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Neural Patterns in Parietal Cortex and Hippocampus Distinguish Retrieval of Start versus End Positions in Working Memory

Giulia Cristoforetti[1], Steve Majerus[2,3], Muhammet Ikbal Sahan[1], Jean-Philippe van Dijck[1,4], and Wim Fias[1]

Abstract

■ Coding serial order of information is a fundamental ability of our cognitive system, and still, little is known about its neural substrate. This study examined the neural substrates involved in the retrieval of information that is serially stored in verbal working memory task using a sensitive multivariate analysis approach. We compared neural activity for memorized items stemming from the beginning versus the end of a memory list assessing the degree of neural pattern discordance between order positions (beginning vs. end). The present results confirmed and refined the role of the intraparietal sulcus in the processing of serial order information in working memory. An important finding is that the hippocampus showed sensitivity to serial order information. Our results indicate that the representation of serial order information relies on a broader set of neural areas and highlight the role of the intraparietal sulcus and the hippocampus, in addition to the supramarginal gyrus and the SMA. The contribution of different neural regions might reflect the involvement of distinct levels of serial order coding (i.e., spatial, attentional, temporal) that support the representation of serial order information. ■

INTRODUCTION

Maintaining events in an appropriate sequence is a fundamental feature of memory, and it is important for many daily activities. Serial order processing concerns information about the temporal succession in which events have occurred and is a major contributor to higher-order cognition such as vocabulary acquisition, language production, and reasoning (Baddeley, 2012). However, how order is represented and processed in the brain remains one of the main empirical challenges in the field of cognitive neuroscience.

Recent neuroscience research has focused on the neural mechanism involved in representing serial order in working memory (WM), which allows the temporary maintenance of information in active and accessible state over a short period of time (Baddeley, 2003). A crucial role in the neural processing of serial order in WM is assigned to the intraparietal sulcus (IPS). Evidence for the involvement of the IPS essentially comes from brain imaging studies that contrast neural activity induced by executing an order processing tasks versus neural activity induced by tasks that do not involve order processing, like item processing (Roberts, Libby, Inhoff, & Ranganath, 2018; Martinez Perez, Poncelet, Salmon, & Majerus, 2015; Majerus et al., 2006, 2010; Henson, Burgess, & Frith, 2000; Marshuetz, Smith, Jonides, DeGutis, & Chenevert, 2000). In the order processing task, participants have to indicate whether two memory probes are presented in the same order as they appeared in the memorized list. In the item processing task, participants simply have to indicate whether both items were or were not part of the memorized list. These studies showed that encoding and recognition of serial order information recruit a frontoparietal network centered on the IPS for sequences in verbal and visual domains compared with item recognition, which recruits frontotemporal cortices to a larger extent (Majerus, 2019). Marshuetz et al. (2000) and Henson et al. (2000) compared item and order recognition for consonant lists and also obtained larger activity in the bilateral IPS for the order condition. More specifically, Majerus et al. (2006) observed stronger right IPS activity for order than for identity, whereas the left IPS showed similar levels of activity for both types of information. Crucially, the left IPS showed functional connectivity to the right IPS only for order information, as well as to frontal and cerebellar areas.

Research building on these seminal studies aimed at further specifying the functional contribution of the IPS. A fundamental characteristic of serial order processing is the ordinal distance effect, the distance between the two serial positions determining performance. Participants make more errors and are slower for determining whether two items are in correct order when they come from close serial positions in the memory list as compared with more

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distant positions. Marshuetz, Reuter-Lorenz, Smith, Jonides, and Noll (2006) and Attout, Fias, Salmon, and Majerus (2014) showed that this behavioral ordinal distance effect was mirrored by an activity gradient within the IPS, smaller distances leading to stronger IPS levels of activity. These findings were confirmed by a recent fMRI study assessing ordinal judgment in WM using a multivariate approach and showed sensitivity to ordinal distance in the bilateral IPS (Attout, Leroy, & Majerus, 2022), particularly observing a more general ordinal processing in the right posterior IPS across different domains (WM and alphabetical domain).

Altogether, these studies highlight the bilateral IPS as being a crucial brain region for serial order coding. Yet, there remain several important questions. First, the full neural system involved in serial order processing may not yet have been uncovered, because contrasting order and item tasks is not optimal in terms of sensitivity given that an item recognition task itself is probably not free of order processing (Abrahamse, van Dijck, Majerus, & Fias, 2014). It has indeed been shown that there is the strong tendency to spontaneously process the order in which items are presented (Kahana, 1996). Consequently, contrasting order tasks with item tasks does not guarantee a maximal contrast between both types of information and may thus not be the most sensitive method to examine the neural underpinnings of serial order processing in WM. Second, evidence so far builds exclusively on tasks involving explicit comparison processes. Other tasks involving similar comparison processes such as numerical or alphabetical comparisons between two stimuli also led to IPS involvement (Fias, Lammertyn, Caessens, & Orban, 2007). In other words, IPS involvement might reflect these more general comparison processes, rather than processes specifically related to the serial order aspect of WM. Computational modeling has shown that the distance effect may be a result of the comparison process rather than reflecting the types of representation on which the comparison process is built (i.e., numerical magnitude or alphabetical position; Van Opstal, Gevers, De Moor, & Verguts, 2008). The fact that distance-related neural activity in a WM order comparison task overlaps with the distance-related neural activity in numerical and alphabetical comparison tasks (Attout et al., 2014) may reflect such overlapping comparison-induced processes rather than of the processing ordinally organized information itself.

An additional area that is relevant for coding serial order information is the hippocampus (HC). Converging evidences for hippocampal involvement in order processes come from work with patient with hippocampal lesions and fMRI studies. In patients' studies, hippocampal damage has been related to greater deficits in order WM relative to item WM, and in making temporal distance judgments (e.g., Shimamura, Janowsky, & Squire, 1990). Similarly, Alzheimer's disease patients, who commonly have progressive hippocampal atrophy, showed a specific impairment in processing serial order, which causes a general reduction in WM functions (De Belder, Santens, Sieben, & Fias, 2017). Recent fMRI studies also suggest a role for the HC in the formation and retention of temporal and sequence information (for reviews, see, e.g., the works of Long & Kahana, 2019; Ranganath & Hsieh, 2016; Eichenbaum, 2014). Roberts et al. (2018) assessed the neural activation in temporal and object WM and observed that the maintenance of temporal WM information was associated with an increased activation in the posterior HC (and posterior parietal cortex [PPC]) compared with the anterior HC for maintenance of WM items. This study provided evidence for the involvement of the HC in temporal/order processing in WM and suggests that the HC exhibits different activation patterns along the longitudinal axis. The HC has been traditionally linked to long-term memory (LTM), and its involvement in retrieving and maintaining temporal and ordinal information has been observed also in LTM. Hippocampal activity has been detected when participants learned stimulus sequences (Ross, Brown, & Stern, 2009; Kumaran & Maguire, 2006) and it increased during encoding and retrieval of serial order information (i.e., Ekstrom, Copara, Isham, Wang, & Yonelinas, 2011; Tubridy & Davachi, 2011). Tubridy and Davachi (2011) had participants study triplets of sequentially presented words and then reorder those items during test. The authors found that increased hippocampal activity during encoding predicted better performance on the subsequent ordering task. These findings suggest that both successful encoding and retrieval of event sequences recruit the HC. Although these studies indicate that the HC is involved in processing and representing sequences of events in memory, direct and robust evidence is still lacking. The vast majority of studies used univariate analysis, comparing order processing to item processing or investigating an explicit order processing. We can argue that by using a univariate approach, these studies lack of sensitivity and explored memory for serial order information rather than the serial order processing per se. Furthermore, evidence of the involvement of the HC in order processing is still inconsistent. Whereas Roberts et al. (2018) observed hippocampal activation by comparing order processing and item processing in a WM task, recent fMRI studies directly focusing on order processing using an explicit comparison order task, such as Attout et al. (2022), have not shown sensitivity of the HC to order processing. New insights are needed to clarify the functional role of HC in order processing.

