Visual working memory representations in visual and parietal cortex do not remap after eye movements

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Abbreviated title: No remapping of VWM after eye movements

Number of pages: 30

Number of figures: 3

Number of words: Abstract = 248, Sig. Statement = 102; Introduction = 549, Discussion = 1008

Acknowledgements: This work was supported by The Netherlands Organisation for Scientific Research Vidi Grant 452-13-016 to F.P.d.L., the EC Horizon 2020 Program ERC Starting Grant 678286 “Contextvision” to F.P.d.L, the James S.McDonnell Foundation 220020373 to F.P.d.L and the China Scholarship Council (CSC; 201608330264) to T.H.. We thank David Richter and Chuyao Yan for helpful comments and discussions of the manuscript.

Competing Interest: The authors declare no competing financial interest.

Author contributions: T.H. wrote the first draft of the paper; T.H., M.E., and F.P.d.L. edited the paper; T.H., M.E., A.V., and F.P.d.L. designed research; T.H. and A.V. performed research; T.H., M.E., and F.P.d.L. analyzed data.

ABSTRACT

Previous studies have suggested that stimulus representations in the visual system are remapped across eye movements during perception. Interestingly, our visual system does not only process stimuli that are directly available to our eyes, but may also have a role in maintaining information in VWM over a period of seconds. It remains unclear if saccadic remapping also occurs for stimuli that are held in working memory and whether eye movements degrade VWM representations in visual cortex. Here, we directly compared the content of VWM in early visual areas for saccade and no-saccade conditions using MVPA of delay-related activity measured with fMRI. Specifically, we probed item-related VWM representations of the remembered grating orientation from contralateral and ipsilateral early visual areas (V1 – V3) and the intraparietal sulcus (IPS). When participants did not make a saccade, VWM representations were robustly present in contralateral early visual cortex. Surprisingly, VWM representations disappeared from contralateral V1-V3 after the saccade shifted the location of the remembered grating to the opposite visual field. In contrast to our saccadic remapping hypothesis, we found no evidence for the representations of the remembered grating at the saccadic target location in the opposite visual field, suggesting that there is no evidence for remapping of VWM in early visual cortex. Interestingly, IPS showed persistent VWM representations in both the saccade and no-saccade condition. Together, our results indicate that VWM representations in early visual cortex are not remapped across eye movements, potentially limiting the role of early visual cortex in VWM storage.

Significance Statement

It has been well documented that our visual system does not only process stimuli that are directly available to our eyes, but may also have a role in maintaining information in visual working memory over a few seconds. Previous research has indicated that stimulus features are remapped across eye movement to aid visual stability. In the current study, we show that visual working memory information does not remap after eye movements. In addition, visual working memory representations are degraded after eye movements in early visual cortex, but not in parietal cortex, potentially limiting the role of early visual cortex in VWM storage.

Introduction

Humans perform about three saccadic eye movements per second in order to guide the fovea toward regions of interest in the visual field (Rayner, 1998). Previous research has indicated that both stimulus features and attentional pointers are remapped across eye movement to aid visual stability (Melcher, 2007; Rolfs et al., 2011; He et al., 2018). Furthermore, research in the last decade has suggested that our visual system may not only process incoming information, but also be relevant for maintaining internal representations of previously observed visual stimuli, i.e. visual working memory (VWM). The ability to maintain information that is no longer in view is critical for reasoning about and mentally manipulating visual information despite temporal discontinuous in visual inputs that occur for example during eye movements, occlusions, and object motion (Curtis and D'Esposito, 2003; Serences, 2016; Lorenc et al., 2018).

VWM information has been observed both in early sensory areas (Ester et al., 2009; Harrison and Tong, 2009; Albers et al., 2013), as well as higher-order parietal (Christophel et al., 2015; Ester et al., 2015; Bettencourt and Xu, 2016; Xu, 2017, 2018), and prefrontal regions (Durstewitz et al., 2000; Riley and Constantinidis, 2016). Moreover, VWM representations in early visual cortex have been found to be spatially specific, maintained in a retinotopic manner (Pratte and Tong, 2014). Crucially however, in these previous studies, participants were instructed to maintain fixation while remembering a visual stimulus during a retention period. While this is a common approach to investigate VWM in a lab environment, it is arguably quite different from real-world settings that are marked by multiple eye movements per second. In our daily life, VWM is typically dynamic and fragile. For instance, when looking for a key in an apartment, one needs to maintain a mental image of the key

while continuously moving one's eyes toward different search locations. It is largely unknown how eye movements impact the mental VWM representations in early visual areas and beyond.

One possibility is that VWM representations are dynamically remapped and follow the shift of the retinotopic location caused by eye movements. In this case, the cortical location representing the VWM would be updated after an eye-movement. Alternatively, working memory information might be maintained across multiple brain regions and not require remapping following eye movements. On this account, after every eye movement, the up-to-date feature of the stimulus (e.g., the latest location of the stimuli) would be integrated with the previous working memory information.

Here, we tested the potential remapping of VWM in the early visual system, by presenting participants with an orientated grating in either the left or right visual field. The grating orientation had to be maintained for a subsequent retention period, while we measured blood oxygenation level-dependent (BOLD) signals with functional magnetic resonance imaging (fMRI). Using multivariate pattern analysis (MVPA), we attempted to decode the remembered orientation in both the contralateral and the ipsilateral hemispheres during trials in which participants performed either a saccade or maintained fixation during the working memory period.

