



No evidence for mnemonic modulation of interocularly suppressed visual input

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ABSTRACT

Visual working memory (VWM) allows for keeping visual information available for upcoming goal-directed behavior, while new visual input is processed concurrently. Interactions between the mnemonic and perceptual systems cause VWM to affect the processing of visual input in a content-specific manner: visual input that is initially suppressed from consciousness is detected faster when it matches rather than mismatches the content of VWM. It is currently under debate whether such mnemonic influences on perception occur prior to or after conscious access. To address this issue, we investigated whether VWM content modulates the neural response to visual input that remains suppressed from consciousness. We measured fMRI responses to interocularly suppressed stimuli in 20 human participants performing a delayed match-to-sample task: Participants were retro-cued to memorize one of two geometrical shapes for subsequent recognition. During retention, an interocularly suppressed peripheral stimulus (the probe) was briefly presented, which was either of the cued (memorized) or uncued (not memorized) shape category. We found no evidence that VWM content modulated the neural response to the probe. Substantial evidence for the absence of this modulation was found despite leveraging a highly liberal analysis approach: (1) selecting regions of interest that were particularly prone to detecting said modulation, and (2) using directional Bayesian tests favoring the presence of the hypothesized modulation. We did observe faster detection of memory-matching compared to memory-mismatching probes in a behavioral control experiment, thus validating the stimulus set. We conclude that VWM impacts the processing of visual input only once suppression is mostly alleviated.

1. Introduction

The visual input to our retinae changes on a moment-to-moment basis. Consequently, we often need to keep visual representations available after the visual input has changed. Visual working memory (VWM) allows for maintaining visual representations available for subsequent, goal-directed behavior. During VWM maintenance, the visual system generally continues to receive visual input. These mnemonic and perceptual processes co-exist (Rademaker et al., 2019), and interact with one-another: visual input can interfere with representations in VWM (Rademaker et al., 2015; Bettencourt and Xu, 2016; Fang et al., 2020; Li, Liang, Lee, Barense, pre-print), and VWM content enhances the neural response to memory-matching relative to memory-mismatching visual input (Kumar et al., 2009; Gayet et al., 2017). Accordingly, observers have increased perceptual sensitivity to memory-matching stimuli (Soto

et al., 2010; Teng and Kravitz, 2019), and memory-matching stimuli attract attention and eye-movements to a greater extent than memory-mismatching stimuli (Soto et al., 2005; Olivers et al., 2006; for a review, see Soto et al., 2008). Far from being an experimental triviality, VWM-based modulations of visual input are believed to underlie goal-directed visual search, by allowing observers to strategically favor visual input that resembles a search-target at the expense of non-relevant visual input (e.g., Duncan and Humphreys, 1989; Wolfe, 1994; Desimone and Duncan, 1995; Kastner and Ungerleider, 2001; Wolfe and Horowitz, 2004; Eimer, 2014). As such, understanding at what stage of visual processing VWM content impacts perception (i.e., before or after conscious access) is vital to our understanding of goal-directed visual search. In this study we investigated whether VWM could impact the processing of non-conscious visual input.

One behavioral finding that is of particular relevance to the present

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question, is that VWM affects the point in time at which initially suppressed visual stimuli can be reported: memory-matching visual stimuli gain conscious access faster than memory-mismatching visual stimuli (e.g., Gayet et al., 2013; Pan et al., 2014), due to an a priori bias toward memory-matching stimuli (Gayet et al., 2016). Moreover, stimuli that remain subjectively invisible, are correctly localized more often (in a two-alternatives forced-choice task) when they match rather than mismatch the content of VWM (Pan et al., 2012). These findings imply that VWM content impacts the processing of visual input *prior* to conscious access.

An alternative view is that VWM content only starts affecting the processing of visual input when suppression is mostly alleviated (i.e., peri-threshold). In line with this view, feature-based attention (which relies on VWM; De Fockert et al., 2001; Günseli et al., 2014) was shown only to affect conscious access around the time of perceptual transitions between the suppressed and the non-suppressed image in binocular rivalry (Dieter et al., 2015). Generally, the extraction of information from (initially) suppressed visual input improves when certain visual attributes (but not others) can be reported upon (e.g., Gelbard-Sagiv et al., 2016). As such, it remains unknown whether the content of VWM modulates the neural response to visual input that is not accessible to consciousness. Here, we directly addressed this question by measuring fMRI responses to perceptually suppressed stimuli that either matched or mismatched the content of VWM. Perceptual suppression was achieved by means of continuous flash suppression (CFS; Tsuchiya and Koch, 2005), in which a low-contrast stimulus presented to one eye is rendered invisible by presenting a high-contrast dynamic pattern to the other eye (i.e., interocular suppression).

In this study, participants were retro-cued to memorize one of two shapes (hereafter: *memory items*) drawn from different shape categories for subsequent recognition. During the retention interval, a different shape (the interocularly suppressed *probe*) was briefly presented at an unpredictable moment and location. The probe could either match the shape category of the cued (i.e., memorized) item, or of the uncued (i.e., discarded) item, and was task-irrelevant to the participants. This procedure allowed for manipulating the contingency between the content of VWM and the probe, while keeping all visual stimulation constant across trials. This experimental design was largely based on that of Gayet et al. (2017), who observed an enhanced neural response to consciously accessible shape stimuli (probes) when they matched rather than mismatched a shape that was concurrently maintained in VWM.

2. Materials & methods

2.1. Participants

The group of participants included in this experiment consisted of 20 students (4 males, 25 years of age, $SD = 4$) that were gathered from either the Humboldt University of Berlin or the Charité medical school of Berlin, participating for monetary reward. All participants confirmed having (corrected to) normal vision, and signed informed consent for this study, which was approved by the local ethics committee.

One participant was removed after a binomial test revealed that the participant was significantly above chance in reporting the location of suppressed stimuli that were subjectively reported as invisible, thus precluding us from asserting invisibility of the suppressed probes (see section on inclusion criteria). A second participant was removed because the participant subjectively reported seeing nearly all stimuli presented to the left visual field, but nearly none of the stimuli presented to the right visual field (~50% subjective visibility reported; near-perfect objective performance on those trials) resulting in a small and unbalanced dataset for this participant.

2.2. Set-up and stimuli

Participants wore prism glasses, to horizontally separate visual input

to the left and right eye. Each eye viewed a different image on the projection screen, and the images presented to both eyes were separated by a custom-made divider, positioned between the eyes of the participants, reaching from the prism glasses to the projection screen. In order to facilitate binocular fusion of the two complementary images presented to each eye, the two presentation areas were enclosed by a circular Brownian ($1/f^2$) noise frame, adjoined by two vertical white lines.

The shape stimuli (displayed in Fig. 1C) consisted of filled rectangles, isosceles triangles, and ellipses of equal surface (and therefore of equal overall luminance). Within each of these three shape categories, nine shape variants were created by varying the height-to-width (h/w) ratio following a sigmoid function. The ranges of h/w ratios within each shape category were manually adjusted to obtain comparable performance on the memory recognition task in all three shape categories in an earlier pilot study. All shapes were presented in light gray (7% Weber contrast) on a dark gray background (30 Cd/m^2), and had a surface area of 0.81° of visual angle (squared).