This study aims at investigating the involvement of the IPS and HC in serial order processing using a WM paradigm that allows greater sensitivity and that is less dependent on explicit serial order comparison processes. In particular, we build on a recently developed paradigm that allows to examine implicitly activated serial order information in WM, and without needing a nonserial order comparison task. This paradigm probes serial order processing by revealing the presence of interactions between spatial and serial order representations. van Dijck and Fias (2011)

showed that serial position in a verbal WM task can be coded as a spatial position within a left-to-right oriented mental representation (for reviews, see the work of Abrahamse, van Dijck, & Fias, 2017). Specifically, they demonstrated that items from the beginning of the memorized sequence were responded to faster with the left hand than with the right hand, and the opposite was true for items toward the end of the sequence. This pattern of findings can be summarized by referring to a metaphor that describes WM as a mental whiteboard on which memorized items are displayed as a function of their position in the WM sequence, depending on reading direction (Guida & Campitelli, 2019; Guida et al., 2018; Abrahamse et al., 2017). This serial order-spatial congruency effect may allow to evaluate the serial position of items that are accessed in WM in a nonexplicit manner. This initial paradigm, though, confounds serial order and spatial-motor congruency effects because the motor response directly involves the task target and its serial position (as in the work of Zhou et al., 2021). An extension of the original paradigm allows to deconfound these two effects, by collecting the motor response on a subsequent task that does not involve the WM items. In this variant, memorized items are presented as cues; the participants have to determine whether the item presented during the retention delay is part of the memory list. If this is the case, the participant detects a target dot appearing on either the left or right side of the screen in a subsequent dot-detection task (by pressing a central response button or by saying "yes"). It was found that the closer the position of the memorized item to the end of in the memorized sequence, the faster the response to detect a dot appearing on the right side of the screen as compared with the left side (van Dijck, Abrahamse, Acar, Ketels, & Fias, 2014; van Dijck, Abrahamse, Majerus, & Fias, 2013). When an item cue is presented, participants are rehearsing and scanning serially across the items stored in memory. Scanning is faster for early list items as they are reached earlier than last list items. It is precisely this serial scanning process that is supposed to induce a spatial attention bias in the dot-detection task, by assuming that earlier items are coded in the left hemispace and later items in the right hemispace (Abrahamse et al., 2014; van Dijck et al., 2013, 2014). Importantly, with this paradigm, processing of the memory cue and its serial position can be temporally isolated from response-related effects (Rasoulzadeh et al., 2021).

In this study, we adopted this paradigm to investigate cue-induced neural responses related to accessing specific positions in serially ordered information, without necessitating comparison processes. This paradigm should also allow for maximal sensitivity as no control task is used to compare order processing with. Instead, we compare cue-induced neural activity for memorized items stemming from the beginning versus the end of a memory list. We used the technique of multivoxels-pattern analysis (MVPA) on fMRI data acquired when retrieving serially stored items that enable us to assess the degree of neural pattern discordance between order positions (beginning vs. end). These methods are more sensitive than standard univariate methods as they allow us to assess the informative value of the functional activity (e.g., Haxby, 2012; Kriegeskorte, Goebel, & Bandettini, 2006; Haynes & Rees, 2006). We specifically looked at cue-related activity reflecting access to a specific position in WM with a ROI approach. Multivariate analyses were conducted over the IPS and the HC primarily. We predicted that the serial position of retrieved items could be decoded from the pattern of neural activity over voxels in these regions. Decodability in the IPS would allow us to refine its functional contribution to process that are directly linked to position-specific access to WM. Moreover, with higher sensitivity, we expect to identify the HC involvement in serial order processing and to provide new insights on its functional role.

METHODS

Participants

The study was preregistered on the Open Science Framework (https://osf.io/86aeu). Thirty-four young adults (mean age = 28.62, range = 18–40; 24 females) were recruited from the Ghent University community. All participants were right-handed (confirmed by the Edinburgh handedness inventory), with no diagnosed psychological or neurological disorders, and MRI safe. The study was approved by the UZ Gent Ethics Committee, and participants gave their written informed consent before their inclusion in the study. Of the 34 participants, 5 were discarded because of low accuracy in the verification phase (more than 2 out of 12 blocks were inaccurate) and 1 for excessive head motion (3-mm translation), resulting in a final sample of 28 participants. Our preregistered sample size was 30 participants with sufficient data quality. The number of participants was based on a power analysis for the MVPA classification analysis. A power analysis for the comparison of mean classification accuracies against chance level classification accuracy (one-sample t test) indicated that 34 number of participants are needed for obtaining a power $> .80$, for medium effect size (Cohen's $d = 0.50$) and an alpha of .5. We could not conclude the collection of two remaining participants because of COVID-19.

Experimental Design

The stimulus material consisted of eight digits (from 1 to 4 and from 6 to 9). An experimental session contained 12 blocks each containing three phases each: encoding of the sequence and rehearsal (Phase 1), dot-detection task (Phase 2), and order verification task (Phase 3; Figure 1). During the Phase 1, four digits (0.45° visual angle, hereafter VA) were serially presented as memoranda at the center of the screen. The participants were explicitly instructed to maintain the items in the order of presentation. All stimuli were presented in white on a gray/background throughout the experiment. Each digit was presented for 800 msec,

