Attention-based rehearsal: Eye movements reveal how visuospatial information is maintained in working memory

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Open Practices Statement

Data and codes are publicly available at the OSF page of the corresponding author: https://osf.io/ehzku/

Author contributions

Muhammet Ikbal Sahan: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization, Funding Acquisition. **Roma Siugzdaite**: Investigation, Writing – Review & Editing. **Sebastiaan Mathôt**: Conceptualization, Mothodology, Writing – Review & Editing. **Wim Fias**: Conceptualization, Methodology, Resources, Writing – Review & Editing, Supervision, Funding Acquisition.

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Abstract

The human eye scans visual information through scan paths, series of fixations. Analogous to these scan paths during the process of actual "seeing", we investigated whether similar scan paths are also observed while subjects are "rehearsing" stimuli in visuospatial working memory. Participants performed a continuous recall task in which they rehearsed the precise location and color of three serially presented discs during a retention interval, and later reproduced either the precise location or the color of a single probed item. In two experiments, we varied the direction along which the items were presented and investigated whether scan paths during rehearsal followed the pattern of stimulus presentation during encoding (left-to-right in Exp 1; left-to-right/right-to-left in Exp 2). In both experiments, we confirmed that the eyes follow similar scan paths during encoding and rehearsal. Specifically, we observed that during rehearsal participants re-fixated the memorized locations they saw during encoding. Most interestingly, the precision with which these locations were re-fixated was associated with smaller recall errors. Assuming that eye position reflects the focus of attention, our findings suggest a functional contribution of spatial attention shifts to working memory and are in line with the hypothesis that maintenance of information in visuo-spatial working memory is supported by attention-based rehearsal.

KEYWORDS: eye-movements, visuospatial working memory, spatial attention, scan paths

Visuospatial working memory (vsWM) is a fundamental cognitive function that enables us to retain visual information to guide future behavior. The efficiency of vsWM depends on the precision with which visually presented objects and their spatial location are stored and remembered in the absence of persistent visual input. The capacity to remember visual information with a high degree of precision is known to be limited (Luck & Vogel, 2013; Ma, Bays & Husain, 2014). Substantial research efforts have been invested in determining the relationship between the number of items to be remembered and the precision of vsVWM. This led to two opposing theoretical viewpoints. According to the slots model (Luck & Vogel, 2013), there is a limited number of memory slots. If set size is smaller than or equal to the available number of slots, precision of item and location memory is highly precise. If set size is larger, those items that do not fall within a slot are not remembered. The resource model does not consider precision to be an all or none phenomenon, but sees precision as gradual (Bays & Husain, 2008). A limited amount of resources has to be divided across the features to be remembered: if there are few items, there are a lot of resources available to encode and remember the identity and location of the objects with high precision. With more items to be remembered, there are less resources per item, leading to a decrease in precision. While vsWM shows varying degrees of precision that depend on its capacity limits, whether in terms of slots or resources, the mechanisms underlying the retention of visuospatial information remain largely unknown. Instead of focusing on how set size has an impact on precision, we here take a different approach to better understand how precision of vsWM is achieved, addressing the question which mechanisms underlie the retention of visuospatial information and how these determine precision.

Sensory input is kept in an active state during a retention interval (i.e. while the input is no longer available) via the recruitment of sensory systems. This is shown by neurocognitive studies that have demonstrated that sensory brain regions that are activated by visual input continue to be active during a retention interval (Serences, Ester, Vogel & Awh, 2009; Harrison & Tong, 2009; Rigall & Postle, 2012) after the stimulus has disappeared. In fact, recruitment is not restricted to sensory representations of visual features (e.g., color, orientation, spatial frequency) or spatial locations of stimuli, but extends more generally to the processes that are involved in the processing of incoming stimuli, including the attentional and oculomotor processes that support the exploration and analysis of the visual scene (Baddeley, 1986; D’Esposito and Postle, 2015). In line with the sensorimotor-recruitment hypothesis, visuospatial information has been suggested to be rehearsed by shifting spatial attention to internal memory representations (Awh and Jonides, 2001; Pearson, Ball & Smith, 2014; Awh, Jonides & Leuter-Lorenz, 1998; , Lawrence, Myerson & Abrams, 2004; Smyth & Scholey, 1994). Convincing empirical evidence for this hypothesis comes from studies in which a secondary task disrupted memory performance when it shifted the spatial focus of attention away from the memorized locations (Awh et al. 1998; Pearson & Sahraie, 2002; Lawrence et al. 2004, see also Hanning, Jonikaitis, Deubel & Szinte, 2016; Postle & Hamidi, 2007). Furthermore, there is increasing evidence that eye movements are spontaneously involved in memory retrieval even in the absence of a disruptive secondary task (Nobre, Gitelman, Dias & Mesulam, 2000; van Ede, Chekroud, Stokes & Nobre, 2019). For example, van Ede et al. (2019) showed that, even in the absence of large eye movements, eye position was slightly biased towards retrospectively cued locations in memory while there was actually nothing physically present anymore. The interplay between spatial attention and WM has so far mostly been studied in the context of cue-based selection. However, WM is a multistage process including stages of encoding, maintenance and retrieval, and our understanding of the role of eye movements before any cue-based selection/interruption has taken place remains limited.

However, some studies have focused on the possible role of eye movements in rehearsal during the retention interval. The strong overlap between brain circuits supporting oculomotor control, spatial attention, and visuospatial WM (Van der Stigchel & Hollingworth, 2018; Jonikaitis & Moore, 2019) suggests that rehearsal in visuospatial WM is accomplished through shifts of the attentional focus that internally cycles through the visuospatial memoranda (Awh and Jonides, 2001). A robust observation supporting this hypothesis is that the patterns of eye movements during imagery or retention of spatial information have been found to closely reflect the patterns of eye movements during visual perception of that same spatial information (Hebb, 1968; Brandt & Stark, 1997; Laeng & Teodorescu, 2002). Similar to the subvocal rehearsal mechanism in verbal WM, rehearsal in vsWM via eye movements and/or shifts of spatial attention has been found to enhance memory performance (Tremblay. Saint-Aubin & Jalbert, 2006; Olsen, Chiew, Buchsbaum & Ryan, 2014; Souza. Czoschke & Lange, 2020; Morey, Mareva, Lelonkiewicz & Chevalier, 2018; Johansson, Nyström, Dewhurst & Johansson, 2022).

Yet, as outlined below, these studies do not conclusively support the hypothesis that precision of vsWM depends on visuospatial attention shifts reflected in oculomotor behavior during retention.

