

# What makes an event significant: an fMRI study on self-defining memories

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Self-defining memories are highly significant personal memories that contribute to an individual's life story and identity. Previous research has identified 4 key subcomponents of self-defining memories: content, affect, specificity, and self-reflection. However, these components were not tested under functional neuroimaging. In this study, we first explored how self-defining memories distinguish themselves from everyday memories (non-self-defining) through their associated brain activity. Next, we evaluated the different self-defining memory subcomponents through their activity in the underlying brain system. Participants recalled both self-defining and non-self-defining memories under functional MRI and evaluated the 4 subcomponents for each memory. Multivoxel pattern analysis uncovered a brain system closely related to the default mode network to discriminate between self-defining and non-self-defining memories. Representational similarity analysis revealed the neural coding of each subcomponent. Self-reflection was coded mainly in the precuneus, middle and inferior frontal gyri, and cingulate, lateral occipital, and insular cortices. To a much lesser extent, content coding was primarily in the left angular gyrus and fusiform gyrus. No region was found to represent information on affect and specificity. Our findings highlight the marked difference in brain processing between significant and non-significant memories, and underscore self-reflection as a predominant factor in the formation and maintenance of self-defining memories, inviting a reassessment of what constitutes significant memories.

**Key words:** self-defining memories; self-reflection; functional MRI; multi-voxel pattern analysis; representational similarity analysis.

## Introduction

As we go through life, autobiographical memories are formed from various events. These memories serve as integrated representations of our personal experiences, self-knowledge, as well as our own interpretations and evaluations of these events, thus enabling a continuous perception of self over time (Conway and Pleydell-Pearce 2000; Levine 2004; Rubin et al. 2019). Some of these memories are more significant than others, as they contribute to our sense of identity and life story and are known as self-defining memories (SDMs) (Singer and Moffitt 1992; Moffitt and Singer 1994; Blagov and Singer 2004; Wood and Conway 2006; D'Argembeau et al. 2014). SDMs have been defined as highly significant personal memories that are vivid, emotionally intense, repetitively recalled, and often relate to important concerns, goals, or unresolved conflicts, forming links with other memories sharing the same theme (Singer and Salovey 1996).

Over the past decades, studies have explored the different aspects of SDMs, as reflected in participants' descriptions of such memories (Singer and Salovey 1996; Singer and Blagov 2000; Thorne and McLean 2001; Cili and Stopa 2015; Blagov et al. 2022; Fritsch et al. 2023). Specifically, these studies have highlighted 4 key subcomponents along which SDMs vary (Blagov and Singer 2004; Lardi et al. 2010). First, the thematic content (*content*) of the memory is the principal theme emphasized in the narrative, reflecting the individual's primary concern (Thorne and McLean 2001), with main categories, such as relationships, life-threatening events, achievements, and leisure (Thorne and McLean 2002;

Blagov and Singer 2004; Thorne et al. 2004; Singer et al. 2007). Second, affective responses (*affect*) to SDMs can vary in valence and intensity during memory retrieval (Wood and Conway 2006). Third, memory specificity (*specificity*) concerns a certain characteristic of sensory and spatiotemporal details of a specific memory. The retrieval process of autobiographical memory can lead to the construction of a specific memory, or to more general memories (Fisher and Geiselman 1992; Conway and Pleydell-Pearce 2000; Singer and Blagov 2000; Blagov and Singer 2004; Memon et al. 2010; Madore and Schacter 2016). The fourth subcomponent involves self-reflective thinking about a past experience, in which one reflects on the meaning and implications of the experience (D'Argembeau et al. 2014). It involves integrating different aspects of one's life and the self, thereby linking past experiences with the present (*self-reflection*, also referred to as *autobiographical reasoning*) (Habermas and Bluck 2000; Singer and Bluck 2001; Lilgendahl and McAdams 2011). The process of self-reflection is of special importance as it contributes to the sense of identity and continuity and is crucial for well-being, maturity, and identity development (King 2000; McLean and Pratt 2006; Singer et al. 2007; Lilgendahl and McAdams 2011).

Previous research has primarily utilized neuropsychological experimental paradigms to investigate SDMs, with a limited number of studies examining the underlying brain activity. For example, D'Argembeau et al. (2014) explored the neural basis of the narrative self and autobiographical reasoning, using SDMs as part of the experimental paradigm. While SDMs and non-SDMs did

not elicit different brain activations, compared to remembering the content of the event, autobiographical reasoning recruited a left-lateralized network, including the dorsomedial prefrontal cortex (dmPFC), inferior frontal gyrus, middle temporal gyrus, and angular gyrus. In the present study, we aimed to define the brain system underlying SDMs and directly assess the involvement of each of the 4 subcomponents of SDMs through their brain representations. To this aim, we asked participants to recall both SDMs and non-SDMs and rate the 4 subcomponents (content, affect, specificity, and self-reflection) under fMRI. Multivoxel pattern analysis (MVPA) was applied to identify brain regions that distinguish between SDMs and non-SDMs, and representational similarity analysis (RSA) was used to explore the brain activity elicited by each subcomponent contributing to the construction of SDMs.