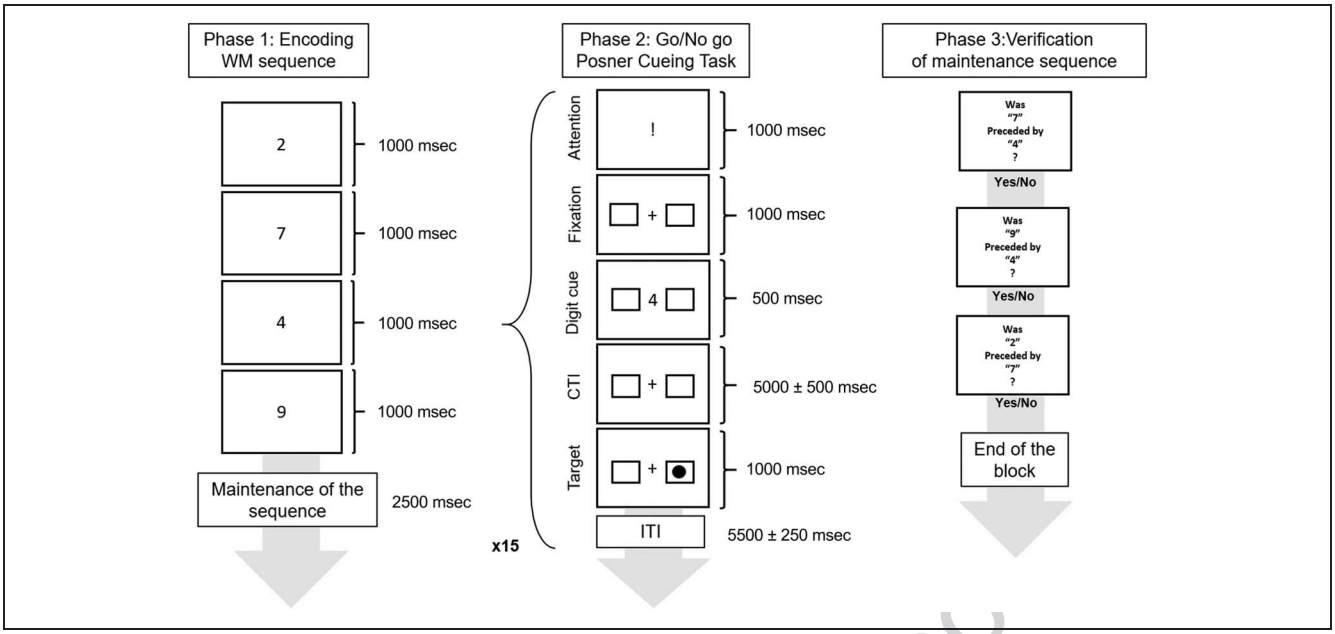

Figure 1. Design of the experiment. After loading the sequence to WM (Phase 1), the illustrated procedure in Phase 2 was repeated for 15 times. In Phase 3, the correct maintenance of the sequence was verified by three questions.

followed by a 200-msec blank screen. Sequences of four digits were pseudorandomly created off-line with MATLAB 2016b and imported to the E-Prime 2.0 software (Psychology Software Tools) program used for presenting the task in the scanner. Each sequence consisted of two "small" digits (1–4) and two "large" digits (6–9). For each participant, we had 12 sequences that contained for each magnitude condition two digits in each possible combination of position. After a rehearsal period (variable duration: random Gaussian distribution centered on a mean duration of 2500 and a standard deviation of 250 msec), Phase 2 started. This was a go/no-go cued dot-detection task. For each sequence, Phase 2 was repeated 15 times. Each trial started with a neutral warning (an exclamation mark, 0.45° VA) displayed for 1000 msec, followed by the presentation of a central fixation cross (0.25° VA) centered between two rectangles (1° × 0.67° VA; 3.20° VA eccentricity). After 1000 msec, a digit (uninformative of the dot location) replaced the fixation cross for 500 msec. After a cue-target interval (CTI; variable duration: random Gaussian distribution centered on a mean duration of 5000 ± 500 msec), the target (a white dot, 0.5° × 0.5°) appeared in one of the rectangles for 200 msec and with a response window of 1000 msec. To ensure WM access, participants were instructed to press a button with their right hand index only on those trials where the cue belonged to the memorized sequence (8 out of 15). When the cue did not belong to the sequence, participants had to refrain from responding to the target (five trials). The remaining two trials were catch trials where the cue was from the sequence, but it was not followed by a dot to prevent anticipatory responses. Each block contained 15 trials. For each block, the first and the fourth order positions were cued 3 times (two go trials and one catch trial), whereas the second and the third items 2 times as go trials. The remaining four digits that were not part of the sequence appeared once (one was presented twice) in each block as no-go trials. Intertrial interval duration was of variable duration and followed a standard normal distribution with a mean of 5000 msec and a standard deviation of 300 msec. During the intertrial interval between probes in the dot-detection task, a fixation cross was displayed on the screen. In Phase 3, the correct maintenance of the elements in the sequence was tested with three questions about the serial order (i.e., "was 1 preceded by 8?"). These questions were on the three possible pairs of subsequent WM items, the order of which either did or did not correspond to the order of the WM sequence (items were vertically arranged to avoid any horizontal association). Each block consisted of one run lasting 3 min and 45 sec. All tasks were presented a Windows PC and back projected onto a screen located behind the scanner. Participants responded using an MRI-compatible button box on the right hand (pressing with the index finger to detect the dot).

As in the work of van Dijck et al. (2013), we computed each participant's mean RT for each condition and subjected them to a 4 (*WM position*: 1/2/3/4) × 2 (*dot location*: left/right) repeated-measures ANOVA. We considered only go trials that were followed by fully accurate responses to the final verification task, ensuring that the memory sequence had been correctly maintained throughout the trial.

MRI Acquisition

Imaging was carried out on a 3 T Magnetom Trio MRI scanner (Siemens MedicalSystems), operated with a standard transmit–receive quadrature 64-channel head coil. T1

weighted image was acquired for anatomical reference using a magnetization-prepared rapid acquisition 594 gradient echo sequence (repetition time = 2250 msec, echo time = 4.18 msec, inversion time = 900 msec, acquisition matrix = 256 × 256, field of view = 256 mm, flip angle = 9°, voxel size = 1 × 1 × 1 mm). fMRI data were acquired using a T2*-weighted gradient echo EPI sequence with the following parameters (repetition time = 1730 msec, echo time = 30 msec, image matrix = 84 × 84, field of view = 210 mm, flip angle = 66°, slice thickness = 2.5 mm, voxel size = 2.5 × 2.5 × 2.5 mm, distance factor = 0%, 50 slices) with slice acceleration Factor 2 (simultaneous multislice acquisition). Each run corresponded to one block of the main task for a total of 12 runs. For each run, 128 slices orientated along the AC-PC line were acquired for each subject. Head movement was minimized by restraining the subject's head using a vacuum cushion. Stimuli were displayed on a screen positioned at the back of the scanner, which the subject could comfortably see through a mirror mounted on the standard head coil.

fMRI Analysis

Preprocessing

Data were preprocessed and analyzed using SPM12 (*v7487*) software (Wellcome Department of Imaging Neuroscience, www.fil.ion.ucl.ac.uk/spm) running on MATLAB R2016b. Functional images were realigned and unwrapped to correct for movement artifacts (using the first scan as the reference slice). A mean realigned functional image was then calculated by averaging all the realigned and unwarped functional scans, and the structural T1 image was coregistered to this mean functional image (rigid-body transformation, normalized mutual information cost function; fourth degree B-spline interpolation). The mapping from subject to Montreal Neurological Institute space was estimated from the structural image with the "unified segmentation" approach. The warping parameters were then separately applied to the functional and structural images to produce normalized images of resolution 2 × 2 × 2 mm^3 and 1 × 1 × 1 mm^3, respectively. Finally, the warped functional images were spatially smoothed with a Gaussian kernel of 4-mm FWHM to improve SNR while preserving the underlying spatial distribution (Schrouff et al., 2013); this smoothing also diminishes the impact residual head motion can have on MVPA performance, even after head motion correction (Gardumi et al., 2016). The scans were screened for motion artifacts, and time series with movements exceeding 3 mm (translation) or 3° (rotation) were discarded. One participant was excluded for excessive movements.

