



Saccades reset the priority of visual information to access awareness

Yun Ding^{a,*}, Marnix Naber^a, Chris L.E. Paffen^a, Jasper H. Fabius^b, Stefan Van der Stigchel^a

^a Department of Experimental Psychology, Utrecht University, Utrecht, the Netherlands

^b Institute of Neuroscience and Psychology, College of Medical, Veterinary and Life Sciences, University of Glasgow, Glasgow G12 8QB, Scotland, United Kingdom



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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.

1. 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, Fracasso, & der Stigchel, 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;

* Corresponding author.

E-mail address: y.ding1@uu.nl (Y. Ding).

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 et al., 2013; Jiang et al., 2007; Rothkirch, Overgaard, & Hesselmann, 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.

2. Method

2.1. Observers

17 observers (7 men; $M_{age} = 26.5$, $SD = 2.94$) 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.

2.2. 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., Matick 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 $9500^\circ/s^2$ and a velocity threshold of $30^\circ/s$. The Eyelink was calibrated using 5-point calibration routine.

2.3. Stimuli

As illustrated in Fig. 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 sine-wave 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.

2.4. Procedure

Before the main experiment, each observer’s dominant eye was determined with a b-CFS task because eye dominance is task specific (Ding, Naber, Gayet, Van der Stigchel, & Paffen, 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,

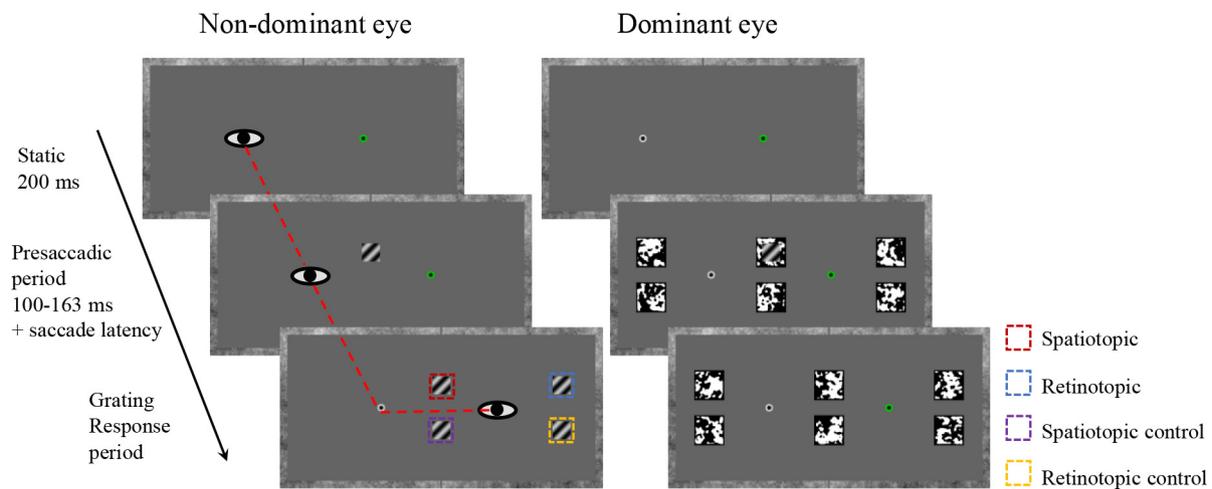


Fig. 1. A schematic depiction of the sequence of events during each trial. Observers were instructed to look at the gray dot, make an eye movement to the green dot at the time of the auditory cue and keep fixating thereafter, and to detect the position at which the grating appeared after the eye movement 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.

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.

2.5. 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.

3. 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 Fig. 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, Paffen, van der Smagt, & Verstraten, 2011; Wilson, Blake, & Lee, 2001; Genc et al., 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 ($F < 3.90$, $p > 0.05$).