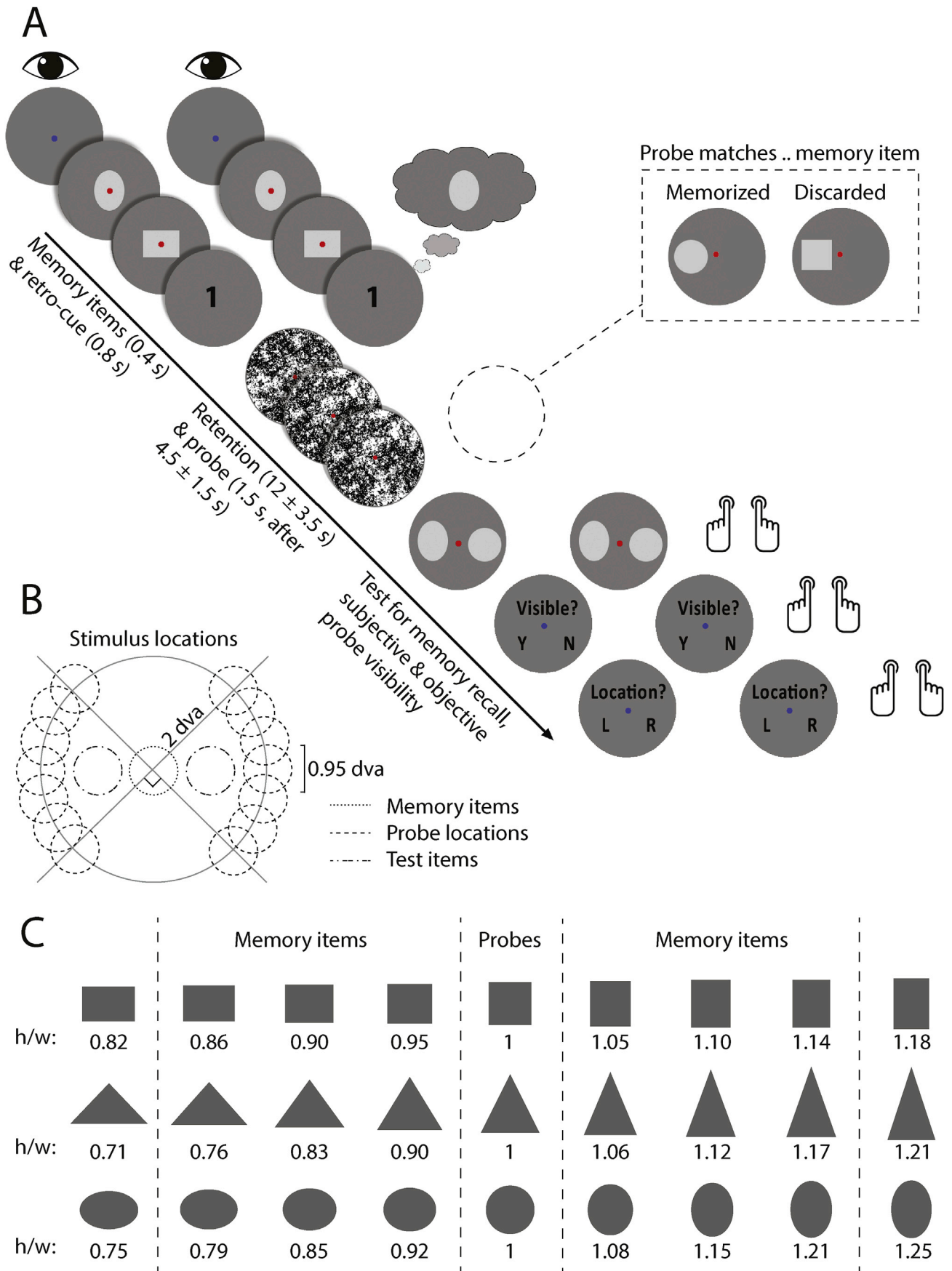
A subset of these shape stimuli was presented during the retention interval: the probes. These rectangles, isosceles triangles, and ellipses had a h/w ratio of 1 (and a height of 0.95° of visual angle), and were presented at a fixed eccentricity of 2° of visual angle on one of seven equally interspaced locations on the left and right arcs of an imaginary circle, delimited by its main diagonals (i.e., at $45, 75, 90, 105, 120, \text{ and } 135^\circ$; Fig. 1B). Six other shape variations of each shape category were used for the memory task and, unlike the peripheral probes, were always presented at fixation. As such, the cued (i.e., memorized) and uncued (i.e., discarded) memory items were never identical to the probe stimulus, and always presented at different retinal locations than the probe stimulus. Finally, the test items presented during the recognition task were presented left and right of fixation at an eccentricity of 1° of visual angle. These test items consisted of the cued (memorized) memory item, and another item drawn from the same shape category, but with a slightly different height-to-width ratio (i.e., either one step left or one step right; Fig. 1C).

The current stimulus set was nearly identical to that of Gayet et al. (2017), but slightly downscaled to fit the smaller presentation area allowed for by dichoptic presentation. Consequently, the surface area of all shape stimuli, and the eccentricity at which the probe stimuli were presented were smaller compared to this earlier study (0.81 instead of 1.00° of visual angle (squared), and 2 instead of 3° of visual angle respectively).

CFS (to perceptually suppress the probes) was achieved by presenting noise masks to one eye (replaced at 10 Hz), while presenting the probe to the other eye (Tsuchiya and Koch, 2005). These noise masks were created by (a) filtering pink ($1/f$) noise using a rotationally symmetric Gaussian low-pass filter ($\sigma = 1.5$) and by (b) making the resulting gray-scale image binary with maximum contrast (as in Gayet et al., 2013). In order to strengthen suppression, CFS onset started 100 ms (one mask) prior to probe onset, and in order to minimize after-images of the probe CFS ended 100 ms (one mask) after probe offset.

2.3. Procedure

Participants took part in 144 experimental trials during the functional scans (divided into 8 runs), and 6 minutes of practice trials during the preceding structural scan. On each trial (see Fig. 1A), participants were subsequently presented with two memory items, drawn from two different shape categories, for 400 ms each. This was followed by a 400 ms interval after which a retro-cue was presented for 800 ms. This retro-cue, the number “1” or “2”, instructed participants to memorize either the first or the second memory item for later recall. After a delay ranging between 3 and 6 s ($M = 4.5$), the probe was presented for 1.5 s. After another delay varying between 5.5 and 9.5 s ($M = 7.5$) two test-stimuli appeared at fixation for 1.5 s, one of which was identical to the cued (i.e., memorized) memory item, and one of which had a slightly different height-to-width ratio (one step in either



(caption on next page)

Fig. 1. Methods of the main experiment. Panel A depicts a schematic depiction of a trial, as presented to the left and right eye. On each trial, participants were presented with two memory items (geometric shapes, retrieved from 2 out of 3 different shape categories), and a retro-cue indicating which of the two items should be memorized for subsequent recognition. During retention, a different shape (the probe) was presented to one eye, and suppressed by a dynamic mask presented to the other eye (continuous flash suppression, or CFS; Tsuchiya and Koch, 2005). The probe either matched the shape category of the cued (i.e., memorized) memory item, or the uncued (i.e., discarded) memory item. After the memory recognition task, participants were asked whether they had seen the probe (subjective assessment), and they were asked to provide a forced-choice answer as to the location of the probe (objective assessment). Panel B depicts stimulus size and positioning: the memory items were presented at fixation, the two test stimuli (for the recognition task) were presented left and right of fixation, and the probes could be presented on one of 14 locations (7 left and 7 right of fixation). Panel C depicts the shapes of all stimuli used in this experiment, and their height-to-width (h/w) ratios (all retrieved from Gayet et al., 2017): the probes were squares, circles and isosceles triangles (h/w = 1), the memory items were either horizontally or vertically elongated versions of the probes (i.e., rectangles, ellipses, and isosceles triangles), and two additional shapes (with more extreme h/w ratios) were added as distractors in the memory recognition task.

direction; see Fig. 1C). Participants were instructed to report which of these two test-stimuli was identical to the cued memory item, by means of a left-hand or right-hand button press. After the participant gave a response, or after 2 s had passed, the fixation dot turned red, and two final questions appeared: the participants had 1.5 s to report whether (yes or no) they had perceived any part of the probe, and another 1.5 s to report (or guess) whether the probe had appeared left or right of fixation. After an inter trial interval that lasted between 1.5 and 4.5 s ($M = 3$) the fixation dot turned blue again, to indicate that the next trial would begin after 1 s.