Univariate Analysis

First, univariate analysis was performed to assess brain activity levels possibly associated with the retrieval of items from the WM sequence. For each subject, brain responses were estimated at each voxel, using a general linear model with event-related regressors. The design matrix included two regressors that modeled cue retrieval; one regressor for the go condition (retrieved item from the sequence), and the second for the no-go condition. Two additional regressors modeled for dot location in the target detection phase (left target and right target) to control for target-related variance. The model also included the realignment parameters to account for any residual movement-related effect. A high-pass filter was implemented using a cutoff period of 128 sec to remove the low-frequency drifts from the time series. Serial autocorrelations were estimated with a restricted maximum likelihood algorithm with an autoregressive model of order 1 (+ white noise). Furthermore, a linear contrast was defined for assessing differential main effects between the go and no-go cue conditions, that is, items retrieved from the WM sequence and items not part of the WM sequence, respectively. The resulting set of voxel values constituted a map of *t* statistics [SPM{T}]. The contrast image was then entered in a second-level analysis to assess with a linear contrast brain regions involved in retrieving items from WM sequence compared with unrelated cues. One-sample *t* tests assessed the significance of the effects. For univariate analyses, statistical inferences were performed at the voxel level at $p < .05$ corrected for multiple comparisons (FWE corrections) across the entire brain volume.

Multivariate Analysis

Multivariate analysis was conducted using PRoNTO, a pattern recognition toolbox for neuroimaging (https://www.mlnl.cs.ucl.ac.uk/ pronto; Schrouff et al., 2013). The analysis was cue-based to the retrieval of an item during the go/no-go cued dot-detection task (Phase 2) as a single event. To investigate the neural patterns associated with serial order information, we trained a classifier to distinguish voxel activation patterns associated with the retrieval of an item located at the beginning (first item) versus an item at the end (fourth item) of the WM encoded sequence (Figure 2B), using a binary support vector machine in the preprocessed and 4-mm-smoothed time-series functional images.

A leave-one-run-out cross-validation procedure was used, resulting in training the classifier on 11 runs and testing the classifier on the remaining one run (Figure 2B). We reconsidered our preregistered analysis, and we did not decode order by grouping together the first and second items for a beginning classifier and the third and fourth items for an end classifier. The reason for this is that the position of the middle items with respect to begin and end might be more ambiguous, which could have a negative impact on the sensitivity that we aim for. We also did not exclude blocks from the analysis in which the verification task was not accurate, because of very high accuracy in the go/no-go cued dot-detection task.

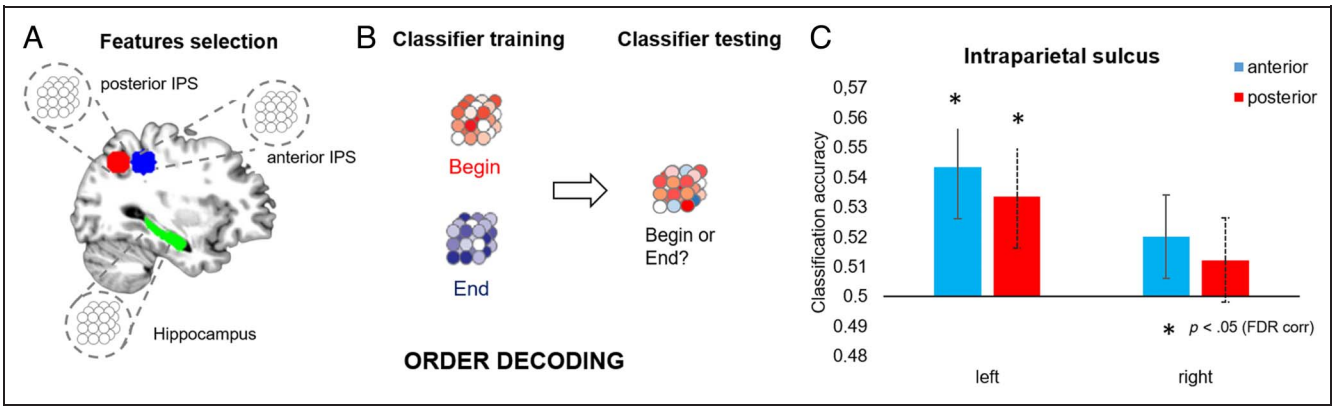

Figure 2. (A) Feature selection: second-level masks. IPS (anterior and posterior) and HC. (Sagittal slice $x = -32$.) (B) Training classifiers to distinguish voxel activation patterns associated with the retrieval of an item located at the beginning (first item) versus items (fourth item) at the end of the WM sequence. (C) Classification accuracy significantly above-chance level in the left anterior and posterior IPS. Error bars represent the standard error of the mean.

To ascertain that the specific neural patterns associated with first versus fourth serial position are really specific to serial position, we also examined whether specific neural patterns could be found that characterize item content, such as small (1 and 2) versus large magnitude (8 and 9) of the cue. A leave-one-block-out cross-validation procedure was used. Research in numerical cognition has indeed highlighted the IPS to represent abstract quantity information (e.g., Nieder & Dehaene, 2009; Ansari, 2008).

A standard mask removing voxels outside the brain was applied to all images, and all models included timing parameters for hemodynamic response function delay (5 sec) and hemodynamic response function overlap (5 sec) ensuring that stimuli from different categories falling within the same 5 sec were excluded (Schrouff et al., 2013). An ROI approach was used by limiting the voxel space to a priori-defined VOIs. Each ROI decoding analysis returned one accuracy value per ROI and participant. Significance of classification accuracy was assessed at the group level by comparing the distribution of classification accuracy to a chance-level distribution with the parametric one-sample t test ($p < .05$ after further false discovery rate correction for multiple comparisons; six ROIs in each hemisphere, for a total of 12 comparisons).

The statistics of the decoding analysis additionally followed a permutation approach assuming that a probability level of 0.5 might be considered precarious (Combrisson & Jerbi, 2015). To confirm the validity of our results, for each ROI, we computed a null distribution by repeating the decoding protocol 1000 times swapping the labels of the true classes. To assess significance at the population level, we first compared accuracy minus chance scores of all participants against 0, using a one-sample t test. Then, we computed the empirical null distribution of t values, on each of 1000 permutations; an effect was considered significant if the observed t value was larger than 95% of the t values in the null distribution (thus, significance level = $p < .05$).

Classification accuracy was also assessed using a Bayesian one-sample t test. The Bayesian approach has the advantage not only to give evidence in favor of the alternative model but also to appreciate evidence in favor of the null model, allowing to reject or not the null hypothesis more confidently (Wagenmakers, 2007). We report BF_{10} values, which represents the result of the likelihood ratio of the alternative model (H1) relative to the null model (H0) and BF_{01}value that represents the likelihood ratio of H0 relative to H1. A BF_{10} of 1 provides no evidence, $3 > BF_{10} > 1$ provides anecdotal evidence, $10 > BF_{10} > 3$ provides moderate evidence, $30 > BF_{10} > 10$ provides strong evidence, $100 > BF_{10} > 30$ provides very strong evidence, and $BF_{10} > 100$ provides extreme/decisive evidence. A BF_{01} value > 3 provides positive evidence for the absence of above-chance-level decoding used (Jeffreys, 1961; Lee & Wagenmakers, 2014). Bayesian analyses were conducted with Version 0.10.2.0 of the JASP software package, using default settings for the Cauchy prior distribution (JASP Team, 2017, jasp-stats.org).

A Priori ROIs

For the multivariate analyses, we performed ROI analyses on brain areas previously shown to support processing and retrieval of serial order information. These ROI were used as inclusive masks for the multivariate analyses (Figure 2A). An overview of the a priori ROIs is presented in Table 1.

