

Visual input that matches the content of visual working memory requires less (not faster) evidence sampling to reach conscious access

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The content of visual working memory (VWM) affects the processing of concurrent visual input. Recently, it has been demonstrated that stimuli are released from interocular suppression faster when they match rather than mismatch a color that is memorized for subsequent recall. In order to investigate the nature of the interaction between visual representations elicited by VWM and visual representations elicited by retinal input, we modeled the perceptual processes leading up to this difference in suppression durations. We replicated the VWM modulation of suppression durations, and fitted sequential sampling models (linear ballistic accumulators) to the response time data. Model comparisons revealed that the data was best explained by a decrease in threshold for visual input that matches the content of VWM. Converging evidence was obtained by fitting similar sequential sampling models (shifted Wald model) to published datasets. Finally, to confirm that the previously observed threshold difference reflected processes occurring before rather than after the stimuli were released from suppression, we applied the same procedure to the data of an experiment in which stimuli were not interocularly suppressed. Here, we found no decrease in threshold for stimuli that match the content of VWM. We discuss our findings in light of a *preactivation* hypothesis, proposing that matching visual input taps into the same neural substrate that is already

activated by a representation concurrently maintained in VWM, thereby reducing its threshold for reaching visual awareness.

Introduction

Consciousness and working memory

Working memory and consciousness are two well-studied phenomena that share a lot of similarities. For instance, both consciousness (Boehler, Schoenfeld, Heinze, & Hopf, 2008; Lamme, & Roelfsema, 2000; Sergent, Baillet, & Dehaene, 2005) and working memory (D'Esposito, 2007; Raffone & Wolters, 2001) have been proposed to rely upon recurrent cortical processing, and both consciousness (Baars, 1997a, 1997b; Dennett, 1991; Edelman & Tononi, 2000) and working memory (e.g., Cowan, 2001; Luck & Vogel, 1997) are of limited capacity. The traditional stance is that working memory only operates on information that is accessible to consciousness (e.g., Baars, 1993; Baars & Franklin, 2003; Stein, Kaiser, & Hesselmann, 2016; but see also Soto & Silvanto, 2014). In fact,

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consciousness has even been described as “the remembered present” (Edelman, 1989), and phenomenal experience and access consciousness have been related to iconic memory and working memory, respectively (Lamme, 2004). Despite the close kinship between consciousness and working memory, the question of how working memory interacts with conscious perception has not received much attention until recent years. Focusing on the visual modality, we investigated the mechanism by which the content of visual working memory (VWM) affects access to visual awareness.

The potency of visual input to reach awareness is affected by concurrent working memory maintenance in a number of distinct ways. The threshold for stimuli to reach visual awareness increases with working memory load (De Loof, Verguts, Fias, & Van Opstal, 2013; Lavie, 2005; Maniscalco & Lau, 2015) and even more so when the working memory content is visual in nature (De Loof, Poppe, Cleeremans, Gevers, & Van Opstal, 2015; Konstantinou & Lavie, 2013). Recently, it has been demonstrated that the specific content of VWM also modulates access to awareness. For instance, visual input that matches rather than mismatches a color maintained in VWM is more likely to dominate in binocular rivalry (Gayet, Brascamp, Van der Stigchel, & Paffen, 2015; but see Scocchia, Valsecchi, Gegenfurtner, & Triesch, 2014). Similarly, maintaining an unambiguous motion direction in VWM biases the perceived motion direction of an ambiguous structure from motion sphere towards the memorized motion direction (Scocchia, Valsecchi, Gegenfurtner, & Triesch, 2013).

Related findings that are of particular interest for the present purpose are those using the breaking continuous flash suppression method (b-CFS; Jiang, Costello, & He, 2007; for a review, see Gayet, Van der Stigchel, & Paffen, 2014). In this method, a target stimulus is initially suppressed from awareness by means of continuous flash suppression (CFS; Tsuchiya & Koch, 2005). The time it takes for observers to report the location of the initially suppressed target provides a measure of access to awareness. Using b-CFS, it has been demonstrated that visual input that matches a color (Gayet, Paffen, & Van der Stigchel, 2013; van Moorselaar, Theeuwes, & Olivers, 2015), shape (Gayet, 2016), or face (Pan, Lin, Zhao, & Soto, 2014) maintained in VWM is released from continuous flash suppression faster than mismatching visual input. Considering that, in these cases, the content of VWM codetermines *when* visual input reached awareness, it can be deduced that the content of VWM impacts the processing of said visual input *before* it reaches visual awareness.

Presenting two models

The shorter suppression durations for stimuli that match, rather than mismatch, the content of VWM is likely potentiated by an enhanced neural response to visual input that matches the content of VWM (Gayet, 2016). Reviews on CFS (Sterzer, Stein, Ludwig, Rothkirch, & Hesselmann, 2014; Yang, Brascamp, Kang, & Blake, 2014), b-CFS (Gayet et al., 2014), and binocular rivalry (Lin & He, 2009) reveal that interocularly suppressed information is processed only to a very limited extent. That is, only coarse processing of visual features is preserved, whereas higher level (e.g., semantic) information is severely disrupted. Considering that, when climbing up the visual processing hierarchy, a decreasing proportion of neurons represents visual input that is interocularly suppressed (Leopold & Logothetis, 1999; Yuval-Greenberg & Heeger, 2013), the content of VWM is most likely to modulate the signal elicited by the suppressed sensory input in early visual areas. The present study is aimed at dissociating between two possible ways in which representations maintained in VWM can modulate concurrent visual input in early visual processing areas. For this purpose, we replicated the finding that visual input matching the content of VWM yields faster access to awareness in a b-CFS task (Gayet et al., 2013; Pan et al., 2014; van Moorselaar et al., 2015), and compared the potency of two models in explaining the observed pattern of results: the *preactivation* hypothesis and the *amplification* hypothesis.

The preactivation hypothesis entails that representations maintained in VWM (say, the color green) elevate the base activation level for concurrent matching visual input (a green stimulus). The preactivation hypothesis builds upon the assumption that a visual representation (the color green) draws upon the same neural population, irrespective of whether its origin is retinal or mnemonic, which is in line with the recent view that content-based VWM processes reside in visual processing areas (for a discussion, see Sligte, Van Moorselaar, & Vandenbroucke, 2013). This view is built upon recent imaging studies that show generalizable patterns of neural activity for perceived gratings and memorized gratings (e.g., Harrison & Tong, 2009), and is corroborated by behavioral findings showing an orientation repulsion effect between perceived gratings and concurrently memorized gratings (Kang, Hong, Blake, & Woodman, 2011; Scocchia, Cicchini, & Triesch, 2013). Considering this common neural substrate, visual input might impinge upon a neural population that was already activated by VWM maintenance. Such an additive effect of matching visual representations would result in enhanced activation of visual input that matches the concurrent content of VWM. By this, preactivation of specific neural popu-

lations by the content of VWM should decrease the effective threshold for matching visual input to affect behavior and perception (a similar view has been proposed in a priming study by Lupyan & Ward, 2013).

The amplification hypothesis proposes that the content of VWM, which modulates the visual input, is maintained in visual areas that are further upstream in the processing hierarchy compared to the visual areas where the interocular competition is resolved. Feedback loops between high-level processing areas containing the VWM representation (e.g., the green color category) and the visual processing areas (processing the green stimulus) allow for enhancing (i.e., amplifying) visual input that complies with the categorical representation maintained in VWM. When considering the influence of VWM on suppression durations in b-CFS studies, there are at least two types of observations, suggesting that the differentiation between matching and mismatching stimuli can only be construed in higher level processing areas. First, in these b-CFS studies, the to-be-memorized stimulus was never presented at the same retinal location as the suppressed target stimulus presented during the delay interval (i.e., typically they are separated by 1 to 2 degrees of visual angle). From this it follows that the effect is either nonretinotopic or originates in processing areas with sufficiently large receptive fields to cover the retinotopic distance between the to-be-memorized stimulus and the suppressed target stimulus. Secondly, in these b-CFS studies, the to-be-memorized stimulus was never identical to the suppressed stimulus. Rather, matching or mismatching conditions reflected whether the suppressed stimulus was drawn from the same or from a different stimulus category than the memorized stimulus (i.e., the effect was categorical). The categorical nature of this effect leads to suggest that the effect originates in higher level processing areas (e.g., object selective areas such as the lateral occipital complex, or nonvisual areas that contain abstract coding of stimulus categories). An important requirement for this hypothesis, however, is that some of the CFS suppressed visual input transpires to higher level visual areas. The view that the modulation of suppression durations in a b-CFS paradigm relies on suppressed visual input transpiring to higher level visual areas is substantiated by the recent finding that certain priming effects under CFS only occur under conditions of partial awareness (Gelbard-Sagiv, Faivre, Mudrik, & Koch, 2016).

