Retrieval orientation alters neural activity during autobiographical memory recollection

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A B S T R A C T

When an autobiographical memory is retrieved, the underlying memory representation is constructed by flexibly activating a broad neural network. As such, the content used to reconstruct a memory can bias activity within this neural network. Here, we tested the hypothesis that focusing on the conceptual and contextual aspects of a memory to construct a memory representation will recruit distinct neural subsystems. To test this hypothesis, we measured neural activity as participants retrieved memories under retrieval orientations that biased remembering towards these elements of a past autobiographical experience. In an MRI scanner, participants first retrieved autobiographical memories and then were re-oriented towards the conceptual or contextual elements of that memory. They then used this re-oriented content (conceptual or contextual elements) to access and elaborate upon a new autobiographical memory. Confirming our hypothesis, we found a neural dissociation between these retrieval orientation conditions that aligned with established models of memory. We also found evidence that this neural dissociation was most prominent when the re-oriented mnemonic content was used to access a new memory. Altogether, the reported results provide critical insight into how and when retrieval orientations alter neural support for autobiographical memory retrieval and inform on the neural organization of autobiographical knowledge.

1. Introduction

Autobiographical memories are mental representations of past experiences that are reconstructed at retrieval (Schacter and Addis, 2007; Schacter, 2012; Sheldon and Levine, 2016). These memories are richly detailed and contain a diverse array of information – including sensory perceptual and contextual event (episodic) details as well as factual knowledge associated with a particular event (semantic details; Tulving, 1983). Autobiographical memory construction relies upon a distributed network of brain regions that includes the hippocampus, medial prefrontal, middle and lateral parietal as well as temporal regions to access this content (Svoboda et al., 2006). While it is known that the hippocampus is critical for associating together the various details of an experience into a memory representation (Moscovitch, 1992; Winocur and Moscovitch, 2011), considerably less is known about how these details (i.e., memory content) are represented within this greater neural network.

One theory is that there are distributed functional neural subsystems prioritized to process specific episodic components of a remembered event, such as subsystems that support accessing the general concept of

what happened to the contextualized details of the remembered environment (Cabeza and Moscovitch, 2013; Sheldon et al., 2019). Support for these subsystems comes from research examining neural support during internally-directed cognitive tasks – those that involve directing cognition towards self-generated thoughts and memories rather than information present in one's external environment (Dixon et al., 2014). These tasks typically activate the default network (DN) – a resting-state network that overlaps considerably with the autobiographical memory network (Buckner et al., 2008; Spreng and Grady, 2009). When internally-directed tasks are directed towards processing conceptual and contextual information, there is evidence that dissociable subsystems within the DN will be active (n.b., other resting state subsystems have been proposed, see Lee et al., 2012). The dorsal medial subsystem comprised of the dorsal medial prefrontal cortex (dmPFC), temporal pole, lateral temporal cortex, and temporoparietal junction processes self-referential and conceptual information and is engaged during evaluative decision-making. The medial temporal subsystem comprised of the hippocampal formation, parahippocampal cortex, retrosplenial cortex, posterior inferior parietal lobule, and ventrolateral prefrontal cortex (vmPFC) processes contextualized information that critically supports

episodic memory (Andrews-Hanna et al., 2010; Andrews-Hanna et al., 2014).

The above-reported division within the DN parallels research that has reported distinct medial temporal lobe (MTL) subsystems for accessing conceptual and situational (i.e., contextual) elements of learned stimuli (Ranganath and Ritchey, 2012; Reagh and Ranganath, 2018). Specifically, there is a memory system that is activated for recalling the conceptual and semantic content of a past episode (an anterior subsystem including the perirhinal, temporopolar, and lateral orbitofrontal cortices) and one for recounting the specific situational context associated with an event (a posterior medial subsystem including the parahippocampal cortex, retrosplenial cortex, vmPFC, precuneus, and angular gyrus; Ranganath and Ritchey, 2012).

We recently proposed a framework (Sheldon et al., 2019) positing that these dissociable systems are engaged during different forms of episodic autobiographical remembering. This framework was based on a prominent theory for autobiographical memory organization in which the conceptual and the contextualized aspects of an event are organized at different 'hierarchical levels' within one's autobiographical knowledge base (Conway, 2001, 2009; Conway and Pleydell-Pearce, 2000). However, with our framework, we suggest that these different aspects of an event are stored at the same level and can co-exist rather than being nested within one another as described in the original model. With a non-hierarchical structure, distinct episodic memory representations of the same autobiographical experience can be built as a function of the relative weight assigned to conceptual (i.e., event-based) versus contextual (i.e., perception-based) event-specific knowledge accessed from one's autobiographical knowledge base (see Fig. 1). This weighting will thus determine how dissociable conceptual and contextual neural networks are recruited during remembering.

We propose that the bias towards these conceptual and contextual neural networks during autobiographical remembering can be determined by a person's retrieval orientation – a retrieval goal-state that is defined by a particular cue to probe a memory (Herron and Rugg, 2003; Morcom and Rugg, 2012). Retrieval orientation effects have been well-established with laboratory-based memories that manipulate orientation by altering the cues used to reactivate memory representations and have shown how retrieval orientation changes the engaged cognitive (Rugg and Wilding, 2000) and neural processes (e.g., Herron, 2018; Herron et al., 2016; Herron and Rugg, 2003; Morcom and Rugg, 2012; Robb and Rugg, 2002; Rugg and Wilding, 2000). This line of work has shown that retrieval orientations biased towards certain modalities

(words, pictures) can change the underlying cognitive and neural processes engaged (e.g., Herron and Rugg, 2003). In addition, findings have shown that retrieval orientations biased towards certain features of studied items, such as the conceptual versus perceptual aspects of those items, also relate to distinct neural correlates during retrieval (e.g., Stenberg et al., 2006). This latter body of work aligns with the conceptual and contextual aspects of autobiographical memories and the finding that a conceptual retrieval orientation relied on anterior aspects of the brain and the perceptual retrieval orientation relied on more posterior aspects of the brain (Stenberg et al., 2006) fits with the proposed distinctions within the autobiographical memory neural network.

In this study, we aimed to test if autobiographical memories retrieved with an orientation biased towards conceptual versus contextual event details will result in dissociations in brain activity. In testing for these dissociations emerging from one's retrieval orientation during autobiographical memory retrieval, we considered additional factors that influence the neural support of autobiographical memory retrieval. One factor that may influence how retrieval orientation affects brain activity is the age of a recollected autobiographical memory (Nadel et al., 2007; Squire et al., 2004). Although evidence favours the view that the same brain systems are needed to construct detailed recent and remote memories (Nadel et al., 2007; Winocur and Moscovitch, 2011), it is not clear if memories from different life periods are modified by retrieval orientation in the same way. Another factor we consider is when during the memory retrieval process retrieval orientation effects are most pronounced – i.e., when retrieval orientation specifies how a memory representation must be initially built or when retrieval orientation updates an existing memory representation. There is evidence that retrieval makes a underlying memory representation malleable and more open change (Alberini, 2011; McKenzie and Eichenbaum, 2011; Nader and Hardt, 2009; Sara, 2010). If this is the case, then retrieval orientation effects should manifest most robustly when reconstructing a memory representation for an already-recalled memory – as this representation will be more labile and susceptible to change – than when constructing a memory representation for a newly-accessed memory. Alternatively, if retrieval orientation effects primarily influence how a memory is cued (Herron and Rugg, 2003), then orientation effects should present most strongly when retrieval orientation specifies how a new memory representation should be initially constructed.

