Processing of Different Temporal Scales in the Human Brain

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Abstract

■ While recalling life events, we reexperience events of different durations, ranging across varying temporal scales, from several minutes to years. However, the brain mechanisms underlying temporal cognition are usually investigated only in small-scale periods—milliseconds to minutes. Are the same neurocognitive systems used to organize memory at different temporal scales? Here, we asked participants to compare temporal distances (time elapsed) to personal events at four different temporal scales (hour, day, week, and month) under fMRI. Cortical activity showed temporal scale sensitivity at the medial and lateral parts of the parietal lobe, bilaterally. Activity at the medial parietal cortex also showed a gradual progression from large- to small-scale processing, along a posterior–anterior axis. Interestingly, no sensitivity was found along the hippocampal long axis. In the medial scale-sensitive region, most of the voxels were preferentially active for the larger scale (month), and in the lateral region, scale selectivity was higher for the smallest scale (hour). These results demonstrate how scale-selective activity characterizes autobiographical memory processing and may provide a basis for understanding how the human brain processes and integrates experiences across timescales in a hierarchical manner. ■

INTRODUCTION

We live our life through time. We grow, age, and collect experiences over the years. These experiences are composed of extended events, ranging usually from several minutes to hours (Bergson, 2014; Husserl, 2012; Varela, 1999). In the scientific investigation of temporal cognition, experiments usually take place across several dozens of minutes, whereas measurements (RTs, neural activities) are in the millisecond range. Attempts to study the difference between processing of different timescales ranged from hundreds of milliseconds to tens of seconds (Nani et al., 2019; Wittmann, 2013; Gooch, Wiener, Hamilton, & Coslett, 2011; Wiener, Matell, & Coslett, 2011; Danckert et al., 2007; Ivry & Spencer, 2004; Ulanovsky, Las, Farkas, & Nelken, 2004), timescales that can still be measured within the laboratory. However, how does the brain organize experiences across longer periods? In addition, how is the processing of shorter and longer periods related?

Several main theories have attempted to answer these questions. The discovery of time cells in rat hippocampus, firing for fixed periods every several seconds (Eichenbaum, 2014, 2017; MacDonald, Lepage, Eden, & Eichenbaum, 2011), suggested that such cells may account for timing not only in this level but also across minutes, hours, and even longer periods (unified representation theory; Spalla, Dubreuil, Rosay, Monasson, & Treves, 2019; Kinsky, Sullivan, Mau, Hasselmo, & Eichenbaum, 2018; Rangel et al., 2014; Ziv et al., 2013; Mankin et al., 2012; Manns, Howard, & Eichenbaum, 2007). On the other hand, neuroanatomical evidence collected separately for the different timescales suggests that distinct systems process each timescale (distinct representation theory). In the milliseconds-to-minutes scale, involvement of the visual system and lateral parietal regions was found (Grossman, Gueta, Pesin, Malach, & Landau, 2019; Nani et al., 2019; Wittmann, 2013; Ulanovsky et al., 2004). Discrimination in the hundreds of milliseconds range elicited frontal activations (van Wassenhove, Herbst, & Kononowicz, 2019; Ng & Penney, 2014; Pouthas et al., 2005); at the scale of memory across years, functional imaging highlighted activations at the medial temporal lobe, TPJ, lateral temporal cortex, insula, and pFC (Bellmund, Deuker, & Doeller, 2019; Gauthier, Pestke, & van Wassenhove, 2019; Gauthier & van Wassenhove, 2016; Peer, Salomon, Goldberg, Blanke, & Arzy, 2015; Arzy, Collette, Ionta, Fornari, & Blanke, 2009; Bueti & Walsh, 2009). Evidence from patients with disorientation disorders in time further shows that temporal disorientation can be limited to a specific scale, according to the underlying lesion (Peer, Lyon, & Arzy, 2014); for example, patients with lesions in the CA1 part of the hippocampus show disorientation in the immediate and recent (hours) timescale (Peer, Nitzan, et al., 2014; Bartsch, Alfke, Deuschl, & Jansen, 2007); in contrast, patients with insular

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and lateral parietal cortex lesions are impaired in age perception in the years range (Naveh & Arzy, 2019; Zangwill, 1953). A similar notion was suggested for the autobiographical memory-related time range of days, weeks, months, and years. The leading hypothesis suggests multiple temporal "codes" for these durations (Conway & Pleydell-Pearce, 2000; Friedman, 1987; Friedman & Wilkins, 1985), because these codes depend on multiple sources of information (e.g., memory trace strength, shared contexts, interevent links [chaining], time tags, intertemporal choice, and temporal discounting; Bulley & Schacter, 2020; D'Argembeau, 2012, 2020; Schacter et al., 2012). The logarithmic character of the mental time line (Gauthier & van Wassenhove, 2016; D'Argembeau, Jeunehomme, Majerus, Bastin, & Salmon, 2015; Arzy, Adi-Japha, & Blanke, 2009) may suggest a bipartition for the time range closer to the "now" on the one hand and the logarithmic series distribution's tail on the other. Another kind of bipartition of the memory time code are "forward" and "backward" forms (see Arzy, Molnar-Szakacs, & Blanke, 2008; Friedman, 1993). A simpler hypothesis suggests a uniform code for time in which long and short timescales are coded similarly. Several neuroimaging studies have investigated the neural correlates of temporal order memory for autobiographical events (D'Argembeau et al., 2015; Nielson, Smith, Sreekumar, Dennis, & Sederberg, 2015; St. Jacques, Rubin, LaBar, & Cabeza, 2008). These studies have shown activations mainly in the precuneus, pFC, visual cortex, and hippocampus during temporal order tasks. St. Jacques et al. (2008) differentiated between long and short lags, yet both were within the hour timescale; D'Argembeau et al. (2015) compared past and future temporal order in the days scale and highlighted temporal order to be reflected in the left posterior hippocampus. Nielson et al. (2015) showed a temporal order for time range in between hours and a month only within the left anterior hippocampus; however, this study focused on analyses of the hippocampus, leaving out cortical representations.

