Representational dynamics of memories for real-life events

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Acknowledgments: This work was supported by the University of Liège (Fonds spéciaux – Crédits sectoriels no. 9893). O. Jeunehomme and A. D'Argembeau are supported by the Fund for Scientific Research (F.R.S.-FNRS), Belgium.

Competing interests: The authors have declared no competing interest.

Abstract

The continuous flow of experience that characterizes real-life events is not recorded as such in episodic memory. The unfolding of events is represented as a succession of moments of prior experience (referred to as "experience units") that are separated by temporal discontinuities, such that events are temporally compressed when remembered. To unravel the neural basis of this temporal structure of episodic memories, we recorded a series of real-life events using wearable camera technology and then used fMRI to investigate brain activity during the temporal unfolding of these events in memory. We found that, compared to the representation of static scenes in memory, dynamically unfolding memory representations were associated with greater activation of posterior brain regions that support episodic recollection (i.e., the precuneus, posterior cingulate cortex, retrosplenial cortex, and angular gyrus). Strikingly, by analyzing the autocorrelation of brain activity patterns at successive time points throughout the retrieval period, we found that these brain regions showed higher temporal dynamics when remembering the unfolding of events compared to static scenes. Furthermore, these effects were more pronounced when recalling events that included a higher density of experience units (i.e., actions compared to spatial displacements). These results reveal the key role of the posterior medial network in representing the dynamic unfolding of event segments that constitute episodic memories.

Keywords:

Episodic memory, fMRI, Temporal structure, Event segmentation, Scene construction.

INTRODUCTION

Decades of cognitive, neuropsychological, and neuroimaging research on episodic memory have deepened our understanding of the neurocognitive processes supporting the ability to remember past events (Conway, 2009; Moscovitch et al., 2016; Rugg & Vilberg, 2013; Schacter et al., 1998; Tulving, 2002). However, most studies have focused on memory for static stimuli (e.g., lists of words or pictures), so important questions remain about how the dynamic unfolding of events is represented in episodic memory. People make sense of the continuous stream of experience by segmenting it into meaningful units (i.e., events and sub-events), with this segmentation process playing a key role in the temporal structure of memory representations (Clewett & Davachi, 2017; Radvansky & Zacks, 2017; Zacks, 2020). Memories are composed of a succession of event segments (i.e., moments or slices of prior experience) that are organized in chronological order (Anderson & Conway, 1993; Radvansky et al., 2005) and usually include temporal discontinuities in the unfolding of events: Parts of the continuous flow of information that characterized the previous experience are omitted during event recall (Folville et al., 2020; Jeunehomme et al., 2018; Jeunehomme & D'Argembeau, 2020). This structure of memories allows one to mentally represent events in a temporally compressed form, such that it usually takes less time to remember an event than it took for this event to occur in the past (Arnold et al., 2016; Bonasia et al., 2016; Chen et al., 2017; Jeunehomme & D'Argembeau, 2019; Michelmann et al., 2019). To date, however, the neural basis of this temporal structure of memory representations remains unclear.

Memory for real-life events is supported by a specific set of brain regions that includes the medial temporal lobes (e.g., hippocampus, parahippocampal gyrus), cortical midline structures (medial prefrontal cortex, precuneus, posterior cingulate cortex, and retrosplenial cortex), and lateral fronto-temporo-parietal areas (Benoit & Schacter, 2015; Cabeza & St Jacques, 2007; Kim, 2012; McDermott et al., 2009; Svoboda et al., 2006). Within this core

memory network, the hippocampus and medial parietal cortex have been associated with the process of "scene construction" (i.e., the generation, maintenance, and visualization of complex spatial scenes), which is considered one of the key components of past event recall (Hassabis & Maguire, 2007). Supporting this view, it has been shown that episodic memory retrieval and the imagination of fictitious experiences are associated with overlapping patterns of brain activation, notably in the hippocampus, parahippocampal gyrus, and retrosplenial cortex (Hassabis et al., 2007). However, most studies on scene construction required participants to mentally represent static scenes (e.g., visualizing an old library) (Zeidman et al., 2015), whereas, as noted above, remembering past events involves a dynamic succession of moments of prior experience.

A recent fMRI study has provided important insight into the neural mechanisms underlying the dynamic unfolding of events in episodic memory (Baldassano et al., 2017). During the initial encoding of events from a movie, event segmentation processes were evidenced at multiple time scales throughout the cortical hierarchy: While early sensory regions represented relatively short-lived segments of experience, the posteromedial cortex and angular gyrus supported more extended episode representations that corresponded closely to event boundaries identified by human observers. Event boundaries in these higher-level areas triggered the hippocampus to encode the current situation model into episodic memory, which was later reinstated in the posteromedial cortex and angular gyrus during memory retrieval (see also Ben-Yakov & Dudai, 2011; Ben-Yakov & Henson, 2018; DuBrow & Davachi, 2016).

While these results present an important first step towards understanding the temporal dynamics of events during their initial experience, the dynamic unfolding of event segments during recollection remains to be elucidated. As noted above, episodic memories are not literal reproductions of past events, but instead consist of a succession of event segments that

typically includes temporal discontinuities. The density of the segments of experience that constitute memories, and therefore the amount of temporal discontinuities within memories, can vary substantially across events, leading to more or less compressed representations (Jeunehomme & D'Argembeau, 2019). Here, we aimed to unravel the neural basis of this dynamic unfolding of the units of experience that constitute episodic memories.

We first sought to examine brain regions that are involved in remembering dynamic and temporally extended events as compared to static scenes. Memories were prompted using a paradigm that capitalizes on wearable camera technology to investigate the remembrance of real-life experiences (Jeunehomme et al., 2018; Nielson et al., 2015; Stawarczyk et al., 2018). Specifically, participants performed a 40-min walk on a university campus during which they experienced a series of daily life events, while the content and timing of these experiences were recorded using a wearable camera (Chow & Rissman, 2017) (Figure 1A). Immediately after the walk, participants took part in an fMRI session in which they had to remember events that were cued by pictures that had been taken during their walk (Figure 1B). By contrasting these episodic memories to a control condition involving the mental representation of static scenes, we identified the brain regions that specifically underlie the recall of temporally unfolding events. We focused on the recall of real-life events rather than movies because the former involve a sense of agency that is absent from passive video viewing but may play an important role in structuring memory representations, given that a key function of episodic memory is to remember actions and goal-relevant information (Conway, 2009; Zimmer et al., 2007).

Another aim of the current study was to compare the neural correlates of episodic memories that are associated with different event compression rates. Previous studies have shown that the density of the units of experience that constitute memories, and therefore the temporal compression of events, is not constant but varies with the content of remembered

events. In particular, memories for actions contain a higher density of experience units than memories for spatial displacements (Jeunehomme et al., 2018; Jeunehomme & D'Argembeau, 2019, 2020). Indeed, spatial displacements involve a relatively simple structure that is primarily organized in terms of changes in direction (i.e., turns), whereas actions typically have a more complex and fine-grained structure in which event segments correspond to changes in goals and sub-goals (Tversky et al., 2004). This difference in the density of event segments should be reflected in the dynamics of neural activity when remembering the unfolding of events.

Our main hypothesis is that the posterior medial network, which is thought to support the representation of event models (Ranganath & Ritchey, 2012; Ritchey & Cooper, 2020; Stawarczyk et al., 2021), plays a key role in representing the temporal structure of memories. Indeed, regions such as the retrosplenial cortex, posterior cingulate cortex, precuneus, and angular gyrus might contribute to the integration of successive changes in experience when remembering the unfolding of events, and might also maintain and elaborate integrated event representations (Ritchey & Cooper, 2020). To test these hypotheses, we not only examined brain activity over the entire duration of the retrieval period using classical univariate analyses, but also investigated to what extent multivariate patterns of brain activity change across time during the unfolding of events in memory. To the extent that memories for actions contain a higher density of experience units, we expected that they would be associated with higher temporal dynamics (i.e., lower autocorrelations) of brain activity patterns at successive time points during the retrieval period.