We designed a novel functional magnetic resonance imaging (fMRI) experiment to specify the effect of retrieval orientation on the neural mechanisms of episodic autobiographical memory retrieval and to
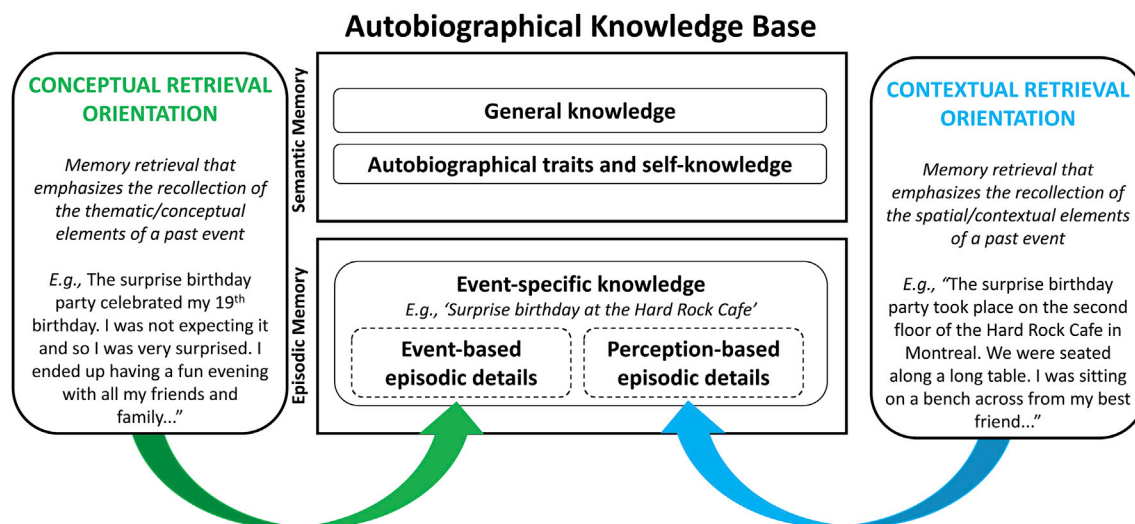

Fig. 1. A schematic of the proposed framework (Sheldon et al., 2019) in which different aspects (i.e., conceptual/event-based and contextual/perception-based details) of an event are simultaneously stored within episodic memory and how retrieval orientation can bias the episodic event-specific mnemonic content that is retrieved from one's autobiographical knowledge base (extending from the autobiographical memory organizational model by Conway, 2001).

determine if this effect depends on a.) the age of the autobiographical memory and b.) the stage of memory retrieval. In the scanner, participants recalled twelve pre-selected recent and remote autobiographical memories equated for a number of subjective ratings (vividness, emotionality, importance, and rehearsal) under conceptual and contextual retrieval orientation conditions that included four sequential retrieval phases (see Fig. 2): (1) recollecting the autobiographical memory without any orientation cue (*full recollection*); (2) re-orienting to the conceptual (the theme/purpose of the event) or contextual (the placement of people and things in the location) elements of that memory (*re-oriented recollection*); (3) accessing a new and related memory using these conceptual or contextual elements from the recollected memories phase (*new memory access*); and (4) recollecting the conceptual or contextual elements of this new memory (*oriented recollection*). In this way, our retrieval orientation manipulation was carried out at two separate timepoints during the retrieval process – first, this manipulation was introduced after an unbiased memory representation had already been established (re-oriented recollection) and, second, the manipulation was introduced prior to the memory representation being built (oriented recollected) – allowing us to establish when during the memory recollection process retrieval orientation exerts the strongest influence on brain activity. Thus, the overall goal of our manipulation was to shift the relative emphasis of the conceptual versus contextual details retrieved when constructing a mental representation for a past event. Specifically, our prediction was that forming a memory representation with more contextual details (i.e., with a contextual retrieval orientation) would activate regions that support visuo-spatial component processes and forming a memory representation with more conceptual details (i.e., with a conceptual retrieval orientation) would activate regions that support schematic and value-based component processes. We further predict that these dissociations will be apparent for both recent and remote memories yet be most robust when orienting within an already-accessed memory (i.e., re-oriented recollection), provided that the latter will require more episodic memory constructive processes to allow one to revise and reconstruct an updated representation specified by the retrieval orientation. Univariate and multivariate analytic approaches were taken to identify regional activation differences and network variability differences related to retrieval orientation, respectively.

2. Methods

2.1. Participants

Twenty-eight participants were recruited to participate. Data from four participants were excluded from our analyses due to indications of anxiety while in the scanner (n = 1) or failure to comply with the task instructions (n = 3). The analyzed dataset included 24 right-handed participants (females = 17; mean age = 21.34 years, SD = 3.3; mean education = 15.26 years; SD = 2.18). All participants had normal or corrected-to-normal vision and were free of any medical conditions, neurological conditions, or contraindications for fMRI experimentation. All experimental procedures were approved by the McGill University Ethics Board and written informed consent was collected from all participants prior to testing. Participants were compensated for their time.

2.2. Procedure

2.2.1. Pre-scan autobiographical memory generation

At least 24 h prior to the scanning session, participants provided a list of at least 10 recent (previous 6 months) and 10 remote (5–10 years ago) autobiographical memories (personal events that occurred at one time and in one specific location). For each memory, participants provided a short event caption (e.g., 'Thanksgiving dinner with my boyfriend's family'), the specific date and location of the event, and ratings on a 6-point Likert scale of vividness (i.e. how vividly they remembered that even), emotionality (i.e., was the event happy or sad), importance (i.e., how important the event was to them), and rehearsal (i.e., how often they thought about the event). For each participant, we selected the six recent and six remote events that were best matched along these dimensions to be used as experimental stimuli in the fMRI experiment.

2.2.2. Scan session

Prior to scanning, the experimenter went over detailed instructions about the format of the experiment and participants completed three practice trials. During the first practice trial, the experimenter gave an example of how to complete the task using a hypothetical event for both experimental conditions (i.e., conceptual and contextual); all participants
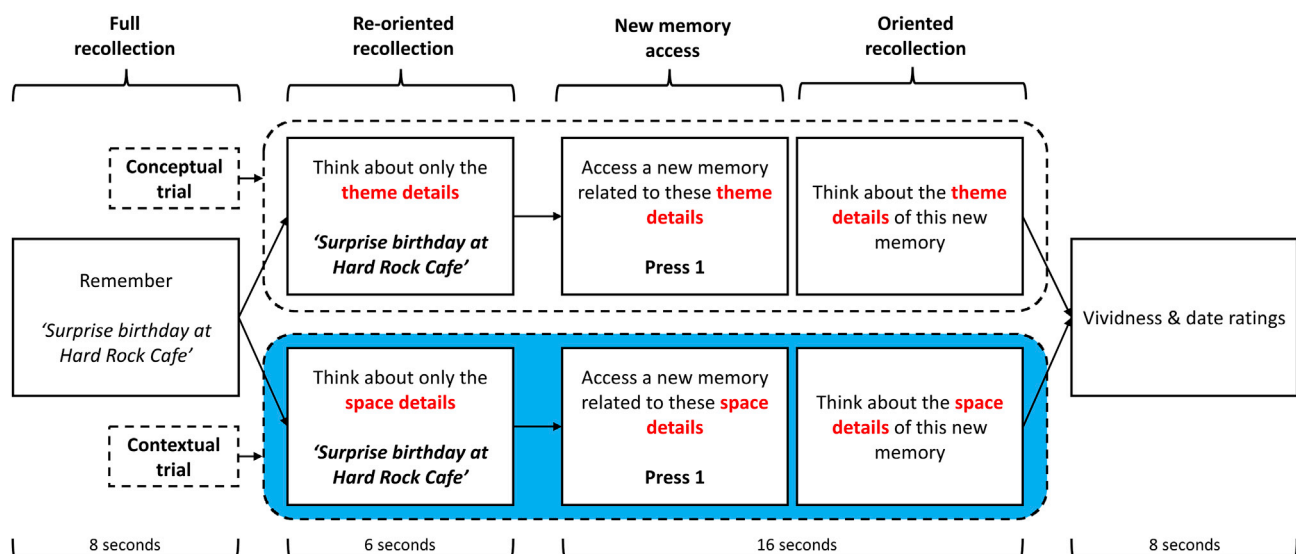

