

Sensory Continuity Across Eye-movements

Forward to a model of visual perception

Sensorische continuïteit tussen oogbewegingen
(met een samenvatting in het Nederlands)

Proefschrift

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dedicated to

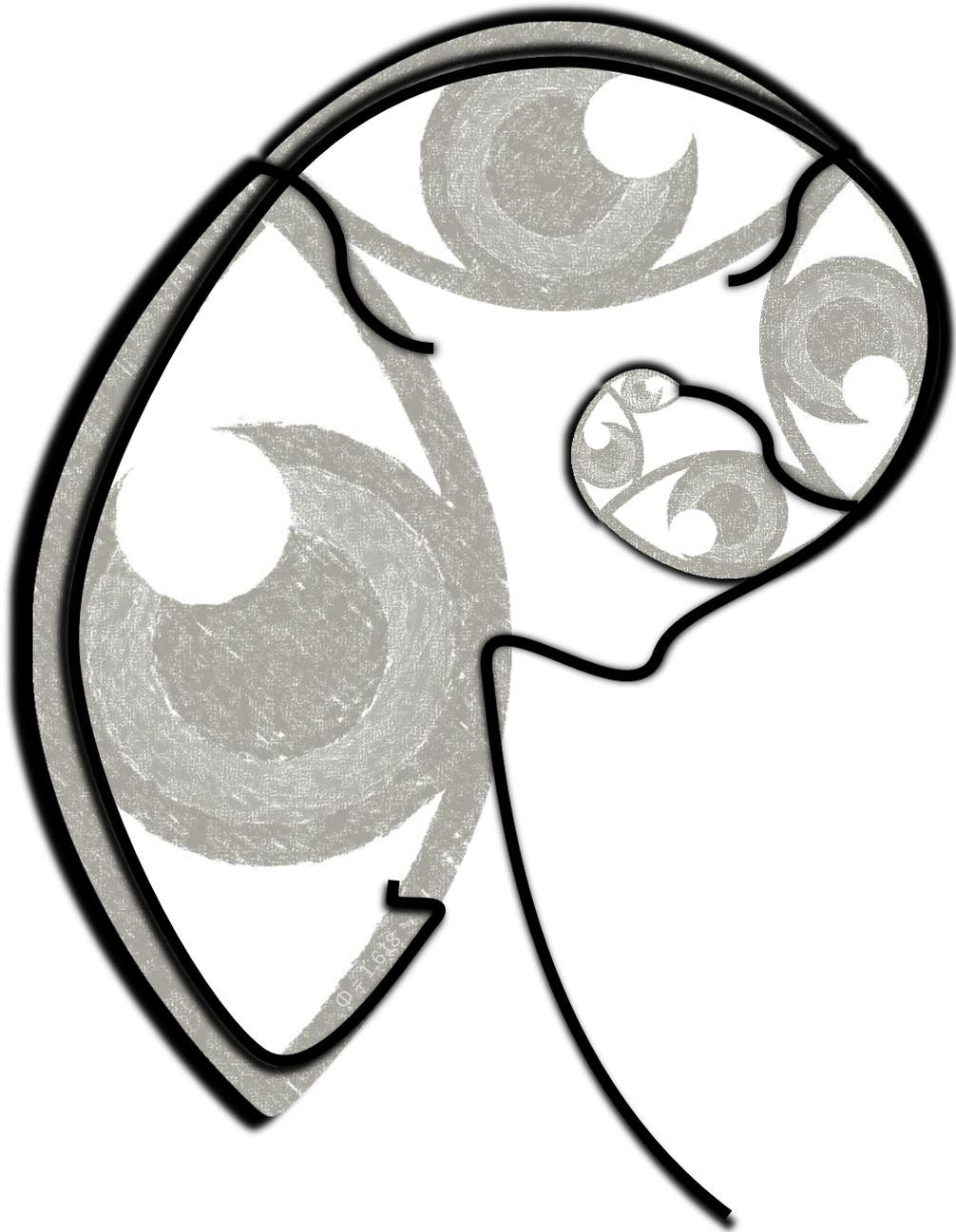
Veronique and Chloe

“Sometimes science is
more art,
than science.”

R. Sanchez, 2013

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Chapter 1

General Introduction

Martijn J. Schut

Vision is the dominant sense of humans. This becomes apparent when considering just how much of our society operates under the assumption of perfectly functioning vision. For example, using an (unaltered) smart-phone or driving a car is virtually impossible without vision. In isolation, our senses are constrained by some limitation due to the physical properties of the information that they detect. Spatial accuracy is somewhat low for the auditory system, touch is limited to only our immediate vicinity, and other senses do not convey much spatial information. At first glance, vision provides unparalleled accuracy and the ability to both sense at close range and long range, making it a top contender for our primary sensory system. However, vision does contain less apparent limitations.

Visual continuity

The first limitation is perhaps the most obvious, as we have some subjective insight in this limitation. By keeping your eye still and shifting the focus of your attention, you may notice that the visual system only provides high resolution vision for input that falls in the center of the retina (fovea). The resolution at which we process visual information is lower in the periphery, due to lower (overall) densities of photoreceptors in those areas [1]. This limits the portion of visual space that we process in high resolution. Color perception, which is dependent on photoreceptors known as cones, declines so sharply with increasing distance to the fovea, that we are effectively color blind in our peripheral vision [1]. Yet, interestingly, we do not perceive this apparent color blindness.

Another limitation of the visual system, illustrated by our previous example, is that humans are only aware of a small portion of visual space at any given time. The only portion of visual information that is processed to reach consciousness is the information that receives visual attention. Visual attention, for the purposes of this dissertation, acts as a selection mechanism for visual input [2–5]. Rather than processing the entire visual field at once, we select information both voluntarily and based on salience, which in turn is the information that reaches our awareness [6]. We are effectively blind for any unattended information, and we are unaware of our apparent blindness.

The last, and most critical, restriction placed on visual processing is the need to make eye-movements (saccades [7–9]). Humans make eye-movements to move the high-resolution fovea to objects of interest. It is during saccades that we largely stop processing visual information [10–12]. This halt in processing is intentional, as processing the visual image fully would lead to retinal smear, like the smear you see

when you take a picture with a camera while moving it. Likely, the visual system solves the problem of retinal smear by reducing visual processing around the time of a saccade. Per second, we make several eye-movements [7–9], and a portion of time is spent in absence of visual processing as a result. Thus, humans only process a small portion of visual space, only during a limited time when the eye is still, and only in high resolution when it is at the center of vision. Yet, these limitations seem completely at odds with our subjective experience of our own visual perception. This stark contrast in our subjective experience and behavior is often coined as the problem of visual continuity; we process information in discrete snapshots, yet our subjective experience of the world is continuous.

Visual continuity is often mentioned as the impetus to do vision research. In this dissertation I will focus on the subjective experience of visual continuity across eye-movements, despite gaps in visual processing due to eye-movements. To accomplish visual continuity across an eye-movement, the visual system must somehow combine two disparate images (before and after a saccade) and do it in such a way that we have no notion of the lack of information processing during the saccade. Within this dissertation I argue that the visual system may accomplish continuity of visual perception across eye-movements through several linking mechanisms: 1) presaccadic shifts of attention, 2) visual working memory, and 3) transsaccadic integration which come together in one common model: a forward model of visual perception.

Presaccadic shifts of attention

To bridge the gap in visual processing during a saccade, information needs to be selected, stored and then compared to the postsaccadic visual input. Many studies have shown that processes of visual attention (i.e. selection) are closely coupled to saccade execution [3,4,13,14]. It is due to these attention shifts that observers have already processed the target of a saccade before the saccade is made. One of the formative theories in the field of visual perception has been the pre-motor theory of attention [15,16]. The pre-motor theory argues that attention mandatorily precedes an eye-movement, and that shifts of attention and saccades are functionally very similar. Early iterations of the theory even argue that attentional selection and saccade target selection are the same process, although the consensus now is that it is likely that these two can be dissociated to an extent [17,18]. Regardless, by selecting the saccade target via visual attention, it is processed in higher resolution than information that saccades are not made towards [3,4,19].

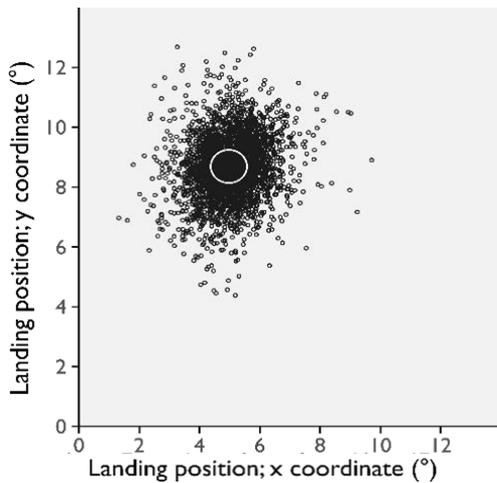


Figure 1. Variance in saccadic landing point.

The white circle denotes the target of the saccade. Each dot is one landing point of an eye-movement to this target. Saccadic onset started at point (0,0).

Attentional selection becomes especially relevant when considering that there is a large amount of variance in saccade landing position across different eye-movements (Fig. 1). Landing point variance further complicates the notion of visual continuity, creating the problem where the visual system needs to dissociate differences in the location of visual information due to saccadic inaccuracies, or spatial differences due to the motion of the object. Recent studies are showing that the locus of the presaccadic shift of attention is not necessarily the actual landing point of the eye, but rather the *intended* landing point [17,18]. Thus, by dissociating actual landing point and intended landing point, the visual system has some notion of the saccadic inaccuracy and can (presumably) correct for these inaccuracies. These studies provide some insight into how the problem of visual continuity in the face of motor variance may be solved, as attention is deployed at the intended landing location of the eye-movement, rather than the actual location.

In sum, before a saccade is made, visual attention shifts to the intended location of the saccade target. This likely occurs to process the saccade target in greater detail so that the visual system can evaluate the visual features and location of the object before a saccade is made.

Visual working memory & Transsaccadic integration

If presaccadic information is indeed compared to postsaccadic information, the presaccadic information needs to be stored for the duration of the saccade. If visual information is stored until postsaccadic visual processing commences, presaccadic and postsaccadic visual input can be compared. Older theories coin the

presaccadic memory buffer as transsaccadic memory [13,20], and later studies have shown that transsaccadic memory is likely (a subjugate of) visual working memory (VWM, [21–24]). VWM allows humans to temporarily store and manipulate visual information, making it a likely candidate for transsaccadic feature storage.

Storing the visual information in VWM could allow humans to detect changes across saccades. However, as this is rarely occurring outside of a laboratory (features do not tend to change in a ~50 millisecond timespan) its use seems limited at first. Additionally, research has shown that human observers are usually quite poor at detecting transsaccadic changes [11,25]. Therefore, even if features are changed in a laboratory setting, participants often do not notice them. Instead, storing the features of the object allows for quick selection after a saccade [24,26]. If a saccade does not land on the saccade target, the features of that object can be quickly retrieved from VWM, after which a corrective saccade can be made [23,27,28]. Storing presaccadic information in VWM most likely primarily serves to correct for oculomotor variance.

Another possible use of presaccadically storing the visual information, is to make a prediction of the postsaccadic visual world based on low-resolution presaccadic visual information [29–32]. Before a saccade is made, visual information is typically low-resolution (as we tend to make saccades towards objects of interest, rather than away from them). Since we have made many saccades during our lives, we have a wealth of experience to base these predictions on. In the studies by Herwig, Schneider, Weiß and colleagues [29–32], participants are making a saccade to an object, which is then altered during a saccade. As a result, the postsaccadic information does not match the presaccadic information, and participants over time change their estimate of the presaccadic visual information. The authors conclude that participants are updating their prediction of the presaccadic low-resolution image due to receiving non-matching postsaccadic visual input, showing that the presaccadic predictions are subject to learning processes.

In light of presaccadic predictions, a theory has been proposed about how the visual system may bridge the gap in visual processing between saccades, by integrating presaccadic and postsaccadically perceived information [30]. In essence, information about the upcoming features are stored, a prediction is made about what these features will look like after the eye-movement, and finally this information is then integrated with the postsaccadically perceived information [30,33–37]. Studies have found that integrative processes are closely linked to selection of visual information by visual attention, as visual distractors deteriorate transsaccadic

integration [37]. Integrating visual information across saccades may allow for the visual system to assume that visual information was always present [30].

The idea that the visual system retroactively ‘fills’ in the information that is not processed during a saccade is not new, nor unique to visual attention research. Researchers have noted that filling in leads to a visual-temporal illusion called saccadic chronostasis [38]. You may have experienced this illusion for yourself when making a saccade to a clock with a second hand and noticing that it takes slightly longer to resume ticking after an eye-movement. What happens in this instance is that your perception of the clock during the saccade is retroactively filled in, making that moment seem a little longer. However, the exact mechanisms of chronostasis have been unclear thus far, and only recently have been connected to transsaccadic integration [30]. In one example that attempted to cross the bridge between temporal and vision research, the authors found that chronostasis only occur at the saccade target, linking it to the presaccadic shift of attention [39]. Again, this seems to mesh well the current ideas on transsaccadic integration and its link to visual attention, suggesting that chronostasis is a side-effect of transsaccadic integration.

Forward model

I hypothesize that most of these concepts fit within a theoretical model known as a forward model. Typically, forward models have been used to describe motor movements and learning from motor errors [40]. The essence of a forward model is that some predictive mechanism uses motor outflow, a copy of the motor command (efference copy) that is sent to the muscles, to predict the outcome of that motor command before the motion is completed [41,42]. The predictive process is known as the forward model. After the movement is completed, the prediction from the forward model is compared to the new state of the world. If the prediction and new state of the world match, predictions for the forward model become more accurate (less variable). However, if the prediction does not match, the system can

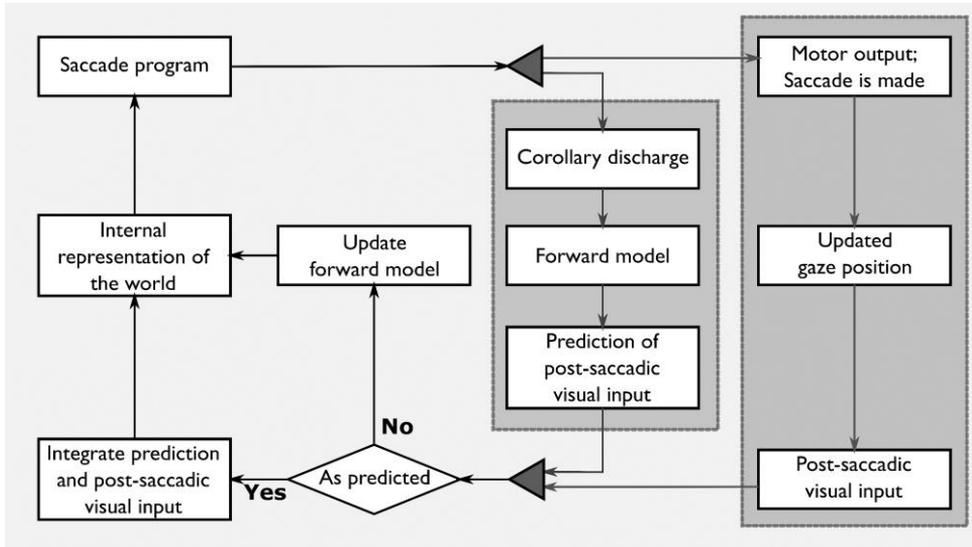


Figure 2. The proposed theoretical model of visual perception across eye-movements.

The model is presented as a box and arrow model. Decision nodes are denoted as diamond shapes, processes as rectangles, and merging nodes as triangles. Connectors are shown as unidirectional arrows.

learn from the mistake by updating the forward model to make new predictions. We argue that visual perception across saccades may fit within a similar theoretical model.

The proposed model for visual perception across saccades is shown in Fig. 2. In short, whenever a saccade is made, the visual system predicts the outcome. This prediction is acquired at the intended location of the saccade, and subsequently stored in VWM to bridge the gap in visual processing across a saccade. Then, the presaccadic visual input is integrated with the postsaccadic visual input. I hypothesized that this integration occurs for features, as well as temporally. Feature integration across saccades has been studied extensively [33,35–37,43]. In essence, when changing a stimulus across an eye-movement, participants report a mixture of the presaccadic and postsaccadic state of the stimulus. Furthermore, temporal integration could explain why we do not detect our lack of visual processing during a saccade. Our visual system assumes the visual information was always present if our prediction of the postsaccadic visual input was not violated. Thus, visual continuity across saccades may be established.

In the following chapters I investigated several components of the proposed forward model for visual perception. First, in Chapter 2, I investigated the cost of storing presaccadic predictions on VWM. I hypothesized that with each eye-movement, a prediction is made, which means that this information is stored in VWM. This information overrides any previously stored information when VWM is at capacity. In Chapter 3 I investigated the implications of selecting visual information with presaccadically linked visual attention. Whether selecting visual information can be inhibited by other non-voluntary ‘negative’ attentional processes. In Chapter 4 I examined the functional link of coupling VWM and attention. Here, I argue that utilizing visual attention and VWM in establishing visual continuity across saccades may ultimately serve to execute corrective saccades. Corrective saccades are a necessity, due to variance in saccadic landing point. Lastly, I have explored the integrative part of the forward model in Chapter 5. Here, I studied how observers integrate feature information across saccades and whether this may relate to saccade accuracy or is independent of variance in saccadic landing point.