One of the first studies that explicitly addressed the link between oculomotor rehearsal and vsWM is Tremblay et al. (2006). In their study, a series of seven dots was presented at different locations, and participants were required to remember these dots in their correct order after a delay period of 10 seconds. During the delay period, all the to-be-remembered dots were simultaneously presented again at the same locations, and remained on the screen while spontaneous eye movements were tracked. The results indicated that the eyes tended to move towards the dot locations and to follow them in the same order as they had appeared at encoding. Moreover, it was found that the number of visits to these dot locations was positively associated with better serial order memory recall. This finding is interesting, but the conclusion of the purported oculomotor rehearsal is not conclusive because the presentation of the dots at the exact same spatial locations as possible targets for oculomotor activity during the delay period could have facilitated rehearsal and its relation to memory performance. Recent studies have shown that using visual grids containing the originally encoded stimuli in the delay period serve indeed as environmental support for spatial rehearsal and therefore result in better memory performance compared to when such a grid is absent (e.g., Lilienthal, Hale & Myerson, 2014; Souza et al., 2020). Moreover, there was only an assessment of the general capacity of serial order recall (Tremblay et al. 2006). What remains unaddressed is how oculomotor rehearsal relates to the precision with which individual visual features and spatial locations are remembered,

Other studies have shown that even in the absence of visual support of possible target locations, delay period eye movements showed remarkable similarities with eye movements at encoding (Olsen et al., 2014; Johansson et al., 2022). For example, Olsen et al. (2014) have shown that in a delayed-match-to-sample task with simultaneous presentation of multiple objects, the patterns of eye movements during encoding and delay periods were similar. Moreover, these similarities predicted memory performance but only for target displays containing multiple objects and not for objects presented in isolation. These findings suggested that eye movements support memory for the spatial relationship between stimuli rather than for absolute spatial locations. It is therefore possible that with the presentation of all items at once, eye movements in the delay period may reflect the maintenance of relational information rather than the item-level information. Moreover, as with the study of Tremblay et al. (2006), it is not clear how oculomotor rehearsal affects the precision with which the visuospatial information was recalled, as the only dependent variable was a binary decision as to whether the visual objects were spatially displaced or not.

While the above-mentioned studies demonstrate that delay period-eye movements relate to various measures of memory performance, suggesting some functional role of eye movements in memory retention (e.g., Lawrence et al. 2004), others have argued for a limited role of the eye movements during rehearsal (e.g., Godijn & Theeuwes, 2012). For example, Godijn and Theeuwes (2012) instructed participants to either maintain fixation or move their eyes freely in a task where the spatial locations of scattered numbers were to be remembered in increasing order. They found that recall performance in the free viewing condition was not better than in the fixation condition, suggesting that overt eye movements do not provide an additional benefit over covert attention. However, while that study directly addressed the contribution of eye movements to memory performance, the task instructions to maintain fixation were interleaved with free viewing on a trial-by-trial basis, which could have restricted the involvement of systematic patterns of natural eye movements (e.g., scan patterns) that would have otherwise resulted in better memory performance during free viewing as compared to fixation. Importantly, the eye movements in that study were only analyzed based on whether the original stimulus locations were re-fixated and not based on whether the order of fixations during retention and encoding were similar, thus leaving the role of sequential patterns of eye movements in visuospatial WM unanswered.

Taken together, while several studies have investigated the role of eye movements during vsWM, only a few studies have established eye movements as an underlying mechanism contributing to the precision with which visual items and their locations are remembered (e.g., Peterson, Kelly & Blumberg, 2019). A first critical question that needs to be addressed is what kind of eye movements people make during a delay period when there is nothing on the screen for stimuli that are presented sequentially. A second important question pertains to the functional contribution of visuospatial rehearsal. If oculomotor rehearsal is not merely a byproduct of attention-based rehearsal, but is an essential part of it, one would expect it to influence the accuracy with which visual information is remembered; hence, the crucial question is whether rehearsal via eye movements is related to the precision of memory representations of visual features and their locations. In order to address these questions, we keep set size constant and investigate the nature of the processes that take place during the retention interval and how they are related to mnemonic precision. Our objective is to reveal oculomotor rehearsal by tracking spontaneous eye movements while participants are maintaining a sequence of visuospatial information, and to evaluate the degree to which the patterns and accuracy of successive eye positions relates to the precision with which the visuospatial information is remembered.

Our main hypothesis is that eye movements reflect refreshing of information in visuospatial memory. Specifically, memoranda are successively brought into the attentional focus, which is a process that can be indexed by eye movements iteratively cycling through spatial locations containing the memory items. To this end, participants performed a continuous recall task in which the precise location and the color of three discs were to be rehearsed during a retention phase and reproduced afterwards. We presented these discs one at a time and without any visuospatial information during the delay period, thus eliminating the role of any relational information at encoding (e.g., Olsen et al., 2014) and during retention (e.g. Souza et al. 2020). After the retention period, participants either had to reproduce the precise location or the exact color of a probed item on a continuous scale. In two separate experiments, we varied the direction along which the items were presented and investigated whether eye movements during rehearsal followed the same pattern of eye movements as during encoding (left-to-right in Experiment 1; left-to-right and right-to-left in Experiment 2). Following the attention-based rehearsal hypothesis (Awh and Jonides, 2001; Baddley, 1989; Postle, 2006), we predicted that the rehearsal pattern of delay period eye movements would follow the encoding direction of the visuospatial memoranda. Another key aspect of our study is that we studied the relationship between oculomotor rehearsal and memory performance. Since we obtained a continuous measure of recall errors on every trial (i.e. the difference between the reported and true location/color values), we investigated whether the delay period patterns of eye movements related to trial-level recall errors.

Experiment 1

Methods

Participants

Forty Ghent University students (5 males, age *M*=18.5, *SD*= 1.15) participated in return for course credits. All participants had normal or corrected-to-normal vision and all but five participants were right-handed. The sample size and number of trials were based on the recommendations of Brysbaert and Stevens (2018). They suggested a minimum of 1600 observations (e.g. 40 participants x 40 trials) for an 80% powered study to detect a small effect (Cohen's d < .2). Since we included 40 participants, we made sure to have at least 40 trials per conditions of interest. The EyeLink data file of one subject was corrupted and therefore removed from the analysis. The research complied with the guidelines of the Independent Ethics Committee of the Department of Psychology and Educational Sciences of Ghent University. All participants gave written informed consent. Data and codes are publicly available at the OSF page of the corresponding author: https://osf.io/ehzku/

Apparatus and fixation extraction

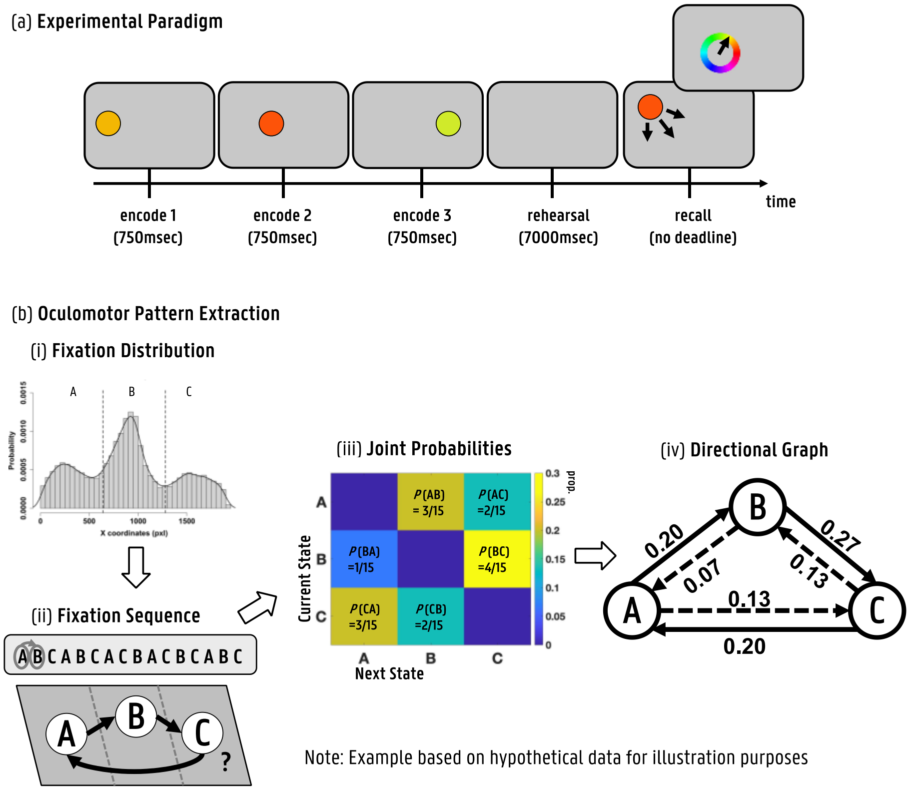
Stimuli were presented at a 70 cm distance from the participants on a 22-inch LCD monitor (1920x1080 pixels, refresh rate: 60 Hz). Stimulus presentation was controlled using Matlab software (Mathworks, Natick, MA) with Psychtoolbox 3 extensions (Brainard, 1997). An Eyelink 1000 tower-mounted eye-tracker (SR Research, Canada) was used to record the eye-movements at 1000 Hz. A chinrest was used to reduce head movements. Prior to each session of 30 trials, the eye tracker was calibrated to the screen using an built-in nine-point calibration protocol. The eye tracker was recalibrated when the calibration accuracy exceeded a mean threshold of 0.5° visual angle (VA). Data samples that were continuously measured were filtered down into saccades, blinks and fixations. We used the EyeLink built-in saccade-detection algorithm where the acceleration (35°/sec) and velocity ($9500°/sec^2$) thresholds were set to detect saccades greater than 0.60°. Blinks are defined as periods of missing data in the sample sequence. The remaining samples after saccade and blink classification were defined as fixations which constitute our primary measure of interest for the following analysis.

