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Eye movements follow the dynamic shifts of attention through serial order in verbal working memory

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How are arbitrary sequences of verbal information retained and manipulated in working memory? Increasing evidence suggests that serial order in verbal WM is spatially coded and that spatial attention is involved in access and retrieval. Based on the idea that brain areas controlling spatial attention are also involved in oculomotor control, we used eye tracking to reveal how the spatial structure of serial order information is accessed in verbal working memory. In two experiments, participants memorized a sequence of auditory words in the correct order. While their eye movements were being measured, they named the memorized items in a self-determined order in Experiment 1 and in a cued order in Experiment 2. We tested the hypothesis that serial order in verbal working memory interacts with the spatial attention system whereby gaze patterns in visual space closely follow attentional shifts in the internal space of working memory. In both experiments, we found that the gaze shifts in visual space correlated with the spatial shifts of attention along the left-to-right one-dimensional mapping of serial order positions in verbal WM. These findings suggest that spatial attention is employed for dynamically searching through verbal WM and that eye movements reflect the spontaneous association of order and space even in the absence of visuospatial input.

In a quickly changing environment, the ability to briefly retain and manipulate information in the absence of steady perceptual input is a crucial function of working memory (WM). To complete the most basic tasks successfully, it is important to remember not only *what* was presented to us but also to remember the *order* in which this information was presented. Without order processing, complex cognitive skills such as language, reasoning, and learning are impossible[1]. How serial order processing is accomplished is therefore considered to be one of the most important problems in cognitive science[2]. The current study aims to investigate how arbitrary sequences of verbal information are retained and flexibly accessed in WM.

The question of how serial order verbal information is retained has been extensively studied within the framework of the phonological loop[3]. As speech progresses in time, its retention has been proposed to rely on the brain's language-specific regions subvocally looping through the memory sequence[4,5]. However, an increasing number of findings suggests that the brain's spatial processing and attentional systems are also recruited[6–9]. Firstly, there is neuroimaging evidence showing that the retention of serial order information relies on parietal brain regions that are typically observed in the perceptual processing of visuospatial information[10,11]. Secondly, a robust behavioral observation indicates that serial order verbal information is spatially mapped, with items from the beginning of the sequence being associated to the left side of space and items from the end to the right[12]. Thirdly, it has been shown that neural correlates of guiding spatial attention in visual space are also involved in the internal search through the spatial mapping of serial order verbal information[13]. Finally, motivated by the idea that brain regions controlling spatial attention are also engaged in saccadic planning[14,15], a recent line of eye tracking studies demonstrated that spontaneous eye movements reveal the serial position of attended items in verbal WM[16,17]. Specifically, gaze position diverted more towards the left side of space when retrieving initial items from the memorized verbal WM sequence, and more towards the right side of space when retrieving later items[17]. Consistent with the notion that serial order information is grounded in the spatial attention system[6], these findings add to the close coupling that has previously been shown between visuospatial WM, spatial attention and the oculomotor system[18,19].

Similar to the subvocal rehearsal mechanism, recurring *patterns of eye movements* have been reported in visuospatial WM that are highly similar to patterns of eye movements at encoding as if the oculomotor system

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is dynamically replaying the sensory information[20–26]. For example, de Vries and van Ede[26] showed that delay period eye movements were biased along the direction of sensory information. While these findings in the visuospatial modality are interesting, they are not so surprising because both sensory processing and retention of visuospatial information share many features supported by common brain regions[18–20]. The involvement of such patterns of eye movements in verbal WM is more interesting as these eye movements allow to track how the focus of attention cycles through serial order verbal information which is inherently non-spatial in nature. In this regard, Viganò et al.[27] observed that spontaneous eye movements closely followed the one-dimensional structure of a mental number line, and the two-dimensional structure of colors represented on a color wheel, thereby reflecting the relational structure of long-term memory (LTM). The aim of the present study is to address the question whether such patterns of eye movements reflect the spatial configuration of verbal WM.

Consistent with the hypothesis that memory for serial order is grounded in the spatial attention system[7,8], there is evidence of left-to-right encoding reflected in horizontal eye movements[16]. However, this effect was found in the context of serial recall respecting the forward order. On itself, this finding might reflect processes related to serial verbal production (e.g., reciting positions) rather than the exploration of a spatially defined representation of ordinal positions. Notably, incremental recitation, such as counting, has been shown to induce rightward eye-movement shifts[28]. However, the fact that systematic horizontal gaze shifts accompany accessing specific positions in working memory[17] shows that oculomotor activity in verbal working memory is not exclusively tied to recitation but also to the exploration of a spatially defined representation of ordinal position. Yet, the latter finding was restricted to the specific situation where access to an item in working memory was followed by a secondary task (i.e., auditory beep detection) and where eye position was measured in absolute terms. This design did not allow to capture the dynamics of exploring the working memory space from one position to the other. Hence, it remains an open question how serial order positions are continuously accessed through successive shifts from one position to the other, allowing relative measurements of space, by distinguishing how an item at a specific position is accessed from different other positions (like for instance position four being accessed via leftward shifts from position five or via rightward shifts from position three) and not just by rightward shifts as studied in earlier work[16,17].

