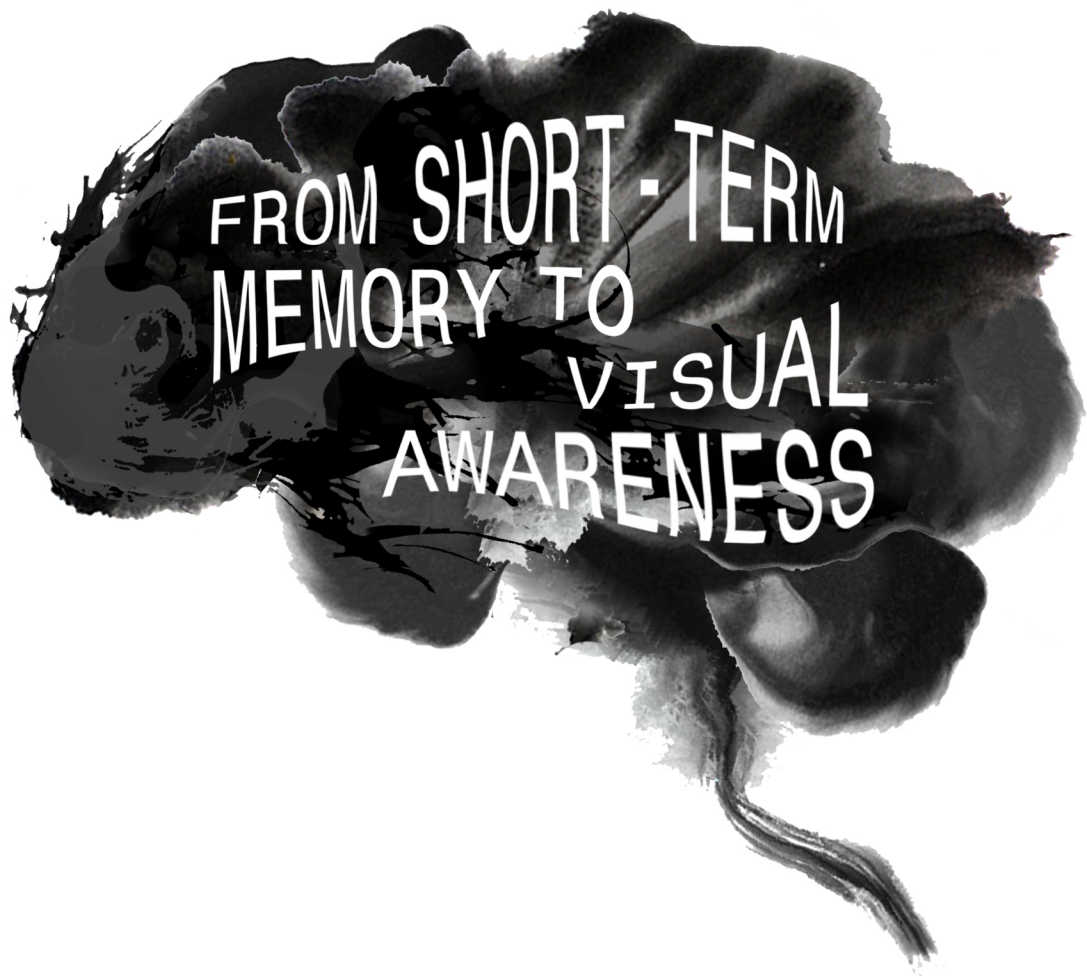


IT ALL COMES BACK TO YOU



It all comes back to you: from short-term memory to visual awareness

Het komt allemaal bij je terug: van kortetermijngeheugen tot visueel
bewustzijn
(met een samenvatting in het Nederlands)

Proefschrift

ter verkrijging van de graad van doctor aan de
Universiteit Utrecht
op gezag van de
rector magnificus, prof. dr. H.R.B.M. Kummeling
ingevolge het besluit van het college voor promoties
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Yun Ding

geboren op 13 October 1988
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Promotor:

Prof. dr. S. van der Stigchel

Copromotor

Dr. C. L. E. Paffen

Dr. M. Naber

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Chapter 1

General Introduction

Example

It was a sunny day. One of our ancestors, a hominid woman, was searching mature wild oats to feed her children among green bushes. To facilitate the visual search task, she maintained the appearance of an oat (e.g., the yellow color, elliptical shape, and size, et cetera) in her mind. When she was concentrating on the current task, at her right side, peripherally, a lion with a yellow appearance, similar in color to the mature oat seed, was sneaking out from the bushes and slowly approaching her. Even though the dangerous beast was projected to the lady's retinae, she did not get aware of the beast. She realized a bunch of oats were present at her right side later and moved her gaze to the plants, bringing the beast near her fovea which resulted in spotting the animal and being aware of the potential risks. Then she immediately climbed on a tree in front of her and successfully escaped from the danger. Her children survived because of the mother's care and the race continued...

Even though a large amount of sensory information is bombarding our brain at any moment in time, our central processing unit (i.e., brain) is not overloaded for most of the time. For instance, the sensory receptors on our skin are always stimulated with sensations such as temperature and airflow; the visual receptors on our retinæ are reacting to the light quantum when the eyes are open (and even closed), et cetera. Even though our brain is bombarded with perceptual information, only a small part of the information can enter our conscious experience at each moment (e.g., Edelman, & Tononi, 2000; Baars, 1997a; Dennett, 1991). In other words, some of the sensory information is prioritized for access to consciousness. This leads to several questions: which factors affect the priority, and how do the factors regulate the access to conscious experience? I have conducted several empirical projects to address these questions in the past four years which papers constitute the current thesis.

Understanding how we can have conscious experience and what regulates the priority of information to access consciousness has been generally attractive since it is crucial to understand human nature. Consciousness is believed to be a prerequisite for performing demanding tasks, such as decision making (see Dehaene & Nacache, 2001 for a review; Hommel, 2007; Van Gaal, Lange, & Cohen, 2012), planning (Crick & Koch, 2003), and memorizing the appearance of objects (Fahrenfort, Lamme, 2012; Treisman, 2003; Tononi & Edelman, 1998). For instance, in the initial fictitious example in the dissertation, the hominid mother needed to consciously maintain a representation of objects in mind and get aware of the lion before deciding to escape. To understand consciousness, theories were proposed by a large number of prominent researchers long before the 1990s (for a review see LeDoux et al., 2020). Since plenty of knowledge about the visual system of the brain has been gathered in the early 1990s, Crick and Koch defined a promising empirical approach to consciousness by focusing on visual awareness (Crick & Koch, 1990; 1995a; 1995b). As the terms “consciousness” and “awareness” are used without clearly defined difference in the field,

both terms are used interchangeably throughout this dissertation. Although different definitions or declarations are used in the literature (Ramsøy, & Overgaard, 2004; Dennett, 1991; Baars, 1998; 2005; Edelman & Tononi, 2000), the definition of consciousness remains controversial. There might be different orders or levels of consciousness, or different kinds of consciousness, or a single kind with non-identical features. In my view, consciousness will remain too mysterious to define if we broadly talk about the whole puzzle (e.g., consciousness *per se*). Instead, I focus on a piece of the whole puzzle, e.g., sensory consciousness in the current dissertation. Sensory consciousness is referred to the subjective experience of information perceived through the senses, as opposed to high-level consciousness, such as self-awareness, which refers to meta-cognitive states of the mind. More specifically, I focus on visual awareness in this dissertation. As Ramsøy and Overgaard (2004) reviewed, consciousness is operationalized as the ability to convey a subjective and spontaneous report of a percept. This description refers to an observer's ability to subjectively answer: "Do you see the lion? Is it a real one or just a pussy-cat?"

If the lady had encountered a lion before, she might have detected the lion earlier in her periphery than the first time. When you look at Figure 1, you might only recognize it as a pattern of randomly organized dots. If you have seen this picture before and are aware of the content it conveys, you can quickly find a spotty dog that has its head down sniffing the ground. This phenomenon suggests that our brain gets aware of visual stimuli based on previous experience (Naber et al., 2010; Suzuki & Grabowecky, 2007). Memory, suggested by the Israeli neurobiologist Yadin Dudai, is the retention of experience-dependent internal representations over time (Dudai, 1989). Typically, memory is categorized into short-term memory (STM) and long-term memory (LTM; Atkinson & Shiffrin, 1968) based on the existing duration of memory content. Working memory (i.e., WM), defined as the storage system which is responsible for maintaining ongoing relevant information, has replaced the

relatively vague concept of short-term memory (Miller et al., 1960; Baddeley, 1986; Luck and Vogel, 2013; Koch, 2004). The late biologist and Nobel laureate Gerard Edelman (1989) termed consciousness as “The remembered present”, highlighting the tight link between consciousness and WM. The neuroscientist Victor Lamme proposed a similar view by relating different forms of consciousness to different stages of working memory (Lamme, 2004). In particular, visual working memory (VWM) is a branch of WM to specifically hold visual information for imminent goal-directed behavior, allowing information to be integrated over time so that it can generate a stable representation of the external world (for a review, see Baddeley, 2003).



Figure 1. Spotty picture of a spotty dog

It has been proposed that VWM representations can improve the priority of memory congruent information for visual processing. Studies revealed that a memory congruent object attracts more attention than a memory incongruent one (Downing 2004; Hollingworth, Matsukura, & Luck, 2013; Hollingworth, & Beck, 2016; Bahle, Beck, & Hollingworth, 2018; Olivers, 2009; van Moorselaar, Theeuwes, & Olivers, 2014; Soto, Heinke, Humphreys, & Blanco, 2005; Dalvit & Eimer, 2011; Kumar, Soto, & Humphreys, 2009; for a review see Olivers et al., 2011) and biases eye movements (Schut, Van der Stoep, Postma, & Van der Stigchel, 2017; for a review see Van der Stigchel & Hollingworth, 2018). However, since

these studies explored VWM regulating visual performance when the stimuli were not suppressed from awareness, this evidence does not address whether VWM regulates the access to visual awareness or post-conscious visual processing (e.g., the visual processing *after* becoming aware of a stimulus). To what degree does the content of VWM regulate the priority of what enters awareness? Relating this back to the example at the start of this thesis, how does memorizing a yellow oat help to detect a yellow lion faster? How does the simple shape of an oat infer with becoming aware of the rather distinct shape of a lion?

Breaking continuous flash suppression & eye dominance

Quantifying the priority of a visual stimulus for access to visual awareness can help us understand the dynamics of visual awareness. For that aim, it is essential to render a visual stimulus invisible first and measure the priority of a stimulus' access to visual awareness. A number of empirical approaches have been invented to study visual awareness: degrade stimulation, visual masking, visual crowding, bi-stable figures, binocular rivalry, motion induced blindness, inattention blindness, change blindness, and the attention blink (for reviews see Kim & Blake, 2005; Sterzer et al., 2009; Stein et al., 2011; Lin & He, 2009). Binocular rivalry is a particularly elegant way to render a stimulus invisible. Let me explain what binocular rivalry entails. In daily life, we perceive our visual environment stably as our two eyes typically receive similar input from the external world. However, when the two eyes view distinct images, the two images rival for conscious visibility. This phenomenon, first reported by Porta in 1593 (Wade, 1998), is named binocular rivalry (see Figure 2 for an example; for a review see Blake, 2001). The tasks which include interocular suppression of binocular rivalry has been used to study the dynamic properties of visual awareness and its neural concomitants (Paffen & Van der Stigchel, 2010; Paffen, Naber, & Verstraten, 2008; Naber, Carter, & Verstraten, 2009; for a review, see Tong et al., 2006; Sterzer et al., 2009; Stein et al., 2011).



Figure 2. Example of a binocular rivalry task in which each eye of an observer is presented with a distinct image (e.g., a house and a grating). Observer’s conscious perception fluctuates back and forth between these two images (Blake et al., 2014). This phenomenon is termed as binocular rivalry (Alais & Blake, 2005).

The duration of a stimulus to enter visual awareness can be used to quantify its priority for access to visual awareness. For instance, a lion with high priority will result in the animal entering visual awareness sooner. It is estimated that at least 60-70ms is needed for a visual stimulus to exert a basic visual experience, as constrained by neural propagation time (Efron, 1967). Jiang and the colleagues (2007) developed a new method named breaking continuous flash suppression (b-CFS, see Figure 3 for an example) based on the classical binocular rivalry paradigm to compare the priority of different stimuli to enter visual awareness. In a b-CFS task, a target presented to one eye is suppressed from awareness initially by the dynamic pattern (e.g., masks) presented to the other eye. The duration a target takes to overcome the interocular suppression is used to quantify the priority of the target for visual awareness. Compared to other methods, b-CFS has several advantages: (i) the

suppressed images can be presented near or at the fovea, which is highly sensitive to visual information, (ii) the rather long suppression durations allow long sub- or unconscious processing of suppressed images, (iii) the suppression time can be relatively easily controlled externally (unlike binocular rivalry in which observers control the dynamics of consciousness internally). This is why this paradigm has been used to explore my research questions in the dissertation.

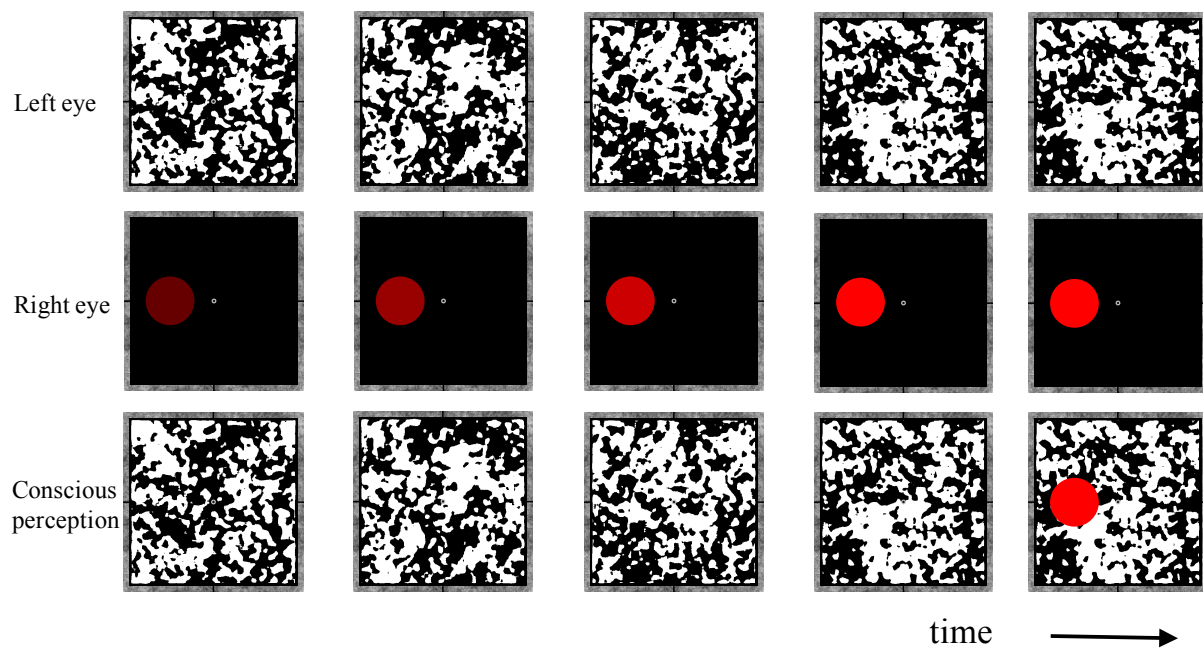


Figure 3. A schematic depiction of the sequence of events in a b-CFS trial. Dynamic masks are presented to one eye while a target ramps up to full contrast for the other eye. The target is suppressed initially and the duration for it to break interocular suppression into visual awareness can be used to quantify the priority of the target.

To ensure prolonged target suppression in a b-CFS task, previous studies have presented the dynamic masks to the dominant eye and suppressed target stimuli to the weaker eye. But what makes an eye a dominant? Researchers have used a number of methods to determine eye dominance. However, different measurements could test different aspects of eye dominance which results in a situation in which one particular eye dominance measure

does not predict the stronger eye in a b-CFS task. For instance, the different definitions of eye dominance that utilize different methods of assessment can be classified into three behavioral categories: (a) sighting dominance (e.g., a dominant eye used for sighting when looking at the distant object through a tiny hole); (b) dominance in visual functions inherent to spatial vision, such as acuity (Mapp, Ono, Barbeito, 2003; Wade, 1998); and (c) sensory dominance (i.e., the eye yielding the most prevalent or the longest percepts) during interocular suppression (Stanley, Forte, Carter, & Cavanagh, 2011; Yang, Blake, & McDonald, 2010). The most commonly used method for assessing sighting dominance for b-CFS consists of a brief and simple test (e.g., the sighting eye dominance test). It is often assumed that this form of dominance generalizes to sensory dominance, but this assumption is not supported by scientific evidence. In Chapter 2 we report an investigation into whether sighting eye dominance is truly linked to sensory eye dominance in several frequently used paradigms that involve interocular conflict. This study was performed first to ensure that we use the right type of eye dominance for the subsequent b-CFS projects reported in this dissertation.

VWM content regulates the access to visual awareness, but at which level?

The content of VWM might be a good candidate to select relevant information for access to visual awareness. For instance, a memory congruent stimulus exerts a greater influence on behavior before the stimulus enters visual awareness than a memory incongruent one (Pan, Cheng, & Luo, 2012). Combining a VWM task with a b-CFS task, researchers observed that an item that was maintained in VWM break interocular suppression to enter visual awareness faster (Gayet et al., 2013; Liu, Wang, Wang, & Jiang, 2016; van Moorselaar et al., 2017). These studies suggest that VWM regulates the priority of visual information for access to visual awareness. In other words, thinking and visualizing oat seeds will help you find them faster.

Visual information can be maintained in VWM in different forms. For instance, we can retain information about four colors, orientations or both the color and the orientation of four objects in VWM at one time (Luck & Vogel, 1997). Given that the VWM capacity is limited around four chunks, this evidence suggests that multiple features of a single item can be maintained in VWM as a bound conjunction. However, the debate whether VWM stores visual information as bound object representations or as independent features of objects is still ongoing since divergent evidence is reported by a number of subsequent studies: some studies replicate results which suggest bound object representations in VWM (Vogel, Woodman, & Luck, 2001; Luria & Vogel, 2010), whereas other studies report that memoranda are maintained as independent features (Delvenne & Bruyer, 2004; Olson & Jiang, 2002; Parra, Cubelli, & Della Sala, 2011; Wheeler & Treisman, 2002; Alvarez & Cavanagh, 2004). The multiple-resource theory assumes that there are separate pools of resources for holding features from different dimensions (Alvarez & Cavanagh, 2004; Delvenne & Bruyer, 2004; Olson & Jiang, 2002; Parra et al., 2011; Wheeler & Treisman, 2002). For example, Alvarez and Cavanagh (2004) reported that the object-based theory fails to entirely explain the VWM capacity. They argue that the VWM load is determined both by the number of objects and the number of features. Simply put, complex objects can be maintained in VWM with less accurate representations. Follow-up studies observed that features from the same dimension (e.g., color) compete for storage space while features from different dimensions (e.g., color and orientation) are maintained in parallel without competition (Wheeler & Treisman, 2002; Delvenne and Bruyer, 2004). On the other hand, the object-based theory of VWM representation suggests that the features of a memorized object are somehow linked as a bound conjunction (Vogel, Woodman, & Luck, 2001; Luria & Vogel, 2010; Balaban & Luria, 2016). These divergent findings inspired me to specifically question whether VWM regulates the priority for access to visual awareness at 1) the

individual feature levels 2) the conjunction of multiple features level or 3) the object level; and whether multiple features from different dimensions regulate access to visual awareness synergistically. These questions were investigated in Chapter 2 and 3 of this dissertation.

Do VWM and saliency interact to regulate visual awareness?

Certain visual information might be prioritized for access to visual awareness. For instance, an upright body, an upright face, and recognizable words are known to be prioritized for visual awareness as compared to other information (Costello, Jiang, Baartman, McGlennen, & He, 2009; Jiang, Costello, & He, 2007; Stein, Senju, Peelen, & Sterzer, 2011; Yang & Yeh, 2011). A particular visual stimulus interacts with the surrounding stimuli to regulate the visual processing through saliency. Saliency is a bottom-up, fast, primitive factor that biases observers to selecting stimuli based on their conspicuity and distinctiveness with respect to other stimuli in the same scene (Itti & Koch, 2000). A body of studies has found that visual awareness could be guided by this bottom-up factor. Paffen and colleagues (2008; 2010) varied the saliency of items and observed that the more salient items are more dominant to overcome interocular suppression to enter visual awareness than the less salient ones. Gayet et al. (2016, Experiment 2) replicated this effect by showing that an increase in saliency through luminance contrast shortened the time to break interocular suppression, which resulted in observers becoming aware of the originally suppressed stimuli faster. With respect to the first example of the dissertation, as the color of the lion is memory congruent and more salient than the surroundings, does VWM as a top-down factor and the saliency as a bottom-up factor synergistically prioritize the lion for the mother's visual awareness?

Previous literature has shown that saliency and VWM can interact behaviorally. For instance, items with higher saliency can be memorized better than less salient ones (Fine & Minnery, 2009; Melcher & Piassa, 2011; Santangelo & Macaluso, 2013). Furthermore, by

varying the validity of VWM content and the saliency of a target, Soto and colleagues (2006) observed that the target is detected faster by subjects when it is both memory congruent and salient, as compared to when the target was either memory congruent or salient. This demonstrates that VWM and saliency can interact to affect visual processing (e.g., attention). However, this evidence does not address whether saliency and VWM can interact to act on the priority for access to visual awareness, since the previous studies did not explore the interaction between these two factors when the stimuli are suppressed from awareness. In Chapter 4 of this thesis I explored this question.

Transsaccadic integration & the stability of visual awareness

Although a large chunk of the external visual environment can be perceived simultaneously, only the part projected to the center of the retina (i.e., fovea) enters awareness with clarity. For instance, when the items are presented at more than 30 degrees from fixation (e.g., peripheral vision), the visual sensitivity is poor due to lower densities of photoreceptors in these areas (Hansen, Pracejus, & Gegenfurtner, 2019). To still be able to explore the external world in detail, we make ballistic eye movements (i.e., saccades) around three times per minute. Remarkably, our visual system is idle to process the information during the saccade motion though the external environment is still projected to the retinae. For instance, you can never see the motion of your own eyes when you are facing a mirror (for a review, see Breitmeyer & Ganz, 1976). Thus we sample the external visual world as discrete snapshots because of the saccades. However, our visual awareness of the world is continuously stable. To maintain the stable visual awareness during a saccade, the presaccadic information needs to be consciously stored until postsaccadic visual processing commences.

Voluntarily, we can store visual information actively in VWM for a specific goal-directed task (e.g., visual search, recognition etc.). Our visual system automatically stores the presaccadic information with little effort. Older theories suspect that the presaccadic memory functions as a buffer for transsaccadic memory (Irwin, 1991; 1992), and more developed theories have argued that transsaccadic memory maintains simple visual stimuli, just like VWM (Luck & Vogel, 1997; Hollingworth & Henderson, 2002; Hollingworth & Richard, & Luck, 2008; Richard & Luck, & Hollingworth, 2008). In particular, it has been proposed that spatiotopic representations, which encode the visual world and its locations in coordinates with respect to external frames (e.g., an object of interest), contribute to visual stability (Burr & Morrone, 2011; Melcher & Morrone, 2015). Indeed, several recent studies provide evidence that visual information can be integrated across saccades to some degree (Ganmor, Landy, & Simoncelli, 2015; Melcher & Morrone, 2003; Oostwoud-Wijdenes, Marshall, & Bays, 2015; Wolf & Schütz, 2015; Fabius et al., 2016). These studies suggest that information of the external world is stored for postsaccadic conscious processing. Although a number of studies have explored the integration of the presaccadic information and postsaccadic information, it is currently unclear whether the prioritization for the processed presaccadic information survives for visual awareness across saccades. In Chapter 6 I investigated this question.

Thesis outline

In chapter 2 of this dissertation, I investigated whether the most commonly used sighting eye dominance determined by the hole-in-the-card test is predictable for the sensory eye dominance in a b-CFS task that involves interocular conflict. Several frequently used interocular conflict paradigms were also used to measure eye dominance and to study whether the unbalance between two eyes is expressed differently across these paradigms. The

outcome of this project suggested which measurement of eye dominance is best suited to define the dominant eye in the main b-CFS tasks.

In Chapter 3 and 4, I investigated whether VWM regulates the priority of an item for visual awareness along a single feature dimension, the conjunction of multiple features dimension or the object dimension; and whether the features of a single object from different feature dimensions regulate access to visual awareness synergistically (i.e., as a bound entity). This evidence would extend our understanding of the architecture of VWM and the pathway that memoranda of congruent visual input use to access visual awareness.

Our visual awareness can be guided both by top-down factors and bottom-up factors. To expand our understanding of these factors and how they affect visual awareness processing we studied, in Chapter 5, whether VWM and visual saliency, as a top-down factor and a bottom-up factor respectively, interact to regulate access to visual awareness.

Although saccades basically pause the visual system from sampling the external world, our visual awareness is stable across saccades. Transsaccadic memory is proposed as a short-term memory that maintains visual information to some extent to facilitate visual stability. Chapter 6 was conducted to explore whether the priority of visual information for access to visual awareness is either reset by each saccade or continuous across saccades because of transsaccadic memory.

With these experiments we cover the most important aspects known to affect visual attention, working memory, and awareness with the all-encompassing goal to study the prerequisites and dynamics of becoming aware of visual information.

2

Chapter 2

Assessing the generalizability of eye dominance across binocular rivalry, onset rivalry, and continuous flash suppression

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Author contributions:

All authors designed the study concept. YD programmed the experiment and tested the observers, YD conducted the analyses and wrote the manuscript.

Critical revisions were provided by all co-authors.

Abstract

It is commonly assumed that one eye is dominant over the other eye. Eye dominance is most frequently determined by using the hole-in-the-card test. However, it is currently unclear whether eye dominance as determined by the hole-in-the-card test (so-called sighting eye dominance) generalizes to tasks involving interocular conflict (engaging sensory eye dominance). We therefore investigated whether sighting eye dominance is linked to sensory eye dominance in several frequently used paradigms that involve interocular conflict. Eye dominance was measured by the hole-in-the-card test, binocular rivalry, and breaking continuous flash suppression (b-CFS). Relationships between differences in eye dominance were assessed using Bayesian statistics. Strikingly, none of the three interocular conflict tasks yielded a difference in perceptual report between eyes, when comparing the dominant eye with the non-dominant eye as determined by the hole-in-the-card test. From this we conclude that sighting eye dominance is different from sensory eye dominance. Interestingly, eye dominance of onset rivalry correlated with that of ongoing rivalry, but not with that of b-CFS. Hence, we conclude that b-CFS reflects a different form of eye dominance than onset and ongoing rivalry. In sum, eye dominance seems to be a multifaceted phenomenon, which is differently expressed across interocular conflict paradigms. Finally, we highly discourage using tests measuring sighting eye dominance to determine the dominant eye in a subsequent experiment involving interocular conflict. Rather, we recommend that whenever experimental manipulations require a priori knowledge of eye dominance, eye dominance should be determined using pre-trials of the same task that will be used in the main experiment.

Keywords: eye dominance, hole-in-the-card test, interocular conflict, onset rivalry, ongoing rivalry, b-CFS

Introduction

When viewing through a small aperture or when aiming to throw a dart, we generally experience a preference for using either our left or right eye. This preference for using one eye over the other is generally defined as ‘eye dominance’. On a physiological level, Coren and Kaplan (1973) regarded (eye) dominance to be the result of any sort of physiological preeminence, priority or preferential activity of one member of a bilateral pair of organs.

Researchers have utilized several methods to determine eye dominance. The different definitions of eye dominance that follow from these different methods of assessment can be classified into three behavioral categories: 1. sighting dominance (e.g. a dominant eye used for sighting when looking at a distant object through a hole), 2. dominance in visual functions inherent to spatial vision, such as acuity (Mapp, Ono, & Barbeito, 2003; Wade, 1998), and 3. sensory dominance (i.e., the eye yielding the longest or most prevalent percepts) during interocular conflict (Stanley, Forte, Carter, & Cavanagh, 2011; Yang, Blake, & McDonald, 2010). In the clinic, the dominant eye is usually determined by using the first method (the ‘hole-in-the-card test’). When an object is viewed with both eyes through an aperture placed at about an arm distance, the retinal images of the eyes differ. Because of this perceptual difference, one eye dominates the other eye in order to see a single, coherent picture of the object. When the dominant eye is closed during the test, the percept of the object is suddenly displaced because the non-dominant eye with the other retinal image becomes visible. A visual displacement after closing one eye is thus indicative of eye dominance in the hole-in-the-card test. The second method also reveals a clear bias towards one of the two eyes, both in terms of a consistent difference in far and near visual acuity between the eyes (Bausch and Lomb Orthorator, Rochester, NY). The third method relies on binocular rivalry: alternations of perception that arise when dissimilar images are presented to the same retinal location of both eyes. This method reveals that the image presented to one eye tends to consistently

dominate perception over the image presented to the other eye (e.g. Blake & Logothetis, 2002). In addition, Wolfe (1983) reported that an initial fused image of the two monocular images will be quickly replaced by the perception of only one of the two images, a phenomenon called onset rivalry. Ongoing rivalry will start if the participant continues to view the images. As with the first two methods, a preference for recruiting one eye over the other can be observed with these phenomena: a stimulus presented to a specific eye can produce the most frequently reported percept during onset rivalry. Likewise, the stimulus presented to a specific eye can be the most dominant percept during ongoing rivalry (assessed by the frequency or duration of the dominant percept).

Recently, researchers started employing a novel experimental paradigm that is related to the phenomenon of binocular rivalry. Tsuchiya and Koch (2005) presented a static target to one eye and a dynamic mask to the other eye, causing perceptual suppression of the static stimulus (i.e., Continuous Flash Suppression, or CFS). In a variation of this paradigm, researchers measure the time it takes before a static target image is released from suppression and, thus, is perceived (breaking CFS, or b-CFS; Jiang, Costello, & He, 2007; Stein, Hebart, & Sterzer; Gayet, Van der Stigchel, & Paffen, 2014). In this paradigm too, a consistent imbalance for one of the two eyes can be observed: on average, a target image presented to one eye is released from suppression earlier in time than the same target image presented to the other eye. The eye eliciting a shorter suppression duration is then labelled as the dominant eye.