Drawing a parallel with spatial receptive fields, the temporal receptive window (TRW) theory suggests a distributed and hierarchical organization of the different timescales, with short timescales (hundreds of milliseconds) represented in primary sensory areas and longer timescales (minutes) represented in higher sensory areas (Baldassano et al., 2017; Chen et al., 2016; Hasson, Chen, & Honey, 2015; Gauthier, Eger, Hesselmann, Giraud, & Kleinschmidt, 2012; Lerner, Honey, Silbert, & Hasson, 2011; Hasson, Yang, Vallines, Heeger, & Rubin, 2008). This so-called gradient of increasing temporal window size was also described from primary sensory to frontal regions and was shown to follow a scale-free distribution ($1/f$; La Rocca, Zilber, Abry, van Wassenhove, & Ciuciu, 2018). In addition, similar gradients of temporal processing were suggested to underlie hierarchical planning in pFC (Wood & Grafman, 2003; Fuster, 2001; Miller & Cohen, 2001). TRW, however, was not extended to periods longer than minutes. Recently, we studied the representation of different spatial scales, from room and building through neighborhood and city to country and continent (Peer, Ron, Monsa, & Arzy, 2019). Similarly to the TRW theory, our results demonstrated gradual progression from small- to large-scale processing, along three gradients extending anteriorly in three scene-responsive brain regions (the retrosplenial cortex, parahippocampal place area [PPA], and occipital place area) and along the hippocampus posterior–anterior axis (Peer et al., 2019). Is this also the case with respect to time? Does temporal cognition rely on a unified system? Or perhaps different cortical regions manage each timescale? In the current work, we sought to characterize human brain activity under ecologically valid experimental settings, across a large range of periods, when directly manipulating only the parameter of temporal scale. To obtain ecological validity, we recruited participants in the same age range who recently completed several months of travel abroad. This enabled us to compare judgments of temporal distances between clearly defined real-life experiences that happened during their trip, across four temporal scales (hours, days, weeks, and months; Figure 1; Friedman, 1987, 2004; Friedman & Wilkins, 1985). We looked for differences in brain response for the different scales to decide whether the underlying system is compatible with either the unified, the distinct, or the gradient/TRW timescale theories.
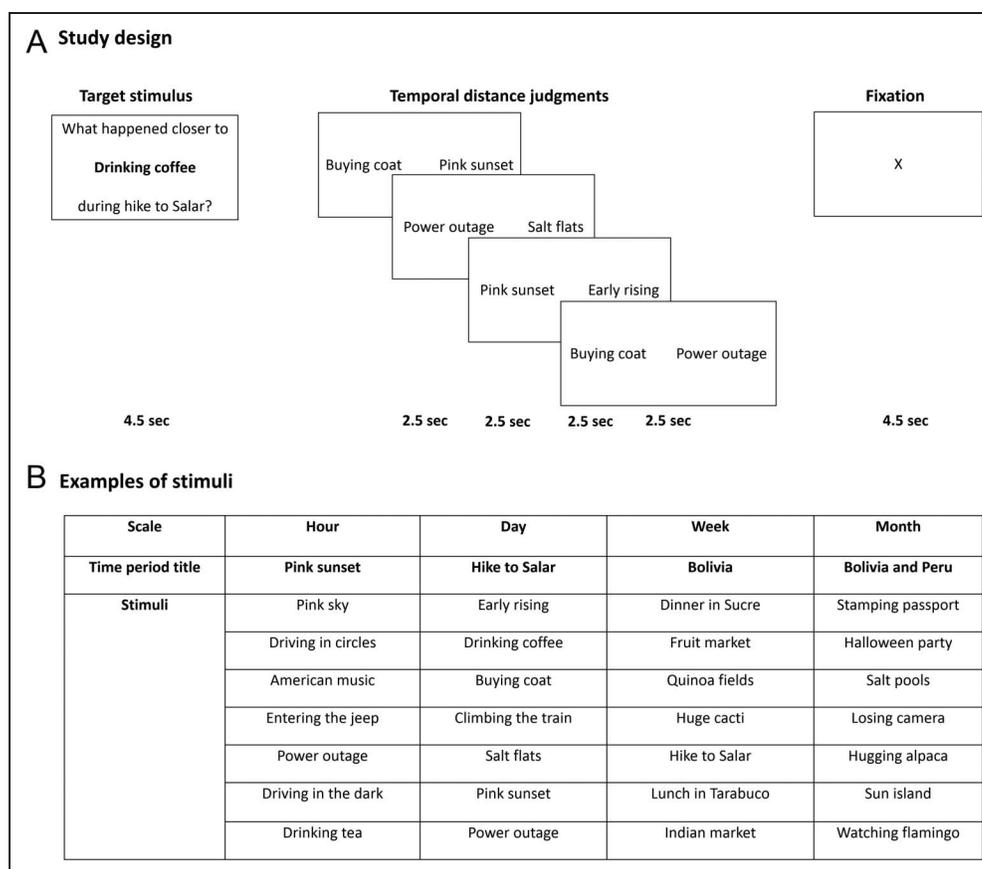
METHODS

Participants

Sixteen healthy participants (13 women, mean age = 24.8 ± 2.2 years), who traveled in the last 4 years for a long period (3–9 months), participated in the study. All participants provided written informed consent, and the study was approved by the ethics committee of the Hadassah Hebrew University Medical Center in conformity with the Declaration of Helsinki (2013).

Experimental Stimuli

Four temporal scales were investigated, representing four ecologically valid durations: hour, day, week, and month (Friedman, 1987, 2004; Friedman & Wilkins, 1985). A week before the experiment, participants were asked to provide, for each timescale, two highly vivid circumscribed periods that took place while they were travelling (e.g., Dinner in Cusco at Jack's Cafe [hours], Day hike to Laguna 69 [day], A week at El Chalten village [week], A month in Argentina [month]). For each of these eight periods, participants provided descriptions of eight distinct events that occurred during these periods and whose temporal order they remembered (e.g., "ordered veggie burger" in "Dinner at Jack's Cafe," "buying empanadas" in "Day hike to Laguna 69"; Figure 1). Participants were explicitly instructed to select events that spanned the entirety of the temporal scale. A test on a subsample of four participants who indicated the specific times in which events occurred demonstrated that the participants did comply with this

Figure 1. Study design and stimuli. (A) Study design. In each block, participants viewed one anchor item in a specific scale and period and then performed four temporal proximity comparisons for pairs of other items from the same period. All stimuli were provided by the participants from events experienced while they were travelling, and anchor and comparison items were chosen randomly from the participants' stimuli set. (B) Examples of stimuli (participant-provided periods and stimuli) in each temporal scale.

A **Study design**

| Target stimulus | Temporal distance judgments | Fixation |

What happened closer to **Drinking coffee** during hike to Salar?

Buying coat — Pink sunset
Power outage — Salt flats
Pink sunset — Early rising
Buying coat — Power outage

x

4.5 sec   2.5 sec   2.5 sec   2.5 sec   2.5 sec   4.5 sec

B **Examples of stimuli**

Scale	Hour	Day	Week	Month
Time period title	**Pink sunset**	**Hike to Salar**	**Bolivia**	**Bolivia and Peru**
Stimuli	Pink sky	Early rising	Dinner in Sucre	Stamping passport
	Driving in circles	Drinking coffee	Fruit market	Halloween party
	American music	Buying coat	Quinoa fields	Salt pools
	Entering the jeep	Climbing the train	Huge cacti	Losing camera
	Power outage	Salt flats	Hike to Salar	Hugging alpaca
	Driving in the dark	Pink sunset	Lunch in Tarabuco	Sun island
	Drinking tea	Power outage	Indian market	Watching flamingo

instruction: Stimuli spanned all periods when dividing them to four quadrants (no significant difference from a uniform distribution, chi-square goodness-of-fit test, all $ps > .05$). They were additionally asked to keep the descriptions short (one to three words) and make sure they represent a unique event. All 16 participants provided all of the required stimuli.

Experimental Paradigm

During the experiment, participants were presented with an anchor stimulus consisting of one of the event descriptions they had provided and its respective period, followed by a pair of other stimuli from the same period on the left and right of the screen (Figure 1A and 1B). In a temporal comparison task, participants were asked to indicate which of the two stimuli happened temporally closer to the anchor stimulus (irrespective of their order of occurrence) by pressing the left or right buttons.