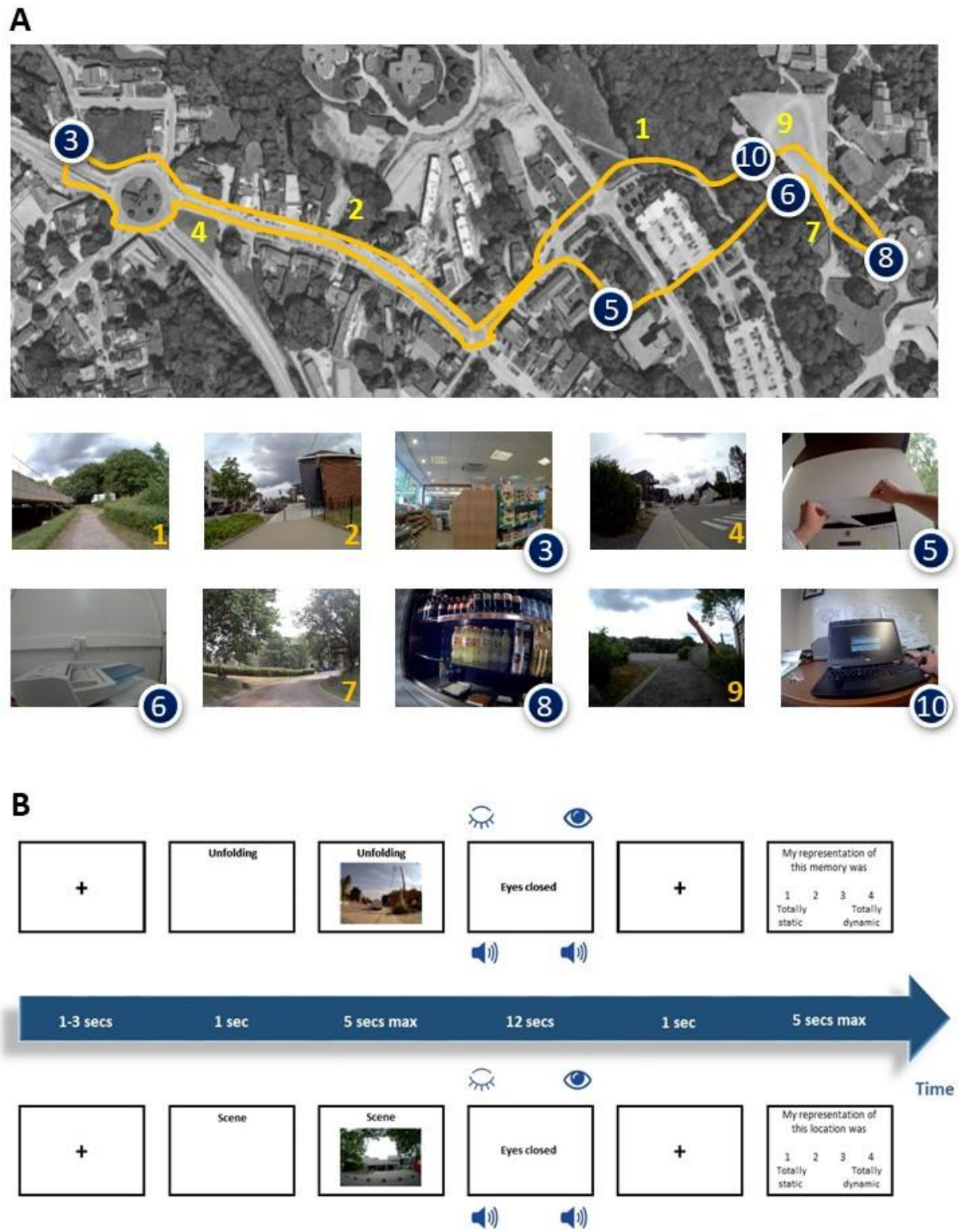

Figure 1: Experimental procedures. (A) Overview of the walk on the campus of the University of Liège. Locations in which participants performed an action are indicated by blue circles and the paths taken to go to these locations are indicated by yellow lines. For each event, an example of picture taken by the wearable camera that was used as cue for the episodic memory task is provided. (B) Trial structure in the episodic memory conditions (top panel) and in the control condition (bottom panel). Participants were first presented with a cue specifying the experimental condition. In the episodic memory conditions, a picture taken during the walk of the participant (corresponding to the beginning of an action or a spatial displacement) was then presented on the screen. As soon as they identified the moment of the walk depicted by the picture, participants were asked to

remember the unfolding of the event, starting at the precise moment they identified on the picture. In the control condition (i.e., scene condition), participants were asked to imagine the visual scene depicted by the picture (which was not part of their walk). For each condition, participants were asked to close their eyes and to press a response key once they started to perform the task; they did the task with eyes closed until the presentation of a sound signal (which was presented 12 seconds after their button press). Finally, each trial ended with the presentation of a Likert scale on which participants rated the temporal dynamics of their mental representation (i.e., static vs. dynamic). In total, 20 trials were presented for each condition. FMRI analyses focused on the time interval between the key press and the end of the 12 second period, thus corresponding to the phase of mental replay.

RESULTS

Behavioral results

Participants successfully identified the presented pictures for nearly all trials (M = 98.24%, 95% CI [98.11%, 98.36%]). Verbal descriptions of episodic memories showed that participants re-experienced a succession of experience units when recalling the events (see Materials and Methods). Memories of actions contained more experience units than memories of spatial displacements, $t = 7.29$, $p < .001$, $\xi = .85$ (Table 1). To assess the density of recalled experience units, we computed the number of reported units per minute of the actual event duration (see Materials and Methods). In line with previous studies(Jeunehomme et al., 2018; Jeunehomme & D'Argembeau, 2019, 2020), the density of experience units was higher when recalling actions than spatial displacements, $t = 6.77$, $p < .001$, $\xi = .88$. As shown in Table 1, all memory representations were judged as clear, easy to recall/construct, and associated with a subjective feeling of re-experiencing the events.

Table 1. Behavioral data for the episodic memory (action, spatial displacement) and control (scene) conditions

	Action	Spatial displacement	Scene
Number of experience units	8.51 [7.51, 9.55]	4.93 [4.08, 5.78]	-
Number of experience units / min	12.42 [10.28, 15.62]	5.02 [4.05, 6.56]	-
Clarity	5.88 [5.48, 6.32]	4.68 [4.31, 5.19]	5.34 [4.80, 5.82]
Easiness	6.09 [5.60, 6.57]	4.93 [4.55, 5.42]	5.32 [5.02, 5.74]
Re-experiencing	5.71 [5.18, 6.20]	4.94 [4.57; 5.43]	-

Note: Data represent 20% trimmed means and their 95% confidence intervals. The score for clarity, easiness and re-experiencing ratings made during the post-scan debriefing ranged from 1 = '*not at all'* to 7 = '*extremely'*.

fMRI results

Episodic memories versus scene representations

We first conducted univariate analyses to identify brain regions within the autobiographical memory network (see Materials and Methods) that showed higher activity when recalling the unfolding of events compared to static scene representations (see Figure 2A, Table 2). Results showed that the recall of actions (action > scene) was associated with increased activation in bilateral parietal areas, including the precuneus, posterior cingulate, retrosplenial cortex, and angular gyrus. Moreover, we found higher activity in the superior/middle frontal gyrus, the posterior middle temporal gyrus, middle occipital cortex, and cerebellum. When looking at memories of spatial displacements (spatial displacement > scene), similar activations were observed in medial parietal areas (i.e., precuneus, posterior cingulate, and retrosplenial cortex). Additional clusters of activation were detected in the right

angular gyrus/middle occipital cortex, and bilaterally in the middle frontal gyrus. Figure 2A also illustrates overlapping activations associated with each contrast, which show that the two types of episodic memories were associated with common activation in medial parietal areas, including the precuneus, posterior cingulate cortex, and retrosplenial cortex.