2.4. Experimental design

The experimental design comprised the within-subject factor Congruence (probes matched the memorized or discarded memory item) as a main factor of interest. The within-subject factor Shape (the shape of the probe was a square, triangle or circle) was a factor of interest for multivariate analyses in which shape-category was classified, and a factor of non-interest for all other analyses. Within-subject factors of no interest included the hemifield to which the probe was presented (left or right of fixation), the retro-cue (instruction to memorize first or second shape), the correct answer in the memory task (left or right of test-stimulus is correct), and the eye to which the probe was presented (left or right). Factors that were randomly distributed over the entire experiment (maximally equating prevalence), but that were not counterbalanced with the other factors, included the height-to-width (h/w) ratio of the cued and uncued shape stimuli (one of 6 variations within each shape category), the h/w ratio of the incorrect answer in the memory recall task (higher or lower h/w ratio than the cued memory item, see Fig. 1C), and the exact angular position of the probe (one of seven positions within each hemifield, see Fig. 1B).

2.5. Functional localizer

We conducted a separate functional localizer run after the experimental runs. The aim of the functional localizer run was to locate the voxels that are responsive to the presentation of our stimuli, relative to baseline (i.e., fixation), as was done in Gayet et al. (2017). The functional localizer comprised mini-blocks of intact shapes, shape outlines, scrambled shape outlines and a baseline condition. Each of these four mini-blocks lasted 12.6 s, and were separated by inter-block-intervals that varied between 1 and 3 s ($M = 2$). The sequence of four mini-blocks was repeated nine times in random order, with the only restriction that two subsequent mini-blocks were of different conditions. Within a single mini-block, shapes from each of the three shape categories were presented three times to the left hemifield and three times to the right hemifield. The exact locations and exact shape variations were drawn at random from a pool that allowed to maximally equate the prevalence of each. Participants were instructed to maintain fixation during the entire run and to press a button whenever they observed a shape of deviating brightness (about -20% luminance contrast). This would occur at an unpredictable moment, three times per mini-block.

2.6. fMRI data acquisition and preprocessing

Functional MRI data were acquired on a 3 Tesla SiemensTrio scanner (Siemens, Erlangen, Germany) equipped with a 12-channel head-coil, using a T2-weighted gradient-echo EPI sequence. The fMRI session comprised 6 experimental runs, in which 322 whole-brain volumes were acquired, and a functional localizer run, in which 271 whole-brain volumes were acquired. The fMRI runs (2000 ms repetition time, 25 ms echo time, 78° flip angle, voxel size 3 mm isotropic, 33 slices acquired in descending order, 0.75 mm inter-slice gap) were preceded by a high-resolution T1-weighted MPRAGE structural scan (192 sagittal slices, 1900 ms repetition time, 2.52 ms echo time, 9° flip angle, 256 mm field of view).

Preprocessing was performed using SPM12 (www.fil.ion.ucl.ac.uk/spm) and included slice-time correction, spatial realignment and co-registration with the structural image. For most analyses, the images were smoothed with a 4 mm Gaussian kernel, and kept in native subject space. For univariate group-level whole-brain analyses, the images were smoothed with an 8 mm Gaussian Kernel, and normalized to the standard Montreal Neurological Institute (MNI) template.

2.7. Regions of interest

In this study, we created two types of regions of interest (ROIs). The first type of ROI was developed to maximize the likelihood of observing the hypothesized effect (i.e., a stronger neural response to probes that match the memorized memory item, compared to probes that matched the discarded memory item), thereby maximizing the evidential strength of a null finding. For this purpose, we retrieved those clusters of voxels from Gayet et al. (2017) that responded more strongly to probes matching the cued (i.e., memorized) memory item than to probes matching the non-cued (i.e., discarded) memory item ($p_{\text{CFWE}} < 0.05$, for cluster-defining voxel threshold $p_{\text{uncorrected}} < 0.001$), at the group level in MNI space. Because stimulus presentation was kept as similar as possible to that of Gayet et al. (2017), voxels within these ROIs (depicted in Fig. 2) are objectively the most likely to elicit a stronger BOLD response to probes that match the content of VWM. These ROIs were reverse-normalized to native subject space.

The second type of ROI was a priori motivated by our research question: is the neural response to interocularly suppressed visual input enhanced when it matches the content of VWM? Following the procedure of Gayet et al. (2017), we constrained our analyses to occipital and parietal voxels that were significantly responsive to our stimuli in the [probe > baseline] contrast of the functional localizer run ($p_{\text{FWE}} < 0.05$). This was achieved by intersecting responsive voxels ($N = 2069$) with anatomical masks derived from the AAL Atlas (Tzourio-Mazoyer et al., 2002). For conducting multivariate analyses, these ROIs were reverse-normalized to native subject space.

2.8. Univariate fMRI data analyses

To assess the influence of the content of VWM on the neural response to interocularly suppressed probes, we estimated a first-level GLM, on the 8 mm smoothed data normalized to MNI space. This GLM included two

regressors tied to the onset of the probe, depending on the different levels of the factor Congruence (memorized, discarded), as well as regressors of no interest tied to the onsets of both memory items, the retro-cue, and the two test items (regardless of the different factor levels). These regressors were modeled as stick functions (i.e., duration set to zero) and were convolved with the canonical hemodynamic response function provided in SPM12. Additionally, six regressors for head motion—from the spatial realignment procedure—were included in the GLM. The whole-brain maps of parameter estimates from the GLM were used to compute contrast images for the response to the probe in the memorized and in the discarded conditions against baseline. Following the approach of Gayet et al. (2017), we performed a whole-brain analysis to investigate which brain regions were modulated by the match between the probe and the content of VWM. For this purpose, we conducted a *t*-test contrasting the two Congruence conditions (memorized, and discarded) at the group-level. Significance was determined at the cluster level (family-wise corrected; i.e., $p_{\text{cFWE}} < 0.05$, for cluster-defining voxel threshold $p_{\text{uncorrected}} < 0.001$).

A second univariate approach was aimed at maximizing the chance of observing a VWM-based modulation of the neural response to the probe. For this purpose, we used the same two contrasts described above (i.e., [memorized probe > baseline] and [discarded probe > baseline]), and extracted the average contrast estimates from those clusters of voxels that showed a significantly stronger response to probes in the memorized condition than in the discarded condition in the group-level data of Gayet et al. (2017) (i.e., the first ROI type described above). We then conducted directional paired Bayesian *t*-tests at the group level, to assess evidence for the null hypothesis (no difference in neural response to probes in the memorized and discarded conditions), and the alternative hypothesis (a stronger neural response to probes in the memorized than in the discarded condition). Following convention, we considered Bayes factors of at least 3 for either the null or the alternative hypothesis as reliable evidence for said hypotheses (Lee and Wagenmakers, 2013; Dienes, 2014; Jeffreys, 1961).