Sequential sampling models

Both the preactivation hypothesis and the amplification hypothesis predict a stronger (neural) response to matching visual input in visual processing areas. If

we consider the time course over which a stimulus is expected to be enhanced depending on its match with VWM, however, the two hypotheses provide very distinct predictions. According to the preactivation hypothesis, matching (but not mismatching) visual input should be immediately enhanced, as it draws upon a preactivated neural population, akin to a decreased threshold. According to the amplification hypothesis, the differentiation between matching and mismatching visual input should occur through gradual evidence accumulation, resulting in a positive gain modulation. Sequential sampling models (for reviews, see Forstmann, Ratcliff, & Wagenmakers, 2016; Mulder, van Maanen, & Forstmann, 2014; Ratcliff & Smith, 2004) provide the means to infer, from response times and response choices, the process of evidence accumulation over time that eventually leads to a perceptual decision. A core assumption in these models is that dichotomous perceptual decisions are the result of gradual evidence accumulation over time. The gradual accumulation of perceptual evidence has been observed for nonconscious stimuli (Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003; for discussions, see Dehaene, 2011; Dehaene, Charles, King, & Marti, 2014). As such, sequential sampling models have been used recently to investigate the mechanisms driving access to awareness of expected versus unexpected stimuli (De Loof, Van Opstal, & Verguts, 2016). In addition, sequential sampling models have been used before to investigate evidence accumulation in early visual processing areas (e.g., Ho, Brown, van Maanen, Forstmann, Wagenmakers, & Serences, 2012).

In the present study, we conducted a modified version of the experimental paradigm used by Gayet et al. (2013). Similarly to the traditional paradigm, suppression durations were inferred from speeded responses to target stimuli that were initially interocularly suppressed. In the present study, there were two targets (one that was related to the memory task and one that was unrelated to the memory task), one on each side of fixation. Participants were instructed to report on which side of fixation a target first appeared, thereby indicating which of the two targets broke through suppression first. The modification of the original one-target paradigm into a two-target paradigm allowed us to obtain response time distributions for two possible response options (responses to targets that were either related or unrelated to the memory task), thereby optimizing the traditional paradigm for fitting sequential sampling models to participants' behavioral responses.

First, we replicated the finding that visual input matching the content of VWM gains preferential access to awareness in a b-CFS paradigm. Next, we implemented both the preactivation and amplification hypotheses as sequential sampling models to compare

which of these best explained the data quantitatively. To ensure that our findings would generalize to the typical b-CFS paradigm, we additionally reanalyzed the data of two experiments retrieved from Gayet et al. (2013) with a sequential sampling model tailored to the type of data typically obtained in the b-CFS paradigm (the shifted Wald model; Anders, Alario, & Van Maanen, 2016; Heathcote, 2004). Together, our results unequivocally favor the preactivation hypothesis over the amplification hypothesis. From this, we conclude that neuronal populations are preactivated by representations maintained in VWM, as a result of which matching visual input is prioritized over mismatching visual input for gaining access to awareness.

Methods

Participants

The participant group consisted of 22 undergraduate students from Utrecht University (eight men, 14 women; mean age 21.6 years, $SD = 3.0$), who participated for course credits or monetary reward after signing informed consent. The experiment complied with all ethical guidelines set out in the Declaration of Helsinki. Participants had normal or corrected-to-normal vision and were tested for color blindness with the Ishihara test plates (Ishihara, 1917) and for stereoscopic vision with the TNO test for stereoscopic vision (12th edition; Walraven, 1972). The number of participants was determined on the basis of prior b-CFS experiments (e.g., Gayet et al., 2015) and experiments with comparable implementations of sequential sampling models (Forstmann, Brown, Dutilh, Neumann, & Wagenmakers, 2010).

Apparatus and stimuli

The experiment was conducted using an Apple dual 2-GHz PowerPC G5 equipped with a linearized 22-in. LaCie Electron Blue IV CRT monitor (1024×768 pixels; 100-Hz refresh rate) and an Apple keyboard, which was used for response registration. There were no light sources in the experiment room, except for the computer monitor. Stimulus presentation and response collection were managed using the Psychophysics Toolbox 3 (Brainard, 1997; Pelli, 1997) in MATLAB (R2009b; MathWorks, Natick, MA). A pair of displays was viewed dichoptically through a mirror stereoscope mounted on a chin rest, which kept the effective viewing distance at 57 cm. To facilitate binocular fusion of the two complementary images, we presented a circular area with a diameter of 8° to each eye, which

was composed of Brownian (i.e., $1/f^2$) noise with a mean luminance of 16.08 cd/m^2 . All stimuli were presented on a uniform gray background, (16.62 cd/m^2), that consisted of two circular areas with a diameter of 4.95° , superimposed on the Brownian noise. Both presentation areas comprised a white (32.15 cd/m^2) fixation bull's-eye composed of a white circle with a diameter of 0.2° of visual angle and a black ($<0.1 \text{ cd/m}^2$) circle in its center with a diameter of 0.04° of visual angle. The retro cues consisted of the Arabic numerals 1 and 2 in white Arial font with a font size of 18.

The masks used for obtaining CFS were created by filtering pink ($1/f$) noise using a rotationally symmetric Gaussian low-pass filter ($\sigma = 3.5$) and making the resulting image binary (black and white, $>99\%$ Michelson contrast). On every trial, 20 new masks were generated, which were presented for 100 ms each (10 Hz) in random order, with the restriction that the same mask was never presented twice in succession. During presentation, a vertical sparing with a width of 0.8° of visual angle divided the CFS presentation into two masked areas on each side of fixation. Because reversals of ocular dominance tend to follow object continuations (Kaufman, 1963), the addition of such a sparing served the purpose of increasing the independency of the two targets' suppression durations (Maruya & Blake, 2009).

The colored stimuli used in the memory task as well as the colored target stimuli used in the b-CFS task consisted of circles with a diameter of 1.08° of visual angle. The colors used for the b-CFS task were comprised of perceptually equiluminant saturated red, green, and blue, and purple, for which the red and blue cannons of the CRT monitor contributed equally. A saturated blue color was used to obtain perceptual equiluminance of the saturated red, green, and purple colors for each subject by means of heterochromatic flicker photometry (Kaiser & Comerford, 1975; Wagner & Boynton, 1972). The target stimuli were presented at a fixed eccentricity of 1.62° of visual angle from fixation, at a random angular position on the left and right arcs of an imaginary circle, delimited by its main diagonals. The 20 colors used for the memory task were based on those of Gayet et al. (2013), extended with the purple color category. These colors consisted of five nonsaturated hues, drawn from each of four different color categories (red, green, blue, and purple). The luminance of all hues was physically matched by means of a PR-650 SpectraScan colorimeter/telephotometer (Photo Research, Inc., Chatsworth, CA). These equiluminant colors were tested informally during the pilot phase of the experiment to assert that (a) they were clearly part of the intended color category, and (b) whether the difference between two hues was visible when juxtaposed. An overview of

all CIE-color values of the stimuli used in this experiment is provided in Table 1.

Procedure

Participants first performed a calibration task, which was aimed at (a) allowing participants to get acquainted with the b-CFS task, and (b) adjusting the intensity of the target stimuli to promote independent breakthrough of the two target stimuli. In case the participants experienced simultaneous breakthrough of the two targets, the experimenter reduced the opacity of the target stimuli from 100% (full opacity) to a minimum of 60% in discrete steps. Lowering the opacity, and thereby the (chromatic) contrast of both targets with the background, causes suppression durations to increase, thereby increasing the difference in suppression durations between both targets. If the participant still experienced simultaneous breakthrough of the two target stimuli at this stage, the participants ($N = 2$) could not take part in the experiment. Next, participants performed 128 experimental trials and 10 catch trials, separated into eight blocks. A schematic depiction of a trial is presented in Figure 1. Each trial started with two successive colored stimuli, drawn from different color categories, followed by a Retrocue (1 or 2) indicating whether the first or second color should be memorized for subsequent recall. During the retention interval, high contrast patterns started alternating at 10 Hz in one eye (now the dominant eye), temporarily suppressing visual input to the other eye (now the nondominant eye). After a variable delay ranging between 300 and 600 ms, two target stimuli (left and right of fixation) were presented to the nondominant eye, ramping up from zero to full intensity in 1000 ms. One of these stimuli was drawn from the same category as either the cued or the uncued color (i.e., related to the memory task), whereas the other stimulus was drawn from neither (i.e., unrelated to the memory task). Participants were instructed to report as fast as possible where (left or right) they first saw a target stimulus appear. After this response (or after 10 seconds had elapsed), two colored stimuli appeared left and right of fixation that were both drawn from the same color category as the cued color. Participants were required to indicate within 4500 ms which of these two stimuli (presented for 1500 ms) was of the exact same color as the cued color. Each trial was separated by an inter trial interval of 1600 ms.