Interaction with other senses

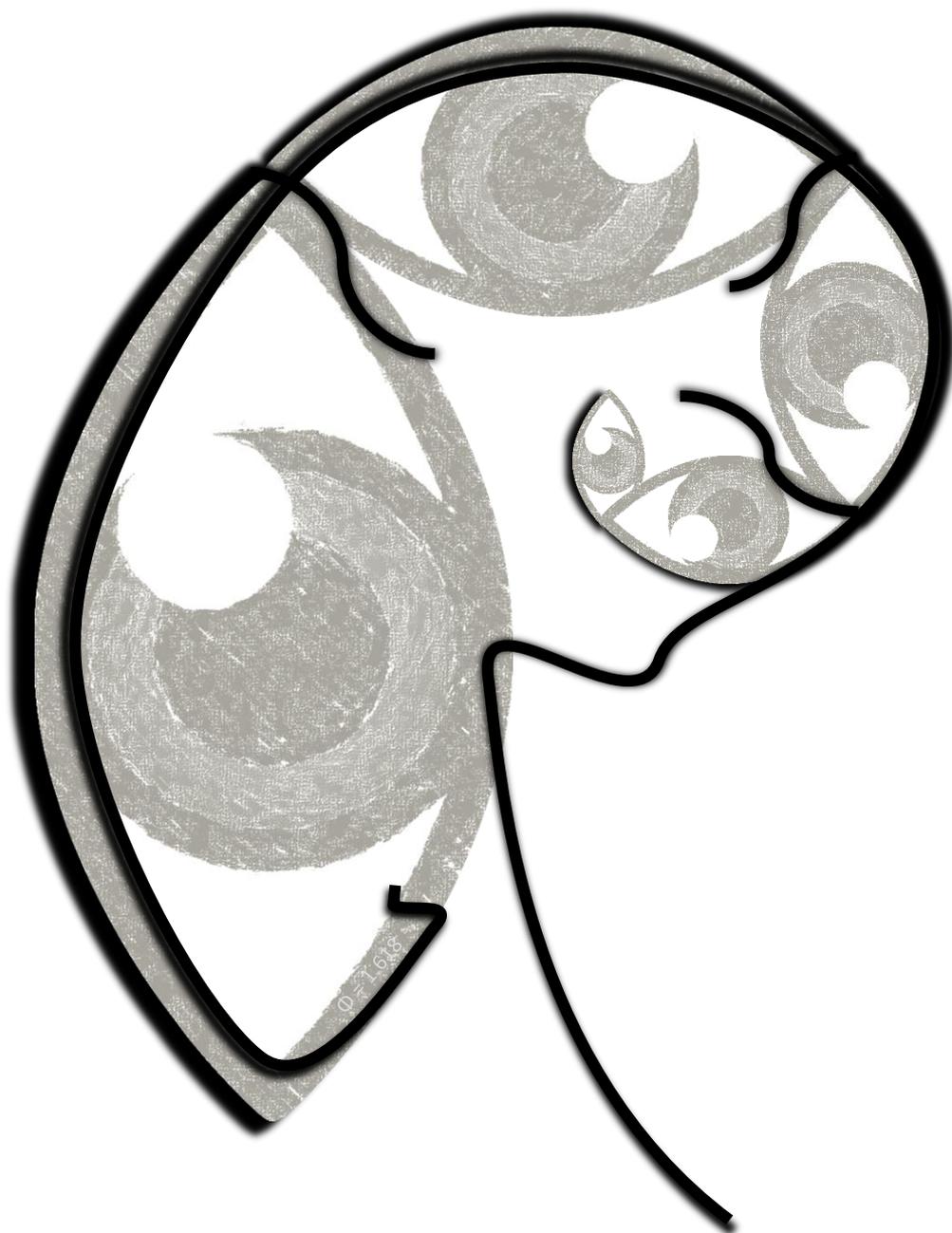
Additionally, many neurophysiology studies have shown that, due to high spatial accuracy of the visual system, it also serves as a calibration mechanism for other sensory systems [44,45]. This is important for e.g. social interaction, coupling the visual motion of a mouth movement to the sound, which helps identifying who is talking and attenuating irrelevant noise. It is thought that because vision is innately spatial (light falls onto a part of the retina), it serves as the calibration mechanism for the auditory system. I hypothesized that, to make comparisons between sensory system possible, cross-modal attention must update in a similar manner to visual attention across eye-movements.

In Chapter 6 I investigated attentional updating across eye-movements and compared them across the visual and auditory modalities. I hypothesized that attentional updating across the modalities is very similar, as to not introduce discontinuity errors between the different sensory systems when a saccade is made. I suspected that many of the processes linked to updating attention across saccades may be relevant for multiple sensory systems, as the visual system is the primary sensory system that provides spatial information.

In sum

Within this dissertation I will explore several topics that link together into a forward model of visual perception. The studies discussed in the following chapters have a strong focus on deepening the knowledge of the visual attentional system and the link with VWM. The results of which will be tied together in the final chapter, the general discussion.





Chapter 2

The cost of making an eye-movement: A direct link between visual working memory and saccade execution.

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Author contributions

MJS, NvdS, AP, & SvdS conceptualized and designed the experiment. MJS programmed the experiment, collected the data and performed the analyses. MJS wrote the manuscript, and NvdS, AP, and SvdS commented on and co-authored the manuscript. SvdS funded the research.

Summary

To facilitate visual continuity across eye-movements, the visual system must presaccadically acquire information about the future foveal image. Previous studies have indicated that visual working memory (VWM) affects saccade execution. However, the reverse relation, the effect of saccade execution on VWM is less clear. To investigate the causal link between saccade execution and VWM, we combined a VWM task and a saccade task. Participants were instructed to remember one, two or three shapes and performed either a No Saccade-, a Single Saccade- or a Dual (corrective) Saccade-task. The results indicate that items stored in VWM are reported less accurately if a single-saccade- or a dual-saccade-task is performed whilst retaining items in VWM. The loss of response accuracy for items retained in VWM by performing a saccade, was similar to committing an extra item to VWM. In a second experiment, we observed no cost of executing a saccade for auditory working memory performance, indicating that executing a saccade exclusively taxes the VWM system. Our results suggest that the visual system presaccadically stores the upcoming retinal image, which has a similar VWM load as committing one extra item to memory and interferes with stored VWM content. After the saccade, the visual system can retrieve the saccade target from VWM to evaluate saccade accuracy. Our results support the idea that VWM is a system which is directly linked to saccade execution and promotes visual continuity across saccades.

Introduction

To process visual information, the visual system redirects the high-acuity fovea to objects of interest in the visual field by rapidly moving the eyes (saccades) [46]. Although saccades dramatically alter the visual input, we subjectively experience a stable visual world: a world in which items of interest are available for processing both before and after a saccade. It is still debated in what manner the visual system stitches together a continuous experience from visual input interrupted by saccades [11,12,25].

One potential candidate to bridge the gaps in visual processing during saccades, is an attentional selection mechanism that is tightly coupled to saccade preparation, i.e. presaccadic shifts of attention [3,4,14]. The coupling between attentional selection and saccades is shown by an increase in the discriminability of visual input near a saccade target (relative to stimuli further away from the saccade target), even when the stimuli are no longer available after the execution of the saccade [19,47]. Information at the attended location is selected by attentional processes and stored in a memory buffer, from which information can subsequently be retrieved after the saccade [3,4]. A presaccadic shift of attention, may allow the visual system to determine whether the stored visual input matches the postsaccadic visual input. By determining congruence between pre- and postsaccadic visual input, motor errors and/or changes in the external world can be detected and compensated for by corrective eye-movements [24,41,48]. Previous research indicates that the presaccadic shift of attention, together with the corollary discharge (an efference copy of the motor command executed by the visual system), underlies visual continuity across saccades [28,49–51].

The storage of presaccadic visual input, or transsaccadic memory, is often thought to be dependent on visual working memory (VWM) [4,9,19,20]. VWM is a buffer, with a limited amount of storage capacity, which we can consciously access and use to update visual information [52–54]. As storage capacity in VWM is limited, when more information is stored in VWM, individual items can be represented with less detail, resulting in a decrease in the precision of responses [53]. Storing presaccadic visual input is important, as it allows for comparison with postsaccadic visual input. For example, after the saccade has been completed, the postsaccadic visual input can be integrated with the visual input stored in VWM, to evaluate saccade accuracy and increase the precision of information that is processed by the visual system [33,35,43]. Other possible mechanisms include transsaccadic

learning. Several authors have shown that transsaccadic changes of stimuli (e.g. shape and spatial frequency) can alter how observers respond to presaccadic retinal stimuli [29,32,55–57]. Transsaccadic learning is thought to occur because the visual system learns to associate presaccadic peripheral visual input and postsaccadic foveal visual input over the course of many saccades [31]. Both transsaccadic learning and transsaccadic integration could underlie comparisons of presaccadic and postsaccadic retinal input, potentially bridging the gap in visual processing during saccades.

The ability of the visual system to evaluate stored presaccadic visual information after a saccade has been made, has been shown in several studies [13,23,24,33]. In particular, studies on gaze correction have shown that visual information selected by presaccadic attentional shifts can be used to re-fixate a target object if it is displaced during a saccade [23]. In the study by Hollingworth and colleagues [23], participants were presented with a circular array of stimuli. The saccade target was indicated by a brief increase and decrease in size of one of the stimuli. When the participant executed a saccade to this cued object, the array rotated, such that the participant landed in between the previously cued object and an uncued (distractor) object. To correctly perform the corrective saccade task, the observers had to execute a corrective saccade based on the available visual information alone, as variance in the motor system was uninformative regarding the postsaccadic location of the target. The study showed that participants consistently executed a secondary (corrective) saccade to the displaced target. The authors thus showed that information about the saccade target is acquired before execution of the saccade, allowing for corrective saccades. Another study on corrective saccades showed that VWM content may bias and increase the latency of visual corrective saccades [27]. In the study by Hollingworth and Luck [27], observers were tasked with remembering the exact color of a stimulus. The crucial manipulation was a distractor object in a visual corrective saccade task, that changed into a color that was being maintained by the participant. Corrective saccades were slower and biased towards a distractor object that matched the features of the colored object when compared to a distractor with irrelevant features. These results indicate that VWM is tightly coupled with motor execution in a visual corrective saccade task.

Overall, prior studies indicate that corrective saccades are guided by VWM content. The opposite relation, how VWM content is affected by the execution of a saccade, is less clearly defined. The proposed interaction between saccade execution and VWM is that visual information at and surrounding the saccade target is

obligatorily and *preferentially* encoded into VWM before a saccade is executed. We hypothesize, that before the eye-movement is executed, a prediction of the visual features of the future fixation target is made. This prediction will most likely be as accurate as possible, which means it will have a VWM load comparable to actively committing one extra item to VWM. We also hypothesize that the visual system will prioritize information acquired by presaccadic attentional shifts, as it is essential for the evaluation of saccade accuracy, which in turn is important for a stable perception of the environment. If this is indeed the case, then the encoding of the saccade target in VWM should decrease the precision of other information that is stored in VWM, as features of the saccade target mandatorily compete for VWM resources.

In the current study, we investigated whether and how VWM content is affected by visual information that is acquired before the execution of a saccade. We expected that information that was present in VWM at the time of saccade execution would be represented less accurately (higher standard deviation in the distribution of responses) because of the encoding of the saccade target into VWM (Experiment 1). In addition, to correctly perform a corrective saccade task, the stored visual features of the saccade target must be retrieved from VWM. We expected this process of retrieval to be delayed when competition for VWM resources was higher. To investigate whether these effects were exclusive to VWM load, and to exclude the effects of task-load in general, we conducted a second experiment. Participants had to perform a dual-task in which they had to retain auditory or visual information and execute a saccade. Prior research has shown, that auditory working memory load affects corrective saccade latency less than VWM load, but that the effect of executing a saccade on items stored in auditory working memory are unknown. We expected items stored in auditory working memory to be less affected by executing a saccade, compared to items in VWM, due to auditory information occupying a resource separate from VWM.

Experiment 1

Method

Participants

Fifteen participants (9 female) aged 18 to 28 ($M = 21.9$) were tested, for 90 minutes each. Participant amounts were chosen to match prior research [23,58]. All observers participated for a monetary compensation of €6,- per hour. Participants reported normal or corrected-to-normal vision and were naïve as to the purpose of

the study. Written informed consent was obtained from all participants. One participant chose to end the experiment prematurely and was excluded from further analyses. The study was reviewed and approved by the Faculty Research Ethics Committee (FETC) of the University of Utrecht. The data and analyses are registered and available online [59].

Stimuli and Apparatus

Participants performed three tasks in blocks of several trials: a saccade task (124 trials per participant), a VWM task (124 trials per participant), or both tasks in dual-task blocks (186 trials per participant). The tasks were presented in blocks of trials and did not differ in stimulus presentation, only in pre-block instructions. Moreover, the order was randomized per participant.

In the VWM task, the participant was instructed to remember one, two, or three shapes presented sequentially at the center of the screen. We chose to present the stimuli in sequence so that we could run an auditory analogue to the VWM task (Experiment 2). The VWM shapes were morphed by manipulating their width and height, whilst keeping the surface area at a constant-value (surface area of the shapes = 2.25°). For example, a square with a width-height-ratio of 1.0:1.0 would be 1.5° wide and 1.5° high. The VWM shape categories used in the VWM task were a square, diamond (a square rotated by 45 degrees), and triangle. The width-height-ratio of the VWM shapes was a continuous value, randomly drawn from one of two uniform distributions (with width-height-ratios ranging from 1.0:1.2 to 1.0:2.0). The participants were instructed to remember the exact form of the VWM shapes, for a maximum of three stimuli. The VWM shape categories and width-height-ratios were randomly chosen per trial, with the constraint that all VWM shapes in a trial were unique in both shape category and width-height-ratio. After a retention interval, a test stimulus was presented. The test stimulus was one of the three VWM shapes categories (e.g. square) with an equal width and height, the width-height-ratio of this stimulus had to be altered to match the remembered object by pressing the arrow keys. The smallest step size of a single press of a key was a change of 0.0025 in width-height-ratio. The step size increased if one of the arrow keys was pressed by: number of seconds since release \times 30. The step size reset to a change of 0.0025 if a key was released. This was done to ensure accuracy in changing the values by tapping the keys, and to avoid frustration by reducing the amount of time needed to indicate a large change by holding down a key. Once the participant thought the response stimulus matched the remembered object, they pressed the space bar to

confirm their answer. The participant could only end the trial if one of the arrow keys had been pressed.

The saccade task was performed in between the presentation of the VWM shapes and the VWM test stimulus. In the saccade task, six colored circles with a diameter of 1.5° were presented on the screen. Colors were drawn from a subset of 4 colors: red (12.1 cd/m^2), green (18.9 cd/m^2), blue (9.9 cd/m^2), and magenta (14.2 cd/m^2). The restriction in assigning the colors was that no neighboring circles could have the same color. The six colored circles were placed equidistantly on an imaginary circle with a radius of 4.5° from the fixation stimulus (a grey dot of 0.6° in diameter, 4.1 cd/m^2). The array of stimuli was rotated randomly clock-wise or counter-clockwise per trial, with the additional restriction that no stimuli could appear on the cardinal axes. One of the circles was cued as the saccade target by expanding its size to 2.1° in diameter for 100 ms.

The experiment took place in a darkened room. Stimuli were presented on an Asus ROG swift PG278Q (27 inch, 60.1 by 34.0 cm) monitor with a spatial resolution of 2560 by 1440 pixels and the refresh rate set at 120 Hz. Participants were seated 70 cm from the monitor with their heads resting on a desk-mounted chin- and headrest. Eye-movement data was collected using an EyeLink 1000 (SR Research Ltd., Canada), positioned at 65 cm from the participant. The left eye was recorded at 1000 Hz. Saccades were detected offline with the default-values of the EyeLink algorithm for saccade detection.

The experiment was programmed in Python 2.7 using the Pygaze library to connect to the eye tracker and to define areas of interest [60]. Eye tracker data files were analyzed with Python 2.7 and statistical analyses were performed using R 3.1.3 [61].

Procedure

Participants completed the experiment in three blocks of trials: a saccade only block, a VWM only block, and a dual-task block in which participants performed both the saccade task and VWM task. A typical trial within the dual-task block occurred as follows (see Fig. 1A): a fixation stimulus was presented, after which one/ two/ or three VWM shapes were shown sequentially in the center of the screen (see Fig. 1B). The VWM shapes were either morphed to have a low width-height-ratio or a high width-height-ratio. Participants were instructed to remember the exact form of all VWM shapes that were presented.

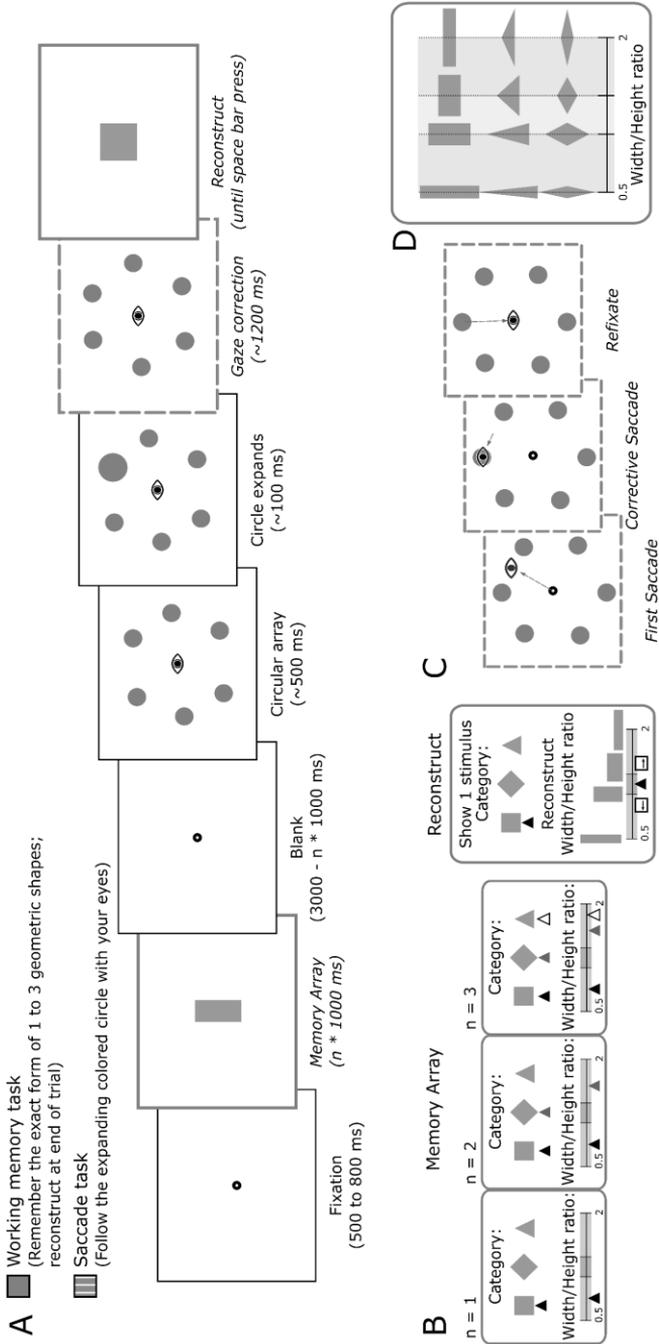


Figure 1. The procedure of Experiment 1.

Square panels indicate the stimuli that were presented (A, C), rounded panels illustrate the experimental design (B, D). A) An overview of a trial. In the given example the memory load = 1. Solid lines indicate the VWM portion of the trial, dashed lines indicate the saccade task portion of the trial. B) An overview of the VWM task. Subjects were tasked with remembering 1 to 3 stimuli during the ‘Memory Array’ phase and were asked to reconstruct the width-height-ratio of one of these stimuli in the ‘Reconstruct’ phase. C) The procedure of the saccade task. The two saccades of importance are shown: ‘First saccade’ and ‘Corrective saccade’. In the VWM only task, the participants kept their gaze on the fixation point for 1200 ms. Note that the circles in c were colored in the actual experiment. D) Example stimuli for the extreme values of the three shape categories.

Each VWM shape was shown for 900 ms, followed by a 100 ms blank interval. After all VWM shapes were presented, a fixation point was shown. In trials in which less than three stimuli were shown, the duration of the fixation period was increased to match the retention time of a trial with three VWM shapes. After an interval of 400 ms, six colored circles were shown. This indicated to the participant that the saccade task had started. One of the circles was cued, by expanding in size for 100 ms and subsequently returning to its original size in the next refresh cycle of the screen. The participant was instructed to execute an eye-movement to this stimulus as soon as a circle was cued. If the participant did not initiate a saccade within 800 ms, the array rotated by itself. During the eye-movement, the entire array of stimuli rotated such that the participant's gaze landed in between the cued stimulus (target) and another stimulus (distractor), a 30-degree rotation. Eye-movements were determined by the recorded gaze position leaving a circular region of 1-degree visual angle around the last sampled point. In one third of the saccade trials, the array did not rotate.