## Materials and methods

### Participants

Twenty-four right-handed healthy young adults (mean age  $\pm$  SD, 26.05  $\pm$  2.17 years, 13 females) with normal or corrected-to-normal vision and with no history of neurologic or psychiatric disorders participated in the study. The study was approved by the ethical committee of the Hadassah Medical Center in accordance with the Declaration of Helsinki (2013), and all participants provided written informed consent.

### Experimental stimuli

At least a week prior to the experiment, participants were asked to provide 5 detailed written descriptions of SDMs (Fig. 1A). The instructions for eliciting these memories were adapted from the SDM task (Singer and Moffitt 1992; Blagov and Singer 2004) and are further detailed in the [Supplementary Methods](#) section. For each SDM, participants were instructed to describe in as much detail as possible the content of the event, explain why it is a significant memory, and estimate how long ago the event took place (temporal distance). The instructions for generating non-SDMs were adapted from a previous neuroimaging study (D'Argembeau et al. 2014) and are further detailed in the [Supplementary Methods](#) section. After providing SDMs, participants were asked to provide detailed written descriptions of non-SDMs, referring to specific events that range across different time periods (Fig. 1B). To account for potential differences in the temporal distances of the SDMs and non-SDMs, participants were asked to provide 2 non-SDMs to correspond with the same time period of each of the 5 previously reported SDMs (resulting in a total of 10 non-SDMs). For each memory, SDM and non-SDM alike, participants were asked to construct a short cue representing that memory. Cue length did not differ between SDMs and non-SDMs (mean  $\pm$  SD number of words; for SDMs: 3.12  $\pm$  0.59; non-SDMs: 3.13  $\pm$  0.53;  $P > 0.8$ , paired two-tailed  $t$ -test). In addition, participants were required to rate in a pre-scan questionnaire each memory's vividness on a 7-point scale (1 = not vivid at all, 7 = extremely vivid) and personal significance (1 = completely insignificant, 7 = extremely significant). Out of the 10 non-SDMs, 5 were chosen for the fMRI session based on having low personal significance ratings and also matching in temporal distance with the 5 SDMs. Analysis of participant responses to the pre-scan questionnaire confirmed significant differences between SDMs and non-SDMs, with SDMs receiving higher average ratings for both personal significance and vividness (Fig. S1A and B; mean  $\pm$  SD, SDMs: 4.64  $\pm$  1.30; non-SDMs: 1.99  $\pm$  0.78 for significance and SDMs: 4.47  $\pm$  1.20; non-SDMs: 3.05  $\pm$  1.22 for vividness;  $P < 0.001$ , paired two-tailed  $t$ -test,

FDR corrected for multiple comparisons). There was no difference in temporal distance between the 2 types of memories (Fig. S1C;  $P > 0.8$ , paired two-tailed  $t$ -test, FDR corrected for multiple comparisons). To counterbalance between positive and negative SDMs, memories were classified according to participants' ratings of 8 emotions (positive: happy, interested; neutral: surprised; negative: sad, angry, fearful, ashamed, guilty). A memory was defined as positive/negative only if the rating was at least 1 SD higher/lower than the mean. This analysis yielded a balanced relationship between the number of positive and negative SDMs ( $Z = 1.46$ ,  $P$ -value = 0.14, Wilcoxon signed rank test). To investigate whether gender affected the behavioral measures, we compared behavioral ratings of personal significance, vividness, emotional intensity, and self-reflection ratings for both SDMs and non-SDMs in men and women separately. Our results showed no significant gender differences in any of these measures (all  $P$ -values  $> 0.05$ , two-tailed  $t$ -tests, [Table S3](#)).

### Experimental paradigm

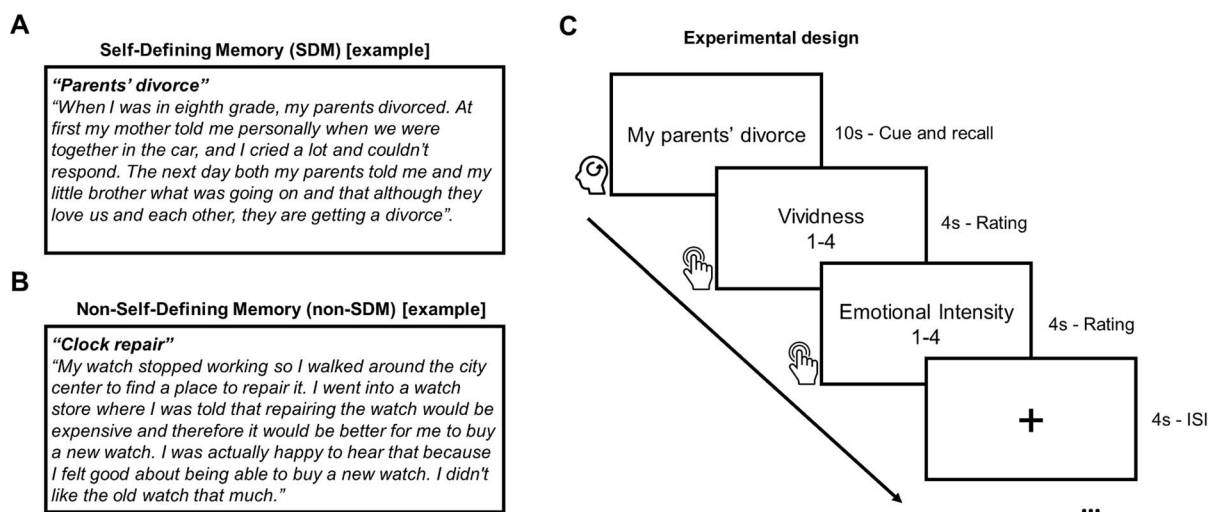
In the experimental task, participants underwent fMRI scanning while recalling their 10 previously provided memories, consisting of 5 SDMs and 5 non-SDMs (Fig. 1C). At the beginning of each trial, a cue was presented for 10 s indicating which memory to recall, and participants were instructed to vividly recall the cued memory. Following each trial, participants rated the preceding recall on a 1–4 scale in terms of vividness (1 = not vivid at all, 4 = very vivid) and emotional intensity (1 = not emotional at all, 4 = very emotionally intense), with each rating screen presented for 4 s and responses recorded using a 4-button response box. A fixation cross was then presented for 4 s before the next memory recall trial. The memories were presented in a pseudo-random order to ensure that the same memory was not repeated twice or more in a row.