Stimuli were presented in a randomized block design. Each block started by presentation of an anchor stimulus for 4.5 sec, followed by a consecutive presentation of four stimuli pairs, each for 2.5 sec (Figure 1A). All stimuli within the same block had to be judged in relation to the block's anchor stimulus time. Each block (14.5 sec) was followed by 4.5 sec of fixation. Participants were instructed to respond accurately, but as fast as possible. The experiment consisted of five experimental runs for each participant, with each run containing 24 blocks in a randomized order (three blocks for each of the eight periods = six blocks in each temporal scale). Anchor items and stimuli pairs were chosen independently and randomly from the eight items the participant provided for each timescale. In addition, participants performed a lexical control task in a separate run, in which they viewed similar anchor stimuli followed by stimuli pairs but were instructed to indicate which of the pair of words is closer in length to the anchor stimulus. A training task using pairs of stimuli derived from the same pool was delivered before the experiment; participants performed the training until they indicated that they felt comfortable doing the task. Stimuli were presented using the Presentation software (Version 18.3, Neurobehavioral Systems, Inc., www.neurobs.com). After the experiment, participants rated the emotional significance of the period, the level of difficulty of judgments at each period, and the vividness of the memory of each period (from 1 to 7). They were also asked to describe the strategy used for determining responses in each of the four temporal scales (free description) and specifically to what extent they used the location of the events to determine responses (spatial strategy; 1–7 ratings).

MRI Acquisition

Participants were scanned in a 3-T Siemens Skyra MRI at the Edmond and Lily Safra Center neuroimaging unit. BOLD

contrast was obtained with an EPI sequence (repetition time [TR] = 2500 msec; echo time = 30 msec; flip angle = 75°; field of view = 192 mm; matrix size = 64 × 64; functional voxel size = 3 × 3 × 3 mm; 46 slices, descending acquisition order, no gap; 200 TRs per run). In addition, T1-weighted high-resolution (1 × 1 × 1 mm, 160 slices) anatomical images were acquired for each participant using the magnetization prepared rapid gradient echo protocol (TR = 2300 msec, echo time = 2.98 msec, flip angle = 9°, field of view = 256 mm).

MRI Processing

fMRI data were analyzed using the BrainVoyager 20.6 software package (R. Goebel, Brain Innovation), Neuroelf v1.1 (www.neuroelf.net), and in-house MATLAB (The MathWorks) scripts. Preprocessing of functional scans included slice timing correction (cubic spline interpolation), 3-D motion correction by realignment to the first run image (trilinear detection and sinc interpolation), high-pass filtering (up to two cycles), smoothing (FWHM = 4 mm), exclusion of voxels below intensity values of 100, and co-registration to the anatomical T1 images. Anatomical brain images were corrected for signal inhomogeneity and skull-stripped. All images were subsequently normalized to Montreal Neurological Institute (MNI) space (functional resolution = 3 × 3 × 3 mm, trilinear interpolation).

fMRI Analyses

Estimation of Cortical Responses to Each Temporal Scale

A general linear model (GLM) analysis (Friston et al., 1994) was applied at each voxel, where predictors corresponded to the four temporal scales. Each modeled predictor included all experimental blocks at one temporal scale, where each block was modeled as a boxcar function encompassing the anchor stimulus and the four temporal distance comparisons following it. Predictors were convolved with a canonical hemodynamic response function, and the model was fitted to the BOLD time course at each voxel. Motion parameters were added to the GLM to eliminate motion-related noise. In addition, white matter and CSF masks were manually extracted in BrainVoyager for each participant (intensity > 150 for the white matter mask and intensity < 10 with a bounding box around the lateral ventricles for CSF), and the average signals from these masks were added to the GLM to eliminate potential noise sources. Data were corrected for serial correlations using the AR(2) model and transformed to units of percent signal change. Subsequently, a random effects analysis was performed across all participants to obtain group-level beta values for each predictor. This analysis yielded five beta estimates (one for each run) for each of the temporal scale conditions (hour, day, week, and month).

Identification of Voxels with Temporal Scale-sensitive Activity

To identify voxels with temporal scale-sensitive activity, we performed multivoxel pattern analysis to estimate the discriminability of the beta estimates using searchlight analysis for each participant (Kriegeskorte, Goebel, & Bandettini, 2006). This approach identifies voxels where the pattern of activation in its local neighborhood can discriminate between conditions. In this analysis, for each participant, the pattern of beta values from the eight conditions (two for each timescale) was extracted from a spherical ROI with a radius of 3 voxels centered in turn on each voxel in the brain, yielding eight multivoxel vectors. A linear discriminant analysis classifier was trained to discriminate between vectors related to the four different timescales. We used a leave-one-out cross-validation splitting: The classifier was trained using the data from four of the five runs and was subsequently tested on its accuracy at classifying the unseen data from the remaining run. The classification accuracy of each sphere was assigned to the central voxel. This procedure was repeated for every voxel in the brain yielding whole-brain classification accuracy maps for each participant. This analysis was performed using the CoSMoMVPA toolbox for MATLAB (Oosterhof, Connolly, & Haxby, 2016; Maris & Oostenveld, 2007).

To assess the statistical significance of searchlight maps across participants, all maps were corrected for multiple comparisons without choosing an arbitrary uncorrected threshold using threshold-free cluster enhancement (TFCE) on the cluster level (Smith & Nichols, 2009). A Monte Carlo simulation permuting condition labels was used to estimate a null TFCE distribution. First, 100 null searchlight maps were generated for each participant by randomly permuting condition labels within each obtained searchlight classification. Next, 100,000 null TFCE maps were constructed by randomly sampling from these null data sets to estimate a null TFCE distribution (Stelzer, Chen, & Turner, 2013), obtaining a group-level z-score map of the classifier results. Scale-sensitive voxels were chosen from the z-score map (z score = 3.8, $p < .005$). After voxel identification, beta values were averaged for each voxel across participants, and two methods were used to identify selectivity to temporal scale at each voxel: (1) fitting a Gaussian function to the betas' graph and identifying its peak and (2) selecting the scale with maximal activity. Gaussian fitting was performed for each beta vector after its normalization by subtracting its minimum value, and fitting was performed using MATLAB, with bounds of 0–100 for amplitude, −100 to 100 for center, and 0–100 for width. Only voxels with fit of $r^2 > .3$ were included in the subsequent analyses of Gaussian fit peaks and maximal beta values.

Measuring Shift in Scale Selectivity along Scale-sensitive Regions

Within the two identified scale-sensitive regions (medial parietal cortex [MPC] and lateral occipito-parietal cortex)

bilaterally, the peak of Gaussian fit and the scale with maximal response were averaged across all scale-sensitive voxels in each MNI coordinate along the y axis, resulting in vectors of scale selectivity across a posterior–anterior axis. A Pearson correlation coefficient was computed to assess the relationship between the location across the posterior–anterior axis (y axis MNI coordinate) and the averaged scale with maximal response.