Design and hypotheses

All factors were manipulated within-participant. The experimental design consisted of one factor of interest,

Color	CIE values*		
	x-value	y-value	Luminance (cd/m ²)
Red 1	0.608	0.364	3.76
Red 2	0.632	0.345	3.50
Red 3	0.651	0.340	3.47
Red 4	0.581	0.312	3.24
Green 1	0.269	0.528	3.31
Green 2	0.287	0.600	3.53
Green 3	0.310	0.597	3.25
Green 4	0.362	0.557	3.33
Blue 1	0.166	0.137	3.45
Blue 2	0.156	0.103	3.37
Blue 3	0.159	0.079	2.87
Blue 4	0.171	0.083	2.66
Purple 1	0.228	0.123	3.47
Purple 2	0.251	0.133	3.34
Purple 3	0.293	0.151	3.40
Purple 4	0.349	0.182	3.22
Blue target**	0.147	0.068	2.64
Red target (SD)	0.635	0.343	2.61 (0.56)
Green target (SD)	0.292	0.612	4.24 (0.97)
Purple target (SD)	0.319	0.165	2.95 (0.50)

Table 1. Overview of the colors used in the main experiment. *CIE values stands for Commission Internationale d'Éclairage values, as measured from viewing distance (i.e., 57 cm) with a PR-650 SpectraScan colorimeter/telephotometer (Photo Research, Inc.). **The saturated blue was the reference stimulus for the perceptual luminance matching (i.e., heterochromatic flicker photometry; Kaiser & Comerford, 1975; Wagner & Boynton, 1972) with the red, green, and purple colors that were used for the target stimuli.

Trial Type, which had two levels. In half of the trials, one of the two target stimuli always matched the category of the cued color (i.e., Memorized trial type). In the other half of the trials, one of the two target stimuli always matched the category of the uncued color (i.e., Discarded trial type). The color of the simultaneously presented second target stimulus was always drawn from the color category that was not used on that trial (i.e., the target was unrelated to the memory task). Four other factors were included as factors of no interest. This included the factors Retrocue (1 or 2), Eye (target presented to left or right eye), Location (unrelated stimulus presented to the left or right of fixation), and Color (the cued stimulus is drawn from the red, green, blue, or purple color category). Together, these factors resulted in 64 unique combinations of conditions, in which the order was randomized. Each unique combination of conditions was presented twice, once in each half of the experiment, resulting in a total of 128 trials. Finally, on each trial, the specific hue of the cued color, the color category and specific hue of the uncued color, and the color category of the unrelated target stimulus were

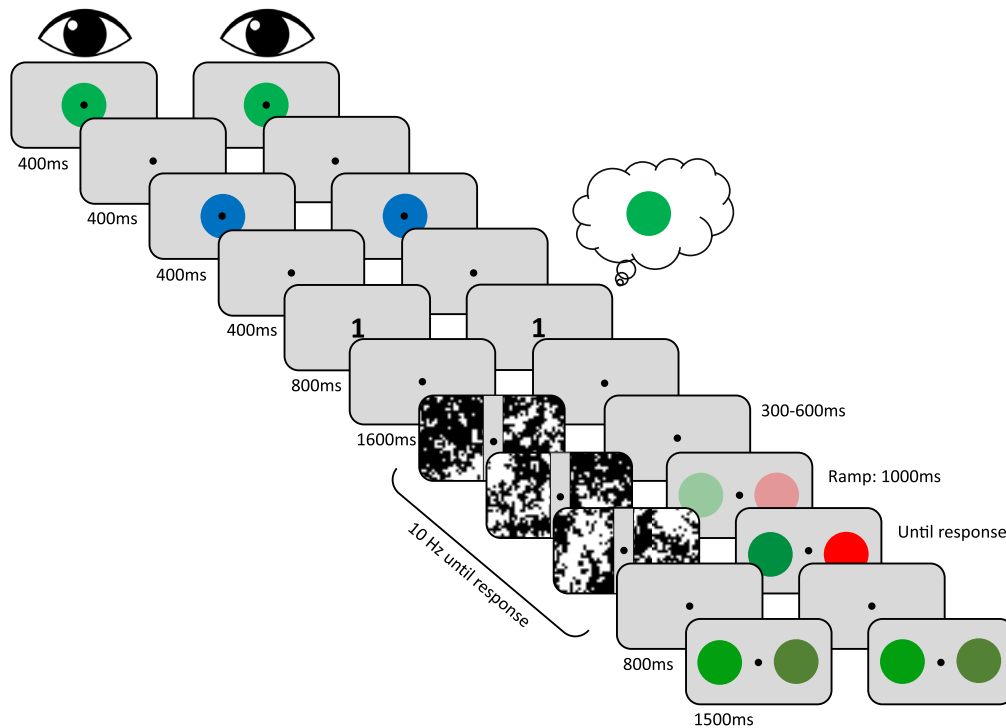


Figure 1. A schematic depiction of a trial. On each trial, participants were cued to memorize one of two sequentially presented hues for subsequent recall. During the delay interval, the participants were required to report as fast as possible the location (left or right of fixation) at which a stimulus emerged through the CFS masks. One of these stimuli was always unrelated to the memory task, whereas the other stimulus was related to the memory task (i.e., either matching the cued stimulus on so-called Memorized trial types or the uncued stimulus on so-called Discarded trial types). Note that the specific stimulus properties used in this illustration differ from those of the actual experiment.

determined at random, with the only constraint that the cued color, the uncued color, and the color of the unrelated target stimulus were drawn from distinct color categories.

In addition to the experimental trials described above, 10 catch trials were interspersed throughout the experimental trials (1 or 2 per block). In these catch trials, only one stimulus was presented; five times left of fixation and five times right of fixation.

Based on previous experiments (notably, Gayet et al., 2013) we expected that target stimuli matching the category of the cued (i.e., memorized) color would break through suppression faster than target stimuli that mismatch this category. Assuming that this effect is engendered by the memorization rather than the presentation of the cued color, we expected that target stimuli matching the uncued color would not break through suppression faster than target stimuli drawn from an unrelated color category. Therefore, we predicted that on trials with a target stimulus matching the category of the cued color (i.e., the Memorized trial type), these target stimuli would be reported (a) more often and (b) faster than target stimuli drawn from an unrelated color category; in line with this, we predicted that (c) these differences should not be observed in

trials comprising target stimuli matching the category of the uncued color (the Discarded trial type).

All analyses provided here are (one-sample or paired-samples) t tests that are regarded as significant when the p -value (two-tailed) is below the α -value of 0.05 after Bonferroni correction.

Modeling analyses

We hypothesized two distinct patterns of perceptual evidence accumulation that could underlie the preferential detection of targets that match compared to targets that mismatch the concurrent content of VWM. Specifically, the preactivation hypothesis predicts a lowered effective threshold for targets that are drawn from the same color category as the cued color. Conversely, the amplification hypothesis predicts a faster accumulation of perceptual evidence for targets that are drawn from the same color category as the cued color. To dissociate between these two possibilities, the preactivation and amplification hypotheses were implemented as two variants of the linear ballistic accumulator model (LBA; Brown & Heathcote, 2008). The LBA model assumes that evidence for each

response option (e.g., the target left or right of fixation) gradually accumulates over time until a preset response threshold is reached. The time required for the first option to reach the threshold constitutes the decision time. This is implemented in the LBA model by a set of parameters that govern the shape of the response time distributions for both response options, as well as the proportion of both response options. These parameters are the response threshold b , the mean rate of accumulation v , and a nondecision parameter t_0 representing components of the response time that capture other processes, such as the time required to press the response button. Additionally, variability in behavior is accounted for by allowing the accumulation rate to vary from trial to trial (represented by a normal distribution with mean v and standard deviation s), and by allowing the response threshold to vary (represented by a uniform distribution with range $[b-a, b]$, which is equivalent to varying the point at which the accumulation starts within the range $[0, a]$). Figure 2 provides an overview of the parameters that constitute each accumulator. Both the response threshold and the accumulation rate may differ across accumulators, yielding differences in response times and response choices.