More specifically, in our preregistration, we had listed the bilateral IPS and the HC as ROIs. As already mentioned, the IPS has been consistently linked to tasks involving serial order processing. Whereas the posterior IPS is part of the dorsal attention network and it has been associated to top–down attentional processes (Corbetta & Shulman, 2002), Attout et al. (2014) showed a more specific involvement of the anterior IPS in serial order coding. Accordingly, and as described in the preregistration, the IPS ROIs

Table 1. A Priori ROI for Multivariate Pattern Analysis

ROI	*Functions*	*Preregistered*
IPS (anterior and posterior)	Order processing (i.e., Attout et al., 2014, 2021; Majerus et al., 2006)	Yes
	Temporal order in WM (Roberts et al., 2018)	
HC (anterior, middle, posterior)	Temporal order in LTM (Davachi & DuBrow, 2015)	Yes
No AG	Memory retrieval, recollection (Sestieri et al., 2017)	
SMG	Memory retrieval (Sestieri et al., 2017)	No
	Serial order coding (Majerus, 2019)	
SMA	Chronotopic maps (Protopapa et al., 2019)	No

were segmented in anterior and posterior portions. The selection of functional IPS ROIs was guided by previous order processing literature. Moreover, we preferred not to use existing anatomically defined ROIs (Caspers et al., 2006, 2008; Choi et al., 2006) as they cover mainly the anterior part of the IPS and do not entirely comprise the posterior part. IPS areas were directly selected from the mean coordinates of functional loci published in previous studies focusing on order processing in WM (Attout et al., 2014, 2022; Majerus et al., 2006). The ROIs were defined as spheres with a radius of 10 mm centered on the following coordinates: anterior ($x = -32, y = -42, z = 42; x = 42, y = -40, z = 42$) and posterior ($x = -28, y = -62, z = 42; x = 28, y = -58, z = 44$) for the left/right IPS, respectively (Figure 2A).

As preregistered, we selected an anatomical hippocampal ROI because of lacking references of functional foci involved in serial order coding in WM and to a greater use in the literature of the anatomical ROI given the conformation of the HC. The hippocampal ROI was constructed in Montreal Neurological Institute space using the Anatomy Toolbox in SPM12 (Eickhoff et al., 2005; Amunts et al., 2005) and by combining CA1, CA2, CA3, and DG subregions separately for each hemisphere. As a descriptive analysis, to look at classification accuracy across the long (anterior–posterior) axis of the HC, we performed additional analysis by dividing the hippocampal mask into three segments of approximately equal lengths along the y axis, using MRI-cron; posterior portion of the HC: from $y = -40$ to -30; mid-portion of the HC: from $y = -29$ to -19; anterior portion of the HC: from $y = -18$ to -4 (Collin, Milivojevic, & Doeller, 2015).

In addition to the preregistered ROIs, we decided to select additional ROIs for exploratory analyses. First, there are a number of brain regions that according to Sestieri, Shulman, and Corbetta (2017) are involved in retrieving information from memory. In the ventral PPC, the left supramarginal gyrus (SMG) is involved in serial order processing (Guidali, Pisoni, Bolognini, & Papagno, 2019; Majerus, 2019), the angular gyrus (AG) has a fundamental role in the recollection of specific information of retrieved items (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008). We also included the SMA as an ROI because this region has been shown to be involved in time processing and to host chronotopic maps of time (Protopata et al., 2019), which could, in principle, contribute to the processing of serial order. SMG, bilateral AG, and bilateral SMA ROIs were obtained from automated anatomical labeling (Tzourio-Mazoyer et al., 2002) using WFU_PickAtlas (Maldjian, Laurienti, Kraft, & Burdette, 2003). We used anatomical ROIs given no a priori hypothesis on the specific functional location within those areas.

RESULTS

Behavioral Performance

Trials from WM sequences with accurate serial order verification (on average, 11.42 of 12 sequences) and correct go trials (accuracy on the dot-detection task was 96.78% and 97%, for the go, no-go, respectively) were considered. Each participant's mean RTs were computed for each condition and subjected to a 4 (WM order position; 1, 2, 3, 4) × 2 (dot location; left, right) ANOVA (Table 2). No effects of WM position, $F(3, 108) < 1, p = .88$, neither dot location, $F(1, 27) < 1, p = .83$, is observable. The interaction between order position and dot location is not observed, $F(3, 108) < 1, p = .68$. The interaction between order position and dot location is not observed, $F(3, 108) < 1, p = .68$. Using the same paradigm but with substantially shorter cue target intervals (250 msec instead of 5000 msec in this study), van Dijck et al. (2013) observed a significant interaction between order position and dot location, and this finding has been replicated over many different studies (Rasoulzadeh et al., 2021; De Belder et al., 2015; van Dijck et al., 2014). The long CTIs between retrieval of items from a specific WM position and the dot detection are very likely to have rendered

Table 2. Average RTs and Standard Deviation for WM Positions and Dot Location

	WM Positions			
Dot Locations	*1*	*2*	*3*	*4*
Left side	388.7 ± 80.9 msec	398.1 ± 83.1 msec	393.9 ± 72.5 msec	393.9 ± 76.1 msec
Right side	394.6 ± 80.9 msec	392.8 ± 83.4 msec	393.0 ± 81 msec	390.6 ± 85 msec

the dot-detection task insensitive to the effects of spatial attentional shifts (Rasoulzadeh et al., 2021; van Dijck et al., 2013).

Univariate Analysis

Retrieving items from the memory list (go condition) was associated with increased activity peaks in a large set of frontal, parietal, and occipital regions, as compared with the no-go condition. As in previous studies (Majerus et al., 2006; Henson, 2000), the frontal peaks included the left middle frontal gyri and the precentral sulcus extending to the anterior part of the inferior parietal lobule, overlapping with the most anterior part of the IPS (Table 3). Moreover, increased activity was detected in the left medial superior parietal lobule; this activation extended to more lateral regions. Finally, there was also a significant activation in the inferior occipital area and the caudate, as reported in the work of Majerus et al. (2006).

Multivariate Analysis

ROI Multivariate Analyses

A first set of classifiers was trained to distinguish voxel activity patterns associated with the retrieval of an item located at the beginning versus the end of the sequence in the parietal ROIs (anterior and posterior IPS). Above-chance-level discrimination of serial position (one-sample t test, $p < .05$, with false discovery rate correction for multiple testing, 12 comparison) was observed in the left anterior IPS, $t(27) = 2.52$, $p = .040$, Cohen's $d = 0.48$; permutation-based one-sample t test (1 k), $p = .006$; mean classification accuracy = .54 ± .09, and in the left posterior IPS, $t(27) = 2.39$, $p = .040$, Cohen's $d = 0.46$; permutation-based one-sample t test (1 k), $p = .01$; mean classification accuracy = .53 ± .07. Bayesian analyses supported these effects with moderate levels of evidence ($BF_{10} = 5.538$ and $BF_{10} = 4.369$, respectively). In the right hemisphere, the anterior and posterior part of the IPS were not associated with significant above-chance classification accuracy (anterior right: $t(27) = 1.19$, $p = .165$, d = .22; permutation-based one-sample t test (1 k), $p = .123$.; mean classification accuracy = .52 ± .09; posterior right: $t(27) = 0.87$, $p = .536$, Cohen' $d = .16$; permutation-based one-sample t test (1 k) $p = .177$; mean classification accuracy = .51 ± .08). Bayesian statistics also provided no definitive evidence *for* chance-level classification in the right hemisphere ROIs ($BF_{01} = 1.539$ and $BF_{01} = 2.232$, respectively; Figure 2C).