The study consisted of 8 experimental runs, with each run comprising 20 trials, including 2 repetitions of each memory provided. Apart from the 8 experimental runs, a lexical control run was also conducted where the same verbal cues were presented, yet here participants were instructed to count how many times a specific letter appeared in the target stimulus. Prior to the experiment, participants underwent a training task using the non-SDMs, which were not included in the fMRI session, to familiarize themselves with the task.

### Post-scan questionnaires

Following the fMRI session, participants were required to complete 2 questionnaires. In the first questionnaire, participants rated on a 7-point scale the level of effort required to recall each memory (1 = very easy, 7 = very difficult). They were also asked to indicate to what extent they recalled the memory from their own eye's perspective or an observer's perspective using a 7-point scale. Additionally, participants were asked whether recalling the memory repeatedly had any impact on the memory, specifically in terms of the consistency of their recollection compared to the original event, using a 7-point scale (1 = not at all, 7 = significant impact) (Fig. S2).

The second questionnaire aimed to extract measurements related to the 4 subcomponents of SDMs. To assess the *content* component, participants rated the extent to which 4 themes (life-threatening, relationship, leisure, and achievement) best described each memory on a 7-point scale (Thorne and McLean 2001, 2002; McLean 2005; Lardi et al. 2010). To assess the *affect* component, they rated the extent to which they felt 8 emotions during memory recall (happy, sad, angry, fearful, surprised,



**Fig. 1.** Experimental design. A) Example of a self-defining memory. B) Example of a non-self-defining memory. C) Participants were instructed to recall their personal memories, prompted by a cue presented for 10 s. Following the recall period, participants rated the preceding recall trial's vividness and emotional intensity on a 1 to 4 scale. Each rating screen was presented for 4 s, followed by a 4 s interstimulus interval before the next memory recall trial.

ashamed, guilty, and interested) on a 7-point scale (Singer and Blagov 2002). To assess the *specificity* component, participants selected the duration of the event itself from 10 possible time scales (ranging from an hour to several years) and indicated the time scale they were thinking of when recalling the memory (D'Argembeau 2020; Monsa et al. 2020; Singer and Blagov 2002; Wittmann and Van Wassenhove 2009). Finally, to assess the *self-reflection* component, participants rated their level of agreement with 8 statements regarding the recollected memory on a 7-point scale (Wood and Conway 2006; statements detailed in the Supplementary Materials). The statements included the extent to which the past event had an impact on them, whether they have grown as a person since experiencing the event, and what they have learned from the event (Wood and Conway 2006).

### Calculation of dissimilarity matrices

For each participant, dissimilarity (distance) matrices in each of the 4 subcomponents (content, affect, specificity, and self-reflection) were calculated as the Euclidean distance between the participant's responses to the specific subcomponent questions (Kriegeskorte et al. 2008). Four  $10 \times 10$  dissimilarity matrices were computed between each of the 10 memories provided by the participant. All measures were normalized to the range of 0 to 1 (normalizing by maximum value).

### MRI acquisition

Participants were scanned in a 3 T Siemens Skyra MRI (Siemens, Erlangen, Germany). Blood oxygenation level-dependent (BOLD) contrast was obtained with a gradient-echo, echo-planar imaging sequence [time to repetition (TR), 2,000 ms; time to echo (TE), 32.430 ms; flip angle,  $78^\circ$ ; field of view, 192 mm; matrix size,  $96 \times 96$ ; functional voxel size,  $2 \times 2 \times 2$  mm; 72 slices, multi-band acceleration factor = 4, interleaved acquisition order; 368 TRs per run, descending acquisition order, no gap; the EPI phase-encoding direction was posterior to anterior]. In addition, T1-weighted high-resolution ( $1 \times 1 \times 1$  mm, 160 slices) anatomical images were acquired for each subject using the MPRAGE protocol [TR, 2,300 ms; TE, 2.98 ms; flip angle,  $9^\circ$ ; field of view, 256 mm].

