaluso, 2020), suggesting that these two regions may participate in the temporal organization of cluster of events along long timescales. Thus, present findings of activation of the right retrosplenial complex together with the right AG suggest that the PCC may be involved in the representation of the order of autobiographical information along the personal timeline, contributing to its organization also along the different lifetime periods (Monsa et al., 2020), and are overall in line with evidence that movement in mental time is conceived in a spatialized manner (Bender & Beller, 2014).

Concerning activation found in the aMTG, anterior temporal regions are commonly activated during processing of PS information (Renoult et al., 2012; Svoboda et al., 2006), and the MTG has been particularly implicated in representing general events and knowledge about significant persons and autobiographical facts (Martinelli, Sperduti, & Piolino, 2013). Thus, present results are consistent with proposals that the anterior temporal lobe contributes specifically to the representation of higher-order aspects of autobiographical memory, such as the organization of autobiographical knowledge into lifetime periods and general events (D'Argembeau, 2020).

Results of the analyses in a series of theoretically motivated ROIs consistently involved in autobiographical memory (Teghil, Bonavita, et al., 2021) further confirmed findings from the voxel-wise analyses. Indeed, we found significantly stronger activation during ordering of enPS compared with EAMs in the bilateral AG; right HC, PCC, aMTG, and pCer; and left vmPFC.

The pCer shows intrinsic connectivity with the right AG, MTG, and medial frontal cortex and, during the retrieval of EAMs, interacts with the right PCC and MTG (Addis et al., 2016), all regions found to be activated in the present study. Moreover, disruption of activity in the right pCer impairs semantic integration and retrieval (Gatti, Vecchi, & Mazzoni, 2021; Gatti, Van Vugt, & Vecchi, 2020), in line with a possible role of this region in the flexible use of stored knowledge. Thus, although the contribution of the right pCer to autobiographical memory is still unclear, our results suggest that this region may contribute to the temporal organization of enPS.

As mentioned in the Introduction, the right HC has also been implicated in representing PS information, such as repeated events (Addis, McIntosh, Moscovitch, Crawley, & McAndrews, 2004). It has been proposed that the involvement of medial temporal lobe structures in PS depends on the extent to which these memories embed a spatiotemporal context: more experience-near enPS, although not to the same degree of EAMs, entail some spatiotemporal information and thus rely on the medial-temporal lobe; conversely, more experience-far PS, which have undergone complete abstraction, map on cortical networks involved in general semantic memory (Grilli & Verfaellie, 2016). Here, we tested the temporal organization of enPS asking participants to retrieve the relative order of names of people associated with different lifetime periods; this type of autobiographical facts embeds a temporal context by definition. Our results are thus compatible with the possibility that a continuum exists between episodic and semantic autobiographical memory, and their phenomenological features depend on the differential weighting of different component processes (Renoult et al., 2016, 2012). This interpretation is in line with the significant correlation we found between activity specifically associated with enPS in the right AG and PCC and the left aMTG with the Episodic subscale of the SAM; also, enPS-specific activity in the right HC was correlated with scores on both the Episodic and Semantic subscales.

Our final set of analyses assessed context-dependent connectivity between the abovementioned ROIs using gPPI (McLaren et al., 2012). The results showed that different regions were more strongly connected during enPS compared with EAM (Figure 6). More in detail, we found increased connectivity during the enPS compared with the EAM condition between the vmPFC and the ipsilateral PCC. Also, the connectivity between this latter region and the right PCC and AG was increased during ordering of enPS compared with EAMs. During the same condition, increased connectivity was also observed between the right AG and the ipsilateral PCC and aMTG. Results of the gPPI analysis are thus consistent with those of the voxel-wise and ROIs analyses and suggest overall that the left vmPFC, the right PCC/pCu, and the right AG and aMTG are key nodes in the network supporting temporal sequencing of autobiographical information.

Notably, the set of brain regions commonly highlighted by the present analyses considerably overlaps with the "core" subsystem of the DMN, including the medial pFC, the posteromedial cortex, the AG, and the aMTG (Andrews-Hanna, Smallwood, & Spreng, 2014; Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010). In line with recent suggestions that regions of the DMN support different forms of complex thought characterized by various degrees of abstraction (Smallwood et al., 2021), including episodic and semantic memory (Irish & Vatansever, 2020), this network has been shown to be involved during tasks requiring the application of previously learned schematic knowledge (Vatansever, Menon, & Stamatakis, 2017), of which enPS is an example. Specifically, the left vmPFC, the AG, the anterior temporal cortex, and the PCC have been strongly implicated in the processing of the so-called "schemas," conceived as high-level knowledge structures abstracted across multiple experiences (Gilboa & Marlatte, 2017). The sensitivity to chronological order has been recently theorized to be among the defining features of schemas, specifically in situations in which temporal order is relevant to guide behavior (Ghosh & Gilboa, 2014). More in detail, together with the other nodes of the DMN, the mPFC, retrosplenial cortex, and AG have been proposed to allow the instantiation of particular types of schemas, the so-called "situation models," that represent different kinds of relations, including temporal ones, within a specific context, supporting a wide range of complex cognitive functions (Ranganath & Ritchey, 2012). Within this network, the AG and pCu/PCC may specifically support the orientation within space and time (Ranganath & Ritchey, 2012), in line with evidence that these regions are involved in spatial navigation (Teghil, Bonavita, et al., 2021; Ekstrom, Huffman, & Starrett, 2017; Spreng, Mar, & Kim, 2009; Aguirre & D'Esposito, 1999) and with studies suggesting that temporal relations between lifetime periods may be represented in a spatialized manner (Teghil, Marc, & Boccia, 2021; Miles, Nind, & Macrae, 2010; Arzy, Adi-Japha, & Blanke, 2009). Present results thus suggest overall that the temporal organization of autobiographical information into different lifetime periods exploits situation models developed within core DMN regions.