In the current study, we aim to investigate to what extent different forms of sensory eye dominance (as engaged by interocular conflict), and sighting eye dominance (as measured by the hole-in-the-card test) are related. We are not the first to address this question: It is commonly assumed that eye dominance measured by different methods shares general properties. Valle-Inclan, Blanco, Soto and Leiros (2008), for example, reported a

statistically significant correlation ($r = 0.375$) between the dominant sighting eye and dominance in onset rivalry. Yang et al. (2010) observed correlations between sighting eye dominance, acuity scores, and dominance durations during b-CFS. However, earlier studies were more cautious in generalizing across different methods for measuring eye dominance. For example, Coren and Kaplan (1973) found consistencies as well as inconsistencies across 13 different eye dominance tests. They therefore claimed that eye dominance is a multifaceted phenomenon, and suggested that it is important to specify which type of dominance is being referred to. More recently, Mapp et al. (2003) reviewed studies measuring eye dominance and concluded that the sighting task is constrained by the fact that only one eye can be used, and that the sighting dominant eye for this task reflects the ease or habit of using this eye for such viewing behavior task (Barbeito, 1981; Ono & Barbeito, 1982). It is important to note that even in Yang et al.'s study (2010), the correlations between preferred sighting eye dominance and eye dominance measured by b-CFS were weak, which suggests that eye dominance as measured by the different methods (preferred sighting eye test and b-CFS) could have similar but not necessarily identical underlying mechanisms.

Many have suggested that differences in the outcomes of paradigms inducing interocular conflict (onset rivalry, ongoing rivalry and (b-)CFS) are also caused by factors other than eye dominance. Leat and Woodhouse (1984), for example, reported that the location of the stimuli on the retinae influences the dominance of onset and ongoing rivalry tasks differently. Also, strong and stable localized biases in perceptual dominance that vary across the visual field have been reported both within and between participants in onset rivalry tasks, but not in ongoing rivalry tasks (Carter & Cavanagh, 2007; Stanley et al., 2011). Based on this, Stanley et al. (2011) concluded that the properties of onset rivalry differ significantly from those of ongoing binocular rivalry and may, in fact, be caused by distinct mechanisms. When comparing CFS and ongoing rivalry, Tsuchiya, Koch, Gilroy, & Blake

(2006) reported that CFS is not only a stronger version of binocular rivalry, but is also affected by the accumulated suppressive effects of multiple flashes, suggesting that CFS could be caused by mechanisms that are different from those involved in onset rivalry and ongoing rivalry.

In sum, only weak correlations have been observed between different methods for assessing eye dominance, and different variations of interocular conflict elicit varying perceptual experiences. Nonetheless, researchers still interchangeably utilize different methods for assessing eye dominance, relying on the tacit assumption that applying one method to assess eye dominance will reveal the same dominant eye as applying another method. Examples of these include studies measuring eye dominance with the preferred sighting eye test (Handa et al., 2004; Salomon, Lim, Herbelin, Hesselmann and Blanke, 2013), onset rivalry (Valle-Inclán, Blanco, Soto and Leirós, 2008), ongoing rivalry (Hastorf & Myro, 1959; Washburn, Faison, & Scott, 1934) and b-CFS (Yang et al., 2010). A potentially more troublesome situation arises when researchers determine eye dominance using one method, and then apply this information in a subsequent part of the experiment in which another method is used (e.g., to elicit b-CFS of the non-dominant eye only). Examples of this include studies in which eye dominance is first established with the hole-in-the-card test, after which this information is utilized in a main experiment involving interocular conflict (e.g., Mastropasqua, Tse and Turatto, 2015; Moors, Wagemans and de-Wit, 2014; Yokoyama, Noguchi and Kita, 2013). The question thus remains whether this approach is valid.

Using different methods to assess eye dominance is only warranted if the different methods produce the same outcome: one method should produce the same result as to which eye is dominant as any other method. In order to investigate whether different measures are correlated, we assessed eye dominance with four methods: the hole-in-the-card test, onset

rivalry, ongoing rivalry and b-CFS. Importantly, we kept the stimuli and procedure in the different methods as similar as possible, thereby allowing us to make a fair comparison between methods. We used two distinct approaches to assess the relationship between the different types of eye dominance. First, we tested whether eye dominance measured in the three tasks involving interocular conflict (onset rivalry, ongoing rivalry, and b-CFS) systematically differed between the observers' dominant eye and non-dominant eye as measured by the hole-in-card test. Second, we tested to what extent eye-dominance in the three tasks involving interocular competition were related to one another.

Method

Subjects

Sample size was determined online using an optional Bayesian stopping rule. We set out to test a minimum of 20 participants, and until at least one of our tests resulted in a Bayes factor of 6 (in favor of either the null or the alternative hypothesis), or until we ran out of participants. Thirty-five subjects took part in the current study for monetary reward after signing informed consent. Two subjects aborted the experiment before the end and another two subjects did not follow instructions (i.e., they forgot which response to give) and were therefore excluded from the analyses. The ages of the remaining subjects ranged from 18 to 33 years old ($M = 24.2$, $SD = 3.24$, 19 females). All the subjects reported having normal or corrected-to-normal vision and having no visual disorders or epilepsy.

Apparatus

The study was conducted on 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) in a dark room. Stimulus presentation and response collection were created in MatLab (R2009b; MathWorks, Natick, MA) using the PsychToolbox extension (Brainard, 1997; Pelli, 1997). A mirror stereoscope mounted on a chinrest was used to achieve dichoptic presentation. The viewing distance was 57 cm.

Stimuli and procedure

The subjects conducted four different tasks in the following order: b-CFS, onset rivalry, ongoing rivalry, and the hole-in-the-card test to determine eye dominances. Subjects could take a break between the tasks.

b-CFS

As explained in the introduction, b-CFS consists of the presentation of a target image to one eye and a dynamic mask to the other eye (Figure 1). We generated 50 different binary masks (0 and 27.3 cd/m² for the black and white parts, respectively) consisting of pink noise images filtered by a Gaussian low-pass filter ($\sigma = 3.2$) (Gayet et al., 2014). We presented the masks for 100 ms each (10 Hz) in random order. For the targets we used 45° oriented (counter clock-wise (CCW) or clock-wise (CW) from vertical) sinewave gratings with a diameter of 2° and spatial frequency of 2 cycles per degree. The presentation areas in both eyes were enclosed by an identical Brownian (i.e., $1/f^2$) noise frame with sides of 8° and a width of 1° to facilitate binocular fusion of the dichoptic images. We also presented gray dots sized 0.5° at the center of the visual field of both eyes to help subjects keep fixating.

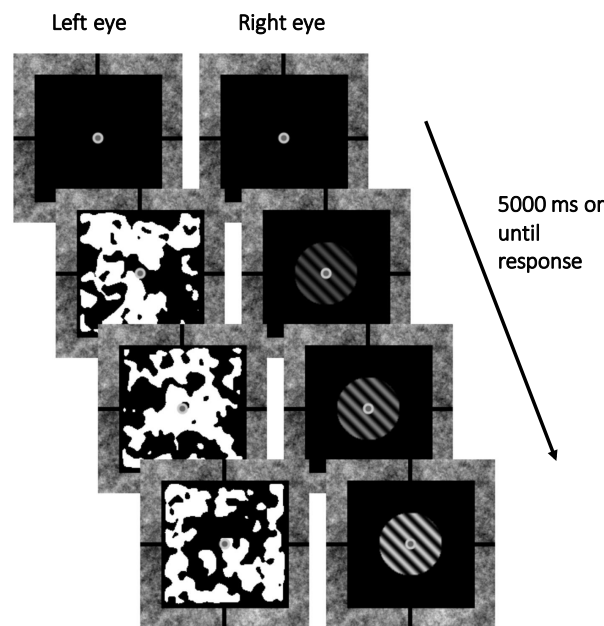


Figure 1. A schematic depiction of the sequence of events in a b-CFS trial. Subjects were instructed to keep gazing at the central gray dot and to indicate the orientation of the grating as fast and accurately as possible after it became visible.

After subjects had read the instructions and understood the task requirements, they performed an eye-alignment task in which stimulus position was calibrated for proper fusion. Then subjects performed 8 practice trials, followed by 96 test trials. Subjects started each trial by pressing the space bar. The sequence of events of a single trial is shown in Figure 1, consisting of the presentation of a mask to one eye and the presentation of the target stimulus to the other eye. The Michelson luminance contrast of the target grating was linearly increased from 0% to almost full contrast (98%) within one second to ensure that the target was first suppressed by the mask and did not break through abruptly at the start of the trial. The subjects were instructed to keep fixating at the central gray dot and to respond to the target orientation by pressing a button as fast and accurately as possible (left-arrow for counter clockwise; right-arrow for clockwise). Each trial lasted until a response was given or when 5 s without a response had passed. The trials were separated by an inter-trial interval of 500 ms. The trials in which no response was given were recycled at the end of the task (i.e., performed again). The b-CFS task consisted of 2 blocks, each containing 48 trials. We counterbalanced the eye to which the stimuli were presented, and the trial order was randomized for each participant.

Onset Rivalry

The stimuli and procedure of the onset rivalry experiment were similar to those of the b-CFS experiment. In this experiment, two target gratings (98% Michelson luminance contrast) with different orientations were presented dichoptically (see Figure 2). The subjects were instructed to report which orientation they perceived first by pressing either the left (CCW) or right (CW) arrow button. Each trial lasted for 5 s or until a response was given. Stimulus presentation was counterbalanced across eyes, and trials were separated by a 5 second fixation interval (based on Leopold, Wilke, Maier, & Logothetis, 2002) to minimize potential history effects of previous percepts on subsequent percepts (Blakemore, & Nachmias, 1971).

After 8 practice trials, the subjects finished a total of 80 trials which were separated into 2 blocks. The trials in which no response was given were recycled.

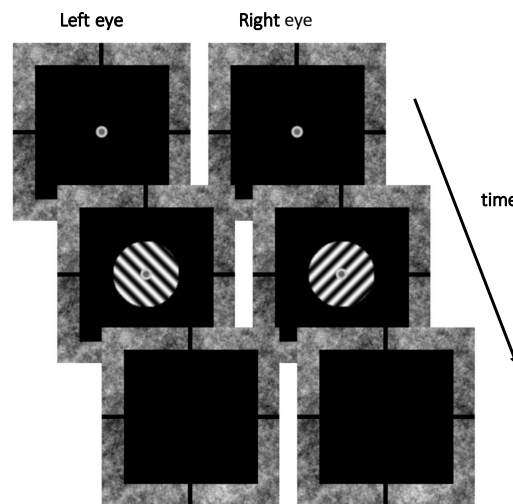


Figure 2. Stimuli used in the onset and ongoing rivalry experiments. The subjects were required to keep fixating at the center dot and to report the first orientation in the onset rivalry experiment and to continuously report the dominant orientation in the ongoing rivalry experiment.

Ongoing Rivalry

The stimuli used in this experiment were identical to those used in the onset rivalry experiment, except for the duration of the target display (60 s instead of 5 s). The subjects were instructed to continuously indicate which orientation was the dominant percept by pressing and holding one of two arrow buttons (left arrow button for CCW; right arrow button for CW). The subjects performed 4 practice trials and 12 test trials.

Hole-in-the-card test

In this experiment, the dominant sighting eye was determined by using the hole-in-the card test (Mile 1929 & 1930; Yang et al., 2010). The subject stretched both arms in front of the face and created a little triangular porthole with his/her thumbs and index fingers. Next, the subject was instructed to look at a small object fixed in the room through the center of the porthole with two eyes open. After this, the subject reported whether the object was still

visible with one eye closed while keeping the hands and head static. When closing one eye (say the right) kept the object visible, the other eye (in this case the left) would be the dominant eye.

Analysis

After removing the data of subjects who failed to understand the instruction or finish all the tasks, the data of 31 subjects was analyzed. Performance in the b-CFS tasks was good: subjects reported the correct orientation in 98.06% (93.75% as the lowest) of the trials. To compare the data between different experiments, we calculated for each subject a so-called dominance index, reflecting perceptual dominance of one eye relative to the other:

- for the b-CFS task, the right eye's median RTs were divided by the sum of the two eyes' median RTs;
- for the onset rivalry task, the number of responses corresponding to the stimulus being presented to the left eye were divided by the total number of trials;
- for the ongoing rivalry task, the median durations of the left eye were divided by the sum of the two eyes' median durations.

The resulting ratios index the relative dominance of the right eye: a value smaller than 0.5 means that a stimulus presented to the right eye (1) broke suppression faster than one presented to the left eye in the b-CFS task; (2) was more often the first percept in the onset rivalry task; (3) and was perceived longer than that presented to the left eye in the ongoing rivalry task. In each case, a value smaller than 0.5 indicates that the dominance of the right eye is stronger than that of the left eye.

For our main statistical analyses, we conducted non-directional Bayesian paired-sample t test or tests (standard Cauchy prior width of 0.707; JASP, 2017), and Bayesian pairwise correlations to support (standard Beta prior width of 1; JASP, 2017). This allows for

providing statistical support for the alternative hypothesis ($BF_{10} > 3$)), as well as for the null hypothesis ($BF_{10} < 0.33$; Dienes, 2014; Jeffreys, 1961).

Results

Results b-CFS

The results showed that one subject had an extremely dominant eye in the b-CFS task (4.02 SD from the mean dominance index, Mahalanobis distance of 11.23), which led us to exclude the subject from further analyses. Figure 3b illustrates the distribution of eye dominance across subjects for the three indices introduced above. When using the index for the b-CFS task, 66.67% subjects were categorized as having a right dominant eye and the rest (33.33%) having a left dominant eye (Figure 3b). The finding that the right eye is dominant over the left eye in b-CFS is in line with a previous study (Yang et al., 2010).

The mean RT observed in the b-CFS task was 1.33 seconds ($SD = 0.68$). Subjects perceived the grating slightly faster in trials when it was presented to the right eye (mean 1.30 seconds; $SD = 0.72$) than when it was presented to the left eye (mean 1.36 seconds; $SD = 0.65$), but the evidence for this difference was statistically inconclusive ($BF_{10} = 0.55$).

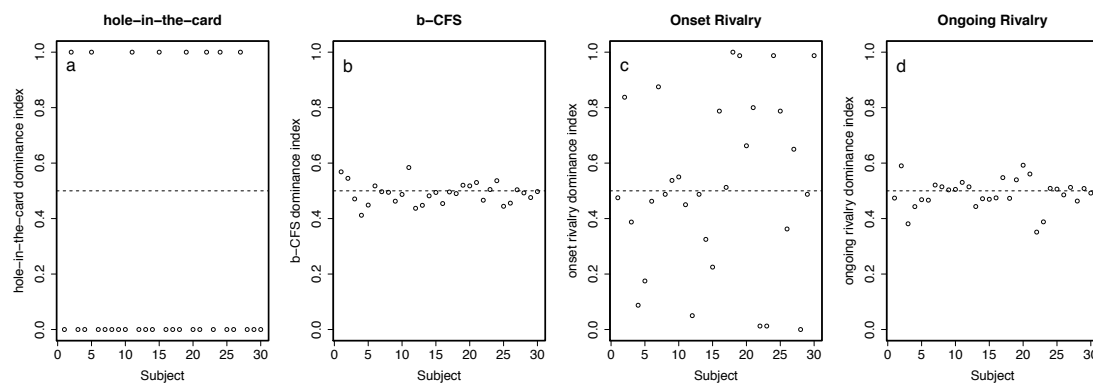


Figure 3. Eye dominance as measured by the hole-in-the-card test (0 stands for right eye dominant and 1 stands for left eye dominant), b-CFS (ratio between right eye RT and the sum of left eye RT and right eye RT), onset rivalry (ratio between left eye perceived trial number

and all the trial number), ongoing rivalry (ratio between left eye duration and the sum of left eye and right eye durations). For all the four plots, a dominance index smaller than 0.5 indicates right eye dominance.

Results Onset rivalry

The number of subjects categorized as having a right dominant eye (53.33%) was slightly greater than the number of subjects categorized as having a left dominant eye (46.67%) (Figure 3c). A Bayesian t-test showed that the eye to which the stimulus was presented did not affect which grating was perceived (left eye perceived trial number: mean, 51.50%) or right eye (right eye perceived trial number: mean 48.50%; ($BF_{10} = 0.20$)).

Results Ongoing rivalry

We measured the dominantly perceived grating durations by each eye as the dependent variable. The first and last reported dominance durations in each trial were excluded from the analyses to exclude truncated percepts. The results are presented in Figure 3d. Based on the index introduced above, we did not observe an eye dominance preference in ongoing rivalry since 50% of the subjects had longer left eye and 50% had longer right eye dominance durations. The Bayesian t-test ($BF_{10} = 0.3$) provided support for the absence of a difference between left and right eye dominance durations (left eye mean: 2.96 seconds; right eye mean: 3.12 seconds)¹.

Hole-in-the-card test

¹ In the ongoing rivalry task, mixed percepts were not recorded. To assess whether such mixed percepts affected our results, we ran a control experiment in which ten new participants (5 females) reported not only exclusive percepts, but also mixed percepts during ongoing rivalry. The results show that participants reported mixed percepts for only a limited proportion of the time (mean proportion: 12.83%; SD = 10%). After removing the mixed percepts, and in line with our original findings, the median phase duration did not differ between the dominant and the weak eye (as measured by the hole-in-the-card test), $BF_{10} = 0.41$.

In the hole-in-the-card test, there were more subjects that used their right eye (73.33%) as their sighting eye, $\chi^2(1) = 6.53$, $p = 0.01$. To test whether the sighting eye dominance affected the dominance measurements in the three interocular conflict tasks, we compared the eye dominance indices within these interocular conflict tasks between the sighting dominant and sighting non-dominant eye. The data provided support for the null hypothesis (i.e., no difference) for onset rivalry and ongoing rivalry, but were inconclusive for b-CFS (b-CFS: $BF_{10} = 1.89$; Onset rivalry: $BF_{10} = 0.20$; Ongoing rivalry: $BF_{10} = 0.26$), which means that sighting eye dominance (as determined with the hole-in-the-card test) did not reliably predict eye dominance in the interocular conflict tasks.

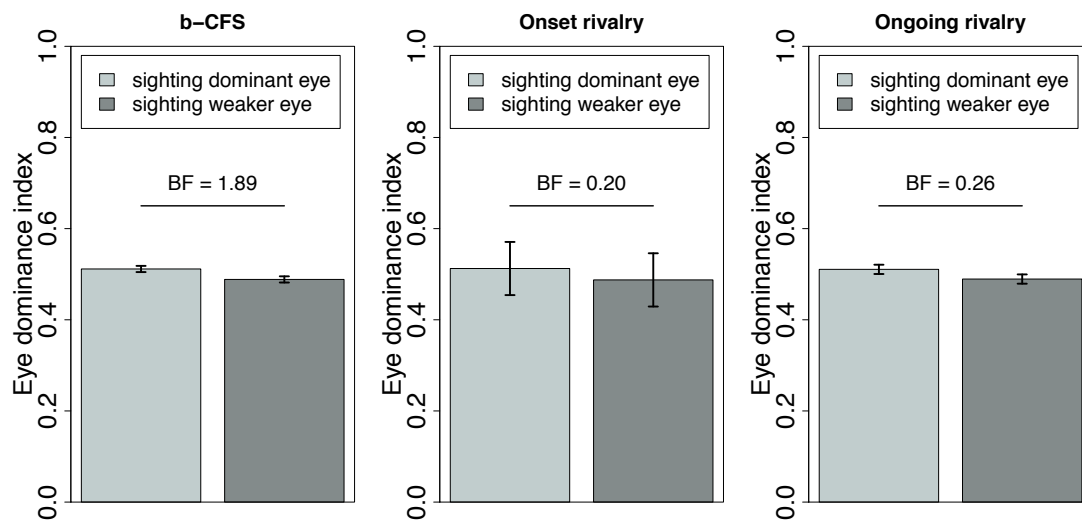


Figure 4. Sensory Eye dominance index of b-CFS, onset rivalry, and ongoing rivalry separated for the dominant (light gray) and non-dominant (dark gray) sighting eye. Error bars depict the standard error of the mean.

Correlations

Bayesian Pearson correlations between the hole-in-the-card test and the interocular conflict tasks and their corresponding Bayes factors are displayed in Table 1. The Bayes factors can be classified as statistically inconclusive for the correlation between b-CFS and the hole-in-the-card-test ($BF = 1.26$), and as evidence for the null-hypotheses (no correlation) for the correlations between the hole-in-the-card test on the one hand, and onset ($BF = 0.35$) and ongoing rivalry ($BF = 0.36$) on the other. This conclusion is further illustrated by sequential analyses of Bayes Factors for the correlations between b-CFS and the hole-in-the-card test (Figure 5a), onset rivalry and the hole-in-the-card test (Figure 5b), and between ongoing rivalry and the hole-in-the-card test (Figure 5c). These results provide evidence that sensory eye dominance, as measured with onset rivalry or ongoing rivalry, does not correlate with sighting eye dominance as measured with the hole-in-the-card test, and that this absence of a correlation cannot be explained by a lack of experimental power. Furthermore, the results show that the correlation between b-CFS and the hole-in-the-card test is weak at most.

Table 1. Correlations between the eye dominance index measured by the hole-in-the-card test and the three interocular conflict tasks.

	b-CFS	onset rivalry	ongoing rivalry
Hole-in-the-card	0.33 ($BF = 1.26$)	0.05 ($BF = 0.35$)	0.07 ($BF = 0.36$)

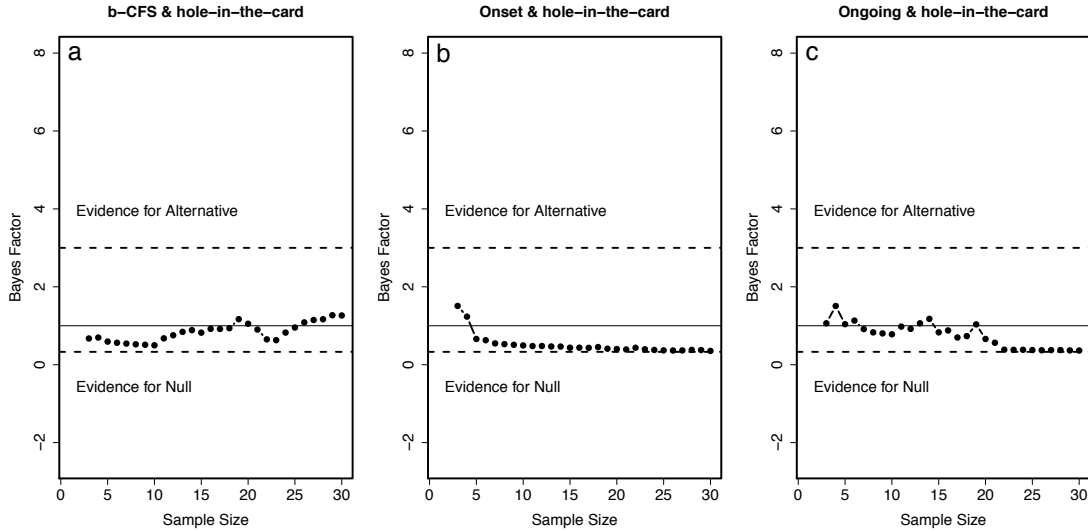


Figure 5. The sequential analyses of Bayes Factors for correlations between sighting eye dominance and b-CFS dominance (a), onset rivalry dominance (b), and ongoing rivalry dominance (c).

To explore whether different experimental paradigms that engender interocular conflict measure the same underlying factor (i.e., a generalized form of sensory eye-dominance), we conducted correlations between the dominance indices obtained from the three tasks involving interocular conflict. We report Pearson’s correlations here since Shapiro-Wilk test suggested the eye dominance indices in the interocular conflict tasks were normally distributed (b-CFS: $p = 0.88$; onset rivalry: $p = 0.11$; ongoing rivalry: $p = 0.18$). As illustrated in Figure 6, the results showed a convincing positive correlation between onset rivalry dominance and ongoing rivalry dominance ($r = 0.57$, $BF_{10} = 29.0$). This indicates that approximately 30% of the variance in eye dominances is shared between ongoing and onset rivalry. The correlations between b-CFS dominance and onset rivalry dominance ($R = 0.36$, $BF_{10} = 1.6$), and between b-CFS dominance and ongoing rivalry dominance ($R = 0.41$, $BF_{10} = 2.5$), were of the expected direction, but were statistically inconclusive.

To further investigate the robustness of these test results, we plotted the evolution of the Bayes Factors after addition of each new subject. These plots confirm that there is no convincing correlation between b-CFS dominance and onset rivalry dominance (Figure 7a), but also suggest that the correlation between b-CFS dominance and ongoing rivalry dominance might eventually emerge with the addition of more participants (Figure 7b). Importantly, however, the evidence for a relation between sensory eye dominance as measured by these different experimental paradigms is clearly weaker than what would be expected if they were fully supported by a single generalized type of sensory eye dominance.

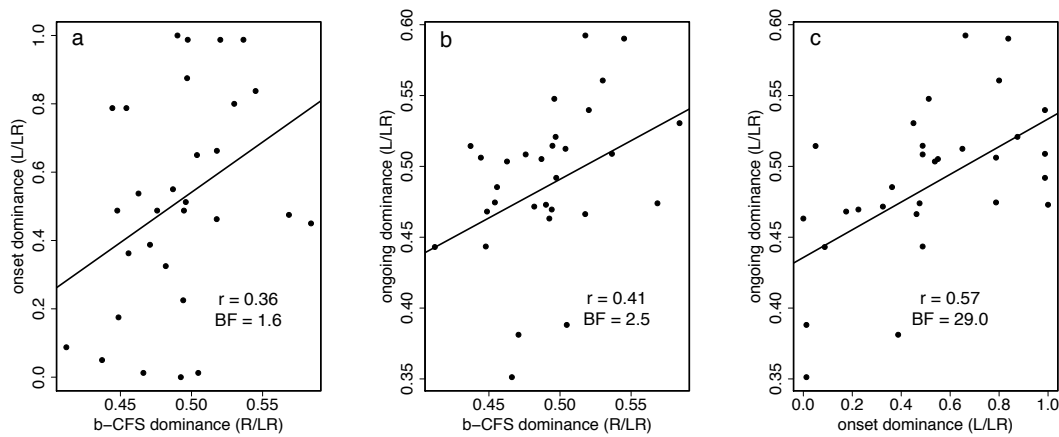


Figure 6. (a) The correlation between the b-CFS dominance index and the onset rivalry dominance index; (b) The correlation between the b-CFS dominance index and the ongoing rivalry dominance index; (c) The correlation between the onset rivalry dominance index and the ongoing rivalry dominance index.

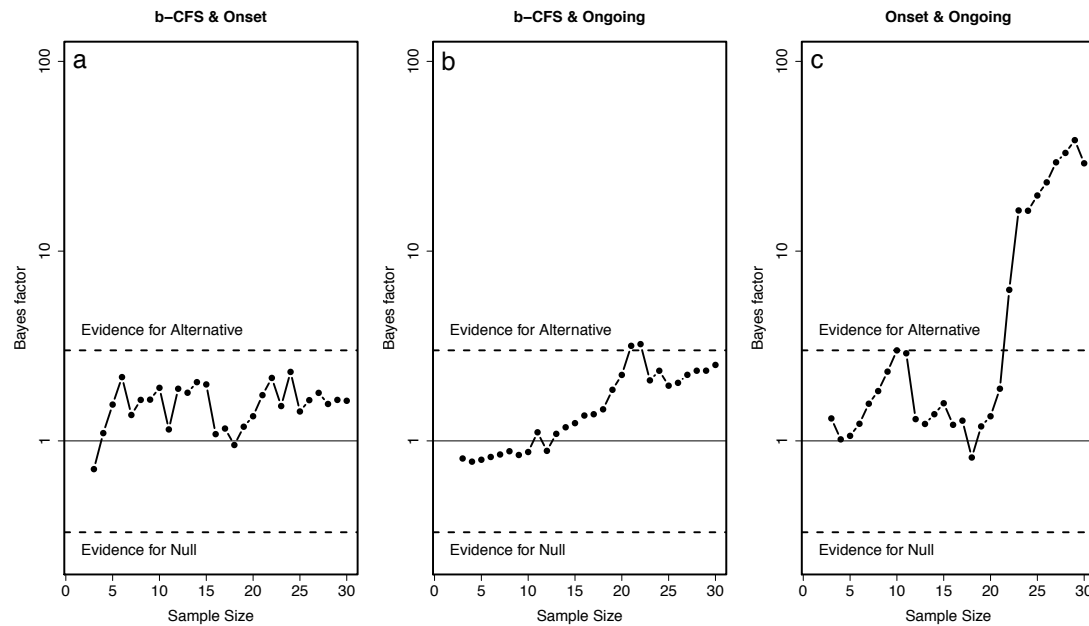


Figure 7. The sequential analyses of Bayes Factors for the correlational analyses between CFS dominance and onset rivalry dominance (a), b-CFS dominance and ongoing dominance (b), and onset rivalry dominance and ongoing rivalry dominance (c).

Following these quantitative analyses, we also investigated to what extent the different eye dominance measures employed in this study yield qualitatively different classifications of eye dominance. To do so, we computed for each pair of interocular suppression tasks the percentage of matching classifications (i.e., both measures classify a participant as being left-eye or right-eye dominant), and of mismatching classifications (i.e., one measure classifies the participant as right-eye dominant, whereas the other measure classifies the participant as left-eye dominant). Mismatching classification rates between pairs of methods ranged between 23.3% and 43.3%, with the most extreme example showing that only 56.7% of participants that were classified as left or right-eye dominant with the hole-in-the-card test, exhibited the same eye as dominant in the ongoing rivalry task (see Supplementary Tables for a full overview of classifications between pairs of tasks).

Effects of task order

We did not randomize the task order in the current study. Together with the fact that we used naïve observers, one could wonder whether practice effects might have influenced the results. To investigate this, we compared the dependent measures per eye for the first half of trials and second half of trials. Breakthrough times in b-CFS (LE: $BF = 0.23$; RE: $BF = 0.23$), number of percept onsets (LE: $BF = 0.32$; RE: $BF = 0.32$), and dominance durations in ongoing rivalry (LE: $BF = 0.25$; RE: $BF = 0.21$) did not differ between the first and second half of trials, implying that our measures were not affected by the effect of practice.