Table 2. Brain regions showing increased activity for episodic memories as compared to scene representations

		MNI coordinates				
Brain regions	Side	*X*	*Y*	*Z*	Cluster Size	*t*
Actions > scenes						
Precuneus/PCC/RSC	R	12	-62	36	2111	11.46
	R	8	-54	44		9.93
	R	8	-38	26		8.35
	L	-12	-60	20		8.79
	R	12	-62	28		10.99
Middle cingulate gyrus	L	-2	-32	40	28	6.71
Middle/superior frontal gyrus	L	-40	10	54	84	6.40
	R	30	14	58	35	5.85
Middle frontal gyrus	L	-24	30	48	172	4.73
AG	R	44	-68	36	165	5.66
	L	-58	-56	26	21	4.40
MTG/AG	L	-48	-54	20	66	5.64
Middle OC	L	-40	-72	38	64	5.38
MTG	R	62	-52	10	20	5.18
Cerebellum	L	-6	-54	-40	28	4.18
Spatial displacements > Scenes						
Precuneus/PCC/RSC	L	-10	-58	18	1983	11.03
	R	12	-52	20		8.64
	R	4	-44	12		7.75
	R	8	-64	44		7.48
AG/Middle OC	R	42	-70	34	92	537
Middle frontal gyrus	R	28	16	54	31	4.91
	L	-34	6	60	40	4.72
	L	-38	8	54		4.40
	L	-22	26	42	23	4.17

Note: PCC = Posterior cingulate cortex; RSC = Retrosplenial cortex; OC = Occipital cortex; AG = Angular gyrus; MTG = Middle temporal gyrus.

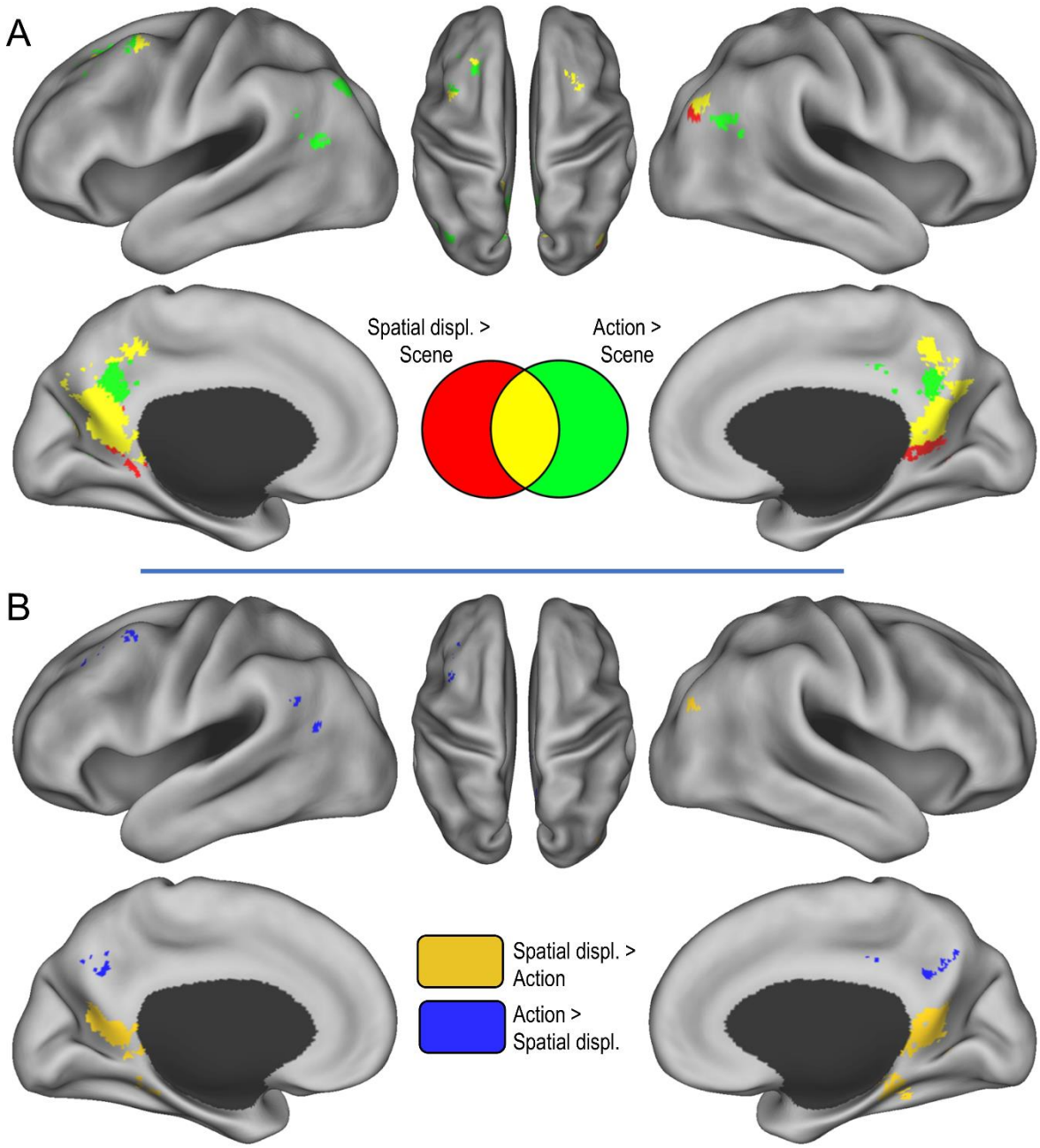

Figure 2. Brain regions activated when recalling the unfolding of events (univariate analyses). (A) Regions that were more activated when recalling actions and spatial displacements compared to the scene construction condition. (B) Regions showing differential activity when recalling actions and spatial displacements. Activations are displayed at $p < .001$ (uncorrected) within the autobiographical network mask.

Remembering actions versus spatial displacements

Next, we compared the two episodic memory conditions (actions vs. spatial displacements; see Figure 2B, Table 3). The retrieval of actions was associated with higher activity in the precuneus, left middle frontal gyrus, right middle temporal gyrus, middle cingulate cortex, and angular gyrus compared to the retrieval of spatial displacements. The reverse contrast (spatial displacements > actions) revealed increased activations in the retrosplenial cortex, the right parahippocampal gyrus, and the right middle occipital gyrus.

Table 3. Brain regions showing differential activity for actions vs spatial displacements

		MNI coordinates				
Brain regions	Side	*X*	*Y*	*Z*	Cluster Size	*t*
Action > Spatial displacement						
Middle frontal gyrus	L	-32	26	36	34	6.25
Precuneus	L	-2	-62	38	131	5.51
MTG	R	64	-48	6	22	5.45
Middle cingulate gyrus	R	2	-26	38	21	5.39
AG	L	-58	-54	30	24	4.82
Spatial displacement > Action						
RSC	L	-12	-52	12	483	9.44
	R	12	-46	6	363	7.84
PHG/FG	R	20	-34	-10	170	7.68
Middle occipital gyrus	R	42	-74	26	21	4.28

Note: RSC = Retrosplenial cortex; MTG = Middle temporal gyrus; PHG = Parahippocampal gyrus; FG = Fusiform gyrus; AG = Angular gyrus.

Distinct brain activity patterns across recall conditions

We next examined whether distributed patterns of brain activity in the autobiographical memory network reflected the content of memories – i.e., whether these patterns differed systematically between experimental conditions. Using representational similarity analysis, we compared all recall trials of the three experimental conditions (actions, spatial

displacements, scenes) with trials of the same condition as compared to trials of other conditions. A repeated measures ANOVA revealed a significant main effect of within versus between similarities ($F(1,20) = 34.58$, $p = <0.0001$, Figure 3A). Post-hoc contrasts showed significantly higher within condition correlations compared to between condition correlations for all three conditions (Figure 3B). Trials within the action condition were more similar to one another compared to trials of other conditions (within: $M = 0.43$, $SD = 0.13$; between: $M = 0.41$, $SD = 0.13$; $t(20) = 3.13$, $p_{\text{Bonferroni}} = 0.015$), and the same pattern was found for spatial displacement (within: $M = 0.44$, $SD = 0.15$; between: $M = 0.41$, $SD = 0.13$; $t(20) = 3.13$, $p_{\text{Bonferroni}} = 0.00044$) and for the control condition (within: $M = 0.43$, $SD = 0.15$; between: $M = 0.39$, $SD = 0.15$; $t(20) = 3.12$, $p_{\text{Bonferroni}} = 0.015$). These results show that voxel patterns indeed reflect the remembered contents and can thus be used to analyze the temporal dynamics of episodic memories, which we did in the next step.