### MRI Preprocessing

Data were preprocessed with fMRIPrep 20.2.1 (Esteban et al. 2019). For the complete preprocessing procedure, please refer to the [Supplementary Methods](#) section. Functional images were motion- and slice-time corrected, aligned to T1 anatomical images, and then warped to MNI space. Subsequent preprocessing and statistical contrasts were performed using the FMRIB Software Library (FSL version 6.0) (Jenkinson et al. 2012), Nilearn (Abraham et al. 2014), and in-house MATLAB scripts (MathWorks, version 2022a). Anatomical brain images were corrected for intensity non-uniformity, skull-stripped, and normalized to MNI space.

### Estimation of cortical responses to each stimulus

Parameter estimates were extracted for each voxel using a general linear model (GLM) that consisted of gamma-variate convolved regressors for each of the 10 predictors (one for each of the 10 memories in the participant's stimulus set). Twenty-four motion parameters were added to the GLM to eliminate motion-related noise; these parameters consisted of the 6 translation and rotation parameters, their temporal derivatives, and the squared values of the 6 parameters and their derivatives (Friston et al. 1996; Charest et al. 2018). This procedure removed variance caused by regressors of no interest and resulted in an estimate of the response of each voxel to each trial type. The resulting GLM  $\beta$  values were converted to  $t$  values using FSL contrasts (1 for each predictor and 0 for all other predictors; Misaki et al. 2010). Finally, the  $t$  values corresponding to each memory were averaged across experimental runs to obtain a single pattern for each memory (Dimsdale and Ranganath 2018).

### Multi-voxel pattern analysis (MVPA)

MVPA was performed using the CoSMoMVPA toolbox (Oosterhof et al. 2016) in MATLAB. In CoSMoMVPA, we performed a whole-brain searchlight analysis (Kriegeskorte et al. 2006) separately for each subject on the voxelwise  $\beta$ -weights (GLM). First,  $\beta$ -weights were demeaned to verify that classification could not be governed by a difference in the amount of activity by condition across all voxels (simple univariate difference). Second, a linear discriminant analysis (LDA) classifier was trained on labeled data from 7 of the 8 functional runs. Following, the trained classifier

was presented with naive data (unlabeled) from the 1 left-out run. This procedure was repeated 8 times, testing different runs each time (leave-one-out cross-validation). These cross-validated analyses were performed within overlapping spherical ROIs of 123 voxels tiling the entire brain. This yielded a whole-brain map for each participant, in which the center voxel of each ROI is assigned with a classification accuracy. To determine whether the classifier performed above chance at the group level, we used random-effects Monte Carlo cluster statistics corrected for multiple comparisons (as implemented by the CosmoMVPA toolbox; Maris and Oostenveld 2007; Oosterhof et al. 2016). Threshold-free cluster enhancement (TFCE; Smith and Nichols 2009) was used as a cluster-forming statistic. To correct for multiple comparisons, the Monte Carlo technique used by CosmoMVPA generates 10,000 null searchlight maps for each participant by performing a sign-permutation test, swapping the signs of the classification accuracy results at random at each data point (voxel). The 10,000 null TFCE maps are then constructed by randomly sampling from these null datasets to estimate a null TFCE distribution (Stelzer et al. 2013), obtaining a group-level z-score map of the classifier results. The z-score threshold was set to 2.33 ( $P < 0.01$ ), yielding clusters for memory type (SDM and non-SDM) classification. Cluster coordinate tables and region labels were generated using AtlasReader (Notter et al. 2019; <https://github.com/miykael/atlasreader>). The anatomical labels of peak searchlight coordinates were determined by the Harvard-Oxford atlas brain template distributed with FSL (<http://www.fmrib.ox.ac.uk/fsl/>, RRID:SCR\_001476; Desikan et al. 2006; Jenkinson et al. 2012).

### Comparison of scale-selective activations to large-scale resting-state networks

Next, we aimed to compare the brain activity associated with SDM versus non-SDM classification to known brain networks. Overlap was calculated between the significant voxels in the MVPA searchlight group analysis results and each of the 7 major resting-state networks as identified by Yeo and colleagues (Yeo et al. 2011; <https://surfer.nmr.mgh.harvard.edu/fswiki/CorticalParcellation>). To characterize the involvement of each resting-state network in processing SDMs, we computed the Jaccard index (intersection over union) between the group-level map and each of the 7 large-scale brain networks. The statistical significance of the overlap with each network was computed by permuting the voxel labels for the 7 networks 1,000 times and looking at the number of permutations reaching the same degree of overlap or higher.

### Representational similarity analysis (RSA)

To investigate the brain's representation of different subcomponents of SDMs, neural pattern similarities were compared with the different behavioral dissimilarity matrices using a whole-brain RSA searchlight approach (Kriegeskorte et al. 2008; Peer et al. 2021). Analyses were performed using CoSMoMVPA (Oosterhof et al. 2016) and in-house MATLAB scripts. A spherical searchlight was run by defining a sphere with a radius of 3 voxels that was moved across the brain. In each sphere location, the  $t$  values for each of the 10 memories were extracted from all voxels included in the sphere. Next, the mean activity pattern across all 10 conditions was subtracted from all activity patterns to eliminate global effects (Diedrichsen and Kriegeskorte 2017). Subsequently, for each searchlight sphere location, a  $10 \times 10$  neural dissimilarity matrix was computed between the 10 memory-specific activity patterns using Pearson's correlation. The neural dissimilarity