Our results may appear somewhat at odd with previous literature, showing that brain regions often associated with episodic autobiographical retrieval (see Boccia, Teghil, & Guariglia, 2019, for a recent meta-analysis) were more activated during temporal sequencing of enPS than of EAMs. It is important to point out that here we aimed to investigate temporal sequencing along one's own personal timeline at the boundary between episodic and

semantic autobiographical memory. Indeed, the results of behavioral analyses on accuracy in the ordering task as a function of temporal distance between stimuli are consistent with the possibility that both EAMs and enPS have a specific temporal organization along the personal timeline. Accordingly, ROI analyses showed that differences in activation between memory categories in the autobiographical memory network were correlated with scores on the Episodic subscale of the SAM, supporting the possibility that these regions contribute to the temporal organization of enPS by processing contextual information. Based on these results, future fMRI studies are warranted to test the effect of temporal distance on regional activation, using event-related designs.

One may also wonder whether the enPS labels triggered the retrieval of specific events related to the cued persons. If this were the case, slower RTs to enPS than to EAMs should be expected, because enPS would entail recollecting both the identity of cued persons and contextual features of EAMs. However, this was not the case, because we observed faster RT to enPS than EAMs and no evidence for significance differences between performances in the EAM and enPS condition. Thus, present results may be especially important to understand neural mechanisms supporting the representation of temporal information for enPS, which has been significantly less investigated compared with EAM. Previous fMRI studies investigating PS mainly required participants to retrieve repeated events (e.g., Levine et al., 2004) or to provide judgments on statements concerning self-knowledge or self-traits (e.g., Araujo, Kaplan, Damasio, & Damasio, 2014; Maguire & Frith, 2003). To our knowledge, none of these studies assessed the temporal organization of this personal knowledge along different lifetime periods. Further studies, using PS characterized by variable contextual specificity (e.g., different types of autobiographical facts, such as one's job, street address, etc., as well as different conceptual categories of PS information) are thus needed to understand whether this temporal organization is common to other types of enPS knowledge.

Finally, temporal sequencing of enPS in our study yielded to stronger activation compared with EAM in different brain regions, whereas ordering of EAMs entailed stronger than enPS activation only of a single cluster. This fits well with findings of a recent fMRI study, reporting that during the recalling of fictional talk show conversations involving three fixed hosts and nine different celebrities, the identity of the (repeated) hosts was strongly reinstated in regions of the posteromedial network, whereas that of the (unique) celebrities was not (Bromis et al., 2022). Our findings that different regions of the DMN are activated more strongly during temporal ordering of personally known individuals than of single experienced events are thus in line with the possibility that repeated elements are more strongly represented at the neural level, further suggesting that this may be also true for autobiographical memory. In a similar vein, core regions of the DMN such as the vmPFC and the PCC have been also reported to be sensitive to the presence of social information (Tso, Rutherford, Fang, Angstadt, & Taylor, 2018). Thus, future studies specifically manipulating social significance are warranted to understand whether and how the degree of social information embedded within EAMs and enPS affects the strength of their neural representation along one's own personal timeline.

Overall, present findings are consistent with the theoretical proposal that autobiographical knowledge is organized along lifetime periods according to temporal and thematic relations (Conway & Pleydell-Pearce, 2000) and suggest that such an organization may be supported by temporal properties of situation models. From a broader perspective, these results are in line with recent theoretical accounts highlighting the privileged role of regions of the DMN in the gathering of multiple sources of information across the cortex and thus in allowing a continuum of abstraction from concrete, sensory-detailed representations typically involved in EAM to more abstract semantic knowledge (Smallwood et al., 2021; Irish & Vatansever, 2020). This conceptualization of PS would fit well with evidence that more experience-near types of autobiographical knowledge possess at least partial spatial and temporal features (Grilli & Verfaellie, 2016, 2014) and would provide a biological substrate to proposals that enPS information represents an intermediate entity between episodic and semantic memory (Renoult et al., 2012).

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Data Availability Statement

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Author Contributions

Alice Teghil: Conceptualization; Methodology; Formal analysis; Investigation; Writing–original draft; Writing–review & editing; Visualization; Project administration; Funding acquisition. Alessia Bonavita: Investigation; Writing–review & editing. Federica Procida: Investigation;

Writing–review & editing. Federico Giove: Methodology; Software; Formal analysis; Writing–review & editing. Maddalena Boccia: Conceptualization; Methodology; Formal analysis; Writing–review & editing; Visualization; Project administration; Supervision.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance. The authors of this article report its proportions of citations by gender category to be as follows: M/M = .485; W/M = .235; M/W = .147; W/W = .132.

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