The amplification hypothesis is implemented as an accumulation rate difference between the Memorized and Discarded trial types. That is, all parameters are assumed to be equal for both conditions, but we included two accumulation rates ($v_{\text{memorized}}$ and $v_{\text{discarded}}$) to account for the hypothesized difference in gain. For scaling purposes, the accumulation rate for responses to the unrelated targets is set at $1-v_{\text{memorized}}$ and $1-v_{\text{discarded}}$ for each trial type, respectively.

The preactivation hypothesis is implemented by including two different response thresholds. Specifically, we estimated the overall threshold b across all trial types and responses, and additionally estimated the deviation of each accumulator from this threshold (Δb), in each trial type. This means that $b_{\text{memorized}} = b - \Delta b_{\text{memorized}}$, and $b_{\text{unrelated}} = b + \Delta b_{\text{memorized}}$, with $b_{\text{memorized}}$ indicating the threshold for the target that matches the cued (i.e., memorized) color category. Similarly, in the Discarded trial type, $b_{\text{discarded}} = b - \Delta b_{\text{discarded}}$, and $b_{\text{unrelated}} = b + \Delta b_{\text{discarded}}$, with $b_{\text{discarded}}$ indicating the threshold for the target that matches the color category of the uncued (i.e., discarded) stimulus. Again, for scaling purposes, the drift rate for the unrelated targets was set at $1-v$, which in this model is the same for both conditions. The present approach is similar to that of earlier studies, in which the influence of a priori information on perceptual decision making was attributed to an initial bias, on the basis of an LBA model in which only the threshold was allowed to vary (Forstmann et al., 2010; van Maanen, Forstmann, Keuken, Wagenmakers, & Heathcote, 2016).

Because changes in the accumulation rate and threshold parameters (v and b) have different effects on the shape of the response time distributions and the choice proportions, one of these models will more closely match the observed data after the best fitting parameters are estimated, providing evidence in favor of that model. We estimated parameters by maximizing the summed log likelihood of the ventiles (i.e., the twenty 5% quantiles; Ratcliff, 1979; Vincent, 1912) of the response times, separated for both response options (i.e., target related or unrelated to the memory task), for both the Memorized and Discarded trial types (i.e., related target is drawn from the same color category as the cued stimulus or uncued stimulus). Maximization was done using particle swarm optimization (Clerc, 2010), to avoid local optima in fitness landscape. The LBA model implementations of the preactivation and amplification hypotheses were subsequently compared by their likelihood ratios, which indicate how likely each model is relative to the other model given the data (Jeffreys, 1961). This comparison can be made directly, as both models comprise the same number of free parameters, such that no correction has to be applied for model flexibility. Finally, the model that was best at describing the observed data was compared to a control model, in which all parameters were fixed. In this case, the likelihood ratio was computed by means of a Bayesian information criterion (BIC) score, which allows selection of the best model from a finite number of models (in this case, three), while correcting for the number of free parameters in each model.

Results and discussion

Preliminary analyses

Three participants were excluded from further analyses for being incorrect in at least 30% of the catch trials. These participants thus repeatedly reported that a stimulus appeared first at a location where no stimulus was presented. Such responses indicate that participants either misattributed features of the CFS masks as being a target stimulus, or reported a target location prior to seeing the target. We removed all trials that yielded response times under 350 ms (1.23% of all trials) as well as those that were not responded to within the 10 s time window (0.04% of all trials). The remaining 19 participants were 95.3% ($SD = 6.8$) accurate on the catch trials. Participants had an average accuracy of 73.2% ($SD = 6.3$) on the working memory recall task, and all included participants performed above chance level, as

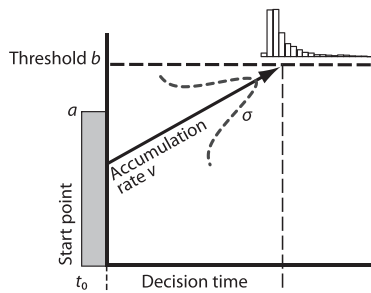


Figure 2. A schematic depiction of a single accumulator and its parameters in the LBA model. On each trial, participants provided a behavioral response that consisted of a response time and a response option (e.g., the target left or right of fixation). The LBA model assumes that evidence for each response option gradually accumulates over time, following an accumulation rate v , until a preset response threshold b is reached. The time required for the first option to reach the threshold constitutes the decision time. Here, we investigate whether the observed pattern of data is best described by either a model in which all parameters are fixed except for the threshold b , or a model in which all parameters are fixed except for the accumulation rate v .

determined by a binomial test against chance level (all $p_s < 0.0145$).

Behavioral analyses

Our first aim was to replicate the finding that visual input matching the content of VWM breaks through suppression faster than mismatching visual input. For this purpose, we computed how likely participants were to respond to the target that was related to the memory task, relative to the target that was unrelated to the memory task. This was done as follows: for each condition (i.e., Memorized and Discarded trial types), we subtracted the number of trials in which participants responded to the related target from the number of trials in which participants responded to the unrelated target, and divided this by the total number of trials in which the participant responded to any of the two targets. This was then multiplied by 100 to obtain percentages:

$$\text{Response preference} = \frac{N_{\text{unrelated}} - N_{\text{related}}}{(N_{\text{unrelated}} + N_{\text{related}})} \times 100. \quad (1)$$

We first conducted planned one-sample t tests against 0 (i.e., no difference). This revealed that target stimuli matching the category of the cued color were responded to 8.8% ($SD = 12.2$) more often than unrelated target stimuli, $t(18) = 3.0605$, $p = 0.0067$, $d = 0.585$ (significant at a Bonferroni corrected α -level of 0.025). This reflects a difference of about 5.6 trials. In

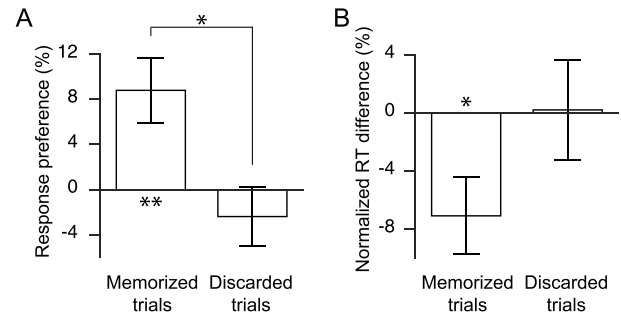


Figure 3. Behavioral results of the main experiment. On each trial, one target (i.e., response option) was unrelated to the memory task, whereas the other one was related to the memory task. The target that was related to the memory task was related to the cued stimulus on Memorized trials, and to the uncued stimulus on Discarded trials. Panel A depicts the percentage of trials in which participants reported seeing the target appear first that was related to the memory task. A positive value indicates that on the majority of trials the related target emerged from CFS before the unrelated target did. Panel B depicts the normalized difference in response time to targets that were related to the memory task compared to unrelated targets. A negative value reflects a faster response time to the related target. Error bars represent the standard error of the mean. * $p < 0.05$, ** $p < 0.01$.

contrast, the same analysis for the Discarded trial type revealed that target stimuli matching the category of the uncued color were responded to 2.3% ($SD = 11.1$) less often than unrelated target stimuli, and this was not significantly different from the null, $t(18) = -0.9059$, $p = 0.3770$, $d = -0.209$ (not significant at a Bonferroni corrected α -level of 0.025). Additionally, a paired-samples t test showed that these fractions differed between the Memorized trial type, in which target stimuli matched the category of the cued color, and the Discarded trial type, in which target stimuli matched the category of the uncued color, $t(18) = 3.1601$, $p = 0.0054$, $d = 0.597$. For paired comparisons, effect sizes were computed by using Cohen's d , following Morris and DeShon's (2002) equation 8, which corrects for dependence between means. The results of these analyses are depicted in Figure 3A.