matrix was then compared with each of the 4 behavioral dissimilarity matrices (content, affect, specificity, and self-reflection dissimilarity matrices) using Spearman's correlation (Nili et al. 2014), resulting in a whole-brain correlation map for each matrix. Group analysis was performed for each matrix's correlation map using permutation testing (10,000 iterations) with TFCE, as implemented in the CoSMoMVPA toolbox (Smith and Nichols 2009; Stelzer et al. 2013). To identify the independent contribution of each SDM-subcomponent dissimilarity matrix, a similar RSA searchlight was performed for each of the 4 dissimilarity matrices (content, affect, specificity, and self-reflection dissimilarity matrices) using a partial correlation approach as implemented in CoSMoMVPA (regressing out from each matrix the contribution of the other 3 matrices to control for their shared variance; Parkinson et al. 2017). Group-level results were again computed using permutation testing with TFCE. Cluster coordinate tables and region labels were generated using AtlasReader (Notter et al. 2019; <https://github.com/miykael/atlasreader>). The anatomical labels of peak searchlight coordinates were determined by the Harvard-Oxford atlas brain template distributed with FSL (<http://www.fmrib.ox.ac.uk/fsl/>, RRID:SCR\_001476; Desikan et al. 2006; Jenkinson et al. 2012).

### Parametric modulation analysis

To examine how variations in the personal relevance of SDMs influenced the underlying brain network, a parametric modulation analysis using the personal relevance ratings from the post-scan questionnaire was performed. Each participant's ratings for each memory were independently normalized by the z-transform. The design matrix included 1 regressor for all memory recall events and 1 parametric regressor reflecting the normalized personal relevance ratings. Random effects group analysis was then performed using the new design matrix to identify regions in which activity was modulated by the subjective level of personal relevance of the memories.

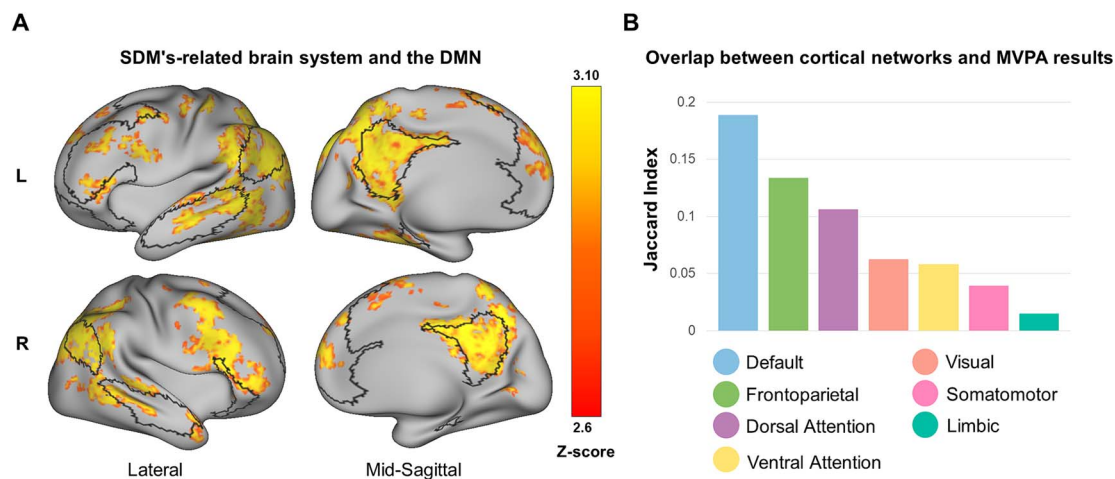
## Results

### The default-mode network is central in differentiating between SDMs and non-SDMs

Applying a classification analysis to our fMRI data identified brain regions that significantly distinguished between SDMs and non-SDMs (Fig. 2A;  $P < 0.01$ , TFCE-corrected). These regions included the precuneus, supramarginal gyrus, lateral occipital cortex, middle frontal gyrus, frontal pole, superior frontal gyrus, and paracalcarine gyrus bilaterally, the left fusiform and parahippocampal gyri, and the right temporal pole (Table S1). Next, we compared the network of brain regions as identified here with a parcellation of the brain into 7 cortical resting-state fMRI networks (Yeo et al. 2011). Specifically, we calculated the Jaccard index (intersection over union) between the group-level map and the 7 large-scale brain networks. This revealed that the default mode network (DMN), frontoparietal, and dorsal attention networks showed significant overlap with the SDM-related regions ( $P < 0.001$ , permutation test). The DMN was most dominant in its similarity to the group-level map (0.19), followed by the frontoparietal (0.13) and dorsal attention (0.10) networks (Fig. 2B).