To address this question, we used an adapted version of the verbal fluency task used by Viganò et al.[27]. Unlike Viganò et al.[27] who relied on prior spatial associations existing in LTM (e.g. mental number line), we presented novel sequences of verbal stimuli (i.e., fruits/vegetables) for temporary storage in verbal WM. In Experiment 1, participants were instructed to *internally* generate an arbitrary stream of verbal items they sampled from the WM sequence. In Experiment 2, the targets for naming these verbal items were defined by *external* cues shifting spatial attention through the WM sequence. We hypothesized that if eye-movements reflect the spatial geometry of verbal WM, then both the size and the direction of eye movements in physical space should be correlated with the size and direction of the shifts along the serial order positions in mental space. Since serial order is mainly represented along a horizontal axis[7,16,17], we predicted that shifts in mental and physical space should be correlated on the horizontal axis but not on the vertical axis.

Results

Experiment 1

The verbal fluency task consisted of three phases. In phase 1, participants memorized a sequence of five auditorily presented words in the right order. In phase 2, participants listened to metronome beeps and had to continuously speak words from the list at the pace set by the beeps in a random order. In phase 3, participants repeated the WM sequence in the right order at their own pace (Fig. 1a).

Only trials with accurate verbal responses in both phases 2 and 3 were included in the analyses. Accuracy in phase 2 was defined as correctly named items belonging to the WM sequences ($M = 64.72\%$, $SD = 26.36\%$). Accuracy in phase 3 was defined as blocks with an entirely correct serially recalled WM sequence ($M = 50\%$, $SD = 25.14\%$). The reaction times (RTs) of the correctly named items did not significantly vary as a function of the absolute serial position (Table 1a) or the relative shifts in serial position (Table 1b) ($F\text{s} < 1.56$). This confirms that participants adhered to the instruction to prioritize accuracy over speed.

Following Viganò et al.[27] and Loetscher et al.[29], median gaze coordinates on the x and y axes were extracted separately from the 500 ms interval before voice onsets. This specific interval was chosen because it aligns well with the estimated interval for initiating articulation after concept selection, which falls between 455 and 600 ms[30,31]. Note that we controlled for word length and lexical frequency to ensure consistent speech production times across all words.

Next, we calculated a trial-by-trial vector of differences in WM position between consecutively named items by subtracting the WM position of the currently named item from the WM position of the subsequently named item (Fig. 1b). The size of the resulting difference indicates the absolute distance of the shift in WM position. The direction of the positional shift in WM was indicated by the negative (backward) or positive (forward) sign of the resulting difference. Similarly, a vector of trial-by-trial differences between the median gaze positions associated to consecutively named items were computed for the x and y axes separately. The size of these differences indicates the visual distance in coordinates between consecutive items. The direction travelled along the visual axes (horizontal/vertical) was indicated by the negative (leftward/downward) or positive (rightward/upward) sign of these differences.

To visualize the associations between the relative changes in gaze position in visual space with the relative changes in the serial order WM position, we computed the average changes in gaze shifts along the axes per subject. These gaze shifts were then regressed onto positional changes along the serial order positions in WM. The paired samples t-tests resulted in a significant correlation between shifts in WM position and shifts in gaze position on the x-axis ($r = 0.12$, $SD = 0.35$, $t(28) = 2.38$, $p = 0.024$, $PCC = 72.41\%$). The correlation between shifts