Effects of task requirements

In the ongoing rivalry task, the participants were required to continuously indicate the perceived dominant orientation. However, enduring interocular conflict typically also included phases in which neither one of the images was dominant in perception. Our final analysis was concerned with the question of whether these so-called mixed percepts or piecemeal rivalry confound our results. To evaluate the potential impact of piecemeal rivalry on our findings, we recalculated the dominance indices from a modified data set in which we treated 50% of the dominance durations as mixed percept (as could be expected for ongoing rivalry between stimuli with a diameter of 2 degrees, based on O'shea et al., 1997). Mixed percept time was not assigned to one of the eyes since we counterbalanced the rivalry inducers' orientation for both eyes, meaning that dominance durations for the left and right eye were equally reduced by 25% of the average dominance duration. This data transformation resulted in a new set of dominance indices for the ongoing rivalry task. Similar to the original results, the piecemeal-corrected dominance indices of ongoing rivalry did not correlate with the other interocular task indices (b-CFS: $r = 0.42$, $BF = 2.87$; Onset

rivalry: $r = 0.57$, $BF = 29.47$). These results show that mixed percepts did not confound our results.

Discussion

This study was conducted to investigate whether the hole-in-the-card test, onset rivalry, ongoing rivalry, and b-CFS tasks indicate similar biases in eye dominance. In line with previous studies (Weinman & Cooke, 1982; Yang et al., 2010), we evaluated eye dominance by calculating the relative eye dominance indices between the eyes, which allowed us to assess imbalances in binocular strength quantitatively. We observed no consistent effect of sighting eye dominance on eye dominance in the three interocular conflict tasks. Specifically, using Bayesian statistics allowed us to establish that perceptual reports in the two rivalry tasks did not differ between the dominant and non-dominant eye, as measured by the hole-in-the-card test, and that reaction time for b-CFS was weakly dependent on the dominant eye. This suggests that preferred sighting eye dominance is a different type of eye dominance than that which is measured through interocular conflict. We did observe a statistically significant correlation between onset and ongoing rivalry eye dominance indices, suggesting that imbalances in perceptual onset frequency and dominance durations between the eyes are affected by a shared mechanism for these two tasks specifically.

Although previous studies reported positive relations between eye dominance measurements, especially those that depend on similar experimental paradigms (Valle-Inclan et al., 2008; Yang et al., 2010), differences across paradigms have been observed as well (Barbeito, 1981; Coren & Kaplan, 1973; Ono & Barbeito, 1982; also see review by Stanley et al., 2011). More specifically, eye dominance in interocular conflict does not correlate well with eye dominance in spatial vision tasks, nor with preferred sighting dominance as assessed with the hole-in-the-card test. Our results concur with these findings.

Surprisingly, Yang et al. (2010) did report a relationship between the eye dominance determined by b-CFS and the hole-in-the-card test, and concluded that b-CFS can be used as an efficient, reliable and quantitative sensory eye dominance measurement. This is in contrast to our observations, which show no convincing relationship between preferred sighting eye dominance and b-CFS eye dominance. Neither did b-CFS eye dominance correlate convincingly with eye dominance assessed in the other two interocular conflict paradigms. It is currently unclear why we have found different results, and we can only speculate that it may be related to the design of the stimuli, which was different from that of Yang et al. (2010). Nonetheless, Tsuchiya et al. (2006) have already hinted at the possibility that CFS relies upon a different suppression mechanism than binocular rivalry, which could explain why eye dominance as measured with b-CFS was not correlated to eye dominance as measured with the other rivalry tasks (Yang & Blake, 2012). It is therefore tempting to suggest that b-CFS measures a different form of eye dominance than onset or ongoing rivalry.

The positive relationship in eye dominance between onset and ongoing rivalry concurs with previous studies (Dieter, Sy, & Blake, 2016; Leat & Woodhouse, 1984). For example, Leat and Woodhouse (1984) observed strong correlations in eye dominance between onset and ongoing rivalry. It is important to note, however, that there are other factors, such as eye movements, stimulus location, and stimulus characteristics that can alter and attenuate biases in eye dominance (Dieter, Sy, & Blake, 2016, 2017; Kalisvaart et al., 2011; for review, see Stanley et al., 2011). For example, Dieter et al. (2017) explored individual's ongoing rivalry biases for eye and color within the visual field and observed idiosyncratic patterns of biases for both eye and color within the visual field. The origin of a perceptual dominance wave during non-exclusive rivalry might also be sensitive to such spatial anisotropies in eye dominance (Paffen, Naber, Verstraten, 2008). In addition, it would be interesting to assess

whether the timing and the speed at which perceptual dominance switches between the eyes (Lee et al., 2005; Wilson et al., 2001; Genc et al., 2013; Genc et al., 2011; Naber, Carter, Verstraten, 2009; Knapen, van Ee, Blake, 2007) is affected by eye dominance. The above observations withhold us to generalize our findings and to conclude that onset and ongoing rivalry share a singular mechanism underlying eye dominance. Before this can be concluded, more work needs to be conducted to map out all the factors that influence eye dominance.

With regard to the neural substrates of eye dominance, one theory prevails in the literature. Visual brain area V1 is commonly assumed to be the neural locus of differences in eye dominance. The striate cortex consists of columns that receive only monocular input. The idea is that the dominant eye is represented by more interconnected and larger monocular columns. Evidence for this comes from a study by Le Vay, Wiesel and Hubel (1980) who sutured one eye of the new born macaque monkey. After a few weeks, the monocular columns in striate cortex (V1) for the closed eye shrunk and were distributed more fragmented. Sengpiel, Blakemore and Harrad (1995) suggested that perceptual dominance might also involve intracortical inhibition between adjacent ocular dominance columns. Indeed, human neuroimaging and psychophysical studies (for review, see Tong, Meng, & Blake, 2006) also indicate neural sites that retain eye-selective information responsible for binocular rivalry. Lastly, amblyopia, a condition in which one eye has weaker eye dominance, is most likely caused by size differences in ocular dominance columns (Goodyear, Nicolle, Humphrey, & Menon, 2000; Wong, 2012). Our results suggest that variable measurements assess different types of eye dominance, despite the potential involvement of a general mechanism underlying interocular suppression.

We conclude that ocular dominance is a multifaceted phenomenon, and that in our search for the function and etiology of ocular dominance we must first specify which type of dominance is referred to (Coren & Kaplan, 1973). This exploration highlights the importance

of considering the factor of eye imbalance strength when drawing inferences about the perceptual processing of images in different paradigms. We suggest researchers to choose appropriate tests to measure the eye dominance or dominant eye. Specifically, whenever experimental manipulations require a priori knowledge about eye dominance, pre-trials of the task at interest (i.e., as used in the main experiment) should be used to determine eye dominance.

Chapter 2 – Supplementary information

Table S1. Frequency of individuals categorized as left or right eye dominant in b-CFS and hole-in-the-card test.

	LED in b-CFS	RED in b-CFS
LED in hole-in-the-card test	16.67%	10.0%
RED in hole-in-the-card test	16.67%	56.67%

Table S2. Frequency of individuals categorized as left or right eye dominant in onset rivalry and hole-in-the-card test.

	LED in onset rivalry	RED in onset rivalry
LED in hole-in-the-card test	13.33%	13.33%
RED in hole-in-the-card test	13.33%	40.0%

Table S3. Frequency of individuals categorized as left or right eye dominant in ongoing rivalry and hole-in-the-card test.

	LED in ongoing rivalry	RED in ongoing rivalry
LED in hole-in-the-card test	16.67%	10.0%
RED in hole-in-the-card test	33.33%	40.0%

Table S4. Frequency of individuals categorized as left or right eye dominant in b-CFS and onset rivalry.

	LED in b-CFS	RED in b-CFS
LED in onset rivalry	20.0%	26.67%
RED in onset rivalry	13.33%	40.0%

Table S5. Frequency of individuals categorized as left or right eye dominant in b-CFS and ongoing rivalry.

	LED in b-CFS	RED in b-CFS
LED in ongoing rivalry	23.33%	26.67%
RED in ongoing rivalry	10.0%	40.0%

Table S6. Frequency of individuals categorized as left or right eye dominant in ongoing rivalry and onset rivalry.

	LED in ongoing rivalry	RED in ongoing rivalry
LED in onset rivalry	36.67%	10.0%
RED in onset rivalry	13.33%	40.0%

3

Chapter 3

**The priority for access to awareness of information matching VWM is
mirror-invariant**

Accepted as:

Ding, Y., Naber, M., Sahakian A., Paffen, C. L. E., & Van der Stigchel, S. (in press)

The priority for access to awareness of information matching VWM is mirror-invariant.
Cognition.

Author contributions:

All authors designed the study concept. YD programmed the experiment and tested the
observers, YD conducted the analyses and wrote the manuscript.

Critical revisions were provided by YD, MN, AS, CLEP, and SVdS.

Abstract

Previous studies suggest that 1) storing a visual representation of an item in visual working memory (VWM) prioritizes access to visual awareness for this item and that 2) VWM can contain representations of bound items instead of separate features. It is currently unclear whether VWM affects access to visual awareness at the individual feature level, the conjunction of multiple features level or the object level. To investigate this question, we conducted a series of experiments in which we combined a delayed match to sample task with a breaking Continuous Flash Suppression (b-CFS) task. On each trial, subjects memorized an object consisting of a disk with two halves with different colors for the later recall test and, between them, had to detect the location of a target initially presented under suppression. We varied the congruence in colors between the memory representation and to-be-detected target. Our results show that memory congruent objects (consisting of a conjunction of features) break CFS faster than memory incongruent objects. Interestingly, we also observe this congruence effect when we presented the memorized object in a horizontally-mirrored configuration of colors. However, we do not observe a faster effect when the target shares only a single feature of a memorized object (semi-congruent) or when the memory congruent target is rotated by 90°. Our results suggest that VWM prioritizes access to visual awareness for complex visual memoranda for which the spatial lay-out of the individual features does not need to exactly match the lay-out of the memoranda.

Keywords: Visual working memory, conjunction, feature, b-CFS, visual awareness

Introduction

When we open our eyes, our visual system is bombarded with visual input. Our brain is not equipped to process all of this information to the same extent and most of the visual information that is presented to our retinæ therefore does not give rise to conscious experience (Baars, 1997a, 1997b; Dennett, 1993). Because of the limited capacity of visual awareness, some of the visual information needs to be prioritized for access to visual awareness. For instance, previous studies observed that upright bodies enter visual awareness more rapidly than inverted bodies and that the same holds for recognizable versus scrambled words and fearful versus neutral stimuli (Costello et al., 2009; Jiang et al., 2007; Yang et al., 2007; Stein et al., 2012; Gayet, Paffen, Belopolsky, Theeuwes, & Van der Stigchel, 2016). The visual system has evidently evolved to prioritize relevant information for access to visual awareness.

To what degree a stimulus receives priority for visual awareness is generally measured with a paradigm termed breaking continuous flash suppression (b-CFS). In b-CFS a target stimulus is rendered unaware by presenting it to one eye while the other eye is presented with strong dynamic stimuli (i.e., a mask). Because the mask suppresses the target, it takes some time until the target enters awareness. This breakthrough period typically lasts a couple of seconds, and the time it takes for a stimulus to be detected by the observer is an index of the degree to which the target received priority to access visual awareness. Importantly, not only stimulus properties impact visual processing and priority to access awareness. By combining b-CFS and a VWM task (Jiang et al., 2007; Mudrik et al., 2011; Tsuchiya & Koch, 2005), Gayet et al. (2013; 2016; 2019) were able to find that a memory congruent target breaks into awareness more rapidly than a memory incongruent target. This means that if an object is held in working memory, it will enter awareness quicker than other objects. This phenomenon also applies when multiple objects are remembered: a later study

showed that when two items (i.e., distinct in color) are memorized one by one, both items will receive priority (van Moorselaar et al., 2017). However, the question remains which aspects of the items are memorized and affect the prioritization for awareness. Previous evidence about the influence of visual memoranda on visual awareness is based on simple targets, typically consisting of a disk with a single specific color. As studies have suggested that even complex visual stimuli (multi-featured, e.g., faces) which are stored in VWM can also facilitate priority to visual awareness (Liu, Wang, Wang, & Jian, 2016; Pan, Lin, Zhao, & Soto, 2014), this means that VWM could regulate the priority for visual awareness of items consisting of multiple features. However, these previous studies do not tell us whether VWM regulates the priority for access to visual awareness at 1) the individual feature level 2) the conjunction of multiple features level or 3) the object level (see Figure 1). For instance, when holding a two-colored Pepsi logo in VWM, it could be that a product which shares one color of the logo enters awareness faster in a supermarket (i.e. at the individual feature level), or that objects share multiple features of the logo but the lay-out of the features does not need to exactly match the lay-out of the logo are prioritized (at the conjunction level). Alternatively, it could be that only an exact copy containing the colors in the same spatial arrangements as the memorized object is prioritized for conscious access (the object level). Our current study aims to answer this question.

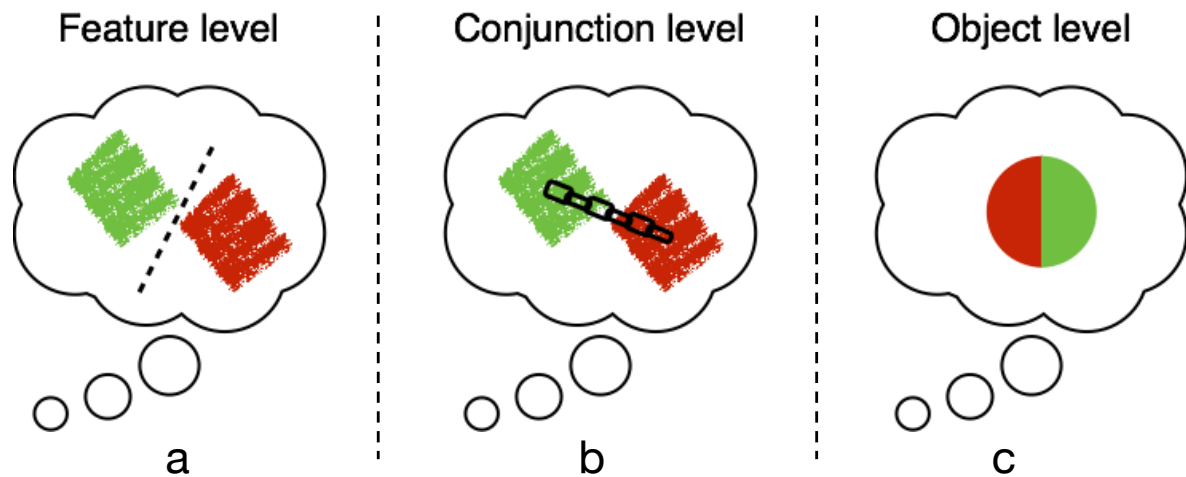


Figure 1. VWM could regulate the priority for access to visual awareness at (a) the feature level, (b) the conjunction level, or (c) the object level. The disk with two colors in the object level (c) is an example of a stimulus used in the current study and here represents an exact copy (i.e., colors combination, orientation, and shape is preserved). Note that the feature level (a) contains only the unbound individual colors of the object while the intermediate, conjunction level (b) also contains spatially-bound colors.

Answering this question addresses one of the most heated debates in VWM literature, namely the extent to which VWM can store items as bound conjunctions or not. For instance, Luck and Vogel (1997) reported that VWM contains representations of conjunctions instead of separate features. They found that the accuracy to memorize multiple stimuli was about equal when the stimuli contained a single varying feature (a single color) or when stimuli consisted of multiple features. However, the debate whether WM stores bound object representation is still ongoing, mainly because a number of subsequent studies reported divergent evidence: some studies find results in favor of bound object representations in VWM (Vogel, Woodman, & Luck, 2001; Luria & Vogel, 2010), whereas other studies reported that memoranda are stored as single features (Delvenne & Bruyer, 2004; Olson & Jiang, 2002; Prira, Cubelli, & Della Sala, 2011; Wheeler & Triesman, 2002; Alvarez &

Cavanagh, 2004). For example, Alvarez et al. showed that the accuracy for remembering complex objects is less than for simple objects. Knowing at which level VWM regulates the access to visual awareness helps us to understand how VWM content is represented.

Our main question is whether VWM affects access to awareness at the feature, conjunction or object level. To answer this question, we combined a VWM task with a b-CFS task in our experiments: on each trial subjects memorized an object which consisted of multiple features for the later recall phase and, between the memorization and recall, indicated the target location during the b-CFS period. We varied the congruency between the b-CFS targets and the memory probes at the single feature level, the conjunction level and the object level. By comparing the durations for the b-CFS targets to break into awareness, we could quantify how and at what level of processing VWM affects access to visual awareness.

Experiment 1

Method

Observers

After informed consent was obtained, 26 observers (5 males; mean age 24.00, SD = 4.02) participated in Experiment 1 for monetary reward. All observers reported having normal or corrected-to-normal sight and having no visual disorder or epilepsy. This study was approved by the Ethics Committee at the Faculty of Social and Behavioral Sciences of Utrecht University and was conducted in accordance with the Declaration of Helsinki.

Apparatus, Stimuli, and Procedure

A PC equipped with a linearized 27-inch LCD monitor (2560 by 1440 pixels, 144-Hz refresh rate) was used to conduct the experiments. A stereoscope with four mirrors (two per eye) was fixed on a chinrest to achieve dichoptic presentation for b-CFS. Stimuli were presented on a gray background and were viewed from approximately 61 cm. As illustrated in Figure 2, the stimulus area presented to each eye was enclosed by a Brownian (i.e., $1/f^2$) noise square frame with a height and width of 7.5° and a thickness of 0.25° . The square was identical for both eyes and was used to promote binocular fusion. The colors used in the WM and b-CFS task (red, green, blue, and purple) were perceptually equal in luminance to prevent differences in luminance to (1) affect memory performance, and (2) to affect b-CFS breakthrough-times². Two hundred different binary patterns (0 and 41.80 cd/m² for black and white parts, respectively), that consisted of pink noise images filtered by a Gaussian low-pass filter ($\sigma = 3.2$), were generated before the experiment as the CFS masks.

² The low-luminance blue color was best suited as the baseline luminance reference to which the other colors were subjectively matched with heterochromatic flicker photometry (Kaiser & Comerford, 1975; Wagner & Boynton, 1972). The hues of each color were slightly different but, about equal in luminance. We produced the hues using two selection steps: First, we identified the location of each of the five color categories into an equiluminant plane in CIE 1931 color space. Next, two more hues of each color category were chosen from this plane.

Before the main experiment, we measured each observer's dominant eye with a b-CFS task because eye dominance is task specific (Ding et al., 2018). In the main experiment, the b-CFS masks were always presented to the dominant eye. As depicted in Figure 2A, each trial in the main experiment started with a fixation point presented for 500 ms. The memory probe consisting of a disk with two halves with different colors (size of 1.2 deg visual angle (VA)) was presented at the fixation position for 2000 ms. The two colors were chosen from the color set (a pair from all possible combinations of red, green, blue and purple) and were to be memorized for later recall. After presenting a blank screen for 2000 ms, the b-CFS task started by presenting a disk of 1.2 deg VA (the b-CFS target) to the non-dominant eye and the CFS mask (refreshing at 10 Hz) to the dominant eye. The intensity (i.e., transparency) of the disk in the b-CFS task increased linearly within 1.5 s. Observers were instructed to respond by pressing the left or right arrow button as soon as they saw the target appearing either to the left or to the right of fixation, respectively. The b-CFS task lasted until observers responded or until 20 s without a response had passed. 500 ms after the disappearance of the b-CFS stimulus, the memory recall task started. During this phase, we presented two discs (size of 1.2 deg VA) left and right of fixation until observers chose which of the two options matched the memorized stimulus. Each disc consisted of two colors: one disc was identical to the probe disc, the other disc had one identical half and one half of which the color was of the same category, but of a slightly different hue. This small adjustment made the task difficult enough to prevent ceiling effects in the memory performance and to prevent that memory stimuli were encoded verbally or categorically. The colors with adjusted hues were equiluminant to that of the memory probe and b-CFS target colors. A trial was ended with feedback to the observers if an incorrect response was given in either the b-CFS and memory task.

The stimuli presented during the b-CFS phase defined five main conditions (Figure 2B). On Memory Congruent trials (condition 1), the b-CFS target was identical to the probe disk. On Memory Congruent Mirrored trials (condition 2), the left and right halves of the disk matched the colors of the *right* and *left* halves of the probe disk, respectively. On Memory Incongruent trials (condition 3), both halves of the disk were of different color categories than the probe disk. On Single Memory Congruent trials (condition 4), the disk contained only one color which was one of the two colors of the probe disk. On Single Memory Incongruent color trials (condition 5), the disk contained only one color category which was different from either one of the probe disks. A total of 5 (main conditions) x 4 (number of probed colors) x 3 (number of hues) conditions was used. As each unique combination was presented for 4 times, each observer performed in 240 trials.

By comparing b-CFS durations on the first three conditions, we investigated whether VWM content affects access to visual awareness at the conjunction level; by comparing the b-CFS durations on the last two conditions, we investigated whether VWM content affects access to visual awareness at the feature level.

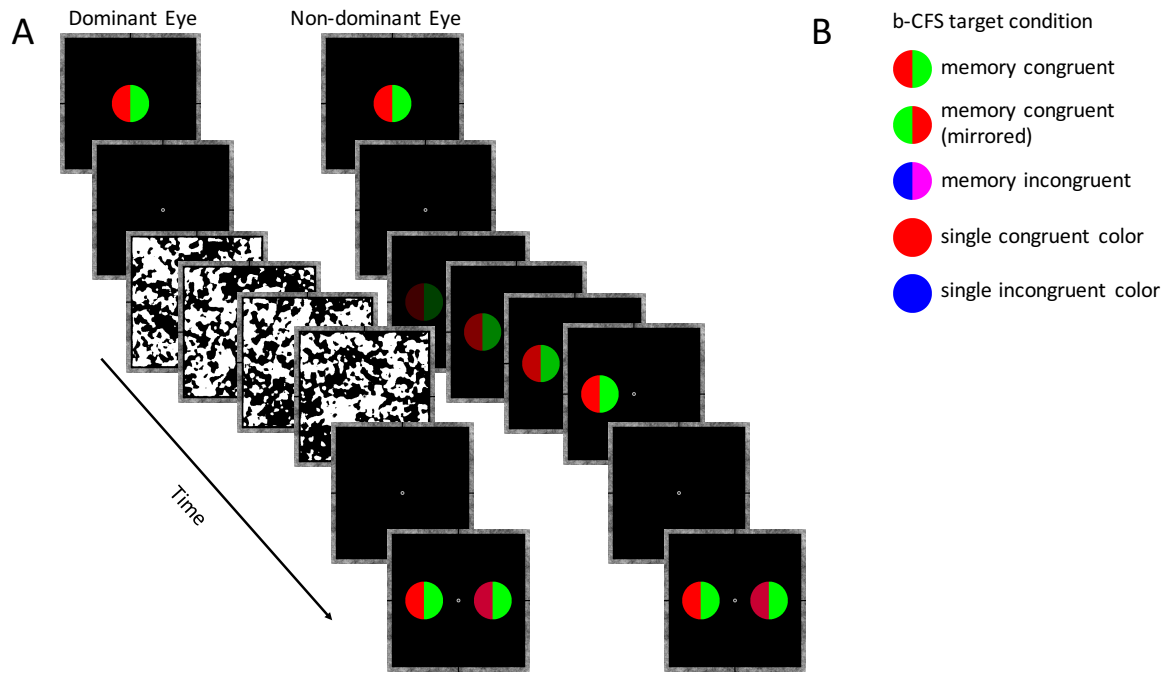


Figure 2. (A) Example trial sequence showing a Memory Congruent trial. Subjects were instructed to memorize the item consisting of two colors in the memory phase. In the suppression phase, the dynamic masks were presented to the dominant eye and a target ramped up to full contrast in the other eye, and observers were required to indicate as soon as possible whether the target appeared to either left or right of the fixation. Trials ended with the recall phase, in which two colored items of same color category but one of the hues was not identical as the memory item, and the observers had to indicate the item which were identical to the memory one. (B) Examples of the b-CFS target conditions.

Data Analysis and Results

One observer was excluded from the analysis because the accuracy on the memory task was lower than the 50% chance level (for the rest subjects, $M = 73.91\%$ correct, $SD = 7.27\%$). Only trials in which observers indicated the correct target location were included in the response-time (RT) analysis of the b-CFS task (fewer than 3% ($SD = 1.86\%$) of the trials were incorrect). We determined observers' median RTs for each memory condition. No trials were lost because of RT outliers. The extent to which observers exhibit

different effects in b-CFS varies extensively (in the range of hundreds of milliseconds) which might result in a large difference in RTs between observers. Since the within-subject comparison does not remove the variability between subjects, we transformed the RTs with a latency-normalization method³ (Gayet & Stein, 2017) for the analyses to remove the between-subject variability in suppression duration from the effect of interest. To facilitate the interpretation for the reader, however, the RTs reported in the text and depicted in the figures express the raw RTs.

The effects of VWM on RTs in the b-CFS task were analyzed with a repeated-measures ANOVA. As depicted in Figure 3, we observed significant main effects of b-CFS condition ($F(4, 96) = 25.08, p < 0.001$). The subsequent paired-sample two-tailed t tests show that: 1) observers detected memory congruent targets and left-right mirrored memory congruent targets faster than memory incongruent targets (Memory Congruent vs. Memory Incongruent: 1277 ms vs. 1326 ms, $t(24) = 2.67, p < 0.02, \eta_G^2 = 0.30$; Memory Congruent Mirrored vs. Memory Incongruent: 1268 ms vs. 1326 ms, $t(24) = 2.66, p < 0.02, \eta_G^2 = 0.33$); 2) there was no difference between detecting memory congruent targets as and the left-right mirrored memory congruent targets ($t(24) = 0.19, p = 0.85, \eta_G^2 = 0.02$); 3) there was no significant difference between RTs of single memory congruent color targets and single memory incongruent color targets ($t(24) = 0.47, p = 0.64, \eta_G^2 = 0.10$). The t -tests were not corrected since we designed the comparisons in the experiments beforehand and we only focused on these comparisons.

The results of Experiment 1 show that 1) a disc containing two colors was detected faster than a disc of one color and we reason that the former is more dominant to break interocular suppression because of a higher spatial frequency, which is not relevant to our

³ The formula here depicts how to transform the RT of condition A with latency-normalization method: $RT_{A\ TRANSFORMED} = 100 * \frac{RT_A}{mean(RT_{OVERALL})}$

current question; 2) a two-color disc was detected faster when the colors matched rather than mismatched the colors of the probe disc⁴. Interestingly, there was no difference in RTs between the identical and mirrored colors disc. One potential explanation for this result is that in Experiment 1, only the colors of the memory disk were tested in the recall task but not the left-right order of the colors. Thus, it is reasonable to query whether the lack of requiring subjects to memorize the left-right order of the disk could result in specific memory strategy (e.g., subjects memorizing the color combination of the memory disk and ignoring the color sequence). Experiment 2 was dedicated to tackle this possible confound.

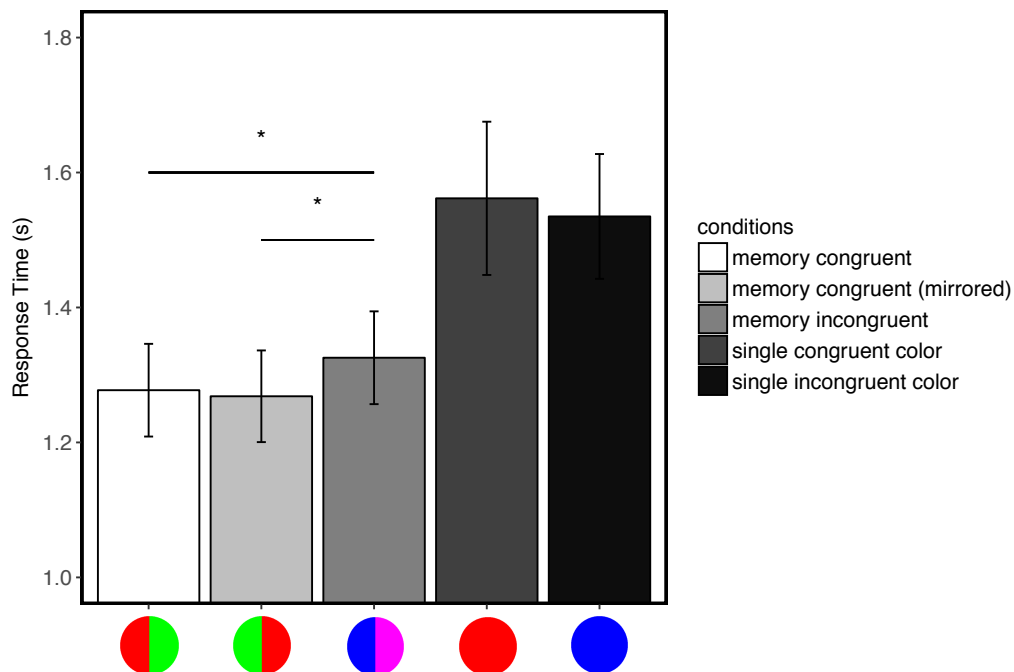


Figure 3. Response times as a function of different b-CFS conditions for the main experiment (* $p < 0.05$). Error bars denote ± 1 SEM.

3 To exclude a potential priming effect, we, as previous studies did (Ding et al., 2019; Gayet et al., 2013), conducted a control experiment in which observers were required to passively view the probe before the b-CFS task. We also removed the recall phase on each trial. The b-CFS target could be either congruent or incongruent with the probe. For 12 observers, our results show that there was no effect of priming ($t(11) = 0.17$, $p = 0.87$, $\eta^2_G = 0.01$): WM-matching targets were not detected faster than WM-mismatching targets when observers passively viewed the probe. These results indicate that the memory congruent facilitation in our experiments cannot be explained by bottom-up priming.

Experiment 2

Method

Observers

To retain the statistical power, we recruited more subjects in Experiment 1 which had five conditions and fewer subjects in Experiment 2 which had three conditions. Sixteen observers participated in Experiment 2, one of them was replaced by a new observer because the memory accuracy was lower than 50% chance level (2 males; mean age 24.13, $SD = 4.30$). All reported having normal or corrected-to-normal sight and having no epilepsy or visual disorder.

Apparatus, Stimuli, and Procedure

The method was the same as in the first experiment except for the following changes: Three of the main conditions of Experiment 1 were included in Experiment 2 (the Memory Congruent condition, Memory Incongruent condition, and Memory Congruent Mirrored condition). In the memory recall task, per trial either hue or the left-right order of the colors were tested with equal chance (50% of the trials randomly occurring for each) to assess whether the memorization of order made the spatial layout relevant for the b-CFS task. When order was tested, observers had to indicate which of the two stimuli, one of which was horizontally mirrored, was the memory probe.