### Partial dissociation between coding of self-reflection and content in SDMs

Similarity matrices were constructed for content, affect, specificity, and self-reflection distances between each participant's personal memories based on their subjective ratings. To measure



**Fig. 2.** The default-mode network is central in the discrimination between SDMs and non-SDMs. A) Color-coded z-score maps illustrating brain regions that discriminate between SDMs and non-SDMs ( $z = 2.33$ ,  $P < 0.01$ , TFCE-corrected). The DMN is indicated by the black line. Note the similarity between the DMN and multivariate pattern analysis (MVPA) results especially at the medial parietal cortex. B) Jaccard index (intersection over union) was calculated between the group-level map and a cortical parcellation to 7 large-scale brain networks (Yeo et al. 2011). The DMN was most dominant in its similarity to the group-level map (0.19), followed by the frontoparietal (0.13), dorsal attention (0.10) networks. Only these 3 networks showed significant overlap with SDM-related regions (permutation tests,  $P < 0.001$ ).

the independent contribution of each factor (similarity in activity explained by the unique variance of each factor, excluding the effect of the common variance), we performed an RSA searchlight using a partial correlation approach (Fig. 3; Table S2). Our findings showed that information on similarity in memories' self-reflection is encoded in regions within the lateral occipital cortex, precuneus, middle frontal gyrus, frontal pole, inferior frontal gyrus, paracingulate cortex, and superior frontal gyrus bilaterally, and the left fusiform and parahippocampal gyri (all  $P$ -values  $< 0.01$ , Monte Carlo permutation test, TFCE-corrected for multiple comparisons). To a much lesser extent, information on similarity in memories' content was found in the left angular gyrus and fusiform gyrus (all  $P$ -values  $< 0.01$ , Monte Carlo permutation test, TFCE-corrected for multiple comparisons). No region was identified to encode information on similarity in memories' affect and specificity (all  $P$ -values  $> 0.5$ , Monte Carlo permutation test, TFCE-corrected for multiple comparisons). Repeating this partial correlation searchlight RSA for each gender group separately did not yield any gender-related differences.

### Personal relevance modulates brain activity in the posterior cingulate cortex (PCC)

Parametric modulation analysis revealed a significant cluster in the left PCC where activity was positively modulated by personal relevance ratings (peak MNI coordinates:  $x: -4.5$ ,  $y: -48.5$ ;  $z: 31.5$ ; peak  $z$ -score: 4.21; cluster size: 227 voxels;  $P$ -value  $< 0.05$ , FDR-corrected).

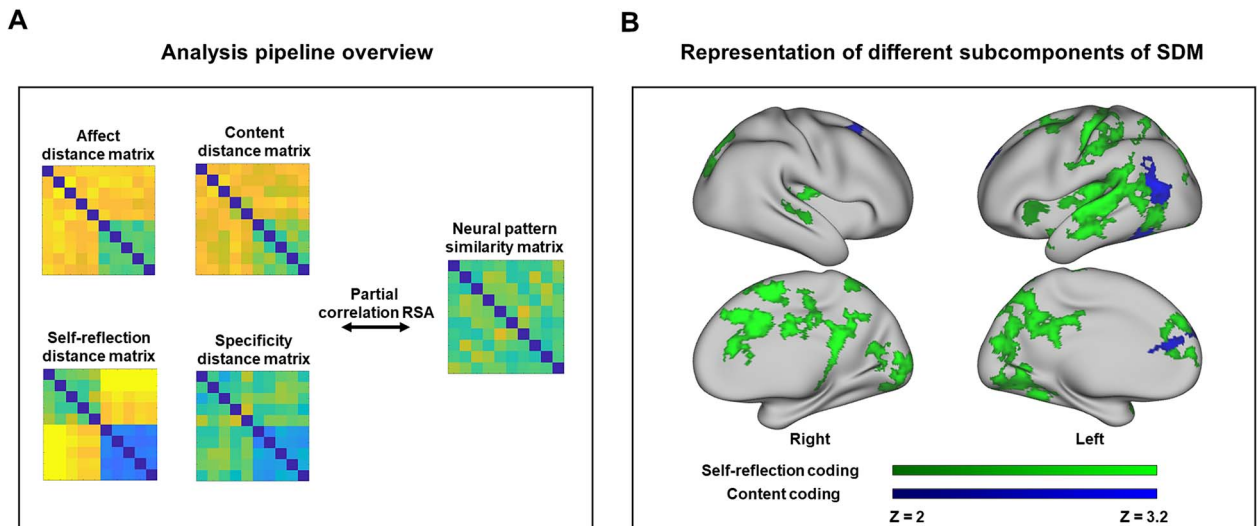
### Brain network distinguishing between SDMs and non-SDMs unaffected by emotional valence

A GLM was applied to investigate whether different brain regions are engaged according to emotional valence within the identified brain network. The model predictors corresponded to the conditions: positive, negative, and neutral with a balanced contrast between "positive" blocks and "negative" blocks. We found no brain regions that showed significantly different activation for positive compared to negative memories (threshold  $P$ -value  $< 0.05$ , FDR-corrected).

## Discussion

Investigation of SDMs under fMRI revealed several novel findings. First, a large brain network, mainly in the medial parietal cortex, temporo-parietal junction, and lateral frontal cortex, distinguished between SDMs and non-SDMs. These regions were found to overlap mostly with the medial and lateral parietal portions of the DMN, as well as the frontoparietal and dorsal attention networks. Moreover, we found that when dissociating the sub-components of SDMs, a substantial network of brain regions was found to represent information related to similarity in self-reflection. Conversely, a more limited set of regions was found to represent information on similarity in the content of the memory. We did not identify any significant voxels that represent information on similarity in the affect or specificity of the memories. Our results are discussed in the following with respect to the theoretical concept of SDMs and the involvement of large-scale brain networks.