2.9. Multivariate fMRI data analysis

Multivariate analyses were conducted for two main reasons. First, they can be more sensitive to uncovering differences between conditions than univariate measures. Second, they offer a means to investigate content (i.e., shape) specific activity patterns in the BOLD response.

The first application of multivariate analyses (increased sensitivity), was aimed at testing for differences in BOLD response between VWM-matching and VWM-mismatching probes that were not picked-up by the univariate analyses. To this end, we estimated a GLM for each subject with the same regressors as in the univariate analyses, but on non-normalized data which were smoothed at only 4 mm to better retain pattern information. To maximize the chance of observing a differential pattern of neural activity between probes that matched compared to probes that mismatched the shape maintained in VWM, we conducted those multivariate analyses in those exact clusters of voxels showing a difference between VWM-matching and VWM-mismatching probes in the whole-brain univariate analysis of Gayet et al. (2017) (i.e., the first ROI type described above).

To investigate shape-specific activity patterns (the second application of our multivariate analyses), we followed the approach of Gayet et al. (2017): we estimated a GLM for each subject, on the 4 mm smoothed and non-normalized data. The GLM included shape specific (i.e., rectangle, ellipse, or triangle shape categories) regressors for the two memory items, for the probe (i.e., rectangle, ellipse or triangle, in either the memorized or discarded condition), and for the two test-stimuli. The estimated beta images from the GLM were used for support vector machine (SVM) classification. SVM classification was performed with The Decoding Toolbox (Hebart et al., 2015), using a linear SVM (libsvm). Classification was performed following a leave-one-run-out cross-validation procedure. On each iteration, the classifier was trained on the

beta maps of five runs and tested on the beta maps of the remaining sixth run. Classification was done separately for the three pairs of shape categories (rectangle versus triangle, rectangle versus ellipse, and triangle versus ellipse) in each of the two Congruency conditions (i.e., memorized and discarded). Classifier performance was then analyzed at the group level, averaged across shape-pairs. We conducted one-sided one-sample *t*-tests to test whether classifier performance was higher than the 50% chance level (we opted for a directional test to keep the approach identical to that of Gayet et al. (2017), and following the reasoning that negative within run-type decoding is theoretically uninterpretable). In order to determine whether the content of VWM affected the neural response to the interocularly suppressed probes, we conducted a paired-samples *t*-test between classification accuracies in the memorized condition and in the discarded condition. These multivariate analyses were conducted in ROIs composed of the occipital and parietal clusters of voxels from the [stimulus > baseline] contrast of the functional localizer (akin to the approach of Gayet et al., 2017; i.e., the second ROI type described above).

2.10. Trial inclusion (fMRI experiment)

In order to ensure invisibility of the probe stimuli, we analyzed only trials in which participants reported subjective invisibility of the probes ($M = 85\%$, $SD = 12$). On these trials, participants were unable to report the hemifield to which the stimulus was presented with above chance level performance ($M = 49\%$ correct, $SD = 5$), $t(19) = -0.862$, $p = 0.340$, $BF_{0+} = 7.31$. This allowed us to guarantee that, for these participants, probes that were reported as invisible were indeed successfully suppressed. Conversely, when participants reported subjective visibility of the probe, they were 69% accurate ($SD = 31$) in reporting the hemifield to which it was presented, which is better than chance, $t(19) = 9.948$, $p = 0.014$. It is worth noting that this statistic included five participant averages based on 4 or fewer responses and, across all subjects, a correct left/right localization response was provided for 80% of the probes that were reported to be subjectively visible. Finally, failed suppression occurred equally often for probes matching the category of the cued ($M = 48\%$, $SD = 14$) and the uncued memory item, $p > 0.5$, $BF_{01} = 3.36$. As such, trial exclusion did not differently affect the two conditions of interest.

2.11. Behavioral control experiment

The behavioral control experiment was aimed at testing the suitability of the stimulus set used in the main (fMRI) experiment, by testing whether interocularly suppressed shape stimuli would be detected faster when they matched compared to when they mismatched a shape that is concurrently maintained in memory for subsequent recognition. Participants ($N = 20$, 8 males, 24 years of age, $SD = 5$) were recruited from the same participant pool as the main experiment. The experiment, which lasted about an hour, was approved by the local ethics committee and participants signed informed consent before participating.

The general experimental procedure (Fig. 3A) was similar to that of Gayet et al. (2013), and stimulus presentation was kept as similar as possible to that of the main experiment. On each trial, participants were retro-cued to memorize one of two presented memory items drawn from different shape categories. During the retention period a probe was initially suppressed by CFS, and participants were instructed to report the location (left/right of fixation) of the probe as fast as possible (i.e., once suppression was sufficiently alleviated). This method is referred to as *breaking* continuous flash suppression (b-CFS; Jiang et al., 2007; Stein et al., 2011; Gayet et al., 2014). After participants provided a response (or 5 s had elapsed), two shapes from the same category were presented, and participants had to indicate which of the two they had memorized at the start of the trial. The probe matched either the category of the memorized memory item, the discarded memory item, or neither (the unused shape category). We predicted that, if VWM

content enhances the response to memory-matching visual input, shape stimuli should be detected faster when they matched (memorized condition) compared to when they mismatched the content of VWM (discarded, and unused conditions).

3. Results

3.1. Behavioral performance on the memory recognition task

Participants were 60% ($SD = 6$) accurate in reporting which of two shape variations was identical to the cued (i.e., memorized) memory item. Performance in the recall task did not depend on whether participants were cued to memorize the first ($M = 60\%$, $SD = 6$) or the second ($M = 60\%$, $SD = 8$) memory item ($p > 0.8$), $BF_{01} = 4.23$, as shown by a paired-samples t -test. Also, repeated measures ANOVA's showed that participants' performance on the recall task did not significantly differ between experimental runs ($p > 0.6$, $BF_{01} = 3.67$), nor did it differ between the different shape categories ($p > 0.9$, $BF_{01} = 6.95$).

3.2. No evidence for mnemonic modulation of the neural response to the probes

To assess the influence of VWM on neural responses to interocularly suppressed probes, we first conducted a mass univariate analysis, to find clusters of voxels in which the factor Congruence explained significant portions of variance in the BOLD response of our current dataset. A whole-brain t -test at the group-level contrasting probes that matched the memorized memory item with probes that matched the discarded memory item, revealed no effect of Congruence (significance threshold: $p_{\text{cFWE}} < 0.05$, for a cluster-defining voxel threshold $p_{\text{uncorrected}} < 0.001$). This stands in stark contrast with the findings of Gayet et al. (2017; with visible probes) in which 5 highly reliable clusters were observed. This finding suggests that the content of VWM does not affect the neural response to visual input that is fully suppressed from awareness by CFS.