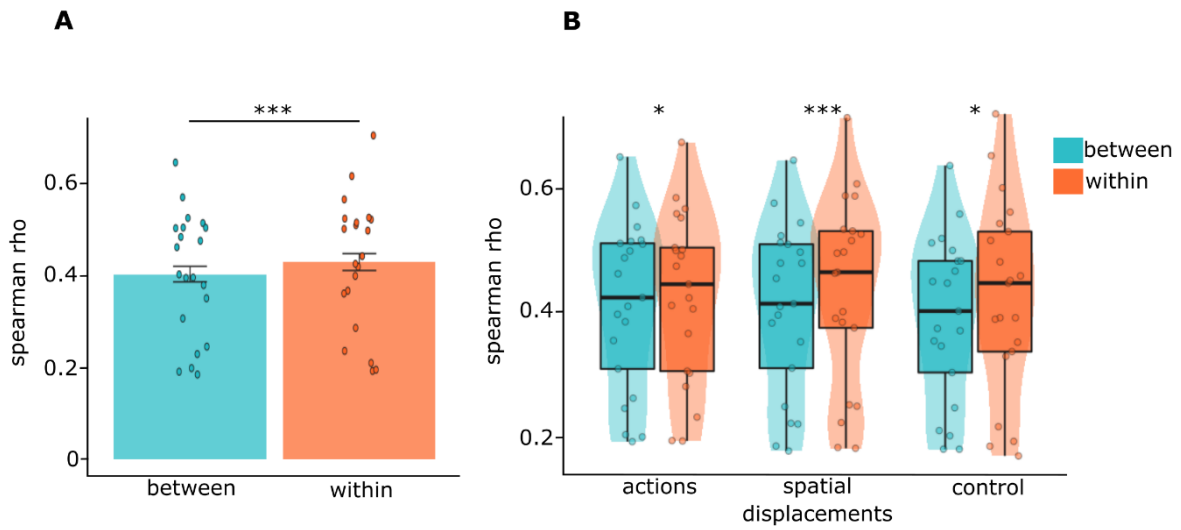

Figure 3. Content-specific memory representations in the autobiographical memory network. (A) Distributed patterns of neural activity are more similar when recalling events from the same category than events from different categories. (B) This higher within- than between-condition similarity is observed for all experimental conditions.

Higher temporal dynamics of brain activity patterns during recall of high-density events

We next computed temporal autocorrelations between successive patterns of brain activity as a measure of the temporal dynamics of memories (see Figure 4A). A searchlight analysis revealed higher temporal dynamics (i.e., lower autocorrelations) during the recall of episodic memories compared to the representation of static scenes. Compared to the control condition, the recall of actions was associated with higher temporal dynamics in the precuneus, posterior cingulate cortex, angular gyrus, and lingual gyrus ($t(20)= 10.8$; $p_{corr} < 0.05$, FWE corrected using TFCE, Figure 4B/C). This extended cluster also included the middle frontal gyrus, frontal pole, middle temporal gyrus, and precentral gyrus. Compared to the control condition, the recall of spatial displacements was associated with higher temporal dynamics in the posterior cingulate cortex, cuneus, angular gyrus, and lateral occipital cortex ($t(20)= 5.48$; $p_{corr} < 0.05$, FWE corrected using TFCE, Figure 6B/C).

Next, we compared the temporal dynamics of the two types of episodic memories and found higher temporal dynamics for the recall of actions than spatial displacements in the lateral occipital cortex, precuneus, posterior cingulate, cuneus, and angular gyrus ($t(20) = 7.06$; $p_{corr} < 0.05$, FWE corrected using TFCE, Figure 4B/C). None of the opposite contrasts showed any significant differences.

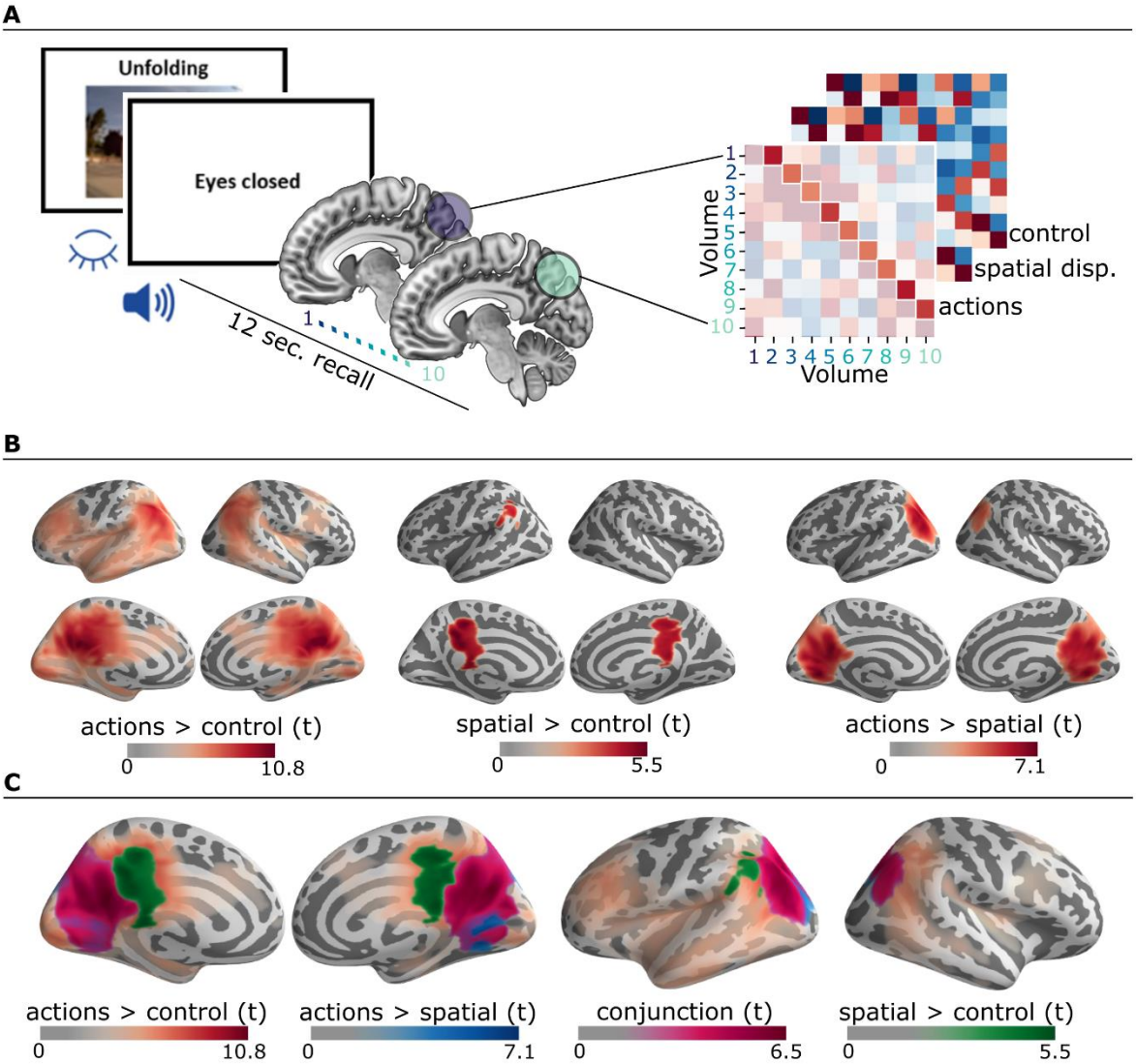

Figure 4. Temporal dynamics of patterns of brain activity during the recall period. (A) Within each searchlight sphere (first volume blue circle), we correlated 10 consecutive volumes (starting with the fifth volume after the recall onset to account for the delayed hemodynamic response function), resulting in a 10x10 spearman rho correlation matrix. From this matrix we extracted the mean of the first off-diagonal (i.e., correlations of patterns between all pairs of temporally adjacent volumes). This procedure was applied to all trials of all conditions and for all sphere locations, resulting in three brain maps (one for each condition) indicating the averaged autocorrelation as an (inverse) measure of the temporal dynamics of episodic recall. (B) The searchlight analysis revealed significantly higher temporal dynamics for the action condition compared to the control and spatial displacements conditions. Spatial displacements showed higher temporal dynamics compared to the control condition. (C) The conjunction of higher temporal dynamics for actions compared to both the spatial displacements and control conditions is shown in purple (The conjunction of spatial displacements vs. control and of action vs. control is not shown as it overlaps completely with the action vs. control contrast.).