Our findings demonstrate that activity patterns in the DMN differentiate between SDMs and non-SDMs. These results may be considered with respect to Conway's self-memory system model, which operates under the central premise that the self plays a crucial part in how memories are stored and recalled (Conway and Pleydell-Pearce 2000). Consequently, memories that lack a connection to the self or are no longer relevant to current objectives tend to be rapidly forgotten or rendered inaccessible since they are not assimilated into long-term knowledge frameworks. Conversely, memories that hold significant importance to the self and align with personal long-term aspirations may gain a heightened level of accessibility. In this sense, the DMN has been shown to play a crucial role in various cognitive processes associated with self-reflection and introspection, including retrieving autobiographical memories, thinking about or planning personal future events, engaging in self-reflection, relating information to one's self, orientation, and evaluating or reevaluating emotional information, among other related processes (Andrews-Hanna et al. 2014; Buckner et al. 2008; Raichle et al. 2001; Peer et al. 2015; Peer et al. 2021; for a recent review, see Menon 2023). Specific DMN hubs that were found in our study to discriminate between SDMs and non-SDMs include the precuneus, PCC, angular gyrus,



**Fig. 3.** Partial dissociation between representations of self-reflection and content distances. A) Similarity matrices for content, affect, specificity, and self-reflection were used in a representational similarity searchlight analysis with a partial correlation approach (regressing the contribution of other matrices from the matrix of interest) to identify the independent variance explained by each factor. The dissimilarity matrices displayed are examples from a single subject. B) Regions encoding similarity in memories' self-reflection include the lateral occipital cortex, precuneus, middle frontal gyrus, frontal pole, inferior frontal gyrus, paracingulate cortex and superior frontal gyrus bilaterally, and the left fusiform and parahippocampal gyri. Regions associated with similarity in memories' content are primarily located in the left angular gyrus and temporal occipital fusiform cortex. No regions were identified for similarity in memories' affect and specificity (RSA searchlight, spherical radius = 3 voxels, all  $P < 0.01$ , Monte Carlo permutation test, TFCE-corrected).

middle temporal gyrus, and mPFC bilaterally. These brain regions are part of the "core network" (Schacter et al. 2007; Buckner et al. 2008; Rabin et al. 2010; Long and Kahana 2015), which has been implicated in cognitive operations, such as episodic simulation of future or fictitious episodes (Benoit and Schacter 2015), and the retrieval of autobiographical memories (Spreng and Grady 2010). The involvement of the "core network" in discriminating between SDMs and non-SDMs may reflect the brain's encoding of memories that are integral to the construction of one's personal narrative identity.

Two of the four subcomponents of SDMs were found to be discernable in the underlying brain activity, namely the process of self-reflection on the memory's meaning and implications and, to a much lesser extent, the memory's content. The process of self-reflective thinking about past experiences, in which one creates connections between different life events and the self, is important to the construction of one's personal narrative identity (Habermas and Bluck 2000; McLean and Fournier 2008). The emergence of the life story during adolescence is linked to the development of a sense of identity, as it helps individuals make sense of their past experiences, understand their present situation, and envision their future goals. Over time, the life story becomes more elaborate and coherent, as individuals acquire more experiences and refine their sense of self (Habermas and Bluck 2000; McLean and Fournier 2008). One study found that the SDMs of adults over the age of 50 contain more integrative meaning compared to college students (Singer et al. 2007). However, a different study found that middle-aged adults gave more integrative meaning to SDMs compared to older-aged adults (Cuervo-Lombard et al. 2021), suggesting that the integrative meaning of SDMs peaks during midlife. A cross-cultural study that examined the differences in the 4 subcomponents of SDMs between Swiss and North American people, found that the only difference was that Swiss young adults attribute more explicit meaning to their memories, suggesting they are more engaged in autobiographical reasoning compared to their North American counterparts (Lardi et al. 2010).

Together, the Israeli young-adults tested here may have attributed more integrative meaning to their SDMs, as reflected in our results, similarly to the Swiss young adults. With respect to the brain network supporting self-reflection in SDMs, D'Argembeau et al. (2014) found that a left-lateralized network, composed of the dmPFC, inferior frontal gyrus, middle temporal gyrus, and angular gyrus was more active when participants engaged in self-reflective processes about their personal SDMs and non-SDMs. According to the researchers, this left-lateralized network has been previously implicated in semantic processing while accessing the meaning of simple non-personal words (Renoult et al. 2012). In our data, left-lateralization was not found, while comparing SDM to non-SDMs. However, we did find strong left lateralization in the lateral wall in our RSA results. In addition, higher personal relevance was found to be associated with increased activation in the left PCC during memory recall. This is in accordance with this region's involvement in the network distinguishing between SDMs and non-SDMs, as well as its role in encoding information related to self-reflection (Moran et al. 2006; Holt et al. 2011; Bluhm et al. 2012). Self-reflection may also relate to the discrimination between self and others, which has also been shown to involve considering one's past or future perspective (Arzy et al. 2008, 2009; Soutschek et al. 2016). Temporoparietal activation, as we found in the angular gyrus, was found to play a crucial role in these processes (Arzy et al. 2008, 2009; Soutschek et al. 2016; Quesque and Brass 2019; Zeugin et al. 2020). This may explain its involvement in distinguishing SDMs from non-SDMs in view of the unique self-referential nature of SDMs as shown here. Namely, SDMs often require individuals to integrate between different aspects of their life and the self, thereby linking past experiences with the present. Moreover, this process may involve shifting between different perspectives, including those of others, to validate the significance of these memories.