Results

The data were analyzed in the same way as for Experiment 1. Observers performed well in both the b-CFS task (fewer than 2% responses were incorrect, $SD = 2.40\%$) and the memory task (accuracy for the color test, $M = 74.48\%$, $SD = 11.68\%$; accuracy for the order test, $M = 90.89\%$, $SD = 11.39\%$).

The transformed RTs were analyzed with a repeated-measures ANOVA, and the results show marginally significant effects of VWM on RTs ($F(2, 30) = 2.69$, $p = 0.08$). Next, post hoc tests were conducted with one-sided t-tests since Experiment 2 involved a

replication of Experiment 1. As illustrated in Figure 4, the results show that: 1) a marginally significant difference between the RTs on the memory congruent trials and the memory incongruent trials was observed (Memory Congruent vs. Memory Incongruent: 1339 ms vs. 1395 ms; $t(15) = 1.68$, $p = 0.057$, $\eta_G^2 = 0.73$); 2) observers detected left-right mirrored memory congruent targets faster than memory incongruent targets (Memory Congruent Mirrored vs. Memory Incongruent: 1329 ms vs. 1395 ms; $t(15) = 2.30$, $p = 0.026$, $\eta_G^2 = 0.89$); 3) there was no difference between RTs on memory congruent targets and left-right mirrored memory congruent targets ($t(15) = 0.43$, $p = 0.34$, $\eta_G^2 = 0.16$).

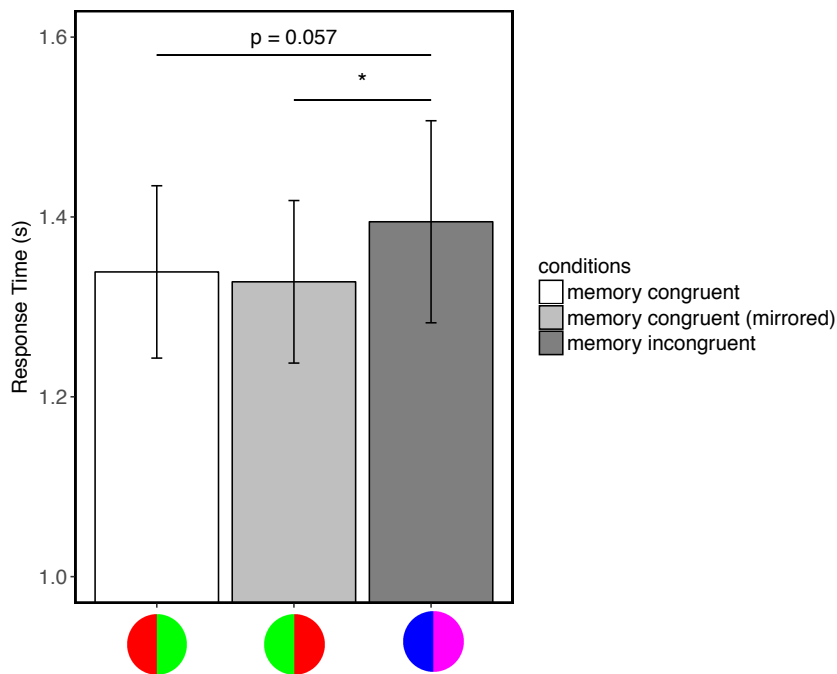


Figure 4. Response times as a function of different b-CFS conditions for the main experiment (* $p < 0.05$). Error bars denote ± 1 SEM.

The replicated facilitated response for both the identical and left-right mirrored memory congruent targets suggests that configuration of the two colors is mirror-invariant for VWM content prioritizing access to visual awareness of matching visual input. However, it is still too preliminary to conclude that VWM prioritizes access to visual awareness at the

conjunction level. This is because, in the memory congruent (mirrored) trials, the targets always consisted of two halves with the same colors (and perhaps different spatial layout), and either of the halves could be a memory feature which resulted in the facilitated response in the b-CFS task. That is to say: perhaps the facilitated response can be observed whenever a single color of a two-color disc matches a color of the memory probe. Experiment 3 was conducted to test whether the combination of two matching colors is necessary for the facilitated response to occur.

Experiment 3

Method

Observers

Sixteen observers participated in Experiment 3, one of them was removed and replaced by a new observer since the individual failed to keep stable binocular vision (6 males; mean age 23.47, $SD = 1.84$). All observers reported having normal or corrected-to-normal sight and having no epilepsy or visual disorder.

Apparatus, Stimuli, and Procedure

The current method was identical to the methods of the previous experiments except that the memory congruent mirrored condition was replaced by a one color memory congruent condition in which the b-CFS target was composed of two colors and where one of the halves was of the same color category as the memory probe (see x-axis of Figure 5).

Results

All observers performed well in both the b-CFS task (fewer than 2% trials were incorrect ($SD = 2.32\%$)) and the memory task (accuracy for the color test, $M = 76.61\%$, $SD = 10.16\%$; accuracy for the order test, $M = 95.72\%$, $SD = 10.16\%$).

The transformed RTs were entered in an analysis consisting of a repeated-measures ANOVA. As Figure 5 illustrates, the results showed that VWM affected RTs in the b-CFS

task ($F(2, 30) = 3.65, p < 0.04$). The post hoc two-tailed t-tests showed that: 1) observers detected memory congruent targets faster than memory incongruent targets and one color memory congruent targets (Memory Congruent vs. Memory Incongruent: 1219 ms vs. 1263 ms; $t(15) = 2.39, p = 0.03, \eta_G^2 = 0.95$; Memory Congruent vs. One Color Memory Congruent: 1219 ms vs. 1266 ms; $t(15) = 2.21, p = 0.04, \eta_G^2 = 0.91$); 2) There was no difference between the RTs on detecting memory incongruent trials and one color memory congruent trials ($t(15) = 0.12, p = 0.91, \eta_G^2 = 0.05$).

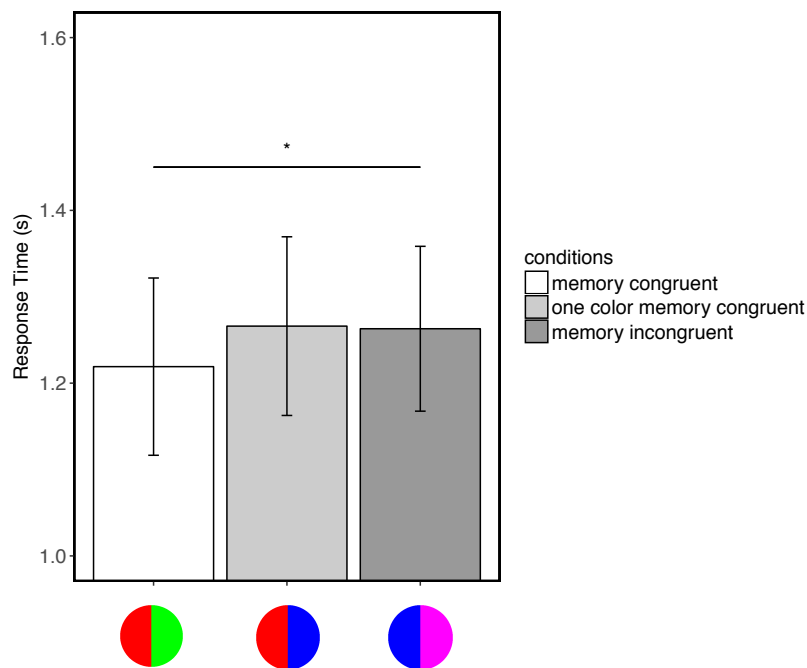


Figure 5. Response times as a function of different b-CFS conditions for the main experiment (* $p < 0.05$). Error bars denote ± 1 SEM.

The results of Experiment 3 show that only when both colors of the disc match the memory probe, access to visual awareness is prioritized. This indicates that VWM regulates the access to visual awareness for the objects at the conjunction level. However, it is still not possible to conclude that the spatial lay-out of the individual features is irrelevant. Such a conclusion would be strengthened when matching probes are also prioritized when probe and

b-CFS target are oriented differently. In Experiment 4, we manipulated the orientation of the b-CFS targets to investigate whether the spatial lay-out of a VWM conjunction affects the priority to access visual awareness.

Experiment 4

Method

Observers

Eleven observers (4 males; mean age 24.36, SD = 5.41) participated in this experiment and all observers reported having (corrected to) normal sight and having no epilepsy or visual disorder.

Apparatus, Stimuli, and Procedure

The current method was identical to the methods of the previous experiment except that we replaced the b-CFS conditions with a horizontally oriented memory congruent condition and a horizontally oriented memory incongruent condition. In these conditions the b-CFS targets were the same as the memory congruent target and memory incongruent target of Experiment 3, except for the fact that they were flipped 90° clockwise or counterclockwise for each trial (see x-axis of Figure 6).

Results

All observers performed well in both the b-CFS task (fewer than 2% responses were incorrect on average; SD = 1.02%) and the memory task (accuracy for the color test: M = 77.46%, SD = 4.82%; accuracy for the order test: M = 92.42%, SD = 6.80%).

As illustrated in Figure 6, the results showed no difference between the RTs on detecting horizontally oriented memory congruent targets (1050 ms) and horizontally oriented memory incongruent targets (1060 ms); $t(10) = 0.39, p = 0.71, \eta_G^2 = 0.19$.

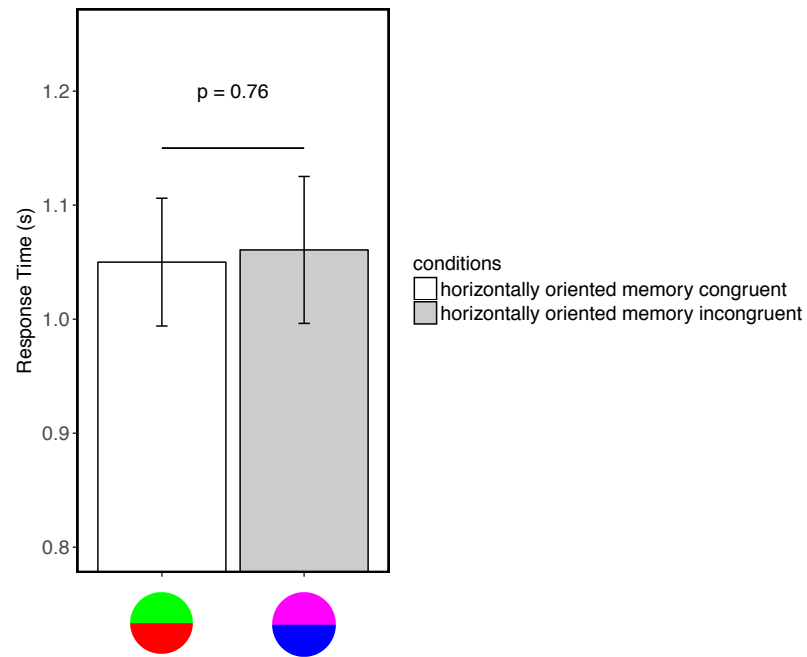


Figure 6. Response times as a function of different b-CFS conditions for the main experiment ($*p < 0.05$). Error bars denote ± 1 SEM.

The results of Experiment 4 show that a disc is not prioritized to visual awareness when it matches the memory probe with respect to its colors but not with respect to its spatial orientation, suggesting that the spatial information of the VWM content, to some extent, regulates the visual awareness access. Combining these results with those of the first three experiments, objects that share multiple but not all features (e.g., the colors and spatial orientation but not the exact lay-out) of the memory object are prioritized, suggesting that VWM prioritizes the access to visual awareness for objects at the conjunction level but not at the object level.

Discussion

Recent research suggests that VWM can regulate access to visual awareness of incoming visual information (Gayet et al., 2013; 2016; 2019; van Moorselaar et al., 2017; Liu et al., 2016; Pan et al., 2014; Ding, Paffen, Naber, & Van der Stigchel, 2019). Here we have

examined whether VWM exerts this influence at the individual feature level, the conjunction level or the object level (see Figure 1). We have combined a unique version of the VWM and b-CFS task to find that a target consisting of two color categories matching the content of VWM probe broke CFS faster than memory mismatching objects. Interestingly, we observe that this congruency effect was preserved when we presented the matching object in a configuration that mirrored the probe colors. Additionally, we did not observe the congruency effect when the object shared only a single feature or when the object did not share the spatial orientation of the memorized probe. It could be argued that the lack of a facilitation effect for a congruent single color target in Experiment 1 was due to observers' shift in post-conscious response criterion instead of conscious access (e.g., response strategy). A monocular control experiment which includes the presentation of the b-CFS target superimposed on the dynamic masks and together presented to the same eye has been used by previous studies to investigate this possibility. Importantly, these studies (Gayet et al., 2013; Ding et al., 2019) observed no facilitation effect of the memory congruent target in monocular control experiments, suggesting that the memory congruent facilitation effect is not due to response strategy. In sum, the results show that VWM prioritizes the access to visual awareness for targets at the conjunction level but not at the individual feature level or at the object level. The priority for access to awareness of the information matching VWM is mirror-invariant.

Van Moorselaar et al. (2017) have observed that multiple memorized colors receive priority to access visual awareness (van Moorselaar et al., 2017). We extend this observation with the finding that also multiple, spatially-bound colors are prioritized to access visual awareness, and we additionally find evidence that this process operates at an intermediate, conjunction level at which the spatial layout of the object does not need to exactly match the lay-out of the memoranda. That the content of VWM interacts with visual awareness at this level is not trivial. To clarify, let us use the search for the logo of a Pepsi can or bottle, as

described earlier in the Introduction, as an analogy. When searching for a Pepsi can in a filled fridge, looking for the exact red-blue color combination through tolerating some variation of the spatial lay-out (e.g., the left-right sequence) of the logo would be the most efficient strategy, because the can might lie upside down. In contrast, using a search (or prioritization) template of the exact Pepsi logo with a specific color arrangement and spatial lay-out will limit search performance. Therefore, a prioritization strategy at the object level will fail to help observers to become aware of relevant objects mismatching any spatial layout. On the other side of the spectrum lies the use of multiple search templates of each individual aspects of the Pepsi logo; a strategy that is too liberal and will prioritize many irrelevant objects in the fridge (e.g., a red Babybel cheese package will cause false alarms and will cause inefficient search). At least within the realm of the current study, and the examples of real-life search mentioned above, it thus most useful to have VWM operate at an intermediate, conjunction level. It will be interesting, though, to investigate in future studies whether the level at which VWM and visual awareness interact can be (in)voluntarily changed depending on the task.

How do our findings relate to previous studies that examined how VWM retains several features? A large body of studies have not yet reached consensus on this topic, withholding us from choosing between the options that VWM representations operate as either the bound conjunctions or independent features level (Luck & Vogel, 1997; Vogel et al, 2001; Luria & Vogel, 2011; c.f., Wheeler & Triesman, 2002; Olson & Jiang, 2002; Parra et al., 2011; Awh, Barton, & Vogel, 2007; Alvarez & Cavanagh, 2004). We can conclude from the current results that the interaction between VWM and visual awareness can be best described by a process that lies in between the two theoretical viewpoints: when two colors are to be encoded simultaneously, the colors are stored as conjunctions and not as independent features (Brady & Alvarez, 2011).

Another interesting line of research to pursue is to use combinations of features from different domains, for example features that define what an object is (i.e., contour and shape; Lamme & Roelfsema, 2000). Instead of using two different colors, follow-up experiments may try to combine colors and shapes to see whether both a b-CFS should share both features with the memory probe in order to be prioritized. For example, a previous study suggests that an object's shape may have different effects on visual processing than colors (Soto et al., 2005). These authors observed that objects matching memorized representations at both color and shape can speed observers' search performance but not when only the shape is matched. As more studies are needed to generalize these findings to other features, we leave the possibility open that not all features can be bound to regulate visual processing.

To conclude, previous studies have repeatedly reported that VWM can modulate the access to visual awareness (Gayet et al., 2013; Pan et al., 2014; Liu et al., 2016; van Moorselaar et al., 2017). Our present experiments provide clear evidence this process can operate at the conjunction level, which is an intermediate stage of the visual hierarchy (Alvarez & Cavanagh, 2004) preceding the stage of binding features into coherent objects.

4

Chapter 4

How retaining objects containing multiple features in visual working memory regulates the priority for access to visual awareness

Submitted as:

Ding, Y., Naber, M., , Paffen, C. L. E., Gayet, S., & Van der Stigchel, S.

How retaining objects containing multiple features in visual working memory regulates the priority for access to visual awareness

Author contributions:

All authors designed the study concept. YD programmed the experiment and tested the observers, YD conducted the analyses and wrote the manuscript.

Critical revisions were provided by all co-authors.

Abstract

The content of visual working memory influences the access to visual awareness. Thus far, research has focused on retention of a single feature, whereas memoranda in real life typically contain multiple features. Here, we intermixed a delayed match-to-sample task to manipulate VWM content, and a breaking Continuous Flash Suppression (b-CFS) task to measure prioritization for visual awareness. Observers memorized either the color (Exp. 1), the shape (Exp. 2) or both the features (Exp. 3) of an item and indicated the location of a suppressed target. We observed that color-matching targets broke suppression faster than color-mismatching targets both when color was memory relevant or irrelevant. Shape only impacted priority for visual awareness through an interaction with color. We conclude that: 1) different features of a memorandum vary in their potency to impact access to visual awareness 2) color dominates prioritization; 3) even when color is irrelevant for the upcoming memory task.

Keywords: Visual working memory, feature binding, continuous flash suppression, visual awareness

Introduction

While reading this text, you might not be aware of other objects on your desk, even if they do project an image on your retinae. Because access to visual awareness is limited, we are not aware of the vast majority of the visual information that is readily available. Our visual system has evolved to prioritize relevant visual information over irrelevant visual information. For example, previous studies have suggested that a fearful face (Jiang et al., 2007), a threatening symbol (Gayet et al., 2016), or a salient item (Ding et al., 2019; Stuit et al., 2010) gains preferential access to awareness.

Besides these intrinsically relevant stimuli, our current mental state also influences the priority of stimuli for access to visual awareness. For instance, by requiring observers to memorize a color for later recognition, Gayet and colleagues (2013; 2016; 2019) observed that memory congruent items break interocular suppression faster than memory incongruent items. This finding reveals that an item which is currently stored in visual working memory (hereafter: VWM) is prioritized to enter awareness compared to other items. A follow-up study showed that when two items (i.e., of two distinct colors) are memorized simultaneously, each of them will be prioritized for visual awareness, suggesting that multiple features in VWM can jointly regulate visual awareness (van Moorselaar et al., 2017). Furthermore, the same principle holds for more complex memoranda that are defined by multiple features, such as faces (Liu et al., 2016; Pan et al., 2014). Interestingly, Liu et al., (2016) observed that faces with threatening expressions are released from suppression faster when observers are memorizing threatening faces; an effect that was not observed for faces with happy or neutral expressions. As differences between emotional expressions are relatively subtle, this raises the question to what degree complex object representations in VWM interact with the dynamics of visual awareness. More generally, as visual items stored in VWM typically

comprise multiple features, it is currently unknown whether and how these features jointly regulate access to awareness.

For the questions introduced above it is important to know how items are represented in VWM. A body of evidence suggests that multiple features of a single item can be maintained in VWM as a bound conjunction. For instance, Luck and Vogel (1997) reported that the number of items stored in memory was not different when only a single feature needed to be remembered (e.g., either their color or their orientation) or when multiple features needed to be remembered (e.g., their color as well as their orientation). Sequential studies replicated this finding thereby supporting this object-based theory of VWM (see Luria et al., 2016 for a review; Luria & Vogel, 2011; Vogel et al., 2001). These studies suggest that the features of a memorized object in VWM are somehow linked together. Alternative to the object-based theory of VWM is the multiple-resources theory which assumes that there are separate pools of resources for maintaining features from different dimensions (Alvarez & Cavanagh, 2004; Delvenne & Bruyer, 2004; Olson & Jiang, 2002; Parra et al., 2011; Wheeler & Treisman, 2002). For instance, Alvarez and Cavanagh (2004) observed that the object-based theory cannot entirely explain the capacity of VWM. Instead, they argue that VWM load is not only determined by the number of objects, but also by the number of features. Furthermore, Wheeler and Treisman (2002) observed that features from the same dimension (e.g., color) compete for storage capacity while features from different dimensions (e.g., color and orientation) are stored in parallel without competition. Delvenne and Bruyer (2004) replicated this finding, revealing that features from different dimensions can be stored without affecting capacity limits.

The discussion about the nature of VWM representations above, leads us to question whether VWM regulates the priority of an item for visual awareness along a single feature dimension and/or whether multiple features from different dimensions regulate access

synergistically (i.e., as a bound entity). In this study, we opted for the feature dimensions ‘color’ and ‘shape’ to facilitate comparison with previous studies investigating the influences of VWM on perception (e.g., Olivers et al., 2006; Gayet et al., 2013; Bahle & Hollingworth, 2018; Soto et al., 2005; Wheeler & Treisman, 2002). To quantify the priority to visual awareness, we used the so-called breaking continuous flash suppression paradigm (i.e., b-CFS; Jiang et al., 2007; Stein, Hebart & Sterzer, 2011; Gayet, Van der Stigchel, & Paffen, 2014; Stein, 2019). In a typical b-CFS task, a target stimulus is initially suppressed from awareness by presenting it to one eye while the other eye is presented with dynamic stimuli (i.e., masks). The duration for a b-CFS target to overcome interocular suppression is an index quantifying the priority of a target to access visual awareness. In the current study, we combined b-CFS and a VWM task. In the first two experiments, we will investigate whether VWM regulates visual awareness at a specific feature dimension. We will ask observers to memorize a single feature (specifically, the color or the shape, respectively) of a memory item that contains multiple features (specifically, both a color and a shape), and vary the congruency between the b-CFS target and the memory item. In the third experiment, we will research whether VWM regulates access to visual awareness of an object along multiple features dimensions (i.e., synergistically) when multiple features of an item are simultaneously maintained in VWM (specifically, as a conjunction of both color and shape).

Experiment 1 – Memorize color

Method

Observers

A planned number of twenty observers (age: $M = 22.7$, $SD = 3.1$; 7 males) participated in Experiment 1 after giving written informed consent. All observers reported normal or corrected-to-normal sight and having no epilepsy. The current study was approved by the local Ethical Committee of the Faculty of Social and Behavioral Sciences of Utrecht University and followed the general guidelines set out in the Declaration of Helsinki.

Design and procedure

The congruency between the memory item and the target during b-CFS defined four main experimental conditions (Figure 1B). On color congruent and shape incongruent trials, the b-CFS target was of the same color category and of a different shape category than the memory item (hereafter: *color only match*). On color congruent and shape congruent trials, the b-CFS target shared both the color category and the shape category with the memory item (*whole object match*). On color incongruent and shape congruent trials, the b-CFS target was of the same shape category and of a different color category than the memory item (*shape only match*). On color incongruent and shape incongruent trials, the b-CFS target shared neither color category nor shape category with the memory item (*whole object mismatch*). The within-subject experimental design comprised a total of 4 congruency conditions (described above) x 3 color categories (a color from the red, green or blue category is memorized) x 3 shape categories (ellipse, triangle or rectangle shaped memory item) x 2 target locations (left or right of fixation) x 2 response options for the memory recognition task (left or right option is correct). Every unique combination of conditions was presented once, resulting in 144 trials for each observer (36 trials per congruency condition). The order of trials was randomized for each participant.

Before the main experiment, we measured each observer's sensory eye dominance using a b-CFS task (this is important because eye-dominance is task-specific; Ding et al., 2018). As illustrated in Figure 1, each trial in the main experiment started with a fixation dot presented for 500 ms. The memory item (i.e., a colored shape) then replaced the fixation dot for 2000 ms. Observers were instructed to memorize the color of the memory item for a memory recognition task at the end of each trial. After a blank screen (2000 ms), the b-CFS target detection task was initiated by presenting a colored shape (the b-CFS target) to the non-dominant eye and dynamic masks (refreshing at 10 Hz) to the dominant eye. The intensity (i.e., opacity) of the b-CFS target increased linearly within 1.5 s and retained the highest intensity until the end of the trial. Observers were instructed to respond as soon as they saw the target appearing to the left or the right of fixation (at an eccentricity of 1.8°), by pressing the left or right arrow button of the keyboard, respectively. The target detection task lasted until observers responded, or until 20 s without a response had passed. A blank screen was presented for 500 ms between the disappearance of the b-CFS stimuli and the onset of the memory recognition task. During the memory task, we presented two stimuli, left and right of fixation, until observers chose which of these two was identical to the memorized stimulus. One item was identical to the memory item, and the other had an identical shape and was chosen from the same color category but with a slightly different hue. It is important to make the hue difference sufficiently small to prevent ceiling effects and to prevent observers from encoding the memory stimuli verbally or categorically (Olivers et al., 2006). In case an incorrect response was given in either the b-CFS task or the memory recognition task, the text 'Incorrect' was presented on the screen. Trials with a localization error or without a response in the b-CFS task were recycled and presented at the end of the experiment to preserve an equal number of trials in all conditions of interest.

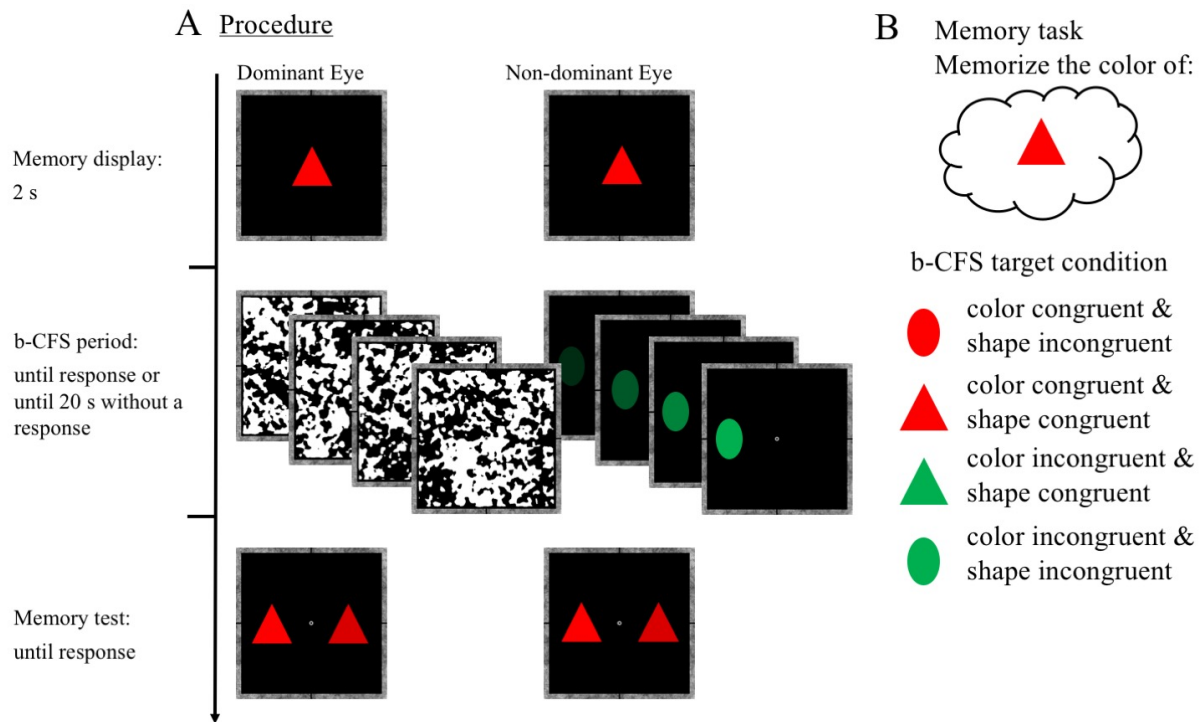


Figure 1. (A) Schematic depiction of a trial sequence showing a shape and color incongruent trial in Experiment 1. Observers were instructed to memorize the color of the memory item in the memory encoding phase. In the b-CFS phase, the dynamic masks were presented to the dominant eye and the target was ramped up from zero to full intensity for the other eye. Observers were required to indicate whether the target appeared to the left or right of fixation as soon as they saw it. In the memory recognition phase, two items from the same shape and color categories were presented, one of which was identical to the memory item, while the other was of a slightly different hue. (B) Illustration of the four congruency conditions of the b-CFS target in case the memory item was a red triangle.

Apparatus and stimuli

We showed stimuli to the observers in a dark room using a desktop computer and a linearized 27-inch LCD monitor (2560 · 1440 pixels, 144-Hz refresh rate). All stimuli were created and presented with MATLAB 2016 (The Math Works, Inc) and its PsychToolbox extension software (Brainard, 1997; Pelli, 1997). The viewing distance was maintained at around 61 cm

with a chin and forehead rest. A stereoscope with four mirrors (two per eye) was fixed on the chinrest to allow for separately stimulating the two eyes of the observer.

In the main experiment, the masks were always presented to the dominant eye to avoid large differences within participants in suppression duration in b-CFS. To promote binocular fusion of the complementary images, the stimulus area presented to each eye was enclosed by a Brownian (i.e., $1/f^2$) noise quadrate frame with a width of 7.5° and a thickness of 0.25° (see Figure 1). The colors (red, green, and blue) used in the memory display, memory recognition task and b-CFS task were subjectively equal in luminance to prevent observers from memorizing the item based on the luminance instead of hue in the memory task (Olivers et al., 2006), and to prevent the difference in luminance between colors to create variance in break-through times in the b-CFS task. Three shape categories (triangle, ellipse, and rectangle) were used in the VWM task and the b-CFS task, and each shape category included three shape variations that slightly differed in terms of height-to-width ratio (i.e., elongation). The CFS masks consisted of two hundred different binary images that were generated by filtering pink ($1/f$) noise using a circular Gaussian low-pass filter ($\sigma = 3.2$), and rounding the resulting images to black ($\sim 0 \text{ Cd/m}^2$) and white (41.8 Cd/m^2).

Data Analysis, Results, and Discussion

Trials without a response (5.17%) or with incorrect localization (2.40%) in the b-CFS task were recycled at the end of the experiment, and the original ones were excluded from further analysis. The accuracy on the memory task was well above the 50% chance level but not at ceiling ($M = 84.31\%$ correct, $SD = 8.04\%$).