Fig. 2. A schematic of the progression of the experimental trials. First, participants are shown a descriptive title of one of their autobiographical memories (e.g., 'Surprise birthday at Hard Rock Cafe') and are instructed to re-experience this event in as much detail as possible by thinking about all the details and images associated with the event (full recollection). Second, participants are instructed to only think about a particular aspect of that memory – theme details for conceptual trials and space details for contextual trials (re-oriented recollection). Third, participants are instructed to use the details from the re-oriented recollection to think of a new, related past event as quickly as possible and indicate with a keypress when they have a new event in mind (new memory access). Fourth, participants are now instructed to think about the theme (conceptual trial) or the space (contextual trial) details of this new memory (oriented recollection).

received the same practice event ('Birthday dinner with grandma'). Next, participants completed two additional practice trials with events chosen from their list of unused autobiographical memories (collected from the pre-scan autobiographical memory generation phase) during which they received performance feedback from the experimenter. These two trials were randomly assigned to the conceptual and the contextual conditions such that all participants completed an example trial for each of the experimental conditions with their own personal memories, exactly as they would be completing them in the scanner.

In the scanner, participants completed six functional runs (four conceptual trials, four contextual trials, and two control trials per run). During each run, eight of the twelve pre-selected autobiographical memories were recalled with half appearing in conceptual trials and the other half appearing in contextual trials. The same memory never appeared more than once within a single run. Both experimental trials began with a trial cue ('Remember') that remained on the screen for 1000 ms. The trial then moved into the three phases of remembering. First, participants saw one of their generated event captions on the screen (e.g., 'Surprise birthday at Hard Rock Cafe') and were given 8 s to silently elaborate on all the details of the event (*full recollection*). Second, participants then focused primarily on the conceptual or contextual details of the retrieved memory for 6 s (*re-oriented recollection*; see Appendix A for specific instructions given to participants). Here, we note that the primary aim of our experimental manipulation was not to induce mutually-exclusive forms of remembering. Rather, the aim of this manipulation was to shift the relative emphasis of the contextual and conceptual details used to construct a memory representation such as to bias retrieval towards conceptual versus contextual event-specific details. Thus, for conceptual trials, participants preferentially focused on the gist or overall theme of the memory (e.g., 'The surprise birthday party celebrated my 19th birthday. I was not expecting it and so I was very surprised. I ended up having a fun evening with all my friends and family.'). For contextual trials, participants preferentially focused on the specific spatial-perceptual details of the memory (e.g., 'The surprise birthday party took place on the second floor of the Hard Rock Cafe in Montreal. We were seated along a long table. I was sitting on a bench across from my best friend.'). Third, participants used the recovered conceptual or contextual details of the retrieved memory to access another past personal event (16 s; e.g., conceptual trial: 'Waiting with family and friends to surprise my cousin for her 23rd birthday'; contextual trial 'Buying a white sweater from the Hard Rock Cafe in New York City'), indicating with a key press when this memory was accessed. Fourth, participants were now asked to elaborate on the conceptual or contextual details of this new memory ('We were all anxiously waiting for my cousin's arrival and discussing the possibility of her not liking the surprise and being mad'; contextual trial 'My family and I were walking around Time Square and stumbled upon the Hard Rock Cafe. We all went in and I bought a sweater'). All trials ended with a vividness rating in which participants indicated how vividly they recalled the new oriented memory (6-point Likert scale) and a date rating (4-point Likert scale) in which the participants indicated when this new memory took place. The control condition was an odd/even number detection task in which participants were shown a series of numbers (0–9) for 45 s. For each number, participants silently determined if the presented number was an odd or even number.

2.2.3. fMRI data acquisition

Images were acquired using a 3T Siemens Magnetom Trio MRI scanner with a 32-channel head coil located at the Montreal Neurological Institute (Montreal, QC). Anatomical scans were obtained using a three-dimensional, T1-weighted, gradient-echo sequence (MPRAGE protocol; 176 1.0 mm thick sagittal slices, TR = 2200 ms; TE = 2.98 ms; FA = 9°). Functional images were obtained using T2-weighted gradient echo, echoplanar imaging (EPI) sequence (TR = 2200 ms; TE = 2.98 ms). Forty-two interleaved slices (voxel size = 3.5 mm × 3.5 mm x 3.5 mm) were collected for each functional run.

2.2.4. Post-scan session

Immediately after the completion of the scan, participant completed a post-scan interview outside of the scanner. In random order, they were presented with each of the event captions that were used as stimuli in the in-scanner experiment on a computer screen. For each caption, participants were asked to describe the associated event aloud in as much detail as possible and were given up to 3 min to do so. After describing each memory associated with the event caption, participants were then asked to generate a list of the new memories they could remember accessing in the scanner (i.e., oriented memories). The post-scan interviews were audio-recorded and transcribed. These data were used to verify that participants were accessing specific details from a personal event during the experiment.

2.3. fMRI preprocessing and statistical analyses

Data were preprocessed and analyzed using Statistical Parametric Mapping (SPM12; Welcome Trust Centre for Neuroimaging, London, United Kingdom). Realignment, unwarping, slice-timing correction, spatial normalization to Montreal Neurological Institute (MNI) space, and spatial smoothing using Full Width at Half Maximum (FWHM) of the Gaussian smoothing kernel (8 mm) were applied to the images. The associated brain regions from our analyses were identified based on the MNI coordinates obtained from SPM and using the Multi-Image Analyses GUI image processing and viewing software (Mango; http://ric.uthscsa.edu/mango/mango.html) and with reference to a MNI atlas.

A general linear model (GLM) approach, using a model of the canonical hemodynamic response function (HRF), was applied to the data to model our task regressors of interest (for details, see Inline Supplementary Table 1a). Each regressor was defined based on the duration that the participant was instructed to think of event details of a memory (re-oriented recollection) or indicated with a button press that they had retrieved a related memory (oriented recollection) and lasted until the end of the trial. This model also included regressors that were not of interest, which were time points associated with the cue presentation, in-scanner ratings, and six motion-related regressors.

A conjunction analysis using AFNI's (Analysis of Functional Neuro-Images; Cox, 1996) 3dcalc procedure was run to verify that the conceptual and contextual conditions were recruiting the core autobiographical memory network (Schacter et al., 2012; Svoboda et al., 2006). We contrasted conceptual and contextual trials separately with the control task (i.e., odd/even number detection task) and thresholded the resulting contrast to identify voxels that were significantly active above T = 1.93 ($p = .03$) to create a conjunction map that identified voxels commonly active at a threshold of $p < .001$. A flexible factorial model analysis with two within-subjects factors – memory retrieval stage (re-oriented and oriented memories) and retrieval orientation (contextual and conceptual) – tested for differences in the hemodynamic blood-oxygen-level dependent (BOLD) response associated with these factors.