Next, we aimed to assess whether the response speed to target stimuli depended on the response choice (i.e., the relation between the target stimulus and the color categories used in the memory task). For this purpose, we computed median response times for each for the two response options (target is related or unrelated to the memory task) in each of the two trial types (Memorized or Discarded trial types). This showed that, in the Memorized trial type, response speeds to target stimuli matching the category of the cued color ($M = 1678$ ms, $SD = 645$) were 160 ms faster than responses to target stimuli drawn from an unrelated color category ($M = 1838$ ms, $SD = 841$), $t(18) = 2.4852$, $p = 0.0230$, $d = 0.816$

(significant at a Bonferroni corrected α -level of 0.025). In the Discarded trial type, however, there was no difference in response speed between target stimuli matching the category of the uncued color ($M = 1691$ ms, $SD = 607$) and to targets drawn from an unrelated color category ($M = 1704$ ms, $SD = 701$), $t(18) = 0.1267$, $p = 0.9006$, $d = 0.024$. The effect of the memory task on response speeds (i.e., in the Memorized trial type) was correlated with participants' average response speed, $R = 0.72876$, $p = 0.0004$. This means that part of the variability in the response speed difference is accounted for by between-subjects variability in absolute response speed (i.e., sensitivity to CFS). To remove this between-subjects variability, we normalized the response times within each trial types as follows:

$$\text{Normalized RT difference} = \frac{RT_{\text{unrelated}} - RT_{\text{related}}}{\frac{1}{2}(RT_{\text{unrelated}} + RT_{\text{related}})} \times 100. \quad (2)$$

A similar approach has been used by Stein (2012). The resulting measure reflects the difference in response time brought about by the manipulation (i.e., the relation between the color of the target and the color category of the cued stimulus in the memory task). After normalization, one-sample t tests revealed that individual response times to target stimuli matching the color of the cued stimulus were 7.0% ($SD = 11.2$) faster than to target stimuli of an unrelated color category, $t(18) = 2.6714$, $p = 0.0156$, $d = 0.613$ (significant at a Bonferroni corrected α -level of 0.025). This reduction of response times was not apparent in the Discarded trial type ($M = 0.2\%$, $SD = 14.6$), $t(18) = 0.0614$, $p = 0.9517$, $d = 0.014$ (not significant at a Bonferroni corrected α -level of 0.025). The difference in response time between responses to the related and unrelated targets did, however, not significantly differ between trial types, as shown by a paired-samples t test, $t(18) = 1.555$, $p = 0.1374$, $d = 0.339$ (see Appendix A and Figure S1 for an alternative analysis, which is more similar to that of Gayet et al., 2013, and does reveal a difference between the Memorized and Discarded trial types). It is possible that the effect of our experimental manipulation on response times was dampened (compared to Gayet et al., 2013) due to the fact that for Memorized trials in which participants reported the unrelated target to appear first, the suppression duration was codetermined by the related target, presented to the same eye (e.g., Ooi & He, 1999). Using a similar paradigm, it has been observed that when multiple objects (of which one target) are presented under CFS, the modulation of response times by the content of VWM is reduced (van Moorselaar et al., 2015).

Taken together, we replicated earlier findings (e.g., Gayet et al., 2013) by showing preferential access to awareness for visual input matching the content of VWM. The present paradigm allowed to corroborate these findings with a modified experimental paradigm,

in which two stimuli directly (i.e., simultaneously) compete for access to awareness. This paradigm was specifically aimed at examining the effect of VWM on access to awareness including measures of response choice as well as response speed. In the next paragraph, these two behavioral measures will allow us to discern whether the effect of VWM on access to awareness is engendered by (a) a lowered effective threshold or (b) a faster accumulation of evidence for detecting visual input that matches rather than mismatches the content of VWM. This would provide support for either (a) the preactivation hypothesis or (b) the amplification hypothesis, respectively.

Modeling analyses

We compared the implementations of the preactivation and amplification hypotheses as variants of the LBA model. A model comparison supported the preactivation hypothesis over the amplification hypothesis, as indicated by a likelihood ratio of 35,186. Specifically, a model with the threshold offset b as the only free parameter is 35,186 times more likely to have generated the data than a model with the accumulation rate v as the only free parameter. Additionally, the preactivation model was 10,459,802 times more likely to have generated the data than a control model in which no parameter was allowed to vary. Figure 4 summarizes that the preactivation model indeed captures important properties of the data. Specifically, Figure 4A shows that the preactivation model roughly captures the participants' response choices (i.e., the fraction of trials in which participants responded to the target that was related to the memory task). Importantly, the model captures the shape of the response time distributions (Figure 4B), as evidenced by the close correspondence between model predictions and data for all deciles (i.e., 10% quantiles) of the response time distribution. In comparison, the losing amplification model failed to capture the tail end of the RT distributions in the observed data (Appendix B).

The parameters of the preactivation model support the perspective that the response threshold is lower for targets that match the content of VWM (Figure 4C). One-sample t tests against no difference show that there was a significant difference in the response threshold parameter b between trials in which targets were either unrelated to the memory task and trials in which target were related to the cued stimulus (i.e., in the Memorized trial type; $M_{\text{memorized}} = 82$, $SD_{\text{memorized}} = 101$), $t(18) = 3.56$, $p = 0.0022$), but not for trials in which targets were either unrelated to the memory task or were related to the uncued stimulus (i.e., in the Discarded trial type; $M_{\text{discarded}} = 9.8$, $SD_{\text{discarded}} = 109$), $t < 1$. In addition, a paired-samples t test showed that this effect of response threshold differed between the

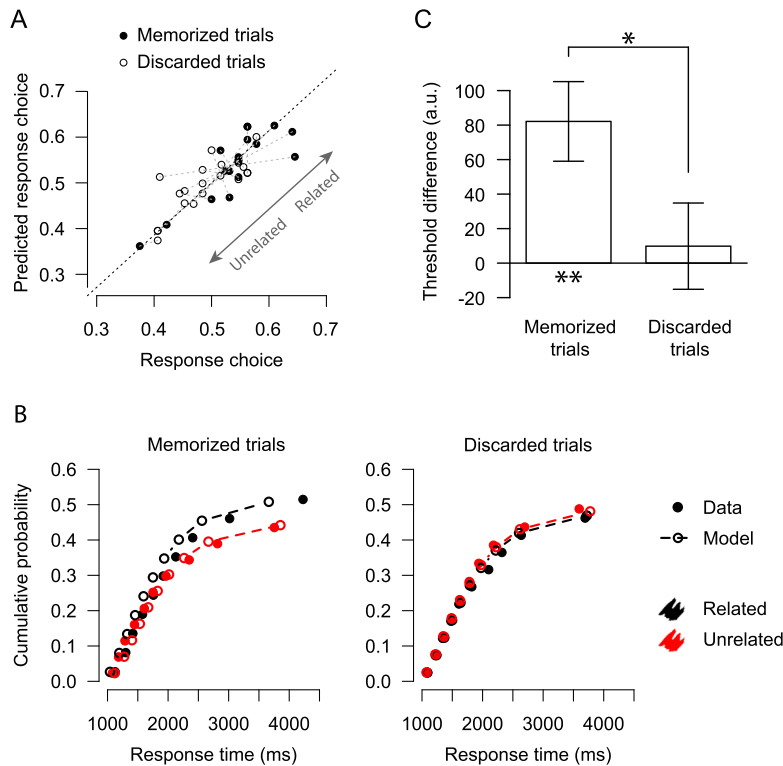


Figure 4. Model predictions and parameter estimates of the preactivation (or threshold) model for the main experiment. On each trial, one target (i.e., response option) was unrelated to the memory task, whereas the other one was related to the memory task. The target that was related to the memory task was related to the cued stimulus on Memorized trials, and to the uncued stimulus on Discarded trials. Panel A depicts the observed (x -axis) and predicted (y -axis) fraction of trials in which participants responded to the related target. The gray dotted lines connect pairs of data points from the same participant. Panel B depicts the defective cumulative density of observed data and model predictions, for 10 response time quantiles (i.e., ventiles binned into deciles for illustrative purposes) averaged over participants. The y -axes represent the probability of observing a response to the related target or the unrelated target on or before a specific RT (depicted on the x -axis). The two trial types are shown in different graphs. Panel C depicts the mean parameter estimates (in arbitrary units) of the preactivation model. The bars indicate the difference in threshold parameters b for the related (to cued or uncued) target responses and the unrelated target responses. * $p < 0.05$, ** $p < 0.01$.

Memorized and Discarded trial types, $t(18) = 2.51$, $p = 0.021$. This shows that the different patterns of findings in the Memorized trial types and the Discarded trial types, which only differ in the contingency between the content of VWM and the target stimuli, is accounted for by a lowered threshold for stimuli matching the content of VWM. This is the pattern of results that would be expected if the content of VWM preactivated neural populations that process concurrently presented visual input.