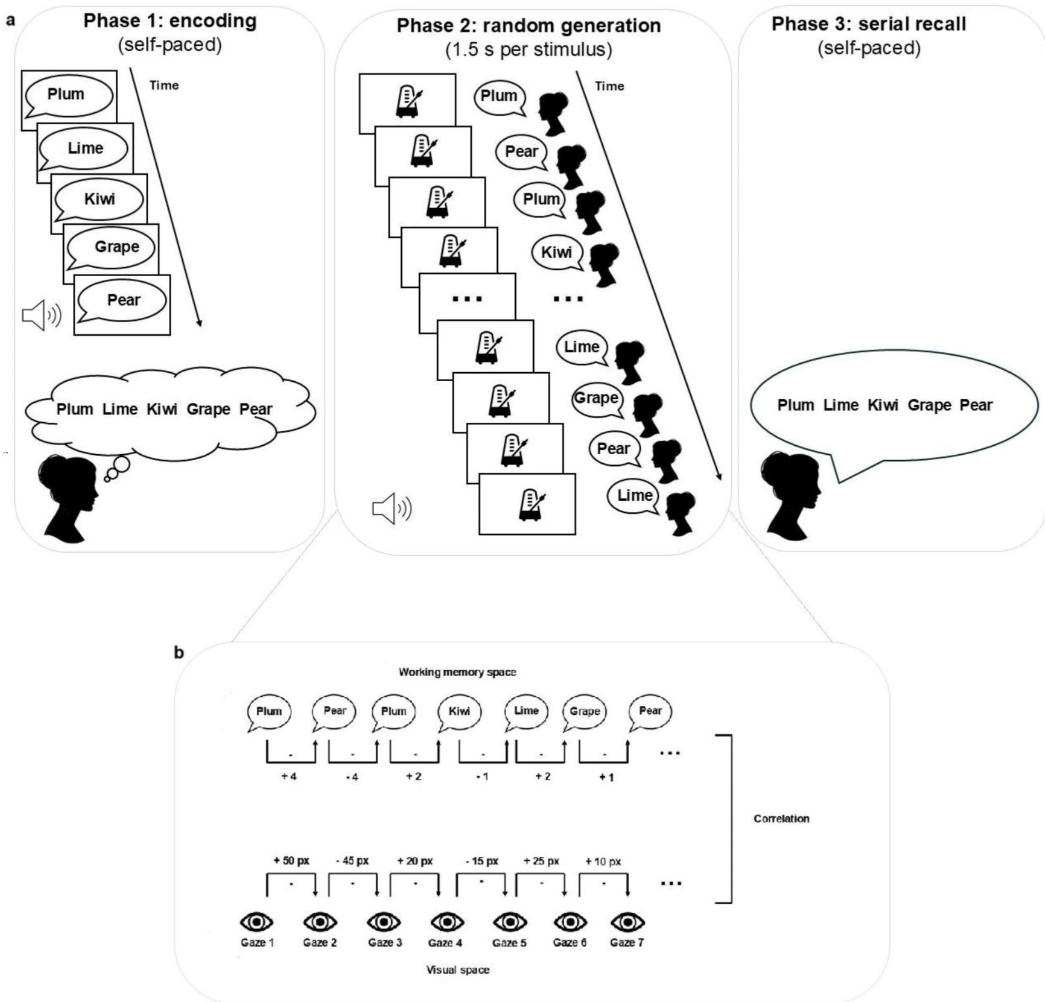

Fig. 1. (**a**) Eye movements were continuously measured while participants performed a random production task sampling from five words belonging to an auditorily encoded WM sequence. Their knowledge of the sequence was tested with a serial recall task at the end of each block. (**b**) Illustration of how difference scores going into the final analyses were obtained with a simulated example. Shifts in WM space were calculated by subtracting the WM position of the named item from the WM position of the successively named item. Shifts in visual space were calculated similarly. Note that all stimuli were presented in the participant's native language (i.e. Dutch).

in WM position and shifts in gaze position on the y-axis did not reach statistical significance (r = -0.01, SD = 0.28, $t(28)$ = 1.23, p = 0.23, PCC = 51.72%) (Fig. 2a).

Regressing the shift in gaze position onto the shifts in WM position, revealed that the slopes of the regression line per participant were significantly increasing on the horizontal axis ($slope$ = 23.02, SE = 12.78, $t(28)$ = 1.8, p = 0.041, PCC = 68.96%; Fig. 2b). but not on the vertical axis ($slope$ = −1.37, SE = 1.83, $t(28)$ = −0.75, p = 0.77, PCC = 48,28%; Fig. 2c). This effect indicates that the distance and direction of the positional changes in serial order WM were associated with the changes in gaze position on the horizontal plane of visual space. Furthermore, we observed that the variance in the changes in gaze position is also greater along the x-axis (Fig. 2b) compared to shifts on the y-axis (Fig. 2c), indicating that the effects are primarily associated to the horizontal dimension. These findings suggest that the spatial shifts of attention, as tracked by the eye movements, systematically followed the distance and direction of internal shifts of attention within the spatial configuration of serial order information in verbal WM.

We investigated whether gaze position followed the absolute positions of serial order verbal items in WM. This analysis focused on the absolute landing position of the gaze before naming an item from each serial order position. To this end, the median gaze coordinates on the x and y axis were separately averaged per participant and regressed onto the serial order position of the named item.

As illustrated in Fig. 2d, the spatial configuration of serial order follows a left-to-right gradient of gaze with increasing position in the WM sequence. A one-tailed one-sample t-test was performed to test whether the resulting slopes were significantly larger than zero, indicating a rightward movement of the gaze with increasing

	Experiment 1		
	WM position	Mean voice onset	SD voice onset
a	1	642.64	245.41
	2	644.54	248.00
	3	622.26	226.66
	4	636.84	223.25
	5	635.18	224.30
	Experiment 1		
	WM position shift	Mean voice onset	SD voice onset
b	−4	619.76	198.91
	−3	632.52	260.32
	−2	631.57	258.17
	−1	636.97	241.68
	0	659.99	259.28
	1	636.23	234.80
	2	625.14	208.02
	3	612.30	208.31
	4	605.14	219.84

Table 1. Average reaction times (ms) experiment 1.