To preview, we found a contralateral VWM representation in the early visual system. This VWM representation disappeared when participants made a saccade and was not remapped to ipsilateral visual cortex. In contrast, VWM representations in IPS persisted after saccades. These findings suggest a limited role of the early visual system in VWM.

Materials and Methods

Data and code availability

All data and code used for stimulus presentation and analysis is freely available on the Donders Repository (https://data.donders.ru.nl/login/reviewer-77603154/wWWKvrhkeJS0w6mNBkWAHBvST_jPJyodeGVyxxYwpLc).

Participants

Thirty healthy participants with normal or corrected-to-normal vision were recruited from the institute's subject pool in exchange for either monetary compensation or study credits. All participants were naive with respect to the purposes of the study. The experiments were approved by the Radboud University Institutional Review Board and were carried out in accordance with the guidelines expressed in the Declaration of Helsinki. Written informed consent was obtained from all participants prior to the start of the study. All participants had to complete the entire experimental protocol (i.e., the behavioral experiment and the two fMRI sessions). Six participants were excluded before the final analysis: one participant didn't complete the fMRI sessions due to discomfort, one participant failed to follow the instructions (i.e., fixate and saccade) during experiment, four participants had excessive head motion (motion cutoff = 1 mm). The remaining 24 participants were included in all analyses (13 female, mean age 23.3 years, range from 19 to 31 years). The desired sample size of N=24 included subjects was based on an a priori power calculation that aimed to achieve 80% power to detect an effect size of at least Cohen's d > 0.6.

Stimuli

Stimuli were programmed in MATLAB (v2016a, The MathWorks, Inc., Natick, MA) using the Psychtoolbox (Brainard, 1997). The circular sinusoidal grating stimulus subtended 10° and was centered with a small jitter (0.3°) on the screen center. The grating was full contrast, with a spatial frequency of 1 cycles/degree, a random phase and an orientation of either 25° or 115° (with a small jitter of 3°) from the horizontal axis. The contrasts of the edges of the grating were linearly attenuated over the distance from 4.5° to 5.0° radius. Two filled dots (0.5°, one green, one black) were presented at the periphery of the screen, which were served as the fixation dot and saccade target in the task. In the behavioral training session, stimuli were presented on a 24-in. flat-panel display (BenQ XL2420T, 1,920 x 1,080 resolution, 60 Hz refresh rate). In the fMRI sessions, stimuli were displayed on a rear-projection screen using an EIKI LC-XL100L (EIKI, Rancho Santa Margarita, CA) multimedia projector (1,024 x 768 resolution, 60 Hz refresh rate).

Experimental design

Behavioral training procedure. Prior to the fMRI scan sessions, all participants completed a one-hour behavioral training session to familiarize themselves with the fMRI main task and to establish their individual orientation discrimination threshold, which served as an initial orientation difference of the gratings in the following fMRI sessions. The experimental design of the behavioral training task was exactly the same as during the fMRI main task, except that the delay period and the inter-trial interval (ITI) were shortened to 3 s to reduce the experimental time. Participants completed two to three blocks of 56 trials until a stable orientation discrimination threshold was obtained, during which the eye movements were continuously monitored by an Eyelink 1000 plus eye tracker. In addition, participants were

158 familiarized with the localizer tasks and the retinotopic mapping procedures that
159 were used in the fMRI session at the end of the behavior session.
160 *fMRI main task.* The experimental design (Figure 1a) was adapted from a well-
161 known delayed orientation discrimination task used before (Harrison and Tong,
162 2009). Each trial began with two filled dots (one green, one black) that were
163 presented at the periphery of the screen (2 s). Participants were asked to fixate at
164 the green dot through the trial. Two oriented gratings were flashed sequentially at the
165 center of the screen (which could be in the left or right visual field of the participants,
166 depending on the location of the green fixation dot) for 200 ms, respectively, with an
167 inter-stimulus interval of 400 ms, and followed by a retro-cue (400 ms, “1” or “2”) to
168 indicate which orientation of the grating should be remembered during the following
169 delay period. The sequence of the orientations (25° and 115°) were randomly
170 chosen on each trial. On one third of trials (No-saccade condition), the two dots did
171 not swap their locations, which indicated to participants that they needed to keep
172 their fixation at the initial fixation location during the 10 s delay period. On the
173 remaining two thirds of trials (Saccade condition), the green dot was shifted to the
174 opposite side of the screen at the beginning of the delay period (2 s after the offset of
175 the retro-cue). This instructed participants to move their eyes to the opposite location
176 of the screen and maintain their fixation at the new position for the remaining 8 s. A
177 probe grating was presented at the screen center after the delay period and
178 participants were required to make a judgement of whether the probe orientation was
179 rotated clockwise or countclockwise relative to the grating they memorized during the
180 delay period. Finally, feedback was provided and a black fixation dot instructed
181 participants to move their eyes to the center of the screen in preparation for the next
182 trial. Trials were separated by an ITI of 9.6 s. The central fixation dot changed its

color from black to gray at the last second of the ITI to indicate that the next trial was going to start.

In order to rule out the potential confound of global representations of VWM, four catch trials were included in each run. Stimuli and timing of the catch trials were identical to the main trials, except for the following changes. During the presentation of the probe in the catch trial, the probe was horizontally shifted 1° to the left or right with respect to the location of the sample gratings. Participants were instructed to not respond when the location of the probe grating did not match with the sample gratings. The rationale of this was that it forced participants to memorize the orientation stimulus at its original location in order to successfully perform the task, resulting in a spatially specific VWM representation.