In addition to this whole-brain analysis, we conducted a second searchlight analysis within the autobiographical network mask that we used for the univariate analyses (Figure 5). This analysis revealed significantly higher temporal dynamics during the recall of actions compared to the control task within the precuneus and posterior cingulate (cluster 1: $t(20)$ =

12.3; $p_{corr} < 0.05$, FWE corrected using TFCE), middle temporal gyrus (cluster 2: $t(20) = 5.52$; $p_{corr} < 0.05$, FWE corrected using TFCE), superior frontal gyrus (cluster 3: $t(20) = 4.48$; $p_{corr} < 0.05$, FWE corrected using TFCE), lateral occipital cortex and angular gyrus (cluster 4: $t(20) = 4.15$; $p_{corr} < 0.05$, FWE corrected using TFCE). We also found higher temporal dynamics for the action condition compared to the recall of spatial displacements within one cluster including the precuneus, lingual gyrus, cuneus, angular gyrus, and the lateral occipital cortex ($t(20)= 8.75$; $p_{corr} < 0.05$, FWE corrected using TFCE). The contrast between the spatial displacements and control conditions did not yield significant differences within the autobiographical network mask.

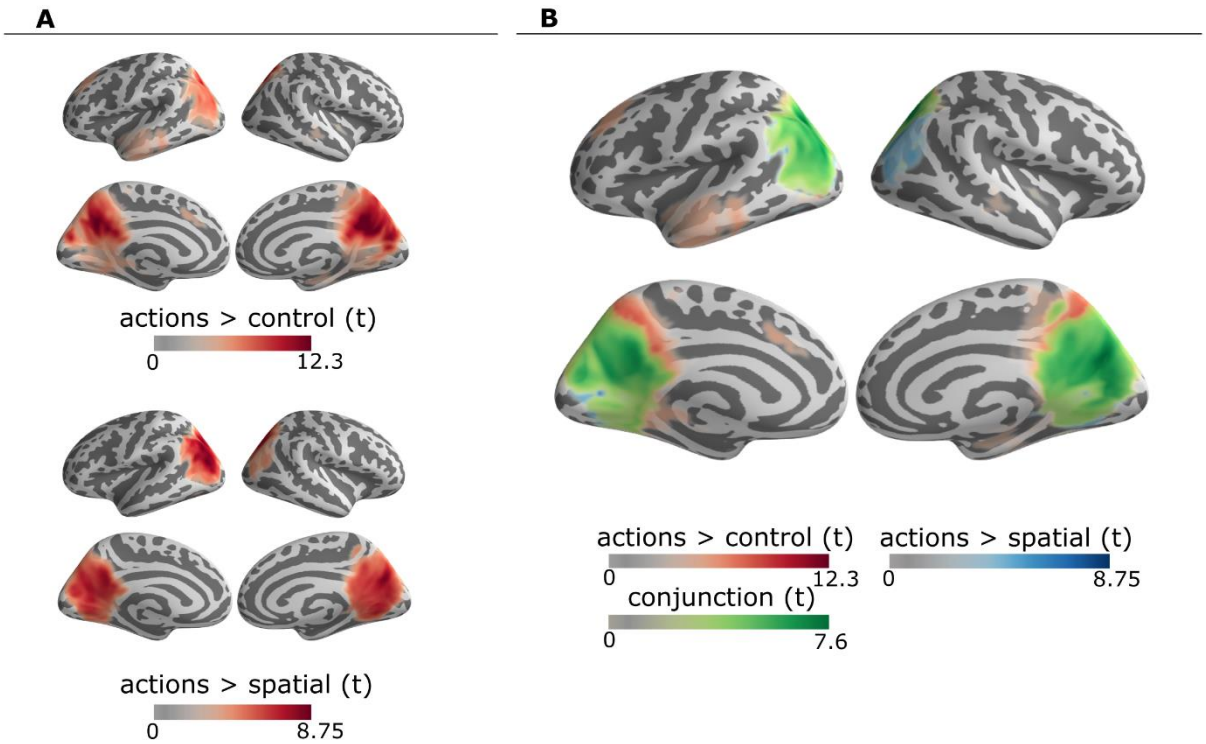

Figure 5. Searchlight analysis of temporal dynamics within the autobiographical network mask. (A). This analysis revealed significantly higher temporal dynamics for the action condition compared to both the control and the spatial displacement condition. (B) Conjunction of higher temporal dynamics for actions compared to spatial displacements and compared to the control condition shown in green

DISCUSSION

The aim of our study was to better understand the neural mechanisms underlying the dynamic unfolding of events within episodic memory representations. Compared to mental representations of static scenes, memories for dynamic events elicited greater activation in medial parietal areas (including the precuneus, posterior cingulate cortex, and retrosplenial cortex) and in the angular gyrus. Furthermore, when investigating the autocorrelation of patterns of brain activity throughout the retrieval period, we found that these posterior brain regions showed greater temporal dynamics when remembering dynamic events compared to static scenes. These effects were more pronounced for memories that included a higher density of experience units (i.e., memories for actions compared to spatial displacements).

Memories for real-life events depend on an extended fronto-temporo-parietal network, but the exact functions of specific regions within this network are not fully understood (Benoit & Schacter, 2015; Cabeza & St Jacques, 2007; Kim, 2012; McDermott et al., 2009; Svoboda et al., 2006). Medial parietal areas, including the precuneus, posterior cingulate, and retrosplenial cortex, are central areas of this network(Svoboda et al., 2006) that share reciprocal connections (Cavanna & Trimble, 2006) and have been referred to as the posterior medial episodic system (Baldassano et al., 2017; Ranganath & Ritchey, 2012; Ritchey & Cooper, 2020). A first contribution of the present study is to show that this posterior network is more active when recalling the dynamic unfolding of events compared to mentally representing static scenes. Remembering the unfolding of events involves the retrieval of moments or slices of prior experience (each moment itself consisting of a bounded set of various event features) that need to be sequenced and integrated into a stable and coherent representation (Conway, 2009; D'Argembeau et al., 2021). The posterior medial episodic network is considered to play a central role in the elaboration and use of event models (i.e., models that specify the spatial, temporal, and causal relationships between entities within a

particular context) (Ranganath & Ritchey, 2012; Ritchey & Cooper, 2020; Stawarczyk et al., 2021), and may thus contribute to organize and integrate the sequence of experience units that represent the unfolding of events during episodic recall.

A second important aim of this study was to compare the neural correlates of episodic memories that are composed of different densities of experience units. Consistent with previous findings (Jeunehomme et al., 2018; Jeunehomme & D'Argembeau, 2019, 2020), our behavioral results showed that the density of experience units was higher when remembering actions compared to spatial displacements. Actions typically have a more complex and fine-grained segmental structure than spatial displacements (Tversky et al., 2004), which is manifest when mentally representing the unfolding of prior experience during episodic recall. At the neural level, we found that some regions of the posterior medial episodic network, including the precuneus, were more active when remembering actions compared to spatial displacements. Furthermore, and most importantly, we observed higher temporal dynamics within patterns of activity in the precuneus, as well as the posterior cingulate and occipital cortex when remembering the course of action events than when remembering spatial displacements or mentally representing static scenes. The precuneus has been associated with central aspects of autobiographical memory retrieval, including visuo-spatial imagery, first-person perspective taking, and an experience of agency (Cavanna & Trimble, 2006). Interestingly, recent findings suggest that the precuneus plays a causal role in the dynamics of memory retrieval (Hebscher et al., 2020), and may notably contribute to the temporal structure and order of moments of past events (Aly et al., 2018; Kwok et al., 2012). The higher temporal dynamics of activity patterns in the precuneus and other posterior regions that we observed suggest that these regions are sensitive to changes in recalled content during the retrieval period and may thus contribute to implementing and organizing transitions between experience units when representing the temporal unfolding of past events. This interpretation

fits with previous research showing that patterns of activity in posterior medial regions are less similar across than within segments of a video episode (Baldassano et al., 2017).