Results Experiment 1

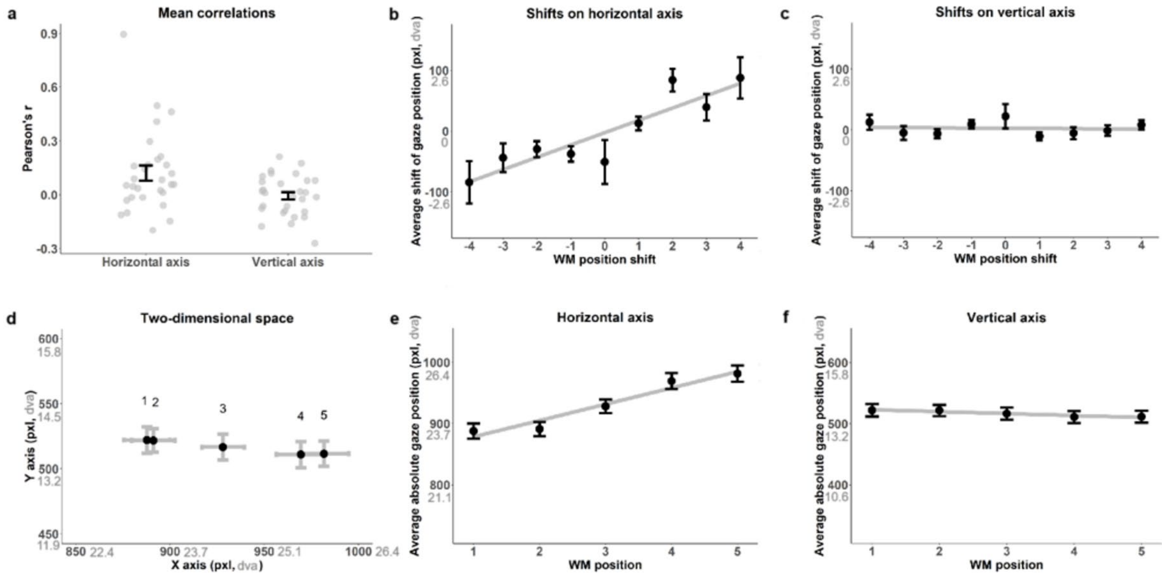

Fig. 2. (**a**) The black dot represents the average correlation between shifts in gaze position and shifts in WM position of the items on the horizontal (left) and on the vertical axis (right) during the random generation task. The grey dots illustrate the average correlation on the participant level. (b + c) Grand average of shift in gaze position (in pixel and degrees of visual angle) in function of shift in WM position of the named items on the horizontal (**b**) and vertical axis (**c**). Shift of gaze position followed a left-to-right gradient with increasingly positive shift in WM position. (**d**) Gaze location corresponding to each item WM position plotted in the two-dimensional space. (e + f) Absolute gaze position in function of WM position of the named item. Gaze progressed to the right with increasing WM position of the named item (**e**). There was no relation found between gaze location on the vertical axis and item position in the WM sequence (**f**). All error bars indicate the standard error of the mean across participants.

WM position (following Rinaldi et al.[16] and Sahan et al.[17]). We found that regressing the absolute gaze coordinates onto absolute WM position of the named item resulted in significantly increasing slopes on the horizontal axis (*slope* = 24.53, *SE* = 13.82, $t(28) = 1.78$, $p = 0.043$, *PCC* = 68.96%; Fig. 2e) but not on the vertical axis (*slope* = −1.49, *SE* = 2.58, $t(28) = -0.58$, $p = 0.716$, *PCC* = 48.28%; Fig. 2f).

In a follow-up analysis we addressed the question whether eye movements are functional or epiphenomenal in verbal WM. To this end, we performed a Pearson correlation analysis between the positional gaze slopes per participant and the average RTs per participant, where the magnitude of the slope reflects the extent of the spatial coding and RTs indicate retrieval efficiency. One could predict that if spatialization is functional, then it should also be beneficial for retrieval (e.g., van Ede et al.[32]). However, none of the effects were significant regardless of whether the analysis was conducted on the absolute positional gaze slopes (X-axis: $r = 0.22$, $t(27) = 1.16$, $p = 0.26$; Y-axis: $r = 0.06$, $t(27) = 0.29$, $p = 0.78$) or the relative positional gaze shift slopes (X-axis: $r = 0.24$, $t(27) = 1.30$, $p = 0.20$; Y-axis: $r = 0.12$, $t(27) = 0.64$, $p = 0.53$).

Experiment 2

The design of Experiment 2 remained largely similar to that of Experiment 1 except for phase 2. To test whether the results of Experiment 1 can be replicated with externally induced shifts of attention, participants were cued to verbally generate the items belonging to the encoded sequence in an experimentally predefined random order instead of internally generating a random order. All preprocessing and analysis steps remained the same as in Experiment 1 (accuracy phase 2: $M = 69.13\%$, $SD = 19.13\%$; accuracy phase 3: $M = 72.32\%$, $SD = 38.25\%$). The RTs of the correctly named items varied significantly as a function of the absolute serial position ($F(3, 87) = 3.57$, $p = 0.02$, $\eta^2_p = 0.11$; Table 2a). A post-hoc Fisher's Least Significant Difference (LSD) test showed that this effect was primarily driven by faster RTs to items in the first or last serial position compared to items in the third serial position ($p < 0.05$). This pattern, contrary to the findings in Experiment 1, suggests a potential primacy and recency effect, evoked by the external cueing paradigm that imposed different cognitive demands than the random generation task used in Experiment 1. However, the RTs of the correctly named items did not exhibit significant variation as a function of the relative shifts in serial position ($F < 1.05$; Table 2b).

The paired samples t-tests resulted in a significant correlation between shifts in WM position and gaze shifts on the x-axis ($r = 0.29$, $SD = 0.36$, $t(29) = 6.46$, $p < 0.001$, $PCC = 93.33\%$). The correlation between shifts in WM position and gaze shifts on the y-axis did not reach statistical significance ($r = -0.01$, $SD = 0.33$, $t(29) = -0.96$, $p = 0.68$, $PCC = 50\%$) (Fig. 3a). Regressing the shift in gaze position onto the shifts in WM position, revealed that the slopes of the regression line per participant were significantly greater than zero on the horizontal axis ($slope = 26.86$, $SE = 8.3$, $t(29) = 3.23$, $p = 0.002$, $PCC = 90\%$; Fig. 3b) but not on the vertical axis ($slope = -0.66$, $SE = 3.66$, $t(29) = -0.18$, $p = 0.571$, $PCC = 40\%$; Fig. 3c). As in experiment 1, we observed that the variance in the changes in gaze position is also greater along the x-axis (Fig. 3b) compared to shifts on the y-axis (Fig. 3c). This effect indicates that the distance and direction of the positional changes in serial order WM were associated with the changes in gaze position on the horizontal plane of visual space.