Each run comprised 28 trials, consisting of 8 no-saccade trials, 16 saccade trials, and 4 catch trials. The order of trials was a pseudo-randomized within each run. Each trial lasted 26.4 s, consisting of a 16.8 s task period and a 9.6 s ITI. Each run lasted 12.32 min and started with 6 s of fixation that was discarded from the analysis.

Staircase Procedure

The staircase procedure was used to ensure equal task difficulty across participants and to equate task difficulty levels across no-saccade and saccade conditions within participants. In the behavioral training session, immediately after the delay period, participants were asked to compare the tilted orientation between the probe and the internal remembered grating. The staircase procedure estimated the difference between probe and remembered grating that ensured 75% performance, using QUEST (Prins and Kingdom, 2018). A maximum orientation difference of 20° between the probe and remembered grating was enforced. The staircase was

initiated with an orientation difference of 10° and dynamically adapted according to participants' performance on previous trial until a stable threshold was acquired. This threshold was used as a seed in the following fMRI sessions and the same staircase procedure was also used during scanning.

Eye tracking

Eye position was monitored with an MR-compatible Eyelink 1000 (SR Research Ltd., Ottawa, Canada) eye tracker. Only the left eye was recorded in the scanner. Pupil and corneal reflection were sampled at 1000 Hz and analyzed offline to ensure that participants fixated at the correct location. The eye tracker was calibrated at the beginning of each session and repeated between runs if necessary. In 10 out of 192 runs, the eye tracker signal was lost during scanning due to subjects' head motion or technical problems. During these runs, the experimenter monitored the eye position online via the live video feed from the camera. All participants were trained on the fixation task and to perform saccades in the behavioral training session prior to the scanning session.

fMRI parameters

Functional and anatomical images were carried out with a 3T Siemens Prisma fit MRI system (Siemens, Erlangen, Germany), using a 32-channel headcoil. Functional images were acquired using a whole brain T2*-weighted multiband-4 sequence (TR/TE = 1,200/39 ms, voxel size 2.4x2.4x2.4 mm, 56 transversal slices, 65° flip angle, A/P phase encoding direction, FOV = 210 mm, BW = 2030 Hz/Px). Anatomical images were acquired using a T1-weighted magnetization prepared rapid gradient echo (MP-RAGE) sequence (TR/TE = 2,300/3.03ms, voxel size 1x1x1 mm, 192 transversal slices, 8° flip angle).

fMRI Preprocessing

fMRI data were preprocessed using FSL (Oxford, UK) (Smith et al., 2004), including motion correction (six-parameter affine transform), temporal high-pass filtering (100 s) and Savitzky–Golay low-pass filter (time window length = 11 TRs, polynomial order = 3; Savitzky & Golay, 1964) for each run separately. No spatial smoothing and slice timing correction was performed. All univariate and multivariate analyses were performed in native subject space using custom python code.

Functional localizers

In addition to the main experiment, participants underwent two localizer runs, which were used to select voxels that maximally responded to stimuli presented in the contralateral hemifield and served as independent training data for the multivoxel pattern analysis. The same grating stimulus parameter were used in localizer runs as those in the main experiment. Participants fixated at the left or right green dot and the grating was presented at the center of screen for 16 s, with a frequency of 4 Hz. Throughout the localizer, participant had to fixate at the green dot and monitor a sequence of rapidly changing letters just above fixation, to which they had to respond by button press whenever a target letter (“X” or “Z”) occurred in a stream of non-target letters (“A”, “H”, “R”, “N”, “T”, “V”, “U”, “Y”). Letters were presented at a frequency of 2 Hz. When the green dot shifted from the left to the right side of the screen (or vice versa) at the end of the trial, participants had to move their eyes to follow the fixation dot. Each trial was separated by a 2 s ITI in which only the fixation cross was presented, to give participants enough time to saccade and stabilize their eyes in the new position. Two blocks of 20 trials (10 trials per visual field: left or right) and orientation (25° or 115°) were collected.

Images of the localizer runs were also preprocessed following the same procedure as the main tasks. Onsets and duration of the localizer blocks were convolved with a single-gamma haemodynamic response function (HRF) and fitted using a general linear model in left and right hemisphere separately. For each participant a two-sided t-contrast was calculated contrasting between left and right hemispheres. Resulting statistical maps were thresholded at $Z > 2.3$ and a corrected cluster significance threshold of $p < 0.05$.

Retinotopic mapping of early visual areas (V1 – V3)

Early visual areas (V1, V2, and V3) for each participant were identified using two retinotopic mapping blocks based on the standard traveling-wave method using rotating wedges (DeYoe et al., 1996; Engel et al., 1997; Wandell et al., 2007), consisting of a clockwise and a counterclockwise-rotating run. Participants were instructed to fixate at the center of the screen and fulfill rapid letter detection task (exact same as that in localizer runs). The BOLD responses to the wedges were used to estimate the polar angle of the visual field representation.

Regions of interest (ROIs)

Early visual areas (V1 - V3) and the intraparietal sulcus (IPS0 – IPS5) within each hemisphere were independently chosen as the ROIs in our analyses. For the ROI of the early visual areas, we first used Freesurfer (http://surfer.nmr.mgh.harvard.edu/, (Fischl et al., 2002)) to define the gray–white matter boundary and perform cortical surface reconstruction. The borders of the early visual areas V1 - V3 were delineated based on retinotopic maps. The ROI of the intraparietal sulcus was defined based on anatomical probability maps of retinotopic areas in the intraparietal sulcus (IPS0 – IPS5) from the Probabilistic atlases (Wang et al., 2015). Finally, all surface-based ROIs were backward-transformed into participant's native space. Next, the visually

active voxels corresponding to the grating that was positioned at the left and right visual field was identified based on statistical activation maps from the functional localizer runs. Two types of ROI were defined in the decoding analyses: contralateral ROIs and ipsilateral ROIs. For instance, when decoding the orientation of the grating that was initially presented at participant's right visual field, regardless of the no-saccade and saccade condition, the left hemisphere would be labeled as the contralateral ROIs, while the right hemisphere would be labeled as the ipsilateral ROIs (see Figure 1b) and vice versa. Finally, we selected the 200 most active voxels across the entire early visual cortex (V1 -V3) and the entire intraparietal sulcus (IPS0 – IPS5) to do the decoding analyses, separately.