The observer's median response-times (RT) to the b-CFS target were determined for each memory-relevant feature condition (i.e., color; congruent and incongruent) and each memory-irrelevant feature condition (i.e., shape; congruent and incongruent). A 2 x 2 repeated-measures analysis of variance (ANOVA) was conducted on these median RTs per condition, to investigate the effects of color and shape congruence on RTs in the b-CFS task. As depicted in Figure 2, we observed a significant main effect of color congruency ($F(1, 19) = 14.04$, $p = 0.001$), but neither a significant main effect of shape congruency ($F(1, 19) = 0.27$, $p = 0.61$), nor an interaction between color and shape ($F(1, 19) = 0.73$, $p = 0.40$). In summary, we observed faster response times for b-CFS targets when they matched compared to when they mismatched the memorized color (1523 ms vs. 1632 ms).

The results of Experiment 1 show that a suppressed target stimulus was detected faster when the color matched rather than mismatched the color of the memory item. Shape congruency, however, did not impact RTs. These results indicate that VWM can regulate the access of visual information to visual awareness along the color feature dimension, at least when color is relevant for the upcoming recognition task.

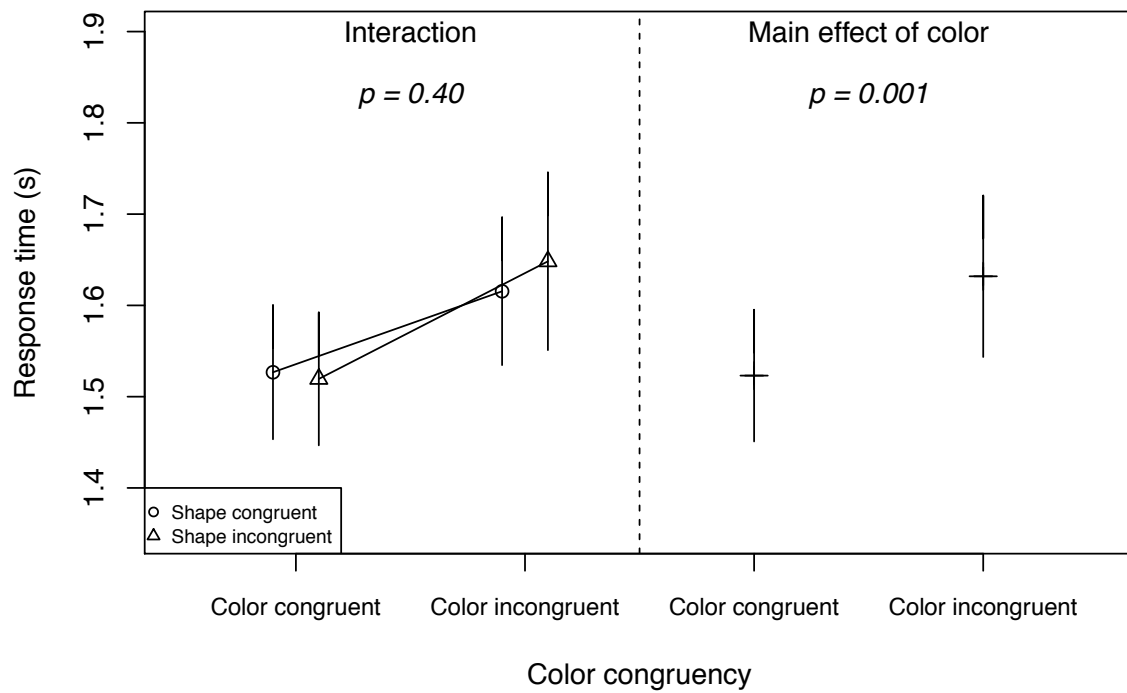


Figure 2. Mean response times across observers as a function of color congruency and shape congruency for Experiment 1. On each trial, participants were required to memorize the color (but not the shape) of the memory item for the subsequent recognition task. Error bars denote ± 1 SEM across observers. The results show a main effect of color congruency.

Experiment 2 – Memorize shape

To investigate whether VWM modulates visual awareness along the shape feature dimension, in Experiment 2, observers were only required to memorize the shape of the memory item for the upcoming recognition task, and not its color. We expected two possible outcomes: first, if b-CFS targets that match the shape of the memory items are detected faster than those with a mismatching shape while color does not affect detection times, this indicates that (1) VWM content can regulate visual awareness along the shape feature dimension, and that (2) only the feature dimension that is relevant for the upcoming memory task can regulate access to visual awareness. A second outcome, however, is also feasible, namely that b-CFS targets with matching colors (i.e., the incidental, non-memorized feature) will be detected faster than targets with mismatching colors. This would indicate that (1) even incidentally stored features in VWM can regulate access to visual awareness but that (2) this effect is restricted to cases in which color is the incidental feature (as no effect of the incidental feature ‘shape’ was observed in Experiment 1).

Method

Observers and procedure

Twenty new observers participated in Experiment 2 (7 males; mean age 24.8, $SD = 4.5$). All reported having (corrected to) normal sight and having no epilepsy. The method was the same as Experiment 1 except that observers were instructed to only memorize the shape of the memory item, and only the shape would be tested at the end of each trial.

Results and Discussion

Observers performed well in both the b-CFS task (only 2.19% trials were recycled because of incorrect localization responses, $SD = 1.83\%$) and the memory recognition task (accuracy for the shape test, $M = 79.58\%$, $SD = 8.25\%$).

Akin to Experiment 1, the median localization RTs of the b-CFS task were analyzed with a repeated-measures ANOVA. As illustrated in Figure 3, the results showed a significant main effect of color congruency ($F(1, 19) = 4.57, p = 0.046$) but again no main effect of shape congruency ($F(1, 19) = 0.41, p = 0.53$). Interestingly, we now observed a significant interaction between color congruency and shape congruency ($F(1, 19) = 7.01, p = 0.016$). To investigate the nature of the interaction, subsequent pairwise *t-test comparisons* were conducted among different congruency conditions (i.e., color congruent only, shape congruent only, both shape and color congruent, and neither shape nor color congruent – see Table 1). This analysis revealed that two pairs of conditions differed significantly from each other: color congruent/shape incongruent versus color incongruent/shape incongruent (the left versus the right triangle of Figure 3; $p = 0.007$), and color incongruent/shape congruent versus color incongruent/shape incongruent (the right circle versus the right triangle of Figure 3; $p = 0.033$). The other comparisons did not reveal significant differences. The overall pattern of post-hoc comparisons suggests that the condition that involved two features that were incongruent with the memory item, lead to *slower* breakthrough times than the other three conditions (which had similar breakthrough times). Therefore, to test whether, generally, a target is prioritized for awareness when it matches *any* feature with the memory item (i.e., color, shape, or both), we collapsed RTs across the three congruent conditions and compared this to the RTs in the color and shape incongruent condition. This analysis revealed that observers detected targets faster when they matched the color, the shape or the color as well as the shape of the memory item, as compared to targets that matched neither feature (1714 ms vs. 1802 ms, $t(19) = 2.88, p = .010$).

Table 1. RT differences between all the different congruent conditions in the b-CFS task.

Condition 1		Condition 2		<i>t</i> (19)	<i>p</i>
Color	Shape	Color	Shape		
Congruent	congruent	incongruent	incongruent	1.44	0.166
congruent	incongruent	incongruent	incongruent	3.01	0.007
incongruent	congruent	incongruent	incongruent	2.31	0.033
congruent	congruent	congruent	incongruent	1.96	0.065
Congruent	congruent	incongruent	congruent	0.03	0.975
Congruent	incongruent	incongruent	congruent	2.02	0.058

We can conclude that VWM content can prioritize stimuli for visual awareness along the color feature dimension, even when the color dimension is irrelevant to the VWM task. This goes against the hypothesis that only the memory-relevant feature dimension impacts access to visual awareness. However, the interpretation of the results of Experiment 2 is more complex than we initially expected. The post-hoc comparisons also hint at the possibility that color dominates over shape in the potency of VWM to regulate access to visual awareness, even when shape is relevant for the upcoming memory task and color is not. Also, these results suggest that VWM content can prioritize stimuli along the shape dimension as well, albeit subtly: shape congruency gates the influence of color congruency on visual awareness, but (perhaps only) when shape is relevant for the VWM task and color is not.

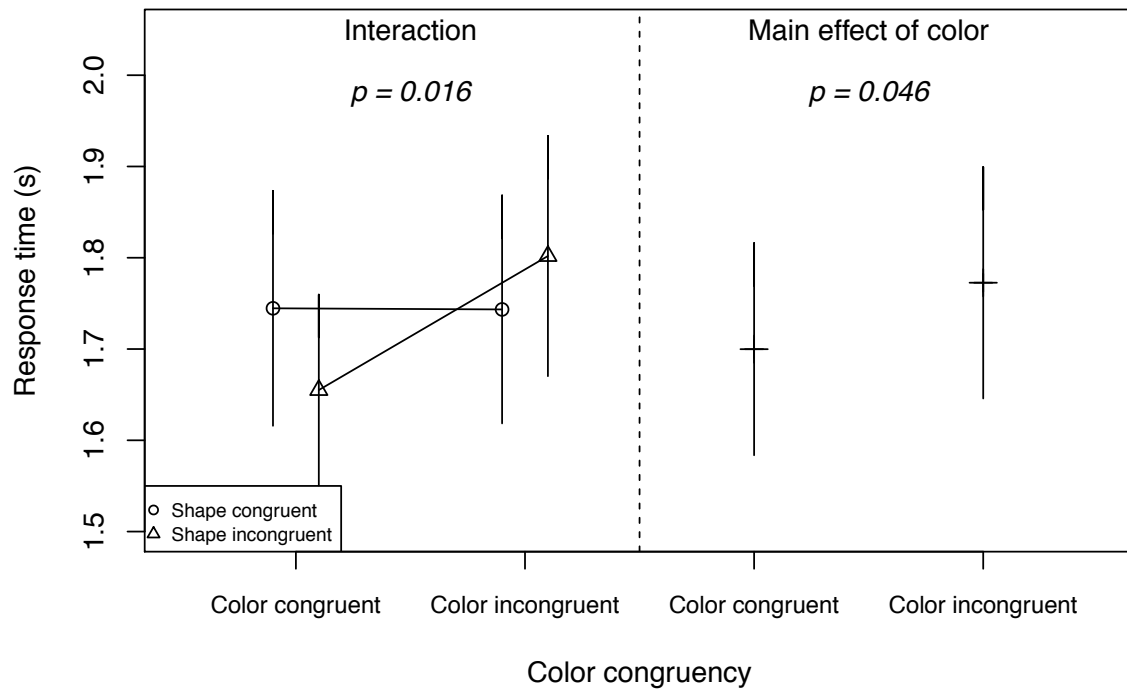


Figure 3. Response times as a function of congruency condition in the b-CFS task of Experiment 2. In this experiment, participants were only required to memorize the shape (but not the color) of each memory item for the upcoming memory recognition task. Error bars denote ± 1 SEM across participants. The results show a main effect of color congruency (right panel) and an interaction between shape congruency and color congruency (left panel).

Experiment 3 – Memorize color and shape

In daily life, when memorizing an object, we typically don't memorize only a single feature dimension (i.e., an orientation or color) but multiple feature dimensions at once (resulting in a face, or a car, etc.). As such, we questioned whether the content of VWM would regulate access to visual awareness of a concurrently presented object along multiple features dimensions (i.e., synergistically) when multiple features of an item are simultaneously maintained in VWM (i.e., as a bound object). To this end, in Experiment 3, we made both

features relevant for the upcoming memory task by requiring observers to memorize the shape and the color of the memory item simultaneously. We expected one of three possible outcomes: 1) If b-CFS targets that match either the color or the shape of the memorized item are detected faster than targets that do not, this indicates that VWM content can regulate visual awareness of a multi-feature object at either memory feature dimension; 2) If only the b-CFS targets that match both the color and the shape of the memory item are detected faster, this indicates that VWM content regulates visual awareness at the conjunction level, as long as the bound feature dimensions are both relevant; 3) Considering that the results of Experiments 1 and 2 suggest that color information in VWM is more dominant than shape information in VWM in regulating access to visual awareness, we also considered the possibility that only color congruent targets are detected faster, and shape congruent targets are not. This would indicate that certain feature dimensions in VWM (e.g., color) can null or suppress the effect of other (e.g., shape) in regulating access to visual awareness, even when both features are memorized.

Method

Observers and procedure

To keep the statistical power equal between experiments, we recruited a new group of 20 observers in Experiment 3 (5 males; mean age 23.41, SD = 3.28). The observers were instructed to memorize both the color and the shape of each memory item, and the feature dimension that was probed during the memory recognition task was determined at random with equal probability (50% color memory recognition, 50% shape memory recognition). This motivated observers to memorize both the color and the shape of the memory item on each trial. When shape was tested, observers had to indicate which of the two stimuli, which were slightly different in shape, was the memory item. All other aspects were identical to Experiment 1.

Results and Discussion

Observers performed well in the b-CFS task (only 2.02% trials were recycled because of incorrect localization responses, $SD = 1.68\%$). The accuracy on the memory recognition task was again above chance and below ceiling, and accuracy was higher on the color-memory than on the shape-memory recognition task (82.41% (7.76%) vs. 73.58% (8.75%), respectively; $t(19) = 4.03, p = 0.0007$).

As illustrated in Figure 4, we observed a main effect of color congruency ($F(1, 19) = 38.79, p < 0.001$), which means that the observers again detected the memory color-congruent targets faster than memory color-incongruent targets (1512ms vs. 1644ms). However, neither the main effect of shape congruency ($F(1, 19) = 0.20, p = 0.66$) nor the interaction between color congruency and shape congruency ($F(1, 19) = 1.48, p = 0.24$) was significant. The results of Experiment 3 show that VWM only accelerates access to visual awareness along the color feature dimension, even though both color information and shape information were made relevant for the VWM task. These findings supported our third prediction: VWM regulates access to visual awareness along the more dominant feature dimension when features from multiple feature dimensions are memorized.

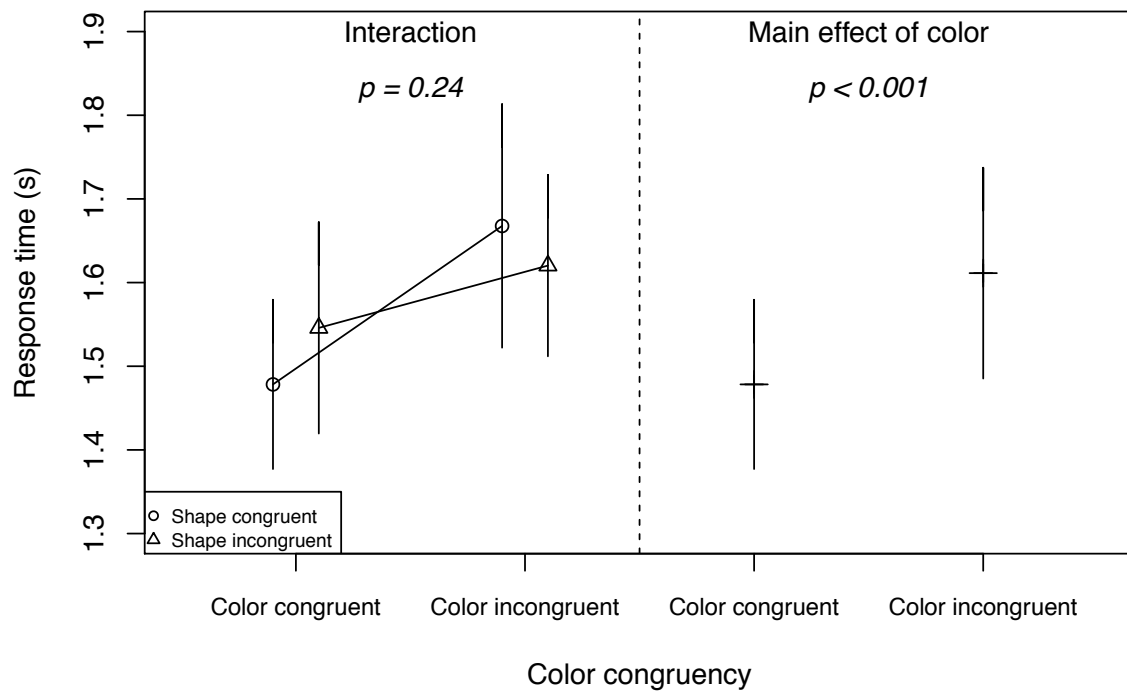


Figure 4. RTs as a function of different congruency conditions of the b-CFS task in Experiment 3. On each trial, participants were required to memorize both the color and the shape of the memory item for the upcoming memory recognition task. Error bars denote ± 1 SEM across participants. The results show a main effect of color congruency.

General Discussion

Recent studies have shown that VWM can regulate the access of visual information to visual awareness, by favoring VWM-matching stimuli compared to VWM-mismatching stimuli (Ding et al., 2019; Gayet et al., 2013, 2019; Gayet, van Maanen, et al., 2016; Liu et al., 2016; Pan et al., 2014; van Moorselaar et al., 2017). In our current study, we combined a VWM task and a b-CFS task to examine whether items in VWM (comprising multiple feature dimensions) exert this regulation along a single or multi-feature dimension, and whether multiple feature dimensions regulate access to visual awareness synergistically. In Experiment 1, when observers were instructed to memorize the color of an item (but not its shape), we observed that stimuli matching the color of the memorandum enter visual awareness faster than stimuli mismatching the color of the memorandum. These results confirm previous findings in showing that VWM can regulate access to visual awareness along the color feature dimension (Gayet et al., 2013). The shape of the memorandum, which observers were not required to remember for the upcoming memory task (i.e., a so-called incidental feature) did not affect access to visual awareness. In Experiment 2, when observers were instructed to memorize the shape of those same items (but not their color), we observed that the color of a memorandum can affect access to awareness, even when it is an irrelevant feature dimension for the upcoming memory task (unlike shape). Strikingly, these findings also reveal that the shape of the memorandum only impacted priority for visual awareness through an interaction with color, selectively when shape was relevant but color was not.

In Experiment 3, observers were required to memorize both the color and the shape of the items for the upcoming memory recognition task. Under these circumstances, we observed that access to visual awareness of concurrently presented stimuli was only affected by the color feature dimension of the memorandum. Combining the results of Experiments 2 and 3, our findings suggest that when multiple features are maintained, the more dominant

feature dimension (here, color) can suppress the influence of the less dominant feature dimension on access to visual awareness.

In line with our current finding that VWM can regulate access to visual awareness along a single feature dimension, previous studies have investigated whether VWM affects conscious processes (e.g., visual attention to unmasked stimuli) at a single feature dimension (Carlisle & Woodman, 2011; Olivers et al., 2006). For instance, Olivers and colleagues (Experiment 4, 2006) required observers to memorize a single feature of an item before a visual search task. In the search task, observers needed longer time to find a target in an array comprising memory-task congruent distractors than in an array with memory-task incongruent distractors, suggesting that attentional capture occurs mostly for items that carried the memory relevant feature. Taking together these findings and our current observations suggests that VWM can regulate visual processing at a single, memory-relevant, feature dimension.

Interestingly, when only the shape of the memorandum was relevant for the upcoming recognition task, we did not observe a main effect of shape congruency, but we still observed a main effect of color congruency. Considering that, across all three experiments, color produced a congruency effect irrespective of whether observers were required to memorize it or not, the observed color congruency effect could be interpreted as a priming effect: repeated presentation (rather than memorization) of a color yields faster access to visual awareness. This interpretation is highly unlikely, however, based on previous studies showing that the color congruency effect disappeared when the color was presented but either not memorized (so-called passive viewing conditions) or dropped from memory (following a retro-cue) (Costello et al., 2009; Pan et al., 2014; Ding et al., 2019; Gayet et al., 2013; Jiang et al., 2007). These studies, with paradigms very similar to ours, observed no effect of priming, indicating

that the color congruency effect observed here is unlikely to be explained by bottom-up priming, but requires the colored item to be maintained in VWM.

In an experiment with an almost identical design as our current Experiment 2, Gayet et al. (2013; Experiment 5) required observers to memorize the shape of a colored memory item but, intriguingly, they did not observe the color congruency effect in b-CFS. This finding is inconsistent with our current results. It is worth noting, however, that the current Experiment 2 had higher statistical power than that of Gayet et al., (2013; Experiment 5), with 20 observers instead of 15, and 144 trials instead of 54. As such, this previous study might have missed out on the color congruency effect, which appears less statistically reliable when color is an incidental feature in our findings as well. In agreement with our current finding, Pratt and Hommel (2003) also observed that the color of a memorandum influenced conscious processes (of unmasked stimuli), even when it was irrelevant for the upcoming memory task. In Experiment 4 of their study, observers were required to search an array of items for a target that matched the shape of the memory item. The memory item varied in color, which was irrelevant for the search target. Akin to our Experiment 2, it is reasonable to assume that observers did not memorize the color of the memory item voluntarily. However, their results showed that search performance improved when the target also matched the (incidental) color of the search target. Considering the qualitative similarities between memoranda following search instructions and memorization instructions (Bundesen, Habekost, & Kyllingsbæk, 2005; de Fockert, Rees, Frith, & Lavie, 2001; Gunseli, Meeter, & Olivers, 2014), their findings suggest that memory task irrelevant features can also affect the prioritization of concurrently presented stimuli (Pratt & Hommel, 2003), at least when consciously perceived. Furthermore, previous studies have shown that memory task irrelevant features could be actively maintained in VWM. For instance, O'Craven, Downing, and Kanwisher (1999) conducted a functional magnetic resonance imaging (fMRI) study and

observed that attending to one feature of an item would result in both the task relevant feature and the task irrelevant feature of the item to be actively maintained. As such, it is possible that when observers memorized the shape of an item in our current study, the color of the memory item was also maintained in VWM. On the other hand, Serences and colleagues showed that color and orientation of a memory item could be decoded from fMRI BOLD activity during the memory delay only when they were relevant for the upcoming memory task, but not when they were irrelevant (Serences, Ester, Vogel, & Awh, 2009). Taken together, whether or not incidental features are maintained in VWM (and thus affect concurrent visual processing) appears to vary from study to study. One possible explanation for this is that only highly discriminable (i.e., pop-out) features are maintained in memory even when they are irrelevant for the upcoming task (Gao et al., 2010; Gao et al., 2011). In light of the present study, this entails that the colors of our memoranda were more discernable than their shapes. Consequently, the instruction to memorize the shape of an item yielded incidental maintenance of its color, so that color congruent stimuli were prioritized for visual awareness, even when color was an irrelevant feature dimension.

The relative dominance of one feature dimension over the other (i.e., color over shape), might also explain why only the color of the memorandum influenced access to awareness when color and shape were both memorized (in Experiment 3). There is some support for our view that color is more dominant than shape for visual processing (Soto et al., 2005; Williams, 1966). For instance, Williams (1966) reported that, when observers are instructed to search for a target number presented within objects of a pre-specified color and shape, observers would mostly fixate objects of the specified color, not of the specified shape. Similarly, requiring observers to memorize both the color and the shape of an item, Soto et al. (2005) observed that a color-congruent stimulus captures more attention than a color-incongruent stimulus, whereas shape congruency did not affect attentional capture. However,

there is also evidence showing that shape information in VWM can affect visual processing of consciously presented stimuli (i.e., attentional processes; Egly et al., 1994; Ghirardelli & Egeth, 1998; Olivers et al., 2006; Bahle, Beck, & Hollingworth, 2018), and even prioritize access to visual awareness in a b-CFS task (Gayet et al., 2020; behavioral experiment). Interestingly, in the study of Gayet and colleagues the shapes were very similar to those used in the current study, but they were grayscale, so that no color information was present. These findings line up with the view that shape information in VWM can – in principle – influence access to awareness of concurrently presented stimuli, unless its influence is negated by the presence of a more dominant feature such as color. Taken together, the interaction between VWM and perception is subject to an intricate interplay of the different feature dimensions of multi-feature objects. While the relative dominance of the different feature dimensions of a memorandum might depend on experiment-specific stimulus characteristics, our current study does show that the influence of a memorandum on access to visual awareness can dramatically vary for the different feature dimensions of that memorandum. Moreover, the more dominant feature can strongly suppress the influence of the less dominant feature.

In sum, our current results suggest that 1) VWM can regulate the priority of visual information to access visual awareness along a single feature dimension; 2) features from different dimensions can impact the competition for awareness to a variable degree, and the more dominant feature may even suppress the effect of the less dominant feature; 3) even stimuli that match an irrelevant feature dimension of the memorandum can be prioritized for visual awareness.

5

Chapter 5

Visual working memory and saliency independently influence the priority for access to visual awareness

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Author contributions:

All authors designed the study concept. YD programmed the experiment and tested the observers, YD conducted the analyses and wrote the manuscript.

Critical revisions were provided by all co-authors.

Abstract

Both visual working memory (VWM) and visual saliency influence sensory processing, as is evident from research on visual attention and visual awareness. It is generally observed that items that are memorized or salient receive priority in visual search and in the access to awareness. Here we investigate whether these two factors interact and together boost access to visual awareness more than each factor independently. In the present experiment, we manipulated the VWM relevance and saliency of an item through a color memorization task and color uniqueness, respectively. We applied continuous flash suppression (CFS) to suppress items from visual awareness. The color of the suppressed items could either be congruent or incongruent with the memorized color, and either stood out from its surrounding distractors (salient pop out) or not. The item's priority for visual awareness was measured by measuring the time it took for an item to "break" into awareness. We first show that VWM relevance and visual saliency each shortened the time needed for an item to access awareness. More interestingly, the combined effect of VWM and visual salience was additive - that is, items that were both congruent and salient broke into visual awareness even faster. A race model further suggests that the interaction between these two mechanisms can be explained by statistical facilitation. Thus, VWM and saliency influence the priority to access visual awareness independently.

Keywords: Visual working memory, saliency, b-CFS, visual awareness

Introduction

Most information presented to our retina does not get enter our visual awareness. Previous research has revealed that certain visual information is prioritized in entering visual awareness. For instance, upright faces, upright body, and recognizable words are known to receive priority to enter visual awareness compared to other information (Costello et al., 2009; Jiang, et al., 2007; Yang et al., 2011, Stein et al., 2012). One distinction that can be made between factors that determine the speed with which information enters visual awareness is that between bottom-up and top-down factors.

First, visual awareness could be guided by bottom-up factors. For example, a green tomato stands out when surrounded by red tomatoes, resulting in higher saliency (Itti & Koch, 2000). To explore the influence of saliency on visual awareness, researchers have used interocular rivalry tasks by presenting different images to subject's eyes and investigate the processing of stimuli accessing visual awareness by measuring the perceptual dominance switch between the two eyes (Lin & He, 2009). Paffen et al. (2008) and Stuit et al. (2010) varied item saliency and observed that salient items break interocular suppression faster than less salient ones. Furthermore, by using the recently developed interocular suppression paradigm called breaking continuous flash suppression (b-CFS; e.g., Jiang et al., 2007; Wang, Weng, & He, 2012; Gayet et al., 2013), Gayet et al. (2016, Exp. 2) replicated this effect. They showed that an increase in saliency through luminance contrast shortened the time to break interocular suppression, which resulted in subjects getting aware of the originally suppressed stimuli faster. The b-CFS paradigm provides a controllable method to compare the potency of different visual stimuli to reach visual awareness. In a b-CFS paradigm, the detection of stimuli presented to one eye is initially suppressed from awareness by the continuous flash presented to the other eye (Tsuchiya & Koch, 2005). The time it takes for a

suppressed stimulus to overcome the interocular suppression provides a measure of the priority a stimulus receives in entering to awareness (Gayet et al., 2014).

The influence of top-down factors on visual awareness has been studied by examining the influence of the visual working memory (VWM) content in b-CFS tasks. For instance, combining a VWM task with a b-CFS task, researchers investigated whether an item that was held in mind also entered awareness faster. The results suggest that items that matched VWM content got released from interocular suppression faster than the items that mismatched VWM content (Gayet et al. 2013; van Moorselaar et al., 2017; Pan, Lin, Zhao, & Soto, 2014; Liu, Wang, Wang, & Jiang, 2016). These studies suggest that VWM can affect visual awareness processing.

Previous literature has shown that saliency and VWM can interact behaviorally. For example, by manipulating the saliency of items in a visual scene, researchers have observed that items with higher saliency improve subjects' ability to recall these items (locations) (Fine & Minnery, 2009; Melcher & Piazza, 2011; Santangelo & Macaluso, 2013). In addition, VWM congruent items capture more attention than incongruent ones during a detection or search task (Downing 2004; Soto, 2005; Olivers, 2009, 2014; Hollingworth, 2013, 2016, 2018). Varying VWM validity and target saliency, Soto et al. (2006) reported that subjects detect a target faster when both salient and congruent with memory as compared to when the target was either memory congruent or salient. However, since the previous studies explored the interaction between saliency and VWM when the stimuli were not suppressed from awareness, it is currently unclear whether saliency and VWM can interact to act on the priority for entering visual awareness. In the current study, we aim to answer this question by combining a VWM task and a b-CFS task. This paradigm also allows us to investigate *how* visual working content and saliency interact in affecting priority to visual awareness. On each trial, subjects memorized one color for a later recall test and, between memorization and

recall, detected the target location during the b-CFS period. During the CFS presentation, 1) we varied the target saliency by manipulating the pop-out of the suppressed stimuli by using a distinct color; 2) we varied the target's match with memory content by changing whether the detected target was a memorized (match) or non-memorized (mismatch) color category.

Given that both working memory congruence and higher saliency can affect priority for entering visual awareness, multiple outcomes are possible. When an item is salient as well as matching the content of VWM, RTs in b-CFS could - in principle - be affected in three ways: subjects could get aware of the item a) as fast as the salient or VWM relevant item; b) faster than either salient or VWM relevant item but not faster than statistical facilitation; c) even faster than the statistical facilitation (the latter would resemble integration, as in multisensory processing). We will test a race model (Miller, 1982, 2007) to investigate whether integration of these two factors exists. The cumulative distributive functions (CDF) of RTs in the memory congruent condition and salient condition were used to calculate how fast responses in the memory congruent and salient condition are expected to be based on statistical facilitation (i.e., independent processing as indicated by the race model (RMI), see Miller, 1982, 1986). If responses to working memory congruent and salient condition are faster than predicted by statistical facilitation, this indicates that integration between the visual working memory and saliency information exists.

Method

Subjects

Twenty subjects participated in the current study for a monetary reward after signing informed consent. All the subjects were naïve to the research purpose. Their age ranged from 23 to 39 ($M = 26.5$, $SD = 4.27$; 7 women). All subjects reported having normal or corrected-to-normal sight and having no visual disorder or epilepsy.