Hippocampus-specific Analyses

To look for hippocampal involvement in the time-comparison task, we have (1) directly compared hippocampal response for the time task with a lexical control task,

by contrasting brain activity for the time-comparison task with a lexical control task (GLM contrast, all $ps < .01$, false discovery rate [FDR] corrected for multiple comparisons), and (2) applied an event-related averaging (ERA) analysis. For ERA, BOLD signals were averaged for all blocks containing each scale across all runs and participants, for the 10 functional volumes after each block's initial display of the target stimulus within the hippocampus.

Analyses of Potential Confounds

Each participant's ratings of difficulty, emotional significance, and vividness of the memory for each timescale were independently normalized by z-transform. The
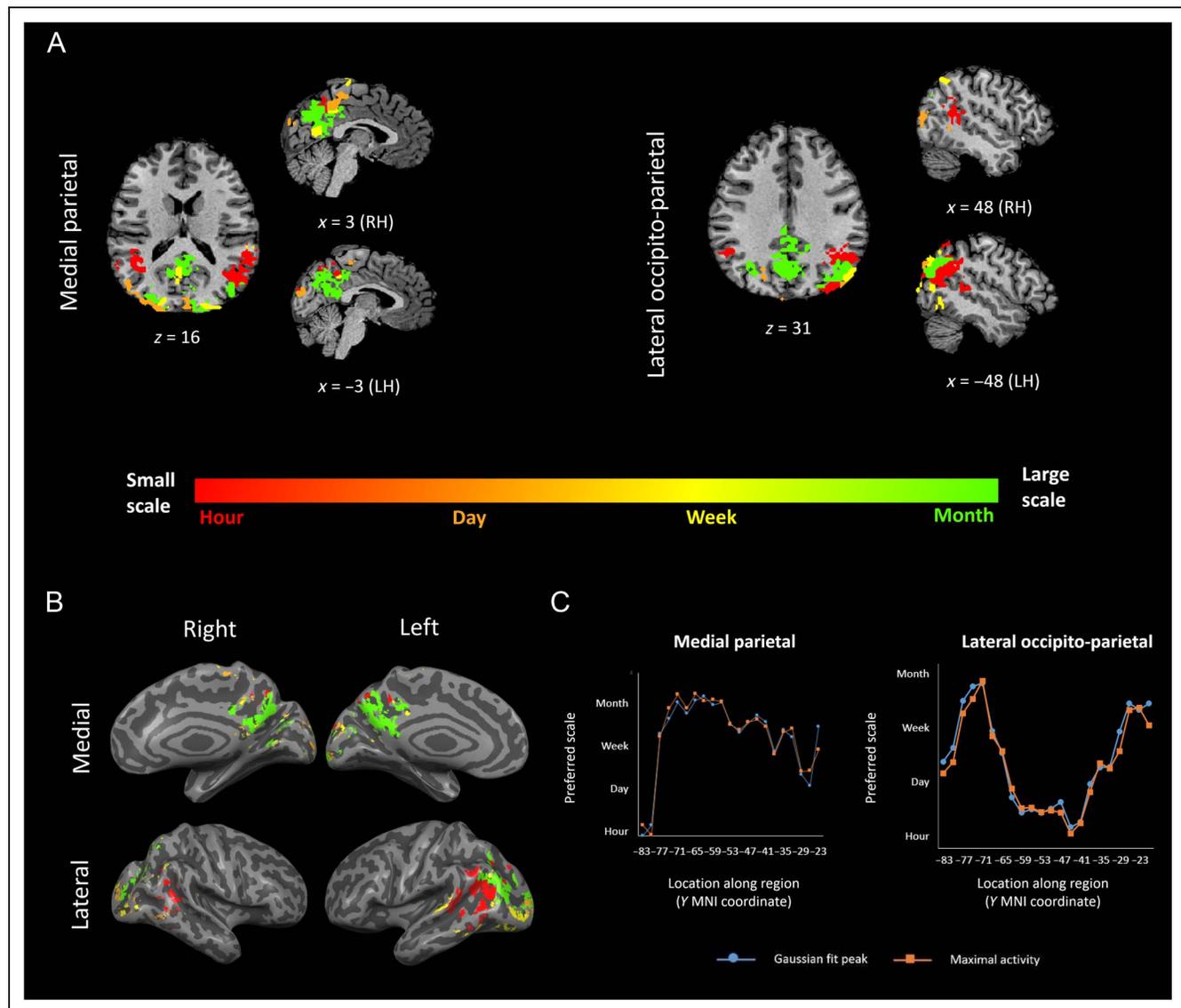
Figure 2. Temporal scale selectivity clusters. (A) Two cortical regions with temporal scale-sensitive voxels, the MPC (left) and the lateral occipito-parietal cortex (right), were identified by searchlight-based multivoxel pattern analysis, classifying between the four different temporal scales (z score = 3.8, TFCE-corrected, cluster threshold: 10 voxels). Colors indicate the temporal scale with maximal beta value at each voxel. (B) Surface view of all scale-selective cortical activations (including regions outside the two scale-sensitive regions). (C) Change in average temporal scale selectivity along the posterior–anterior axis of each region (x axis represents MNI coordinates from posterior to anterior, blue = average position of a Gaussian fit peak for all scale-sensitive voxels at each coordinate, orange = average position of scale with maximum activity for all scale-sensitive voxels at each coordinate). RH = right hemisphere; LH = left hemisphere.

Table 1. Coordinates of All Scale-selective Areas, Sorted by the Temporal Scale with Maximal Activity

MNI Coordinates			Activation Size (Voxels)	Region Name (AICHA Atlas)
x	y	z		
Scale 1: Hour				
62	−51	12	15	STS R
54	−51	29	23	Angular gyrus R
45	−48	15	58	STS R
17	−83	−27	22	Cerebellum
5	−54	46	37	Precuneus R
−5	−47	42	11	Precuneus L
−9	−70	47	32	Precuneus L
−8	−94	22	15	Superior occipital gyrus L
−33	−81	32	30	Middle occipital gyrus L
−51	−54	21	446	STS L
−43	−82	22	19	Middle occipital gyrus L
Scale 2: Day				
57	−57	−1	25	Middle temporal gyrus R
32	−89	11	104	Lateral occipital gyrus R
22	−72	27	13	Parieto-occipital sulcus R
3	−35	52	57	Cingulate sulcus R
0	−89	22	34	Cuneus L
−20	−93	4	112	Lateral occipital gyrus L
Scale 3: Week				
50	−57	47	20	Angular gyrus R
39	−85	0	18	Lateral occipital gyrus R
19	−92	20	26	Superior occipital gyrus R
1	−42	38	15	Precuneus R
4	−60	13	26	Precuneus R
−13	−60	67	24	Superior parietal gyrus L
−30	−85	−3	143	Lateral occipital gyrus L
−50	−69	37	38	Angular gyrus L
−41	−53	−27	14	Cerebellum
−49	−70	6	13	Inferior temporal gyrus L
−50	−64	−10	35	Inferior temporal gyrus L
−61	−28	9	20	Superior temporal gyrus L

Table 1. (*continued*)

MNI Coordinates			Activation Size (Voxels)	Region Name (AICHA Atlas)
x	y	z		
Scale 4: Month				
3	−58	28	642	Precuneus R
28	−86	11	70	Lateral occipital gyrus R
32	−68	−36	14	Cerebellum
22	−60	53	17	Intraparietal sulcus R
−22	−92	5	105	Lateral occipital gyrus L
−40	−72	28	274	Angular gyrus L

Activation clusters with less than 3 voxels are not shown. Labels are by the AICHA (Atlas of Intrinsic Connectivity of Homotopic Areas) parcellation atlas (Joliot et al., 2015). Coordinates indicate location of center of mass for each cluster. L = left; R = right.

resulting values were then added as separate parametric modulation regressors (after convolution with the hemodynamic response function) to the original scale-specific design matrix, according to each experimental block's temporal scale and specific period. A RT predictor was added in a similar manner according to each trial's RT. Random effects group analysis (corrected for serial correlations, AR(2)) was then performed using the new design matrix within each scale-sensitive ROI identified earlier, to identify activity modulation by each potential confound. In addition, one-way ANOVA (Tukey–Kramer post hoc test, $p < .01$) was used to identify significant differences in the ratings between the four temporal scales.