Univariate fMRI analyses

To estimate the BOLD response of each hemisphere in each condition, we selected the same voxels as those used for decoding. We separately modeled the onset of each trial for each hemisphere and for no-saccade and saccade condition separately. To quantify BOLD activity during the trial, contrasts between left and right hemisphere regressors for each condition were created. All fMRI data were transformed from MRI signal intensity to units of percent signal change, calculated relative to the average level of activity for each voxel across the first volume of each trial within each run.

Multivariate fMRI analyses

We used multivariate pattern analyses (MVPA) to determine whether the pattern of activity in each ROI and each hemisphere contained orientation information, as implemented in Scikit-learn 0.20.3 (Pedregosa et al., 2011). To this end, linear support vector machines (SVMs) were trained to discriminate between the two grating orientations based on the pattern of BOLD activity over voxels. In this study

we used classification distance as an indication of the amount of orientation information being maintained in each hemisphere. To calculate the classification distance, we measured the distance of each sample to the separating hyperplane that was trained by a linear SVM with a positive/negative sign (the sign indicates the class). We then averaged the distance within each class and calculated the absolute distance between these two classes. While this approach can give us a binary predicted label (25° or 115°), which can be used to calculate classification accuracy, it additionally allows one to review the confidence of this classification and provide a continuous metric of the decoding performance. In each ROI, the larger the classification distance, the more confident the classifier is in determining the stimulus class based on the BOLD activity pattern, and hence the more orientation information is contained within the pattern of BOLD activity.

When training and testing within the main experiment we averaged the BOLD activity over time points 7.2 - 10.8 s after the onset of the delay period. This time period was selected to be as far from the onset of the two gratings at the beginning of the trial as possible, and therefore not reflect activity elicited by the stimuli, but also prior to the onset of the probe stimulus. These time series were then normalized using a z-scored transformation within each run. For generalization from perception to VWM, the classifier was trained using a full time series (0 - 16 s) of the average BOLD activity in the localizer and then applied to the averaged VWM period.

A leave-one-run-out cross-validation procedure was used to train the classifier where we trained in 7 out of 8 runs and tested on the remaining run. We also used this cross-validation procedure on the time-resolved decoding analysis, but within each time point independently. BOLD activity and classification distance over time were statistically tested using nonparametric cluster-based permutation t test (10,000

permutations; two-sided $p < 0.05$; cluster formation threshold $p < 0.05$) (Maris and Oostenveld, 2007).

Bayesian analyses

In order to further evaluate non-significant tests, we performed the Bayesian equivalents of the above outlined analyses. JASP 0.10.2 (JASP Team, 2019, RRID:SCR_015823) was used to perform all Bayesian analyses, using default settings. Thus, for Bayesian t-tests a Cauchy prior width of 0.707 was chosen. Qualitative interpretations of Bayes Factors are based on criteria by Lee & Wagenmakers (2014).

Results

Our primary goal was to investigate whether VWM representations in early visual cortex (V1-V3) are remapped after eye movements. We used MVPA (Kamitani and Tong, 2005; Haynes and Rees, 2006; Norman et al., 2006) to determine whether the contents of VWM that was initially represented in the contralateral hemisphere (corresponding to the stimulus location) was remapped to the opposite (ipsilateral) hemisphere following an eye movement to the opposite visual field during the retention period. Twenty-four participants performed a delayed orientation discrimination task, in which they initially fixated at the peripheral fixation dot while passively viewing two successive grating stimulus orientations (25° and 115°) in one visual field, followed by a cue and a delay period. Importantly, in two third of the trials (*saccade condition*), participants were asked to saccade to the opposite side of the screen during the delay period, while in the remaining third of trials (*no-saccade condition*), participants maintained fixation at the initial side through the entire trial. A probe grating was presented at the end of the trial (Figure 1a, b).

In order to ensure that participants memorized the grating in its original location and thereby rule out of the potential confound of spatially unspecific representations of VWM in early visual cortex (Ester et al., 2009; Pratte and Tong, 2014), we also included catch trials in which the probe grating was horizontally shifted 1.2° with respect to the location of the sample gratings. Participants were instructed to discriminate the orientation between the probe and the memorized grating only when they were presented at the same location (see Methods for details). This experimental design was chosen to encourage participants to maintain both the orientation and location of the presented grating. Indeed, behavioral data showed that participants could successfully withhold their response at an accuracy of 66.67% (SD 12.25) when the probe was presented at a displaced location, demonstrating that participants remembered the orientation in a spatially specific way.