Finally, the spatial configuration of serial order is equivalent to that observed in Experiment 1 (Fig. 3d). We found that regressing the absolute gaze coordinates onto absolute WM position of the named item resulted in slopes significantly larger than zero on the horizontal axis ($slope = 27.11$, $SE = 8.78$, $t(29) = 3.09$, $p = 0.002$, $PCC = 83.33\%$; Fig. 3e) but not on the vertical axis ($slope = -0.18$, $SE = 3.63$, $t(29) = -0.05$, $p = 0.519$, $PCC = 56.67\%$; Fig. 3f). Therefore, we replicated the left-to-right gradient of gaze with increasing position in the WM sequence found in Experiment 1, but as a function of *externally* cued attentional shifts.

As in experiment 1, we addressed the question whether eye movements are functional or epiphenomenal in verbal WM. The correlation analyses between the absolute gaze slopes and average RT per participant were not significant (X-axis: $r = -0.11$, $t(28) = -0.57$, $p = 0.57$; Y-axis: $r = -0.07$, $t(28) = -0.39$, $p = 0.70$). The relative positional gaze shift slopes did also not result in a significant correlation with the average RT per participant (X-axis: $r = -0.09$, $t(28) = -0.50$, $p = 0.62$; Y-axis: $r = -0.03$, $t(28) = -0.17$, $p = 0.87$).

General discussion and conclusion

The question of how arbitrary sequences of verbal information are retained and manipulated in the mind has a long research tradition[2]. We addressed this question by continuously recording eye movements during a

	Experiment 2		
	WM position	**Mean voice onset**	**SD voice onset**
a	1	1377.42	394.72
	2	1452.60	415.96
	3	1462.91	410.12
	4	1342.38	401.13
	Experiment 2		
	WM position shift	**Mean voice onset**	**SD voice onset**
b	−3	1428.70	29.57
	−2	1472.00	21.29
	−1	1427.78	17.16
	1	1326.64	17.78
	2	1411.07	20.35
	3	1401.16	27.52

Table 2. Average reaction times (ms) experiment 2.

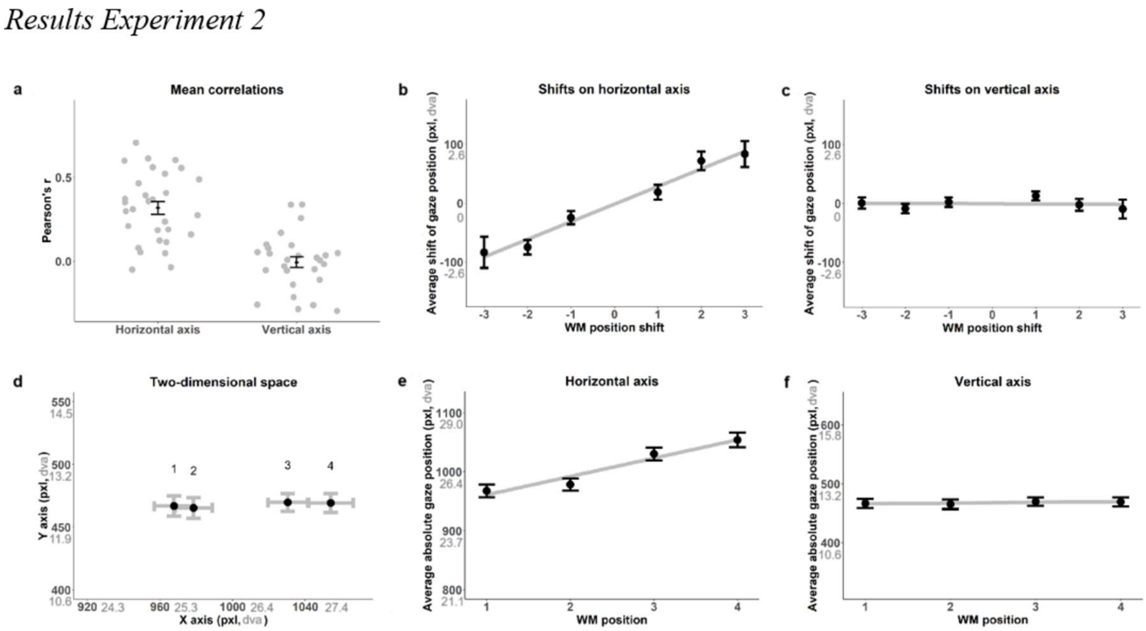

Fig. 3. Same conventions apply as in (Fig. 2). Note that Experiment 2 used sequences of four items instead of five.

verbal memory-based fluency task and observed a close relationship between eye movements and dynamic shifts of spatial attention through serial order verbal WM. In Experiment 1, we found that *internally* generated shifts through serial order in verbal WM were reflected in the patterns of eye movements. Specifically, both the direction and size of shifts through serial positions in verbal WM were associated to the direction and size of gaze shifts in visual space. In Experiment 2, we found that this effect generalized to *externally* induced shifts of attention. While none of the stimuli or cues were spatial in nature, space is an important feature of organizing serial order verbal WM. Accordingly, we found that the progression of absolute gaze position followed a left-to-right gradient along the order of the verbal WM sequence from which the items were sampled[16,17]. These findings are consistent with the hypothesis that the representation of serial order in verbal WM is accomplished by spatially organizing the memoranda according to reading direction (e.g., from left-to-right in Western languages; see Fischer-Baum & Benjamin[33] and van Dijck et al.[9]).