Comparison of Scale-selective Activations to Large-scale Resting-state Networks

A previously published whole-brain parcellation into seven large-scale brain networks was used as a template for resting-state networks' location (Yeo et al., 2011). For each scale-selective area, the percentage of overlap with each of the seven resting-state networks was measured (percentage of voxels from this region within each network).

Comparison of Activity to the Lexical Control Task

Regressors for the lexical control were added to the scale predictors in the GLM analysis, and a new design matrix was computed for each participant. A group analysis (corrected for serial correlations, AR(2)) was performed in each scale-selective area. We used paired two-tailed t tests between the average beta values of each area's preferred scale and the average beta values corresponding to the respective control condition (FDR-corrected for multiple comparisons across areas). In addition, to identify regions that were engaged in the task and not only areas that were scale selective, we contrasted brain activity for the time-comparison task with the lexical control task (GLM contrast, all $ps < .01$, FDR-corrected for multiple comparisons).

RESULTS

Two Scale-sensitive Cortical Regions

To investigate temporal scale-sensitive activity, we looked for voxels showing difference in response to task performance at the different scales and characterized their response profiles by choosing the scale with maximal response. This analysis identified two main cortical regions that displayed temporal scale sensitivity: the MPC and the lateral occipito-parietal cortex bilaterally (Figure 2A and B; for a complete list see Table 1). In addition, activity in the medial parietal region displayed a gradual posterior–anterior shift of selectivity between the different temporal scales (hour, day, week, and month; Figure 2C). Fitting a Gaussian function to the beta value graphs at each voxel also demonstrated the same response along the two scale-sensitive regions (Figure 2C). A negative correlation was found between the y axis MNI coordinate and the preferred scale (Pearson correlation coefficient $r = -.72, p < .001$). No gradient-like activity within the two scale-sensitive regions was found along the x and z axes. To further examine the relation between these regions and temporal cognition, we compared brain activity related to the temporal comparison task to a lexical control task. This contrast revealed significant activations within the two scale-sensitive regions as well as several other regions including the right parahippocampal gyrus and the middle temporal gyrus bilaterally (GLM contrast, all ps < .01, FDR-corrected for multiple

comparisons; Table 2). Analysis of the lexical control task within the two scale-sensitive regions revealed significantly higher activity for the temporal comparison task in all scale-selective areas except of the day- and week-related regions in the medial parietal region (paired two-tailed t test, all ps < .05, FDR-corrected for multiple comparisons across regions). Finally, despite a previously identified gradient organization of spatial scales along the long axis of the hippocampus (Peer et al., 2019; Brunec et al., 2018) and known hippocampal involvement in autobiographical memory, no scale-selective activity was identified at this region for any timescale (see Discussion section for possible explanations). To further look for hippocampus involvement in the temporal comparison task, we have (1) directly compared the hippocampal response for the time task with a lexical control task and (2) applied an ERA analysis. Both analyses did not reveal any significant hippocampal activity.

Differences in Scale Selectivity between the Two Scale-sensitive Regions

The previous analyses identified two cortical regions with scale sensitivity. We next attempted to identify differences between these two regions that may indicate their function in temporal cognition. To this aim, we analyzed the number of voxels with preferential activity for each scale within each region. The number of voxels with preferential activity

Table 2. Pairwise Contrast of Experimental Conditions

Region Name (AAL3 Atlas)	MNI Coordinates			Activation Size (Voxels)
	x	y	z	
Precuneus L	1	−63	18	2376
Middle temporal gyrus L	−57	−6	−16	297
Middle temporal gyrus L	−58	−42	6	54
Parahippocampal gyrus R	29	−34	−13	54
Inferior frontal gyrus L	−44	17	25	108
Inferior frontal gyrus R	35	19	23	729
Angular gyrus L	−41	−70	36	108
Angular gyrus R	44	−71	41	108
Superior frontal gyrus L	−25	−5	60	378
Superior frontal gyrus R	24	23	44	54
Superior frontal gyrus R	18	−9	67	81
Superior temporal gyrus R	58	−6	−13	216
Fusiform gyrus L	−30	−38	−16	108
Thalamus L	−7	−7	4	405

Brain regions involved in the temporal task as compared to the lexical control task are listed, with MNI coordinates and number of voxels involved. Activation clusters with less than 3 voxels are not shown. Labels are by the AAL3 parcellation atlas (Rolls, Huang, Lin, Feng, & Joliot, 2020; Tzourio-Mazoyer et al., 2002). Coordinates indicate location of center of mass for each cluster.

Table 3. Lateralized Distribution of Scale-selective Areas

	Left Hemisphere					Right Hemisphere				
Scale-selective Area	Hour	Day	Week	Month	All Scales	Hour	Day	Week	Month	All Scales
MPC										
Activation size (voxels)	100	43	81	392	616	54	99	51	241	445
Percentage of voxels	16%	7%	13%	64%	100%	12%	22%	11%	54%	100%
Lateral Occipito-parietal Cortex										
Activation size (voxels)	673	133	316	342	1464	173	87	95	95	450
Percentage of voxels	46%	9%	22%	23%	100%	38%	19%	21%	21%	100%

Activation size of scale-selective areas in each hemisphere within the two scale-sensitive regions is detailed. Whereas areas in the left hemisphere were larger than those in the right hemisphere, relative distribution was found to be similar in between hemispheres.

for each scale within each region was similarly distributed in between hemispheres (Table 3). Therefore, we further analyzed this distribution in a bilateral manner (Figure 3). The medial parietal region was mostly active for the month scale (59%), indicating a role for this region in processing large temporal scales. In contrast, the lateral occipito-parietal region contained mostly voxels selective to scales at the hour scale, the smallest scale in the current experiment (49%). These findings demonstrate that the two scale-sensitive cortical regions have different scale preferences, indicating possible different temporal processing functions.

Overlap of Scale-selective Activations with the Default-Mode Network

To relate the two scale-sensitive regions to large-scale brain organization, we compared their anatomical distribution to a parcellation of the brain into seven cortical networks (as derived out of resting-state fMRI). This analysis indicated

that the two scale-sensitive regions overlap mainly with the default-mode network (DMN). Within the two scale-sensitive regions, in the medial parietal region, the main overlap with the DMN involved the largest scale-selective area (the month scale), whereas in the lateral parietal region, overlap involved mostly the smaller scales (hour, day, and week; Table 4).