Apparatus

The current experiment was conducted on a PC equipped with a linearized 27-inch LCD monitor (2560 · 1440 pixels, 144-Hz refresh rate) in a dark room. Stimulus presentation and response registration were controlled by MATLAB (R2016; MathWorks, Natick, MA) using the PsychToolbox extension (Brainard, 1997; Pelli, 1997). Subjects gazed at the monitor through a stereoscope with four mirrors (two per eye) to achieve dichoptic presentation for b-CFS. The viewing distance was maintained at about 61 cm with a chin and forehead rest.

Task and conditions

The main part of a single trial consisted of a b-CFS task to test the effects of saliency and working-memory content on how fast targets break into visual awareness. As illustrated in Figure 1, all stimuli were presented on a uniform black background (7.00 cd/m^2). To facilitate binocular fusion of the dichoptic images, the stimulus areas presented to each eye were enclosed by an identical Brownian (i.e., $1/f^2$) noise square frame with a height and width of 7° and a thickness of 0.4° . We presented a gray dot with a diameter of 0.27° at the center of each frame for fixation. The effect of working-memory content was manipulated by combining a color memory task with the b-CFS task (Figure 1A).

Before the b-CFS task, subjects were first shown a color for memorization (Figure 1A). This color could either match (congruent condition) or not match (incongruent condition) the color category of the target during b-CFS (Figure 1B). The effect of saliency

was manipulated by moderating the stimuli's appearance. The suppressed stimuli could display three identical colors and one odd color (salient condition) or display four dissimilar colors (non-salient condition). The memory congruency and saliency conditions could be combined in any way, resulting in a two-by-two factor design.

Stimuli and procedure

Per trial a color was randomly chosen from five main color categories (red, green, blue, brown, and purple) for memorization. Colors were equal in luminance to prevent that subjects relied on luminance instead of hue as a memorization strategy. To prevent a ceiling effect in task performance and a linguistic instead of visual memorization strategy, subjects had to choose the memorized one from two colors, of which one was the memorized color, and the other one was a distractor color that looked similar but had a different hue (Olivers et al., 2006; see the supplementary material for details of generating the colors). In between the memorization probe and memorization test, subjects performed a b-CFS task (Figure 1A). The b-CFS method typically consists of the presentation of a target stimulus to the non-dominant eye, and strong, dynamic masks to the dominant eye to ensure prolonged visual suppression of the target⁵. We measured each subject's dominant eye with a b-CFS task before the main experiment. We used b-CFS instead of another eye dominance test (e.g., hole-in-the-card) to determine because eye dominance is task specific and thus variable across tasks (Ding et al., 2018). We generated 200 different binary patterns (0 and 41.80 cd/m² for black and white parts, respectively), that consisted of pink noise images filtered by a Gaussian low-pass filter ($\sigma = 3.2$, Gayet et al., 2014), as the b-CFS masks.

In the main task, subjects performed 20 practice trials, followed by 160 test trials. Every trial started by subjects pressing the space bar of the keyboard. After this, an upright

⁵ To check whether the dynamic interocular masks suppressed the targets, we recruited 10 subjects and conducted the salient condition with and without interocular suppression. The subjects detected the target location significantly slower in the suppression condition than in the non-suppression condition (difference = 438 ms, $t(9) = 4.95$, $p < 0.001$) which implies that our b-CFS manipulation was working as intended.

colored triangle was presented at the center of fixation for 1000 ms (Figure 1A). Subjects were instructed to remember the color for later recall and were informed that the memory color was irrelevant for the suppression task. After a blank screen (1250 ms), four colored triangles with randomly arranged different orientations (upright, upside down, leftward oriented and rightward oriented) were presented to the nondominant eye at 2 degrees center-to-center eccentricity on the cardinal axes (i.e., left, right, above and below fixation dot). The intensity of the triangles increased gradually from 0% Michelson luminance contrast to a contrast of 26.35% within 1 s. We presented a different mask every 100 ms (10 Hz) in random order to the dominant eye. Subjects were required to keep fixating at the center dot and report the upright triangle (e.g., the target during CFS) location as soon as they located it. The target color could be either congruent or incongruent with the memory color in the memory congruent or memory incongruent conditions respectively. The colors of the three non-target triangles were chosen from the memory incongruent colors: the non-target triangles shared a same color in the salient condition and had different colors in the non-salient condition (see Figure 1 for specific examples). Considering the statistical power, we designed to balance the memory content congruent and incongruent trials to have the same number of trials (e.g., 50% for each). The suppression task lasted until a response was given or until 20 s without a response had passed. We presented text feedback in trials with an incorrect localization response. Trials with a localization error or without any response were recycled at the end of the experiment. Subjects received feedback about their accuracies in the working memory task every 10 trials.

To exclude potential priming and predictive effects of the memory probe, we conducted a control experiment which was identical to the main experiment except for the fact that we removed the recall phase on each trial and instructed the subjects ($n=10$) to just passively view the cue before the b-CFS task.

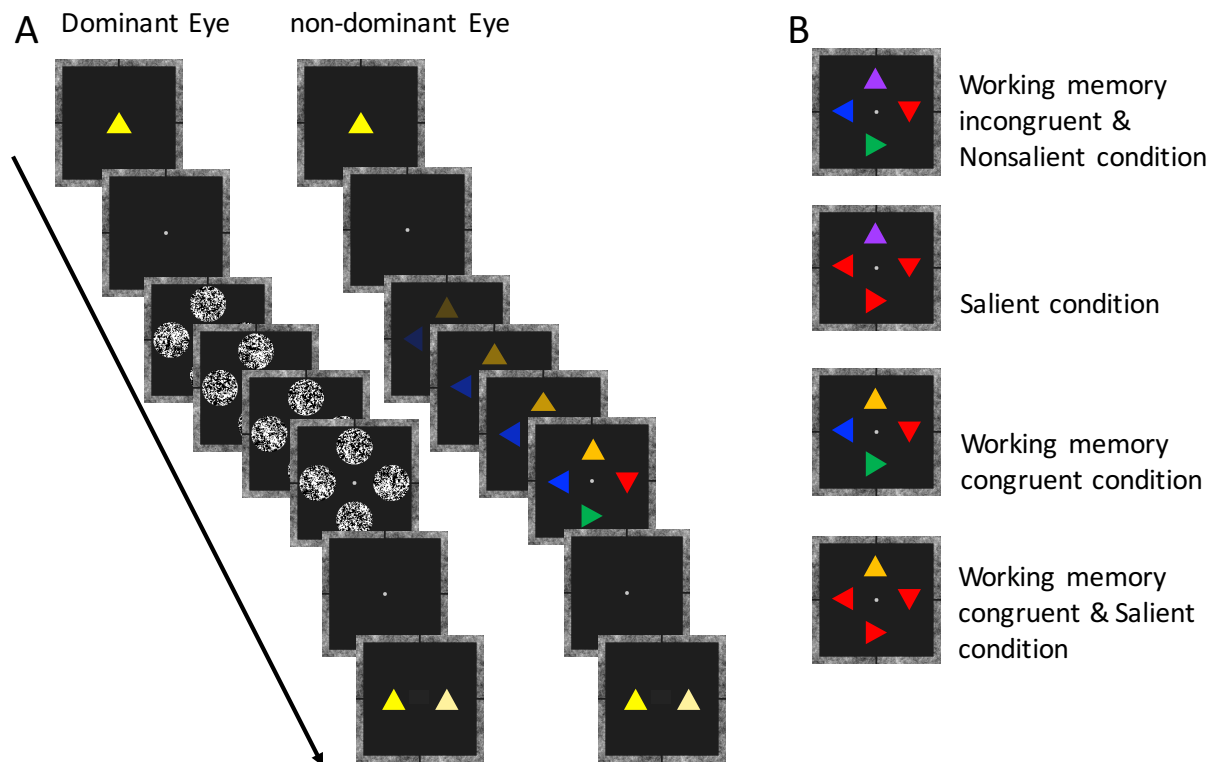


Figure 1. (A) A schematic depiction of the sequence of events in a trial. Subjects were instructed to remember a color for later recall at the beginning of each trial and detect the location of target (e.g., the upright triangle) during the dynamic masks display. The target triangle color during the visual detection task could be working memory (in-)congruent as well as (non-)salient. (B) Examples of the different memory congruence and visual saliency conditions.

Results

Subjects correctly indicated the b-CFS target location in 98.44% ($SD = 2.00\%$) of the trials. Trials with incorrect localization during the suppression task were excluded from further analysis. The localization accuracy was analyzed with a two-factor repeated-measures ANOVA with the predictors memory congruence and saliency. We observed both main effects of visual saliency (salient vs. non-salient: 98.94% ($SD = 1.59\%$) vs. 97.93% ($SD = 2.26\%$); $F(1, 19) = 5.89$, $p = 0.03$) and memory congruence (congruent vs. incongruent:

98.93% ($SD = 1.60\%$) vs. 97.94% ($SD = 2.26\%$); $F(1, 19) = 6.48, p = 0.02$) and a trend-level interaction ($F(1, 19) = 3.27, p = 0.09$).

We compared the subjects' memory accuracies in memory congruent and incongruent conditions and observed no difference ($m = 79.67\%$; $t(19) = 1.12, p = 0.28$). This suggests that the congruent color display during the suppression period did not affect subjects' performance in the memory test.

The effects of congruence and saliency on RTs in the suppression task were also analyzed with a repeated-measures ANOVA. As illustrated in Figure 2, we observed significant main effects of memory congruence ($F(1, 19) = 23.45, p < 0.001$) and visual saliency ($F(1, 19) = 18.39, p < 0.001$) but no significant interaction between them ($F(1, 19) = 1.79, p = 0.20$). These results point at a faster break through suppression by memory congruent as compared to memory incongruent targets (1440 ms vs. 1562 ms) and at visually salient targets having broken through suppression faster than nonsalient targets (1433 ms vs. 1569 ms). Furthermore, subjects detected targets that were both memory congruent and salient faster than targets that were only memory congruent or only salient (memory congruent & salient vs. memory congruent & nonsalient: 1323 ms vs. 1401 ms, $t(19) = 3.69, p < 0.002$; memory congruent & salient vs. memory incongruent & salient: 1323 ms vs. 1349 ms, $t(19) = 3.71, p = 0.001$). Considering the main effects of memory congruence and visual saliency on detection response accuracy reported above, the faster RTs in memory congruent and salient conditions rule out the possibility of speed-accuracy trade-off.

The results of the control experiment show that the differences in RTs for the main experiment were not caused by priming or making use of the predictability of the cue ($F(1, 9) = 0.03, p = 0.86$): WM-matching targets were not detected faster when passively viewing the cue. Interestingly, we even observed a negative priming effect, i.e., subjects detected the target locations slower in the probed & salient condition than in the salient-only condition

($t(9) = 2.44, p < 0.04$). These results indicate that the facilitation of detection times in the top-down condition cannot be explained by bottom-up priming or top-down prediction.

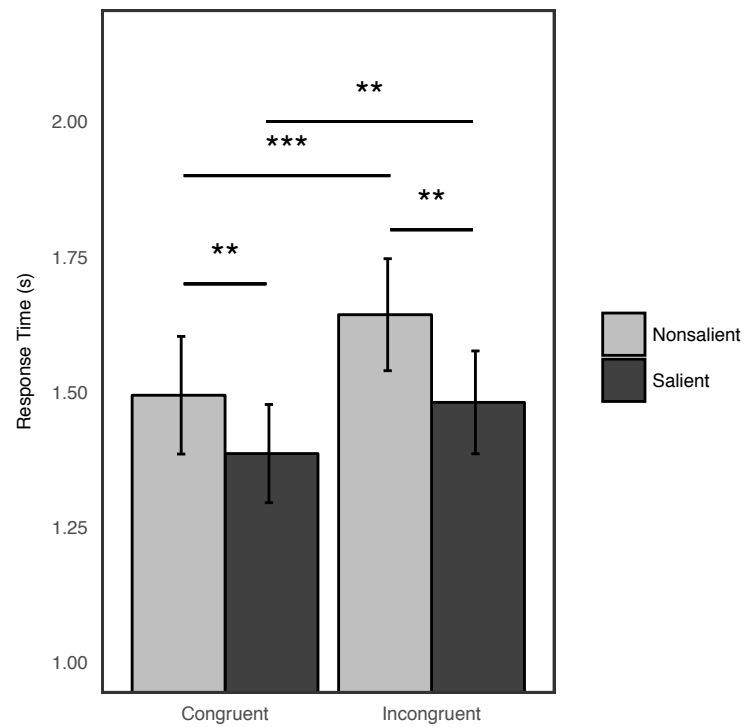


Figure 2. Response times as a function of memory Congruence and visual Saliency for the main experiment. Error bars denote ± 1 SEM.

In order to investigate whether the speedup in the memory congruent and salient condition compared to either memory congruent condition or salient condition could be explained by an independent processing model (i.e., working memory and saliency act independently on RT), or by a coactivation model (i.e., working memory and saliency integrate), we analyzed violations of a race model (Miller, 1982). The race model places an upper limit on the cumulative probability (CP) of a response at a given response time for redundant signals (i.e., the memory congruent and salient condition in the current study). The race model holds, for any response latency, when the CP value from redundant signals does not exceed the sum of the CP from each of the single signals. If violated, this means that working memory and saliency information integrates. As illustrated in Figure 3, for the entire curve, the CP of observed memory congruent and salient condition was smaller than the sum of the CP of memory congruent condition and salient condition, indicating no violation of the race model. This suggests that working memory and saliency independently influence access to visual awareness.

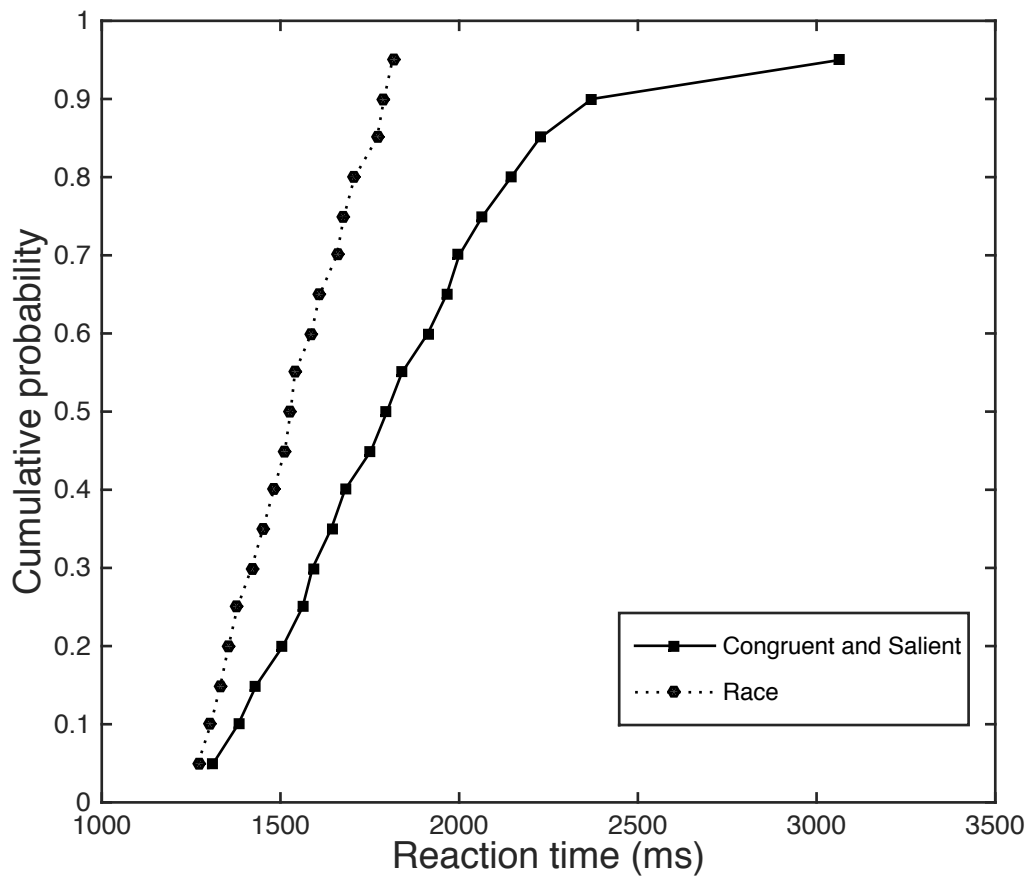


Figure 3. Redundancy gain analysis for violation of the race model inequality. The solid and dashed line stand for the cumulative probability distributions of RTs with memory Congruent and Salient target and with the race model bound computed from memory Congruent target and Salient target, respectively.

Discussion

The aim of the present study was to investigate 1) whether saliency and VWM-content interact in affecting priority for access to visual awareness, and if so, 2) *how* saliency and VWM interact. To this end, we combined a b-CFS task with a VWM task. We replicated two previously reported findings. First, we observed that VWM content-congruent items broke interocular suppression faster than incongruent items (Gayet et al., 2013; van Moorselaar et al., 2017); Second, we replicated that salient items receive priority over non-salient items to break interocular suppression (Gayet, Paffen, Belopolsky, Theeuwes, & Van der Stigchel, 2016; Paffen, Naber, & Verstraten, 2008; Stuit, Verstraten, & Paffen, 2010). Importantly, we observed that items which were both salient and memory-content congruent broke CFS even faster than either salient or memory-congruent items. This novel finding suggests that saliency information and VWM content interact in affecting priority for access to visual awareness. To study *how* saliency information and VWM interact, we conducted a race model analysis which revealed that the interaction between these two mechanisms can be explained by statistical facilitation.

Saliency and VWM, as bottom-up and top-down factors respectively, are known to act on sensory processing. Salient items are prioritized during search tasks (Theeuwes, 1991; 1994; 1992) and consciousness paradigms (Gayet, Paffen, Belopolsky, Theeuwes, & Van der Stigchel, 2016; Naber, Carter, & Verstraten, 2009; Paffen, Naber, & Verstraten, 2008; Stuit, Verstraten, & Paffen, 2010), even when subjects are not aware of the stimuli (Hsieh, Colas, & Kanwisher, 2011; Lin & Murray, 2015). For instance, McCormick (1997) originally observed that attention was captured by a subliminal exogenous cue, and a number of studies replicated this finding with different designs (for reviews, see Mulckhuyse & Theeuwes, 2010; Lamme & Roelfsema, 2000). Using a similar paradigm (e.g., CFS) as the current study, Hsieh et al. (2011) observed that a salient though invisible item captured more attention and

subsequently improved sensory processing more than a less salient one. Similarly, VWM content-congruent items also receive priority in sensory processing, which results in an automatic capture of the focus of selective attention (Bahle, Beck, & Hollingworth, 2018; Hollingworth & Beck, 2016; Maxcey-Richard & Hollingworth, 2013; van Moorselaar, Theeuwes, & Olivers, 2014; Olivers, 2009; Olivers, Meijer, & Theeuwes, 2006) and a boost in priority for access to awareness (Gayet et al., 2013; van Moorselaar et al., 2017). Our results are thus in line with these previous studies.

The current study took the investigation into the role of bottom-up and top-down processes in prioritizing items one step further by combining their effects. In classical search paradigms (Theeuwes, 1991; 1994; 1992), subjects detect the target with a short reaction time which could result in too limited temporal space to observe the possible additive effects of saliency and VWM (e.g. RTs cannot become faster due to a floor effect). The b-CFS paradigm used in the current study provides a proper method to avoid this issue. Typically, CFS delays the process of becoming aware of the items (e.g., seconds or even longer), allowing to measure the effects of saliency and working memory in a broader and therefore more sensitive range of RTs. This prolonged processing allowed us to observe the interaction between saliency and VWM directly in the current study.

Our race model results reveal that salient and VWM content congruent items broke interocular suppression faster than either salient or VWM relevant items alone. However, the model did not violate statistical facilitation, suggesting that the visual system does not integrate (or ‘bind’) saliency and VWM-congruent information to multiply their effects. When an item is salient, processing is therefore not yet at its optimum; when the salient item also matches the content of VWM, processing can become even more efficient (resulting in even shorter RTs in the current experiment). The reverse also applies: when an item matches the content of VMW, processing can become even more efficient when the item is also

salient. One other possible outcome option (integration) was also falsified: saliency and VWM information do not integrate in affecting visual processing: apparently, the visual system does not contain a mechanism akin that in multisensory processing; bottom-up saliency and top-down VWM information is not integrated in a specialized super-facilitation mechanism. Instead, the current results provide evidence that saliency and VWM content affect processing independently: On the one hand, items compete against each other to receive priority for visual processing based on the saliency (Itti & Koch, 2000). On the other hand, the VWM enhances the neural response to the concurrent visual input which matches the VWM content (Gayet et al., 2017). In conclusion, independent, parallel processing explains why we did not observe integration between saliency and VWM.

To ensure that the difference in RTs between conditions reflected conscious access instead of a shift in post-conscious response criterion, previous studies included a monocular control experiment. Such as experiment includes the presentation of a single item (the target) and the dynamic pattern (e.g., masks in b-CFS condition) to the same eye and therewith the measurement of RTs without an episode of item invisibility due to visual suppression (Jiang et al., 2007; Gayet et al., 2013; Pan, Lin, Zhao, & Soto, 2014). No difference observed in RTs in the monocular task then (according to these studies) excludes the response criteria issue (Jiang et al., 2007; Gayet et al., 2013; Pan, Lin, Zhao, & Soto, 2014). However, van Moorselaar et al. (2017) observed a difference in RT between memory-congruent and memory-incongruent items in the monocular experiment, but only when an item was presented among distractors. This suggests that a part of the priority enhancement by VWM results from the interactions between items and distractors outside the operations of interocular suppression. Our aim was to study how saliency and VWM content interact in prioritizing access to awareness, thereby making the monocular control condition redundant. The results of the passively viewing control experiment suggest that it is unlikely that the

subjects made use of the predictive value of the memory probe for the b-CFS task, however, it could still be argued that the items in the memory condition could be memorized more easily than the items in the passively viewing condition. This limitation needs to be studied in further research. Although out of the scope of the current study, it would be interesting to investigate at what stages – from unconscious (e.g., by interocular and spatial suppression) through preconscious (e.g., only by monocular spatial suppression) to conscious – VWM and saliency operate.

Supplementary material

The low-luminance blue color suited best as the baseline luminance reference to which the other colors were subjectively matched with heterochromatic flicker photometry (Kaiser & Comerford, 1975; Wagner & Boynton, 1972). The hues of each color were slightly different to each other and also similar in luminance. We achieved the hues with two selection steps. First, we identified the location of each of the five color categories into an equiluminant plane in CIE 1931 color space. Then two more hues of each color category were chosen from this plane.

6

Chapter 6

Saccades reset the priority of visual information to access awareness

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Author contributions:

All authors designed the study concept. YD programmed the experiment and tested the observers, YD conducted the analyses and wrote the manuscript.

Critical revisions were provided by all co-authors.

Abstract

Subjectively, we experience a stable representation of the outside world across saccades. Although previous studies have reported that presaccadically acquired visual information influences postsaccadic perception, whether such information's priority to access visual awareness is either reset by each saccade or continuous across saccades remains unclear. To investigate this issue, we combined a breaking continuous flash suppression (b-CFS) with a saccade task. Before each saccade, a grating was presented in the peripheral visual field under suppression. After the saccade, the same grating was again presented under suppression at either the retinotopically matched, the spatiotopically matched, or a control location. By measuring the duration of the grating to break through CFS into awareness after a saccade, we could compare the breakthrough times across stimuli presented at the different locations. No difference in the reaction times between the spatiotopic and control location was observed, indicating that a saccade resets the buildup of an object's priority to access visual awareness. However, a longer breakthrough time was observed for the retinotopic as compared to the control location, suggesting that a form of retinotopic adaptation to the grating suppressed the priority to access visual awareness after a saccade.

Keywords: visual awareness, saccade, spatiotopic, retinotopic, b-CFS

Introduction

We make fast, ballistic eye movements ('saccades') around three times per second to sample the external visual world. After each saccade, stimuli in the visual world are projected onto different locations of the eye's retina compared to before the saccade. Although saccades produce abrupt and large changes on the retina, our subjective visual awareness consists of a remarkably stable representation of the outside environment, given that the retinotopic coordinates of stimuli are largely maintained throughout the visual system (Wandell, Dumoulin, & Brewer, 2007).

Why is our awareness of the visual world stable across saccades? It has been proposed that spatiotopic representations, which encode the visual world and its locations in coordinates with respect to external frames (e.g., an object of interest), contribute to visual stability (Burr & Morrone, 2011; Melcher & Morrone, 2015). Such a representation might be used to inform the visual system to anticipate and integrate the change in sensory input caused by a saccade into a coherent and less transient percept. For instance, research using neurophysiological recordings has provided evidence for presaccadic shifts of retinotopic representations (also called 'remapping'). This suggests that a single neuron could be sensitive to a stimulus that remains in its classical receptive field after the saccade, thereby supposedly bridging the change in retinotopic coordinates introduced by the saccade (Duhamel, Colby, & Goldberg, 1992; Kusunoki & Goldberg, 2003; Umeno & Goldberg, 1997). Indeed, several recent studies provide evidence that visual information can be integrated across saccades to some degree (Ganmor, Landy, & Simoncelli, 2015; Melcher & Morrone, 2003; Oostwoud-Wijdenes, Marshall, & Bays, 2015; Wolf & Schütz, 2015; Fabius et al., 2016). For example, Ganmor et al. (2015) and Wolf and Schütz (2015) reported that observers detect the orientation of a grating better when it is visible *both* before (peripherally) and after a saccade (foveally) than when the stimulus is *only* presented before a saccade

(peripherally) or *only* after a saccade (foveally). Such transsaccadic updating is, however, not undisputed, as some studies found no transfer of visual information from retinotopic into spatiotopic representations (Knapen, Rolfs, & Cavanagh, 2009; Mathôt & Theeuwes, 2013; Morris et al., 2010; Wenderoth & Wiese, 2008).

Although these findings appear discrepant, it could be that the studied phenomena operate in different reference frames depending on (among others) conscious access to visual information. It is currently unclear how unconscious information processing is affected by saccades. More specifically, as not all stimuli enter awareness – especially those in the periphery – and some stimuli may be prioritized to enter visual awareness (e.g. fearful stimuli or stimuli of special interest; Gayet, Paffen, & Van der Stigchel, 2013; Jiang, Costello, & He, 2007), it is currently unknown whether such prioritization survives across saccades. As an example, consider standing in front of a fruit stall while searching (via making saccades) for your favorite fruit, say a pineapple. While looking at a different fruit, the pineapple might just run short of crossing the threshold for reaching visual awareness. After making an additional saccade to another location, the pineapple is located at a different retinal location. Does the pineapple reach awareness faster, since it was already processed before the saccade, thereby allowing you to find it sooner? Our current study is conducted to explore this question.

Binocular rivalry is one of the main phenomena broadly used to study visual awareness. By presenting two distinguishable images to the same locations of each eye respectively, an observer experiences alternations in perception between these two images. A recently developed interocular rivalry method called ‘breaking continuous flash suppression’ (e.g., b-CFS; Ding, Paffen, Naber, & Van der Stigchel, 2019; Gayet, Paffen, & Van der Stigchel, 2013; Jiang, Costello, & He, 2007; Rothkirch et al., 2018; Stein, 2019) is now being used by a growing body of studies. In a b-CFS task, a target presented to one eye is initially rendered unaware by dynamic patterns (i.e. masks) presented to the other eye. The

suppression exerted by the masks on the target presented to the other eye typically lasts for seconds, and the time it takes for the stimulus to break through the interocular suppression into awareness is used as a measure of the priority it receives to access visual awareness (Jiang et al., 2007; Mudrik, Breska, Lamy, & Deouell, 2011; Sklar et al., 2012; Stein, Hebart, & Sterzer, 2011; Wang, Weng, & He, 2012). Here we use a b-CFS task to explore whether saccades reset the prioritization of visual information to enter visual awareness. A probe stimulus will be presented before the execution of a saccade and an identical stimulus will be presented at the spatiotopically matched, the retinotopically matched, or a control location, while undergoing CFS. If prioritization for visual awareness is continuous across saccades, the prioritization of the probe stimulus will continue after a saccade, onwards from the level already reached before the saccade. In contrast, if prioritization is reset after a saccade, prioritization will start anew.

When considering the above hypotheses, we also have to consider that the presentation of a stimulus can result in some sort of visual aftereffect. For instance, the ability to discriminate contrast decreases after being presented by a contrast adapting stimulus (e.g., the contrast aftereffect; Greenlee & Heitger, 1988). Therefore, such an aftereffect may reset or even suppress the process of prioritization. Moreover, previous studies have used orientation adaptation to examine visual processing across saccades. While some observed adaptation at both spatiotopic and retinotopic locations (Melcher, 2005; Nakashima & Sugita, 2017; Parwaga, Buckley, & Duke, 2016), others observed adaptation only at retinotopic locations (Knapen, Rolfs, Wexler, & Cavanagh, 2010; Mathôt & Theeuwes, 2013). Using different complexities of stimuli as adaptation stimuli, van Boxtel, Alais, and van Ee (2008) observed an adaptation effect at retinotopic locations for less complex stimuli (e.g., gratings and scrambled faces) and at both retinotopic and spatiotopic locations for more complex stimuli (e.g., faces and houses). Considering that the spatiotopic adaptation effect could

potentially neutralize the buildup of prioritization to awareness, we only used less complex stimuli (e.g., gratings) as the targets during CFS display to avoid adaptation effects at the spatiotopic location. Moreover, we presented stimuli only briefly before a saccade, thereby limiting any potential adaptation effect.

Method

Observers

17 observers (7 men; $M_{\text{age}} = 26.5$, $SD = 2.94$) participated in the experiment for monetary compensation and were naïve as to the purpose of the study. All observers reported normal or corrected-to-normal vision and provided written informed consent prior to the experiment. This experiment was conducted with approval of the Ethics Committee at the Faculty of Social and Behavioral Sciences of Utrecht University and in accordance with the Declaration of Helsinki.

Setup

In a darkened room, a PC equipped with 2 linearized 27-inch ASUS LCD monitors (1920 by 1080 pixels, 120 HZ refresh rate) was used to conduct the experiment. A stereoscope with 2 mirrors (one per eye) was fixed on a chinrest for dichoptic presentation. All stimuli were created and presented using MATLAB (the MathWorks Inc., Natick MA, 2012), the PsychToolbox (Brainard, 1997; Pelli, 1997) and the Eyelink Toolbox (Cornelissen, Peters & Palmer, 2002). An Eyelink 1000 (SR Research Ltd. Ottawa ON; sampling rate 1000 HZ) - a video-based eye tracker sampling at 1000 Hz, was used to record eye movements. Eye movements were recorded monocularly. Saccade initiation was detected online, with an acceleration threshold of $9500^\circ/\text{s}^2$ and a velocity threshold of $30^\circ/\text{s}$. The Eyelink was calibrated using 5-point calibration routine.