We also found that the angular gyrus was more active and showed greater temporal dynamics when remembering actions compared to spatial displacements. Several studies have established relationships between activity in the angular gyrus, especially left-lateralized, and the amount of recollected information and strength of recollection (Gilmore et al., 2015; Rissman et al., 2016; Vilberg & Rugg, 2007; Wagner et al., 2005). Although the exact role of this region has been a matter of considerable debate (Cabeza et al., 2012; Seghier, 2012), a recent unifying framework has proposed that the angular gyrus supports the integration and representation of the multimodal contextual details that constitute a mnemonic representation and promote vivid re-experiencing (Ramanan et al., 2018). The present findings suggest that this integration process contributes to representing the dynamic unfolding of experience units within episodic memory representations.

Compared to the recall of actions, the recall of spatial displacements was associated with increased activity in the retrosplenial cortex and parahippocampal gyrus. These regions are well known for their role in spatial navigation, and notably respond to relevant spatial elements of the environment such as landmarks (Epstein et al., 2017). Interestingly, the parahippocampal gyrus coordinates observed in the present study overlap with those reported in a previous study on the role of the parahippocampal place area on scene perception (Park & Chun, 2009). Evidence suggests that the parahippocampal place area and the retrosplenial cortex might play complementary functions in building a coherent and detailed representation of a scene across several viewpoints (Epstein et al., 2003; Park & Chun, 2009). Specifically, it has been proposed that when viewpoint changes occur continuously in a scene, the parahippocampal place area is sensitive to changes in physical details across each view, thereby representing scenes as a succession of individual representations of each view rather

than a unique and integrated representation of multiple views. On the other hand, the retrosplenial cortex links the current and previous views of the same scene, creating an integrated representation of this scene over changes in visual perspective (Park & Chun, 2009). In the current study, it is therefore possible that the parahippocampal gyrus and the retrosplenial cortex were more active when remembering the unfolding of spatial displacements compared to actions because the former implied more important updating and integration of successive views of the surrounding environment when mentally travelling from one particular moment of past experience to the next.

The critical role of the hippocampus in the retrieval of episodic memories is now well established (Moscovitch et al., 2016). This region is considered to play an important role in binding the various elements that constitute memories, including information about the sequence of events (Bellmund et al., 2020; Clewett et al., 2019; Lee et al., 2020). Therefore, one could have expected that, in the present study, the hippocampus would be differentially activated when remembering events with different densities of experience units, but this is not what we found. We have no ready explanation for this null result, but it is worth noting that in previous work on memory for dynamic events, hippocampal activity was observed during encoding but not during event recall (Baldassano et al., 2017). One possible explanation could be that hippocampal activity during retrieval is transient in nature (Vilberg & Rugg, 2012) and thus was not captured by our analysis. Alternatively, the episodic segments supported by the hippocampus may be substantially longer (~1 minute) (Baldassano et al., 2017) than the relatively short recall periods that we analyzed (12 seconds). Future studies should analyze the contribution of the hippocampus to the temporal dynamics of memories in more detail.

From a methodological perspective, it would also be interesting in future studies to compare our method of analysis of the temporal dynamics of brain activity patterns with other methods that detect state boundaries in activity patterns using hidden Markov models (HMM)

(Baldassano et al., 2017) or greedy state boundary search (GSBS) (Geerligs et al., 2021). HMM and GSBS were not applicable to our data for several reasons. First, these methods have been applied to fMRI recordings ranging from 8 minutes (Geerligs et al., 2021) up to 45 minutes (Baldassano et al., 2017), whereas recall trials in our study were limited to 12 seconds. State boundaries might not be detectable within such short trials, as Geerligs et al. (2021) found that the algorithms start to struggle with short state durations. Second, HMM and GSNS methods are applied to group data, detecting state boundaries across participants. The real-life events experienced by our participants were not completely comparable across participants, contrary to the standardized movies used in the aforementioned studies. In future studies, applying state detection algorithms on the recall of real-life events while taking these issues into account would be a promising next step for further characterizing the representational dynamics of memories.

Here, we investigated the temporal dynamics of brain activity as a function of the density of recalled experience units by comparing memories for two types of events that have been repeatedly shown to differ in terms of event compression rates (i.e., actions vs spatial displacements) (Jeunehomme et al., 2018; Jeunehomme & D'Argembeau, 2019). However, it should be noted that, in addition to these overall differences between event types, compression rates can be voluntarily modulated according to retrieval goals (Bellmund et al., 2020). For example, when people scan their memory for a particular piece of information, they skip more event segments and thus compression rates are higher than when they try to mentally relive the events (Michelmann et al., 2019, 2021). An interesting avenue for future research would be to use the method we developed to analyze the temporal dynamics of brain activity patterns to study the neural basis of this flexible modulation of event compression during episodic retrieval.

In sum, the present study provides first insights on the neural correlates of the dynamic succession of the experience units that constitute memories for real-life events. Our results showed that remembering the unfolding of events activates posterior brain structures (including the precuneus, posterior cingulate cortex, retrosplenial cortex, and angular gyrus) that support event models and may contribute to the representation and integration of episodic details to form coherent representations of the succession of moments of prior experience. Furthermore, an important finding of the current study is that changes in patterns of activity within these regions reflect differences in the density of recalled experience units, suggesting that the posterior medial network plays an important role in the temporal dynamics of event recall and may notably contribute to implement transitions between the units of experience that represent the unfolding of events.

MATERIALS AND METHODS

Participants

Twenty-one right-handed young students (9 women, mean age = 22.29 years, SD = 2.12, range = 18-27 years) from the University of Liège took part in this study. All participants were highly familiar with the university campus where the pre-scan walk took place. None of the participants reported a current use of psychoactive medication or a history of a neurological or psychiatric disorder. Five additional participants were tested but were excluded from the analyses due to noncompliance with the task, either during the pre-scan walk (one participant) or in the scanner (four participants). All participants gave their written informed consent to take part in the study, which was approved by the ethics committee of the Medical School of the University of Liège and was performed in accordance with the ethical standards described in the Declaration of Helsinki (1964).

Materials and procedure

Pre-scan session

Immediately before scanning, participants performed a series of daily-life activities at different locations on the campus of the University of Liège while wearing an Autographer (OMG Life Ltd., Kidlington, UK) tied around their neck. The Autographer is a small wearable camera that automatically and silently takes a continuous series of pictures from the first-person perspective through a 136° fish-eye lens, depending on several electronic sensors (e.g., temperature, accelerometer, magnetometer, etc.). This device has been used in recent neuroimaging and behavioral studies investigating episodic memories for real-life events (Chow & Rissman, 2017). To record the entire set of events as completely as possible, the Autographer was set to the fastest capture rate (approximatively 10 pictures per minute).

The entire set of events was designed to simulate activities that college students would perform in their daily life. It consisted of two kinds of events: goal-directed actions at specific locations, and spatial displacements that did not involve any particular action other than walking from a place to another. These two kinds of events correspond respectively to what Tversky et al. (2004) referred to as “events by hands” (i.e., interactions with objects; e.g., buying a snack) and “events by feet” (i.e., changes of location; e.g., going from the laboratory building to the bus stop). We initially planned to examine a third kind of events that consisted in waiting at specific locations without doing any particular action (e.g., waiting at the bus stop); this condition was included as we assumed it would involve fewer perceptual changes than the two previous types of events. However, preliminary behavioral analyses revealed that the variance in recalled elements (i.e., information about persons, objects, thoughts, perceptual details, and spatial details) was much higher in memories for waiting moments than in memories for actions and spatial displacements, showing that the former condition did not involve a homogenous set of events (the waiting moments took place in public spaces, such as a bus stop, where many different events could occur while participants were waiting). Thus, we do not report analyses about waiting moments (but note that these moments were modeled in the design matrix; see below) as this heterogeneity in recalled contents make the results difficult to interpret.

Participants were instructed to conduct the following series of successive actions: First, they left the laboratory, went to the bus stop, and stayed there as if they were waiting for the bus. After having waited approximately two minutes, they went to the campus shop to buy a snack of their choice. Next, they went to the elementary school near the University campus and stayed in front of the school for approximately two minutes as if they were waiting for a kid. After that, participants went to the Speech and Language Therapy Service to post a letter in a particular mailbox. Having posted the letter, they came back to the laboratory building to

print a document and to wait in the laboratory building hall (again for approximately two minutes) as if they were waiting for an appointment with a professor. Then, they went to a cafeteria to buy a drink of their choice, after which they chose a table inside the cafeteria to wait as if they were waiting for a friend. Next, participants went to a classroom and waited outside as if they were waiting for the beginning of a course. Finally, they were instructed to return to the laboratory and answered an email sent by the experimenter during the walk.