The participant was tasked with executing a saccade to the postsaccadic position of the cued stimulus (Fig. 1C). After a second saccade was detected, 200 ms passed and all circles were removed from the screen. Finally, a stimulus representing a shape category was presented in the center of the screen. Participants were tasked with manipulating the width-height-ratio of the response stimulus (by using the arrow keys) to match the shape they had seen at the start of the trial. To reduce end-point biases, participants could manipulate the width-height-ratio of the response stimulus 30% further than the range of the distribution the VWM shapes were drawn from (examples of extreme VWM shape values shown in Fig. 1D). The participant confirmed their answer by pressing the space bar. In saccade only trials, the stimulus presentation matched the dual-task trials, but participants were required to maintain fixation for 1200 ms instead of initiating saccades.

Data analysis

Our parameters of interest were: the performance on the VWM task in the VWM only block as compared to the dual-task block, and the saccade latency and accuracy during the saccade only block as compared to the dual-task block. We calculated the difference between the shown width-height-ratio of the correct VWM shape and the width-height-ratio that was reported by the participant. The parameters of interest were mean error and precision (the inverse of the standard deviation). As shown by Bays and colleagues [53], when working memory resources are occupied,

response precision decreases. We investigated whether mean error was significantly different between the conditions using a Bayesian repeated measures ANOVA. A difference in mean error would indicate bias, rather than less accurate reporting. If no difference was present, we fit a linear mixed model predicting the precision of responses to the VWM task with the fixed factors of Task (VWM only or dual-task) and Working Memory Load as a contrast-coded factor (one, two or three items). We checked the normality of the residuals in the linear mixed models using a Shapiro-Wilk test, and reported the mean and standard deviation of the residuals. We linearized the responses on the VWM task (reported width-height-ratios), to make the distance in the width-height-ratio identical between ratios above zero and below zero, where zero indicates a width-height-ratio of 1:1.

We compared corrective saccade latency and accuracy within the saccade only block and the dual-task block. We were particularly interested in the relation between VWM and corrective saccades, as we reasoned that corrective saccades can only be correctly executed if the saccade target is retrievable from VWM. First, to determine at which moment the corrective saccade occurred, we analyzed the offset of the first saccade. The first saccade was defined as the saccade with an offset of 60 to 800 ms relative to saccade target onset (99.2% of trials). The next saccade with an onset of 60 to 800 ms relative to the offset of the first saccade, was taken as the corrective saccade (95.7% of remaining trials). We chose a lower bound of 60 ms since the conduction delay for afferent signals to transform retinal input into an oculomotor response, is around 30 to 60 ms at minimum [62–66]. This suggests that, for visual information to be processed, saccades must have a latency beyond 30 to 60 ms. The upper bound reflected the time it took for the array to rotate by itself if a participant did not initiate a saccade after the saccade cue appeared. A corrective saccade was categorized as being correctly executed if the saccade landed in the direction of the corrective saccade target (i.e. the angle between the target and the saccade, should not be greater than 90°) and within 2° of the corrective saccade target. Saccades that did not meet these two criteria were categorized as incorrect, but not excluded (485 out of 2243 trials).

We also performed control analyses using linear mixed models with the latencies of the first saccades as the dependent variable. Previous research has shown that first saccade latency and corrective saccade latencies may be closely linked in a corrective saccade paradigm [58]. Therefore, we wanted to establish whether the potential effect of altered corrective saccade latencies with higher VWM load were not simply due to altered first saccade latencies.

We opted for Bayesian statistics, which can differentiate between significant null results versus non-conclusive evidence [67]. Bayes Factors (BF) can be interpreted as the ratio of evidence for one hypothesis over another. For example, a test which shows $BF = 100$ for the alternative model, indicates that there is 10 times more evidence than a test in which the evidence for the alternative model shows $BF = 10$. To interpret the strength of evidence of a BF, Kass & Raftery [68] have provided guidelines. A BF of between 1 and 3 is described as providing evidence that is ‘not worth more than a bare mention’. A BF of 3 to 20 provides ‘positive’ evidence, 20 to 100 ‘strong’ evidence and above 100 ‘very strong’ evidence [68]. For readability, we report all BFs in favor of one model over the other, BF_{10} is the evidence for the alternative hypothesis over the null hypothesis and BF_{01} is the evidence for the null hypothesis over the alternative hypothesis (since BF_{10} is equal to BF_{01}^{-1}).

Bayesian linear mixed models were constructed with the BayesFactor package [69]. The BF was calculated for the models that included the fixed effect and was divided by the BF of the models that did not include the fixed effect to test the predictive value of adding that factor to the model (Bayesian Model Averaging; [70]). Interaction effects were only tested for models that included all main effects present in the interaction effect, similar to the approach used in the Bayesian ANOVAs in JASP [71]. Each BF was multiplied by the proportion of models that included the factor (prior probability). Additional fixed effects were only included if the BF was 3, indicating positive evidence, or higher in favor of the more complex model. As a measure of uncertainty we provided the (Bayesian) 95% confidence intervals, also known as the 95% credible intervals (95% CI) [72]. The 95% CI s represent the 2.5th and 97.5th quantile of the posterior density function. This interval can be interpreted as being 95% confident that the true value of a parameter lies within the calculated 95% CI , after observing the data. These results were corroborated with frequentist linear mixed models, which were constructed using the lme4 R package [73]. Between frequentist linear mixed models, we compared Bayesian Information Criteria (BIC s), as a measure of model performance. For model comparison purposes, an interaction effect was only included if both main effects were present in the model. A fixed effect was only included if the BIC was 10 points lower in the complex model as compared to a simpler model without the factor.

For frequentist linear mixed model comparisons, the X^2 and p values are reported per model comparison, with a significance criterion of $\alpha = 0.05$. For the

best performing model, we report the parameter estimates β and the corresponding t -values. Lastly, linear mixed models were visualized by plotting the linear fit of the best performing model. The fit was plotted without the random effects (i.e., removing the influence of separate intercepts per participant).

To test similarity of remembering an extra item or performing a saccade, a Bayesian hypothesis-test was performed using the Savage-Dickey method [67,74], in which the difference between the reduction of precision by addition of a saccade task and the reduction of precision per additional VWM item in the posterior distributions were compared. Thus, a difference between conditions (δ) would indicate the relative cost of performing the saccade task, with $\delta = 0$ showing that performing a corrective saccade has the same cost, as remembering an additional memory item. We compared the distribution to the prior distribution (a Cauchy distribution with a width of 0.707) centered on 0, as a null hypothesis that $\delta = 0$.

The Bayesian models were checked for autocorrelation and failure to converge, by examining the trace of the Markov-chain Monte Carlo (MCMC) sampling process. A failure to converge would indicate that the MCMC sampling process was not able to estimate a parameter correctly. The measure of convergence between MCMC chains (*Rhat*) in every model was not higher than 1.1, indicating that's there was no serious convergence issues in the MCMC process, and thus there was reliable parameter estimation [75,76]. For all analyses that required resampling we ran 10000 iterations.

As an exploratory analysis, we investigated the effect of stimulus history on working memory precision. The effect of stimulus history was particularly present in the study by Bays [54], items closer to the saccade onset were reported with more precision. We were interested whether the effect of performing a dual-task differed between items within the sequence. To analyze this, we only included trials in which three working memory items were presented in the analyses. We used model comparison techniques as described previously, reporting *BIC* values and results for Bayesian model averaging tests. Based on these tests, we examined the best performing model in better detail, to investigate which items in the sequence were remembered better than others.

For exploratory purposes, we investigated the differences of random guesses between VWM conditions with a mixture model analysis. As described by Bays [54], working memory performance can be deconstructed into a gaussian component, and a uniform component. The uniform component is a better model for trials in which participants guessed, where any answer is equally likely. The mixture models contain

Table 1. Parameter estimates for Bayesian Model Averaging analysis. Bayes Factors have been rescaled to the participant model for readability.

<i>Model parameters</i>	<i>BF₁₀</i>	<i>Error</i>
<i>WM Load + Participant</i>	1509.66	±1.14%
<i>Task + Participant</i>	5.64	±3.46%
<i>WM Load + Task + Participant</i>	23876.38	±3.38%
<i>WM Load * Task + Participant</i>	5604.96	±1.94%
<i>Participant</i>	1.00	±0.01%

three parameters: (1) the mean of the gaussian distribution as a measure of the response bias, (2) the standard deviation of the gaussian distribution as a measure of the response precision, and (3) the height of the uniform component as a measure of the guess rate. With these analyses, we could identify whether participants guessed more as working memory load increased. When we modelled these (more complex) mixture models, we found that there were no differences in guess rates between conditions (single task vs. dual-task, and one, two or three VWM items, $BF_{01} > 70$). Furthermore, using the product-place method [77], we found that the more parsimonious gaussian only model (as described in the prior paragraphs of the methods section) outperformed the mixture model. Since the mixture model did not outperform the gaussian only model, and there were no differences between guess rates in any of the conditions, we chose to describe the data with a gaussian component only. Likely, the uniform component required an experimental design with a larger number of random guesses. The model code and analysis script are available online [59].

Results

Visual working memory precision

First, we analyzed whether the VWM task was performed less precisely if the participant was also performing the saccade task. As a control analysis, we first determined whether a significant response bias was present between conditions. We did not expect any differences in the mean response, but rather for participants to be less precise as working memory resources were occupied by an eye-movement task. A Bayesian analysis of variance confirmed these hypotheses, showing that

Table 2. Parameter estimates for frequentist linear mixed model predicting performance on the working memory task.

<i>Fixed effects</i>	<i>β-estimate</i>	<i>Standard Error</i>	<i>t-value</i>
<i>Intercept</i>	9.99	0.65	15.42
<i>WM Load : 2</i>	-2.19	0.67	-3.24
<i>WM Load : 3</i>	-3.59	0.68	-5.30
<i>Task : dual-task</i>	-1.77	0.56	-3.14

differences in mean-error was not predicted by task ($BF_{01} = 13.9$), working memory amount ($BF_{01} = 134.0$), task and working memory amount ($BF_{01} = 1993.0$) or a full factorial model ($BF_{01} = 1.21 \times 10^5$). Therefore, a derivative of the standard deviation could be used for further inferences. Our mean data suggested that participants, on average, performed the VWM task less precisely in the dual-task condition ($M = 6.29$, $SD = 2.73$) as compared to the single task condition ($M = 8.06$, $SD = 3.54$). Furthermore, the mean data suggests that participants were more precise in answering when one item was retained ($M = 9.10$, $SD = 3.87$) compared to when two ($M = 6.97$, $SD = 2.64$) and three items were retained ($M = 5.45$, $SD = 1.99$).

To quantify this, we constructed a linear mixed model, with the precision of responses on the VWM task as the dependent variable and Task (VWM only block or dual-task block), and Working Memory Load (one, two or three items presented) as fixed effects. Lastly, a random intercept per participant was added to the model. To test the predictive value of the addition of the fixed effects and interaction effect, BF of the models that included our effects were compared to models that did not. The models including Task (VWM only or dual-task) as a fixed effect were 11 times more likely to explain the data than models that did not include the factor Task ($BF_{10} = 11.72$). Similarly, the models that included a fixed effect for Working Memory Load were about 7000 times more likely to explain the data than models that did not, $BF_{10} = 7038.70$. Conversely, the models that included an interaction effect between Task and Working Memory Load were less likely given the data, $BF_{01} = 26.85$. The parameter estimates are shown in Table 1.

These results were consistent with the frequentist linear mixed models, showing that the best performing linear mixed model (including Task and Working Memory Load without interaction effect, $BIC = 428$) had more explanatory value than models that only included Task as a fixed effect ($BIC = 444$, $X2(2) = 24.818$, p

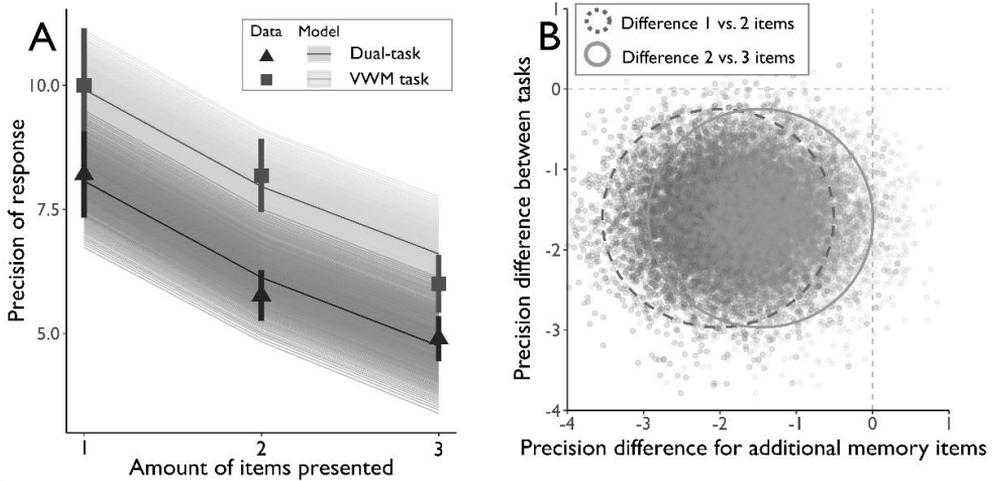


Figure 2. Main results from Experiment 1

A) The fit of the mixed effects model, which predicts precision based on Working Memory Load and Task. The measured precision per Task and Working Memory Load is indicated by the squares and triangles. The 95% CI is shown as a gradient, with higher densities being less transparent. B: The joint posterior of the parameters Task and Working Memory Load. Negative values on the y-axis indicate lower precision on the dual-task with respect to the VWM task. Negative values on the x-axis indicate lower precision per addition of a working memory item. The darker points indicate the difference between 1 and 2 items retained, the lighter points indicate the difference between 2 and 3 items retained. The joint 95% CIs are shown as a dashed and a solid ellipse.

< 0.01) and models that only included Working Memory Load as fixed effect (BIC = 433, $X^2(1) = 9.59$, $p < 0.01$). The more complex model that included the interaction effect between Task and Working Memory Load (BIC = 436, $X^2(2) = 0.95$, $p = 0.62$), did not outperform the simpler models without an interaction effect. A Shapiro-Wilk test suggested that the residuals of the model with Task and Working Memory Load as fixed effects were normally distributed ($M = 1.7 \times 10^{-15}$, $SD = 0.73$, $W = 0.91$, $p = 0.14$), indicating it is an appropriate model for the data. The predicted β -coefficients and corresponding t-values of the model with two fixed effects are shown in Table 2. Together, the analyses supported our hypothesis that performing a saccade task whilst retaining unrelated items in VWM, reduces response precision for the subsequent VWM task. Furthermore, the addition of a saccade task to a working memory task as well as memory load in a VWM task do

not interact. This indicates that the amount of VWM working memory items did not affect the magnitude of the reduction of VWM precision.

The fit of the model and the measured mean performance are shown in Figure 2A. The model shown includes fixed effects for Task and Working Memory Load and a random intercept per participant. The average response precision on the tasks as predicted by the model is lower in the dual-task ($M = 6.37$, 95% $CI = 5.23$ to 7.48) compared to the VWM only block ($M = 7.96$, 95% $CI = 6.86$ to 9.11). Participants were less precise as the number of items increased (1 item: $M = 8.92$, 95% $CI = 7.69$ to 10.19, 2 items: $M = 6.98$, 95% $CI = 5.77$ to 8.21, 3 items: $M = 5.60$, 95% $CI = 4.32$ to 6.85). Fig. 2A visually indicates a slight overlap of the 95% CI between the two tasks and the working memory load, due to uncertainty in the estimate of the mean score that the other scores are centered around. Therefore, we also plotted the joint posterior distributions of Task and Working Memory Load in Fig. 2B. Negative values for Task, shows that the dual-task block was performed less accurately than the VWM only block. Similarly, negative values for VWM precision show the decrease of precision per added item. Two separate point clouds are plotted, one for the difference in precision between 1 and 2 items and the other for the difference in precision between 2 and 3 items. A Bayesian hypothesis test supports that the difference between dual task and VWM task is different from 0, $BF_{10} = 23.93$, 95% $CI = -2.72$ to -0.53 . Furthermore, the difference between 1 and 2 items retained as well as the difference between 2 and 3 items retained is different from 0, $BF_{10} = 23.43$, 95% $CI = -3.26$ to -0.63 and $BF_{10} = 3.11$, 95% $CI = -2.69$ to -0.08 . Lastly, we found marginal evidence for no difference between 1 and 2 items retained versus 2 and 3 items retained, $BF_{01} = 1.49$. We hypothesized that the cost of making a saccade may be close to the cost of remembering an additional item, as saccade targets have been shown to be mandatorily encoded into VWM prior to a saccade. A Bayesian hypothesis test indicates that performing the saccade task elicits a similar load on working memory as remembering an additional item ($BF_{01} = 3.74$, when comparing the dual-task versus the VWM task to 1 versus 2 items, $BF_{01} = 3.85$ when comparing single task versus dual-task to 2 versus 3 items). These results are similar to results from a frequentist paired t-test, $t(12) = -0.40$, $p = 0.35$. Thus, participants were significantly less precise in reporting the items when they were instructed to perform a concurrent saccade task. The loss of precision of performing a dual-task is comparable to remembering an extra item.

To test whether the execution of a *corrective* saccade was the driving factor behind decreased memory performance in the dual-task, we compared trials in which

the array rotated during the first saccade (corrective saccade trials) to trials in which the array did not rotate during the first saccade (single saccade trials). When adding the additional fixed effect of rotation (single saccade trials vs. corrective saccade trials) to the mixed effects model with task and VWM load as fixed effects, we found no predictive value of corrective saccades for the precision of VWM responses, $BF_{01} = 4.08$. We infer that VWM information seems to be in competition with resources acquired around the time of the execution of the first saccade, as executing a corrective saccade did not significantly influence precision of responses in the VWM task.

First saccade latency and accuracy

As a control analysis, we examined differences in first saccade parameters between conditions before examining differences in corrective saccade metrics. We observed that the median first saccade latency in the dual-task was 206 ms ($SD = 79.4$ ms, *Mean amplitude* = 4.94°) if one item was being retained, 203 ms ($SD = 79.1$ ms, *Mean amplitude* = 4.96°) if two items were retained, and 199 ms ($SD = 81.5$ ms, *Mean amplitude* = 4.82°) if three items were retained. In the saccade only block, the first saccade latency was 213 ms ($SD = 92.5$ ms, *Mean amplitude* = 4.96°) if one item was presented, 205 ms ($SD = 104.3$, *Mean amplitude* = 4.86°) and 203 ms ($SD = 84.5$ ms, *Mean amplitude* = 4.99°) if two or three items were presented, respectively. Using a one-sided Bayesian t-test, we tested the effect of Task (saccade only vs. dual-task) on first saccade latency. This test provided evidence that there was no effect of Task on first saccade latency, $BF_{01} = 121.88$ and that there was no effect of Working Memory Load on first saccade latency, for 1 versus 2 items: $BF_{01} = 3.54$ and for 2 versus 3 items $BF_{01} = 8.23$. Similarly, the data provides more evidence for no differences for Task in first saccade amplitude, $BF_{01} = 9.47$. Similar results were found for the effect of items presented on first saccade amplitude, for 1 versus 2 items: $BF_{01} = 8.31$ and for 2 versus 3 items: $BF_{01} = 4.19$.