Design, Procedure and Stimuli

Eye-movements were continuously measured while participants were performing a delayed continuous reproduction task (Figure 1a). No explicit instructions were given regarding the eye movements and therefore participants could engage in free viewing throughout the task. Each trial started with the presentation of three colored discs (radius 15px or 0.34°, same disc sizes were used throughout the trial) that sequentially appeared from left to right at a pace of 750 ms per disc on different locations of the screen. The spatial coordinates of the discs were randomly drawn from predefined regions on the horizontal plane of the screen while the vertical plane was kept constant at the center of the screen (x = variable, y = constant). More precisely, we divided the entire screen in five bins of equal length (i.e., 1920/5=384 pixels or 8.6°) and presented each consecutive disc on randomly drawn locations within the leftmost, middle and rightmost bins. The bins in-between were not stimulated and served as buffer zones. We deemed these manipulations necessary because (i) the distinct bins allow for large-scale saccades across the entire screen which we then could use to study for the rehearsal patterns and (ii) the continuous variations within a bin enable us to study to what extent the fixated locations during rehearsal overlap with the exact disc locations. As for the colors of the discs, color hues were sampled from a list of color values that spanned the full color space of 360° in increments of 1°. This color list was generated from an evenly distributed circle on the CIE L*a*b color space, centered at (L =80, a = 20, b = 20) with a radius of 60. The white point for the CIE XYZ space defining the LAB colors was set to (1, 1, 1). All colors had an equal luminance and brightness and only varied in hue. We constrained the color hues of the presented discs to a minimal angular separation of 90° relative to each other. The reason for employing a minimal angular separation was similar to the binning applied to the spatial locations, in that the minimal angular separation was employed in order to have visually distinguishable colors but at the same time still variable which allowed us to analyze the continuous estimation of the remembered colors.

Both the precise colors and locations of these discs were to be retained during a delay period of 7000 ms. After the delay period, participants were probed to report either the color or the spatial location of a single disc without a response deadline. Participants were informed about the target feature they had to report by means of the type of probe. If location was to be reported, then a color probe was randomly presented at either one of the four corners of the screen with an offset of 100 pixels (2.27°) horizontally and vertically towards the center of the screen (140 pxs Euclidean diagonal distance, 3.17°). The color of the probe was the same as the target disc instructing the participants that the location of this target disc was to be moved to its precise location. Participants used the mouse cursor to move the probe disc to its exact location and pressed the left mouse button to confirm their response. Recall errors for location were stored as the distance between the center of the target disc location and the center of the chosen location of the disc. If the color was to be reported, then the target location was highlighted with a randomly colored disc, instructing the participants to report the precise color of the disc that appeared at the probed location. A color wheel was presented around the disc and participants could select the precise color from this color wheel by moving the mouse cursor on the wheel which simultaneously updated the color of the probe disc accordingly. Participants clicked on the left mouse button to indicate the color of the probed location. The color wheel contained all 360 color hues arranged on an annulus with inner radius of (25pxs) 0.57° and outer radius of (50pxs) 1.13°. Recall errors for the color were stored as the circular distance between the target disc color and the color chosen by the subject on the color wheel.

Responses were immediately followed by feedback. For spatial location, feedback consisted of highlighting the correct location with an empty disc as initially presented at the start of the trial (750 ms). The visual feedback was then followed by a qualitative feedback evaluating the level of performance (750ms; errors ≤28pxs (.63°) elicited "great," >28pxs (0.63°) and <128pxs (2.90°) elicited "good," and ≥128pxs (2.90°) elicited "poor"). As for the color feature, feedback consisted of filling up the discs with the colors as initially presented at the start of the trial followed by the qualitative evaluation of performance (errors ≤15° elicited "great," >15° and <30° elicited "good," and ≥30° elicited "poor"). An intertrial interval of 750ms was administered. The task consisted of 150 trials where the probed spatial locations (left, middle, right) and feature types (color and location) were fully crossed and randomly interleaved with an equal probability, hence being unpredictable to the participants. Prior to the actual task, participants performed a practice block of 10 trials to get acquainted to the task.



Note: Example based on hypothetical data for illustration purposes

Figure 1 (a) Experimental Paradigm. Eye-movements were continuously measured during free-viewing while participants performed a delayed continuous color/location reproduction task. (b) Illustration of the steps involved in the extraction of scan patterns based on hypothetical example data. (i) Fixation distribution. The distribution of the fixated x-axis locations during the retention period were first obtained across trials and participants. The visual field was divided into three regions of interest (ROI) where the left, middle and right ROIs were assigned the letters A, B and C, respectively. (ii) Fixation Sequence. For each trial, the sequences of fixations were then labeled according to which ROI was fixated in order to form letter strings. These letter strings are then processed in terms of the types of successive letter pairs (AB, BC, CA, CB, BA, AC) indicating the transition from the current to the next ROI and stored in an adjacency matrix. (iii) Adjacency Matrix. The adjacency matrix is a 3x3 matrix where each row represents the current state (i.e., A,B,C) and each column the next state in the letter string (i.e., A,B,C). The types of successive letter pairs are counted and stored in the corresponding cells of the adjacency matrix, by progressively moving towards the end of the letter string. The joint probabilities of the pairs in the adjacency matrix are then calculated as a proportion of total number of transitions in the trial sequence. The example letter string ABCABCACBACBCABC contains 15 transitions. The proportions of each successive letter pair is represented with colors. (iv) Directional graph. The contents of the adjacency matrix are then presented in a directional graph, where each node represents three possible states, the arrows the direction of transitions between these states along with the proportions. The solid lines represent the encoding direction of eye movements (here, left-to-right) whereas the dashed lines indicate the opposite direction.

Eye-tracking data preprocessing and analyses.