AFNI's 3dClustSim and 3dFWHMx procedures were used to establish a minimum cluster extent of 82 voxels to correct for multiple comparisons made across the whole brain with a primary voxel-level threshold of $p = .001$ and alpha = 0.05. Following the flexible factorial model analysis, we ran a series of second-level one sample t-tests that contrasted neural activity for our contrasts of interest. We contrasted whole-brain activity associated with the contextual and conceptual trials during the re-oriented recollection separately for recent or remote memory trials. A second set of contrast were run with the oriented memories.

Following these univariate analyses, we conducted a multivariate analysis using partial least squares (PLS; Krishnan et al., 2011; McIntosh et al., 1996; McIntosh and Lobaugh, 2004) analysis. PLS is a data-driven multivariate analysis technique which assesses the relationship between measured neural activity and an experimental design. This technique uses singular value decomposition (SVD) to extract latent variables (LVs) which define patterns of neural activity that covary across the specified conditions. A block design approach was taken to define the data

matrices for our conditions of interest (for details, see Inline Supplementary Table 1b), meaning that activity corresponding to each block (i.e., condition of interest) was averaged across all runs. First, permutations tests (500 permutations) were run to determine the significance of the identified LVs. Second, salience scores are calculated for each voxel as a metric for how reliably the pattern determined by the LV is represented in that voxel with bootstrap estimates (300 iterations) of the standard errors. The reported results were thresholded such that neural activity within clusters of at least 15 voxels and with a bootstrap ratio (salience/standard error) of ± 2.8 (approximately equal to p < .0051) were considered for interpretation. We report the results of two mean-centered blocked task PLS analyses and one mean-centered event-related task PLS analysis. Our first blocked analysis focused on exploring the patterns of neural activity during memory elaboration associated with our retrieval orientation manipulations during both our re-oriented recollection and oriented recollection (after the button press) phases. Following-up on the findings from this analysis, our event-related analysis investigated the time course of our retrieval orientation effects across the length of our experimental trials. Lastly, our second blocked analysis focused on investigating how re-orienting the construction of a memory to converge onto conceptual versus contextual elements diverges from a more unconstrained or naturalistic form of remembering.

3. Results

3.1. Behavioural results

The average of the in-scanner ratings (vividness, date categorization) and reaction times for the oriented memories were examined with separate repeated measures ANOVA with retrieval orientation (conceptual versus contextual) and memory age (recent versus remote) as factors. None of main effects of retrieval orientation were significant (vividness: $F(1, 22) = 0.795$, $p = .382$; date categorization: $F(1, 22) = 0.082$, $p = .778$; reaction time: $F(1, 23) = 1.930$, $p = .178$). The main effect of memory age was significant for vividness ($F(1, 22) = 24,936$, $p < .001$) and date categorization ($F(1, 22) = 90.478$, $p < .001$), but not reaction time ($F(1, 23) = 1.194$, $p = .286$). Participants generated new memories (i.e., oriented memories) that were rated as less vivid and were older for trials that began with a remote memory as compared to trials that began with a recent memory. There were no significant interaction effects between these factors. See Inline Supplementary Table 2 for average ratings.

3.2. fMRI results

3.2.1. Common patterns of activity

The conjunction analyses between the contextual and conceptual conditions revealed overlapping clusters in structures of the core autobiographical memory network. This included the medial temporal (bilateral fusiform gyri, parahippocampi, and hippocampi), lateral temporal (bilateral middle and superior temporal gyri), frontal (bilateral inferior and middle, and superior frontal gyri), cingulate (anterior and posterior gyri), and parietal (bilateral lingual gyri, inferior and superior parietal lobules) cortices. This analysis confirmed that our task was engaging autobiographical memory processes.

3.2.2. Distinct patterns of activity

The flexible factorial analyses (See Inline Supplementary Table 3 for detailed reporting of significant activity) that included both retrieval orientation condition (conceptual vs. contextual) and memory retrieval stages (re-oriented vs. oriented memories) revealed a main effect of both factors. The effect of retrieval stage was associated with large clusters of activity that centered on bilateral posterior parietal cortex (clusters with peak activity in the left precuneus and right cuneus) and left frontal cortex (clusters with peak activity in the precentral and superior frontal gyri). The effect of retrieval orientation was associated with distributed

cortical activity centering on the bilateral medial temporal lobes (clusters with peak activity in the left fusiform gyrus and right parahippocampus) as well as activity centered on posterior regions (clusters with peak activity in the left precuneus and bilateral inferior parietal lobules and bilateral posterior cingulate cortices). There was also an interaction between the factors that was evident in regions typically associated with the autobiographical memory network. These regions included the MTL as well as posterior cortical areas (clusters with peak activity in the right superior occipital gyrus and right inferior parietal lobule) and bilateral frontal regions (clusters with peak activity in the bilateral middle frontal gyri and right inferior frontal gyrus). Based on this interaction effect, we contrasted activity for the two retrieval orientation conditions for the two memory retrieval stages independently.

3.3. Univariate analyses

3.3.1. Orientation effects during re-oriented recollection

We contrasted whole-brain neural activity at a group level between our two retrieval orientation conditions across recent and remote memory trials as an initial analysis revealed no differences in brain activity between these trials. Regions preferentially involved in the contextual compared to the conceptual condition included posterior brain regions (clusters with peaks in the bilateral posterior cingulate cortices (PCC) that extended into the precuneus; the right inferior parietal lobule), the MTLs (clusters with peaks in the bilateral parahippocampal gyri (PHG) that extended into the fusiform gyri, the right inferior and middle temporal gyri, and left middle frontal gyrus). Regions preferentially active for the conceptual compared to the contextual condition included the left superior frontal gyrus, left precentral gyrus, and inferior frontal gyri as well as the left cingulate cortex and lateral temporal lobe regions. See Fig. 3a and Inline Supplementary Table 4.

3.3.2. Orientation effects during oriented recollection

Regions preferentially active for the contextual compared to the conceptual condition included the bilateral middle frontal gyri, left superior occipital gyrus, left superior parietal lobule, and right inferior parietal lobule as well as the left fusiform gyrus (extending into the PHG) and right PHG. Regions preferentially active for the conceptual compared to the contextual condition included the left superior frontal gyrus (a cluster that extended into the right superior and bilateral middle frontal gyri) and lateral frontal brain regions (peaks in the bilateral superior frontal gyri). See Fig. 3b and Inline Supplementary Table 5.