Table 3. Parameter estimates for Bayesian Model Averaging analysis. Bayes Factors have been rescaled to the participant model for readability.

Model parameters	Corrective saccade latency		Corrective saccade accuracy	
	BF_{10}	Error	BF_{10}	Error
WM amount + Participant	0.08	$\pm 1.60\%$	0.03	$\pm 0.59\%$
Task + Participant	8.71	$\pm 1.70\%$	5.09	$\pm 1.96\%$
WM amount + Task + Participant	0.78	$\pm 2.21\%$	0.17	$\pm 2.93\%$
WM amount * Task + Participant	0.02	$\pm 2.24\%$	0.004	$\pm 1.65\%$
Participant	1.00	$\pm 0.01\%$	1.00	$\pm 0.01\%$

Corrective saccade latency and accuracy

After investigating the effect of corrective saccades on VWM precision, we examined the effect of VWM load on corrective saccade metrics by comparing the saccade only block and the dual-task. We investigated the effect of Task (saccade only vs dual-task) and Working Memory Load (one, two or three items presented) on two corrective saccade metrics: a saccade accuracy (proportion of saccades landing within 2° of the target) and saccade latency (time in ms between previous saccade offset and corrective saccade onset). We expected corrective saccades to be performed less accurately or initiated more slowly in the dual-task.

Examining the data showed that the median corrective saccade latency in the saccade only block was 243 ms ($SD = 127$ ms) and for the dual-task was 232 ms ($SD = 124$ ms). When one item was presented, median saccade latency was 236 ms ($SD = 121$ ms). The median saccade latency was 238 ms ($SD = 118$ ms) when two items were presented, and 242 ms ($SD = 138$ ms) when three items were presented. The mean proportion of accurate corrective saccades was 0.83 ($SD = 0.38$) in the saccade task and 0.76 ($SD = 0.43$) in the dual-task. For Working Memory Load, we find a proportion of 0.81 ($SD = 0.40$) correctly executed saccades when one item is presented, and proportions of 0.77 ($SD = 0.42$) and 0.77 ($SD = 0.42$) correctly executed saccades for two and three items presented, respectively.

Table 4. Parameter estimates for frequentist linear mixed models on corrective saccade latency and accuracy.

Model parameters	Corrective saccade latency			Corrective saccade accuracy		
	β -estimate	SE	t-value	β -estimate	SE	z value
Intercept	259.4	11.09	23.39	1.61	0.22	7.24
Task: dual-task	17.2	5.44	3.16	-0.37	0.12	-3.11

Two linear mixed models were constructed to analyze corrective saccade latency and accuracy. One model contained corrective saccade *latency* as a dependent variable and the other with corrective saccade *accuracy* as a dependent variable. The fixed effects in the model were: Task and Working Memory Load, with an interaction effect between the fixed effects. A random intercept was added for each participant. Model comparison for corrective saccade latency showed that the model including only Task as a fixed effect outperformed the models that did not, $BF_{10} = 12.3$. Working Memory Load was not predictive within our models, $BF_{01} = 1.06$, and neither was the interaction effect between Working Memory Load and Task, $BF_{01} = 1532$. A similar pattern of results was found for corrective saccade accuracy. Whereas Task was predictive ($BF_{10} = 8.13$) for corrective saccade accuracy, Working Memory Load and the interaction between Working Memory Load and Task were not ($BF_{01} = 1.05$, $BF_{01} = 696$). This shows that in the dual-task corrective saccade accuracy was lower and latency was higher than in the single-task condition. The BF_{10} for the models are shown in Table 3.

The model comparison using frequentist linear mixed models, yielded congruent results. The model including Task as a fixed factor and a random intercept ($BIC = 27952$) outperformed models with fixed effects for Working Memory Load and Task ($BIC = 27954$ to 27954 to 27975 , $p > 0.25$). We constructed a generalized linear mixed model with one fixed effect (Task) and random effects for saccade accuracy. This model showed that the inclusion of the factor Task had significant predictive value, $z = -3.11$, $p < 0.01$, similarly outperforming more complex models including parameters for Working Memory Load, $BIC = 2209$ for the model including Task, $BIC = 2221$ to 2223 , $p < 0.01$, for the other models. The estimates for the frequentist linear mixed models for saccade accuracy and saccade latency are

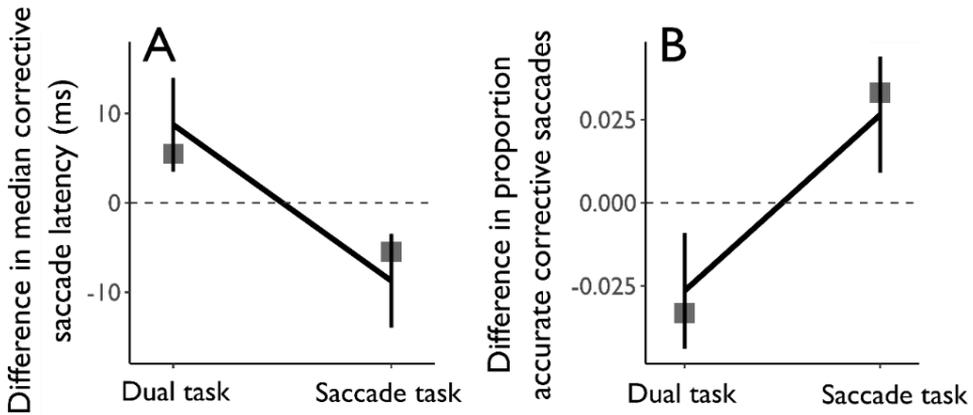


Figure 3. Fit of the Bayesian linear mixed model including Task as fixed effect to the measured corrective saccade latency (A) and proportion of accurate corrective saccades (B). The dark line is the calculated model; the error bars indicate the 95% CI. The transparent squares show the observed point estimates. Note that the figure shows relative values, rather than absolute values.

shown in Table 4. Both models showed normally distributed residuals for the random intercept per participant, $M = 3.71 \times 10^{-12}$ ms, $SD = 36.93$ ms, $W = 0.96$, $p = 0.79$ for saccade latency, $M = -0.01$ ms, $SD = 0.74$ ms, $W = 0.92$, $p = 0.22$ for saccade accuracy.

Based on these model comparisons, we further examined the models that only included Task as a fixed factor and a random intercept per participant to predict corrective saccade latency and corrective saccade accuracy. We normalized the means, which were centered around a latency of 268 ms (95% CI 239 ms to 297 ms) and a 0.78 proportion correct (95% CI = 0.68 to 0.88). Within the Bayesian linear mixed models, saccade latency in the dual-task was 17.4 ms (95% CI = 28.3 ms to 6.67 ms) which was higher than in the saccade only task. Similarly, the model for saccade accuracy showed that the proportion of accurate corrective saccades was, on average, 0.05 ms lower in the dual-task when compared to the saccade only task (95% CI = 0.02 to 0.09). These results are shown in Figure 3.

Exploratory analysis: Stimulus history

Next, we examined the effect of stimulus history on the cost of a saccade. For these analyses, we only investigated trials in which three items were presented. First, we performed a Bayesian model comparison, which included precision on the

VWM task as a dependent variable, as well as Task (VWM only versus dual-task) and Item Index (first, second, third item shown) as fixed variables. The results show positive evidence for models including the factor Task, $BF_{10} = 6.7$. For the fixed effect Item Index, we found inconclusive evidence, $BF_{01} = 1.01$. The results show evidence against the inclusion of an interaction effect between Task and Item Index, $BF_{01} = 17.0$. We further analyzed the model with Task and Item Index as fixed effect and found that the second item was reported worse ($M = -1.25$, $95\% CI = -2.26$ to -0.27) compared to the first item ($BF_{10} = 4.01$, $M = 0.50$, $95\% CI = -0.44$ to 1.44) and third item ($BF_{10} = 7.19$, $M = 0.74$, $95\% CI = -0.21$ to 1.72). Together, these results speak in favor of a difference in working memory precision between the position of items in a sequence. Importantly, the models suggest that this effect does not interact with the cost of a saccade task on visual working memory precision.

Discussion Experiment 1

Our results in Experiment 1 showed that participants were less precise on a VWM task when performing an additional saccade task. Furthermore, corrective saccades within the dual-task were executed slower and less accurate on average compared to saccades in the saccade only condition. Although the corrective saccades were slower and less accurate, the first (or prior) saccade seemed unaffected by the addition of a VWM task. Presumably, a corrective saccade requires information to be successfully retrieved from VWM, whereas initial saccade execution does not depend on VWM encoding. The cue to execute the first saccade is externally available, leading to increased saccade latency for corrective saccades, but not first saccades. The results indicate that the cost of performing a saccade is similar to storing an additional item in VWM. Performing a corrective saccade does not seem to influence VWM precision, indicating that prior to the first saccade, feature information is already mandatorily encoded in VWM. To assess whether these differences are strictly tied to storing visual information in VWM, rather than these results being explained by the added demands of performing two tasks, we conducted a second experiment. Experiment 2 was similar to Experiment 1, but now also included trials in which participants performed an Auditory Working Memory (AWM) task.

Experiment 2

Method

Participants

In Experiment 2, 13 observers (10 female) aged between 18 and 28 ($M = 22.9$ years) participated. The study was approved by the faculty ethics committee and followed the same guidelines as Experiment 1. Experiment 2 lasted for two hours, participants were monetarily compensated with €6,- an hour.

Stimuli and Apparatus

The experiment consisted of three tasks, mixed per block: working memory (WM) trials, saccade only trials, and dual-task trials (WM and saccade task). The modality of WM trials was either visual (VWM) or auditory (AWM). For the VWM trials, the same rectangular morph stimuli were used as in Experiment 1. Sine waves in a range between 350 Hz and 2000 Hz were used in the AWM task. The auditory stimuli were presented on a single speaker placed behind the monitor. To be able to match the characteristics of the two stimulus modalities, we opted for a two-alternative forced choice paradigm. To match the difficulty of the tasks, a *QUEST* staircase procedure was used [78]. Three stimuli were presented, followed by a retention interval. After the retention interval, one of the remembered stimuli and a novel stimulus (i.e. the remembered stimulus plus or minus a staircased value) were presented in a random order. Participants responded by indicating which of the two sounds was the remembered stimulus. The threshold was set at a performance of 75% correct and 100 trials were run. If a difference lower than 1.0 in width-height-ratio was not detectable by the participant in the visual task, or a difference lower than 0.227 in log space was not detected in the auditory task (a difference of approximately 100 Hz at the low end of the frequency range and 485 Hz at the high end of the frequency range), the participant was excluded from the experiment (2 participants). Stimuli for the saccade task were identical to Experiment 1.

Procedure

The experiment was divided into two phases: the threshold phase and the experimental phase. First, participants completed a staircase procedure in the threshold phase for the VWM task and the AWM task. During the threshold phase, participants performed 42 saccade trials to familiarize them with the task. After the staircase procedure, the experimental phase began. The aim of the thresholding phase

was to find a magnitude of modification that resulted in a performance that was not at chance (or at ceiling) between AWM and VWM trials (around 75%). To illustrate, in the VWM thresholding phase three rectangles were shown to the participants (Fig. 4). Participants were instructed to remember the exact shape of the rectangles shown. The rectangles were presented in sequential order and were presented for 600 ms on the screen followed by a 400 ms blank. After all stimuli were presented, a blank screen was shown for 1000 ms (the retention interval). Afterwards, participants were presented a response cue in the form of a number. The number indicated to which stimulus participants were supposed to respond. For example, after being presented three items, the number 3 instructed the participants to report the shape of the third rectangle that was presented previously. Next, the two rectangles appeared, one of which was the actual n^{th} stimulus the other being a rectangle with a modified width-height-ratio. Trials in the AWM thresholding phase were similar, but rather than finding a 75% correct threshold for the width-height-ratio, the 75% correct threshold for differences in tone frequency was determined. The third task during the thresholding phase, the saccade task, was identical to the saccade task described in Experiment 1 and only served as a round of practice trials.

After the thresholding phase was completed, the experimental phase started. Experiment 2 had a 2 (Modality: AWM versus VWM) by 3 (Task: dual-task, WM only, or saccade only) by 2 (Working Memory Load: two or three items) design. The procedure was like the thresholding phase, only the retention interval was replaced by the saccade task. The trials were presented in a block where we predetermined whether participants had to perform the VWM or AWM task. Within this block, participants completed WM only, saccade only and dual-task trials in randomized order. In contrast to Experiment 1, the different conditions did not differ in pre-block instruction, but rather in the stimuli presented on the screen, due to the mixed design nature of Experiment 2. That is, if part of a trial (WM only, or saccade only) did not have to be performed, it was simply replaced by a fixation point.

Data Analysis

Similar analyses were used as for Experiment 1. However, since our dependent variable was dichotomous (i.e., correct/incorrect) we used generalized linear mixed models with a logit link function. This means that the model is linearly fit in log space [79]. This is good practice for binomial data, as the model never reaches values below 0 or above 1 [79]. To fit the generalized linear mixed model, we used the lme4 package (as previously described), for the Bayesian generalized

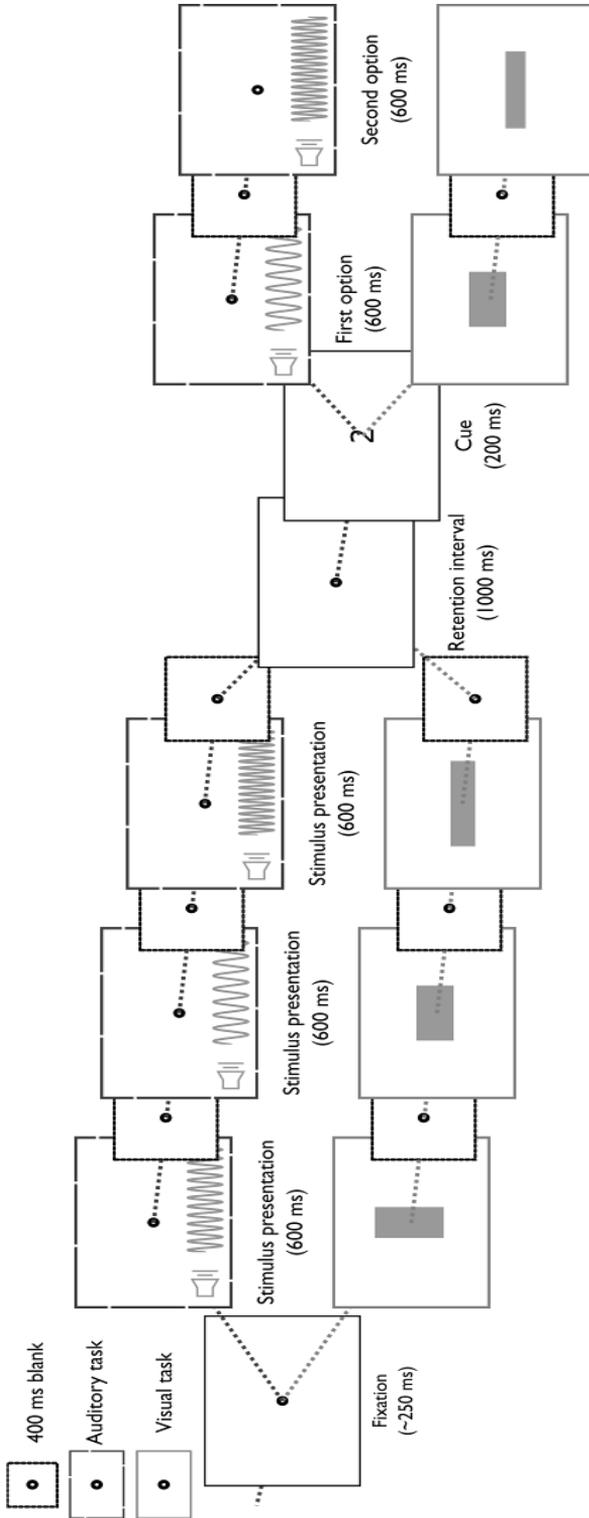


Figure 4. Procedure of the thresholding task in Experiment 2. The smaller black squares indicate that the fixation cross was presented for 400 ms. The dashed line follows the procedure for the auditory task, the solid line for the visual task. The dual-task followed a similar procedure, but the retention interval was replaced by a gaze correction task (see Figure 1 for a graphical representation).

linear mixed model we used the MCMCglmm R package [80]. Importantly, we expected a difference between the dual-task and WM only in the VWM condition, whilst not being present in the AWM condition. To this end, we modeled the response as being predicted by the Task (WM only or dual-task), Working Memory Load (two or three items), and an interaction effect between Task and Modality (VWM vs. AWM). Random intercepts were added per participant for each model, residuals were checked for normality with Shapiro-Wilk tests.

We excluded saccade trials based on the same criteria used in Experiment 1. We excluded trials based on first saccade latencies and corrective saccade latencies being smaller than 50 ms or larger than 800 ms (11 trials out of 1440 excluded). The exclusion rate in Experiment 2 was likely lower than in Experiment 1 because participants had more practice with the saccade task prior to starting the experimental trials.

Results and discussion

Working memory performance

To analyze the data in a similar manner to Experiment 1, we constructed a generalized linear mixed model for working memory performance, but rather than only including Task (WM only vs. dual-task) and Working Memory Load (as a factor: two or three stimuli presented) we added an interaction effect for Modality (visual or auditory). The model with Task and Working Memory Load, together with the added interaction between Task and Modality ($BIC = 2166$) significantly outperformed a null model, in which only a random intercept per participant was modeled ($BIC = 2179$, $X^2(4) = 43.5$, $p < 0.01$) and a full-factorial model, $BIC = 2187$, $X^2(3) = 1.4$, $p = 0.70$. The estimates of the best performing model are shown in Table 5, the residuals for this model were normally distributed, $M = -0.004$, $SD = 0.21$, $W = 0.94$, $p = 0.51$. Results for a Bayesian model comparison between the proposed model and a null model yield similar results, $BF_{10} = 33000$, as well as comparing the proposed model to a full-factorial model, $BF_{10} = 982$. This indicates that the linear mixed model including Task, Working Memory Load, and an interaction effect between Modality and Task is an adequate model for the data.

To recapitulate, we expected to replicate the effects we found in Experiment 1 for the VWM task. That is, better performance in the VWM only condition as

Table 5. Parameter estimates for frequentist generalized linear mixed model predicting performance on the working memory task.