Aside from revealing the absolute gaze positions associated to serial order, our study captured the relative shifts in size and distance between the serial positions. When searching through verbal WM, people generally use forward scanning, starting with the first item and progressing sequentially to the last[34]. Compared to previous work where serial order was maintained with high accuracies (above 90% in[9,17]), performance in our tasks was relatively low (50% in Experiment 1, 65% in Experiment 2). Interrupting forward rehearsal and requiring random generation places higher executive demands with a consequence of reducing memory performance[35]. Experiment 1 was more demanding as it involved self-determined random generation from WM loaded with five items compared to cue-based retrieval from WM loaded with four items in Experiment 2. Despite these differences, our findings suggest that when the forward chain of scanning is disrupted, the ability to flexibly access different positions is retained. This entails that later items, like position four, can also be accessed via leftward shifts from position five, and not just by rightward shifts as defined by the absolute positions as observed in earlier work[16,17]. These findings align with the notion that similar mechanisms of spatial attention involved in visuospatial WM are also recruited when searching through verbal WM that is nonspatial by nature[6,7].

Going beyond the key observation of a close relationship between spatial attention, the oculomotor system and visuospatial WM[18,19], our findings extend this link to the verbal domain of WM. Similar to the subvocal rehearsal mechanism[4], the oculomotor system is also recruited to cycle through the ordered sequence of verbal information. The observation that patterns of eye movements are reflective of attentional processes in verbal WM, suggests that verbal WM is not exclusively supported by a domain-specific (i.e., phonological) rehearsal mechanisms. To the contrary, our findings indicate that spatial attention is adopted as a domain-general selection mechanism operating similarly in verbal WM as in visuospatial WM. However, unlike the visuospatial modality where patterns of eye movements follow the rather large layout of the visual information[24], we observed that the gaze shifts only scaled to a small portion of the visual space. While our findings are of a comparable range to the gaze shifts observed in the semantic spaces of LTM (e.g., approximately 100 pixels or 2.5 degrees of visual angle in Viganò et al.[27]), it remains interesting for future research why and how this spatial compression takes place. Moreover, it is important to note that even though there is a strong link between covert attention and eye movements[15], these mechanisms are dissociated[36]. It is therefore possible that the range of overt attention does not align with covert attention, and that covert attention may operate along the vertical dimension, even if this was not reflected in the eye movements. To our knowledge, there is no evidence for this suggestion in verbal

WM research yet. While we acknowledge the importance of the vertical dimension, serial order is inherently unidimensional, and it appears sufficient to observe positional effects on the horizontal dimension alone[16,17]. The extent to which the vertical domain contributes to verbal WM remains a matter for future research. Similar to Vigano et al.[27], it would be interesting to explore whether conceptual distances between memory items in semantic space are represented along the vertical dimension.

Accepting the idea that the position of the eye reflects the focus of attention, one may wonder whether the link between eye movements and serial order processes is a functional one, or if it is simply an epiphenomenon. In an attempt to address this question, we correlated the gaze slopes (as an index of spatialization) with the average RTs (as an index of retrieval efficiency). We reasoned that if spatialization is functional, then it should follow that the extent of one's spatial coding should lead to more efficient memory retrieval. However, we could not find evidence in our data supporting this hypothesis. In fact, the current study cannot make any claims about the functionality of eye movements based on the absence of such a correlation. Firstly, our experiments emphasized accuracy over speed as we also controlled for effects of word length and lexical frequency, ensuring an approximately equal time course of production across all words. Indeed, the RTs for naming memory items showed no strong evidence of variation based on absolute positions or relative shifts between positions. Secondly, our experiments were not designed to directly address this question, as we did not explicitly manipulate eye movements. De Belder et al.[37] directly manipulated covert attention and found that retrieving items from the start of a sequence was facilitated when the left side of space was cued, while retrieving items from the end of a sequence was facilitated by rightward spatial cues. Whether eye movements serve a similar functional role in verbal WM as covert spatial attention remains an open question. Future research is needed to examine if memory performance is influenced by gaze positions, potentially being enhanced or hindered depending on the congruency with the serial position.