3.4. Multivariate analyses

A mean-centered blocked task PLS analysis that included the experimental factors of retrieval orientation (conceptual and contextual), memory age (recent and remote), and retrieval stage (re-oriented and oriented) revealed two significant latent variables (LVs). The first LV distinguished between the stage of retrieval, irrespective of orientation or memory age (p < .001, 58.42% of the crossblock covariance). Oriented recollection was associated with a brain pattern that included the bilateral superior and middle temporal gyri and middle frontal and cingulate cortex, the left supramraginal gyrus and caudate and the right parietal lobule, pre- and postcentral gyri, and MTL, namely anterior aspects of the hippocampus (warm colors in Fig. 4, top). Re-oriented was associated with the bilateral insula and precuneus/cuneus, the right superior parietal lobule, cingulate gyrus as well as the left lingual gyrus and middle/superior temporo-frontal cortex (cool colors in Fig. 4, top). See Inline Supplementary Table 6 for full reporting of clusters. The second significant LV distinguished the orientation conditions during the re-oriented recollection stage (p < .001, 18.23% of the crossblock covariance). The contextual orientation trials were associated with activity that included the right superior occipital gyrus, precuneus, inferior parietal lobules, superior frontal cortex, ventromedial prefrontal cortex (VMPFC), the PCC as well as the left PHG (warm colors in Fig. 4, bottom). The conceptual
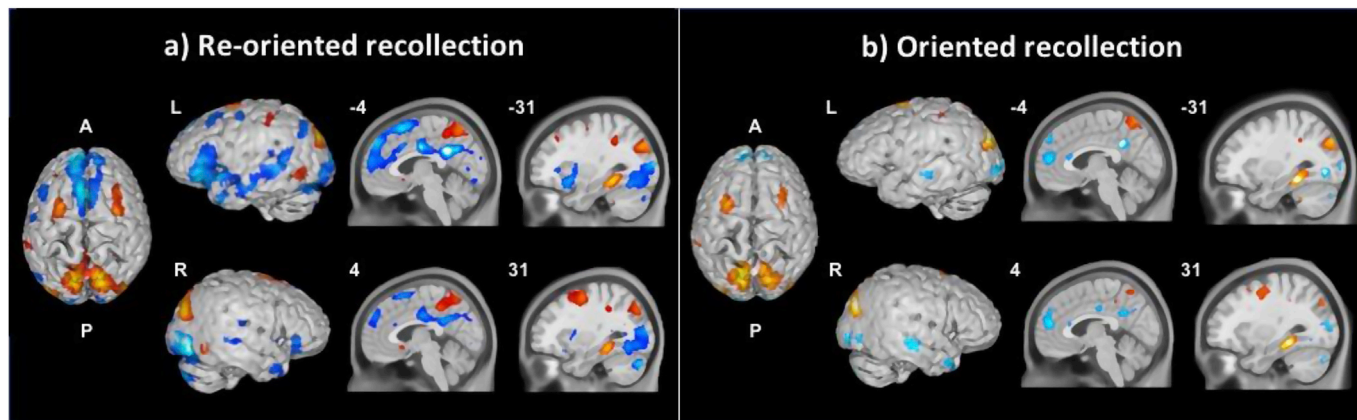
Fig. 3. Results from the univariate analysis contrasting neural activity during the contextual (warm colors) and conceptual (cool colors) retrieval orientation trials for a) re-oriented recollection and b) oriented recollection. Images are thresholded at p < .005 and k > 82 voxels. Note: A = anterior, P = posterior, L = left, R = right.

orientation trials were associated with common activity in the right superior temporal and inferior parietal lobule, the left inferior frontal, insula and cingulate gyrus and the bilateral superior and middle frontal as well as occipital cortices (cool colors in Fig. 4, bottom). See Inline Supplementary Table 7 for full reporting of clusters.

To follow-up on these results, we conducted a mean-centered event-related PLS analysis to disentangle the effects of our tested retrieval orientations from temporal effects. For this analysis, we modelled the trials associated with our two retrieval orientations (conceptual and contextual), separately for recent and remote memories, resulting in 4 event types (recent conceptual trials, recent contextual trials, remote conceptual trials, and remote contextual trials) modelled from the timepoint at which our initial retrieval orientation manipulation was introduced (i.e., the beginning of re-oriented recollection) to the end of the trial (total duration ∼ 22 s; 10 lags). One significant LV was identified (p < .001, 65.70% of the crossblock covariance) revealing a pattern of distinct activity associated with the conceptual and contextual retrieval orientations, irrespective of memory age, that aligned with the patterns identified by LV2 of the above-reported blocked PLS analysis (Fig. 5A, right panel, See Inline Supplementary Table 8 for full reporting of clusters). The temporal brain scores indicated that this dissociation was maximally expressed at lag 4 (Fig. 5B), which corresponds to the new memory access phase of the trials, suggesting that the effect of retrieval orientation is predominantly driven by processes used to probe a memory. The plot of the temporal brain scores further suggests that the pattern of neural activity for the contextual trials is maintained from the new memory access phase into the oriented retrieval recollection phase (i.e., into lags 6–9).

Finally, we ran a mean-centered blocked task PLS analysis that included the initial full recollection phase – when participants were recollecting autobiographical memories without a retrieval orientation – and the stage in which the retrieval orientations were introduced (re-oriented recollection phase). This resulted in two significant LVs. The first LV distinguished the full recollection phase from the re-oriented recollection phase across orientation condition and memory age (p < .001, 57.81% of the crossblock covariance; see Fig. 6 (top) and Inline Supplementary Table 9). The second LV (p < .001, 26.55% of the crossblock covariance) established common activity between the full recollection phase and the contextual orientation condition, primarily in MTL (e.g., left PHG) and frontal regions (cool colors in Fig. 6, bottom) and a dissociated activity pattern for the conceptual condition that included frontal, parietal, and lateral temporal regions (warm colors in Fig. 6, bottom). See Inline Supplemental Table 10 for full reporting of clusters.

4. Discussion

Retrieving an episodic autobiographical memory is a constructive act

that requires flexibly forming mental representations of past events (Bartlett, 1932; Tulving, 1983, 2002). This construction requires accessing separately-stored episodic event-specific information at the time of retrieval, from the conceptual meaning of the event to the sensory-perceptual contextual elements of the experience (Conway, 2001), which are predicted to be supported by distinct neural processes (e.g., Sheldon et al., 2019). Here, we investigated if emphasizing these different types of information during retrieval (i.e., by manipulating retrieval orientation) altered the underlying neural activity associated with reconstructing the same autobiographical experience.

Participants retrieved pre-selected autobiographical memories – events that occurred at one time and in one place (Tulving, 2002) – under two retrieval orientation conditions while undergoing an fMRI scan. In one condition, they recalled these events by focusing on associated thematic (i.e., conceptual retrieval orientation condition) episodic details. In another condition, they recalled these events by focusing on the perceptual-spatial (i.e., contextual retrieval ordination condition) episodic elements of the memory. With this condition manipulation, we tested the prediction that an individual's retrieval orientation will lead to predictable changes in neural activity (Robin and Moscovitch, 2017; Sheldon and Levine, 2016). In confirmation, we found the conceptual orientation condition engaged a broad and distributed network of brain regions, particularly in lateral temporal, superior frontal, and medial prefrontal regions whereas the contextual orientation condition concentrated activity on medial temporal (e.g., parahippocampal cortices) and posterior brain areas (e.g., posterior cingulate cortices and precuneus).

Our experiment included personalized event cues from different time periods in the participant's life. This allowed us to show that retrieval orientation similarly influenced the neural support for recent and remote autobiographical memories. This finding is consistent with the Multiple Trace Theory (MTT; Nadel and Moscovitch, 1997; Nadel et al., 2000; Winocur and Moscovitch, 2011) that suggests that richly contextualized memory recollections from all time periods are supported by similar underlying neural mechanisms (Gilboa et al., 2004; Steinvorth et al., 2005; Viard et al., 2007).