<i>Fixed effects</i>	<i>β-estimate</i>	<i>Standard Error</i>	<i>z value</i>
<i>Intercept</i>	1.48	0.16	9.19
<i>Modality: A</i>	0.53	0.20	2.61
<i>WM Load: 3</i>	-0.27	0.11	-2.46
<i>Modality: V; Task : dual-task</i>	-0.35	0.16	-2.22
<i>Modality: A; Task : dual-task</i>	-0.20	0.18	-1.10

compared to the VWM dual-task condition. Additionally, we expected no difference between the AWM only and AWM dual-task condition. First, we describe the average proportion of correct responses per variable that was entered in the model as a fixed effect. When two items had to be remembered the proportion of correct responses was 0.82 ($SD = 0.39$). The proportion of correct responses was 0.78 ($SD = 0.41$) when three items were presented. In the AWM trials, a proportion of 0.85 ($SD = 0.36$) of responses was correct. In the VWM trials this proportion was 0.75 ($SD = 0.43$). In the AWM only trials the proportion of correct responses was 0.86 ($SD = 0.35$), and in AWM dual-task trials we observed a proportion of 0.84 ($SD = 0.37$). For VWM only trials, the proportion of correct responses was 0.79 ($SD = 0.41$) and in the VWM dual-task trials the proportion of correct responses was 0.73 ($SD = 0.44$) correct.

The model revealed a significant effect of Task, $z = 2.61$, $p < 0.01$, and Working Memory Load, $z = -2.46$, $p = 0.01$, 95% CI -0.56 to -0.06. Importantly, the results show that participants performed the VWM task worse in the dual-task VWM condition than in the single task VWM condition, $z = -2.22$, $p = 0.03$. There was no effect of Task for the AWM condition, $z = -1.09$, $p = 0.27$. Fig. 5 shows both the model (Fig. 5A) and the joint posterior of the difference between the AWM dual-task condition and the VWM dual-task condition (Fig. 5B). The interaction between Task and Modality shows that the cost of making a saccade for the VWM dual-task is on average 0.07 greater (in proportion space) than for AWM dual-task (95% CI -0.02 to 0.16).

To quantify the difference in performance between the AWM dual-task and the VWM dual-task, we performed a Bayesian hypothesis test. The data was 7 times

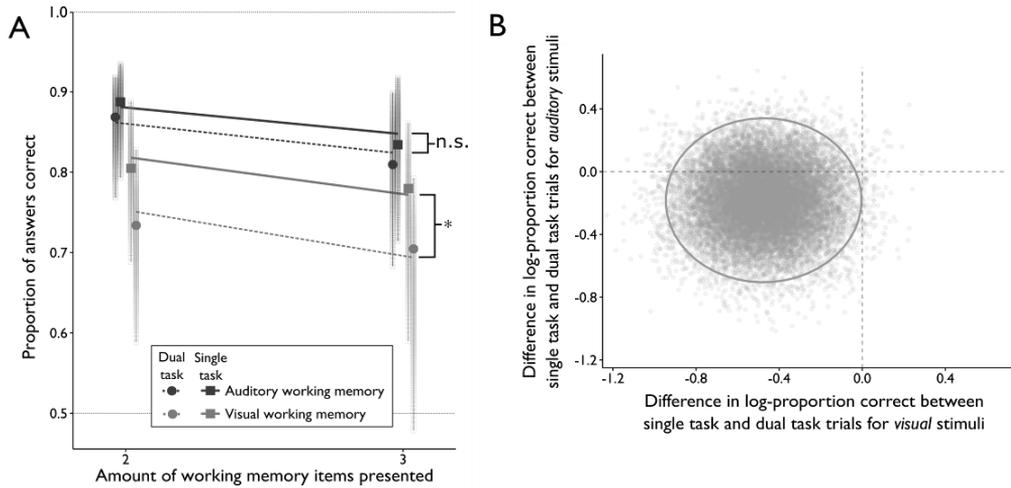


Figure 5. The effect of performing a dual-task on both auditory and visual working memory performance. A) fit of the linear mixed model, 95% CI's are shown as smears, with density of the interval as the alpha value. B) the joint posterior between single task and dual-task trials for auditory stimuli (y-axis) and visual stimuli (x-axis). The 95% CI of this plot is indicated by an ellipse. $*p < 0.05$

more likely to be explained under the model where there was a difference between the AWM dual-task and VWM dual-task ($BF_{10} = 7.08$). Therefore, our hypothesis that the effect of a saccade task would have less effect on an AWM task than on a VWM task was supported. A Bayesian hypothesis test was performed for the difference between the performance in the AWM dual-task and the AWM single task. The results indicated that the model which assumed no difference between the AWM dual-task vs. AWM single task was more likely to explain the data than a model which assumed a difference, $BF_{01} = 32$. We conclude that performing a saccade task while retaining unrelated items in AWM does not affect AWM performance, whereas it does affect VWM performance. Thus, the decrease in WM performance between a dual-task and a single task in Experiment 1 was not exclusively due to increasing task demands.

First and corrective saccade latency and accuracy

When investigating the effect of Working Memory Load on corrective saccade latency in Experiment 2 we used the best fitting model from Experiment 1. In the AWM task, first saccades in the dual-task condition had a median latency of

208 ms ($SD = 88$ ms) and 218 ms ($SD = 77$ ms) in the saccade only condition. In the VWM trials, the median corrective saccade latency in the dual-task condition was 218 ms ($SD = 91$ ms) and 199 ms ($SD = 81$ ms) in the saccade only condition. The model used to describe the corrective saccade latency included a fixed effect of Task, and an interaction effect between Task and Modality, and a random intercept per participant. The model comparison revealed that the model with fixed effects ($BIC = 12062$) performed worse than the model with only a random intercept per participant ($BIC = 12042$, $X^2(3) = 1.52$, $p = 0.68$). A Bayesian linear mixed model analysis provided positive evidence in favor of the null model ($BF_{01} = 9.4$), indicating that the parameters in the model were not predictive. Thus, we can conclude that the parameters in the model do not significantly predict corrective saccade latency. We also ran the analyses with corrective saccade end-point accuracy as the dependent variable. Like the saccade latency results, the null model outperformed the model with fixed effects, $BF_{01} = 153$. We concluded that in Experiment 2, saccade latencies and saccade accuracy were not significantly affected by the modality of items retained or the number of items retained.

General Discussion

In the current study, we have investigated the relation between executing a saccade and the visual working memory (VWM) system. The results of Experiment 1 indicated that the cost of performing a saccade was similar to storing one extra item in VWM. Participants were less accurate in reporting a VWM stimulus after executing a saccade during the retention of the stimuli. The accuracy reduction of items held in VWM was present whether participants executed a single saccade or two saccades (i.e., a saccade to the target followed by a corrective saccade). This accuracy reduction implies that before executing a saccade, information is mandatorily encoded in VWM. Moreover, corrective saccades were executed slower and less accurately in Experiment 1, when participants were retaining VWM items. This increase in corrective saccade latency could have reflected a slowed retrieving of the corrective saccade target from VWM when other items are occupying VWM. The results indicated that predicting future visual input had similar implications for VWM as actively committing an item to VWM, which in turn showed a direct link between VWM and saccade execution.

The results from Experiment 1 demonstrated that VWM precision decreased with an increasing VWM load. A targeted eye-movement lead to a VWM performance reduction that was similar to storing an extra item. We describe the loss

of precision of a saccade as a cost compared to remembering an extra item, yet VWM does not seem to be a resource with discrete ‘item slots’ that can be stored. Instead research suggests that VWM is a continuous resource that can be distributed over multiple objects [52,53,81]. We argue that under either model of VWM resources (i.e., discrete or continuous), our results would be possible.

We also investigated to what extent the results in Experiment 1 were due to increased task-load in general. The results of Experiment 2 indicated that the costs of an eye-movement for WM precision is specific to VWM. It does not affect Auditory Working Memory (AWM). These results were consistent with the traditional models of working memory (WM), in which VWM (visuospatial sketchpad) and AWM (phonological loop) are systems with separate capacities connected by a central executive [82,83]. Due to the separation of these capacities, it is generally easier to perform a multimodal dual-task, rather than a unimodal dual-task [84]. It seems that performing an eye-movement and storing the presaccadic information of the saccade target taxes the VWM system, rather than the AWM system.

The performance in the thresholding phase of Experiment 2 did not perfectly map onto the performance in the experimental phase of Experiment 2. The participants were overall better at the AWM than the VWM task. In Experiment 1, an effect of performing a saccade on the accuracy of items held in VWM was observed, which did not vary with VWM load. We expected performance to be reduced by adding a secondary saccade task to the AWM task. Additionally, we chose an analysis method which was less at risk of interference due to ceiling effects, i.e. a log-linear model. Even if the AWM condition resulted in less overall WM load, an effect of executing saccades on AWM should have been observable, as it was in Experiment 1, and in the VWM condition of Experiment 2. Therefore, the difference in thresholding performance was not problematic for the conclusions drawn.

While the effect of eye-movements on VWM precision were clear, the effect of VWM load on *corrective* saccade latency was less consistent. First of all, we did not find an effect of VWM load on corrective saccade latency or on corrective saccade accuracy, which has been found previously for both endogenously- and exogenously driven saccades [27,85]. The only effect of task-load on eye-movements that we observed, was an effect of whether participants were performing a VWM task next to the corrective saccade task on corrective saccade latency and accuracy. These results may be explained by the visual system prioritizing presaccadically acquired information, as this information is utilized to maintain

visual stability across saccades [23,86]. Moreover, there was no difference between single- and dual-task corrective saccade latency in Experiment 2, in contrast with the results of Experiment 1. This suggests that the effect of VWM load on corrective saccade latency was not very robust when compared to the inverse relation (the effect of saccades on VWM load). Whereas previous studies did observe a consistent effect of VWM load on corrective saccade latency (i.e., higher VWM load increased corrective saccade latency, [23,27]), we only found this effect in Experiment 1.

Alternatively, the difference with previous studies may have arisen because in previous research, the features that were held in the VWM task were similar to, instead of different from, the items in the saccade task (i.e. remember a color and saccade to a colored object) [27]. Even if the features did not directly interfere with each other due to similarity, both features at least occupied the same feature space. Research has indicated that VWM capacity may be modulated by the similarity of items in feature space. For example, remembering a large amount of colors is more difficult than remembering objects with more diverse features, because of potential binding errors [53,87–89]. By design, we opted to keep the features that had to be retained in the visual task (width-height-ratio of a grey object) as dissimilar as possible from the features in the saccade task (one of four colors of a circular object). The slight discrepancy between previous research and our current conclusions may be due to using unrelated features in the memory task and the saccade task. We suggested that the effect of VWM load (of items that are unrelated to the saccade task) on corrective saccade latency, is quite small at baseline, but may become more pronounced when the features of items in a saccade task and a VWM task overlap.

Furthermore, spatial properties of memorized items have been shown to be important for the cost of a saccade. In a study by Williams and colleagues [90], observers were tasked with remembering the features of a stimulus. When unconstrained in their viewing behavior, participants executed more saccades to the location of the items they had to remember than to other, less relevant, locations. The authors hypothesized that visuospatial selection mechanisms aid in the maintenance of object representations. Additionally, the authors show that when attention is drawn away from the location of a remembered object by a distractor, participants report memorized items less accurately. Studies that dissociate the location of the saccade target and the location of remembered items, showed that saccades away from the location of a memorized item resulted in worse memory performance [67, 68]. Tas and colleagues [93] found that saccades to a secondary object during the retention interval of a visual working memory task interfered significantly with the

proportion of correct answers. In contrast, this effect was not present when the participants were instructed to make a free saccade (in a certain direction). The lack of a reduction in memory performance when making a saccade to a blank portion of the screen, showed the necessity of the presence of a visual stimulus for VWM to be affected by a saccade, rather than the saccade itself affecting VWM. In the current study, the saccade targets and working memory items were presented at different locations and contained non-overlapping features. These divergent spatial properties likely resulted in a larger cost due to presaccadic attentional shifts away from the remembered location.

As spatial properties were of great importance to performance on the VWM task, we note that in the AWM task the perceived location of the stimulus was hard to determine. Prior research has shown that auditory information is typically localized towards a visual target [94–96]. This could have caused participants to perceive the sound coming from the center, where the visual stimuli were presented as well. Alternatively, participants could have disregarded the spatial properties of the auditory stimulus entirely, as processing of the spatial location of the auditory stimuli was not emphasized in the current study and the location of the speaker was hidden from view. Two processes may have played a role in the current set of experiments: AWM was less affected by saccades due to the loading of VWM (rather than AWM) by saccades, and/or AWM was less affected by saccades due to a lack of spatial conflict between auditory working memory items and saccades (i.e., the storage of non-spatial features in the AWM task; [97]).

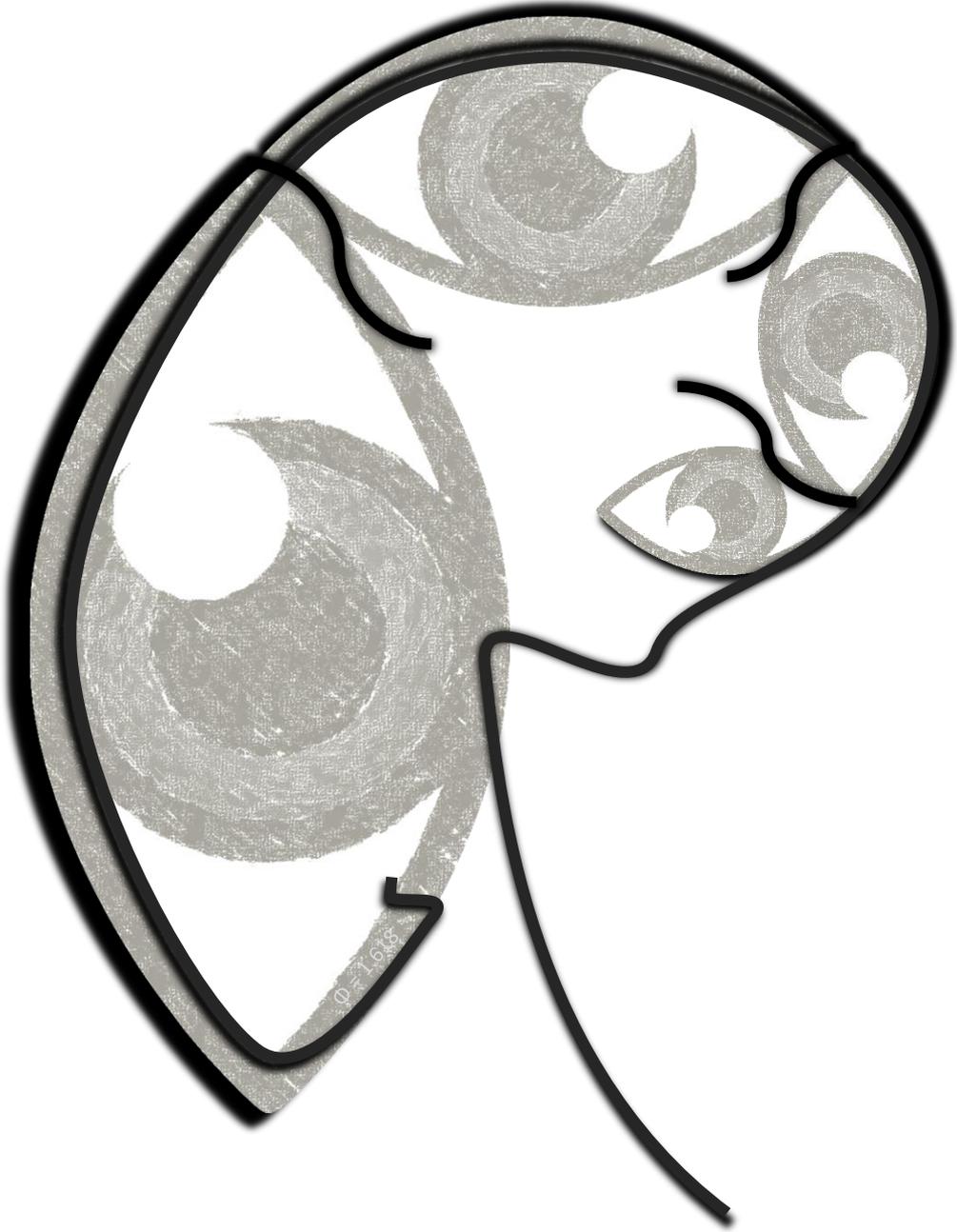
Storing a representation of the object in VWM prior to executing a saccade might serve several functions. First, based on the current literature on transsaccadic integration, we assume that the visual system is constantly storing presaccadic representations of visual input in VWM [30,33,35,43]. The stored representations of presaccadic visual input are integrated with the postsaccadic foveal image. A possible function of integration is to compensate for the reduction of visual processing during a saccade and bridge the delay between pre- and postsaccadic visual input [32,41,98]. Secondly, stored presaccadic visual input, when integrated with the postsaccadic foveal image, increases the precision of the representation of the objects (similar to cue-integration processes) [43,99,100]. Presumably, when a discrepancy (of a large magnitude) is detected between stored presaccadic visual input and a postsaccadic foveal image, the stored presaccadic and postsaccadic visual input are not integrated [101–103]. Furthermore, in case a mismatch is perceived

between the stored visual input and foveated postsaccadic image, the information stored in VWM could guide corrective saccades [28,40,41,98].

Forward models contain the assumption that motor systems predict (before a movement is initiated) the state of the system after the movement. However, it is currently unclear whether the presaccadic visual input is stored or that a prediction of postsaccadic visual input is made and stored prior to the saccade. Several studies on transsaccadic learning have, by inducing changes to saccade targets during the saccade, shown that observers could be taught to associate different presaccadic images with postsaccadic visual input [29,32,55,57]. These studies provide evidence that what was stored in VWM is, at least partly, a prediction of upcoming retinal input. In either case, whether visual information was presaccadically stored, or both stored and influenced by prediction, our study provided evidence that these presaccadic processes tax the VWM system. We propose that VWM is, amongst others, a buffer system, directly linked to saccade execution. VWM can be used to bridge the lack of visual processing during a saccade and may guide corrective saccade by retrieving the state of the world prior to the initial saccade, promoting visual stability.

In conclusion, this study shows that saccades are tightly coupled to the allocation of items to VWM. The visual system must consistently commit predictions of upcoming visual input to a temporary buffer, which can retroactively be compared with the postsaccadic visual input. Our results demonstrate that the cost of predicting the upcoming visual input was quite high, or at least similar to items committed volitionally to VWM. The cost of executing an eye-movement on VWM in this experiment most likely reflects an extreme situation in which the cost of an eye-movement is high. The visual environment within the task was highly mutable (i.e. it changed 66% of the time during an eye-movement), and the stimuli were shown at different locations throughout a trial, requiring saccades away from memorized items. The current findings indicate that the visual system can flexibly allocate the resources of VWM for either saccade tasks or actively committing items to working memory, and that making an eye-movement compulsorily and exclusively uses these visual resources.







Chapter 3

Inhibition of return reduces information acquisition near a saccade target.