Before starting the walk, participants were given the letter that they should post, as well as 5 euros for purchasing the snack and the drink. They were told that they could take the route they wanted to go from each location to the next, but not to perform any additional actions during spatial displacements or waiting moments (e.g., using their smartphones, listening to music, or counting down time). In addition, participants were asked to avoid obstructing the lens of the camera and to behave as naturally as possible. Finally, they were informed that pictures taken during their walk would be presented during a subsequent fMRI session, but no mention was made of the memory task. Instead, we used a cover story in which participants were told that they would have to perform aesthetic judgments on the pictures in the scanner.

FMRI Session

Immediately after the walk on campus, participants took part in an fMRI session that involved the recall of events experienced during the walk on campus, as well as a control condition. The entire task comprised 80 trials (20 trials in each condition). The order of trial presentation was randomized with the constraint that two subsequent trials of the same condition were not presented in direct succession or with an interval of more than five trials.

Episodic memory tasks. In the episodic memory conditions (i.e., action, spatial displacement, and waiting conditions), participants were asked to remember the unfolding of actions, spatial displacements, or waiting periods. Each trial started with a fixation cross (with a variable duration ranging between one and three seconds) followed by the presentation of a written experimental instruction (for one second), specifying the task that participants should perform on the trial (i.e., remembering the unfolding of an event or remembering a particular moment of waiting). Then, a picture taken during the pre-scan walk of the participant was presented, which corresponded to the beginning of either a particular goal-directed action, a spatial displacement, or a waiting moment. Experimental instructions specified that each picture would be displayed several times during the fMRI session. In total, 20 trials were presented in each of the episodic memory conditions (five pictures that were each repeated four times).

For each picture, participants were first asked to identify the corresponding moment of the walk (without starting to remember the corresponding event); all pictures were presented to the participants before the scan session to ensure that they would be able to easily identify the corresponding moment of their walk during the fMRI session. As soon as they identified the moment depicted, participants were instructed to close their eyes and then to press a response key to indicate that they began their mental replay (their button press was confirmed by a sound signal). Depending on the condition, they were asked to mentally replay either the unfolding of the event (for actions and spatial displacements) or the waiting period, in as much detail as possible, starting at the precise moment they identified on the picture. Participants were told that their mental replay could be of anything that they encountered during the walk (e.g., people, objects, actions, thoughts, etc.). Moreover, in the unfolding conditions, it was specified that the task was not to proceed as far as possible in the recall of the walk or action, but rather to be as precise and detailed as possible. In the waiting

condition, participants were told that they should only remember what they experienced during the moments in which they waited at a particular location (without remembering the unfolding of what happened after these waiting moments). The mental replay phase lasted 12 seconds after which a sound signal prompted participants to stop their mental replay and to open their eyes.

Following the mental replay phase, a one-second fixation cross was shown, immediately followed by the presentation of a four-point Likert scale assessing the extent to which participants' mental replay was static (meaning that it was focused on a particular moment of past experience) or dynamic (meaning that it involved the unfolding of several moments of past experience; see Figure 1B). Responses were self-paced with a maximum of five seconds to respond.

Control task. In the control task (scene condition), participants had to form mental images of static scenes. The structure and timing of the control condition was identical to the episodic memory conditions: Each trial started with a fixation cross, followed by written instructions. Then a picture of a scene was presented in the middle of the screen. Each picture was selected to represent a specific location on the campus of the University of Liège that participants did not visit during their walk. In total, five different pictures were presented for four times each, resulting in 20 trials. As in the episodic memory conditions, each picture was also presented to the participants before the scan. After having examined the picture, participants were asked to close their eyes and then to press the response key to indicate that they began forming a mental representation of the scene (a sound signal confirmed their button press). They were instructed to maintain their mental representation of the scene in as much detail as possible until the presentation of a second sound signal (i.e., after 12 seconds). It was specified that their task was not to retrieve personal memories (e.g., past events

experienced at the presented location or past experiences that happened at similar locations) but only to mentally represent the scene that was depicted on the picture. The control condition trials ended with the presentation of a four-point Likert scale assessing to what extent each trial involved a static representation or the unfolding of several moments (as in the episodic memory conditions).

Post-scan debriefing

Immediately after the fMRI session, participants were shown the 20 pictures presented during the scanning session (i.e., 5 pictures per condition) and, for each picture, they were asked to describe the content of the mental representation they formed in the scanner (i.e., their memories or scene representations). Verbal reports were recorded using a digital audio recorder. Furthermore, in the episodic memory conditions, each verbal report was followed by a review of the pictures that had been taken during the walk and participants were instructed to select the picture that best corresponded to their mental representation of the last moment they remembered while mentally replaying the unfolding of the event in the scanner (i.e., the moment they remembered when hearing the second sound signal). These tasks allowed us to determine (a) whether the participants correctly performed all conditions in the scanner and (b) to estimate the density of experience units recalled (see Behavioral data analyses).

Finally, participants were asked to rate the overall clarity of the memory or scene they formed in response to each picture (from 1 = *not clear at all*, to 7 = *extremely clear*), as well as the easiness of remembering/imagining (from 1 = *not easy at all*, to 7 = *extremely easy*). Furthermore, for trials of the episodic memory conditions, participants were asked to estimate their overall feeling of re-experiencing the unfolding of events (from 1 = *not at all*, to 7 = *completely*).

Behavioral data analyses

Verbal descriptions of the memories reported during the post-scan interview consisted of a succession of distinct moments of past experience (referred to as experience units; see (Jeunehomme et al., 2018; Jeunehomme & D'Argembeau, 2019, 2020). For example, a typical verbal report would start by "I got out of the building" (first experience unit), "then I walked along the parking" (second experience unit), "then, I saw a man I know on the opposite side of the road" (third experience unit), and so on. The segmentation of verbal reports into distinct experience units was performed by the first author based on indications of transitions or temporal discontinuities between reported moments of experience (i.e., verbal clues such as "then", "next", and "after that" or moments of silence); most of the time, transitions between experience units involved significant changes in actions, environmental elements, and/or thoughts (e.g., "I saw a sheet of paper on the ground just in front of the door of the cafeteria," followed by "Once inside of the cafeteria, I was happy to see that there were few students queuing"). Although in most cases this segmentation procedure was obvious, we nevertheless assessed its reliability by asking a second trained rater to independently segment a random selection of 20% of verbal reports. The Intraclass Correlation Coefficient (ICC) computed on the number of experience units that were identified within verbal reports showed an excellent agreement between the two raters (ICC = 0.91).

In addition to computing the number of experience units reported by participants, we estimated the density of recalled experience units in the two episodic memory conditions by using temporal information associated with the pictures acquired during the walk. More specifically, for each trial, we estimated the actual event duration by calculating the amount of time between the beginning of each event and the end of the event. The beginning corresponded to the picture presented on the computer screen during each fMRI trial. The end of the event corresponded to the picture selected by participants as the last moment of the

experience they remembered in the scanner. Then, we estimated the density of recalled experience units as the number of experience units reported per minute of the actual event duration (Jeunehomme et al., 2018; Jeunehomme & D'Argembeau, 2019).