Oculomotor Rehearsal Patterns. Eye movement data collected during the rehearsal period were used to investigate the sequential *patterns* of fixations in a primary analysis. To be able to study the sequence of fixations, we divided horizontal plane of the entire screen in three large bins of equal size (i.e., 1920/3=640pxs, 14.2°), where each regions of interest (ROI) overlaps with the initial disc locations. Note that these large regions allowed us to classify fixations falling inside the buffer zones (i.e., regions outside the initial leftmost, middle and rightmost bins). Each region is then assigned with a letter (i.e., A, B, C) and every fixation falling inside either one of these large regions is labeled accordingly forming letter strings (see Figure 1b). These letter strings both carry spatial and sequential information of the fixations which we used to reveal the type of scan patterns that are made within a trial. Multiple fixations (with a minimal spatial difference of 0.60°) within the large ROI (14.2°) are likely and therefore resulting in repetitions of letters. Because we are interested in the large scale scan patterns oriented towards the disc locations, we only considered the distinct sequences of letters within a trial. For instance, the letter string “ABBBCCAACBBC” containing repetitions was transformed into the sequence “ABCACBC” so that it only contained distinct states. We defined trials containing at least three distinct ROI fixations as “movement” trials and included only these trials in the analysis. Trials on which not all ROIs were fixated were defined as “fixated” trials and are therefore not considered in the following analysis. Participants who “fixated” in the majority of the trials, that is more than half of the trials, were defined as “fixators”, whereas participants with “movement” trials in the majority were defined as “movers”. For the following analysis related to the oculomotor rehearsal patterns and precision, we only considered the “movement” trials of the “mover” subjects. In this way, we included a total number of 4176 out of 5850 trials of the mover participants in the analysis. Note that this amount of trials is comparable to the movement trials observed in the study of Tremblay et al. (2006).

For each letter string, we stored the types of successive letter pairs in an adjacency matrix. The adjacency matrix is a 3x3 matrix where each row represents the current state (i.e., A, B, C) and each column the next state in the letter string (i.e., A, B, C; see Figure 1b, iii). By progressively moving towards the end of the letter string, the types of successive pairs are counted and stored in the corresponding cells of the adjacency matrix. This operation is iterated until every successive pair within the entire letter string is covered. The joint probabilities of the pairs in the adjacency matrix are then calculated as a proportion of total number of transitions in the trial sequence. For instance, a letter string “ABCABCACBACBCABC”, contains the following successive pairs of states, AB, BC, CA, AC, CB, BC. With 15 transitions, the proportion of these successive pairs are AB=3/15, BC=4/15, CA=3/15, AC=2/15 and CB=4/15. Notice that the diagonal is empty given that the repetitions within a sequence were removed. The advantage of using the adjacency matrix is that its contents can also be presented in a directional graph summarizing the type of scan patterns occurring in the data (Figure 1b, iv).

We investigated whether eye movements during rehearsal systematically followed the directional scan pattern from left-to-right as during encoding, marked by consecutive sequences of letter pairs. To statistically test if forward pairs (i.e., AB, BC, CA) were more likely than the backwards pairs (i.e., BA, CB, AC) to occur in the letter strings, we subjected the proportions of the following pairs AB vs BA, BC vs CB and CA vs AC to paired *t*-tests and corrected for multiple testing using Bonferroni correction. We also quantified a general score for the forward rehearsal pattern (which we denote as the forward rehearsal index, FRI) by adding up the AB, BC and CA proportions for each trial. Trials with higher FRI scores indicate that the eyes generally moved more in accordance with the left-to-right direction of encoding. We compared the forward rehearsal patterns against the complement, which we defined as the backward rehearsal index (BRI) by adding up the BA, CB, and AC proportions. A paired t-test was conducted to evaluate whether these rehearsal (FRI vs BRI) indices significantly differed. An alpha level of 0.05 was applied throughout the analysis.

Oculomotor Rehearsal Precision. We investigated the *precision* with which the fixated locations during rehearsal overlapped with the initial disc locations without considering the sequential order of the fixated locations. As with the rehearsal pattern analysis, only ”movement” trials of the “mover” subjects were considered here. A measure of error was obtained for each trial by averaging the absolute differences between the fixated and disc locations on the x-axis within a ROI. Contrary to the rehearsal pattern analysis, we used all fixations thus including the repetitions of fixations within a ROI. These fixations are considered as sampling points around the disc locations. Trials with lower errors indicate that the disc locations were revisited by the eyes with a higher precision.

Behavioral analyses.

The recall errors for color and location features were measured as the absolute difference between the true and reported feature values. To be able to analyze these recall errors across different feature dimensions, we scaled the location and color errors relative to their respective feature spaces. To demonstrate, a location error of 192 pixels is converted to a relative error of 0.10 (192/1920). Similarly, a color error of 36° is converted to a relative error of 0.10 (36°/360°). Although color hues strictly speaking form a circular distribution (an error of 190° is the same as an error of 170°), it is very rare for recall errors to be so large that they reach the 'wrap-around point' of 180°; for this reason as well as to simplify the analysis, we treated color errors as coming from a non-circular space (i.e. using a gaussian distribution as opposed to a von Mises distribution). The relative recall errors were analyzed using the linear mixed effects (LME) framework in R software using the lme4 package (Bates, Mächler, Bolker & Walker, 2015).

Prior to the analysis related to the oculomotor rehearsal patterns and oculomotor rehearsal precision, we first wanted to establish whether eye-movements play a functional role in the overall recall performance. We observed that a subset of participants (*N*=8) fixated in the majority of the trials; that is, more than half of the trials were "fixation" trials. We therefore defined these participants as "fixators" and contrasted their recall performance with the remaining participants who we defined as "movers" as more than half of the trials were "movement" trials. The rationale was to verify whether participants who did not make eye movements also differed from participants who made eye movements. For this purpose, *Feature Dimension* (location vs color), *Subject Type* (movers vs fixators), *Trial Type* (movement vs fixation) and their interactions were entered as fixed effects factors in the LME with recall performance as the dependent variable. In the following analysis, we then examined the role of oculomotor rehearsal patterns on recall performance: does oculomotor rehearsal in a left-to-right direction predict recall performance? To this end, the recall errors were entered the LME model with the *FRI scores*, *Feature Dimensions* (location vs color) and their interactions as fixed effects. In a final analysis, we examined the role of oculomotor rehearsal precision on recall performance: are oculomotor rehearsal errors related to recall performance? The recall errors were entered the LME model with *Rehearsal Error*, *Feature Dimension* (location vs color) and their interactions as fixed effects. The random effects structure of the models included a random intercept for the variable *Subject* (maximal models with by-participant random slopes failed to converge). The models were fitted with restricted maximum-likelihood (REML) and Satterthwaite approximations were used to assess the significance of individual predictors. The results are reported using a type III Wald chi square test.[1]

Results and Discussion

Functional involvement of eye movements. There was only a main effect of *Feature Dimension* with overall higher recall errors in the color condition compared to the location condition [$\chi^2(1, N = 39) = 4.27$, $p < 0.05$]. No main effects of *Participant Type*, *Trial Type* or interactions including the *Feature Dimension* were observed on the recall errors [all χ^2s < 1.65]. Crucially, the analysis yielded a significant interaction between *Participant Type* and *Trial Type* [$\chi^2(1, N = 39) = 4.77$, $p < 0.05$], suggesting that participants performed better under their preferred state of eye movements (Figure 2a). In particular, post-hoc tests revealed that "movers" had generally smaller recall errors in movement trials compared to "fixators" (diff = 0.01, t (204)=2.07, 95%CI [.001, 0.03], $p < 0.05$). Note that this difference is relatively small and corresponds to 19.2 pixels for the location and 3.6° for the color conditions. These findings suggest that eye movements, as a measure of overt spatial attention, are not necessarily required for at least a minority of participants (N = 8) who mainly fixated and therefore could do the task on the basis of covert attention (Godijn & Theeuwes, 2012).