Generalizing to the traditional b-CFS paradigm

Introduction and methods

Using a modified version of the b-CFS paradigm, we replicated earlier findings that visual input matching

the content of VWM is released from interocular suppression faster than visual input that mismatches the content of VWM. This modified paradigm allowed us to identify that the reduced suppression durations are potentiated by a decreased threshold for stimuli matching the content of visual working memory, akin to an initial bias towards VWM matching stimuli. To ensure that the present results generalize to the typical b-CFS paradigm in which one target (i.e., response option) is provided, we reanalyzed the data of Gayet et al.'s (2013) experiment 4. Details of the participant groups from which the data is retrieved for the supplemental modelling analyses can be found in Gayet et al. (2013). In this experiment ($N = 15$), only one target was presented simultaneously. The target stimulus either matched the color category of the cued stimulus (in Memorized trial types) or that of the uncued stimulus (in Discarded trial types), in 24 trials each. Trials in which the target was drawn from an unrelated color category were not included in the

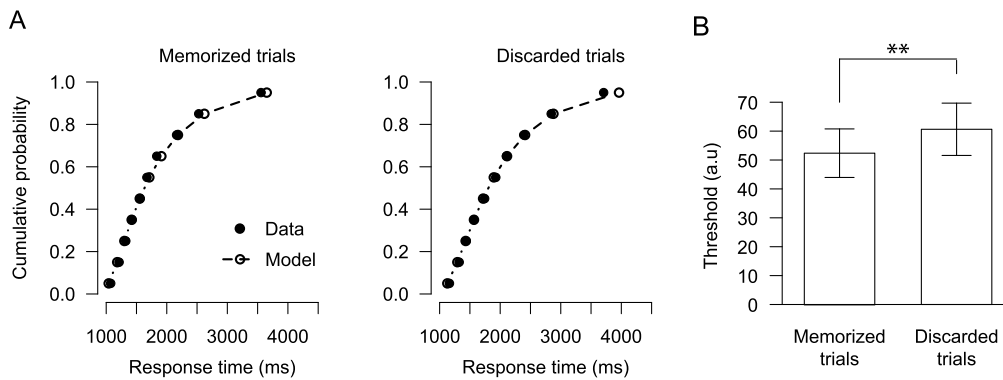


Figure 5. Model predictions and parameter estimates of the preactivation (or threshold) model, for a dataset retrieved from Gayet et al. (2013; experiment 4). On each trial, one target was presented that was either related to the cued stimulus (Memorized trial type) or uncued stimulus (Discarded trial type) from the memory task. Panel A depicts the defective cumulative density functions, illustrating the probability of observing correct and incorrect responses for the data and model predictions, in 10 response time quantiles (ventiles binned into deciles for illustrative purposes), averaged over participants. The y -axes represent the probability of observing a response to the target on or before a specific RT (depicted on the x -axis). The two trial types are shown in different graphs. Panel B depicts the mean parameter estimates of the preactivation model. The bars indicate the mean parameter estimates (in arbitrary units) for the threshold b for each of the two trial types. Error bars represent the standard error of the mean. ** $p < 0.01$.

present analysis. This experiment does not use a binary forced choice paradigm, and therefore an LBA model is inappropriate. Instead, we fitted the response times of the correct responses (97.9%) using a one-sided accumulator model (the shifted Wald model; Anders et al., 2016). This model is suitable for decomposing response time distributions into accumulation rate ν , response threshold b , and nondecision time t_0 in case of only one (meaningful) response. The amplification and preactivation hypotheses were again implemented by allowing separate accumulation rates and thresholds respectively, for the Memorized and Discarded trial types. Again, we compared model implementations of the amplification and preactivation hypotheses using their likelihood ratio, after optimizing the parameters using particle swarm optimization.

Results

Model comparisons of the data of experiment 4 of Gayet et al. (2013) were in line with the findings of the main experiment reported above. The likelihood ratio of the different models revealed that a model with the threshold b as the only free parameter (the preactivation model) is 19 times more likely to have generated the data than a model with the accumulation rate ν as the only free parameter (the amplification model). Also, the preactivation model explained the RT distribution data very well (Figure 5A), and, similarly to the main experiment, we again observed that the threshold parameter b is lower in Memorized than in Discarded trials (Figure 5B, $M_{\text{Memorized}} = 52$, $SD_{\text{Memorized}} = 33$,

$M_{\text{Discarded}} = 61$, $SD_{\text{Discarded}} = 35$), as revealed by a paired-samples t test, $t(14) = 3.98$, $p = 0.0014$.

Dissociating perceptual decision threshold from response criterion

Introduction and methods

The current findings demonstrate that the faster access to awareness of target stimuli matching the content of VWM is potentiated by a lowering of the effective threshold (i.e., the threshold b) for matching compared to mismatching target stimuli. From these data, however, it is unclear whether the difference in threshold reflects differential processing of a matching target stimulus (a) before or (b) after the target stimulus is released from interocular suppression. Gayet et al.'s (2013) experiments 2 and 3 demonstrate that when the target stimulus is not interocularly suppressed, response times do not differ between targets that match and mismatch the content of VWM. In these so-called monocular control experiments, the target stimuli are presented to the same eye as the CFS masks, and their opacity is gradually ramped up. Because the target stimuli are presented to the eye that already dominates perception, these experiments only capture differences in response time that are initiated after the interocular competition is resolved. As response times did not differ between trial types in these experiments, we concluded that the difference in response time that is obtained in conditions of interocular competition (e.g.,

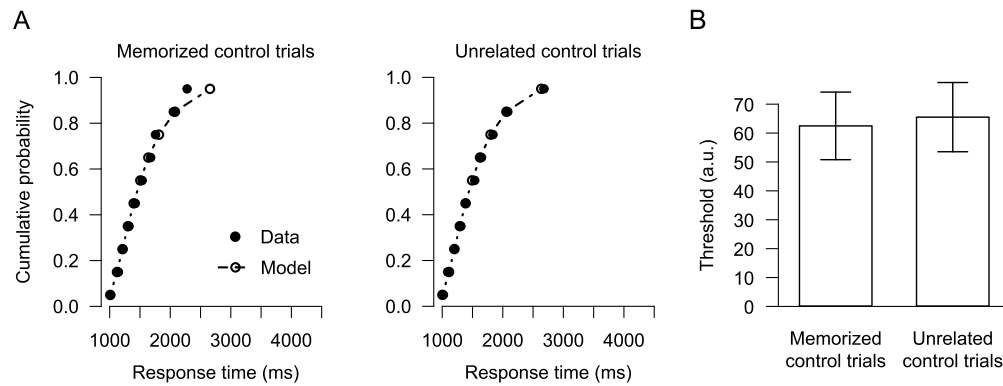


Figure 6. Model predictions and parameter estimates of the preactivation (or threshold) model, for a dataset retrieved from Gayet et al. (2013; experiment 3). On each trial, one target was presented that was either drawn from the same (Memorized trial) or a different (Unrelated trial) color category than the stimulus that participants were instructed to memorize. Importantly, target stimuli in this experiment were presented to the same eye as the masks, such that no interocular suppression was elicited. Panel A depicts the defective cumulative density of observed data and model predictions, for 10 response time quantiles (i.e., ventiles binned into deciles for illustrative purposes) averaged over participants. The y-axes represent the probability of observing a response to the target on or before a specific RT (depicted on the x-axis). The two trial types are shown in different graphs. Panel B depicts the mean parameter estimates of the preactivation model. The bars indicate the mean parameter estimates (in arbitrary units) for the threshold b for each of the two trial types. Error bars represent the standard error of the mean.

the current experiment, and experiments 1, 4, and 5 of Gayet et al., 2013) reflects a difference in suppression duration, rather than a difference in response speed to the target stimulus once it is no longer suppressed (for more elaborate discussion on this topic, see Gayet et al., 2014; Gayet, Paffen, Belopolsky, Theeuwes, & Van der Stigchel, 2016; Stein, Hebart, & Sterzer, 2011). Similarly, we aimed to assert that the lowered effective threshold for stimuli matching the content of VWM reflects a difference in processing before the target stimuli are visible. For this purpose, we reanalyzed the data of Gayet et al.'s (2013) experiment 3, in which the targets were not interocularly suppressed, by fitting it using a one-sided accumulator model (the shifted Wald model; Anders et al., 2016). In this experiment ($N = 11$), targets either matched the color category of the memorized stimulus or not (36 trials per trial type). Only correct trials (99.4%) were included in the analyses.

Results

The preactivation model, in which only the threshold b was allowed to vary between the two trial types, was nine times better in describing the observed data compared to a model in which only the accumulation rate v was allowed to vary between the two trial types (i.e., the amplification model). In this control experiment, however, the threshold b did not significantly differ between Memorized trials and Unrelated trials, as shown by a paired-samples t test, $t(10) = 1.5355$, $p = 0.1557$ (see Figure 6). We advocate caution in

interpreting these findings, however, as a Bayesian paired-samples t test revealed that the null hypothesis (both threshold values are drawn from the same distribution) is only 1.3 times more likely than the alternative hypothesis (both threshold values are drawn from different distributions). This lack of evidence for either hypothesis is indicative of having insufficient power for convincingly demonstrating the absence of a difference in the threshold parameter b between Memorized and Unrelated trials. Nonetheless, the finding that neither the difference in response times nor the difference in the threshold parameter b are significantly reduced for Memorized trials in this control experiment suggests that when targets are presented to the eye that is already dominant, the effects of VWM reported in the previous experiments are, at least partly, abolished. As such, the reduction in threshold for targets matching the content of VWM reflects a processing difference that originates before the target is released from suppression.