Next, we aimed to ensure that the absence of a differential response to probes matching the memorized and probes matching the discarded shape was not due to experimental insensitivity but rather reflected a genuine null effect. To this end, we tested whether the average response

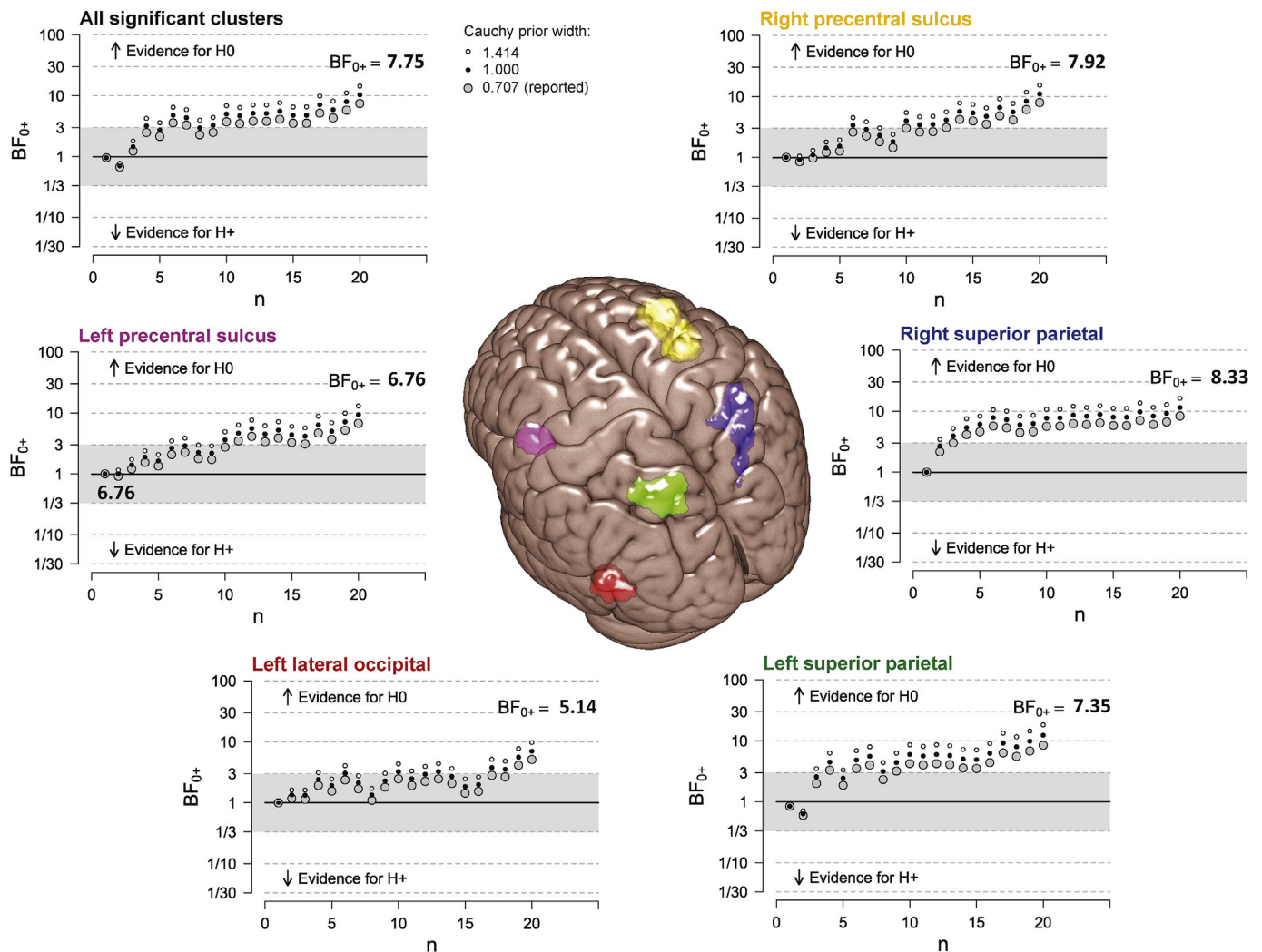


Fig. 2. Evolution of the Bayes factor (over participants) for directional Bayesian t -tests, testing for a stronger BOLD response to memory-matching probes than memory-mismatching probes at the group-level, in each of the five regions of interest (ROIs), shown at the center of the image. These ROIs are clusters of voxels retrieved from Gayet et al. (2017) that showed a significantly stronger BOLD response to memory-matching than memory-mismatching probes, at the group level (using the exact same stimulus set). Consequently, these ROIs constitute the most likely candidate brain regions to exhibit an enhanced BOLD response to memory-matching probes. Here, we observed substantial evidence for the null hypothesis: in neither of the regions of interest did memory-matching probes elicit a stronger BOLD response than memory mismatching probes. Bayes factors that reach beyond the shaded areas in the plots reflect substantial evidence for either one or the other hypothesis (Lee and Wagenmakers, 2013; Dienes, 2014; Jeffreys, 1961). These plots are adapted from JASP 0.9.2 output (JASP Team, 2018).

to probes in the memorized condition was stronger than the average response to probes in the discarded condition, within those voxels that showed this exact modulation for visible probes in Gayet et al. (2017). A directional Bayesian paired-samples *t*-test revealed that the data were 7.75 times more likely to reflect the null hypothesis (i.e., the observed data is drawn from a distribution with a mean of 0), than the alternative

hypothesis (i.e., the observed data is drawn from a distribution with a mean that is larger than 0), thus demonstrating a genuine null effect. Next, we separated this ROI into five separate ROIs, corresponding to the five significant clusters of voxels that were found in the [memorized > discarded] contrast of Gayet et al. (2017; depicted in Fig. 2): a left lateral occipital cluster, left and right superior parietal clusters, and left and