The fact that retrieval of order information from verbal WM relies on the brain's spatial attention system resonates with the ideas of the neuronal recycling hypothesis[38]. According to this view, evolutionary older mechanisms of the brain are recycled for supporting complex skills such as language processing, mathematical cognition or abstract reasoning, that have a relatively recent emergence in the evolutionary timeline. Accordingly, it has been suggested that the spatial attention system recruited to scan the visual space is also re-used to navigate the internal space of WM[6,7,9]. A number of neuroimaging findings support this idea. In the brain various regions involved in exploring and navigating the visual space such as respectively the parietal cortex and the hippocampus have also been identified as active during serial order processing in verbal WM[10,11]. To navigate visual space we rely on an internal structure of the perceptual world known as cognitive maps[39,40], and according to Bellmund et al.[41], the structure of semantic knowledge also relies on the same neural systems to structure and navigate representational spaces[42]. Our results are in line with these hypotheses and suggest a close interplay between representing serial order verbal information and spatial processes. How these two processes precisely interact with each other in the brain is a matter for future research.

To conclude, the results of the current study offer converging evidence for the grounding of serial order in the spatial attention system by demonstrating this relationship in the context of successive dynamic shifts. The recurring observation of eye movements expressing this connection accordingly makes the oculomotor system an interesting target for further neuroscientific research on the topic of serial order processing in WM.

Methods

Experiment 1

Participants

30 Ghent University first year Psychology students (7 males, age: $M = 18.67$ years, $SD = 1.74$ years) participated in the study for course credits. The sample size was a priori determined based on Viganò et al.'s[27] study. Three participants were excluded and replaced due to not performing the task correctly or calibration failure. All participants were Dutch native speakers. Before starting the experiment participants signed an informed consent form. The experimental protocols of this study were approved by the Independent Ethics Committee of the Department of Psychology and Educational Sciences of Ghent University (EC2020157). The study was performed in accordance with the guidelines and regulations of the Independent Ethics Committee of the Department of Psychology and Educational Sciences of Ghent University.

Apparatus

The instructions were displayed at a viewing distance of 60 centimeter. Participants were presented with all auditory stimuli through a headset. Stimulus timing and presentation was managed by the Python-based software PsychoPy (Open Science Tools Ltd.).

Eye movements were recorded throughout all phases of the experiment with an EyeLink 1000 tower mounted eye tracker (SR Research) at a sample rate of 1000 Hz. No chin rest was used as to not restrict the participants' ability to talk. The eye tracker was calibrated before the start of the experiment using the built-in thirteen-point calibration protocol. Drift correction was performed at the beginning and after the first six experimental blocks. The eye tracker was recalibrated after every failure to perform the drift correction. Missing gaze data resulting from blinks were extended backward and forward in time by 100 ms and linearly interpolated (following Geller et al.[43]).

Stimuli

Stimuli consisted of a closed set of twenty Dutch mono- and disyllabic fruit and vegetable words, ten of each category (Supplementary Table 1). We extended a selection of stimuli used in van Dijck & Fias[12] with additional words with an equal Zipf-score range of 2.2–3.5 (SUBTLEX-NL[44]). Restricting our closed set of stimuli with similar Zipf frequencies allowed us to control for effects of word length and lexical frequency, ensuring a consistent time course of production across all words. The auditory stimuli were generated in a synthetic female voice using the Mac OS X text-to-speech "say" command.

Procedure and design
First, participants went through a familiarization phase where the whole stimuli set was presented once, simultaneously in auditory and visual modality. All light sources were turned off. We continuously recorded participants' spontaneous eye movements while they were facing a black screen. Two practice blocks preceded twelve experimental blocks comprising three phases each (Fig. 1a).

In phase 1, participants memorized a sequence of five auditorily presented words in the right order. These items were randomly sampled without replacement from the fruit category in the first six blocks and from the vegetable category in the last six blocks. Participants listened to each word successively by pressing the "j" key (hereafter the response button). A click tone was presented after the last word to signal the end of the encoding phase. Participants were then provided with a self-paced break to rehearse the sequence.

With pressing the response button, participants initiated phase 2. Here, participants heard a metronome of 15 beep tones at 1500 ms intervals. With the presentation of each beep tone, participants were instructed to randomly name a word belonging to the previously encoded WM sequence, generating the words as randomly as possible while sampling each word approximately equally often (Supplementary Fig. 1). Verbal responses were recorded and stored. Voice onsets were obtained from the voice recordings by using a custom-made Python algorithm and visual verification based on the spectrograms in Praat[45]. On the occasion of technical failure, voice onsets were substituted with the average of the remaining registered voice onsets. Blocks in which participants failed to name a word after presentation of the metronome or produced items that did not belong to the original sequence were excluded.

Phase 3 started with the synthetic voice instructing the participants to repeat the WM sequence in the right order at their own pace. The next block was initiated upon pressing the response button.

Statistical analyses
Only trials with correctly recalled WM sequences in phase 3 were included in the final analyses to make sure we analyzed trials where participants correctly maintained all items in the correct order during phase 3. These trials are crucial for meaningful analysis of phase 2, as they depend on the combined accuracy of item content and their serial positions. Furthermore, every trial in phase 2 where participants made mistakes in the verbal random production task, such as skipping the metronome (i.e., omission errors) or producing words that were not part of the original sequence (i.e., commission errors) were excluded as well. RTs as a function of the absolute positions as well as the relative shifts in WM are also reported. Note that, although we emphasized accuracy over speed, we also conducted separate repeated measures ANOVA with the absolute WM positions and relative serial position shifts as independent variables, and mean RT as dependent variable.