General discussion

Summary of the findings

The content of visual working memory (VWM) affects the processing of concurrent visual input. It has been demonstrated across multiple paradigms that visual input matching the content of VWM elicits stronger behavioral responses than visual input that mismatches the content of visual working memory

(e.g., Gayet et al., 2015; Olivers, Meijer, & Theeuwes, 2006; Pan, Cheng, & Luo, 2012). In order to elucidate the perceptual processes leading up to this phenomenon, we conducted a modified version of the b-CFS paradigm, in which stimuli matching the content of VWM have been shown to gain accelerated access to awareness (Gayet et al., 2013; Pan et al., 2014; van Moorselaar et al., 2015). This modified paradigm allowed us to implement the predictions of two hypotheses as sequential sampling models, and compared which of these quantitatively best explained the data. The preactivation hypothesis, which predicts an initial bias towards VWM matching visual input, was implemented as a model in which the threshold was allowed to vary between matching and mismatching visual input. The amplification hypothesis, which predicts a gradual enhancement of VWM matching visual input, was implemented as a model in which the slope of perceptual evidence accumulation was allowed to vary between matching and mismatching visual input. Model comparisons revealed that the data was best explained by a decrease in threshold for visual input that matches the content of VWM, thereby supporting the preactivation hypothesis. In light of this hypothesis, representations elicited by visual input rely on the same neural substrate as representations that are concurrently maintained in VWM. Consequently, the effective threshold for visual input to reach visual awareness is reduced if the visual input matches the content of VWM.

Neural basis of the preactivation account

Whereas the execution of the VWM task is operated in a top-down manner, its effect on concurrent perception is not under volitional control (Gayet et al., 2015). In line with this, the preactivation hypothesis provides a bottom-up account of the modulation of interocularly suppressed information by the content of VWM. That is, the modulation of visual processing areas, engendered by VWM maintenance, precedes the presentation of the stimulus. In contrast, one of the critical prerequisites for the alternative hypothesis, the amplification hypothesis, is that the interocularly suppressed information should at least partly transpire beyond early visual processing areas. This goes against a broad range of findings showing that interocularly suppressed information (either through CFS or binocular rivalry) is processed only to a limited extent (e.g., Lin & He, 2009; Sterzer et al., 2014; Yang et al., 2014). As such, a manipulation that modulates interocular suppression is increasingly likely to affect the processing of suppressed visual input at lower levels of the visual processing hierarchy. The present findings provide an account for the influence of working

memory on suppression duration, for which low-level visual processing of interocularly suppressed information suffices.

There are, however, two possible issues with the view that preactivation of early visual areas accounts for the preferential access to awareness of stimuli that match the content of VWM. First, the effect is categorical; that is, the target stimuli that are presented during the delay interval are never identical to those that are maintained in VWM. Rather, they are drawn from the same category (e.g., in the b-CFS paradigm, Gayet et al., 2013; van Moorselaar et al., 2015; in the binocular rivalry paradigm, Gayet et al., 2014; in attentional capture paradigms, Olivers et al., 2006; van Moorselaar, Theeuwes, & Olivers, 2014). Considering the distinction between higher and lower visual areas, as described in the previous paragraph, categorical representations of stimulus features would be expected to rely on higher level visual processing areas. One explanation is that stimuli that are sufficiently similar will elicit responses in overlapping neural populations. In this view, the enhanced response to a target stimulus that matches a concurrently memorized stimulus is not caused by its inclusion in a feature category, in which case one would expect the enhancement to be all or none (i.e., the target stimulus is either drawn from the same category as the memorized stimulus or not). Rather, the enhanced response might rely on the perceptual overlap between the target stimulus and the memorized stimulus, in which case one would expect the magnitude of response enhancement to correlate with the similarity between the memorized stimulus and the target stimulus. This latter view finds support in a recent study in which participants were primed with an auditory cue (the word *square* or *circle*) prior to performing a breaking continuous flash suppression task with so-called *squircle* stimuli (Lupyan & Ward, 2013). These are stimuli that range on a continuum that is delimited by a perfect square and a perfect circle. Shapes that matched the cue (e.g., a square after the word *square*) yielded the shortest suppression durations, and suppression durations increased linearly with decreasing resemblance between the target stimulus and the cued shape. In line with this, the present findings can be explained without resorting to categorical representations of colors. Rather, the overlap in color-space between the color of the target stimulus and the color of the memorized stimulus can account for the facilitatory effect that we observe.

The second issue is that the target stimulus was (a) presented at an unpredictable location, and (b) was never presented at the same retinal location as the to-be-memorized stimuli. In fact, in some studies using this paradigm (e.g., the current study and Gayet et al., 2013) the stimuli were separated by a degree of visual angle or more, which is more than the receptive field

size of foveal V1-V2 cells (e.g., Harvey & Dumoulin, 2011). Also, studies using related paradigms have shown various forms of enhanced processing of stimuli that match the content of VWM at even larger retinotopic distances between the to-be-memorized stimulus and the target stimulus (e.g., Olivers et al., 2006; van Moorselaar et al., 2014). In the particular case of color stimuli, one could argue that participants memorize the color per se, rather than the colored stimulus. That is, the color representation maintained in VWM is not necessarily spatially delimited, but rather virtually covers the entire visual field. Considering that the color of a presented stimulus can be decoded from early visual areas, including V1 (Brouwer & Heeger, 2009), maintaining a color in VWM could potentially bias interocular competition of colored stimuli in early visual areas. In the case of face stimuli (Pan et al., 2014) or shape stimuli (Gayet, 2016; Lupyan & Ward, 2013), however, this explanation is rather unlikely. While one could imagine retaining a color in VWM, across the visual field, this is not probable for stimuli that are defined by their spatial configuration, such as faces. For these types of stimuli, the most likely explanation is that the response enhancements of matching stimuli originate in higher visual areas with receptive field sizes that encompass the retinal distance between the target stimulus and the to-be-memorized stimulus. It is important to emphasize that, while the present finding (i.e., the difference in effective threshold rather than rate of evidence accumulation) supports a model in which the processing of the target stimulus and of the memorized stimulus rely on a shared neural substrate, it is not informative as to which processing areas this entails. It has been argued that the biasing of interocular competition finds its origin at different levels of the visual processing hierarchy (e.g., Blake & Logothetis, 2002). As such, it remains unclear at what stage of the visual processing hierarchy the contents of VWM impacts the processing of concurrent matching visual input. It is possible that the contents of VWM affects the processing of visual input in later stages of the visual processing hierarchy.

Sequential sampling models and the b-CFS paradigm

The present data reveals that VWM modulation of suppression durations in a b-CFS paradigm is driven by a reduction in effective threshold for matching visual input. This does not (necessarily) imply that other modulations of suppression durations in b-CFS paradigms are also driven by a difference in threshold between experimental conditions. For instance, the well-established finding that upright faces break through interocular suppression faster than inverted

faces (e.g., Jiang et al., 2007; Stein et al., 2011) might be driven by a higher rate of perceptual evidence accumulation (reflecting higher processing efficiency for more familiar stimuli) rather than a lower threshold (reflecting an initial bias towards any of the stimulus conditions). In contrast, differences in suppression durations between stimuli differing in low-level visual characteristics, such as luminance (Tsuchiya & Koch, 2005) or spatial frequency (Yang & Blake, 2012), might provide an initial difference in competitive strength, leading to a difference in threshold. To our knowledge, De Loof et al. (2016) and the current study constitute the first implementations of sequential sampling models in a b-CFS paradigm. Recent findings using the b-CFS paradigm ignited the discussion on the extent to which interocularly suppressed stimuli can be processed (for the full scope of the discussion, see Gayet et al., 2014; Hesselmann & Moors, 2015). We believe that sequential sampling models can be employed to gain more insights in this discussion, by modeling the behavioral data of different types of manipulations used in b-CFS experiments (including monocular control conditions). In particular, the shifted Wald model (Anders et al., 2016) allows for decomposing response time distributions into an accumulation rate and a response threshold in case of only one (meaningful) response. In the present study, we provided the first application of the shifted Wald model on an existing dataset. Importantly, fitting the one-sided shifted Wald accumulator to data from the original experiment led to a qualitatively similar pattern of results as fitting the two-sided accumulators on the data obtained with the modified paradigm. As such, the shifted Wald model allows for gaining novel insights from existing b-CFS datasets without resorting to collecting new data in a modified paradigm (tailored to the typical two-sided accumulator models). Our understanding on the scopes and limits of nonconscious perception has been clouded by the discrepancy in recent CFS findings (e.g., Gayet et al., 2014; Hesselmann & Moors, 2015). We make the case that the field could hugely benefit from such methods that allow for decomposing the perceptual processes that dictate what part of our visual world gains prioritized access to awareness.