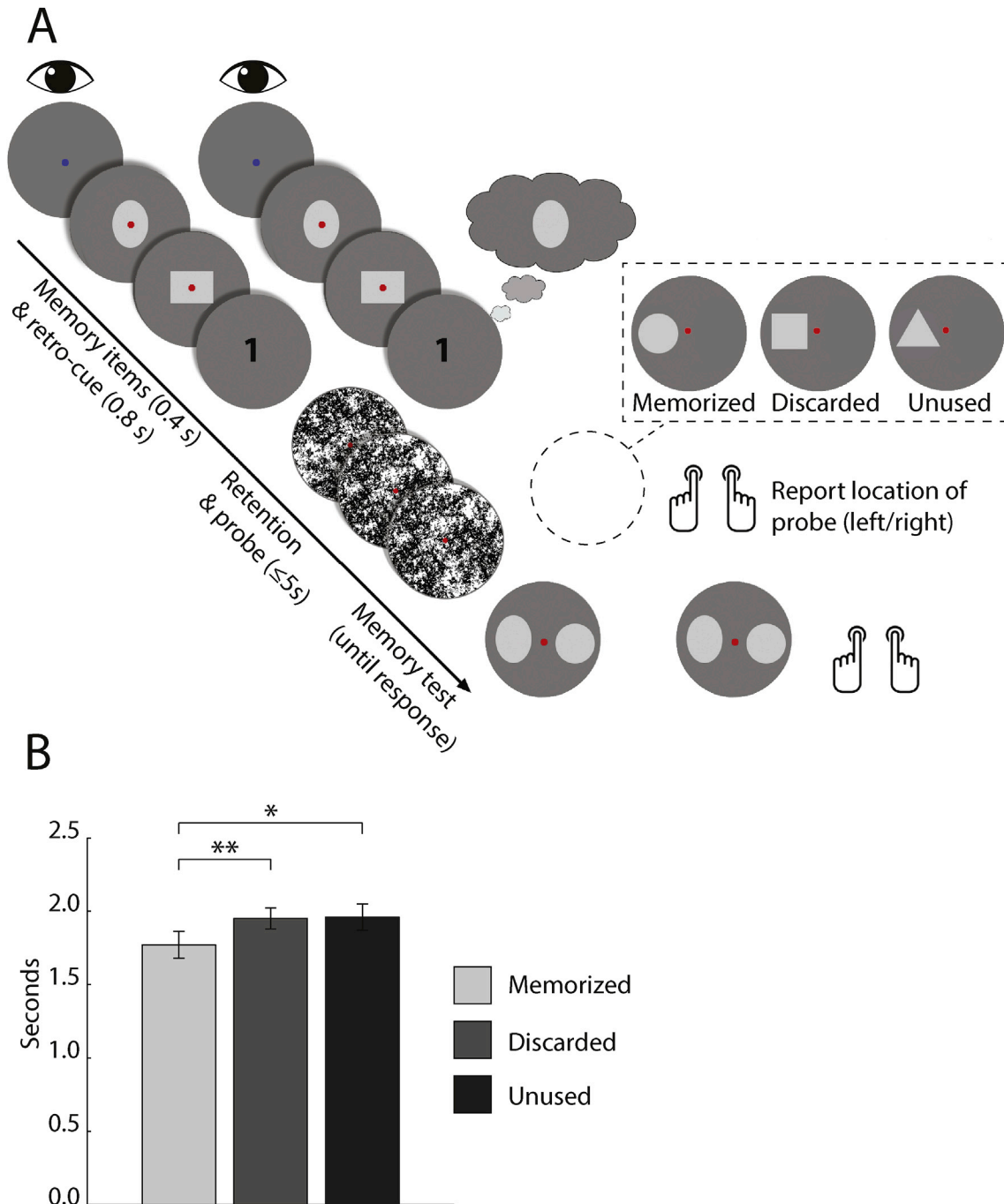


Fig. 3. Behavioral experiment (N = 20). Panel A depicts the outline of a typical trial in the behavioral experiment. Similar to the fMRI experiment, participants were retro-cued to memorize one of two presented memory items drawn from different shape categories, and during the retention period a probe was presented under continuous flash suppression (CFS). The main difference with the fMRI experiment, is that here the time is measured until participants can report the location (left/right of fixation) of the initially suppressed probe. Also (as in Gayet et al., 2017) the probe can now match the category of the memorized memory item, the discarded memory item, or neither (the unused shape category). It was hypothesized that probes elicit an enhanced response when they match the content of visual working memory (VWM), and are therefore released from suppression (i.e., detected) faster than probes than mismatch the content of VWM. Panel B depicts the results of the behavioral experiment. Following our predictions, memory-matching probes (memorized condition) were detected faster than memory-mismatching probes (discarded and unused conditions). As such, it also holds for our present stimulus set that visual input is released from CFS suppression faster when it matches the content of VWM. Error bars reflect the 95% confidence intervals of the condition averages (computed following the method of Morrey, 2008). **p* < 0.05, ***p* < 0.01.

right precentral clusters. For all ROIs, the data were between 5.14 times and 8.33 times more likely to support the null hypothesis than the alternative hypothesis (Table 1). Finally, for the ROI based on the functional localizer of the current experiment (the second ROI type described above), the data was also 7.88 times more likely to reflect the null hypothesis than the alternative hypothesis.

Because multivariate approaches can be more sensitive in uncovering differences in BOLD response between conditions, we next assessed whether a linear classifier could distinguish between probes in the memorized condition and probes in the discarded condition within these same ROIs. We found that the classifier was unable to distinguish between the pattern of activity elicited by memory-matching and memory-mismatching trials in the ROI retrieved from Gayet et al. (2017): classification accuracy was 47.9% ($SD = 13.2$), and a Bayesian t -test confirmed that this result was 6.74 times more likely to reflect a null effect than to reflect above chance classification. Similarly, classification in all individual clusters constituting this ROI was more likely to reflect a null effect than above chance classification (although in some cases inconclusively), with Bayes factors ranging between 1.96 and 9.96. Together, these findings provide compelling evidence that BOLD responses to the interocularly suppressed probes were not enhanced when they matched compared to when they mismatched the content of VWM.

3.3. No evidence for mnemonic modulation of shape-specific information

Although suppressed visual input did not elicit a stronger BOLD response when it matched compared to when it mismatched the concurrent content of VWM, it is nonetheless possible that these two conditions elicited distinguishable patterns of neural activity: that is, the BOLD response might comprise more shape-specific information on VWM-matching than on VWM-mismatching trials, as is the case for

Table 1

Results of directional Bayesian t -tests for distinguishing between memory-matching probes and memory-mismatching probes, in all ROIs derived from Gayet et al. (2017).

Region of interest ^a		Univariate contrast (a.u.)		Multivariate classification (%)	
Location	k voxels (SD)	Mean (SD)	BF ₀₊	Mean (SD)	BF ₀₊
All significant clusters	512 (40)	-0.84 (3.81)	7.75	-2.08 (13.21)	6.74
Left lateral occipital	72 (6)	-0.27 (4.77)	5.14	1.67 (11.67)	2.47
Left superior parietal	93 (9)	-0.95 (4.88)	7.35	-2.08 (17.07)	6.17
Right superior parietal	125 (12)	-1.03 (4.03)	8.33	-5.00 (13.89)	9.96
Left precentral sulcus	62 (6)	-0.68 (4.29)	6.76	-1.25 (19.17)	5.28
Right precentral sulcus	160 (13)	-0.97 (4.21)	7.92	2.92 (15.60)	1.96

Note. Univariate results reflect a paired comparison between the average parameter estimates (in arbitrary units) from the contrasts between probes in the memorized and discarded conditions against baseline; multivariate results reflect classifier performance (in percentage) for dissociating between probes in these two conditions. Directional Bayesian t -tests test the hypothesis that the group average is drawn from a distribution with a mean that is greater than 0. In this case, a Bayes factor (BF_{0+}) above 1 reflects support for the null hypothesis, whereas a Bayes factor below 1 reflects support for the alternative hypothesis. Typically, a Bayes factor above 3 (or below 1/3) is regarded as reliable evidence for said hypothesis (Lee and Wagenmakers, 2013; Dienes, 2014; Jeffreys, 1961). Bayes factors were computed in JASP 0.9.2 (JASP Team, 2018), following the method of Wagenmakers (2007).

^a The regions of interests were based on clusters of voxels retrieved from Gayet et al. (2017) that showed a significantly stronger BOLD response to memory-matching than memory-mismatching probes, at the group level in MNI space.

unsuppressed probes (in Gayet et al., 2017). To investigate whether such a difference would also emerge for interocularly suppressed probes, we conducted multivariate analyses in the occipito-parietal compound ROI that was based on the functional localizer (i.e., the second ROI type), following the approach of Gayet et al. (2017). Bayesian t -tests against chance were performed, to assess whether the absence of a significant effect genuinely reflects a null effect. Unlike when probes were visible, in the present case the classifier was unable to dissociate between shape categories of the suppressed shape stimulus ($M = 48.7$, $SD = 8.5$), $t(19) = -0.698$, $p > 0.1$, $BF_{0+} = 6.72$. This was the case for both the memorized ($M = 47.9\%$, $SD = 12.4$), $t(19) = -0.771$, $p > 0.4$, $BF_{0+} = 6.97$, and the discarded condition ($M = 49.5\%$, $SD = 9.7$), $t(19) = -0.243$, $p > 0.8$, $BF_{0+} = 5.12$. Crucially, shape classification performance did not differ between the memorized and discarded conditions, $t(19) = -0.504$, $p > 0.6$, $BF_{0+} = 6.02$. Thus, using the same procedures as Gayet et al. (2017), we found no evidence for the presence of shape category information of interocularly suppressed probes, nor for a modulation of shape category information by the content of VWM, despite having 33% more participants and 50% more trials per participant.