In the next analyses, we assessed decoding accuracy of serial order information in the hippocampal ROIs. Significant classification was observed in the main left hippocampal ROI, $t(27) = 2.29$, $p = .040$, Cohen's $d = .42$; permutation-based one-sample t test (1 k) $p = .012$; mean classification accuracy = .53 ± .06, and was associated with moderate Bayesian evidence ($BF_{10} = 3.639$). On the other hand, no above-chance-level classification accuracy was observed in the corresponding right hemisphere ROI, $t(27) = 0.22$, $p = .413$, Cohen's $d = .03$; permutation-based one-sample t test (1 k) $p = .405$; mean classification accuracy = .50 ± .08; Bayesian evidence actually supported the null hypothesis ($BF_{01} = 4.180$).

As a descriptive analysis, we explored the significant order discrimination across the long (anterior–posterior) axis of the HC; we split the HC into three parts with approximately equal lengths along the y axis; anterior, middle, and posterior HC (Collin et al., 2015). The higher mean classification accuracies were detected in the middle and posterior part of the left HC (middle; $t(27) = 1.75$, $p = .06$, Cohen's $d = 0.38$, mean classification accuracy = .52 ± .07; posterior $t(27) = 1.76$, $p = .06$, Cohen's $d = 0.33$, mean classification accuracy = .53 ± .078). These finding represent anecdotal evidences with a $BF_{10} = 1.465$ and $BF_{10} = 1.485$. Importantly, no above-chance-level accuracy was observed in the anterior part of the left HC, $t(27) = 0.01$, $p = .496$, $d = .03$ mean classification accuracy = .50 ± .076, and Bayesian evidence supported the null hypothesis ($BF_{01} = 4.949$). These results do not allow us to draw conclusions on where to locate order decoding in the HC, but it can be indicative for future studies investigating a dissociation in the type of information processed across the long axis of the HC. In the right hemisphere, no sub region showed discrimination of order (anterior: mean accuracy = .51 ± .0.07; $p = .33$; $BF_{01} = 3.460$; middle: mean accuracy = .49 ± .0.8; $p = .57$; $BF_{01} = 5.714$; posterior: mean accuracy = .49 ± .0.07; $p = .49$; $BF_{01} = 4.926$).

In the left SMG, significant above-chance classification accuracy was observed (mean accuracy = .54 ± .09; $t(27) = 2.43$, $p = .04$, Cohen's $d = 0.46$; permutation-based one-sample t test (1 k), $p = .009$; $BF_{10} = 4.783$), whereas this was not the case for the right SMG (mean accuracy = .51 ± .09; $t(27) = 0.40$, $p = .38$; permutation-based one-sample t test (1 k), $p = .32$; $BF_{0\ 1} = 0.280$) and the bilateral AG (left AG mean accuracy = .52 ± .09;

Table 3. Maxima within Regions Showing BOLD Signal Changes for the Differential Main Effect between Go and No-Go Cue Trials

Anatomical Region	*No. Voxels*	*Left/Right*	*Broadmann Area*			*SPM {Z} value*
			x	*y*	*z*	
Middle frontal gyrus	1283	L	−30	−4	52	5.0
Precentral sulcus		L	−36	−2	62	4.38*
Inferior parietal		L	−42	−34	38	4.34*
Thalamus	695	R	2	−10	4	4.83
Caudate		R	8	12	8	4.79
Caudate		L	−8	6	2	4.09*
Inferior occipital	390	L	−20	−96	−6	4.79
Lingual		R	−36	−86	−16	3.78*
Solitary nucleus	269	L	−8	−22	−12	4.63*
Superior parietal	471	L	−30	−58	62	4.57*
Precuneus		L	−14	−58	48	4.54*
Parietal superior		L	−18	−64	66	3.7*
Middle occipital	335	R	28	−96	2	4.38*
Calcarine		R	20	−98	−2	4.35*

All regions are significant at $p < .05$, with voxel-level and/or cluster-level FWE corrections for whole-brain volume.

* $p < .05$ for cluster-level FWE corrections only, with a cluster-forming threshold of p uncorrected $< .001$ at the voxel level.

$t(27) = 1.60, p = .09$; permutation-based one-sample t test (1 k), $p = .052$; $BF_{01} = 0.859$; right AG mean accuracy = .52 ± .09; $t(27) = 1.62, p = .09$; permutation-based one-sample t test (1 k), $p = .056$; $BF_{01} = 0.843$). Note, however, that the Bayesian analysis does not support the null effect either for the AG.

Regarding the SMA, above-chance classification accuracy was observed in the right SMA (mean accuracy = .53 ± .07; $t(27) = 2.24$, $p = .04$, $d = 0.42$; permutation-based one-sample t test (1 k), $p = .011$; $BF_{10} = 3.31$) but not in the left SMA (mean accuracy = .528 ± .08; $t(27) = 1.174$, $p = .09$, $d = 0.33$; permutation-based one-sample t test (1 k), $p = .038$; $BF_{01} = 0.693$; Figure 3).

In addition, we conducted univariate analysis on activity peaks for first versus fourth serial positions. We did not observe any significant differences in activity peaks either at the whole level or using our a priori defined ROIs. This result was indeed expected as early versus late items are not supposed to be encoded and maintained with different levels of neural activity but the information encoded by the neural activity should be different, and only multivariate analyses can reveal the informational value encoded by neural pattern activity.

We also investigated whether subregions of the IPS were able to distinguish number magnitude associated with the item cues. We trained classifiers to distinguish IPS voxel activity patterns associated with the retrieval of an item associated to a small magnitude (1 and 2) versus large magnitude (8 and 9) of the WM sequence. None of the subregions of the IPS showed magnitude decoding (left anterior IPS, mean accuracy = .47 ± .09; $t(27) = -2.278$, $p = 0.98$; BF01 = 14.6; left posterior IPS, mean

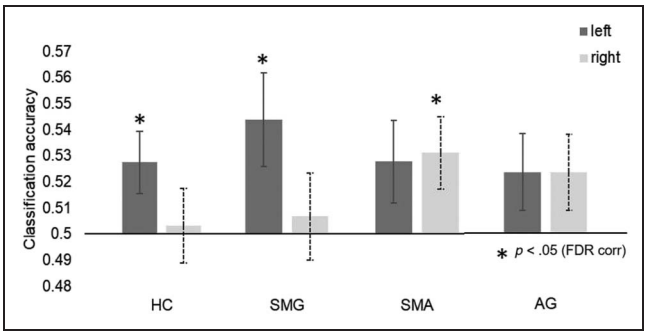

Figure 3. Classification accuracies for the discrimination of order position in the HC, SMG, SMA, and AG.

accuracy = .505 ± .07; $t(27) = 0.429$, $p = .365$; BF01 = 3.475; right anterior IPS, mean accuracy = .506 ± .09; $t(27) = 0.334$, $p = .371$; BF01 = 3.793; right posterior IPS, mean accuracy = .503 ± .07; $t(27) = 0.186$, $p = .427$; BF01 = 4.305). This result suggests that magnitude is not processed implicitly in the IPS while performing an order task not requiring magnitude processing.