Behavioural data confirmed that participants could successfully discriminate small differences between the cued grating and the probe grating (mean discrimination threshold, no-saccade condition: 8.17°, SD 4.80; saccade condition: 8.69°, SD 4.61) at an accuracy of 81.7% (SD 4.96) and 81.4% (SD 4.90) in both no-saccade and saccade trials. Notably, there was no difference in accuracy between trials with and without a saccade ($t_{(23)} = 0.33$, $p = 0.7465$, Cohen's $d = 0.07$; $BF_{01} = 4.426$), and no differences in the mean discrimination threshold ($t_{(23)} = 1.04$, $p = 0.3085$, Cohen's $d = 0.21$; $BF_{01} = 2.866$), indicating that the VWM performance was not impaired by the eye movement during the delay period.

A univariate BOLD analysis showed that the presentation of the grating stimuli induced stronger BOLD activity in contralateral than ipsilateral early visual areas (cluster permutation test, $p = 0.0001$). As expected, probe presentation at the end of

the trial led to a BOLD activity increase in the contralateral hemisphere during no-saccade trials and a BOLD activity increase in the ipsilateral hemisphere, corresponding to the updated stimulus location after the eye movement, in the saccade condition (Figure 1c). Taken together, these results suggest that participants engaged successfully in the task.

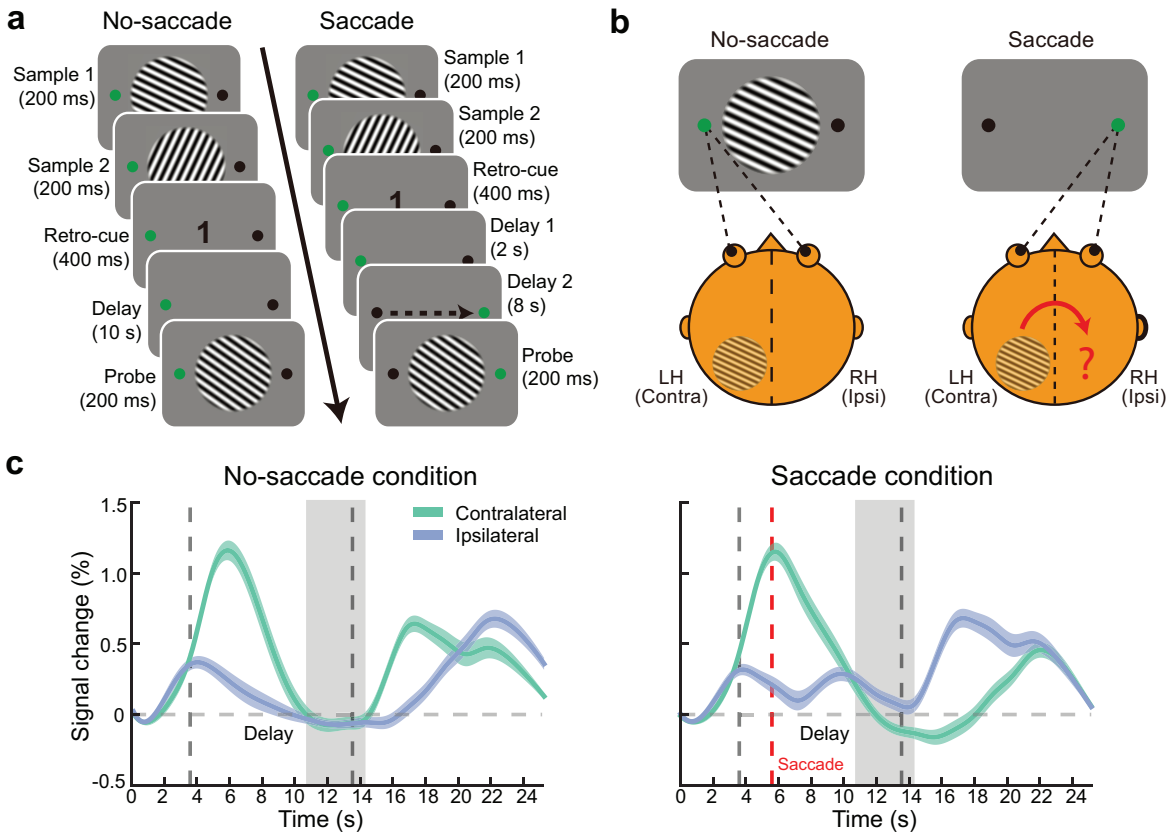

Figure 1. Experimental paradigm and BOLD activity in the early visual cortex. (a) Participants performed a delayed orientation discrimination task. At the start of each trial, two dots were presented at the periphery of the screen and participants were instructed to fixate at the green dot. Two orientated gratings (25° and 115°) were successively flashed in the center of the screen, followed by a retro-cue (1 or 2) that indicated which grating to remember in the following delay period. Crucially, during a 10 s delay period, if the green dot shifted to the opposite side of the screen (*saccade condition*), participants had to make an eye movement to the opposite side and maintained at the new location through the following time period (the dashed arrow is for illustration only, not present in the actual test). Conversely, in the no-saccade condition, the green dot did not change its position and participants maintained fixation at the initial side throughout the entire trial. After the delay period a probe was presented, and participants indicated whether the probe was tilted clockwise or

counterclockwise relative to the remembered grating. **(b)** Illustration of the experimental design probing remapping. In the no-saccade condition (left), the remembered grating presented in right visual field is initially represented in the left (contralateral) early visual cortex. In the saccade condition (right), after participants saccade from the left to the right side of the screen, we set out to examine whether VWM contents that initially generated in contralateral (left) early visual cortex transfer to the ipsilateral (right) visual cortex. **(c)** Group averaged (N=24) BOLD time course in contralateral and ipsilateral early visual areas (V1 – V3). In the no-saccade condition, the presentation of grating stimuli evoked a higher BOLD response in contralateral than in ipsilateral early visual areas. In the saccade condition, while the BOLD activity was still higher in contralateral relative to ipsilateral early visual areas after presentation of the grating stimuli, the pattern inverted after presentation of the probe – BOLD activity became higher in ipsilateral than in contralateral early visual areas. Shaded areas denote SEM.