Generalizing to other paradigms

The b-CFS method is particularly well suited to investigate how VWM modulates access to awareness because, unlike bistable perception (e.g., binocular rivalry), it allows for controlling which percept is initially dominant. Because the CFS masks are initially dominant, observers cannot know which target (i.e., matching or mismatching the content of VWM) is presented before it gains access to awareness. This

allows us to ensure that the VWM modulation of perceptual reports indeed reflects differences in access to awareness (i.e., suppression durations) of the targets, rather than criterion-driven, attention-driven, or strategy-driven effects that require conscious knowledge of the targets' identities (also, for crucial control experiments, see Gayet et al., 2013).

It remains open for debate whether or not preactivation can account for VWM influences in paradigms other than b-CFS. The main argument in favor of such generalizability is that preactivation refers to a modulation in the state of the observer preceding the initiation of the perceptual task (in which perceptual selection is measured). In addition, preactivation capitalizes on the existence of a shared neural substrate for visual representations elicited by both VWM and visual input. There is therefore no reason to assume that such a shared neural substrate is specific to the b-CFS paradigm.

Our results are in line with findings that the enhancement of visual processing by the content of VWM is immediate. For instance, VWM maintenance enhances visual processing of matching motion (250 ms; Mendoza, Schneiderman, Kaul, & Martinez-Trujillo, 2011), color (35 ms; Pan et al., 2012), and color and shape stimuli (99 ms; Soto, Wriglesworth, Bahrami-Balani, & Humphreys, 2010). Based on their data (and similar to our present conclusions), Soto and colleagues proposed that the enhanced sensitivity to (even briefly presented) VWM matching stimuli was caused by a baseline shift in the response to matching features. A recent line of research focusing on the prolonged effect of VWM content on concurrent perception of bistable stimuli (for a review, see Scocchia, Valsechi, & Triesch, 2014) provides evidence against the idea that the content of VWM has an immediate effect on concurrent stimulus processing, however. Using ambiguous structure-from-motion stimuli (Scocchia, Valsecchi et al., 2013) and binocular rivalry (Gayet et al., 2015; but see Scocchia, Valsecchi, Gegenfurtner et al., 2014) prolonged effects of VWM were observed in the absence of immediate effects, which is hard to reconcile with a preactivation account. In both studies, however, the variability in the responses was much higher in the onset measure compared to the prolonged-report measures. This raises the question of whether those studies allowed for discerning the occurrence of an immediate effect of VWM on perceptual selection. In the context of binocular rivalry specifically, it has been argued that onset rivalry (as opposed to prolonged rivalry) relies more heavily on factors that are stable over time within observer (Carter & Cavanagh, 2007). To sum up, although preactivation explicitly aims to offer a general mechanism for VWM modulations of perception, the above considerations call for caution in translating the

immediate effects of VWM reported here to other paradigms.

Conclusion

Visual input that matches the content of VWM is released from interocular suppression earlier in time than mismatching visual input. Thus far, the perceptual processes underlying this facilitatory effect were unknown. By using sequential sampling models, we were able to gain insights in the perceptual processes leading up to the moment in time at which interocularly suppressed visual input was released from suppression. Model comparisons revealed that the threshold for visual input to break through suppression is lower for visual input that matches compared to visual input that mismatches the content of VWM. This is in line with predictions of our preactivation hypothesis, which entails that the effective threshold for visual input to reach awareness is lowered, when neural populations that process the visual input are preactivated by the concurrent maintenance of a similar representation in VWM.

Keywords: visual working memory, visual awareness, continuous flash suppression, sequential sampling model, consciousness

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response speed between target stimuli matching the category of the uncued color ($M = 1696$, $SD = 589$) and to targets drawn from an unrelated color category ($M = 1713$, $SD = 712$), $t(18) = 0.0421$, $p = 0.9669$, $d = 0.010$. In addition, the difference in response times between responses to the related targets and the unrelated targets was larger in the Memorized trial types than in the Discarded trial type, $t(18) = 2.156$, $p = 0.0448$, $d = 0.453$. The results of this analysis is depicted in Figure S1. Although the present analysis is more similar to the original analysis conducted by Gayet et al. (2013), and is arguably a superior method, we can only advocate caution in interpreting an effect that is not robust to different averaging approaches.

Appendix A: Alternative response time analysis

We conducted secondary RT analyses in a way that mirrored those used by Gayet et al. (2013; experiment 4), whose findings we aimed at replicating. In these analyses, we computed average RTs for each response condition (related and unrelated), while taking into account that the different factors-of-no-interest (Eye and Postcue) also elicit different RT distributions. To account for the effect that this has on the computation of median RTs, we computed the median RT for each factor level (both factors-of-interest and factors-of-no-interest) separately, and subsequently averaged those within each response condition (related and unrelated). Conducting statistical analysis on these measures revealed patterns of significance and effect sizes that were more similar to those observed by Gayet et al. (2013; experiment 4): in the Memorized trial type, responses to target stimuli matching the category of the cued color ($M = 1680$ ms, $SD = 629$) were 285 ms (11.6%) faster than responses to target stimuli drawn from an unrelated color category ($M = 1965$ ms, $SD = 589$), $t(18) = 2.5443$, $p = 0.0203$, $d = 0.514$. In the Discarded trial type, there was no difference in

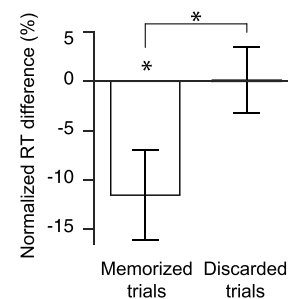


Figure S1. Alternative analysis of the normalized response time differences in the main experiment. A negative value reflects a faster response time to the related target compared to the unrelated target. Error bars represent the standard error of the mean. * $p < 0.05$

Appendix B: Losing accumulator model

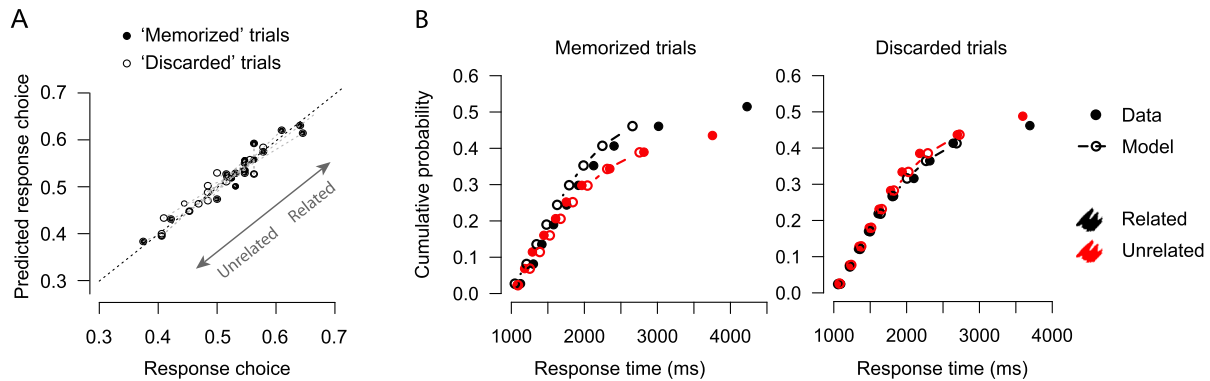


Figure S2. Model predictions of the losing amplification (or accumulator) model for the main experiment. Panel A depicts the observed (x-axis) and predicted (y-axis) fraction of trials in which participants responded to the related target. The gray dotted lines connect pairs of data points from the same participant. In comparison with Panel A of Figure 4 (depicting the winning threshold model), it appears that the losing accumulator model was slightly better at predicting the observed response choices than the winning model. Panel B depicts the defective cumulative density of observed data and model predictions, for 10 response time quantiles (i.e., ventiles binned into deciles for illustrative purposes) averaged over participants. The y-axes represent the probability of observing a response to the related target or the unrelated target on or before a specific RT (depicted on the x-axis). The two trial types are shown in different graphs. In comparison with Panel B of Figure 4 (depicting the winning threshold model), it appears that the losing accumulator model mainly failed at predicting the observed response times in the tail end of the RT distributions.