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Author contributions

MJS, JHF, & SvdS conceptualized and designed the experiment. MJS programmed the experiment, collected the data and performed the analyses. MJS wrote the manuscript, and JHF, and SvdS commented on and co-authored the manuscript. SvdS funded the research.

Summary

A limited amount of visual information is retained between saccades, which is subsequently stored into a memory system. Since the capacity of transsaccadic memory is limited, selection of information is crucial. Selection of relevant information is modulated by attentional processes such as the presaccadic shift of attention. This involuntary shift of attention occurs prior to execution of the saccade and leads to information acquisition at the saccade target. The aim of this study was to investigate the influence that another attentional effect, inhibition of return, has on the information that gets stored into transsaccadic memory. Inhibition of return is an attentional phenomenon where participants are slower to respond at a previously attended location. To this end, we used a transsaccadic memory paradigm in which target stimuli are only visible to the participant before executing a saccade. Previous research showed that items near a saccade target are likely to be reported more accurately. In our current study participants were cued to fixate one of the stimulus locations and subsequently fixated the center fixation point before executing the transsaccadic memory task. Results indicate that information at a location near a saccade landing point is less likely to be acquired into transsaccadic memory when this location was previously fixated. Furthermore, we found evidence which implicates a reduction of the overall number of elements retained in transsaccadic memory when a location had been previously fixated. These results suggest that the presaccadic shift of attention may be modulated by inhibition of return and thereby reduces information acquisition by transsaccadic memory.

Introduction

The way our visual system deals with the challenge of processing visual information across eye-movements (saccades) is both complex and fascinating. While viewing a scene, the eyes saccade about three times per second to foveate specific parts of the scene for high acuity processing [104]. One of the challenges of integrating visual information is the inability of the visual system to process all information simultaneously [105]. Selection of visual information is crucial as we are only able to attend to a small amount of information at any given time, and unattended information is lost over time [106]. Loss of information can occur during different stages of visual processing but is especially true whilst executing a saccade. Between saccades, a limited amount of objects are retained in a memory buffer, coined transsaccadic memory [3,20,34,54].

The crucial factor to select relevant information and subsequently store this information is visual attention [3,34]. Prior studies have shown that visual attention plays a role in both maintaining feature memory and binding features into representations of objects [48]. After selection, visual information is stored in transsaccadic memory. For instance, before executing an eye-movement, attention is shifted to the intended location of the eye-movement [4,107]. The presaccadic shift of attention is thought to be both involuntary and mandatory. Information at the intended target location of an eye-movement is attended before the movement is executed, due to the presaccadic shift of attention [3,4]. In what manner the presaccadic shift of attention affects transsaccadic memory has been explored in the paradigm used by Irwin and Andrews [11]. In this paradigm a stimulus array is presented before executing an eye-movement. As the eye-movement is cued, and subsequently executed, the stimulus is removed. Results show that the information in proximity to the intended saccade target is more accurately acquired than information further away from a saccade target, due to the presaccadic shift of attention.

Besides the presaccadic shift of attention, other attentional processes may modulate information acquisition by transsaccadic memory, yet these factors remain unknown. One such candidate is inhibition of return (IOR) [108]. IOR has been described as an attentional effect where a slowed reaction time is observed to information at a previously attended location [109]. In the IOR paradigm by Posner and Cohen [12] the participants are presented with a cue, followed by a target to which the participant responds. The presented cue is uninformative and draws

attention by its onset (exogenous cue). When the interval between cue presentation and target is short, a facilitation of reaction time is observed. However, when this interval is relatively long a slowed reaction time is observed, resulting from attentional disengagement [108,110].

Other than reaction time, IOR may also affect sensory-perceptual processes and thereby influence performance on certain discrimination tasks [111]. Research has indicated a reduced ability for human observers to discriminate contrast differences at a location associated with IOR [112]. Yet, it is currently unclear how IOR modulates information acquisition across saccades by transsaccadic memory. Studies show that IOR is closely related to the oculomotor system and that IOR and oculomotor activation are integrally linked together [113]. As acquisition of information into transsaccadic memory is dependent on attentional processes such as the presaccadic shift of attention, we inferred that transsaccadic memory and IOR may also interact at a target discrimination level.

The aim of the current study was to investigate how information acquisition across saccades is modulated by IOR. Under normal circumstances, information in the near proximity of a saccade target is encoded into transsaccadic memory. We hypothesize that when information is located near a saccade target at a location that is associated with IOR, that this information would be encoded into transsaccadic memory to a lesser extent. Therefore, information at a previously fixated location should be reported less accurately. To test this hypothesis, we used an adapted version of the original transsaccadic memory paradigm by Irwin & Gordon [12]. In the current study, one of the stimulus locations was previously fixated by the participants. This paradigm allowed us to investigate how IOR influences the overall number of items acquired in transsaccadic memory. If only the information that appears at a saccade goal is acquired due to presaccadic shift of attention and IOR would reduce information acquisition we should observe a reduction in overall number of items acquired by transsaccadic memory. However, if observers can compensate for this proposed loss of information, by more accurately acquiring stimuli further away from the saccade target, the hypothesized effect of IOR would not decrease overall transsaccadic memory capacity.

Experiment 1

Method

Participants

Fourteen participants, of which ten female, aged 19 to 35 ($M = 23.3$) from the Utrecht University community participated for monetary compensation of 6,- Euros per hour. Participants completed 500 trials in a two-and-a-half-hour session. All participants reported normal or corrected-to-normal vision and were naïve to the purpose of the study. Written informed consent was obtained from all participants. The study was reviewed and approved by the Faculty Research Ethics Committee (FETC) of the University of Utrecht.

Stimuli and Apparatus

Stimuli were white letters (font height 1° visual angle) on a black background. The letters used were drawn from a subset of 11 letters (A, S, D, F, G, H, J, K, L, V, and N) with no repeating letters present in one trial. Fixation dots and probes were presented as white circles of 0.6° with a centered black circle of 0.1° . The fixation dot was placed in the center of the screen. Stimuli and probes could appear at 10 locations, placed on two imaginary horizontal axes (3° upwards and downwards from fixation; Fig. 1). The stimuli and probes were evenly spaced along these horizontal axes subtending 4° left and right from fixation. During the experiment two saccade targets appeared along the horizontal axis on the same height as the fixation target, also subtending 4° left and right.

The experiment was performed in a darkened room. Stimuli were presented on a LG 24MB65PM LCD monitor with a spatial resolution of 1280 by 800 pixels and a refresh rate of 60 Hz. The screen size was 50.8 cm wide and 33.9 cm high. The participant was seated 70 cm from the monitor. Participants placed their heads on a desk-mounted chin rest to reduce head movement. Eye-movements were tracked with an EyeLink 1000 (SR Research Ltd., Canada) sampling at 1000 Hz. All participants were calibrated using the standard 9-point calibration procedure. For offline saccade detection the SR research saccade detection algorithm was used, where an eye-movement was classified as a saccade when the movement velocity exceeded $35^\circ/\text{s}$ or when the movement acceleration was greater than $9500^\circ/\text{s}^2$. The left eye was tracked for all participants.

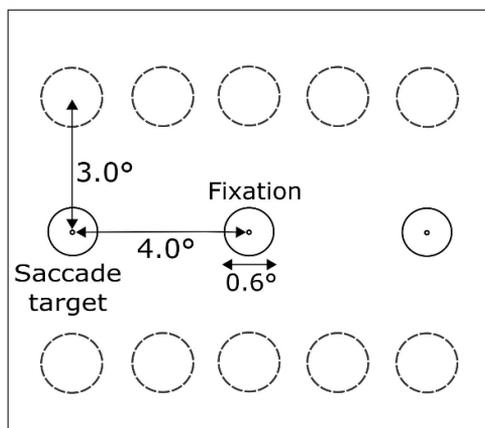


Figure 1. The possible locations of the stimuli used in Experiment 1 and Experiment 2. The dashed circles are placeholders and were not presented during the experiment. The figure presented here is not drawn to scale and is shown in inverted contrast.

The paradigm was programmed in Python 2.7. The Pygaze library was used to connect to the eye tracker using the native Pygaze event detection to detect saccades online [60]. Eye tracker data files were analyzed with Python 2.7 and R 3.1.3 was used for statistical procedures [61]. The lme4 R package was used for statistical analyses [73].

Procedure

The experiment was divided into ten blocks of 50 trials. Prior to starting the experiment, the eye tracker was calibrated using a standard 9-point calibration procedure. After that, a practice block of 15 trials was initiated. If the participant did not perform correct saccades (within 2° of the saccade targets) on at least 5 trials, the practice block was repeated (one participant). Practice trials were identical to regular trials. Before every trial a drift check was performed. If drift was greater than 1.5° visual angle, the eye tracker was recalibrated.

The procedure of the experiment is depicted in Fig. 2. Participants fixated on a central stimulus for 750, 1000 or 1250 ms. The variable interval was used to prevent preemptive saccades. A probe would then appear at one of ten locations. This location will be referred to as the onset location. Participants were instructed to make a saccade to this stimulus as quickly as they could in response to its onset. When the stimulus disappeared, participants had 500 ms to make a saccade back to the fixation point. After this, the letter stimulus array and the saccade targets appeared. After a variable interval of 750 to 1250 ms a tone was played for 400 ms, alerting participants to initiate a saccade. In half of the trials this was a low tone of 200 Hz, instructing a leftward saccade. In the other half the tone was a high tone of

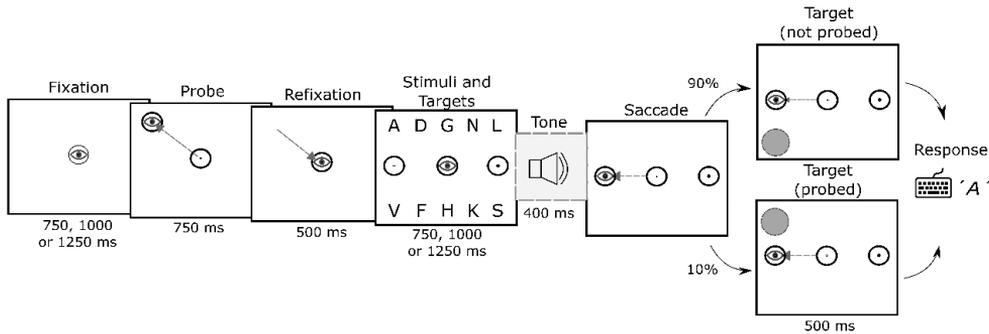


Figure 2. Sequence of events as they occurred in Experiment 1.

Dashed lines with arrows indicate eye-movement and the eye graphic indicates eye position. The tone played is either a high tone, indicating a saccade to the right, or a low tone, indicating a saccade to the left. The panels in the figure are presented in inverted contrast and are not drawn to scale.

1000 Hz, instructing a rightward saccade. When the saccade was completed, a period of 500 ms passed, after which a target probe briefly appeared at one of the 10 locations for 100 ms. The location of this probe will be referred to as the ‘answer location’. Participants then typed in their answer by keyboard. Responses were shown on screen and could be changed until participants confirmed their answer by pressing the Enter key or the Space bar. The subset of letters was chosen due to the location of the letters on the keyboard, which eased the difficulty of typing in the dark. To facilitate performance, participants received feedback on their performance at the end of every block of trials. To reduce fatigue in participants, at the end of every block of trials the participants had the opportunity to take a short break. We also gave the participants a ten-minute break outside of the lab when they were halfway through the experiment.

Combinations of onset location and answer location were counterbalanced per participant and appeared equally often, but in quasi-random order. Thus, there was a 10% chance that the answer location and the onset location were the same. Participants were informed that probes were equally likely to appear at any location. The location of the onset was therefore completely uninformative of the location of the answer. Right and leftward saccades were also counterbalanced with the combination of onset and answer locations. Lastly, the stimuli could not appear more than twice in succession at the same location. Locations of onset and answers were

re-randomized if an experiment was generated in which stimuli did appear more than twice at the same location in succession.

To determine whether IOR would be induced at the onset location, as expressed in prolonged reaction times, we performed a pilot study with a different set of participants. The same locations, timing and stimuli were used as in Experiment 1. One saccade was made to an onset location and subsequently back to fixation. After this, the stimulus array appeared with one target letter highlighted. The letter was highlighted using a grey circle (2° diameter). Participants were encouraged to type a letter as quickly as possible. A slowed response of 30.6 ms ($SD = 125.6$ ms) was observed for stimuli that were previously cued, $F(1, 11) = 5.09$, $p < 0.05$. We therefore concluded that IOR, in terms of prolonged reaction times, could be induced with the onset cues used in this paradigm.

Data analysis

Analyses and associated data are available online [114]. Trials were excluded on basis of any saccades missing their target by more than 2° or by participants not returning to the central fixation dot after fixating the onset position. Trials were also excluded based on saccade latency, using a recursive trimming procedure [115]. If a saccade latency deviated more than 2.5 SD from the participant's median latency it was excluded. Two participants were excluded from further analysis due to not meeting these criteria on more than 50% of their trials. Of the remaining participants 14.2% of the trials were excluded due to saccades not landing within 2° of a saccade target, either the cued location, saccade back to fixation or to saccade target. Another 7.5% of the trials were excluded on basis of saccade latencies.

Answer locations were collapsed vertically to analyze the effect of the location of the onset relative to the saccade direction. This collapsing was performed after tagging the trials as either onset and answer congruent or incongruent trials, to ensure that only the trials in which the participants fixated the exact same location as where the answer appeared were tagged as target congruent trials. By collapsing the positions of the answer in relation to the saccade target, two stimuli appearing on the same vertical axis were encoded as one answer location to a total of 5 answer locations. The locations were encoded relative to the saccade target: Location 1 being the two answer stimuli appearing above and below the saccade target, in equal steps up to Location 5 (the two stimuli furthest away from the saccade target). The performance is expressed as a proportion of correct answers.

Statistical analyses included a repeated measures analysis of variance and a generalized linear mixed (GLM) model. The repeated measures analysis of variance used the mean proportion of answers correct as dependent variable. Independent variables were location of the answer (five locations, from closest to saccade target to furthest from saccade target) and whether the location of the answer probe had been previously fixated (either true or false). A significance criterion of $\alpha = 0.05$ was used for these analyses, additionally effect sizes are reported as eta squared (η^2). Post-hoc tests consisted of Holm-Bonferroni corrected paired t-tests, Cohen's d is reported as a measure of effect size for post-hoc analyses.

The GLM analyses allowed us to examine the fit of the participant data to the model, as analyzing proportions per participant may be less informative for the small amount (10) of critical trials per participant in this experiment [116–118]. GLM models may be a stronger approach in examining participant variance than using proportions, as trial by trial data is not collapsed in a GLM model (like in more traditional statistics) but added as a random effect to the model. As a result, a GLM model is less sensitive to unbalanced data than a type 3 sum of squares analysis of variance [118,119]. The GLM model included correct answers per trial as dependent variable, with location of answer probe as a 2nd degree polynomial and answer probe appearing at previously fixated location as fixed effects. The 2nd degree polynomial was added as the response pattern in the task used typically shows a 'U' shape, where end-point locations are reported better than central locations [3]. A random intercept per participant was added to the model, to account for variance per observer. Significance of fixed effects were tested by a z test of which the p values are reported. Lastly, the model was compared to a null model, which excluded any interaction between fixed effects. A chi square test was used to test the two models against each other and Bayesian Information Criteria (BIC) were reported for both models.

As saccades are somewhat inaccurate [120,121] and foveated points thus differ between trials, we controlled for saccade landing and starting position. As it could be possible that these landing and starting position differ between trials, it could affect which information is acquired. To this end, we added the deviation from the perfect starting and landing position (with regards to the saccade that was cued by tone to a saccade target) as fixed effects to the GLM model to test their predictive qualities. Saccade latencies were similarly controlled for and investigated using a repeated measures analysis of variance.

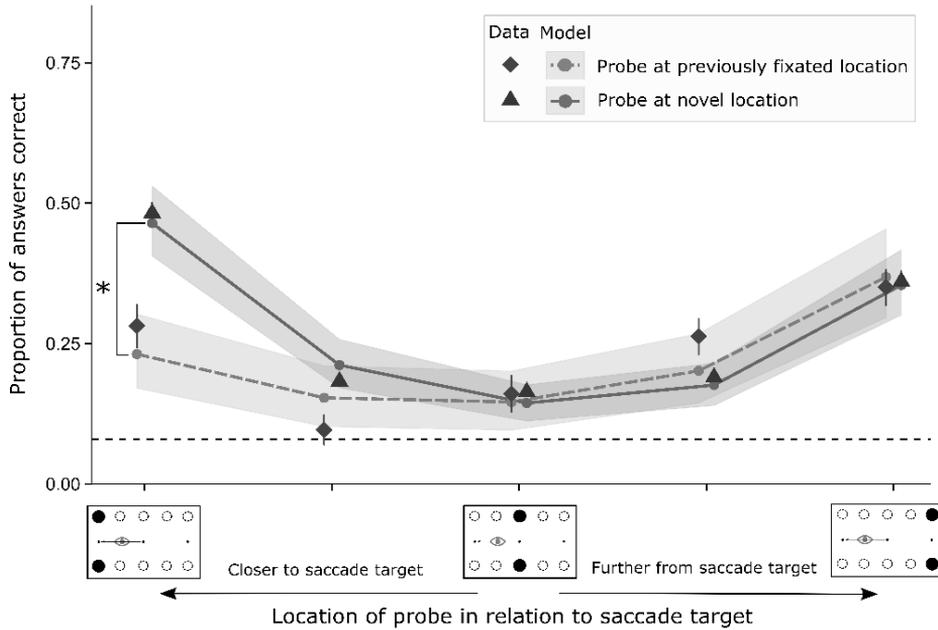


Figure 3. Generalized linear mixed model and mean data for mean proportion of answers correct in relation to saccade target between onset appearing at same location as the answer and onset not appearing at the same location as the answer. The shaded region represents the 95% confidence interval for the model, error bars around the ‘data’ points show standard error. The x axis shows an illustration of where the answer probe appeared. The dashed black line shows performance at chance level (0.08). In the figure the two conditions are horizontally offset as to not overlap visually.

Results

The main results are shown in Fig. 3. A main effect was found for answer location in relation to saccade target $F(4, 44) = 11.84, p < 0.01, \eta^2 = 0.29$. Post-hoc tests exploring the main effect for location show that participants were more accurate at the location closest to the saccade target (Location 1: $M = 0.49, SD = 0.50$) as compared to locations in the middle of the array: Location 2 ($M = 0.19, SD = 0.39$), Location 3 ($M = 0.17, SD = 0.38$) and Location 4 ($M = 0.21, SD = 0.41$), $p < 0.01, 0.67 < d \leq 0.72$. Participants were more accurate at the location furthest from the saccade target as compared to the locations in the middle of the stimulus array, $p < 0.05, 0.39 < d \leq 0.44$. Participants were more accurate at Location 1 (the location

closest to the saccade target) than at Location 5 (furthest from the saccade target, $M = 0.36$, $SD = 0.48$), $p < 0.01$, $d = 0.24$.