With respect to content, Thorne et al. (2004) found that memories considered to be the most meaning-making were memories of life-threatening or relationship-related events, while memories

of positive achievements and leisure events were considered less meaning-making. The RSA results highlighted the left angular gyrus and fusiform gyrus to be more active for the SDM's content. On the contrary, D'Argembeau et al. (2014) found that the memory content involved brain regions within the retrosplenial cortex, precuneus, amygdala, hippocampus, parahippocampal gyrus, dorsolateral prefrontal cortex, and medial orbitofrontal cortex, similar to the regions found here to be active for self-reflection. This discrepancy may be related to the different instructions given in the experiments. While D'Argembeau et al. (2014) asked participants to concentrate either on the specific content of the events or to reflect on their meaning and relation to the self, here we asked participants to vividly recall the event without explicitly addressing any SDM component. Moreover, in our study, we addressed the SDMs' content type (Thorne et al. 2004) and not the concrete content of the SDM (what the participants saw, heard, felt, etc.; D'Argembeau et al. 2014).

Affect and specificity were not found to be significant in our neuroimaging findings, surprisingly given their role in autobiographical memories (Damasio 2003; Schacter et al. 2009). Blagov and Singer (2004) have shown that achievement events are less specific, while life-threatening events are more specific, suggesting specificity to correlate with the content subcomponent (Thorne et al. 2004). Affect was also found to correlate to content, as achievement events produced more positive affect, while life-threatening events produced more negative affect. This may also explain the surprising finding regarding affect and specificity. Perhaps they serve as a proxy for self-reflection, that is higher affect and specificity may point on a higher self-reflection. Alternatively, since our analysis is based on a winner-takes-all strategy (the subcomponent that is found most relevant to the voxel's response marks the voxel), it may be the case that self-reflection yields a stronger brain response, therefore accounting for most of the involved voxels.

Theories of emotion have long proposed that our visceral sensations significantly shape and inform our experiences of life events (James 1894; Damasio 1999). These bodily responses not only influence our experiences as the events occur but also persist and impact how we remember these events (Forte et al. 2019; Sheldon et al. 2020; Bögge et al. 2022). Further, lower-level sensory processing was found to significantly influence higher-level cognitive and emotional responses (Pamplona et al. 2022). While analysis of participants' subjective trial-by-trial ratings revealed a difference in emotional intensity between the first and fifth runs, objective lower-level inputs were not recorded in this study. Future research is needed to explore how such inputs might influence the representation of SDMs and their subcomponents.

Our study is not free of limitations. First, other potential characteristics of SDMs may be important for their representation. This initial study investigated the 4 predominant components suggested by the literature (e.g. Blagov and Singer 2004; Lardi et al. 2010). Further studies may explore other potential subcomponents of SDMs and their underlying brain representation. Second, repeatedly recalling memories may have affected the SDM subcomponents; however, analyzing the post-scan questionnaire confirmed that repeated recall did not alter our participants' memories. Analysis of participants' trial-by-trial ratings revealed a decrease in both vividness and emotional intensity across experimental runs. However, these differences were observed only between the first run and subsequent runs, indicating a similar recall experience throughout most of the experiment. Finally, personal memories are associated with

other shared contextual factors, such as the people in the event (Hayman and Arzy 2021), people's role in one's life (Ron et al. 2022), or similar places or situations. Thus, we cannot rule out an interaction of other contextual factors with the coding of the subcomponents.

In conclusion, this work demonstrates that the brain processing of SDMs is markedly different from that of non-SDMs. SDM's underlying brain system was found to be closely related to the DMN. Moreover, our brain-based approach demonstrated dissociable coding of different subcomponents of SDM in different brain regions. Specifically, *self-reflection* was found to be represented in extensive brain regions, suggesting it is a crucial factor in the formation and maintenance of SDMs. The *content* subcomponent was shown to play a more minor role, while the subcomponents of *affect* and *specificity* did not elicit any evident brain regions for SDMs as compared to non-SDMs. Taken together, these results highlight the importance of SDMs in autobiographical memory, calling for extensive research of the relation between self-referential processing and autobiographical memories (Conway and Pleydell-Pearce 2000). Finally, our study invites further efforts to the neuroscientific exploration of significance and significant life-events as processed in the neurocognitive system (Kringelbach et al. 2024).

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## Author contributions

Rotem Monsa (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing—original draft, Writing—review & editing), Amnon Dafni-Merom (Visualization, Writing—original draft, Writing—review & editing), and Shahar Arzy (Conceptualization, Supervision, Writing—original draft, Writing—review & editing).

## Supplementary material

Supplementary material is available at *Cerebral Cortex* online.

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