3.4. Orthogonal assessment of data quality

In order to ensure that our current dataset, ROIs, and analysis procedure were suitable at all for shape category classification of our stimuli, we computed classifier performance for the shape categories of the test-stimuli that were presented at the end of the delay interval. These classification analyses were conducted in the main occipito-parietal ROI (i.e., the second ROI type), following the procedures of Gayet et al. (2017). Classification accuracy for these test-stimuli was 59.9% ($SD = 13.0$), which is better than chance, $t(19) = 3.46$, $p = 0.002$, and numerically better than the same analysis performed on the data of Gayet et al. (2017; $M = 56.4$, $SD = 6.6$). As such, the inability to decode the shape category of the suppressed stimulus in the current study (as compared to Gayet et al., 2017) is not caused by potential problems in the data or ROI definition. Rather it is caused by the CFS-based suppression of the probes.

3.5. Behavioral control experiment: testing the suitability of the stimulus set

We considered one final possibility that could explain why VWM content did not affect the neural response to interocularly suppressed probes in the current fMRI experiment: because different visual features rely on different VWM storage sites (Christophel et al., 2017), it is possible that the shape of a stimulus (unlike its color) is disrupted by interocular suppression before it can interact with shape-specific VWM content. Indeed, while VWM does enhance the neural response to shape-matching visual input that is consciously accessible (Gayet et al., 2017), it has not been tested before whether VWM accelerates detection of shape-matching stimuli that are interocularly suppressed (as is the case for color-matching stimuli; e.g., Gayet et al., 2013). As such, we next conducted a behavioral control experiment with the same stimulus set used in the fMRI experiment, to test whether interocularly suppressed shape stimuli (i.e., probes) are detected faster when they match, compared to when they mismatch the content of VWM.

On average, participants were 64% ($SD = 9$) accurate on the memory recognition task, which was better than chance, $t(19) = 32.55$, $p < 0.001$, and 99.1% accurate on the left/right detection task. This confirmed that participants complied with the task demands. The main findings are depicted in Fig. 3B. A repeated measures ANOVA showed that response times depended on the congruency between the probe and the content of VWM, $F(2, 38) = 5.969$, $p = 0.006$, $\eta^2 = 0.24$. Subsequent planned comparisons revealed that probes were detected faster in the memorized condition ($M = 1.742$ s, $SD = 0.615$) than in the discarded condition ($M = 1.912$, $SD = 0.743$), $t(19) = 3.09$, $p = 0.006$, $d = 0.69$, as well as in the unused condition ($M = 1.922$, $SD = 0.731$), $t(19) = 2.69$, $p = 0.015$, $d = 0.60$, while response times in these latter two conditions did not differ, $t(19) = 0.176$, $p = 0.862$, $d = 0.04$. Virtually identical results were

observed when applying the response time normalization procedure proposed by Gayet and Stein (2017). In sum, we observed accelerated detection of interocularly suppressed shape-stimuli that matched rather than mismatched a shape concurrently maintained in VWM, thus validating our current stimulus set.

4. General discussion

Previous findings show that VWM maintenance accelerates conscious access of memory-matching compared to memory-mismatching visual input (e.g., Gayet et al., 2013). This led us to enquire whether VWM content can enhance neural responses to visual input that is not yet consciously perceived. We addressed this question by measuring fMRI responses to CFS-suppressed stimuli, while participants performed a delayed-match-to-sample task. Despite convincing effects obtained in a highly similar study with non-suppressed visual input (Gayet et al., 2017), applying the same analysis pipeline to the current data yielded no evidence that VWM content modulated interocularly suppressed visual input (despite having 33% more participants, 50% more trials per participant, and numerically higher classification accuracy of the test-stimuli than this previous study). Compellingly, a second analysis step that was maximally biased toward observing this predicted effect by (1) restricting our analyses to clusters of voxels that were responsive to the same contrast in non-suppressed stimuli (in Gayet et al., 2017), and by (2) employing directional Bayesian tests explicitly favoring an effect in the expected direction, provided support for the null hypothesis in all ROIs. Thus, despite leveraging a highly liberal analysis approach, we did not observe any evidence that the content of VWM enhances neural responses to visual input that is still interocularly suppressed.

It is important to stress that, while we found no evidence that VWM impacted visual processing of interocularly suppressed visual input, this observation does not necessarily generalize to other forms of perceptual suppression. It has been argued that other perceptual masking techniques (e.g., inattention blindness, crowding, etc.) interrupt visual processing at higher levels of the perceptual hierarchy (e.g., Breitmeyer, 2015). Accordingly, stimuli suppressed with these methods could be more susceptible to VWM-based modulations, even in the absence of conscious access. To the best of our knowledge, however, there is no evidence that the impact of VWM on stimulus detection is more pronounced with the use of these other masking techniques (if at all) as compared to interocular suppression. Conversely, although we utilized interocular suppression precisely because it was shown to be heavily influenced by the content of VWM, it remains unsure to what extent our findings generalize to other masking techniques (and therefore to non-conscious processing per se). It is also worth noting that even Bayesian support for the null cannot preclude the existence of a reliable effect, provided that it is sufficiently small. As such, we cannot rule out the possibility that VWM modulates the processing of suppressed visual input to some extent. Considering our failure to detect such an effect despite our extremely liberal analysis approach, and considering the compelling effect size in our behavioral control study, however, this unobserved effect is unlikely to explain a substantial portion of advantage of memory-matching visual input in overcoming perceptual suppression.

How could this observation be reconciled with the consistent finding that visual input is released from interocular suppression faster when it matches rather than mismatches the content of VWM (Gayet et al., 2013, 2016; Pan et al., 2014; Van Moorselaar et al., 2018; Gayet et al., 2019), in so-called b-CFS experiments that measure how long it takes to report upon initially suppressed stimuli? Possibly, VWM content accelerates detection of memory-matching stimuli when they reach the limen of visibility, rather than when they are still fully suppressed (as was the case in the current fMRI experiment). It has often been argued that the modulation of detection times cannot be unambiguously attributed to processes occurring before the stimuli were released from interocular suppression, even when conscientiously developed control conditions are included (Stein et al., 2011; Stein and Sterzer, 2014; Gayet et al., 2014;

Yang et al., 2014; Gayet and Stein, 2017; Moors et al., 2019). A key challenge in this paradigm lies in establishing whether or not a stimulus is still interocularly suppressed at a particular point in time. One factor complicating this distinction is that interocular suppression is not homogenous across the visual field, as a result of which the dominant percept can be a patchwork of the two eyes' images (e.g., Meenes, 1930; Kovacs et al., 1996; Alais and Blake, 1998; Alais and Blake, 1999; Stuit et al., 2011). Consequently, parts of a predominantly suppressed stimulus might be locally dominant (i.e., not interocularly suppressed), but disregarded by the observer as being part of the dominant sequence of dynamic masks (for a similar argument, see Peremen and Lamy, 2014). A second complicating factor is that interocular suppression (and CFS in particular) tends to break up visual stimuli into their constituent features (Hong and Blake, 2009; Zadbood et al., 2011; Gelbard-Sagiv et al., 2016; for a review see Moors et al., 2017), so that some features of a stimulus (e.g., color) can be reported by the observer, while other features (e.g., its orientation) cannot be reported. As a result of this, it may depend on the specific feature that the observer is required to report, whether or not some manipulation appears to affect processing of a 'suppressed' stimulus (e.g., Gelbard-Sagiv et al., 2016), as the feature-of-interest might in fact not be suppressed. Similar dependencies have been observed with backward masking (Hortensius et al., 2014), thus making it equally difficult to interpret studies showing an influence of VWM on backward-masked stimuli (e.g., Pan et al., 2012). Taken together, while the content of VWM does affect relatively early processes in perceptual selection (e.g., affecting first saccades and detection times), the current literature cannot yet ascertain that VWM modulates the processing of visual input that is (interocularly) suppressed from consciousness. The current findings strongly suggest that the neural response to interocularly suppressed visual shape stimuli insufficiently propagates through the visual processing hierarchy to be affected by VWM content.