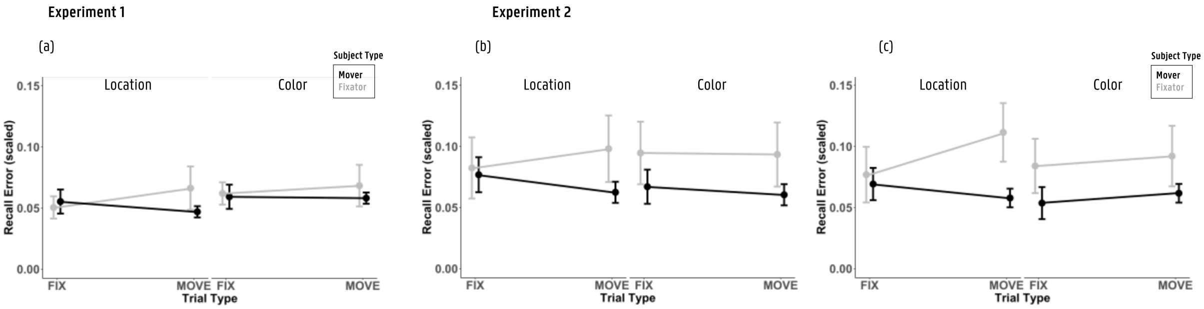


Figure 2 (a) Experiment 1. The average recall errors as a function of Feature Dimension, Trial Type and Subject Type. (b, c) Experiment 2. The average recall errors as a function of Feature

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[1] A direct comparison as to whether the oculomotor precision or the oculomotor patterns contribute more to visuospatial memory is interesting. However, this was not the main purpose of the current study as the paradigm was not designed to assess the reliability of the sequential order information but only focused on item-specific precision. In additional analyses, we investigated the relationship between oculomotor precision and rehearsal patterns, and addressed their relative contribution to visuospatial memory for both experiments (see Supplementary Material).

Dimension, Trial Type, Subject Type and Direction (b, left-to-right and c, right-to-left direction condition). Error bars denote 95% confidence intervals.

***Oculomotor Rehearsal Patterns*[2].** For the rehearsal patterns, we found that the eye movements were characterized more by a forward rehearsal pattern (FRI: $M = .70$, $SE = .025$) than a backward rehearsal pattern ($M = .30$; $SE = .25$; $t(30) = 8.14$, $p < .001$, 95%CI= [0.30, 0.51]). Figure 3a (i and ii) illustrate how the eye movements are characterized in terms of the preferred directionality of successive eye movements. In particular, the proportion of AB was higher than BA ($t(30) = 9.87$, $p < .001$; 95%CI = [0.13, 0.20]), BC higher than CB (t(30) = 6.67, $p < .001$; 95%CI [0.09 0.17]) and CA higher than AC ($t(30) = 44.31$, $p < .001$; 95%CI [0.27, 0.30]).

Next, we addressed whether the rehearsal patterns could predict the recall errors by means of the LME framework (Figure 3a, iii). A main effect of *FRI* was observed with higher FRI scores associated with smaller recall errors [b=-0.015, $\chi^2(1, N = 31) = 9.32$, $p < .01$]; participants were more precise when their eyes followed the same locations and directions as where the discs had initially been presented. A main effect of *Feature Dimension* was also observed with overall higher recall errors in the color condition compared to the location condition [$\chi^2(1, N = 31) = 8.59$, $p < 0.01$]. However, the *Feature Dimension* did not modulate the effect *FRI* [$\chi^2(1, N = 31) = 1.52$, $p = 0.22$], suggesting that the FRI affected recall performance comparably in both conditions.

Oculomotor Rehearsal Precision. In the final analysis (Figure 3a, iv), we tested whether the oculomotor rehearsal errors were also associated to recall errors. We observed a main effect of the rehearsal error, with higher rehearsal errors predicting higher recall errors [b=0.25, $\chi^2(1, N = 31) = 26.56$, $p < .001$]. In other words, participants were more precise in reproducing the features if their eyes fixated the initial disc locations with higher precision. No main effect of *Feature Dimension* or an interaction including this term was observed [χ^2 s <1.1].

Encoding Phase. The distinction between “movers” and “fixators” was only based on the eye-movement data of the delay period. In order to rule the possibility that the eye movements

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[2] The main manuscript focused on first order sequential patterns, that are pairs of successive fixation locations constituting “local” scan paths during rehearsal. The additional analyses investigated the second order sequential patterns which takes into account triplets of successive fixation locations constituting the more “global” scan paths during rehearsal. Similar results for the second order sequential patterns were obtained as for the first order sequential patterns reported here in the main manuscript for both experiments (See Supplementary Material).

during the delay period are merely a reflection of the gaze behavior at encoding, we investigated whether the fixators and movers of the delay period were also the fixators and movers of the encoding period. Repeating the main analysis but now applied to the encoding phase yielded the following results: (i) All participants qualified as “movers” when taking into the eye movement data of the encoding phase suggesting that the gaze behavior during rehearsal is more than just a rehearsal of gaze behavior at encoding. (ii) We further tested whether the patterns and precision of eye movements during encoding differed between the “movers” and “fixators” (as defined by the gaze behavior of the rehearsal phase). The oculomotor encoding patterns did not significantly differ between the fixators (*M*=.94, *SE*=.006) and movers (*M*=.94, *SE*=.001*;* diff = 0.005, *t* (37)=-.31, 95%CI [-.04, .03], *p* = 0.76). Neither was the oculomotor encoding precision significantly different between the fixators and movers (diff = 0.0001, *t* (37)=-.05, 95%CI [-.004, .004], *p* = 0.96). Hence, encoding differences can be excluded as an explanation for the differences between “movers” and “fixators” during rehearsal.