Behavioral Ratings and Their Relation to the Scale Effects

Analysis of participants' ratings of emotional significance, task difficulty, and vividness of memories for each temporal period indicated no significant differences between scales (Figure 4A–D; all $ps > .05$, one-way ANOVA; Tukey–Kramer post hoc test). RTs did not significantly differ between scales (Figure 4E). In a parametric modulation analysis using participants' ratings, no factor showed any significantly active region.

Figure 3. Preferred temporal scale at the two scale-sensitive cortical regions. The maximal beta values at each voxel were used to quantify the preferential activity to each temporal scale. Percentage of voxels with maximal activation for each temporal scale is shown for each scale-sensitive region. Results indicate that the two regions demonstrate preference for processing different temporal scales: The medial parietal gradient mostly represents scales at the largest (month) level, and the lateral occipito-parietal regions mostly represent scales at the smallest (hour) level.
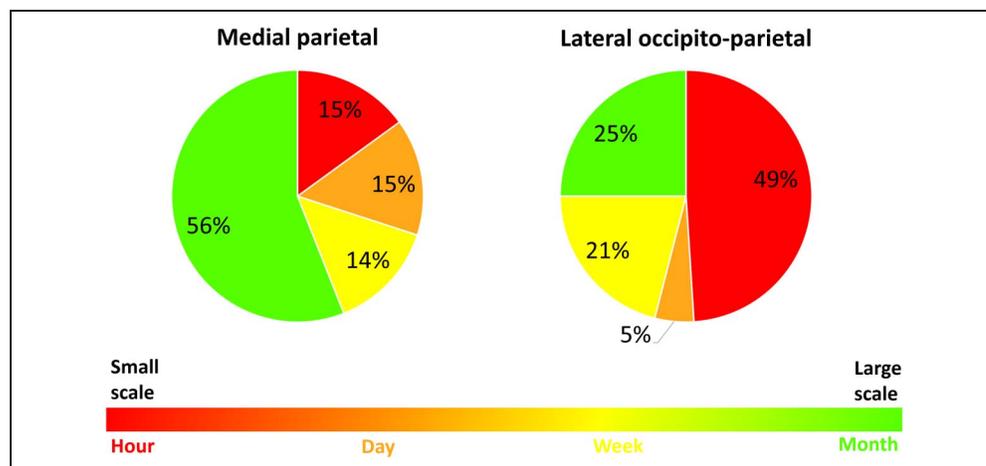
Table 4. Scale Selectivity and the DMN

	Medial Parietal Region				Lateral Occipito-parietal Region			
	Hour	Day	Week	Month	Hour	Day	Week	Month
Visual network	9%	15%	13%	13%	1%	0%	7%	7%
DMN	34%	23%	35%	73%	54%	36%	52%	31%
Dorsal attention network	29%	12%	34%	3%	16%	22%	24%	29%
Frontoparietal control network	21%	18%	7%	1%	5%	0%	10%	6%
Medial-temporal-orbitofrontal network	0%	0%	0%	0%	0%	0%	0%	0%
Ventral attention network	2%	7%	1%	1%	12%	39%	0%	8%
Sensorimotor network	5%	25%	10%	0%	12%	3%	7%	19%

Percentage of overlapping voxels between each scale-selective area (within the two scale-sensitive regions) and a cortical parcellation to seven large-scale brain networks (Yeo et al., 2011). Maximal overlap was found with the DMN, mostly for the month scale in the medial parietal region.

Figure 4. Behavioral results. Participants' ratings of difficulty (A), emotional valence (B), vividness of memory (C), and use of a spatial strategy (D) for each timescale used in the experiment, and average participants' RTs (seconds) in each of the four conditions (E). Error bars represent *SEM*s across participants. No significant differences were identified between scales in any of the behavioral parameters (all $ps > .05$, one-way ANOVA, Tukey–Kramer post hoc test). Analysis of participants' responses regarding any additional strategy used in their response (e.g., imagining a timeline, social context) did not elucidate any significant difference between strategies.
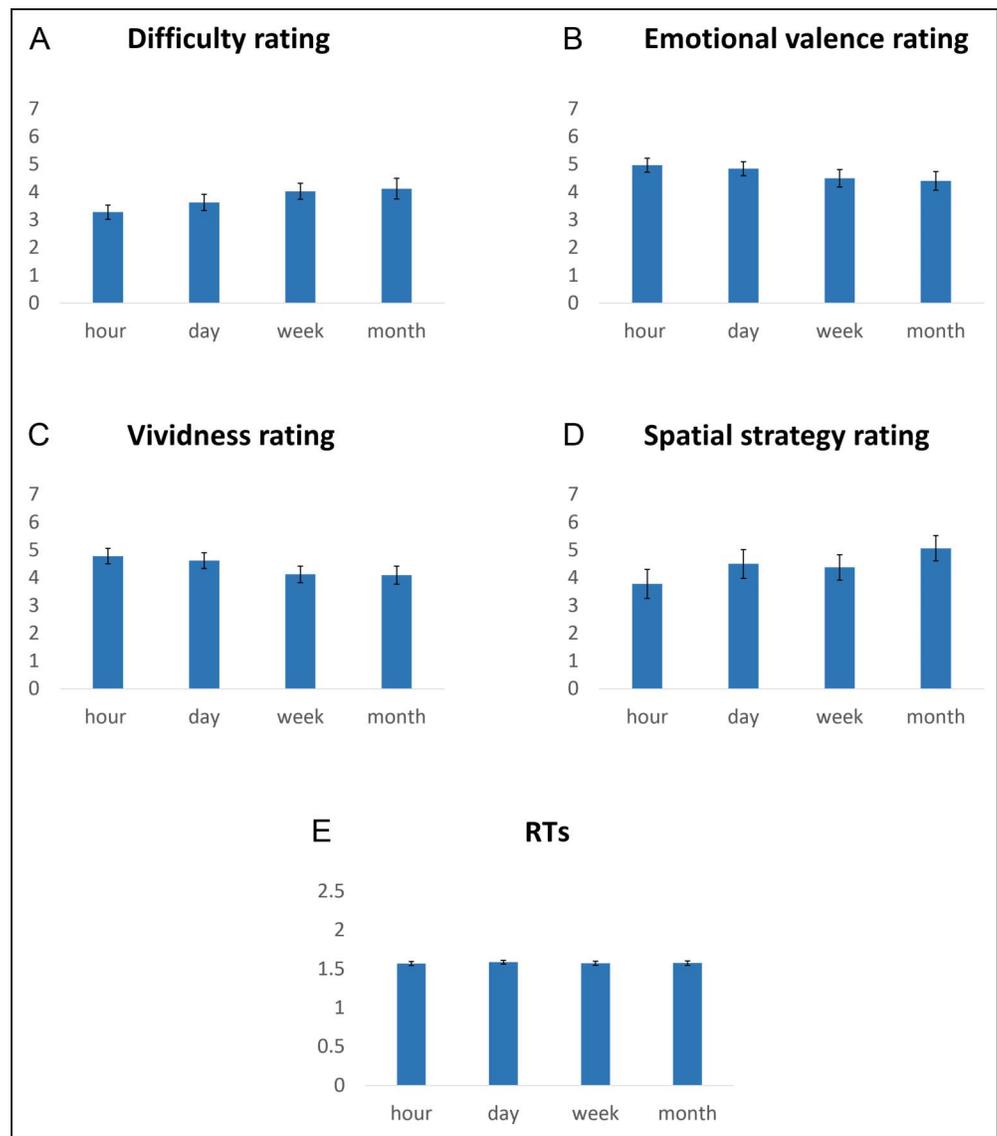
DISCUSSION