The locus of VWM content (i.e., stimulus-specific neural activity that is preserved throughout a retention period) depends in part on the specific feature that is memorized. In the case of visual shapes, storage loci mainly comprise higher-tier visual processing regions, located in the lateral occipital cortex, posterior parietal areas, and frontal eye fields (for a review, see Christophel et al., 2017). These same higher-tier visual processing regions showed an enhanced response to VWM-matching compared to VWM-mismatching visual shape stimuli in our earlier work (Gayet et al., 2017). A straightforward account that could explain why this enhancement is observed in VWM storage sites is that visual representations recruit the same neural populations, irrespective of whether their origin is perceptual or mnemonic, a stance known as *sensory recruitment* (extensively discussed in Xu, 2017, 2018; Gayet et al., 2018; Scimeca et al., 2018). While the interaction between mnemonic and sensory representations thus presumably occurs in such higher-tier processing regions, interocular suppression starts to attenuate neural responses to visual input in early visual processing areas (Polonsky et al., 2000; Tong and Engel, 2001; Haynes et al., 2005; Lee et al., 2005; Yuval-Greenberg and Heeger, 2013; De Jong et al., 2016), and does so increasingly while climbing up the perceptual hierarchy (e.g., Logothetis, 1998). In the present case, interocular suppression might have precluded the extraction of location-invariant, shape-specific information from the probe, required for a VWM-matching effect to arise.

We considered the possibility that the null effect observed in the fMRI experiment could be explained by an excessive suppressive strength of the masks, and/or by probe stimuli that were too weak to elicit any kind of perceptual signal, thus prohibiting them to interact with the contents of VWM. One argument against this possibility is that participants subjectively reported having seen at least part of the probe stimulus on an average of 15% of the trials (with individual participants ranging between 1.3% and 40%). As such, the perceptual signal produced by the probe stimuli was sufficient for the probes to overcome suppression on a substantial proportion of trials, but was not remotely sufficient to be impacted by the concurrent content of VWM. One could argue that suppressive strength was quasi-dichotomous, so that suppression would

either be so weak that probes were visible, or so strong that no residual perceptual signal remained. In line with this view, the proportion of trials in which participants subjectively reported having seen (at least some part of) the probe did not differ between VWM-matching and VWM-mismatching probes, in the fMRI experiment. This stands in stark contrast with the behavioral experiment (and with Gayet et al., 2013, 2017; 2019) where VWM-matching probes are detected faster than VWM-mismatching probes, when the paradigm allows for suppression to weaken over time. Together, these data show that suppression needs to be reduced below a certain threshold for probes to be impacted by the content of VWM, which essentially matches with our conclusions that VWM does not impact visual processing of interocularly suppressed visual input. It remains unknown, however, what exact degree of conscious access accompanies this threshold.

The interaction between mnemonic and sensory representations provides a top-down mechanism to favor particular (e.g., behaviorally relevant) visual objects within the visual field at the expense of others, thus providing a basis for biased competition (Duncan and Humphreys, 1989; Wolfe, 1994; Desimone and Duncan, 1995; Kastner and Ungerleider, 2001; Wolfe and Horowitz, 2004; Eimer, 2014). In line with this view, it was shown that sustained visual search requires VWM (Hodsoll and Humphreys, 2005; Chun et al., 2011; Chun, 2011; Carlisle et al., 2011), and that instructions to memorize or to search for a visual object induces qualitatively equivalent mnemonic representations (De Fockert et al., 2001; Carlisle et al., 2011; Gunselli et al., 2014). There is a clear advantage for such interactions to occur in high-level processing regions, such as lateral occipital cortex in humans (e.g., Gayet et al., 2017) or inferotemporal cortex in non-human primates (Chelazzi et al., 1998): object representations in these regions are relatively invariant with respect to such visual attributes as location, scale, or rotation (Eger et al., 2008; Grill-Spector et al., 1999), allowing for effective object-based search under naturalistic viewing conditions (but for an alternative mechanism, see Gayet and Peelen, 2019). The clear disadvantage is that constructing such invariant object representations requires complex integration of multiple visual features, a cognitive function that is believed to require some degree of consciousness (e.g., Fahrenfort, Lamme, 2012; Treisman, 2003; Baars, 2002; Tononi and Edelman, 1998; but, see Mudrik et al., 2014). We tentatively conclude from the present data that memory-based visual search of objects at the category level requires at least some degree of conscious access to the visual input.

5. Conclusions

The present study found no evidence for VWM modulation of interocularly suppressed visual input. That is, despite using the exact same stimulus set that was successful at reliably demonstrating mnemonic modulation in earlier studies (with less experimental power), and despite biasing our statistical tests as well as our voxel selection to maximize the chance of detecting such effects, we observed reliable evidence for the null in every single ROI. The absence of such VWM-based modulation has profound implications for memory-based strategies of top-down visual search: for memory templates to favor template-matching over template-mismatching visual objects, some degree of conscious access may be required. Finally, we advocate caution in interpreting the results of studies measuring conscious access as a means of probing unconscious processes: although VWM was shown to accelerate conscious access of memory-matching visual input, in this study VWM did not measurably modulate the neural response to non-conscious visual input. Possibly, modulations of detection times might reflect processes arising around (rather than below) the limen of consciousness.

Significance statement

The visual input on our retinae is constantly changing. Consequently, the human brain needs to maintain relevant visual information available for goal-directed behavior, while concurrently processing novel visual

input. Mnemonic and sensory representations have been shown to coexist, and interact with one another. It is believed that humans capitalize on this interaction for top-down visual search: by maintaining a representation in memory, concurrent visual processing favors memory-matching over memory-mismatching visual input. In the current study we find no evidence that these mnemonic biases impact the processing of visual input that is suppressed from consciousness. This would pose severe constraints to the usefulness of memory-based visual search strategies for object detection during human visual foraging behavior.

Ethics statement

All participants gave their informed written consent before participating in this study, which complied with the guidelines set out in the Declaration of Helsinki, and was approved by the local ethics committee.

Data and code availability statement

All data, experiment, preprocessing, and analysis scripts are available at this Open Science Framework project: <https://osf.io/md8rb/>

Declaration of competing interest

The authors declare no competing (financial) interests.

CRediT authorship contribution statement

All authors contributed to the conceptualization and the methodology of the study. Surya Gayet wrote the original draft of the manuscript. All co-authors contributed to the writing (review and editing) of the manuscript. Surya Gayet conducted the formal analyses and developed the analysis software. Surya Gayet, Matthias Guggenmos, Thomas Christophel, and Philipp Sterzer performed the data collection.

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Appendix A. Supplementary data

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