The reported distinctions between the conceptual and contextual retrieval orientation conditions align with those identified within resting-state subsystems and during laboratory-based memory tasks. First, our findings map onto neural dissociations established within two subsystems of the default network (DN), a network that shares considerable neural resources with autobiographical memory (Andrews-Hanna et al., 2010; Buckner et al., 2008; Spreng and Grady, 2009; Spreng et al., 2009). The pattern associated with the contextual retrieval orientation condition resembles the medial temporal DN subsystem, which has been implicated in processing situational (contextual) aspects of mental
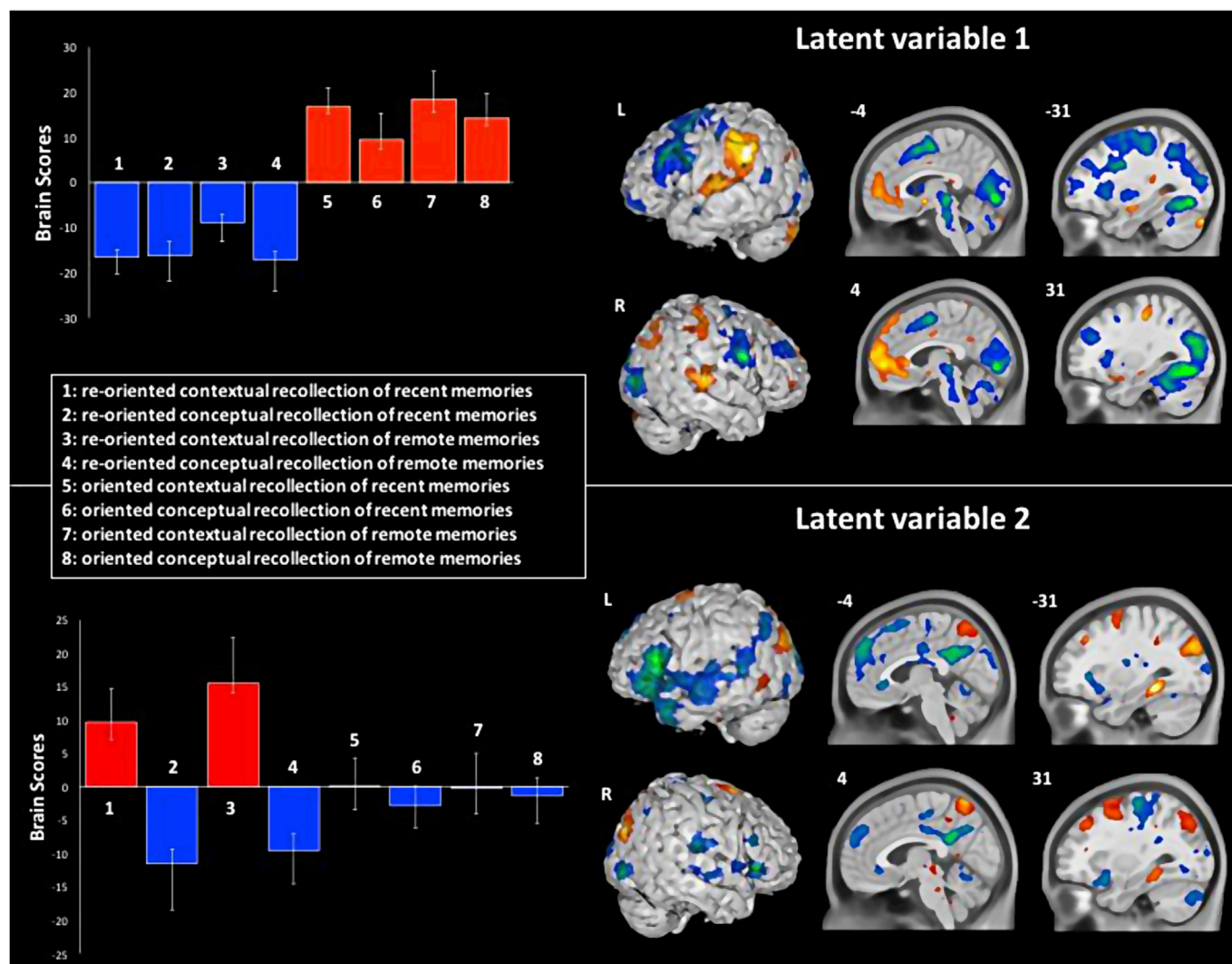
Fig. 4. Brain scores (left; group average brain scores are shown with 95% confidence intervals) and activity patterns (right) of a mean-centered blocked PLS that included the re-oriented recollection and oriented recollection phases for recent and remote memories under the tested retrieval orientation conditions. The top panel illustrates the first significant latent variable (LV; $p < .001$, explaining 58.42% of the crossblock covariance). The experimental conditions with significant positive brain scores (conceptual and contextual trials of oriented memories, irrespective of age) are associated with the neural activity patterns presented in warm colors and the experimental conditions with significant negative brain scores (conceptual and contextual trials of re-oriented recollection, irrespective of age) are associated with the neural activity patterns presented in cool colors. The bottom panel presents the second significant LV ($p < .001$, explaining 18.23% of the crossblock covariance). The experimental conditions with significant positive brain scores (contextual re-oriented recollection of recent and remote) are associated with the neural activity patterns presented in warm colors and the experimental conditions with significant negative brain scores (conceptual re-oriented recollection of recent and remote memories) are associated with the neural activity patterns presented in cool colors.

simulations. The pattern associated with the conceptual orientation condition resembles the dorsal medial DN subsystem, which has been implicated in self-referential and evaluative processing (Andrews-Hanna et al., 2010, 2014). Second, our findings align with evidence for separable MTL memory systems for processing distinct informational components of laboratory-learned stimuli (Ranganath and Ritchey, 2012). This evidence has led to a proposed model of memory that includes an anterior temporal lobe subsystem that supports evaluating information and processing conceptual elements of a memory and a posterior medial network that supports processing contextualized as well as perceptual elements of a memory (Reagh and Ranganath, 2018). Regions within this anterior temporal system overlap with those reported during the conceptual retrieval orientation condition while regions within the posterior medial system overlap with those reported during the contextual retrieval orientation condition.

This collective evidence of a common distinction between processing conceptual and contextual information during autobiographical memory