DISCUSSION

This study aimed at identifying the neural substrates supporting the coding of serial order information retrieved from a memory sequence. Most research so far contrasted neural activity foci associated with the maintenance and recognition of serial order versus item information of a WM sequence, or by examining neural substrates associated with a serial order distance effect. As item recognition is probably not free of order processing, contrasting order versus item maintenance and recognition conditions is not the most sensitive procedure (although it has been shown to be sufficient for highlighting dissociations between item and serial order processing; e.g., Majerus, Attout, Artielle, & Van der Kaa, 2015; Hachmann et al., 2014; Majerus et al., 2006) for distinguishing between memory and comparison processes when retrieving serial order information in WM. This study re-examined the neural substrates associated with serial order codes in WM by using a multivariate analysis approach and by eliciting the activation of serial order codes in an incidental manner requiring no explicit judgment and comparison processes of serial order information.

By comparing the neural signals associated with retrieving of items from the beginning versus the end of a memory sequence, we confirmed the involvement of the IPS, in particular in the left hemisphere, in the representation of serial order information in WM. Importantly, we also observed sensitivity to serial order information in the HC, and this is specifically for the left HC. Finally, whereas neural activity patterns in the bilateral AG did not allow for decoding of serial order information, additional sensitivity to serial order information was observed in left SMG, as well as in the right SMA.

The most important serial order models in WM are based on the idea that serial order coding is achieved by binding the serially coded elements to fixed position markers and that recalling this combination allows access to stored information (Polyn & Kahana, 2008). Although a variety of position indicators have been suggested, these models are still on theoretical ground. According to this idea, each position is based on a frame of reference; whereas some authors suggested that position markers are locations in a spatially defined system (Abrahamse et al., 2014; van Dijck & Fias, 2011), others proposed that position markers are incorporated in a time frame in which the encoded elements are linked to time markers derived from temporal oscillators in the brain (Brown, Preece, & Hulme, 2000).

In a series of studies of van Dijck and Fias (2011), van Dijck et al. (2013) pinpointed the nature of position markers defining them as spatial coordinates to encode serial order information within a mental space representation. Retrieving items stored in a WM sequence involves serial scanning across the items in the sequence, which induces an implicit spatial attention bias based on the WM position of the retrieved item (Rasoulzadeh et al., 2021; van Dijck et al., 2013, 2014). Importantly, Rasoulzadeh et al. (2021) provided evidence of the involvement of spatial attention processes by observing that memory search in serial order verbal WM shares the same electrophysiological signatures as those operating on the visuospatial WM and external space. Serial order also relates to primacy and recency effects, which are positional effects *per se*. The attentional spatial account of serial order provides a specific explanation of primacy and recency effects, with primacy associated to the most leftward endpoint of a mental horizontal line and recency to the most rightward endpoint. Recall advantage for primacy and recency portions of a WM list would stem from the fact that items are associated to the most salient positional markers, that is, the endpoints of the horizontal spatial frame.

Considering this framework in combination with available knowledge about the cognitive roles of different sections of the IPS can benefit to disentangle the different contributions of specific parts of the IPS that we observed being able to decode begin versus end serial positions. Anterior and posterior IPS subserve different functional roles, the anterior part being involved in order coding across different domains and the posterior part being associated to attentional processing (Attout et al., 2014; Nobre et al., 2004).

Indeed, Attout et al. (2014) observed distance effects for serial order WM, alphabetical and numerical order comparison task in common areas of bilateral anterior IPS, but not in the posterior IPS, suggesting different functional roles. The anterior part of the IPS has been argued to be involved in order coding across different domains (Attout et al., 2014). This study can exclude comparison processes as possible contributors to the joint activation in WM order, alphabet and numerical order comparison, as accessing WM on the basis of the presented cue does not entail any comparison process. Recently, Attout et al. (2022) adopted a multivariate approach to study the communality of ordinal representations across different domains and observed that the right posterior IPS characterizes processing of ordinal information in WM and alphabetic domains. However, this commonality might represent more attentional processes involved in ordinal judgments than order processing (Attout et al., 2022). As opposed to the role of the anterior IPS, the posterior IPS has been associated with attentional processes by being part of the dorsal attention network, which is associated with top–down attention, guiding the voluntary allocation of attention to positions (Corbetta & Shulman, 2002). Moreover, Nobre et al. (2004) observed that orienting

attention to locations in external and internal space shared common substrates and the posterior IPS is one of the areas that subserve both types of orienting.

Hence, there is good evidence to support the hypothesis that the posterior IPS is involved in the attention-based search processes that were triggered by the cue. Although we were not able to establish the directional spatial attention shifts as a function of serial position at a behavioral level, we confidently assume that the attention shifts had indeed occurred, based on the robust observation of the effect in the works of van Dijck et al. (2013, 2014) and Rasoulzadeh et al. (2021). These findings indicated an association between serial order WM and spatial attention and confirmed that a digit's WM position modulates dot-detection performance. The fact that our results did not show an interaction is not really surprising. van Dijck et al. (2013) indicated that the effect was most consistent at the 250-msec CTI compared with 100-msec CTI and 400-msec CTI. Rasoulzadeh et al. (2021) provided electrophysiological evidence that the shift of attention while retrieving an element from WM happens between 350 and 450 msec. The effect is supposed to occur at the moment when the memory item is retrieved, with a carry-over effect on the dot-detection task if temporally very close to the retrieval of the memory item. In the current study, we used a much longer CTI of 5000 msec to control for hemodynamic delay in brain response when examining brain activity associated with memorized items and to minimize overlap with the ensuing dot-detection phase. However, with such long intervals between the memory item cue and the dot-detection response, the spatial bias induced by the cue is likely to have dissipated when the behavioral responses is collected. Critically, at the neural level, our measurements were locked to the memory cue itself, ensuring that cue-related neural changes can be examined in a direct and nonambiguous manner.

Overall, the present results confirm and refine the role of the IPS in processing serial order information in WM. This may involve the representation of serial order information per se by the anterior IPS, spatial attentional processes shared with exploring physical space, and mental space in posterior IPS. We should also note that we did not observe the neural response to order processing in the right posterior IPS as in the work of Attout et al. (2022). This could be explained by different task designs used to examine order processing. This will be further discussed.

As we used digits as stimuli, we were also able to investigate the extent to which the number items were processed up to the level of their semantic magnitude. Knowing that the IPS is also related to processing of long-term magnitude/ordinal knowledge (such as involved in numbers or the alphabetic sequence; Fias et al., 2007), we checked whether the IPS regions were sensitive to number magnitude. This was not the case: In none of the IPS subregions, multivoxel patterns were able to distinguish small from large digits. This concurs with earlier demonstrations that items stored in verbal WM do not necessarily imply full activation of associated semantic features (Baddeley, 1966a, 1966b; Kowialiewski & Majerus, 2020).