4. 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 & Schütz,

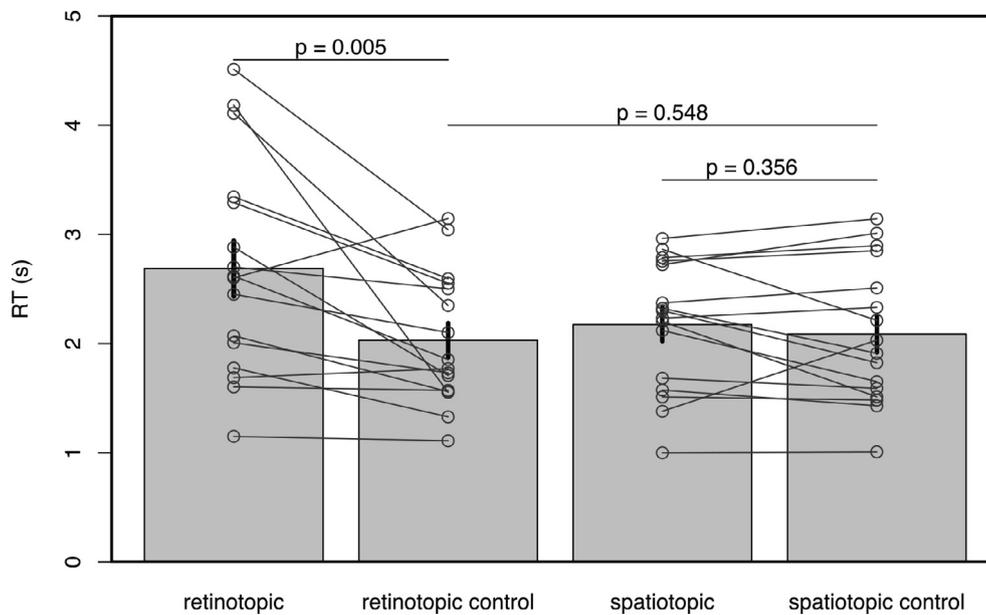


Fig. 2. Mean target RTs of all conditions. The reaction times for the retinotopic location were longer than that for the retinotopic control location. The reaction times for the spatiotopic and spatiotopic control locations were not different. Error bars denote ± 1 SEM.

2015, Oostwoud-Wijdenes et al., 2015, Fabius et al., 2016; Fairhall, Schwarzbach, Lingnau, Van Koningsbruggen, & Melcher, 2017). For example, Fabius, Fracasso, Nijboer, and der Stigchel (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, VanRullen, and Cavanagh (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, Ovaysikia, Logothetis, & Hoffman, 2011; Wutz, Muschter, van Koningsbruggen, Weisz, & Melcher, 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 (Knäpen et al., 2009, Mathôt & Theeuwes, 2010; He, Ekman, & A., & de Lange, F., 2019; Lescroart, Kanwisher, & Golomb, 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 et al., 1985). Though previous evidence showed that the stimuli under suppressed from awareness still can capture attention (Jiang, Costello, Fang, Huang, & He, 2006; Sun, Stein, Liu, Ding, & Nie, 2017), this evidence does not mean that attention affects the duration of breaking CFS. For instance, Gayet, Douw, van der Burg, Van der Stigchel, and Paffen (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, 2000). 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 et al., 2008; Blake & Overton, 1979; Blake, Sobel, & Gilroy, 2003; Noest, van Ee, Nijs, & van Wezel, 2007). It is possible that making a saccade increases retinotopic adaptation (in the same manner as blinks do – Van Opstal, Loof, Verguts, & Cleeremans, 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, Hunt, Afraz, & Rolfs, 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.

CRedit authorship contribution statement

Yun Ding: Conceptualization, Methodology, Software, Investigation, Formal analysis, Writing - review & editing. **Marnix Naber:** Conceptualization, Methodology, Supervision. **Chris L.E. Paffen:** Conceptualization, Methodology, Supervision. **Jasper H. Fabius:** Conceptualization, Methodology. **Stefan Van der Stigchel:** Conceptualization, Methodology, Supervision.

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