Behavioral data were analyzed using robust statistical methods (i.e., Yuen's *t* test) (Field & Wilcox, 2017) because the assumptions underlying classical inferential methods (normality and homoscedasticity) were violated for our main measures of interest (i.e., the number of reported experience units per minute of the actual event duration). These methods perform well in terms of type I error control and statistical power, even when the normality and homoscedasticity assumptions are violated (Erceg-Hurn & Mirosevich, 2008). All descriptive statistics refer to the 20% trimmed means and their 95% confidence intervals.

fMRI data acquisition

All MRI data were acquired on a whole-body 3T scanner (Magnetom Prisma, Siemens Medical Solutions, Erlangen, Germany) operated with a 20-channel receiver head coil. Multislice T2*-weighted functional images were acquired using a gradient-echo-planar imaging (EPI) sequence (TR = 1170 ms, TE = 30 ms, FA 90°, matrix size 72 × 72 × 36, voxel size 3 × 3 × 3 mm^3). Thirty-six 3 mm thick transverse slices (FOV 216 × 216 mm^2) were acquired, with a 25% interslice gap, covering the whole brain. Around 1400 functional volumes were obtained for the entire task and we dropped the five initial volumes to avoid T1 saturation effect. After image acquisitions, we generated field maps using a double echo gradient-recalled sequence (TR = 634 ms, TE = 10 and 12.46 ms, FoV = 192 × 192 mm^2, 64 × 64 matrix, 40 transverse slices with 3 mm thickness and 25% gap, flip angle = 90°, bandwidth = 260 Hz/pixel) that we used to correct echo-planar images for geometric distortion due to field inhomogeneities. Finally, we acquired a structural MR scan [T1-weighted 3D magnetization-prepared rapid acquisition gradient echo (MP-RAGE) sequence, TR = 1900

ms, TE = 2.19 ms, FOV 256 × 240 mm², matrix size 256 × 240 × 224, voxel size 1 × 1 × 1 mm]. All experimental stimuli were presented on a screen positioned at the rear of the scanner, which the subject could see through a mirror mounted on the head coil.

fMRI data preprocessing

Image preprocessing was performed using the SPM 12 software (Wellcome Department of Imaging Neuroscience, http//www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB R2017a. EPI time series were corrected for motion and distortion artefacts using Realign and Unwarp (Andersson et al., 2001) with the Fieldmap Toolbox (Hutton et al., 2002). The mean realigned EPI image was coregistered with the structural T1 image, and the coregistration parameters were applied to the realigned EPI time series. The T1 image was segmented into gray matter, white matter, and cerebrospinal fluid, using the unified segmentation approach (Ashburner & Friston, 2005), and we used the normalization parameters obtained from the segmentation procedure to normalize the functional images to MNI space (2×2×2 mm voxels). Finally, we performed a spatial smoothing of functional images using an 8 mm FWHM Gaussian kernel.

For the representational similarity analyses, volumes coregistered to the first scan of each subject were used to perform the searchlight in the native space of each subject. To exclude variance explained by motion, regressors from motion correction were used as predictors in a GLM for the voxel time series in every voxel. The resulting residuals were then used as the final input for the analyses. To exclude that the searchlight results are influenced by condition differences in motion inside the MRI we analyzed the motion parameters resulting from fMRI preprocessing. As the assumptions for an analysis of variance (ANOVA) were violated we evaluated motion effects with a non-parametric permutation test

using ez-Perm (Lawrence, 2016) in R (R Core Team, 2021). No significant differences of the motion regressor between the three conditions were found.

fMRI data analyses

Univariate analyses

Univariate analyses were performed using SPM 12. For each participant, BOLD responses were modeled at each voxel, using a general linear model (GLM). The memory/scene representation phase of each trial was modeled separately for each condition (i.e., action, spatial displacement, waiting, and scene representation) as epoch-related responses (beginning at the key press and ending at the second sound signal after 12 seconds) and convolved with the canonical hemodynamic response function to create the regressors of interest. Trials for which participants did not press the response button to indicate that they identified the picture and trials for which ratings indicated that they did not perform the requested task were modelled in a separate regressor of no interest. This corresponds to trials for which they provided a rating of 1 or 2 in the two episodic memory conditions (indicating that they mentally represented only one single moment of past experience), or a rating of 3 or 4 in the scene condition (indicating that they mentally represented the unfolding of several moments of past experience). Experimental phases corresponding to the presentation of the pictures and the presentation of the Likert scales were also modelled as epoch-related responses with two regressors of no interest (i.e., a single regressor for each phase across all conditions). Finally, we also modelled the two beeps presented respectively at the beginning and the end of each task as an event-related response, with a single regressor across all conditions. Finally, the design matrix included the realignment parameters to account for any residual movement-related effect. The canonical hemodynamic response function was used

and a high-pass filter was implemented using a cutoff period of 128 seconds to remove low-frequency drifts from the time series.

A series of linear contrasts was computed to identify the brain regions involved in the processing of episodic versus scene representations, and in the retrieval of actions versus spatial displacements. More specifically, we first investigated brain regions showing higher activity during each episodic memory condition compared to scene representation (i.e., Action > Scene; Spatial displacement > Scene). Next, we examined brain regions showing differential activity during the retrieval of the goal-directed actions and spatial displacements (Action > Spatial displacement, and vice versa).

The contrasts of interest were first computed for each participant and were then entered into random effects one-sample *t*-tests. For all analyses, statistical parametric maps (SPMs) were thresholded at $p < .001$, uncorrected, and statistical inferences were corrected for multiple comparisons at the voxel level ($p < .05$, FWE-corrected) using a small volume correction (SVC) within a priori regions of interest. These a priori regions of interest corresponded to brain areas that have been previously related to autobiographical memory, as determined by a meta-analysis of 84 studies performed with Neurosynth (www.neurosynth.org) (Yarkoni et al., 2011). Only clusters with a size of k > 15 voxels are reported.

Representational Similarity Analysis

In addition to the univariate analyses, we conducted a representational similarity analysis, a well-established method to study neural representational structures in brain activity patterns (Kriegeskorte & Kievit, 2013). First, we used this method to assess whether the different conditions (i.e., mental representations of Actions, Spatial Displacements, and Scenes) showed distinct patterns of voxel activity during the recall period. This would

substantiate further analysis of the temporal dynamics of multi-voxel pattern activity (see below). We computed a single-trial GLM for each subject with one regressor for each recall period of 12 seconds, resulting in 60 beta weights for each subject. Within the autobiographical network mask, we tested whether trials within one condition were more similar to each other compared to trials of other conditions. We calculated the cross-correlation between all trials using spearman rank correlations, resulting in a 60 x 60 matrix. Correlation coefficients between all pairs of trials in each condition were used to build the mean within-condition correlation coefficient. Correlations of each trial with itself were excluded before computing the mean. To generate between-condition correlation coefficients, trials of one condition were correlated to trials of the other conditions. Differences for within and between condition similarities were analyzed using a repeated measures ANOVA implemented in the ez-package (Lawrence, 2016) in R (R Core Team, 2021).

Analysis of temporal dynamics

Next, we investigated the temporal dynamics of patterns of brain activity during the memory/scene construction period by computed correlations between consecutive MRI volumes during the recall phase. We expected dynamic and high-density events to show higher differences in brain activity patterns across time, as indicated by smaller volume to volume correlations. The analysis was limited to grey matter voxels by applying a subject specific grey matter mask segmented using Freesurfer (version 6) (Fischl, 2012). We constructed a sphere with a radius of 6 voxels which was centered at each voxel. If the sphere consisted of fewer than 20 voxels no further analysis was performed at this location. At each valid sphere location, 10 consecutive volumes from the recall period, starting with the fifth volume after the recall onset to account for the delay of the hrf, were used to compute a 10x10 cross-correlation matrix (Figure 4A). To analyze consecutive changes in voxel patterns, the

first off-diagonal was used to extract Spearman's rank correlations of each volume with the next (i.e., volume 5 was correlated with volume 6; volume 6 with volume 7; etc.). Then, we computed the mean over the first off-diagonal for the resulting 9 volume-to-volume correlations. This was done for each trial in each condition. In a final step, the mean over all fisher-z-transformed volume-to-volume correlations in all trials per condition was saved at the current sphere location. Thus, three correlation coefficient maps, one per condition, were created for each subject. For group level analysis, the subject-wise correlation coefficient maps were normalized to the FSL standard 2mm 152 MNI template using a non-linear registration in FSL (version 5.0.9, http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/).

On the group level, the correlation coefficient maps were used to identify regions with consistent differences in correlations between the conditions. Using *randomise* in FSL (Winkler et al., 2014), a non-parametric version of the paired one-sample t-test for each condition pairing was conducted. *Randomise* analysis was performed using 10,000 random sign-flips and threshold-free cluster enhancement (TFCE) (Smith & Nichols, 2009) was used to identify significant clusters. TFCE has been shown to be more sensitive than clusterwise thresholding methods by taking both voxelwise signal strength and extent of neighboring voxels into account without relying on an absolute threshold (Smith & Nichols, 2009). All results reported are FWE corrected based on TFCE and thresholded at $p < 0.05$ to control for multiple comparisons. We used the Harvard-Oxford Cortical Structural atlas (Desikan et al., 2006) for anatomical labels.

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