No main effect was found for onset location, $F(1, 11) = 1.93$, $p = 0.19$, $\eta^2 = 0.02$. An interaction effect was present for answer location and onset location $F(4, 44) = 6.14$, $p < 0.01$, $\eta^2 = 0.09$. Post-hoc tests compared the onset location with each answer location in relation to the saccade target. The interaction effect comparing performance for responses at Location 1 with the onset at the same location, and responses at Location 1 with onset at a different location was significant (difference in mean proportion = -0.21 , $p = 0.04$, $d = 0.40$). Comparisons for the other four locations (e.g. answer at location x, onset at exact same location or at a different location) were not statistically significant (ranging all p 's > 0.8 , $0.02 < d \leq 0.17$). The results suggest that only the information closest to the saccade target is less acquired by prior orienting to the onset. An additional post-hoc analysis shows that performance at Location 1 is significantly better than at Location 5 in trials where the onset and probe were presented at different locations, $p < 0.01$, Cohen's $d = 0.27$. In contrast, in trials in which the onset and the probe appeared at the same location there was no significant performance difference between Location 1 and Location 5, $p = 0.18$, $d = 0.12$. Therefore, participants only scored significantly higher at the location closest to the saccade target for trials in which the answer probe was not presented at a previously fixated location.

Data for individual participants is shown in Fig. 4. The figure shows individual scores for the relevant interaction effect we found, at the location closest to the saccade target. Results from a logistic regression suggests that half of the participants show significant reduction in their performance when onset and probe were presented at the same location, $p < 0.05$, as shown in Fig. 4. To further quantify the contribution of individual participants a GLM model was fit, the results are shown 'Model' points of Fig. 3. This model shows significance for the fixed effects: answer probe at same location as the onset, $z = 3.73$, $p < 0.01$, and probe location in relation to saccade target, $z = -7.89$, $p < 0.01$. The interaction effect between the two fixed factors were significant, $z = -2.51$, $p < 0.01$. We found that this model ($BIC = 5435$) significantly outperformed a null model ($BIC = 5910$) in which no interaction effects were present, $\chi^2 = 474.79$, $p < 0.01$. The results from this analysis converge with our previous results. Visually inspecting the mean data suggests that the model fits the data well. Analyzing the fit of this model per participant indicated that 6 out of 12 participants significantly fit the model (odds ratio > 1.2). Furthermore,

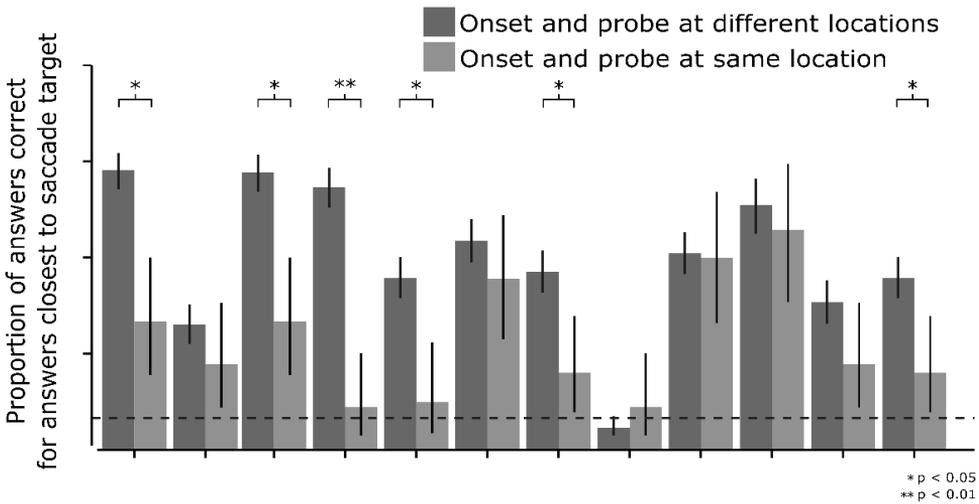


Figure 4. Mean proportion of answers correct per participant at the location closest to the saccade target. Each set of bars, separated by ticks at the bottom of the graph, represents one participant. Significant differences between the onset appearing at the location at the onset or a new location are indicated by asterisk for each participant. The dashed black line is performance at chance level (0.08).

investigating the fit of the participants for the location closest to the saccade target reveals that 7 out of 12 participants fit the model for this location (odds ratio > 1.2).

To examine the effect of saccade starting and landing positions on responses to the letters, we tested our previously constructed GLM model to a model that also included saccade starting and landing position as fixed effects. We found that the GLM model without saccade landing position or starting position ($BIC = 5435$), as used in the previous analysis, outperformed the models that included saccade landing ($BIC = 5890$) or saccade starting position ($BIC = 5880$). Thus, we conclude that the actual starting and landing position of the saccade to a cued saccade target did not affect the ability to report information near that saccade target.

To control for saccade latency, we analyzed the effect of onset location on saccade onset. As IOR may affect saccade latency [122,123] it was crucial to exclude a possible interaction between delayed saccades towards a location associated with IOR. No indication of an effect was found for onset location on saccade latency, $F(4, 44) = 0.54, p = 0.48, \eta^2 < 0.01$. To follow-up on our findings, we investigated whether the reduction of accuracy, when answers and onset appeared near the saccade target, would also mean that less elements were retained overall. Our results imply that,

when the onset appeared near the saccade target, a reduction of accuracy can be observed for elements that appear at the same location as the onset. Thus, we recoded the onset position, and assumed that this loss of information was always present when the onset appeared near the saccade target. This assumption had to be made due to restrictions in our data set, as only one answer/onset location combination was reported per trial.

The onset position was recoded to be either near the saccade target (onset appeared at Location 1) or away from it (onset appeared at Locations 2 to 5). This allowed us to examine whether Locations 2 through 5 received an increase in accuracy from the onset appearing near the saccade target. To analyze the effect of the recoded onset position on accuracy we used a 2x5 repeated measures analysis of variance as before. We entered two factors into the analysis: the recoded onset location (2 levels: onset at Location 1 or onset at Location 2 through 5) and location of answer probe (Locations 1 through 5). As before, the analysis showed a main effect for location $F(4,44) = 12.41, p < 0.01, \eta^2 = 0.38$. No main effect was observed for the recoded onset probe locations, $F(1,11) = 1.03, p = 0.33, \eta^2 < 0.01$. Lastly, no interaction effect was identified between the recoded onset probe locations and the answer locations, $F(4,44) = 0.47, p = 0.90, \eta^2 = 0.01$ suggesting that no difference was observed when onset appeared at the location closest to the saccade target or further away from it in terms of overall accuracy for information at Locations 2 to 5. Therefore, locations further from the saccade target received no compensation in information acquisition from the reduction of information acquisition after the onset appeared near the saccade target.

Discussion

In this experiment we studied the association between IOR and transsaccadic memory using an adapted transsaccadic memory paradigm previously used by Irwin & Andrews [19]. We hypothesized that IOR would interact with transsaccadic memory by reducing the information acquisition at a previously fixated location. Our results indicate an interaction between IOR and transsaccadic memory: we found a reduction of correct answers for elements associated with IOR compared to elements that were not associated with IOR. This effect was only present for the elements at the closest proximity to the saccade target and was not present for elements further from the saccade target. This indicates that processes prior to the execution of the saccade were affected by IOR which resulted in a reduction of accuracy for elements near a saccade target.

In the current experiment IOR only affected transsaccadic memory for elements close to a saccade target. To explore how this interaction affects the overall memory capacity of transsaccadic memory we recoded our data relative to the location where the onset appeared. In this manner, we could investigate whether the less accurately reported information, that was previously fixated, was compensated for by higher accuracy for items that were not previously fixated. Our results show that no benefit was observed for the other locations when the information near the saccade target was previously cued and thus less correctly reported. These results suggest that the reduction of accuracy, when the onset and stimuli both appeared at the same location close to the saccade target, did not relocate attentional resources to other locations.

IOR has been associated with increases in saccade latency when making a saccade to a previously cued location [123]. For this reason, we wanted to examine the possibility that our results could be explained through differences in saccade latencies. IOR being associated with a location within the stimulus array did not cause delays in saccade execution to the saccade targets and does therefore not add any explanatory value to our results. Similarly, we investigated whether information acquisition in the paradigm used was influenced by saccade landing and starting position. We found no such effect, which is in line with the studies indicating that the presaccadic shift of attention moves to the intended location of an eye-movement, rather than the actual landing position [4,18].

We note that in the previous implementations of the paradigm [3,19,20] the stimuli to be attended to via the presaccadic shift of attention were located in closer proximity than in our current study. Although the distance between the saccade target and the stimuli were increased (from a maximum of 2.2° in the original paradigm to 3.0° in the current paradigm) we found a pattern of results that matched the results found previously (i.e. information near saccade end-points is better reported when blanked during saccadic suppression). This effect is not entirely unexpected, as early research has shown that task demands may dictate the size of the attentional focus [124]. Thus, we have shown that the presaccadic shift of attention can at least have an asymmetric spread of 3.0° with the task described in our current study.

In this paradigm, overall target discrimination was best at the location closest to the saccade target. This effect has been previously observed and attributed to the presaccadic shift of attention in the study by Irwin & Andrews [19]. However, the proportion of correct answers on the location furthest away from the saccade target was also better than for stimuli that appeared in the middle of the stimulus

array. We suggest that these results might have been due to the design of the paradigm. To reiterate, in the current study the stimulus array was shown after making a saccade to a cued location. The stimulus array and saccade targets were then visible until a saccade was executed to a saccade target. These saccades were cued with a tone that had a mean onset of 1000 ms after stimulus presentation. The participants may have been preemptively attending both saccade targets before the onset of the tone, as the saccade targets were relevant to perform the task correctly. This form of attending in preparation of the tone would explain the increase in performance at locations furthest from saccade target as compared to stimuli that appeared in the middle of the array. Our results show that overall performance was significantly higher at the location closest to the saccade target when compared to the location furthest from the saccade target. This result indicates a possible added benefit for memory acquisition when executing a saccade. Interestingly, no effect was present for target discrimination when onset and answer appeared furthest from the saccade target and at the same location. Therefore, we postulate that IOR may affect attentional processes linked to the saccade, such as the presaccadic shift of attention, by disrupting the benefit in information acquisition of executing a saccade to the saccade target.

However, our model of the effect may be supported by the similar properties between the presaccadic shift of attention and exogenously captured attention. IOR has been associated with exogenous cueing [108], which directs attention automatically. Similarly, the presaccadic shift of attention is drawn involuntarily to a saccade location. The area that the presaccadic shift of attention is directed to has a range that is bigger than the target itself [3,4,19]. Through this, the participants were better able to report information not only at the saccade target, but also near a saccade target. The increased performance for stimuli near the saccade target suggests that the location that was cued and subsequently associated with IOR also falls within this range of attention. Research has shown that the size and shape of the attentional window can be modulated and can contain fields in which information is unattended [124,125]. This leads us to postulate that information acquisition in transsaccadic memory may be affected by IOR through inhibition of the presaccadic shift of attention. We do note that IOR is an effect which may be disentangled in a motor and attentional component [126,127]. In the current study IOR was induced by the participants executing a saccade to a probe, rather than through attentional orienting alone. Although our current design would most likely elicit both attentional

and oculomotor IOR, at current, it is possible that the effect found may be specific to IOR induced by executing a saccade to a location.

Lastly, it should be noted that we base our conclusions on a relative effect. First, we observed an increase in performance near the saccade target relative to the performance furthest from the saccade target, which may be attributed to presaccadic attentional processes. Second, we observed an *absence* of this increase when IOR was induced near the saccade target, affecting the initial presaccadic shift of attention. To verify the validity of our conclusions, we wanted to ensure that the observed increase in performance near the saccade targets was not due to confounding factors. As noted by Irwin and Gordon [3] performance is generally increased for targets at the end positions in this task and in linear arrays in general. Irwin and Gordon argue that this advantage is due to less visual crowding, since the stimuli at the endpoints have only one stimulus besides them. As we wanted to control for this possibility, a follow-up experiment was performed to examine the effects of flanking stimuli on the observed increase in performance near the saccade target. Our results, thus far, indicate that stimuli that are in the middle of the stimulus array are less accurately reported and may therefore be less attended to, due to not receiving a presaccadic attentional benefit. We propose that flanker stimuli will not receive this presaccadic benefit in a similar manner and therefore not interfere with performance in this paradigm. However, visual crowding has been linked to reducing the ability to identify stimuli [128], and adding more stimuli to the array would reduce the accuracy for the elements at the end positions. To test for this possibility, we added four flanker stimuli next to the end positions in the stimulus array.

Experiment 2

Method

Participants and procedure

The procedure for the second experiment was identical to Experiment 1 except for the following details. The study consisted of 12 participants from the Utrecht University community (11 female) aged 18 to 25, $M = 21.8$, that completed

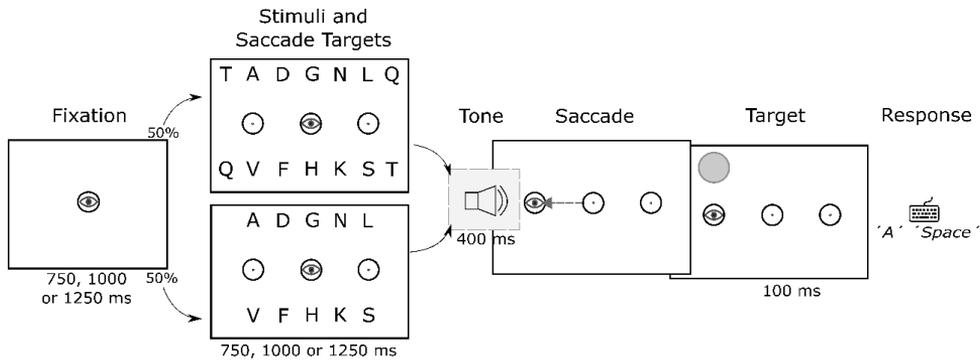


Figure 5. Sequence of events as they appeared in Experiment 2. Dashed lines with arrows indicate eye-movement and the eye graphic indicates eye position. The top panel, second from the left shows an example trial with crowding stimuli. The figure is presented in inverted contrast and is not drawn to scale.

120 trials in one 30-minute session. We chose this amount of trials for Experiment 2 to closely match the amount of critical trials in Experiment 1. All participants reported normal or corrected-to-normal vision.

The procedure used for the experiment is shown in Fig. 5. The main difference is that we only included a crowding condition, where half of the trials four additional stimuli appeared next to the end point stimuli. In the remaining half of the trials the four additional stimuli did not appear. The crowding stimuli were either the letter ‘T’, or the letter ‘Q’. We opted for these crowding stimuli as they are highly similar to the target stimuli (a necessity for crowding to occur) [128–130]. With respect to Experiment 1, the onset stimulus has been removed and thereby the IOR condition. Timing for the experiment remained unchanged as compared to Experiment 1.

Data analysis

Trials were excluded on basis of the saccade missing its target by more than 2° or saccade latencies greater than 2.5 standard deviations from the median saccade latency. By these criteria 10.8% of the trials were excluded. Like Experiment 1, statistical analyses included a GLM model and a repeated measures analysis of variance. The fixed factors in the GLM model were location (5 levels, from closest to saccade target to furthest) and whether the trial contained crowding stimuli or not

(2 levels). A random effect was added for participant. For analyses between locations we used Holm-Bonferroni corrected paired t-tests.

Results

We investigated the effects that crowding stimuli have on the linear array used in Experiment 1. To this end, we added stimuli next to the end point positions of the linear array in half of the trials and compared these with performance on trials without the extra stimuli. The results are shown in Fig. 6. First, results for the GLM show a main effect for the location of answer probe, $z = 1.99$, $p = 0.04$. A repeated measures analysis confirmed this result, $F(1,11) = 11.69$, $p < 0.01$, $\eta^2 = 0.08$. Post-hoc paired t-tests show that proportion of letters correct is higher at the location closest to the saccade target (Location 1, $M = 0.51$, $SD = 0.50$) as compared to locations further from the saccade target (Locations 2 through 4, $M = 0.24$, $SD = 0.43$) with $p < 0.01$, $d = 0.58$. Moreover, performance at the location furthest from the saccade target was significantly higher ($M = 0.42$, $SD = 0.50$) than at the center locations, $p = 0.01$, $d = 0.39$. Performance at the location closest to the saccade target was significantly better than at the location furthest from the saccade target (Location 5), $p = 0.03$, $d = 0.18$. No main effect was present for presence of the crowding stimuli, $z = -0.12$, $p = 0.89$ and no interaction effect was present for location of answer probe and presence of crowding stimuli, $z = -0.20$, $p = 0.84$. A repeated measures analysis of variance confirmed these results: no significant effect of crowding stimuli, $F(1,11) = 0.02$, $p = 0.89$, $\eta^2 < 0.01$, and no evidence for an interaction effect between presence of crowding stimuli and location of answer, $F(1,11) = 0.03$, $p = 0.87$, $\eta^2 < 0.01$.

To provide further evidence that the added crowding stimuli did not interfere with performance on the task we performed a Bayesian t-test. We choose a Bayesian approach since it allowed us to further examine whether the null hypothesis, i.e. crowding does not affect accuracy on the transsaccadic memory paradigm, was rightly rejected or that our test was inconclusive [131]. This distinction cannot be made by using p values. To quantify this concept: if the Bayes factor is less than 0.33 it indicates evidence for the null hypothesis and there is evidence to support the alternative hypothesis when the Bayes factor is greater than 3. Conversely, if the Bayes factor is between 0.33 and 3 it indicates a lack of sensitivity and neither the null hypothesis or the alternative hypothesis is supported. We conservatively modeled the prior distribution as a uniform distribution with a lower bound of 0 (no correct answers) and an upper bound of 1 (all answers correct). This analysis

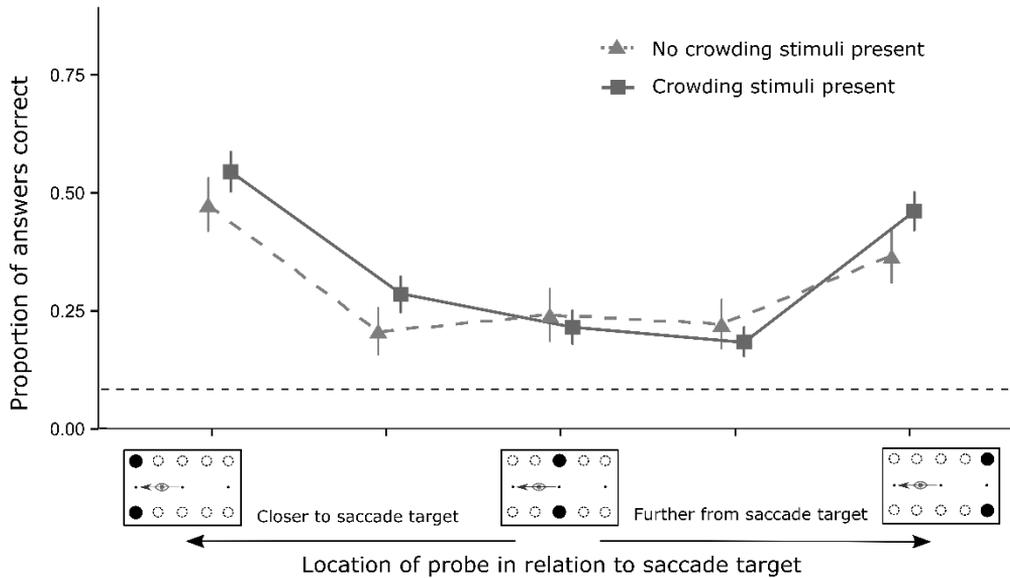


Figure 6. Mean proportion correct answers for locations in relation to saccade target between crowding stimuli and no crowding stimuli. Error bars show standard error. The dashed black line shows performance at chance level (0.08). In the figure the two conditions are horizontally offset as to not overlap visually.

indicated significant support for the null hypothesis, $BF_{10} = 0.08$. We conclude that the crowding stimuli did not affect the performance on the transsaccadic memory task.