To test whether the relative shifts in WM position are correlated with shifts in gaze position, we calculated the Pearson correlation coefficient between the difference vectors of the shifts in gaze position and the shifts in WM position. These correlations were calculated for each participant on a block level and were then averaged per participant. All correlations were Fisher z-transformed [$z=\text{atanh}(r)$] to allow for statistical testing. We statistically tested our observed correlations against simulated correlations. Comparing against correlations with a random gaze pattern made our analysis statistically more stringent than comparing against the hypothetical null distribution. Simulated coordinates were obtained by randomly generating gaze data from a range of screen resolution values and calculating the Pearson correlation coefficient between the random gaze data and the observed WM position shifts. A two-tailed paired samples t-test was then applied to compare between the Fisher z-transformed simulated and observed correlations for the horizontal and the vertical axis separately. An alpha level of 0.05 was applied for all analyses. Following Grice et al.[46], we report person-centered effect sizes as the percentage of participants showing the effects in the expected direction, providing an indication of the consistency of the effect across participants. This is presented as the percent correct classification (*PCC*) of participants demonstrating the expected effect[46].

Experiment 2
Participants
We tested a sample of 30 participants (3 males, age: $M=19.81$ years, $SD=4.65$ years), applying the same selection criteria as in Experiment 1.

Apparatus and stimuli
The stimuli content and set-up remained the same as in Experiment 1 except for using an Eyelink 1000+ (SR research) desktop mounted eye tracker.

Procedure and design
The procedure and the design of the study remained largely similar to Experiment 1 except for the following changes (Fig. 4). In phase 1, the memory load and presentation modality differed: Sequences of four items were presented one by one in the middle of the screen. Each word was printed in a specific color (blue, green, red, yellow). Each participant was presented with a fixed order of colors that remained the same across blocks. The order of the colors was sampled from ten predefined combinations (Supplementary Table 2) and counterbalanced across participants.

In phase 2, the order in which participants produced the words was now *externally* cued by auditorily presenting 16 color words as positional cues spoken by the synthetic voice every 2500 ms. The positional color

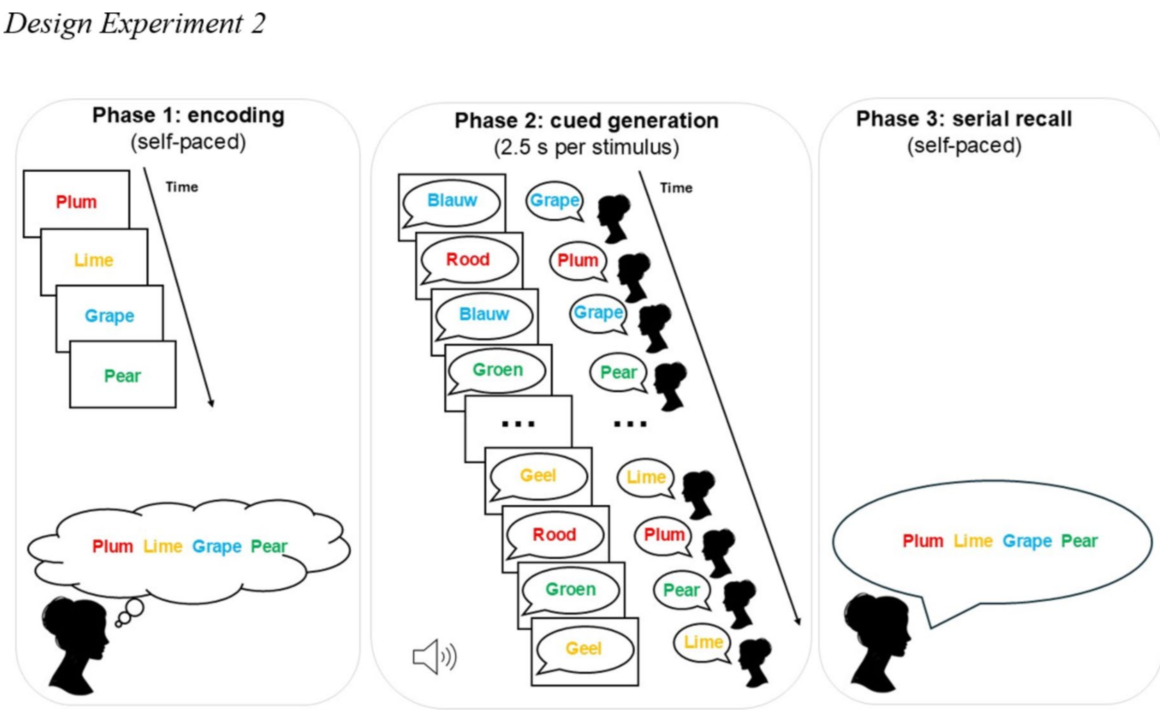

Fig. 4. Eye movements were continuously measured while participants performed a cued verbal production task. Their knowledge of the sequence was tested with a serial recall task at the end of each block. Note that all stimuli were presented in the participant's native language (i.e. Dutch).

cues were pseudorandomly sampled: each color cue appeared equally often, and the same color cue could not be presented twice in a row. Participants were required to name the items associated with the color cues.

Data availability
All data and analysis scripts are available on OSF (https://osf.io/q9mbn/?view_only=a14d32cf62654170a47cec30ecb5c93f.

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Declarations

Competing interests
The authors declare no competing interests.

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