In order to evaluate the potential remapping of VWM in early visual cortex, we assessed whether the patterns of activation in both the hemispheres, contralateral and ipsilateral to the item location, contained the remembered orientation information during the delay period (Figure 1c, gray region). We trained a pattern classifier to discriminate the grating orientation (25° vs. 115°) during an independent, passive-viewing localizer run. The classifier was then used to discriminate the gratings during the retention period of the main experiment. We used classification distance to measure the amount of orientation information present in the activity patterns (Buitinck et al., 2013). This approach results in a binary prediction (25° or 115°), but additionally yields a continuous metric of the decoding performance that can be seen as the confidence of the classification (see Methods for additional details).

No remapping of VWM in early visual cortex following eye movements.

During the no-saccade condition, activity patterns in the contralateral early visual areas (V1 -V3) contained information about the maintained orientation during

the delay period (7.2 s - 10.8 s after onset of maintenance) (Figure 2a, left green bar; $t_{(23)}$ = 3.60, p = 0.0015, Cohen's d = 0.73), whereas there was no orientation information in the ipsilateral hemisphere (Figure 2a, left purple bar; $t_{(23)}$ = -0.25, p = 0.8078, Cohen's d = 0.05), in line with a retinotopically specific VWM storage (Pratte and Tong, 2014). Indeed, Bayesian analyses indicated moderate support (BF_{01} > 3) for the null hypothesis of no VWM representations in ipsilateral early visual areas (BF_{01} = 4.531). In the saccade trials, however, orientation information in the contralateral early visual cortex could no longer be significantly discriminated by the classifier (Figure 2a, right green bar; $t_{(23)}$ = 1.9, p = 0.0706, Cohen's d = 0.39), suggesting that the VWM content that was initially maintained in contralateral regions is degraded by an eye movement during the delay period. Interestingly, the VWM representations in contralateral early visual areas did not remap to its ipsilateral hemisphere, given that the classifier could not infer, above chance, the remembered orientation from activity patterns in ipsilateral early visual areas (Figure 2a, right purple bar; $t_{(23)}$ = 0.69, p = 0.495, Cohen's d = 0.14). Bayesian analyses also showed moderate support for the absence of orientation information in ipsilateral early visual areas in saccade condition (BF_{01} = 3.743).

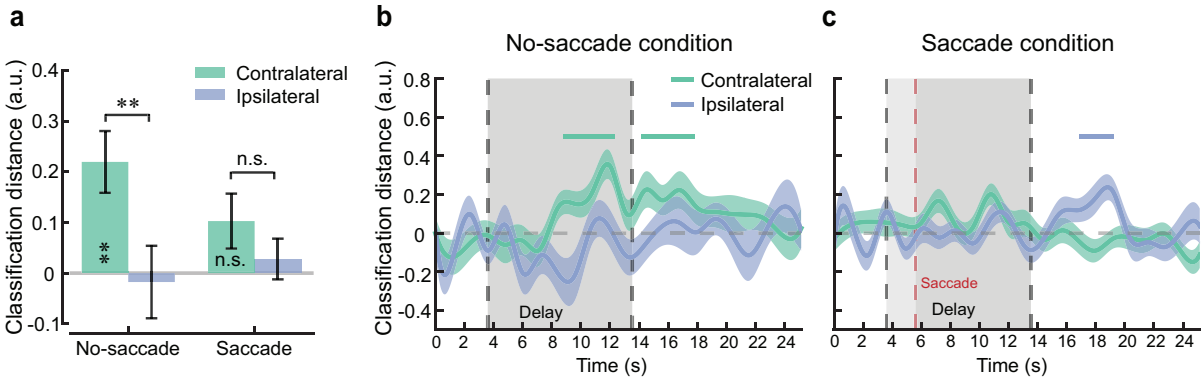

Figure 2. VWM representations in ipsi- and contralateral early visual areas (V1 - V3). (a) Orientation classification performance for gratings presented to the contralateral and ipsilateral hemispheres during the delay period (7.2 s – 10.8 s after onset of maintenance). In the no-saccade condition, only the contralateral early visual areas (V1 -V3) maintained the

orientation information during delay period, whereas following an eye movement from one side to the opposite side during the delay period, the remembered orientation could no longer be reliably decoded from either the contralateral or the ipsilateral early visual areas, suggesting that no remapping of VWM occurred around the eye movement. **(b)** The time course of orientation classification performance in both contralateral and the ipsilateral early visual areas in the no-saccade condition. Information about the orientation of the remembered grating was present in the contralateral early visual areas during delay period. No remembered orientation information was present in the ipsilateral early visual areas. The horizontal bars indicate statistically significant different from zero (cluster permutation test, 1st cluster: $p = 0.0011$; 2nd cluster: $p = 0.0346$). **(c)** The time course of orientation classification performance in both contralateral and ipsilateral early visual areas in the saccade condition, in which participants had to make a saccade to the opposite side of the screen at the beginning of the delay period. The remembered orientation information was degraded in the contralateral visual cortex but did not remap to the ipsilateral hemisphere. The horizontal bars indicate statistically significant different from zero (cluster permutation test, $p = 0.008$). Error bars and shaded areas denote SEM. *$p < 0.05$; ** $p < 0.01$; n.s., $p > 0.05$.