retrieval, resting-state, and MTL-mediated episodic memory tasks suggests that there may be inherent neural systems tuned towards generating certain mnemonic content (Sheldon et al., 2019). Component processing views suggest that there are dissociable brain structures that support processing separate elements of a memory (Cabeza and Moscovitch, 2013; Moscovitch, 1992; Moscovitch et al., 2016; Rubin, 2005). Our findings further expand on this view and propose that certain components work together to evaluate information at a higher-order event level (e.g., lateral temporal and medial prefrontal regions) while other components work together to re-activate sensory and perceptual information (e.g., posterior parietal and parahippocampal regions). Although there is evidence that conceptual and contextual 'remembering' can systematically engage distinct neural subsystems as a result of one's retrieval orientation, it is likely that both forms of remembering are simultaneously engaged, albeit to different degrees, whenever autobiographical memories are retrieved (Reagh and Ranganath, 2018; Sheldon et al., 2019).
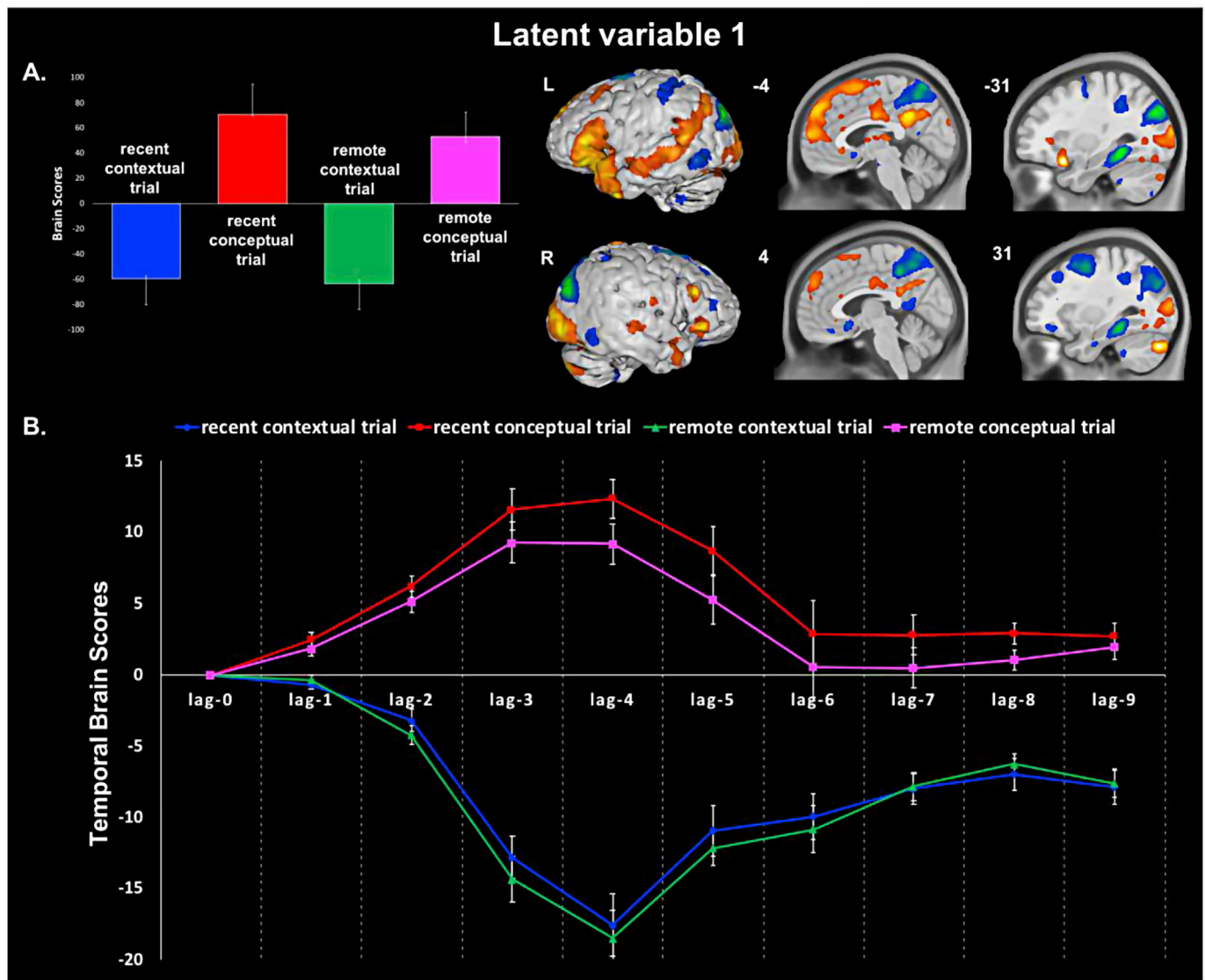
Fig. 5. A. Brain scores (left; group average brain scores are shown with 95% confidence intervals from lag 4) and activity patterns corresponding to lag 4 (right) of a mean-centered event-related PLS that modelled conceptual and contextual trial, separately for recent and remote memories for the significant latent variable (LV1; P < .001, explaining 65.70% of the crossblock covariance). The experimental conditions with significant positive brain scores (conceptual retrieval orientation trials) are associated with the neural activity patterns presented in warm colors and the experimental conditions with significant negative brain scores (contextual retrieval orientation trials) are associated with the neural activity patterns presented in cool colors. B. Temporal brain scores (shown with standard error bars) for each trial type (recent conceptual trials, recent contextual trials, remote conceptual trials, and remote contextual trials) indicating that the identified pattern from LV1 is maximally expressed at lag 4 (i.e., during the new memory access phase of the trial). Note: lags 0–2 correspond to the re-oriented recollection phase of the trials, lags 3–5 correspond to the new memory access phase of the trials, and lags 6–9 correspond to the oriented recollection phase of the trials.

We also examined retrieval orientation effects at different stages during the memory retrieval process and found that these effects were most robust when recollection emphasized particular details of an already-established memory (i.e., during re-oriented recollection) than when recollection was guided by those details (i.e., during oriented recollection). One possibility is that this reflects the fact that memory representations are most malleable – and subject to orientation shifts – after they have already been established compared to when different orientations are used to search and establish a new memory representation. This interpretation runs parallel with work that have shown that a memory becomes susceptible to being changed or updated when recalled (Alberini, 2011; McKenzie and Eichenbaum, 2011; Nader and Hardt, 2009; Sara, 2010). Thus, when a change in retrieval-goal is introduced, dynamic constructive memory processes are engaged to update an already-formed memory representation. However, experiments with laboratory stimuli indicate that orientation effects are the result of how a memory is cued (Herron, 2018; Rugg and Wilding, 2000), presenting the possibility that the retrieval orientation effects during memory recollection we report are driven by differences in the pre-retrieval processes that guided the search for mnemonic content. To test for this, we ran an event-related PLS analysis that examined the effects of the orientation manipulations across the trial period and found that the dissociable neural activity patterns associated with the conceptual and contextual orientations were maximally expressed during time points associated with searching for a new autobiographical memory. This result supports the proposal that the orientation effects during autobiographical memory are primary driven by pre-retrieval processes, however, this analysis also showed that these differences seem to be maintained into the subsequent memory elaboration stage. This latter finding fits with the PLS analysis results reported above.

Analyzing the time course of the retrieval orientation effect with an event-related PLS approach revealed other interesting findings. First, we
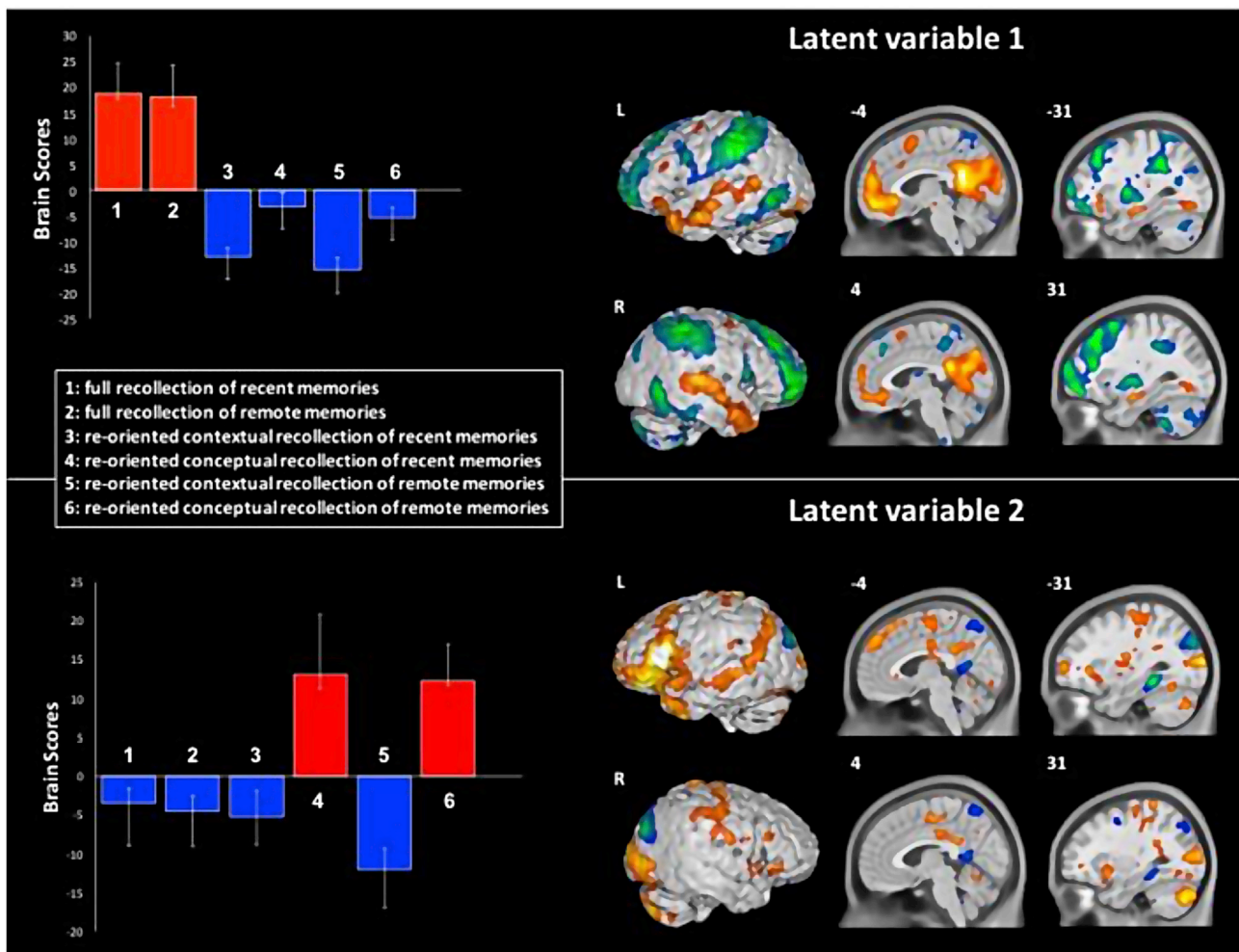
Fig. 6. Brain scores (left; group average brain scores are shown with 95% confidence intervals) and activity patterns (right) of a mean-centered PLS that included the full recollection phase and the re-oriented recollection phase for recent and remote memories under the tested retrieval orientations. The top panel illustrates the first significant latent variable (LV; p < .001, explaining 57.81% of the crossblock covariance). The experimental conditions with significant positive brain scores (full recollection) are associated with the neural activity patterns presented in warm colors and the experimental conditions with significant negative brain scores (conceptual and contextual trials of re-oriented recollection, irrespective of age) are associated with the neural activity patterns presented in cool colors. The bottom panel presents the second significant LV (p < .001, explaining 26.55% of the crossblock covariance). The experimental conditions with significant positive brain scores (conceptual trials of re-oriented recollection, irrespective of age) are associated with the neural activity patterns presented in warm colors and the experimental conditions with significant negative brain scores (full recollection and contextual re-oriented recollection of recent and remote recollected memories) are associated with the neural activity patterns presented in cool colors.