Our investigation into the question of temporal processing across various timescales revealed several novel findings. First, two cortical regions in the MPC and the lateral occipito-parietal cortex were found to be sensitive for specific temporal scales. Second, the medial parietal scale-sensitive region was found to be organized along a posterior–anterior cortical gradient, extending anteriorly at the MPC. This gradient was organized such that its posterior part was most active for the larger temporal scales and the anterior part most active for the smaller scales. Finally, temporal scale selectivity was differentially distributed between the two regions, with the medial parietal gradient preferentially active for the largest scale and the lateral occipito-parietal regions preferentially active for the smallest scale. In the following, we discuss our results with respect to previous theories of temporal cognition as well as findings regarding the spatial system's gradient-like organization.

Several theories on how the cognitive system processes different timescales have been proposed. On the basis of their discovery of time cells, Eichenbaum and associates have suggested a scale-independent unitary brain system to underlie temporal cognition across scales (Eichenbaum, 2014, 2017; MacDonald et al., 2011). Others, as based on different findings in functional imaging studies, suggested different brain systems to underlie each cognitive scale (Grossman et al., 2019; Nani et al., 2019; Wittmann, 2013; Ulanovsky et al., 2004).

This approach was also suggested for the longer periods in the time range compatible with autobiographical memory (Conway & Pleydell-Pearce, 2000; Friedman, 1987; Friedman & Wilkins, 1985). Many psychological theories have been developed regarding memory for time (for comprehensive reviews, see D'Argembeau, 2020; Friedman, 1993). Different theories describe potential ways in which temporal information may subserve memory for events. Such information includes the temporal distance between encoding of events and the present time (Brown, Rips, & Shevell, 1985; Murdock, 1974; Hinrichs, 1970); the temporal order of events (Cotton, Tzeng, & Hardyck, 1980; Hintzman, Summers, & Block, 1975); or contextual information about people, places, or activities that are linked to an event in memory (Brown, 2005; Brown et al., 1985). However, these theories have not explicitly addressed the different timescales involved. Furthermore, the different sources of temporal information of events in memory do not necessarily vary within different timescales. Three efforts to differentiate between the different scales are noteworthy. First, Friedman (Friedman, 1987, 2004; Friedman & Wilkins, 1985) examined memory accuracy in five different timescales, similar to the scales used in this work. When asked to state the exact hour, day of the week, day of the month, month, and year of notable past events, participants were more accurate stating the exact hours than the exact months. This finding led the authors to conclude that temporal information is separately processed over multiple timescales. Second, Conway and Pleydell-Pearce (2000) differentiated between three levels of autobiographical knowledge varying in their specificity and temporal scale: lifetime periods, general events, and event-specific knowledge. Lifetime periods include general knowledge represented by features such as people and locations, confined to the scale of months or years. General events are more specific and include repetitive and single events that are extended in time. Event-specific knowledge involves experiences that occur at a specific time and place. With respect to this differentiation, the suggested cortical gradients reported here may represent an intrinsic hierarchical organization in which shorter periods ("specific events") are part of longer ones ("general events") that, in turn, are part of "lifetime periods" (Conway, 2005; Conway & Pleydell-Pearce, 2000). Finally, in a most recent theoretical article based on these previous efforts, D'Argembeau (2020) suggested to view the different temporal scales as a hierarchy of autobiographical representations from the lifelong (many years scale) to the seconds time range. It is this hierarchy, he suggests, that enables humans to detach from the here and now to simulate future and past events through the construct of mental time travel (Dafni-Merom & Arzy, 2020).

Gradient-like activity is a main feature in the TRW theory, proposed by Hasson, Norman, and colleagues (Baldassano et al., 2017; Chen et al., 2016; Hasson et al., 2008, 2015; Honey et al., 2012; Lerner et al., 2011). According to TRW, events are processed on a postero-anterior cortical gradient, beginning with short events (tens of milliseconds) in primary visual and auditory cortices up to a few seconds in midlevel sensory areas, and building to multimodal situation models in long timescales (hundreds of milliseconds) in anterior regions, including the angular gyrus and posterior medial cortex. Moreover, this theory of cortical process-memory topography argues that information is integrated at different timescales throughout the cortex (Baldassano et al., 2017; Chen et al., 2016; Hasson et al., 2008, 2015; Lerner et al., 2011). La Rocca et al. (2018) extended these findings using magnetoencephalography to show that the gradient of increasing temporal integration window extends from posterior sensory to anterior executive regions in pFC and that this gradient follows a scale-free ($1/f$) distribution. The TRW theory further reflects on hierarchical organization between timescales in the very small to small timescales, which may also apply to the longer ones (although in an opposite direction). The division we identified between gradient-like organization in the medial parietal region and selective, nongradient-like organization in the occipito-parietal region may reflect a division between hierarchical and nonhierarchical characters of the different temporal scales in the different regions. Whereas activation at the MPC fits with hierarchical models, lateral occipito-parietal activation may be compatible with models of information integration such as multiscale recurrent neural networks (Chung, Ahn, & Bengio, 2017), which do not involve hierarchical—and

therefore gradient-like—organization. This difference reflects also the functional role of these regions—whereas the medial parietal cortex provides a map-like organization of the environment and a common brain area for spatial, temporal, and social processing, and the lateral parietal cortex is involved in high-level, multimodal scene processing (Baldassano, Esteva, Fei-Fei, & Beck, 2016; Maguire, Intraub, & Mullally, 2016).

Notably, the TRW theory is based on language-based narrative interpretation (from phonemes to paragraphs) that is shared between individuals, unlike the current experimental results that are based on autobiographical memory, which differs between individuals. Moreover, although our analysis is based on temporal scale selectivity, the TRW analysis approach assumes a sequence of discrete events and/or a hidden Markov model. Finally, the TRW theory relates to event segmentation (Kurby & Zacks, 2008) of a continuous narrative, noting clear event boundaries for each timescale. Although our current design involves event boundaries, we did not supply participants with a continuous narrative but relied on their own recall of specific events within a longer time duration. Event segmentation would not explain the continuous cortical organization of activations in a gradient-like manner as found here. Importantly, the only difference between conditions in the current experimental setting was the scale itself. Taken together, our findings show two scale-sensitive regions to be active across a range of temporal scales, with activity shifting along functional gradient only in the MPC. Therefore, our findings seem to reconcile the different theories, showing a general system that is involved in processing a range of temporal scales, while having an internal organization according to scale in the MPC.