Next, we examined the time course of VWM representations in the contralateral and ipsilateral early visual areas separately. To this end, we applied the classifier that was trained using the passive localizer session to each time point of the working memory task, including no-saccade and saccade trials. During no-saccade trials, the classifier could initially not discriminate between orientations of the remembered grating in either the contralateral or the ipsilateral early visual areas. However, after a few seconds following the stimulus presentation, the classifier was able to select the remembered orientation in the contralateral early visual cortex, while there was no orientation information in the ipsilateral early visual cortex (Figure 2b, cluster permutation test, $p < 0.05$). Compared to the saccade trials, after the eye movement during the delay period, we found that orientation information was strongly degraded in contralateral early visual areas. Crucially, the remembered orientation information could not be decoded at any time point during delay period from activity patterns in

481 the ipsilateral early visual areas (Figure 2c), suggesting that VWM contents were not
482 remapped after the eye movement.

483 Our primary approach to quantify orientation-specific activity patterns in early
484 visual cortex was based on a separate data set, during which participants viewed the
485 grating stimuli while their attention was engaged elsewhere. While this approach
486 allows for strong inference (i.e., patterns of activity during the maintenance period
487 resemble those elicited by the physical presentation of the same stimuli), it cannot
488 detect consistent orientation-specific activity patterns during VWM maintenance that
489 are only robustly present during the VWM task, and not during passive viewing.
490 Therefore, in an exploratory analysis, we used a leave-one-run-out cross-validation
491 approach to train the classifier within the working memory period and test on the left-
492 out run.

493 Unlike in the decoding analysis trained on the localizer, we found that in no-
494 saccade trials, orientation information was present in both the contralateral (Figure
495 3a, left green bar; $t_{(23)} = 3.29$, $p = 0.0032$, Cohen's $d = 0.67$) and the ipsilateral
496 (Figure 3a, left purple bar; $t_{(23)} = 3.18$, $p = 0.0042$, Cohen's $d = 0.65$) early visual
497 areas. This indicates that there were consistent differences during VWM
498 maintenance of the different orientations not only in the contralateral but also the
499 ipsilateral early visual areas during the delay period. However, also here, the
500 classifier was not able to distinguish between grating orientation in either the
501 contralateral (Figure 3a, right green bar; $t_{(23)} = 1.50$, $p = 0.1469$, Cohen's $d = 0.31$;
502 $BF_{01} = 1.738$) or the ipsilateral (Figure 3a, right purple bar; $t_{(23)} = 1.94$, $p = 0.0642$,
503 Cohen's $d = 0.40$; $BF_{01} = 0.936$) early visual cortex after the eye movement during
504 saccade trials.

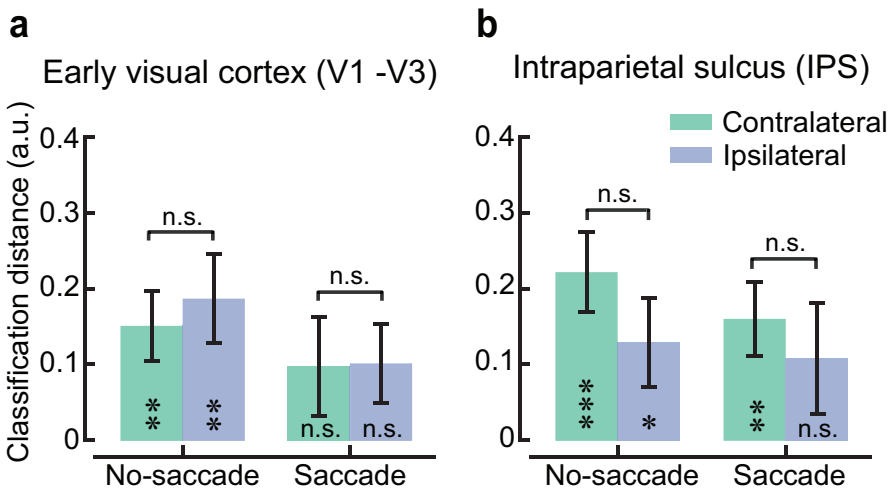

Figure 3. Orientation classification performance during the delay period in early visual cortex (V1 – V3) and intraparietal sulcus (IPS) using a leave-one-run-out cross-validation approach. (a) In the no-saccade condition, both the contralateral and the ipsilateral early visual areas contained orientation information during the delay period. In the saccade condition, however, the orientation information degraded in both hemispheres. **(b)** In the IPS, the classifier could select the remembered orientation in both the contralateral and the ipsilateral hemisphere in the no-saccade trials, in line with the findings in early visual cortex. In the saccade condition, after the eye movement there was still reliable orientation information in the contralateral IPS. Error bars denote SEM. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s., $p > 0.05$.

Persistent VWM representations after an eye movement in the IPS.

Our findings revealed that VWM representations in early visual cortex during maintenance were not remapped following eye movements. Bettencourt & Xu (2016) have recently shown that while remembered orientation information was degraded by irrelevant distractors in early visual cortex, VWM information remained available in the superior intraparietal sulcus (IPS). We sought to test whether we could observe similar results in our study. To this end, we applied the leave-one-run-out cross-validation method to IPS. First, we found that both the contralateral (Figure 3b, left green bar; $t_{(23)} = 4.24$, $p = 0.0003$, Cohen's $d = 0.86$) and the ipsilateral IPS (Figure 3b, left purple bar; $t_{(23)} = 2.22$, $p = 0.0369$, Cohen's $d = 0.45$) contained

information about the remembered orientation in no-saccade trials during delay period, as also observed in early visual cortex. However, in contrast to the early visual cortex, the remembered grating orientation could also be decoded from the contralateral IPS after an eye movement (Figure 3b, right green bar; $t_{(23)} = 3.33$, $p = 0.0029$, Cohen's $d = 0.68$), while there was no reliable orientation information in the ipsilateral IPS (Figure 3b, right purple bar; $t_{(23)} = 1.48$, $p = 0.1515$; $BF_{01} = 1.775$).