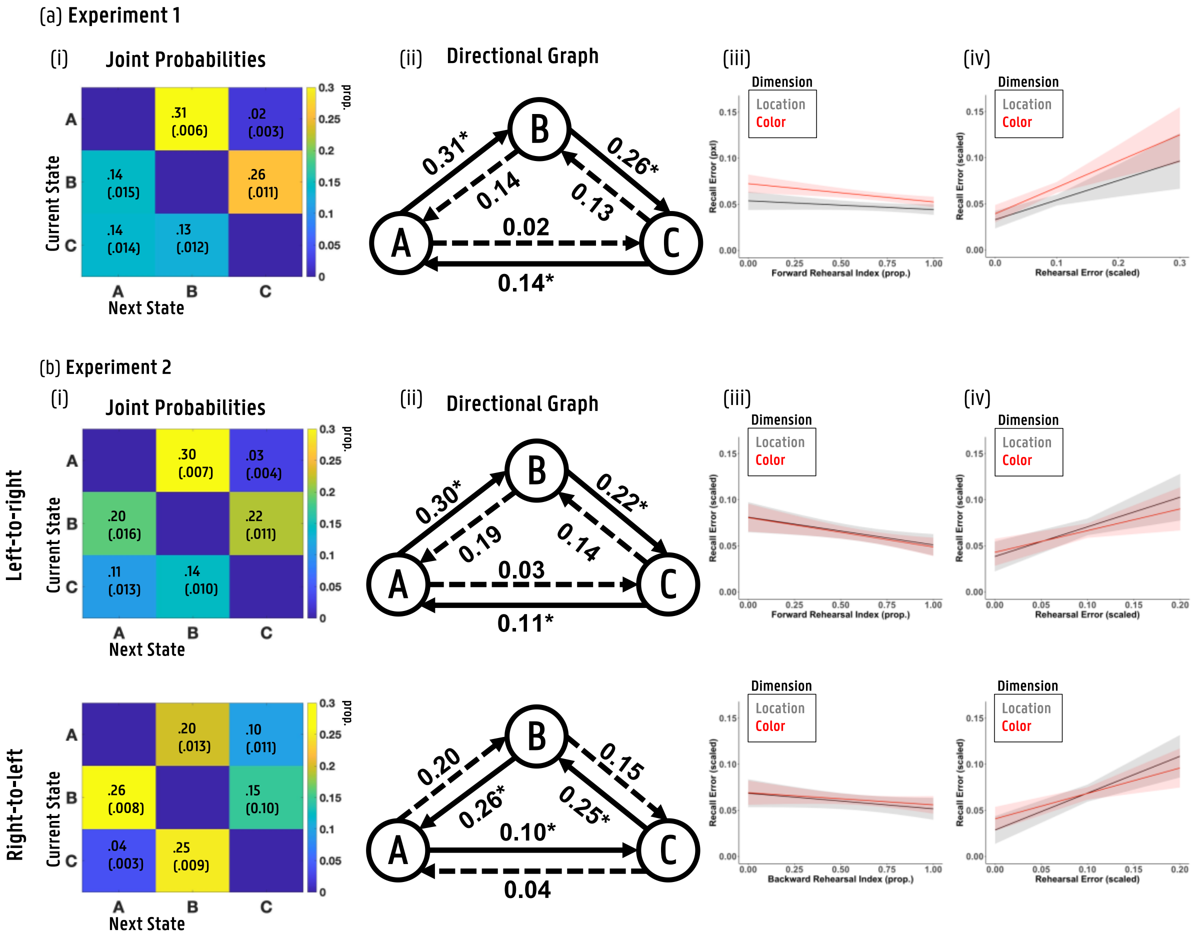

Figure 3. (a) Experiment 1. (i) Oculomotor Scan Patterns. The mean proportion of successively fixated locations within the fixation sequences presented in the adjacency matrix, with standard errors within brackets. (ii) Directional graph. The contents of the adjacency matrix presented in a directional graph. The rehearsal patterns during the retention period follow the encoding direction (solid lines), $*p<0.001$. (iii) The relationship between oculomotor scan patterns and recall Errors. (iv) The relationship between oculomotor rehearsal errors and recall errors. Shaded areas denote confidence intervals. (b) Experiment 2. Same figure conventions apply for panels i-iv as in Experiment 1, with the middle row presenting the left-to-right and bottom row the right-to-left encoding direction condition.

Experiment 2

In the first experiment we showed that participants who move their eyes do so in the same direction in which the sequence was presented. Additionally, we observed that this particular behavior of the eyes correlates with recall performance. In the second experiment we address the question whether our findings generalize to the reverse direction. Specifically, we conducted an exact replication of the first experiment but interleaved with trials where the colored disc sequences were presented from right-to-left. Based on the attention-based rehearsal hypothesis, we predict that the eyes would follow the same the encoding direction.

Methods

Participants

Forty-one different Ghent University students (14 males, age *M*=19.9, *SD*= 3.05) participated in return for course credits. All participants had normal or corrected-to-normal vision and all but eight participants were right-handed. The research complied with the guidelines of the Independent Ethics Committee of the Department of Psychology and Educational Sciences of Ghent University. All participants gave written informed consent.

Procedure, Design and Statistical Analyses

The procedure and design are identical to experiment 1, but with the addition of a *Direction* factor to the design. The discs were now either presented from left-to-right or from right-to-left. The task consisted of 168 trials where the feature types (color and location) and encoding direction (left-to-right and right-to-left) were fully crossed. These trials were randomly administered with an equal probability, hence being unpredictable to the participants. The analyses followed the same analysis protocol as in experiment 1, but with the addition of a *Direction* (i.e., left-to-right and right-to-left) factor.

Results and Discussion

Functional involvement of eye movements. As in the first experiment, we investigated the functional role of eye-movements on the recall performance. A subset of participants (N=5) fixated in the majority of the trials (i.e., “fixators”) whose performance we contrasted with the remaining participants (i.e., “movers”). We observed a significant main effect of only *Participant Type* with “fixators” displaying overall a higher degree of recall errors compared to “movers” [$\chi^2(1, N = 40) = 8.01, p < 0.01$]. There were no significant main or interaction effects of *Direction* (all χ^2s <2.56). As in the first experiment, we observed an interaction between *Participant Type* and *Trial Type* [$\chi^2(1, N = 40) = 8.07, p < 0.01$], suggesting that participants performed better in their preferred state of eye-movements (Figures 2b, c). In particular, post-hoc tests revealed that “movers” had generally smaller recall errors than “fixators” in movement trials (diff = 0.04, t (50.3)=3.66, 95%CI [0.018 0.059], $p < .001$). Moreover, “fixators” displayed a higher degree of errors when they moved compared to when they fixated their eyes (diff =-0.015, t (6831)=-2.36, 95%CI [-0.028 -0.026], $p < .05$). Furthermore, “movers” had also smaller errors when they fixated compared to “fixators” when they made eye movements (diff = 0.033, t (58)=3.02, 95%CI [0.011, 0.055], $p < .001$). Finally, “movers” had an overall lower degree of errors in trials in which they moved compared to the recall errors of “fixators” in their fixation trials (diff =- 0.023, t (45.7)=2.27, 95%CI [.003 .04], $p < .05$).

Interestingly, the analysis further revealed a three-way interaction between *Participant Type, Trial Type and Feature Dimension* [$\chi^2(1, N = 40) = 6.40, p = 0.011$]. To further investigate this interaction, we split the analysis for the Feature Dimension (Location vs Color) and found that in both conditions, there was a significant main effect of Participant Type with higher recall errors for “fixators” compared to “movers” [location: $\chi^2(1, N = 40) = 4.14, p < 0.05$, color: $\chi^2(1, N = 40) = 12.53, p < .001$]. Crucially, the two-way interaction between *Participant Type and Trial Type* was only significant in the location condition [$\chi^2(1, N = 40) = 11.39, p < 0.01$], but not in the color condition [$\chi^2(1, N = 40) = 0.23, p = 0.63$]. Post-hoc test yielded similar results suggesting that participants performed better in their preferred state. “Movers” had generally smaller recall errors than “fixators” in movement trials (diff = 0.05, t (57.4)=3.28, 95%CI [0.018 0.073], $p = .001$). Furthermore, “movers” had also smaller errors when they fixated than when “fixators” were making eye movements (diff = 0.03, t (70.1)=2.23, 95%CI [0.003 0.061], $p < .05$). Moreover, “fixators” displayed a higher degree of errors when they moved compared to when they fixated their eyes (diff =- 0.026, t (3404)=-2.56, 95%CI [-0.046 -0.006], $p < .05$). Finally, “movers” displayed smaller recall errors when they moved their eyes compared to when they fixated (diff = 0.01, t (3352)=2.23, 95%CI [0.002 0.023], $p = .018$). For the remainder of the analyses related to the oculomotor rehearsal patterns and precision, we only considered the “movement” trials of the “mover” subjects. We included a total number of 5103 out of 6888 trials in the analyses.