Apart from strengthening and refining the contribution of the IPS to serial order processing, an important finding of this study is the involvement of the HC in decoding serial order information in a WM task. This finding is in line with emerging evidence for the involvement of the HC in sequential processing of the order of events in memory and provides new insight on the functional role of the HC (Long & Kahana, 2019; Roberts et al., 2018; Davachi & DuBrow, 2015). However, the debate regarding the precise mechanism underlying how the HC supports serial order memory is still open. Long and Kahana (2019) proposed that the HC contributes to serial order memory by associating the elements in a space–time context. HC contains neurons that process sequences of events at different levels potentially providing abstract representation of sequences. Studies have highlighted specialized hippocampal neurons that fire for different locations in physical space (place cells and grid cells) and that discharge at successive moments for temporally structured experiences (time cells; Eichenbaum, 2014; Hafting, Fyhn, Molden, Moser, & Moser, 2005; O'Keefe & Nadel, 1978; O'Keefe & Dostrovsky, 1971). Whereas place cells and grid cells provide a cognitive representation of specific location, time cells represent the flow of time. Place and grid cells are also involved in the construction of cognitive maps in humans (Bottini & Doeller, 2020; Garvert, Dolan, & Behrens, 2017; Constantinescu, O'Reilly, & Behrens, 2016; Schiller et al., 2015; Milivojevic & Doeller, 2013), which were defined as tools for systematically organizing information across multiple cognitive domains (Tolman, 1948). It has been argued that similar principles might also apply to the HC in a WM context (Axmacher et al., 2007, 2010; Ranganath & D'Esposito, 2001).

Our observation that HC can distinguish beginning from end serial positions is in line with this proposal and suggests a more specific contribution of HC in serial order processing in a WM task. In the context of verbal WM sequences, the HC may provide a spatially defined template that can be used for position marking by representing serial order in the form of a unidimensional cognitive map. Bellmund, Gärdenfors, Moser, and Doeller (2018) proposed that HC might have developed from mapping navigable space to representing cognitive space, enabling flexible mapping of different environments through space that can be explored through mental navigation, in either LTM or WM contexts (Eichenbaum, 2017; Buzsáki & Moser, 2013). Importantly, HC has been observed to be involved in both temporal and spatial mental navigation. In one study, participants were asked to project themselves into time and space and to order historical events (Gauthier, Prabhu, Kotegar, & van Wassenhove, 2020; Gauthier, Pestke, & van Wassenhove, 2019). Both temporal and spatial ordering were linked to the HC, but Gauthier et al. (2020) also noticed a lateralization of the

two processes; whereas temporal coding of serial order engaged more in left HC, spatial coding of serial order engaged mostly the right HC. Interestingly, order decoding in this study is also left-lateralized in the HC. This further observation could suggest that the order coding observed in this study may be related to temporal rather than spatial mechanism or a cooperation between the two mechanisms.

One could argue that the hippocampal involvement in our tasks reflects LTM processes contributing to performance in our WM task. There are indeed reasons to believe that memory tasks build on a mixture of processes that support immediate aspects of memory and processes that support longer term storage of information. Depending on the procedural specificities of the memory task, there may be more or less contribution of the more immediate WM mechanisms and the longer term memory mechanisms. In our task, there is a pronounced contribution of WM: Participants need to constantly reactivate the sequence to compute the task, and hence, its representation is necessarily in a WM format when being retrieved. However, as opposed to more typical WM paradigms (such as the work of Attout et al., 2022) in which performance is tested a single time immediately after memory encoding, it is likely that our task also comprised some LTM involvement, as an LTM trace may progressively develop over repeated retrievals.

Interestingly, recent theoretical work developed in the domains of WM and LTM do not consider WM and LTM as two distinct mechanisms. Recent models of WM claim structural and functional overlap between WM and LTM (Oberauer, 2002, 2009) by conceptualizing WM as a subset of activated LTM representations each of which has been brought—for a limited time—to an active state via attentional processes (Oberauer, 2002; Cowan, 1988). A parallel line of research provides a comparable functional model for LTM. Cabeza et al. (2008) proposed an attentional account for memory retrieval in LTM. They observed that parietal regions support the shift of attention to internally generated mnemonic representation, with the dorsal PPC that mediate the allocation of attentional resources for memory retrieval (Cabeza et al., 2008; Ciaramelli, Grady, & Moscovitch, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). In summary, we can suggest that WM and LTM are less distinct than we think, and that attention plays a fundamental role in selecting an item represented in an active state and both models highlight the involvement of attentional resources allocated to retrieve stored information. Our findings might reflect a reactivation of an LTM representation through a WM component or an attentional process that brings it active and temporarily accessible through the focus of attention by uplifting the state of one selected item. This process allows the retrieval from memory.

In Cabeza's model, other regions are known to be involved in memory research activities (Sestieri et al., 2017; Cabeza et al., 2008). Apart from the involvement of the dorsal PPC, also the ventral region of the PPC plays a role in memory retrieval. Differently from the AG, the SMG allows for decoding of serial order position in the current study. Although the functional role is still controversial (Majerus, 2019; Majerus et al., 2006, 2010), in some previous studies, this region has been associated more specifically with serial order processing in a WM context. Papagno et al. (2017) and Guidali et al. (2019), using direct electrical stimulation or TMS, showed an increase in serial order errors during WM recall tasks, a stronger role of this region for serial order maintenance, and this is across verbal and visual domains. This region might support serial order coding via phonological codes (Majerus, 2019) or domain-general relational representations (Papagno et al., 2017). The AG has been usually associated to content processing rather than order processing allowing decoding for the content of the retrieved information. Consistently with the literature, the AG did not allow for decoding of serial order information in the current study.

Apart from the IPS, HC, and SMG, we also observed decoding of serial order information in the SMA. This region had been included for the ROI analyses as it had been shown to be involved in in time processing and the topographic representation of time (Protopapa et al., 2019). This represents potential evidence for additional temporal coding of serial order information. This is compatible with the idea that not only space, but also time, can be used as a position marker. By marking stimuli or events with a time stamp that expresses the moment of their occurrence, the sequential order in which these stimuli or events occurred can be derived. Possibly, such time-based sequential processing may be performed in concert with the coding of sequences by time cells in the HC.

Neurocognitive research on space and time in the brain assumes that space and time retain their independence from each other and are considered distinct axioms. Buzsáki and Tingley (2018) questioned the supposed independence of space and time. Space and time in modern physics are inseparable concepts, and the authors claimed that new experimental approaches in neuroscience research require a new conceptual framework to investigate space and time in the brain. Buzsáki and Tingley (2018) have proposed that space and time represent a succession of events and are just examples of a general mechanism that computes the sequence of variables. According to this conceptual framework, it is not possible to untangle space and time and consequently measure them separately. This may lead us to think that the position markers associated with an item in memory are a combination of space–time and a result of a more general mechanism.

Overall, this study suggests that coding of serial order information is not supported by a single mechanism, but that spatial, temporal, and attentional all contribute to the coding of a type of information that is very difficult to code because of its transient and changing nature (Majerus, 2019). Multimodal coding may provide the most robust representation of temporary serial order information, by involving different representational and neural systems.

Each mechanism might be involved in one or more processes like maintenance, representational, and retrieval.

Conclusion

In conclusion, this study examined the neural substrates involved in access to serial order information in WM by using optimally sensitive experimental and analytic procedures. Our results show that the representation of and access to temporary serial order information relies on a broader set of neural areas than previously thought. We confirmed the role of the IPS in serial order coding, but also highlighted the role of the HC, in addition to the SMG and the SMA. Although it is likely that these different neural regions reflect the intervention of distinct levels of serial order coding (at spatial, temporal, and attentional levels), future studies need to specify more directly the different codes that support the representation of temporary serial order information.

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AUTHOR CONTRIBUTION

Steve Majerus: Conceptualization; Funding acquisition; Supervision; Writing—Review & editing.

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Diversity in Citation Practices

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

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