Discussion

In the current study, we investigated whether VWM representations are remapped following eye movements and whether VWM information persists in the early visual and parietal cortex after the execution of a saccade. We found robust encoding of maintained orientation information in the contralateral hemisphere of early visual cortex. However, this information degraded upon making a saccade to the opposite hemifield and did not remap to the ipsilateral hemisphere in early visual cortex. This suggests that there is no remapping of VWM representations across eye movements in the early visual cortex. Additionally, VWM representations in early visual cortex were impaired by the saccade during the retention period. In contrast, there was orientation information in the IPS contralateral to the remembered item, that remained reliably present also after execution of a saccade. These findings show that early visual cortex is susceptible to interference of eye movements during a working memory period, while IPS appears less sensitive to this interference.

Retinotopically specific encoding of VWM information in early visual cortex

In contrast to previous studies that have shown that VWM in early visual cortex is represented in a spatially global mode (Ester et al., 2009), our study indicates that

552 the orientation information can be restricted to the contralateral hemisphere when
553 the orientation and location of the stimulus need to be jointly maintained, in line with
554 several recent studies (Pratte and Tong, 2014; Lorenc et al., 2018). In Ester et al.
555 (2009), although the remembered grating was always presented in one of the
556 hemifields, participants could use a strategy in which they memorized the orientation
557 of the grating perifoveally instead of at its original location (Williams et al., 2008).
558 This strategy would lead to a bilateral VWM representation irrespective of where the
559 grating is presented. In order to encourage our participants to represent the grating
560 in its original location, we inserted catch trials, in which the probe grating and the
561 remembered gratings were horizontally offset one visual degree. Participants were
562 instructed to respond only when the probe location matched the location of the
563 initially presented grating. Therefore, they had to maintain the orientation of the
564 gratings at the presented location in order to be able to successfully complete the
565 task. Our results revealed that VWM representation during our task were indeed
566 retinotopically specific (see Figure 2a), in line with previous findings (Pratte and
567 Tong, 2014).
568
569 **No remapping of VWM following eye movements.**
570 Attentional or feature based remapping of visual input just prior to a saccade has
571 been well established from a variety of studies and is thought to maintain visual
572 stability across eye movements. For instance, Rolfs et al. (2011) found that attention
573 could be predictively remapped to the future retinotopic location of an upcoming
574 target, even before the execution of the eye movement. In the current experiment,
575 we asked whether memory traces would also be updated with eye movements.
576 However, we found no evidence that visual working memory representations were

remapped following eye movements. At least two reasons should be emphasized to address the discrepancy in remapping between the attention and VWM. First, to survive in a multifaceted and dynamically changing world, our attention needs to be selectively shifted to the most important stimuli that are goal-relevant. In order to be competent for such a complicated task, remapping of attention could be one of the most crucial mechanism to prepare information in advance. In contrast, the main function of working memory is to temporarily retain information available for processing. While attention could be flexibly remapped to different locations to extract information, storing working memory information in one or several stationary regions could be potentially an efficient way for retrieval. Second, in line with the arguments of 'activity-silent' models of WM when compared to the persistent activity models of WM (Stokes, 2015; Wolff et al., 2017), remapping of VWM after each eye movement could also be energetically expensive, especially if VWM is maintaining an up-to-date information of the external environment. Therefore, a stationary working memory representation could be an ideal way for ecologically maintaining and manipulating information in the brain.

Parietal cortex may subserve VWM representations after saccades.

In recent years, the parietal cortex has been repeatedly implicated in VWM maintenance (Todd and Marois, 2004; Christophel et al., 2015; Ester et al., 2015; Bettencourt and Xu, 2016), alongside the involvement of sensory areas (Harrison and Tong, 2009; Serences et al., 2009; Emrich et al., 2013). Our results indicate that the early visual cortex is susceptible to the interference of eye movements during the delay period, potentially limiting the role of the early visual cortex in VWM. Similarly, Bettencourt and Xu (2016) observed that VWM representations in early visual cortex

were degraded by the presentation of distractors, while superior IPS exhibited persistent activity that was not impaired by the presentation of intervening distractor stimuli. In our experiment, the eye movements during the delay period potentially may also generate distracting new input to the visual system, which could disturb the VWM representations. Intriguingly, while VWM representations in early visual cortex were degraded following the eye movement, these representations were still maintained in IPS. Behaviorally, participants' memory performance was indistinguishable between the saccade and no saccade trials. Therefore, it could be that the preserved behavioral performance we observed is supported by these IPS representations, rather than the early visual cortex representations. In a more recent study, Lorenc et al. (2018) found that the VWM information could be reliably maintained only in early visual cortex without distractors. However, these early visual cortex representations seem to transfer to the IPS representations when distractors were presented, which suggesting a flexible coding of VWM between the early visual cortex and the IPS depending on the task demands. This shows that VWM information maintained in visual cortex is susceptible to interference, in line with the idea that the early visual cortex may only play a limited role in VWM storage.

In conclusion, our results indicate that VWM representations in early visual cortex are degraded and not remapped after eye movements, limiting the role of early visual cortex in VWM storage.

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