Stimuli

As illustrated in Figure 1, all stimuli were presented on a gray background. To promote binocular fusion, the stimulus area presented to each eye was enclosed by a Brownian (i.e., $1/f^2$) noise square frame with a height and width of 21.5° and 10.75° respectively and a thickness of 0.5° . A gray dot and a green dot (sized 0.28°) were displayed with a horizontal separation of 8° in the middle of the noise square frame, as fixation and saccade target, respectively. Two hundred different binary patterns (0.33 and 105.00 cd/m^2 for black and white parts, respectively), sized 2° by 2° , were generated as CFS masks. All the masks consisted of pink noise images and were filtered by a Gaussian low-pass filter ($SD = 3.2^\circ$). On each trial, a randomly oriented quadrature sinewave grating with a diameter of 1.2° , Michelson luminance contrast of 98.82% and spatial frequency of 1.5 cycles per degree was presented as the presaccadic stimulus and the to-be-detected target. An auditory cue signal was used to alert observers to move their eyes to the green dot.

Procedure

Before the main experiment, each observer's dominant eye was determined with a b-CFS task because eye dominance is task specific (Ding et al., 2018). In the main experiment, the b-CFS masks were always presented to the dominant eye. Observers performed 25 practice trials and 192 test trials (48 per condition). An experimental trial had the following order of events: At the beginning of each trial, the fixation and the saccade target were presented to each eye. Only after the observer's gaze was within 1° of the fixation dot and he or she pressed the space bar simultaneously, the trial would continue. Continuation of the trial was marked by the appearance of 6 dynamic masks (refreshed at 10 Hz), presented with a vertical separation of 1.5° and a horizontal separation of 4° . Concurrently with the onset of the masks, the presaccadic grating was presented to each eye at one of the corresponding positions of the center masks. After a latency of 100 to 163 ms, the auditory cue signaled the observers to move their eyes from the fixation to the saccade target. As the eye movement response

started, the presaccadic grating was removed. Also at the same time, a grating with the same size, spatial frequency and orientation, but with an intensity increasing from 0% to 98.82% Michelson contrast was presented to the non-dominant eye at either the presaccadic stimulus location (a spatiotopic match), the location that retinotopically matched the presaccadic stimulus location (a retinotopic match), the spatiotopic control location, or the retinotopic control location. To prevent observers from expecting the postsaccadic grating location based on the presaccadic grating location, all the four location conditions were tested with an equal amount of trials (e.g., 25% of the trials for each condition). The task of the observer was to keep fixating at the saccade target and to detect whether the second grating appeared above or below the saccade target as soon as they saw it. A trial was recycled when observers (1) moved their eyes at a moment not corresponding to that of the auditory cue (e.g., the eye movement happened before the onset of the auditory cue or within 100 ms after the onset), (2) pressed a button unrelated to the grating presented after the saccade (e.g., pressing any button before or within 200 ms after the onset of the eye movement response), (3) executed an eye movement that landed more than 2° away from the saccade target, (4) did not execute either saccade or grating detection response, or (5) responded to the second grating by pressing an irrelevant button. At the end of each trial, a white dot was presented at the observer's final gaze position to motivate the observer to keep fixating at the green dot after the saccade.

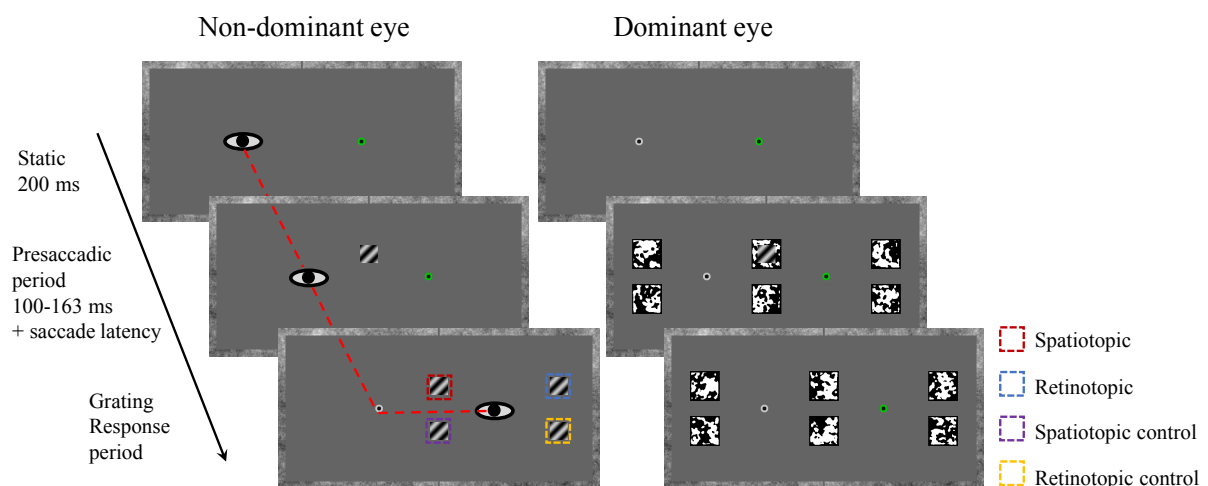


Figure 1. A schematic depiction of the sequence of events during each trial. Observers were instructed to look at the gray dot, make an eye movement to the green dot at the time of the auditory cue and keep fixating thereafter, and to detect the position at which the grating appeared after the eye movement during the dynamic masks display. A grating was presented as the presaccadic stimulus before the eye movement. After the saccade ended at the green dot, the target grating was presented at either the spatiotopic location, the retinotopic location, or one of the control locations.

Data analysis

The data of one observer was removed from the analysis because the individual did not finish the experiment. Trials were excluded based on the following criteria: the response resulted in recycling, or observers moved eyes away from the green dot more than 2° after the saccade response, and saccade response ended before removing the presaccadic stimulus from the screen (as determined offline). More than 10 trials (ranged from 11 to 46, $M = 30$, $SD = 7$) for each condition of each observer were included in the final analysis.

Results

Observers responded with high accuracy to the vertical hemifield of the target grating (with response accuracies ranging from 88.89% to 100%, $M = 97.23\%$, $SD = 3.17\%$).

We quantified the location-specific saccadic shifting effect by comparing the durations for breaking the interocular suppression of different locations. A 2×2 repeated measures analysis of variance (ANOVA) was used with reference frame (spatiotopic, retinotopic) and control location (yes, no) as independent variables and the latency of the second grating location detection response as dependent variable. The analysis revealed main effects of reference frame ($F(1, 15) = 4.90$, $p = 0.043$) and control location ($F(1, 15) = 15.86$,

$p = 0.001$). Crucially, we also observed an interaction between reference frame and control location ($F(1, 15) = 5.46$, $p = 0.034$), revealing different effects of locations for different reference frames. Planned comparison showed that the reaction times for the retinotopic location were longer than that at the retinotopic control location (2.69 s vs. 2.03 s; $t(15) = 3.33$, $p = 0.005$). No significant difference was observed between the reaction time for the spatiotopic location and for the spatiotopic control location (2.17 s vs. 2.09 s; $t(15) = 0.95$, $p = 0.356$) (see Figure 2). Since the retinotopic locations remained in the same visual hemifield across saccades while the spatiotopic locations shifted hemifields, it is possible that the different RT patterns of the retinotopic condition and the spatiotopic condition were caused by the hemifield change. This is of relevance given the fact that distributing dichoptic stimuli within or between hemifields affects interocular suppression (Stuit et al., 2011; Wilson, Blake, & Lee, 2001; Genc, Bergman, Tong, Blake, Singer, & Kohler, 2011). To investigate this possibility, we compared the RTs to the retinotopic control locations and to the spatiotopic control locations and observed no difference ($t(15) = 0.61$, $p = 0.548$), suggesting that our current finding is not due to the visual hemifield change.

The difference in RTs between the different conditions could potentially be caused by differences in the characteristics of the saccade. To test this possibility, we used reference frame and control location as independent variables and both the latency and the amplitude ($M_{\text{latency}} = 358$ ms, $SD_{\text{latency}} = 66$ ms; $M_{\text{amplitude}} = 8.27^\circ$, $SD_{\text{amplitude}} = 0.37^\circ$) landing eccentricity of the saccade response as dependent variables. The analysis showed no main effects or interaction effects for both dependent variables ($F < 3.90$, $p > 0.05$).

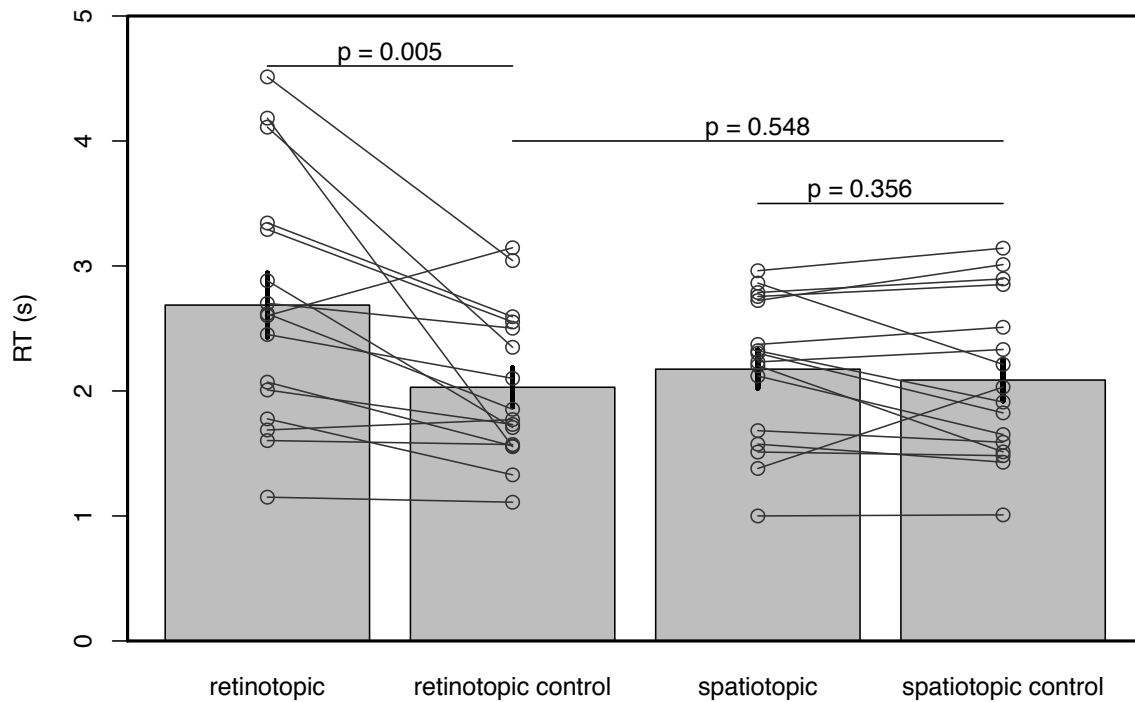


Figure 2. Mean target RTs of all conditions. The reaction times for the retinotopic location were longer than that for the retinotopic control location. The reaction times for the spatiotopic and spatiotopic control locations were not different. Error bars denote ± 1 SEM.

Discussion

In the present study, we investigated whether a target's priority to access visual awareness is either reset or continuous across saccades. We compared the time needed for a grating to overcome interocular suppression after observers executed a saccade. Our results show that the post-saccadic stimulus broke interocular suppression slowest when it was presented at the same retinotopic location as the presaccadic stimulus. However, when the stimulus was presented at the same spatiotopic location as the presaccadic stimulus, and when it was presented at several control locations, the breakthrough time was similar. These results show that processing for awareness at the spatiotopic location is *not* continuous across saccades.

At first glance these results seem to be in contrast with studies that reported evidence for continuous processing of a stimulus in spatiotopic coordinates (e.g. Melcher 2005, Ganmor et al, 2015, Wolf & Schutz, 2015, Oostwoud-Wijdenes et al. 2015, Fabius et al. 2016; Fairhall et al., 2017). For example, Fabius et al. (2019) used the high phi illusion across saccades. In the high phi illusion, a slow rotating ring with a random texture (inducer) induces the percept of a fast, rotational jump backward to the slow rotation when its textures are rapidly replaced with different random textures. When the inducer was presented before a saccade, it induced a stronger illusory percept of backward jumps in the same spatiotopic location, than when the inducer remained static before the saccade. Therefore, the conclusion of the authors was that the rotational information of the inducer had been updated in spatiotopic coordinates. In a similar fashion, Edwards et al (2018) decoded stimulus category (face vs. house) with EEG across saccades. When the stimulus remained the same across the saccade, decoding reliability increased faster after saccade offset. Additional converging evidence observed that saccades affect neural (Bartlett et al., 2011; Wutz et al., 2016) and perceptual (Benedetto & Morrone, 2017) oscillations, implying that saccades and visual processing are coupled. Together these previous findings suggest that some information of a presaccadic stimulus can influence the processing of post-saccadic stimuli in spatiotopic coordinates. The current findings suggest that, possibly, a stimulus' priority to access awareness is reset spatiotopically by a saccade. Such a reset operation might be comparable to the exertion of saccadic suppression that is time-locked to both saccade onsets and the troughs of neural and perceptual oscillations (Bartlett et al., 2011; Wutz et al., 2016; Benedetto & Morrone, 2017).

However, despite these findings, there are also several studies that reported an absence of spatiotopic effects (Knapen et al. 2009, Mathot & Theeuwes 2013; He et al., 2019; Lescroart et al., 2016). Together, these different sets of findings argue against a version of

spatiotopic processing that is omnipresent in visual perception across saccades. Rather, spatiotopic effects seem to be limited to specific conditions in the experiment. The current findings add to this specification that stimuli that have not reached awareness (i.e. under CFS) will probably not be processed in spatiotopic coordinates, suggesting that the spatiotopic effects reported in other studies might be limited to conditions where an observer is already aware of some of the stimulus features before saccade onset.

Although we did not observe any remapping effect at the spatiotopic location in the current experiment, we did observe slower breakthrough times of post-saccadic stimuli at the retinotopic location. Why did it take longer for a post-saccadic stimulus to overcome interocular suppression at the retinotopic matched location than at the control location? One possibility is that it took longer to switch attention back to the presaccadic location (e.g., inhibition of return, IOR; Posner, 1985). Though previous evidence showed that the stimuli under suppressed from awareness still can capture attention (Jiang et al. 2006; Sun et al., 2017), this evidence does not mean that attention affects the duration of breaking CFS. For instance, Gayet et al. (2018) observed that suppressed probes were not released faster from interocular suppression when they were presented at a previously attended location, implying that attention does not modulate the race to awareness in b-CFS. What's more, the difference between the RTs at the retinotopic location and at the control location was 657 ms which is not a typical size of IOR (Klein, 2000s). Therefore, the delayed response to the retinotopic location in our current study is unlikely to be explained by attentional IOR. A more likely explanation is that presaccadic exposure to a stimulus results in a visual aftereffect at the post-saccadic location (e.g., adaptation). Because adaptation results in a weaker representation of the stimulus, it will take longer for the stimulus to overcome interocular suppression (van Boxtel, 2008; Blake & Overton, 1979; Blake et al., 2003; Noest et al., 2007). It is possible that making a saccade increases retinotopic adaption (in the same manner as

blinks do – Van Opstal et al., 2016), but since our design lacked a no-saccade condition, we leave this question open.

One might argue that the beneficial effect of remapping at the spatiotopic location was actually present, but that this effect was cancelled out by the 'negative' effects of spatiotopic adaptation. Spatiotopic adaptation effects have indeed been reported before (Melcher, 2005; Nakashima & Sugita, 2017; van Boxtel et al., 2008). It should be noted, however, that for simple stimuli like those in our study, adaptation influences interocular rivalry when adaptation and rivalry locations are retinotopically matched, but not when they are spatiotopically matched (van Boxtel et al., 2008). Furthermore, spatiotopic aftereffects build up faster and last longer for complex stimuli than simple stimuli, suggesting that spatiotopic adaptation is caused by top-down feedback (e.g., attention) instead of bottom-up visual processing (Alais & Melcher, 2007; van Boxtel et al., 2008). Based on these findings, we conclude that no adaptation effect was induced at the spatiotopic match location in our study.

It should be noted that we do not argue that no information was remapped in our experiment. For instance, the attentional pointer theory argues that it is the spatial information instead of the feature information that is remapped across saccades (Cavanagh et al., 2010). This theory describes the process of updating visual location across saccades as predictive shifts of location “pointers” to attended targets and proposes that these location pointers are the core operators of spatial attention. However, given that spatial attention does not influence the priority of a location to access awareness (Gayet et al., 2018), it could be that these spatial pointers are updated across saccades, but that these do not influence the race to awareness.

To conclude, the current results provide support that the visual awareness processing at a spatiotopic location is reset by each saccade and confirm that adaptation affects the prioritization of stimuli for awareness at a retinotopic level.

7

Chapter 7

General Discussion

In the final part, I will first discuss the theoretical insights based on the experimental chapters which constitute the main body of the dissertation. Subsequently, I will discuss the implications for the neural basis of consciousness. Lastly, I will put a spotlight on the limitations of the current projects but also their implications for the field.

A theoretical perspective

It is impossible to objectify consciousness per se since it is a subjective experience. However, I believe we are following the footprint of the bear (e.g., consciousness) and estimate the weight and shape of the animal. Here, the footprint is the priority for visual awareness assessed with b-CFS and binocular rivalry.

Visual information has variable scales of priority for access to visual awareness, and only part of it can bring us conscious experience at any moment. The priority of a stimulus can be modulated by different factors and one distinction between these factors is that between top-down and bottom-up. Until now, the modulation of top-down factors and bottom-up factors on visual awareness has been explored by examining the influence of the short-term memory representation and the saliency of the stimulus respectively. In the current dissertation, to investigate how memory representations and saliency regulate visual awareness, we quantified the priority of a stimulus for visual awareness by using the suppression duration in b-CFS.

A rapidly growing number of studies have used the recently developed behavioral paradigm named b-CFS to study the priority of visual input for visual awareness. In a b-CFS task, dynamic masks are presented to the dominant eye to prolong the suppression of information presented to the other, weaker eye. The more dominant the masked eye, the longer it takes for the content presented to the non-dominant eye to be prioritized for visual awareness (Mastropasqua, Tse, & Turatto, 2015; Moors, Wagemans, & de-Wit, 2014; Yokoyama, Noguchi, & Kita, 2013). In Chapter 2, we compared multiple measurements of eye dominance to explore whether the measurements reflect the same aspect of eye dominance. This is important because a proper measurement can help us to correctly determine the dominant eye in a b-CFS task.

VWM, as a top-down factor, has been proposed to closely interact with visual awareness. Specifically, the content of VWM regulates the priority of visual input for access to visual awareness by facilitating the memory congruent information to enter awareness (Gayet et al., 2013; van Moorselaar et al., 2017; Liu et al., 2017). As supported by divergent evidence, a complex object, which consists of multiple features, can be maintained as different *combinations* of independent features in VWM. In daily life, we typically memorize multiple features of an object when memorizing it. But is a single memory congruent feature enough for the stimulus to receive prioritized for access to visual awareness? For instance, when maintaining the appearance of a mature oat seed in mind, will a lion sharing only one feature (e.g., the color, but not the shape, size and et cetera) with the seed get prioritized for visual awareness? In Chapters 3 and 4, we addressed 1) whether VWM regulates the priority of an item for access to visual awareness at the individual feature level, the conjunction of multiple features level, or the object level; and 2) whether features from different dimensions regulate awareness synergistically.

Given that visual stimuli can compete against each other for the priority for access to visual awareness (with the stronger visual information entering visual awareness faster), visual awareness can also be guided by bottom-up factors (e.g., saliency). Previous literature has reported that saliency and VWM can interact behaviorally to regulate visual processing (e.g., attention; Soto et al., 2006). Given that it was still unclear whether saliency and VWM can interact to specifically affect the priority of visual input for visual awareness, we explored this question in Chapter 5.

Finally, we make ballistic eye movements (i.e., saccades) to perceive different positions of the external visual world. Although our eyes almost stop sampling the external world during a saccade, visual awareness is generally stable (for a review, see Breitmeyer & Ganz, 1976). Evidence suggests that visual information is automatically stored in

transsaccadic memory before a saccade takes off, in order to facilitate visual stability across saccades. We explored whether transsaccadic memory maintains the priority of a presaccadic stimulus for visual awareness in Chapter 6. To summarize our current findings, I provide an overview of all observations from the current experimental chapters below.

In Chapter 2, we demonstrated that eye dominance measurements with different tests do not necessarily result in the same outcomes. Specifically, the preferred sighting eye dominance (determined by the hole-in-the-card test) does not predict the bias in eye dominance measured by the interocular conflict tasks (i.e., onset rivalry, ongoing rivalry, and b-CFS). Different from previous studies, we did observe a positive relationship between the eye dominance measured by the onset rivalry task and ongoing rivalry task (i.e., the interocular conflict tasks), suggesting that the same mechanism might be underlying these two paradigms. What's more, we observed that eye dominance measured with the b-CFS task does not correlate with that assessed in the other interocular conflict tasks. This evidence implies that b-CFS might be assessing a different aspect of interocular conflict compared to the other two tasks. In other words, our results suggest that ocular dominance is a multifaceted phenomenon. Therefore, we decided to determine eye dominance with the same paradigm (i.e., b-CFS) used in the main experiments of our follow-up projects.

In Chapter 3, when observers were required to memorize complex objects with multiple features, our results showed that memory congruent objects (consisting of a conjunction of features) enter visual awareness faster than memory incongruent objects. Importantly, we also observed this memory congruency effect when the objects were presented in a horizontally-flipped configuration of colors but not when the objects shared only a single feature of the memoranda. These results demonstrate that VWM exerts the influence on visual awareness at the conjunction of multiple features level but not at the

individual feature level or at the object level. In Chapter 4, we required observers to memorize a single feature or multiple features from different dimensions (e.g. color and shape) of an item before the b-CFS task. Our results suggest that 1) VWM can regulate the priority of visual information for access to visual awareness along a single feature dimension; 2) features from different dimensions (e.g., color and shape) can influence the regulation to a variable degree, and the more dominant feature (i.e., color) may even suppress the regulation of the less dominant one (i.e., shape); 3) even a memory task-irrelevant but dominant feature can be maintained and thus facilitates stimuli matching the current feature for visual awareness. Combining these two chapters, the findings provide novel insights into how memory content regulates the priority of visual input: memoranda consisting of multiple features (e.g., red and green) from the same feature dimension (e.g., color) regulate visual awareness along the conjunction level. In contrast, when the features are from different dimensions (color and shape), the dominant feature can suppress the less dominant one from regulating access to visual awareness.

Different from our current findings in Chapter 3, when asking observers to memorize multiple colored items simultaneously, van Moorselaar and colleagues (2017) observed that an item with a single memory congruent color had a higher priority than the memory incongruent ones for visual awareness. However, when observers were required to memorize a single item consisting of two colors (Exp. 1 of Chapter 3), an object which shared only one color of the memory item did not get prioritized for visual awareness, suggesting that the colors are bound together in VWM. Moreover, in Chapter 4, the memory-irrelevant color was still maintained when only the shape of the item was required for the memory task. This evidence suggests that the VWM content is somehow structured as the physical presentation of the to be memorized stimuli during encoding. That is, the features belonging to a memory

item are linked to each other to some extent when either one or multiple of them are memorized.

What binds the memorized features? Attention has been proposed to be necessary for encoding and integrating the distributed visual information into complex but unified/bound objects (Rensink, 2001; Wolfe, 1999; Wheeler & Treisman, 2002; Bays 2011). For instance, the binding of some features of an object, such as its color and shape, might require attention, whereas other feature combinations are detected preattentively (Driver et al., 2001 but see Di Lollo et al., 2001). Although attention and awareness are proposed to be coupled, some other evidence suggests that attention can operate subliminally (Kentridge, Nijboer, & Heywood, 2008; Koch & Tsuchiya, 2006; Lamme, 2003; Naccache et al., 2002; Hsieh, Colas, & Kanwisher, 2011). I propose that attention might be the factor that regulates the integration of multiple features during visual information entering visual awareness. More evidence is however needed to test this hypothesis.

VWM does not regulate the priority of visual input as the exact memoranda for visual awareness. In Chapters 3 and 4, the b-CFS targets never had a hue identical to the memory items. For instance, in a memory congruent condition, the colors of the memory items and the b-CFS targets were different hues which belonged to the same color category, suggesting that the regulation of VWM for visual awareness operates at the categorical level. This makes sense: firstly, we can hardly represent the visual information in exactly the same way as the memory items since our memory resolution varies (Zhang & Luck, 2008). Secondly, it saves time and energy for our brain to quickly become aware of the memory relevant objects by compromising the precision.

In Chapter 5, we replicated that both a VWM content-congruent item (e.g., a red color as the memorandum) and a salient item (e.g., a red item among yellow ones) break interocular suppression to enter visual awareness faster than the memory incongruent and

non-salient ones. Importantly, we observed that items that were both memory congruent and salient were even more prioritized for awareness than either the salient only or memory congruent only. We used a computational modeling approach (i.e., a race model) to investigate how VWM and saliency information interact. Our results demonstrate that statistical facilitation explains the interaction which suggests that the visual system does not integrate saliency and VWM-content information to multiply their effects. We conclude that independent, parallel processing of VWM and saliency explains why we did not observe integration between the bottom-up and top-down factors.

In Chapter 6, we combined a b-CFS task and a saccade task to investigate whether saccades reset the priority of visual information to access visual awareness. We observed that a presaccadically perceived item did not break interocular suppression faster when it was presented at the spatiotopic location compared to when it was presented at the control location after a saccade. This finding demonstrates that the priority of an item at the spatiotopic coordinate to access visual awareness is reset by each saccade. Note, however, that this suggestion does not mean that saccades reset all the visual processing, since a body of studies has shown that the consciously perceived visual information before a saccade at the spatiotopic coordinates survives somehow and is integrated across saccades (Edwards et al., 2018; Fabius et al., 2019; Ganmor, Landy, & Simoncelli, 2015; Melcher & Morrone, 2003; Oostwoud-Wijdenes, Marshall, & Bays, 2015; Wolf & Schütz, 2015; Fabius et al., 2016).

Transsaccadic memory, as a kind of short-term memory, is generally proposed to integrate low-level sensory representations across saccades to constitute a stable image of the external visual world (McConkie & Rayner, 1976). For instance, transsaccadic memory can facilitate observers to identify a stimulus when a preview of the item was presented before a saccade (Henderson, Pollatsek, & Rayner, 1987). However, follow-up evidence suggests that the spatial information instead of the feature information is actually stored in transsaccadic

memory (Cavanagh et al., 2010). Our current findings are in line with a body of studies which argue that transsaccadic memory does not maintain the low-level visual information but the “location pointer” (Irwin, Yantis, & Jonides, 1983; O’Regan & Levy-Schoen, 1983; Rayner & Pollatsek, 1983; Grimes, 1996; Henderson & Hollingworth, 1999, 2003b; Simon & Levin, 1998).

In sum, our observations in this dissertation suggest that: 1) different eye dominance tests measure non-identical aspects of the imbalance between two eyes which could result from different mechanisms; 2) VWM prioritizes access to visual awareness for complex visual memoranda and the regulation is affected both by the memory content and the property of the memoranda; 3) both VWM and saliency regulate visual awareness and the regulation of these two factors operate independently; 4) features from different dimensions of memoranda compete against each other for the dominance to regulate visual awareness; 5) transsaccadic memory does not affect the priority of the presaccadically perceived visual information for visual awareness.

Neural implementation: implications

To understand how short-term memory regulates the priority of visual input for visual awareness, it is interesting to examine the underlying neural mechanisms and relate this to the findings reported in this thesis. Although I did not use neuroscientific methods to investigate the research questions in the current dissertation, our psychophysical results can still be inspiring to understand the neural mechanisms of the regulation. Below, I first discuss the potential brain areas where VWM content and interocular conflict reside respectively, based on previous studies, and then discuss the potentially correlated activity between the brain areas which might result in the observations in our studies.

To maintain visual information temporally, it is generally assumed that the brain areas involved in VWM show elevated activity during memory maintenance (Courtney, 2004; Postle, 2006; Sligte et al., 2013). Subsequent studies show that the activation of visual cortical areas is not significant during VWM maintenance, suggesting that VWM retention does not depend on the activity in the visual areas (for a review see Xu, 2017). Rather, the activity of the parietal and prefrontal cortex was shown to be correlated with VWM maintenance (Pessoa et al., 2002). There is a growing number of studies that observed that a widespread network of brain areas contributes to maintaining visual information in VWM (Harrison and Tong, 2009; for a review see Christophel et al., 2017). For instance, Christophel and colleagues (2012) required observers to temporally memorize complex colored items and explored the content-specificity of BOLD signals from multiple brain areas using multivariate pattern classification. Their results revealed that storage in VWM extends beyond visual areas. What's more, the maintenance of features from different dimensions (e.g., color vs. shape) might be correlated with the activity of different brain areas. Specifically, it has been shown that there is content-specific delay-period activity in the prefrontal cortex (Buschman et al., 2011) for colored objects (Mayer et al., 2011; Miller et al., 1996; Rao et al., 1997) and persistent stimulus-selective activity for shapes in V4 and the temporal cortex (Chelazzi et al., 2001; E. K. Miller et al., 1993; Miyashita & Chang, 1988) and for color in the inferior temporal cortex (Fuster & Jervey, 1981, 1982). In summary, this evidence suggests that the features of an item are maintained in VWM by different brain areas (e.g., visual areas, high-level processing areas, and etc.).

Now we know which areas are involved in VWM, let me review the neural mechanisms of visual perception during interocular conflict before discussing the neural mechanism of VWM regulating the duration of interocular suppression. The neural signal relating to interocular conflict could be located in the visual processing hierarchy where eye-

selective information is still retained, as most cells in early visual areas (80% in V1/V2 and 60% in V4/V5) respond to stimulation from either eye, regardless of which eye's input dominates the conscious experience (Logothetis, 1998). On the other hand, it is also reasonable to assume that the conflict is resolved in the higher processing areas (e.g., IT, LOC, FFA, and PPA) where activity predominantly reflects the dominant conscious experience resulting from the local competition (Tong, Nakayama, Vaughan, & Kanwisher, 1998; Tong, Meng, & Blake, 2006). Together, this evidence suggests that interocular conflict could be registered in widespread brain areas.