Oculomotor Rehearsal Patterns. For the rehearsal patterns, we found that the eye movements in the left-to-right condition were characterized more with a forward rehearsal pattern (FRI: $M = .62, SE = .018$) than a backward rehearsal pattern [$M = .38; SE = .017; t(35) = 6.35, p < .001$, 95%CI= [0.17, 0.33]. Conversely, eye movements in the right-to-left condition were characterized more with a backward rehearsal pattern (*M* = *.60*, *SE* = .017) than a forward rehearsal pattern [*M =.40; SE =.017;* *t*(35) = -5.54, *p* < .001, 95%CI= [-0.27, -0.12]. Figure 3b illustrate how the eye movements are characterized in terms of the preferred directionality of successive eye movements. In the left-to-right condition in particular (figure 3b, i, ii, middle row), the proportion of AB was higher than BA (*t*(35) = 7.68, *p* <.001; 95%CI = [0.08 0.14]), BC higher than CB (t(35) = 4.8, *p* < .001; 95%CI [0.04 0.10]) and CA higher than AC (*t*(35) = 6.83, *p* < .001; 95%CI [0.055, 0.10]). The opposite results were obtained in the right-to-left condition figure 3b, i, b, ii, bottom row) with the proportion of BA was higher than AB (*t*(35) = -4.40, *p* < .001; 95%CI = [-0.09, -0.03]), CB higher than BC (t(35) = -9.07, *p* < .001; 95%CI [-0.13, -0.08) and AC higher than CA (*t*(35) = -6.26, *p* < .001; 95%CI [-0.078, -0.040]).

The patterns of eye movements were then related to the recall performance by including *Feature Dimension, Direction* and the *Rehearsal Index,* and their interactions as fixed factors in the LME. The Rehearsal Index represents the degree with which the patterns of eye movements correspond to the direction in which the eye movements were encoded (FRI in the left-to-right and BRI in the right-to-left condition). The analysis yielded only a main effect the Rehearsal Index [*b*=-.028, $\chi^2(1, N = 36) = 16.55$, $p < .001$] indicating the smaller recall errors were obtained with higher degrees of systematic patterns of eye movements following the encoding direction. The effect of Rehearsal Index was not modulated by any interactions with Direction or Feature Dimension ($\chi^2 < 1.81$). Figure 3 (b, iii) illustrates these effects across the different conditions.

Oculomotor Rehearsal Precision. In the final analysis (Figures 3b, iv), we tested whether the oculomotor rehearsal errors were also associated to recall errors. We only observed a main effect of the rehearsal error, with higher rehearsal errors predicting higher recall errors [*b*=0.31, $\chi^2(1, N = 36) = 40.65$, $p < .001$]. In other words, participants were more precise in reproducing the features if they fixated the initial disc locations with higher precision during the retention interval. No main effect of *Feature Dimension, Direction* or an interaction including these terms were observed [χ^2 s <2.8].

Together, the key findings of experiment 1 were replicated in that the eye movements followed the direction of the serial order information. Crucially, the patterns of eye movements and the precision with which the locations in perceptual space were revisited correlated with recall performance. This observation corroborates the evidence that the maintenance of visuospatial information is supported by attention-based rehearsal which we can follow by tracking the eyes just like verbal information is maintained via subvocal rehearsal.

Encoding Phase. As in experiment 1, the distinction between “movers” and “fixators” was only based on the eye-movement data of the delay period. In order to rule the possibility that the eye movements during the delay period are merely a reflection of the gaze behavior at encoding, we investigated whether the fixators and movers of the delay period were also the fixators and movers of the encoding period. Repeating the main analysis but now applied to the encoding phase yielded the following results: (i) All participants qualified as “movers” when taking into the eye movement data of the encoding phase. (ii) Testing whether the patterns and precision of eye movements during encoding differed between the “movers” and “fixators” (as defined by the gaze behavior of the rehearsal phase) yielded similar results as in experiment 1. The oculomotor encoding patterns did not significantly differ between the fixators (M=.93, SE=.003) and movers (M=.91, SE=.001; diff = 0.02, t (38.9)=1.06, 95%CI [-.01, .05], p = 0.30). Neither was the oculomotor encoding precision significantly different between the fixators (M=.02, SE=.001) and movers (M=.02, SE=.0001; diff =- 0.0009, t (39)=-.04, 95%CI [-.006, .005], p = 0.71). Hence, encoding differences can be excluded as an explanation for the differences between “movers” and “fixators” during rehearsal.

General Discussion

The question of how the mind is able to retain a visuospatial sequence has been extensively studied. Many prominent models, like the sensorimotor-recruitment hypothesis (D’Esposito & Postle, 2015), are conceptual in nature and do not directly address how specific mechanisms of attention are involved in WM. The current study aimed to investigate the attention-based rehearsal hypothesis as a mechanistic explanation of how retention is accomplished. We tested the predictions of the attention-based rehearsal hypothesis that visuospatial memoranda are successfully retained by recruiting the same oculomotor codes that were also recruited during sensory encoding (Awh & Jonides, 2001). Consistent with this hypothesis, our data demonstrate that delay period eye movements cycle through the locations where stimuli had originally been presented. In Experiment 1, we demonstrated that the patterns of eye movements follow the left-to-right direction of the colored discs (i.e., oculomotor rehearsal patterns). The fact that the stimuli were presented one at a time at encoding and without any visual information during the delay period eliminated any form of environmental support for oculomotor rehearsal (Tremblay et al., 2006; Olsen et al., 2014). Moreover, we show that the degree to which the direction of eye movements aligns with the direction of stimulus presentation predicts recall performance. Specifically, smaller recall errors for both color and location information were observed on trials where delay period patterns of fixations moved in the left-to-right direction. In addition to the oculomotor rehearsal patterns, we demonstrate that the precision with which the eye positions overlap with the original spatial locations also predicted lower recall errors for both color and location features. In Experiment 2, we replicate the findings of Experiment 1 and extend them by demonstrating that the oculomotor rehearsal patterns are not limited to left-to-right stimulus presentation, but also generalize to right-to-left stimulus presentation. As in Experiment 1, the more this oculomotor rehearsal pattern was followed, the better the recall performance was. Moreover, we observed that the oculomotor rehearsal precision was predictive for the recall precision of both color and location. The stronger the overlap between original locations and delay-period fixations, the better the performance. While our findings are in line with the idea that the maintenance of visuospatial information is grounded in the oculomotor system (Ballard, Hayhoe, Pook & Rao, 1997; Postle, 2006; D'Esposito & Postle, 2015), we further provide a mechanistic implementation of visuospatial memory retention. Eye movements not only indicate where spatial attention is oriented (oculomotor rehearsal precision), but also reveal how spatial attention shifts during visuospatial memory maintenance (oculomotor rehearsal pattern).