A previous experiment of scale selectivity in the spatial domain identified four different cortical gradients in the MPC, the PPA, the occipito-parietal lobe, and the long axis of the hippocampus (Peer et al., 2019). The existence of the gradient-like activity of temporal selective activations in the MPC suggests this region to encompass a general system for the processing of different cognitive maps at varying scales (Arzy & Schacter, 2019; Bicanski & Burgess, 2018). Although we identified a significant negative correlation in scale selectivity along the posterior–anterior axis of the medial parietal region, the detected activations are not perfectly aligned with this axis and their spatial organization on the cortex is probably more complex. The PPA did not show any temporal scale selectivity and was not active for the current time task, most probably because this region is sensitive for places. Scale-selective activation was found at the occipito-parietal area, although not with a gradient-like organization. In the spatial task, this scene-selective region showed gradual activity from the visual cortex (for concrete, immediate scenes; e.g., within a room) to anterior associative areas (for the more distant and imagination-based larger scales; e.g., within a continent). In the current task, it is improbable that imagined situations differ in their visuality and concreteness in

between temporal scales. Therefore, although this area codes for temporal selectivity, gradient-like activity from concrete/visual to more abstract/imagery ones may not apply. A similar argument may also explain the absence of task-related activity in the hippocampus. According to current models of episodic memory (Moscovitch et al., 2005; Norman & O'Reilly, 2003), the hippocampus binds together representations of an experience during encoding, which are reinstated in the cortex during subsequent retrieval (Danker, Tompary, & Davachi, 2017). Long-term memory therefore relies on a combined activity of a network of brain regions, including the MPC and TPJ (Ranganath & Ritchey, 2012; Kravitz, Saleem, Baker, & Mishkin, 2011), representing multimodal, abstract features of the current event ("situation models"; Zwaan & Radvansky, 1998; Zwaan, Langston, & Graesser, 1995; Johnson-Laird, 1983; Van Dijk & Kintsch, 1983). This notion complements recent suggestions that the hippocampus may represent abstract and conceptual relations, which are not involved in the current design (Behrens et al., 2018; Nau, Schröder, Bellmund, & Doeller, 2018; Epstein, Patai, Julian, & Spiers, 2017; Parkinson & Wheatley, 2013). Therefore, hippocampal activity per se should not be expected in a cued recall, as seen in our results (Peer et al., 2015; Arzy, Bick, & Blanke, 2009; Hassabis, Kumaran, Vann, & Maguire, 2007). However, the absence of hippocampal activity may be artifactual in nature, in view of known susceptibility of this region to imaging artifacts (Peer, Abboud, Hertz, Amedi, & Arzy, 2016). From a clinical perspective, temporal disorientation is the hallmark of Alzheimer's disease, where the two main regions of degeneration are both the medial-temporal and parietal cortices (Peters-Founshtein et al., 2018; Peer, Lyon, & Arzy, 2014).

In all implicated regions, responsive areas in the left hemisphere were larger than areas in the right hemisphere. This left lateralization is in accordance with previous findings showing involvement of predominantly left-lateralized regions in the processing of time and personal past events (Peer et al., 2015; St. Jacques et al., 2008; Svoboda, McKinnon, & Levine, 2006; Maguire, 2001). Furthermore, activation distributions were more extensive for the hour and month ranges, compared to the week or day ranges. Although this may be related to the preferred scale, this finding might also relate to the ecological character of the events—namely, shorter scales represent the most ecological framework of the event (happening across several hours or many minutes), whereas the longer scales represent the general duration of the travel. Further research with life-logging devices may shed further light on this aspect (Nielson et al., 2015). Ideally, we would like our task to encompass timescales ranging from milliseconds to years. However, here, we adopted ecologically valid timescales in the autobiographical memory range (Friedman, 1987; Friedman & Wilkins, 1985). To maintain homogenic stimuli within each participant, we only included events from a specific travel period, which lasted not more than several months.

Our personalized, ecologically valid paradigm included, by definition, different events for each participant. This did not allow us to control for individualized parameters, besides those reported by participants and compared in the data. Finally, as the events used here were part of a well-defined trip, they may be intimately related to specific locations. However, although the events occurred in specific locations, the spatial and temporal sizes were uncorrelated and the temporal activations/gradients differed from the spatial ones. It has been demonstrated that memories of specific events are often embedded in memory structures that organize information about thematically related events (Brown, 2005; Brown & Schopflocher, 1998). Such thematic embeddedness that covaries with temporal scales can be another potential explanation for the cortical gradients found here. Ratings of vividness, difficulty, and emotion were collected for each of the scales after the entire experiment and not after each trial, in accordance with previous studies (Auger & Maguire, 2013; Bonnici et al., 2012). Although rating these subjective parameters only after completing the experiment may present a potential caveat, rating these parameters after each trial would have disturbed the task's flow and consequently the participants' performance. Therefore, although our data did not show evidence for a difference in vividness, difficulty, or emotion for comparison at different timescales, we cannot completely exclude these factors from having a role in memory at different timescales. Participants used the same distance comparison approach across all scales and did not adopt any additional coherent strategy, as based on their postexperiment report. However, the amount of episodic versus conceptual/semantic knowledge involved in the processing of different timescales may vary (D'Argembeau, 2020; Irish & Vatansever, 2020; Conway, 2005, 2009; Conway & Pleydell-Pearce, 2000). Future experimental studies may specifically test the involvement of different memory systems in the processing of different timescales.

Our findings showed that the two scale-sensitive cortical regions have different scale preferences. Another possible explanation for the preference to either the smallest or largest scales is that the identified regions are responsible for cognitive processes that are maximally involved in large timescales and whose involvement diminishes as the scale decreases, or vice versa. For example, our findings show that the overlap of the medial parietal region and the DMN appears to be mainly with the largest temporal scale areas. This might indicate a role in a cognitive process that is maximally active for large timescales. Such a role could be representing an abstract "mental time line" and ordering events along it—a function that would be less important within short time frames, when the actual sequence of events can be fully remembered. Indeed, the MPC/retrosplenial cortex is involved in the integration of allocentric and egocentric spatial information, and this process might similarly function in time to create a mental time line (Arzy & Schacter, 2019; Byrne, Becker, & Burgess,

2007). In contrast, the overlap of the lateral parietal region and the DMN was found higher in the smaller timescale areas, with decreased overlap with the larger ones; this may indicate processes related to direct imagery/memory of an event from the observer's perspective, in accordance with the lateral parietal lobe's role in immediate environment processing (Rolls, 2020; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008). Such direct imagery may be less important for larger scales of time, in congruence with this region's reduced activity for longer timescales. Finally, another factor that may have an effect is the amount of temporal details available to participants at each timescale. Although we did not find a significant difference in vividness ratings between scales, shorter events may be remembered as more "crowded" with details, invoking a richer representation; if that is the case, then the difference in activity may indicate preferential representation of rich memories in the lateral parietal cortex, compared to more schematic representations in the MPC. Overall, our findings suggest a role for the DMN in processing both small and large temporal scales, with subspecializations for processing and representing small and large timescales in its lateral and medial parts, respectively.

In conclusion, the present results demonstrate temporal scale-selective activity for autobiographical memories in the lateral and medial posterior cortex, with the latter also showing gradient-like postero-anterior organization. These findings may provide a basis for understanding how the human brain processes and integrates experiences across timescales in a hierarchical manner and its potential cognitive and computational basis.

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