did not find a dissociation between the stages of retrieval like we did when we ran the blocked PLS. This suggests that the first latent variable of the initial PLS analysis that revealed dissociable neural patterns between re-orienting retrieval of an already-established memory (re-oriented recollection) versus elaborating on a newly-accessed memory (oriented recollection) could reflect different temporal stages of retrieval. The patterns associated with the oriented recollection stage, which involves a guided search for particular event details, versus the re-oriented recollection stage, which focuses more on elaborating on specific details of a memory, are reminiscent of the patterns reported during an initial memory access (construction) and later detailed elaboration stages of autobiographical memory retrieval (McCormick et al., 2018; McCormick et al., 2015). Both memory 'construction' and the tested oriented recollection stage engaged regions like the lateral prefrontal cortices and the anterior hippocampus, which coincides with the idea that this hippocampal subregion is critical for accessing memories and initiating mental construction (Addis and Schacter, 2012; Campbell et al., 2018; Zeidman and Maguire, 2016). Both memory 'elaboration' and the tested re-oriented recollection stage engaged brain regions involved in attending to sensory and perceptual information that are critical for

vividly re-experiencing a past event (e.g., lateral parietal and posterior occipital cortices; Inman et al., 2018; Monge et al., 2018).

In addition, the event related PLS analysis indicated that the neural pattern associated with the contextual orientation subsystem was maintained from the initial memory access period into the oriented recollection (i.e., elaboration) phase of autobiographical memory retrieval. This finding suggests that spatial contextual information may act as a framework or 'scaffold' for accessing more specific details of a recalled event compared to conceptual information (for a review, see Robin, 2018). This interpretation aligns with the results from the mean-centered blocked PLS analysis comparing the stages of recollection with (i.e., re-oriented recollection) and without (i.e., full recollection) a retrieval orientation. This analysis revealed brain activity common between the full recollection and the re-orientated stage for the contextual but not conceptual trials, which we take as evidence that contextual processes are more similarly recruited for various types of remembering (for related evidence, see Hebscher et al., 2018; Robin et al., 2016). This idea is similar to scene construction theory that suggests that autobiographical memory retrieval hinges on the availability of a context or scene onto which event details are projected (Hassabis and Maguire, 2007; Robin, 2018; Rubin and

Umanath, 2015). When remembering the personal past, contextual information is more likely to be first reactivated to form the autobiographical memory representation, which is then followed by the addition of evaluative, perhaps more effortfully retrieved, conceptual information.

5. Limitations and conclusion

Here, we provide new evidence for discrete functional brain systems for accessing two critical components of autobiographical memories – conceptual and contextual details. However, there are a few methodological issues to consider when interpreting these findings. First, the design of our study required that participants recall the same twelve preselected memories multiple times during the full recollection and re-oriented recollection phases (twice during the conceptual retrieval orientation trials and twice during the contextual retrieval orientation trials). These personalized cues were included in the experimental design in an effort to ensure that participants could recall memories vividly and thus access the targeted memory content (i.e., conceptual and contextual details). This method of collecting personalized stimuli prior to scanning has been used successfully in the past in imaging studies of autobiographical memory (e.g., Addis et al., 2004; Maguire et al., 2001; Sheldon and Levine, 2013; Svoboda and Levine, 2009). This design choice raises questions about whether there are repetition effects influencing the reported neural pattern. Repetition effects, particularly within the MTL, have been documented with laboratory-based episodic memory retrieval tasks (Brozinsky et al., 2005; Gonsalves et al., 2005; Grill-Spector et al., 2006; Henson and Rugg, 2003; Suzuki et al., 2011), however, there is also evidence that neural distinctions between different forms of memory remain stable over repeated retrieval (e.g., Svoboda and Levine, 2009). Thus, we do not suspect that the reported retrieval orientation effects would be affected by repeated remembering.

Another limitation of our study was that we did not collect verbal descriptions during the scan given the burden this would have placed on participants while they were in the scanner. Nevertheless, we think our reported neural dissociations would manifest behaviourally, based on evidence that the contextual and conceptual elements of autobiographical-like events dissociate in terms of forgetting rates (Sekeres et al., 2016) and how certain aspects of memory are impaired from brain damage. For example, patients with MTL dysfunction have specific impairments in recollecting contextual but not general (i.e., conceptual) details from autobiographical memories (St-Laurent et al., 2014; St-Laurent et al., 2009).

To conclude, our data show that biasing memory reconstruction towards either conceptual or contextual mnemonic content will shift underlying neural activity towards specific brain networks. This 'shift' leads to different forms of episodic autobiographical remembering, highlighting the dynamic way we reconstruct the past. With this established, future research can explore the reasons why the same autobiographical memory can be retrieved in different ways (Alea and Bluck, 2007; Conway and Pleydell-Pearce, 2000; Pillemer, 2003; Sheldon et al., 2019). We speculate that retrieving memories as conceptual or contextual entities fulfill different retrieval goals. Remembering an event with an emphasis on conceptual details or evaluating the meaning of a memory can be useful for accessing autobiographical experiences to help think about a solution to a current personal problem that is ambiguous. Alternatively, remembering an event with more contextual details is useful when the goal of remembering is to recall the past as it occurred, such as when accurately recounting memories to other individuals (Prebble et al., 2013; Sheldon et al., 2019). As such, these different forms of remembering allow for mental representations of past experiences to be reconstructed based on evaluations of the meaning of an experience (conceptual remembering) as well as based on the particular experienced elements of the remembered event (contextual remembering). These possibilities all hinge on the idea that the neural processes that support this autobiographical memory construction are determined by one's current mental (retrieval) state.

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