Thus, across two experiments, we provide clear evidence that the retention of sequential visuospatial memory information is tightly coupled to spatial attention and eye movements (e.g., Van der Stigchel & Hollingworth, 2018; Jonikaitis & Moore, 2019). Tremblay et al. (2006) were the first to directly address the oculomotor rehearsal hypothesis for spatiotemporal memory information. They found that eye movements were engaged in rehearsing the spatial locations that were presented one by one at encoding according to their presentation order. Note that, in their study, the to-be-remembered locations were made visible to the participants in the delay period, which could have supported oculomotor rehearsal (Lilienthal et al. 2014;Souza et al. 2020). Here, we tested and confirmed the hypothesis that oculomotor rehearsal also takes place in the absence of visual support during the delay period. A second question that we addressed in the current study was related to the item-level information itself, namely whether oculomotor rehearsal is related to the precision of memory representations in isolation. Contrary to Olsen et al. (2014), who did not find a link between oculomotor rehearsal and memory performance for individual items, our findings clearly demonstrate such a link with better recall performance on trials where the eyes moved along the encoding direction. Furthermore, while past research mainly focused on the retention of spatial memory, here we present evidence that oculomotor rehearsal is also associated to memory performance for color information. For instance, Souza et al (2015) demonstrated that colors were recalled with lower errors with the number of times these items were retrospectively cued, and thus covertly attended, during retention. Here, we extend these findings by demonstrating that overt eye movements spontaneously re-fixating the spatial locations where the color stimuli were presented were associated with lower recall errors.

The finding that delay period eye movements follow the same direction of encoding is in line with the assumption that holding a mental representation is a reinstatement of the perceptual processes. A framework for this assumption has been provided by the scanpath theory whereby it has been stated that oculomotor codes are stored along with the stimulus features that are then reused to reactivate the internal stimulus representations during subsequent retrieval from memory (Noton & Stark, 1971). The delay period eye movements could therefore reflect the *retrospective* scanning of the mental space in order to reactivate the visuospatial memory information (Olsen et al. 2014, Laeng & Teodorescu, 2002, Wynn, Shen & Ryan 2019). Alternatively, the assumption that oculomotor codes are stored for future performance resonates with the “memory for action” accounts of WM where it holds that WM reflects the preparation for future actions whether it be oculomotor, verbal or manual (Olivers & Roelfsema, 2020; Stokes & Nobre, 2019). According to this view, the delay period eye movements could be a reflection of *prospective* scanning of the external physical space serving the purpose of better behavioral performance. Given that brain areas planning eye movements are also involved in planning spatial shifts of attention (Corbetta, 1998; Rizzolatti, Riggio, Dascola & Umiltá, 1987), it is therefore likely that the patterns of delay period eye movements are essentially a reflection of the oculomotor action planning. Further research is needed to resolve the question whether the prospective or retrospective scanning account better supports visuospatial WM. For example, one could test the effect of task-relevant and task-irrelevant features on the patterns of delay period eye movements, where the prospective scanning account predicts patterns of eye movements only following task-relevant features.

Accepting the assumption that delay period eye movements reflect attention-based rehearsal, one may wonder to what extent these patterns of eye movements play a functional role in the rehearsal processes or, alternatively, whether they are merely epiphenomenal. According to the epiphenomenal explanation, oculomotor rehearsal could be the consequence of sequencing the internal commands to shift the focus of covert attention. Within this framework, Godijn and Theeuwes (2011) explicitly manipulated the instructions as to whether to move the eyes or to keep them fixated. They did not observe any behavioral advantage of overt (eye movements) compared to covert shifts of attention during rehearsal suggesting that eye movements are not useful for rehearsal. Our findings, however, argue against a strictly epiphenomenal explanation. Across two experiments, we observed that the majority of participants spontaneously moved their eyes according to the encoding direction and, more importantly, that these participants performed better than the minority of participants who preferred not to move, suggesting that the precise and orderly patterns of eye movements play a functional role in the retention of visuospatial information (Hebb, et al., 1968; Pearson et al. 2014). Even if they would produce accurate eye movements because they already have a precise representation of the memory items, eye movements likely help to maintain the finely tuned memory representations which could otherwise decay rapidly (Pertzov, Bays, Joseph & Husain, 2013; Pertzov, Manohar, & Husain, 2017). Although our findings suggest that the reactivation of memory representations is likely (Noton & Stark, 1971; Olsen et al. 2014, Laeng & Teodorescu, 2002, Wynn, et al 2019), our study does not provide direct evidence as it is correlational in nature. Future research needs to address this possibility by explicitly manipulating the eye-movements.

The fact that participants differed in their oculomotor behavior highlights the importance of taking into account the individual differences in scanning strategies (Boot, Kramer, Becic, Wiegemann and Kubose, 2006; Boot, Becic & Kramer, 2009). For instance, Boot et al. (2006) classified participants as naturally overt or covert searchers in a visual scanning task where changes to a dynamically moving visual grid were to be detected. They observed that task performance of naturally covert searchers relative to the overt searchers was disrupted when instructions imposed overt scanning suggesting that eye-movements are not universally beneficial. Analogously, oculomotor rehearsal in vsWM might be adaptive (or maladaptive) for some participants who engage in it, and when behaving otherwise, would impact their overall performance. It is possible that the “fixators” in our study could be classified as covert searchers and when they engage eye movements, their recall performance is disrupted. Yet, due to the correlational nature of our study, a question remaining to be addressed in future work is whether eye movements of naturally covert searchers cause interference with memory precision or whether loss of memory causes their engagement of eye-movements.

While WM models commonly agree that rehearsal is a mechanism for maintaining novel information in an accessible state in order to guide behavior over the short-term, it is currently unknown how rehearsal can be implemented in current models of WM. From the current study, we can conclude that a sequence of visuospatial information is rehearsed, similar to how a sequence of verbal information is subvocally rehearsed, in a cumulative forward direction that starts from the first item, then moves to the second, and so on until the last item, and then back to the first item (Oberauer and Lewandowsky, 2011). This attention-based rehearsal process has recently been rephrased as a process of *refreshing* which has been defined as a domain-general process that is used to prolong the attended visual, spatial and verbal memory representations (Johnson, 1992; Camos, Johnson, Loaiza, Portrat, Souza & Vergauwe, 2018; Vergauwe & Langerock, 2017). Rehearsal in WM is thus not exclusively supported by a domain-specific store with a domain-specific rehearsal mechanism, but also by attentional processes that are part of a unitary WM system (Cowan, 1995; Oberauer 2009).

According to the resource view, the precision of memory depends on the quantity of the available resources divided across the number of memory items (Bays & Husain, 2008; Wilken & Ma, 2004). However, our findings suggest that the memory precision is not only defined by the number of items but also by the precision and type of patterns of eye movements made during retention. For instance, Udale, Tran, Manohar and Husain (2022) have recently shown that in a sequence of saccades during memory encoding of a simultaneously presented array of visual information, memory precision was highest for the final saccade target even when this item was blanked away from vision and could therefore not be fixated. These findings suggest that making eye movements towards a target item, or shifting covert attention to this item, causes a higher proportion of memory resources to be flexibly assigned to this item during visual encoding, and therefore leading to higher recall precision. Within this framework, our findings highlight the fact that retention could be accomplished by a similar mechanism of resource allocation that is continuously reallocated in a cyclic manner to the memoranda during memory maintenance. Hence, one implication of our findings is that models assuming resource allocation among memory items need to incorporate how these resources are dynamically reallocated to memoranda during retention (Bays & Husain, 2008; van den Berg, Shin, Chou, George, & Ma, (2012).

To conclude, the results of the present study align with the attention-based rehearsal mechanism whereby eye movements not only indicate where spatial attention is oriented, but also reveal how spatial attention shifts during visuospatial memory maintenance. The observation that rehearsal is characterized by oculomotor patterns provides a promising novel approach to get insights into the online attentional processes involved in WM (Awh and Jonides, 2001).

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