The regulation of VWM on resolving interocular conflict could happen in a combination of the just described brain areas. The representations maintained in VWM could amplify the base activation level for the memory congruent visual input. Since content-based VWM processes and interocular conflict might reside in overlapping visual processing brain areas, the memory congruent input might be amplified by the base activation of the current VWM maintenance. By this, the specific neural populations could be activated by the VWM content and thereby decrease the effective threshold for memory congruent input to break through the interocular suppression (Lupyan & Ward, 2013). This hypothesis has been supported by a computational model study (Gayet et al., 2016). However, a limited area of the brain might be involved during the memory maintenance when only one category of memory stimuli is used (e.g., color; Gayet et al., 2016), which might have led to limited regulation of VWM in the Gayet et al. study (2016). If features from more dimensions are maintained, then more brain areas could be activated to maintain the features, thereby potentially leading to a larger regulation of VWM on interocular conflict.

Although it is generally believed that higher-level cerebral areas play an important role in producing visual awareness, recent studies have suggested that feedback from higher- to lower-level cortex areas is necessary for conscious experience (for a review see Li & Geng,

2009). Thus, the feedback loops between the high-level processing brain areas which contain the VWM representation and the visual processing areas might amplify the memory congruent input, which results in a faster release of interocular suppression. Our current observations support this hypothesis: as discussed above, the memory congruency effect in this dissertation was categorical, which suggests that the memory congruency effect might originate in the higher-level cortex areas (e.g., object selective regions such as the lateral occipital complex; Emberson et al., 2017; Grill-Spector et al., 2001). Although some evidence does argue that the interocular suppression is mainly located in the visual processing area (Polonsky., et al., 2000; Tong & Engel, 2001; Lee et al., 2005; Haynes & Rees, 2005; Meng et al., 2005), a growing number of studies suggest that the higher-level areas could be involved in regulating the interocular conflict in a b-CFS task as semantic information and emotional information affects the suppression duration (Liu et al., 2016; Jiang et al., 2007; Costello et al., 2009). I therefore propose that the feedback loops between different brain areas may also be the neural mechanism through which VWM modulates memory congruent input for visual awareness.

Limitations and implications for future studies

Different paradigms might reflect different visual processing

As described in the general introduction, a number of experimental paradigms have been invented to study visual awareness. Binocular rivalry is generally regarded as the gold standard to study visual awareness ever since Crick and Koch endorsed this paradigm (Crick & Koch, 1998; for a review, see Giles et al., 2016). b-CFS, an adapted version of binocular rivalry, has recently been used by a growing number of studies (for a review see Stein et al., 2011). Here, we quantified the priority of a certain stimulus for visual awareness with the suppression duration in b-CFS.

However, some exceptions suggest that the perceptual shifts in binocular rivalry may not perfectly correlate with subjective visual experience shifts. For instance, Zou and colleagues (2016) observed that even an invisible flickering grating presented to one eye can decrease observer's sensitivity of a visible low contrast grating presented to the other eye, suggesting that invisible stimuli can induce binocular rivalry. This evidence suggests that interocular conflict might be processed at the low-level visual processing stage (e.g., perception) without giving rise to conscious experience (Gile et al., 2016). Also, the results of the current Chapter 2 show that the eye dominance measured by a b-CFS task is not correlated with that of an onset rivalry or ongoing rivalry task, suggesting that different interocular conflict paradigms could reflect different visual mechanisms. However, this evidence does not falsify the validity of studying visual awareness with interocular conflict paradigms. Importantly, in the current dissertation, we ensured that the stimuli and observer's perceptual capacity were matched among different conditions during CFS (e.g., memory congruent condition vs. memory incongruent condition) which rules out the possibility of low-level perceptual differences confounding our results. It would be interesting to collect more evidence to see whether our findings generalize to other consciousness paradigms, such as motion-induced blindness, change blindness (Simons & Rensink, 2005; Rensink, O'Regan, & Clark, 2000), and inattentional blindness (Simons & Chabris, 1999; Mack, Pappas, Silverman, 2002; Geng & Cai, 2007).

Are we exploring preconscious processing?

In a b-CFS task, the difference between RTs of different conditions might result from the different priorities for visual awareness, but might also reflect a shift in post-conscious response criteria. To exclude the latter, we conducted a monocular control condition in Chapter 5 as previous studies did (Gayet et al., 2013; van Moorselaar et al., 2017; for a

review see Stein & Sterzer, 2014). This control condition is basically identical to the main b-CFS task except for the fact that we simultaneously presented the target and the masks to the same eye. Thus, the measurement of RTs in such a condition is without any episode of item invisibility due to interocular suppression (Gayet et al., 2013; Jiang et al., 2007; Pan et al., 2014). No difference of RTs to different conditions in the monocular task is assumed as evidence against the possibility of response criteria shift. However, it took a shorter time for the observers to report the target in this control condition because of a lack of interocular suppression. To ensure that the RTs in the control condition are comparable to the ones in the b-CFS task, the ramp-up duration of the target intensity is typically prolonged by decreasing the transparency of the target. Importantly, the intensity at which observers detect the target is generally much lower in the control condition than in the b-CFS condition. For instance, in Chapter 5, targets with the same colors in the monocular condition and b-CFS condition were apparently different because of the different intensities when observers reported seeing the target (30% vs. 100%; see Figure 1 for an example). It is therefore reasonable to suspect that the differences in color between the targets in the monocular condition and the memorized color resulted in the lack of a memory congruency effect in the monocular condition. Thus, the monocular condition might be not a proper one to test the possibility of any shift in post-conscious response criteria.

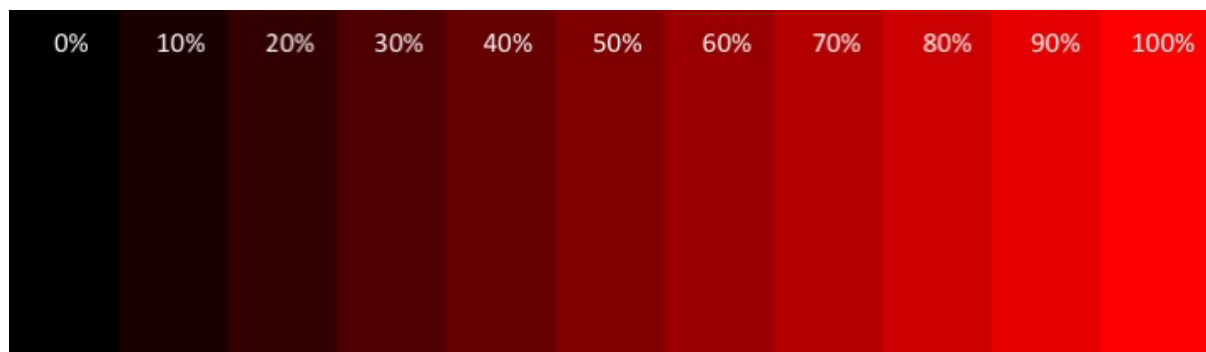


Figure 1. The same red colors with different intensities are presented on a black background. The numbers on the top of each bar stand for the color intensities. The black background renders the red color to darker when the intensity of the red color is lower.

Passively viewed stimuli might be memorized

Observers typically have a lower threshold to identify repeated stimuli (e.g., priming effect; for a review, see Wiggs & Martin, 1998). This phenomenon suggests that the memory congruency effect in our current chapters could perhaps be due to priming effects. To exclude this possibility, a control experiment is sometimes used in which observers are required to passively view the item before the b-CFS task. In such a passive viewing task, no difference between the RTs to the memory congruent and incongruent targets in the b-CFS task is assumed as evidence to exclude the presence of any priming effect. In Chapters 3 and 5, we conducted such a control experiment to convince the reviewers that the memory congruency effect in our studies was not due to priming effects in the process of review. Our results showed no difference between the RTs to the memory congruent targets and memory incongruent targets in the passive viewing condition which suggests that the priming effect was not present.

Visual information can be stored as active or accessory states in VWM. A number of studies suggest that only the active representation but not the accessory ones can facilitate the processing of the memory congruent input (e.g., an actively maintained item captures more attention than the memory incongruent ones, but the accessory ones do not; see Oliver et al., 2011 for a review). Interestingly, more and more studies report that observers can unconsciously learn the experiment design (e.g., statistical learning; Wang & Theeuwes, 2018; Jiang et al., 2015) to adjust their strategy for the current task. For instance, in a passive viewing condition, the observers might learn that the items that appeared before b-CFS can

somehow predict the target appearance (e.g., in 33% trials) during CFS presentation which might lead them to storing the items to some extent. It is plausible that observers maintained the passively viewed items as accessory which did not affect the suppression duration of the memory congruent input. This possibility needs to be addressed in the future.

Epilogue

In the beginning example of the dissertation, maintaining the appearance of an oat seed in VWM helped the hominid woman to guide her visual search as VWM prioritizes memory content-congruent inputs for visual awareness. The yellow-colored lion was prioritized as the color is more dominant than the shape in regulating visual awareness along the single color dimension. Although her saccades reset the priority of the lion for her conscious experience, the lion entered her visual awareness faster than the green bush since the lion had the memory congruent color and the color was more salient than the green background.

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Appendix - English Summary

Summary

Understanding how we consciously experience the visual world around us has attracted the interest of researchers from different scientific disciplines. Our visual system is bombarded with visual information when we open our eyes. However, only a little part of the information that is presented to our retinæ enters visual awareness since our brain is not equipped to process all of this information to the same extent. To deal with this limited capacity, visual information receives variable degrees of priority for access to visual awareness. Even though it is impossible to observe visual awareness per se (since it is a subjective experience), we can study it by quantifying the priority that a visual stimulus receives for entering visual awareness. We do this by measuring the duration it takes for the stimulus to enter visual awareness.

To measure the duration for a stimulus to enter visual awareness, it is essential to render the stimulus invisible. A paradigm named breaking continuous flash suppression (b-CFS) is a good candidate and has already been used by a number of studies. In a b-CFS task, a target is presented to one eye while masks presented to the other eye suppress the target. The duration of the suppression of the target is then used to quantify the priority of the target for visual awareness. Previous studies have generally presented the masks to the dominant eye to prolong the suppression. A number of methods to determine eye dominance have been used as it was commonly assumed that eye dominance measured by different methods produce the same outcome for eye dominance. However, awkwardly, different measurements might test variable aspects of eye dominance which lead to a particular eye dominance measurement that does not predict the stronger eye in a b-CFS task. Therefore, in Chapter 2, we compared several measurements of eye dominance and chose the right type of eye dominance for our subsequent b-CFS projects.

Awareness has been proposed as “the remembered present” which highlights the tight link between awareness and memory and specifically, working memory (WM). WM is a storage system which is responsible for maintaining relevant information. Visual working memory (VWM) is a branch of WM to specifically maintain visual information temporally. In order to build a stable representation of the external world visual information needs to be integrated in VWM over time. Combining a VWM task and a b-CFS task, previous studies reported that an item that was stored in VWM breaks interocular suppression to enter visual awareness faster than memory incongruent items, suggesting that VWM content-congruent information is prioritized for visual awareness. It is currently unclear whether a complex object which consists of multiple features (e.g., shape, color, etc.) is represented in VWM as independent features, a conjunction of multiple features, or a bound object representation. This lack of knowledge inspired us to query whether VWM regulates the priority of a visual stimulus for access to visual awareness at 1) the individual feature level; 2) the conjunction of multiple features level or 3) the object level; and whether multiple features from different dimensions regulate visual awareness synergistically.

Apart from top-down factors such as VWM, visual awareness can also be guided by bottom-up factors (e.g., saliency). Saliency is a fast, primitive factor that biases observers to select information based on their conspicuity and distinctiveness with respect to other stimuli in the same scene. A number of studies have observed that visual awareness can be guided by saliency. What’s more, saliency and VWM can interact behaviorally and interact to regulate visual processing (e.g., attention). In Chapter 4, we explored whether saliency and VWM can interact to regulate the priority of visual stimuli for access to visual awareness.

We make saccades to perceive different positions of the external world around three times per second. Even though each saccade changes the position of the external objects on our retinæ, our visual awareness of the environment remains stable across saccades.

However, our visual system rarely processes the visual information projected to the retinae during the saccade motion. For instance, you do not see your own eyes when you are facing a mirror. Transsaccadic memory has been proposed as a storage mechanism to store the presaccadic information until postsaccadic visual processing takes off. It is currently unclear whether transsaccadic memory affects the priority of the processed presaccadic information for visual awareness across saccades. This question was addressed in Chapter 6.

The results of Chapter 2 demonstrate that eye dominance measurements with different tests do not result in the same dominance outcomes. In other words, our results suggest that ocular dominance is a multifaceted phenomenon. Therefore, we determined eye dominance with b-CFS as the main experiments of the follow-up projects.

In Chapters 3 and 4, we combined a VWM task and a b-CFS task to study the effect of VWM on regulating priority for visual information to access visual awareness. When asking observers to memorize a complex object consisting of multiple features from the same dimension, our results demonstrate that VWM regulates visual awareness at the conjunction level but not at the individual feature level or the object level. In Chapter 4, we asked observers to memorize a single feature or multiple features from different dimensions of an object before the b-CFS task. Our results of Chapter 4 suggest that 1) VWM can regulate the priority of visual information for access to visual awareness along a specific feature dimension; 2) features from different dimensions (e.g., color and shape) can influence the regulation to a variable degree, and the more dominant feature (e.g., color) may even suppress the regulation of the less dominant feature (e.g., shape); 3) even a memory task-irrelevant feature can be actively maintained in VWM thus boosts stimuli with the current feature for visual awareness.

Our results of Chapter 5 replicated that both VWM and saliency can regulate the priority of visual input for access to visual awareness. What's more, we observed that items that were both salient and memory congruent had a even higher priority for awareness than either the salient or memory congruent ones. Importantly, our modeling results demonstrate that the visual system does not integrate saliency and VWM-content information to multiply their effects, instead, VWM and saliency regulate visual awareness independently.

In Chapter 6, we combined a saccade task and a b-CFS task to study whether transsaccadic memory affects the priority of a presaccadically perceived stimulus for visual awareness. We presented observers an item before a saccade and required observers to detect the same grating at different locations in a b-CFS task after the saccade. We observed that the presaccadically perceived item did not break interocular suppression faster when it was presented at the spatiotopic location (e.g., the same location on the screen) than at the control location. These results suggest that the priority to access visual awareness of an item at the spatiotopic coordinate is reset by each saccade.

Conclusion

Understanding how we can consciously experience the visual world is a complex issue with many unresolved questions. In the experimental chapters of this dissertation, I and my co-authors have shown that 1) eye dominance is a multifaceted phenomenon thus should be determined based on the specific aspect of eye dominance of interest. 2) The content of VWM regulates the priority of visual input along the conjunction level when the memoranda consist of multiple features from the same feature dimension. In contrast, when the features are from different dimensions, the regulation can happen along a single feature dimension and the dominant feature can suppress the less dominant one from regulating access to visual awareness. 3) VWM and saliency independently influence the priority of visual information

for access to visual awareness. 4) saccades reset the priority of visual information to access visual awareness. Collectively, these results expand our understanding of visual awareness and provide clear evidence for further research in both short-term memory and visual awareness.

Appendix - Dutch Summary

Samenvatting

De vraag hoe wij de visuele wereld om ons heen bewust waarnemen heeft interesse gewekt in verschillende wetenschappelijke disciplines. Ons visuele systeem wordt overspoeld met visuele informatie wanneer wij onze ogen openen. Echter, slechts een klein deel van de informatie die door onze netvliesen wordt opgepikt, bereikt het visuele bewustzijn, omdat ons brein niet in staat is om al deze informatie volledig te verwerken. Om met deze beperkte capaciteit om te gaan, krijgen verschillende delen van de visuele informatie een verschillende mate van prioriteit om het visuele bewustzijn te bereiken. Ook al is het onmogelijk om het visuele bewustzijn op zich te observeren (want het is een subjectieve ervaring), we kunnen het bestuderen door het kwantificeren van de mate van prioriteit die een visuele stimulus krijgt om het visuele bewustzijn te bereiken. We doen dit door het meten van de tijd dat het duurt voordat de stimulus het visuele bewustzijn bereikt.

Om te meten hoe lang het duurt voor een stimulus om het visuele bewustzijn te bereiken, is het essentieel om de stimulus tijdelijk onzichtbaar te maken. Een methode genaamd '*breaking continuous flash suppression*' (afgekort: b-CFS) is een goede kandidaat die al in een aantal studies is toegepast. In een b-CFS-taak wordt een object getoond aan één oog terwijl maskers, die aan het andere oog getoond worden, voorkomen dat het object in het visuele bewustzijn terechtkomt; het object wordt door de maskers perceptueel onderdrukt. De duur van het onderdrukken van het object wordt dan gebruikt om de mate van prioriteit te kwantificeren die het object krijgt voor het visuele bewustzijn. Duurt dit niet lang, dan heeft het object hoge prioriteit gekregen voor het bewustzijn. In eerdere studies werden de maskers over het algemeen getoond aan de het dominante oog om de duur van de onderdrukking te verlengen en zodoende de sensitiviteit van het paradigma te verhogen. Daarin werd oogdominatie bepaalt met verschillende methodes, omdat het werd aangenomen dat dezelfde

oogdominantie gevonden zou worden ongeacht de methode. Echter, het kan zijn dat verschillende methodes verschillende aspecten van oogdominantie testen, wat zou kunnen leiden tot een bepaalde oogdominantie-meting die niet voorspelt wat het dominante oog in een b-CFS-taak is. Daarom hebben wij, in Hoofdstuk 2, een aantal verschillende methodes van oogdominantie-metingen vergeleken en de juiste methode gekozen voor de daaropvolgende b-CFS-projecten.

Een voorgestelde definitie van bewustzijn is “het herinnerde heden”, wat de nauwe band benadrukt tussen bewustzijn en het geheugen, en specifiek het werkgeheugen (WG). WG is een opslagsysteem dat verantwoordelijk is voor het kort vasthouden van relevante informatie. Het visuele werkgeheugen (VWG) is een tak van het WG om specifiek visuele informatie tijdelijk vast te houden. Om een stabiele representatie op te bouwen van de buitenwereld, is het nodig dat visuele informatie geïntegreerd wordt in het VWG gedurende een korte tijd. Door het combineren van een VWG-taak en een b-CFS-taak, lieten voorgaande studies zien dat een object dat leek op hetgeen werd vastgehouden in het VWG, de interoculaire onderdrukking sneller doorbrak dan een object dat niet leek op hetgeen werd vastgehouden. Dit suggereert dat inhoud die congruent is met het prioriteit krijgt om het visuele bewustzijn te bereiken. Tot op heden is het echter onduidelijk of een complex object dat bestaat uit verschillende kenmerken (bijv. vorm, kleur, enz.), in het VWG gerepresenteerd wordt als onafhankelijke kenmerken, als een combinatie van meerdere kenmerken, of als één geheel object. Daarom vroegen we ons af of het VWG de prioriteit van een visuele stimulus voor toegang tot het visuele bewustzijn reguleert op 1) het niveau van het individuele kenmerk; 2) het niveau van de combinatie van meerdere kenmerken of 3) het niveau van het gehele object; en we vroegen ons af of meerdere kenmerken van verschillende dimensies het visuele bewustzijn synergetisch reguleren.

Afgezien van top-down factoren zoals VWG, kan het visuele bewustzijn ook worden beïnvloed door bottom-up factoren (bijv. saillantie). Saillantie is een snelle, basale eigenschap die mensen doet neigen om informatie te selecteren op basis van hun hoeveel het opvalt en hoe anders het is dan andere stimuli in dezelfde omgeving. Een aantal studies hebben aangetoond dat het visuele bewustzijn kan worden beïnvloed door saillantie. Bovendien kunnen saillantie en VWG interacteren in gedrag en interacteren om visuele verwerking (bijv. aandacht) te reguleren. In hoofdstuk 4 hebben we onderzocht of saillantie en VWG kunnen interacteren om de prioriteit van visuele stimuli voor toegang tot het visuele bewustzijn te reguleren.

In het dagelijks leven voeren we gemiddeld drie keer per seconde saccades uit om verschillende posities van de buitenwereld waar te nemen. Hoewel elke saccade de positie van de externe objecten op ons netvlies verandert, blijft ons visuele bewustzijn van de omgeving stabiel tussen saccades. Ons visuele systeem verwerkt echter zelden de visuele informatie die tijdens de saccadebeweging op het netvlies wordt geprojecteerd. Zo zie je bijvoorbeeld je eigen ogen niet bewegen als je voor een spiegel staat en oogbewegingen maakt. Het transsaccadisch geheugen is voorgesteld als een opslagmechanisme om de presaccadische informatie op te slaan totdat de postsaccadische visuele verwerking van start gaat. Het is momenteel onduidelijk of het transsaccadisch geheugen de prioriteit van de verwerkte presaccadische informatie beïnvloedt voor het visuele bewustzijn na een saccade. Deze vraag is behandeld in hoofdstuk 6.

De resultaten van hoofdstuk 2 laten zien dat metingen van oogdominantie met verschillende methodes niet resulteren in dezelfde dominantie-uitkomsten. Met andere woorden, onze resultaten suggereren dat oogdominantie een fenomeen met meerdere aspecten is. Daarom hebben we oogdominantie vastgesteld met b-CSF in al onze vervolprojecten.

In de hoofdstukken 3 en 4 hebben we een VWG-taak en een b-CSF-taak gecombineerd om het effect van het VWG op de regulering van prioriteit voor visuele informatie om toegang te krijgen tot het visuele bewustzijn te bestuderen. Wanneer we participanten vroegen om een complex object te onthouden dat bestaat uit meerdere kenmerken van dezelfde dimensie, tonen onze resultaten aan dat het VWG het visuele bewustzijn reguleert op het niveau van samenhang van kenmerken, maar niet op het individuele kenmerkenniveau noch op het objectniveau. In hoofdstuk 4 vroegen we participanten om een enkel kenmerk of meerdere kenmerken uit verschillende dimensies van een object te onthouden voorafgaand aan de b-CFS-taak. Onze resultaten van hoofdstuk 4 suggereren dat 1) VWG de prioriteit van visuele informatie voor toegang tot het visuele bewustzijn langs een specifieke dimensiedimensie kan reguleren; 2) kenmerken van verschillende dimensies (bijv. kleur en vorm) de regulering in variabele mate kunnen beïnvloeden, en het meer dominante kenmerk (bijv. kleur) zelfs de regulering van het minder dominante kenmerk (bijv. vorm) kan onderdrukken; 3) zelfs een geheugentaak-irrelevant kenmerk kan worden vastgehouden in het VWG en dus stimuli met dat kenmerk kan prioriteren voor het visuele bewustzijn.

Onze resultaten van hoofdstuk 5 repliceerden dat zowel het VWG als saillantie de prioriteit van visuele input voor toegang tot het visuele bewustzijn kunnen reguleren. Bovendien merkten we op dat objecten die zowel saillant als geheugencongruent waren, een nog hogere prioriteit voor bewustzijn hadden dan de enkel saillante of geheugencongruente objecten. Belangrijk is dat onze modelleringsresultaten aantonen dat het visuele systeem geen informatie over saillantie en VWG-inhoud integreert om hun effecten te vermenigvuldigen, maar dat het VWG en saillantie onafhankelijk van elkaar het visuele bewustzijn reguleren.

In hoofdstuk 6 hebben we een saccadetaak en een b-CFS-taak gecombineerd om te onderzoeken of het transsaccadisch geheugen de prioriteit voor het bewustzijn van een

stimulus beïnvloedt die overeenkwam met een presaccadisch waargenomen. We presenteerden aan participanten een object vóór een saccade en vereisten dat waarnemers na de saccade hetzelfde patroon op verschillende locaties in een b-CFS-taak detecteerden. De resultaten tonen aan dat het presaccadisch waargenomen object de interoculaire onderdrukking niet sneller doorbrak wanneer het werd gepresenteerd op de spatiotopische locatie (bijv. dezelfde locatie op het scherm) dan op de controlelocatie. Deze resultaten suggereren dat de prioriteit voor toegang tot het visuele bewustzijn van een object op de spatiotopische positie door elke saccade wordt gereset.

Conclusie

Begrijpen hoe we de visuele wereld bewust kunnen ervaren, is een complex vraagstuk met veel onopgeloste vragen. In de experimentele hoofdstukken van dit proefschrift hebben ik en mijn co-auteurs laten zien dat 1) oogdominantie een veelzijdig fenomeen is en daarom moet worden bepaald op basis van het specifieke aspect van oogdominantie in kwestie. 2) De inhoud van VWM reguleert de prioriteit van visuele input op het niveau van samenhang van kenmerken wanneer de memoranda bestaan uit meerdere kenmerken uit dezelfde kenmerkdimensie (bijvoorbeeld als twee kleuren allebei onthouden worden). Daarentegen, wanneer de kenmerken uit verschillende dimensies (zoals kleur en vorm) komen, kan de regulering plaatsvinden langs een enkele kenmerkdimensie en kan het dominante kenmerk de minder dominante onderdrukken om de toegang tot het visuele bewustzijn te reguleren. 3) Het VWG en saillantie beïnvloeden onafhankelijk van elkaar de prioriteit van visuele informatie voor toegang tot het visuele bewustzijn. 4) Saccades resetten de prioriteit van visuele informatie om toegang te krijgen tot het visuele bewustzijn. Gezamenlijk verbreden deze resultaten ons begrip van het visuele bewustzijn en bieden ze duidelijk aanleiding voor verder onderzoek naar zowel het kortetermijngeheugen als het visuele bewustzijn.

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Jasper, thank you for picking me up for the meetings, club events, music days, and dinners. I appreciate all the interesting and inspiring chats about science and life in general. I enjoyed

our train ride to Italy very much. It is so exciting to have you in my saccadic remapping project. I admire your programming code and the way you consider science.

Nathan, thanks for introducing the race model to me and answering the relevant questions! Your revision of my letters helped me a lot, too! Also thanks for organizing the arm wrestling club. Let's play this game together somewhere in ten years and, hopefully, we are both professors at that time.

Jessica, I was surprised by your successful combination of your family and work. Especially you went to Canada for research projects for a while. BRAVE!! Thanks for driving me to the Perception day at Donders. I enjoyed our conversation a lot in your car. Thanks for being a nicely inspiring colleague.

Jim, thanks for bringing me so many smiles, giggles, and laughs. Please keep it, even I beat you in the arm wrestling games. And please do continue the exercise until you can beat Stuit, OK?

Fengbin, thank you for always supporting me to chase my dream. You have changed me a lot in a good way. I appreciate the time we spent together and wish you all the best.

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Lei Wang, I am glad to have you as my roommate and friend. Thanks for the drinks, nail polish, and listening to my stories.

Andre, I appreciate your contribution to our conjunction project. It is also my pleasure to help you with the experiment set-up and programming script. You have excellent sensors of science and I am looking forward to seeing you grow as a cutting-edge scientist!

Yue Song and **Yuru**, thank you for your helpful advice! I wish you have a nice life in our motherland.

Gijs, thanks for all the interesting chats, bicycle touring, warm chocolate, and wonderful dinner. Thanks for being my paranymp!

Martijn, thanks for playing organ for us. It was exciting to play arm wrestling with you. Hopefully, I can beat you with the right hand and you can beat me with your left hand one day. Thanks for being my paranymp!

Alyanne, eventually, I can pronounce your name correctly (I think). I am happy to share the office with you. It is impressively surprising that you can find a balance between work and family, especially you have 3 lovely kids around you. I think I will ask for your advice about it one day.

Muge, thanks for your helpful information! I am always bad at hunting the administrative but important information. Somehow, I have learned interesting opinions about politics, art, and life in general from you. I wish you to find an ideal job in China.

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My Ph.D. would not have any chance to be successful without all the participants volunteering in my experiments. I thank them gratefully for their contribution.

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Curriculum Vitae

Yun Ding was born on the 13th of October, 1988 in Jiangsu, China. He studied Psychology at Hangzhou Normal University and received his Masters degree in 2016. Yun was accepted as a PhD student at the Department of Experimental Psychology at Utrecht University under the supervision of Stefan Van der Stigchel, Chris Paffen, and Marnix Naber. Yun worked on visual working memory, visual awareness, and the link between these two functions. This eventually resulted in the present PhD thesis. While writing the last chapter of his PhD thesis, Yun was looking for a post-doctoral position as he was still as keen on doing research as ten years ago.



Publications

- Ding, Y., Naber, M., Paffen, C. L. E., Gayet, S., & Van der Stigchel, S.** How retaining objects containing multiple features in visual working memory regulates the priority for access to visual awareness. Manuscript submitted for publication.
- Ding, Y., Naber, M., Sahakian A., Paffen, C. L. E., & Van der Stigchel, S.** (in press) The priority for access to awareness of information matching VWM is mirror-invariant. *Cognition*.
- Ding, Y., Naber, M., Paffen, C. L. E., Fabius, J. H., & Van der Stigchel, S.** (2020) Saccades reset the priority of visual information to access awareness. *Vision Research*, 173, 1–6 doi.org/10.1016/j.visres.2020.04.010
- Ding, Y., Paffen, C. L. E., Naber, M., & Van der Stigchel, S.** (2019) Visual working memory and saliency independently influence the priority for access to visual awareness. *Journal of Vision*, 19(11), 9–9 doi.org/10.1167/19.11.9
- Ding, Y., Naber, M., Gayet, S., Van der Stigchel, S. & Paffen, C. L. E.** (2018) Assessing the generalizability of eye dominance across binocular rivalry, onset rivalry, and continuous flash suppression. *Journal of Vision*, 18(6), 6–6 doi.org/10.1167/18.6.6

Presentations

Yun Ding, Marnix Naber, Chris Paffen, & Stefan Van der Stigchel. (May, 2020). How the content of visual awareness regulates the priority for access to visual awareness for memoranda with multiple features. Virtual Vision Sciences Society.

Yun Ding, Marnix Naber, Chris Paffen, & Stefan Van der Stigchel. (Dec, 2019). How the content of visual awareness regulates the priority for access to visual awareness for memoranda with multiple features. Nederlandse Vereniging voor Psychonomie, Netherlands.

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Yun Ding, Marnix Naber, Surya Gayet, Stefan Van der Stigchel, & Chris Paffen. (Dec, 2017). Assessing the generalizability of eye dominance across binocular rivalry, onset rivalry, and continuous flash suppression. Nederlandse Vereniging voor Psychonomie, Netherlands.