Discussion

We added crowding stimuli to the paradigm described in Experiment 1 to assess the influence that endpoint advantages have on correctly reporting the stimuli near saccade targets. Our conclusions in Experiment 1 could have been confounded by the finding that the end point stimuli have an advantage over the center stimuli due to a lack of visual crowding. Our results for Experiment 2 indicate that endpoint advantages, due to a lack of crowding, did not influence performance. To elucidate these results: in both Experiment 1 and Experiment 2 a main effect for location was found, where elements in nearest proximity to the saccade targets were reported more accurately than elements further from the saccade target. These results are in line

with the findings in the original experiment by Irwin and Andrews [19]. The stimuli that are further away from the saccade target are not reported as accurately. The flanker stimuli appeared at a similar distance from the saccade target as the stimuli that were further from the saccade target. We suggest that crowding stimuli were not selected by the presaccadic shift of attention in a similar manner as the less accurately reported stimuli in the middle of the stimulus array. Thus, the crowding stimuli would not compete with the stimuli closest to the saccade target for storage in transsaccadic memory and thereby not elucidate effects of performance on the transsaccadic memory task.

General discussion

In this study we investigated how IOR affects information acquisition into transsaccadic memory. To this end, we used a transsaccadic memory paradigm previously used by Irwin & Gordon [3], with an added exogenous cue to which an additional saccade was made. In both our experiment and the original paradigm, it was found that information that is presented near a saccade target is reported more accurately, due to the presaccadic shift of attention. The presaccadic shift of attention has been described as an effect that facilitates information acquisition, whereas IOR is a negative attentional effect, increasing reaction times and reducing target discrimination. Our main finding was that IOR near a saccade target reduces accuracy for stimuli at that same location. This implies that previously fixated elements were less accurately acquired by transsaccadic memory, and thus reduced the participants ability to report this information. We did not observe a reduced performance for previously fixated stimuli that were positioned further from the saccade target. These results implicate that the attentional benefit provided by the presaccadic shift of attention can be reduced by the negative attentional effect of IOR.

As we can only observe a relative effect in the current study, we examined the validity of our conclusions by investigating possible confounding factors. Linear stimulus arrays, as the one used here, have been associated with endpoint advantages [3]. Thus, we needed to exclude the possibility that the increased performance for stimuli at the endpoint positions in Experiment 1 was not due to a lack of visual crowding. In Experiment 2, we investigated the effects of crowding stimuli on the linear stimulus array used in Experiment 1, by using crowding stimuli which were like the experimental stimuli. We found that the linear array was not affected by visual crowding. The results indicate that the increased performance at the endpoint

positions in Experiment 1 were not due endpoint advantages. Thus, even though the effect we observed in Experiment 1 is relative, it seems unaffected by the lack of crowding for the elements near the saccade targets. However, the effect we have observed in Experiment 1 was found by inducing IOR through instructing the participants to execute a saccade to a probe and refixating the center stimulus. We cannot disentangle the oculomotor and attentional component of IOR in our current series of experiments. Yet, we hypothesize this effect to be most strongly present in the design as described in Experiment 1, as the effects of IOR may be reduced in the absence of saccadic eye-movements [126].

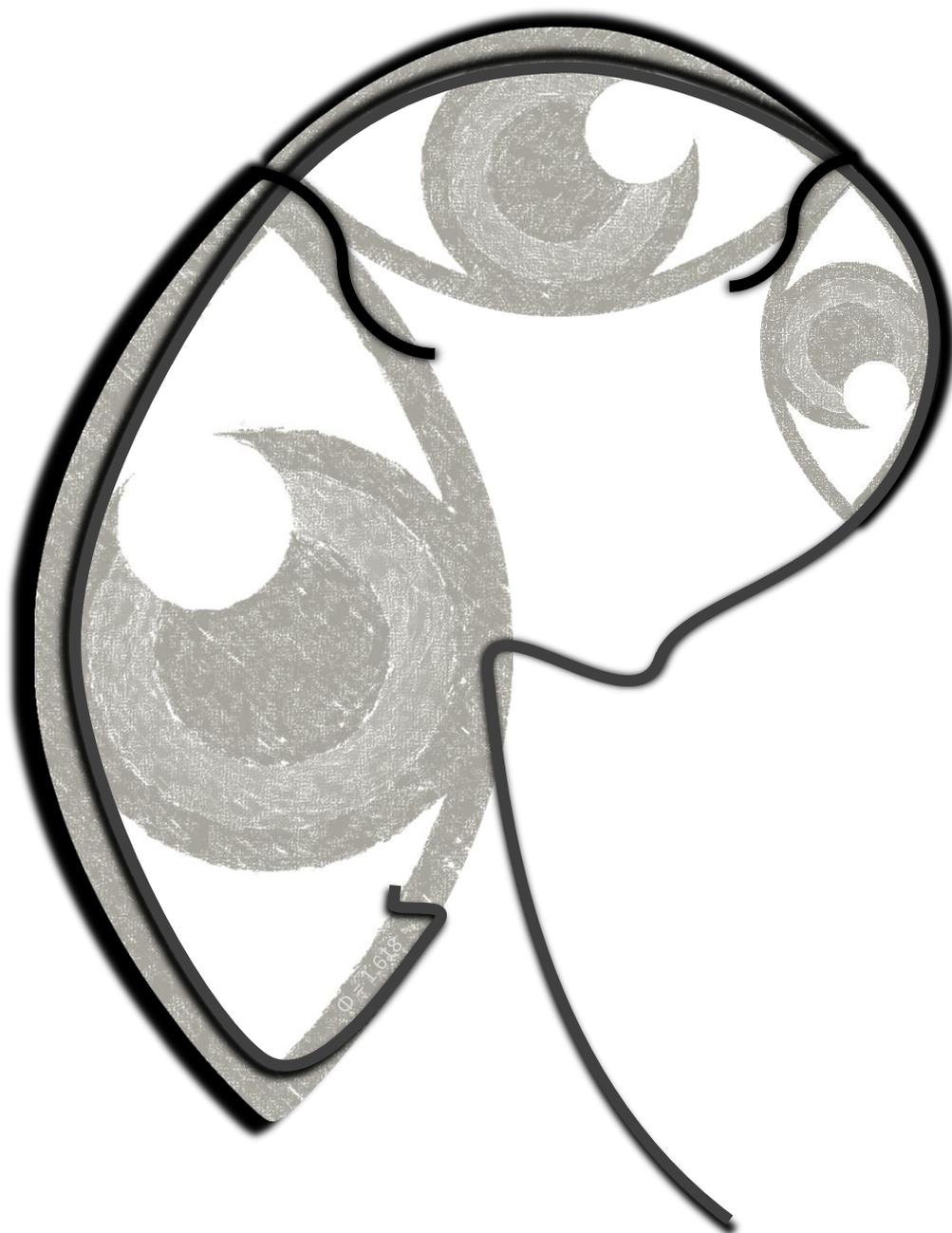
Previous research shows that a limited amount of objects are stored in transsaccadic memory [3,21,52,132]. Thus, we analyzed whether the reduction of accuracy when a location near a saccade target is associated with IOR influences the total amount of elements stored in transsaccadic memory. To this end, we recoded the data relative to the onset position. Our results show that when the elements near a saccade target are less accurately reported, other elements remain unaffected and are reported as accurately as otherwise. This implicates that lessened information acquisition, near a saccade target, is not compensated for by increased performance at other locations. This suggests that IOR does not only modulate the accuracy of information acquisition but may reduce the number of elements that are acquired between saccades.

The nature of transsaccadic memory has been a point of discussion since it was named. Similarities between visual working memory (VWM) and transsaccadic memory have been noted since the term has arisen [20]. VWM is the memory storage where a small amount of visual information is held for a limited time [133,134]. Transsaccadic memory is described to exclusively stores this visual information between saccades [11,19]. Research has shown that transsaccadic memory carries many similarities to VWM, such as the limited amount of objects retained and information being selected by similar attentional processes [9]. As such, transsaccadic memory may be a subsystem of VWM [23]. Importantly, previous studies have linked VWM and IOR closely together. Both VWM and IOR are thought to be used in visual search tasks, as to respectively remember the locations of previous fixations and to inhibit revisiting previously attended locations [110,135,136]. Although our study does not necessarily support the notion that VWM and transsaccadic memory may consist of the same system, our study adds that previously fixated locations within the field of the presaccadic shift of attention

are affected in terms of information acquisition, which may implicate both VWM and transsaccadic memory.

To summarize, this study provides evidence that IOR and transsaccadic memory are functionally linked. Our results are in line with the notion that IOR prioritizes information presented at uninspected locations [109], and adds that there is less benefit from the attentional processes that are closely linked to execution of saccades at locations associated with IOR. The reduction of preferential processing is not compensated for by increased performance at other locations in the visual field and thus results in lessened acquisition of information.







Chapter 4

Object files across eye-movements: Previous fixations affect the latency of corrective saccades.

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Author contributions

MJS, JHF, NvdS, & SvdS conceptualized and designed the experiment. MJS programmed the experiment, collected the data and performed the analyses. MJS wrote the manuscript, and JHF, NvdS, and SvdS commented on and co-authored the manuscript. SvdS funded the research.

Summary

One of the factors contributing to a seamless visual experience is object correspondence, i.e. the integration of pre- and postsaccadic visual object information into one representation. Previous research suggests that before the execution of a saccade, a target object is loaded into visual working memory and subsequently used to locate the target object after the saccade. Until now, studies on object correspondence have not taken previous fixations into account. In the current study, we investigated the influence of previously fixated information on object correspondence. To this end, we adapted a gaze correction paradigm in which a saccade was executed towards either a previously fixated target or a novel target. During the saccade the stimuli were displaced such that the participant's gaze landed in between the target stimulus and a distractor. Participants then executed a corrective saccade to the target. The results indicate that corrective saccades have lower latencies towards previously fixated targets than to non-fixated targets, indicating object-specific facilitation. In two follow-up experiments we show that presaccadic spatial and object (surface feature) information can contribute separately to the execution of a corrective saccade as well as in conjunction. Whereas the execution of a corrective saccade to a previously fixated target object at a previously fixated location is slowed down (i.e., inhibition of return), corrective saccades towards either a previously fixated target object or a previously fixated location are facilitated. We conclude that corrective saccades are executed based on object files rather than unintegrated feature information.

Introduction

The human visual system does not build a complete representation of our environment, but retains a limited amount of information between eye-movements [8,19,137]. This information is stored in transsaccadic memory, which is thought to be (at least partially) dependent on visual working memory (VWM) [20,23,27,138]. However, due to the limited amount of information that can be stored in this memory, selecting relevant information is crucial [13,21,52]. Voluntary and involuntary orienting of attention guide this selection process [139]. Interestingly, visual attention is involuntarily shifted to the location of an intended saccade target just before saccade initiation [3,11,18,107]. The presaccadic acquisition of information may be a crucial factor in enabling visual stability (i.e., the sense of a continuous visual world across saccades) [140]. Identifying pre- and postsaccadic information and attributing this information to a specific object facilitates object correspondence across saccades [23].

Saccades are somewhat imprecise, therefore presaccadic acquisition of object information may be particularly useful to be able to distinguish retinal displacement from object displacement after a saccade. It has been hypothesized that some form of visual search, guided by the surface features in VWM, is used to detect the intended saccade target after the execution of a saccade [23,24,140]. When the intended target is detected, a corrective saccade can be executed to properly foveate the target. To investigate corrective saccades, Hollingworth et al. [5] designed a gaze-correction paradigm. In this paradigm, participants made a saccade toward one of twelve colored disks. During a saccade, the array of disks rotated in such a way that participants had to execute a second (corrective) saccade to land on the target. This corrective saccade process is most likely enabled by the observer presaccadically acquiring the saccade target into memory. The initial saccade target can then be relocated after a displacement of visual information. In a study using the same corrective saccade paradigm, participants were tasked to remember unrelated color information for a memory task in addition to performing a gaze correction task [27]. In the dual-task experiment, it was observed that, when the color information in VWM was conflicting with the color of the saccade target, the participants made more erroneous corrective saccades and corrective saccades with longer latencies. Based on these results, the authors concluded that gaze correction targets are acquired into VWM and are therefore in competition with other VWM content. These results indicate that features relevant to corrective saccade are indeed stored

in VWM and can bias corrective saccade execution. It is currently unknown, however, in what manner previous *attentional* orienting (selection) may affect corrective saccades.

Visual attention shares neural substrates with VWM [141] and is thought to underlie the binding of visual features into object representations in VWM [88,142,143]. Therefore, visual attention allows for retrieval of stored object representations. Currently, it is unclear how previous deployment of attention could affect corrective saccade latency. Previous fixations have been shown to significantly alter saccade latency in visual search tasks. We hypothesized that if a corrective saccade is preceded by a VWM visual search task, that previously attended objects and locations (through fixation) would affect the latency of corrective saccades. For instance, when searching for a particular target, previously fixated objects and locations are typically less likely to be re-fixated than novel objects and locations [144,145]. Based on previous literature, there are two possible influences of previous fixations on corrective saccade latency.

First, corrective saccades towards a previously fixated target could be executed slower because of inhibition of return (IOR [136]). IOR is the slowed response (after approximately 200 milliseconds) to previously exogenously attended stimuli [108] and is present for both saccadic and manual responses [111]. These effects are tied to objects (instead of retinal coordinates) as illustrated by IOR effects at the location of moving objects [146–148]. In dynamic stimulus displays an ‘object’ is defined by previously fixated surface features, such as color or shape, at an updated spatial position. This definition of an object would also be applicable for corrective saccades in the paradigm described by Hollingworth and colleagues [23]. Furthermore, IOR may slow down decision making in discrimination tasks [149,150], which could express itself as slowed target acquisition in a gaze correction task.

A second mechanism affecting corrective saccade latencies through previous fixation may be priming effects, in which participants are *faster* to respond (saccadically or manually) to previously attended information [151–153]. A facilitation of response times to presaccadically acquired information has been observed previously [153]. In prior experiments, facilitation in response to presaccadically attended stimuli were present even when the object had shifted location during the saccade [153]. Possibly, the results might generalize to the latencies in corrective saccades as well. In the study by Henderson and Anes [153] participants used presaccadically acquired information in a passive manner as the

presaccadically acquired information was not explicitly relevant to the manual response task. This contrasts the gaze correction paradigm used by Hollingworth and colleagues [5] in which the presaccadically acquired information is necessary to perform the corrective saccade. Moreover, it has been observed that a target letter is more quickly identified when a similar object (such as another letter) has been previously fixated [154], indicating that priming effects may carry over between objects if they belong to the same category.

The aim of the current experiment is to examine in what manner corrective saccades to previously fixated objects differ from corrective saccades to non-fixated objects. We expect corrective saccades to a previously fixated target to either be facilitated through object-specific priming or to be inhibited through IOR. To this end we adapted the gaze correction paradigm previously described by Hollingworth and colleague [5], with the addition that participants had fixated one stimulus in the display prior to executing the gaze correction task. In short, an eye-movement to one of six objects was executed before the actual gaze correction task was performed. After refixation, the participant was cued to reorient to the same object or to a different object. During this eye-movement, the array rotated, and the participant executed a corrective saccade to the object's updated position.

Experiment 1

Method

Participants

Twelve participants, of which ten female, aged 19 to 32 ($M = 22.5$) from the Utrecht University community participated for a monetary compensation of €6,- per hour. All participants reported normal or corrected-to-normal vision and were naïve as to the purpose of the study. Written informed consent was obtained from all participants. The study was reviewed and approved by the Faculty Research Ethics Committee (FETC) of the University of Utrecht.

Stimuli and Apparatus

In this experiment, six randomly colored circles with a diameter of 1.6° were used as stimuli. The colors were drawn from a subset of red (12.4 cd/m^2), green (18.9 cd/m^2), blue (10.9 cd/m^2), and magenta (13.6 cd/m^2). The limitation in this selection was that no circle could be the same color as one of its neighboring circles. The stimuli were presented on a black background (0.34 cd/m^2). The six colored discs

were equidistantly positioned along the circumference of a circle (radius of 4.5°) around a central fixation dot. One circle was cued by expanding its size to 2.1° . A fixation dot (0.6° in diameter, 4.5 cd/m^2) with a centrally located single black pixel was used as fixation target and remained on screen throughout the experiment. During each trial, the entire stimulus array rotated by $\pi / 6$ radians (i.e. 30 degrees: half of the distance between the stimuli) clockwise or counter-clockwise. The rotation event was triggered by gaze positions (see *Procedure*). At the end of a trial, an outline of a box (2.0° by 2.0°) was drawn around the target stimulus to signal the end of a trial.

The experiment took place in a darkened room. Stimuli were presented on an LG 24MB65PM LCD monitor with a spatial resolution of 1280×800 pixels and a refresh rate of 75 Hz. The size of the screen was 50.8 cm by 33.9 cm. Participants were seated 70 cm from the monitor with their heads resting on a desk-mounted chin- and headrest. Eye-movement data was collected using an EyeLink 1000 (SR Research Ltd., Canada) sampling the left eye at 1000 Hz. Saccades were detected offline with the default-values of the EyeLink algorithm for saccade detection.

The experiment was programmed in Python 2.7 using the Pygaze library to connect to the eye tracker and to define areas of interest [60]. Eye tracker data files were analyzed with Python 2.7 and statistical analyses were performed using R 3.1.3 [61].

Procedure

Participants performed 460 trials, evenly divided across 10 blocks. The eye tracker was calibrated using a standard 9-point calibration procedure prior to starting the experiment. Every trial started with a drift check, which was initiated by the participant by pressing the space bar. The eye tracker was recalibrated whenever the drift was greater than 1.0° . Preceding the experiment, 15 practice trials were performed, which were identical to the experimental trials (see below for a description). Practice trials consisted of 5 control trials (no rotation during saccade) and 10 experimental trials, in which target locations were randomly chosen.

The procedure for the experiment is shown in Fig. 1. After the drift check, a fixation dot (which remained on screen throughout the experiment) was presented for 200 milliseconds. Six colored circles were then displayed in an equidistant circular pattern surrounding the fixation point. To eliminate location-specific effects carrying over between trials random orientation offsets (between 1.0 and 35.0 degrees) were added to the rotation of the entire array. This orientation offset caused

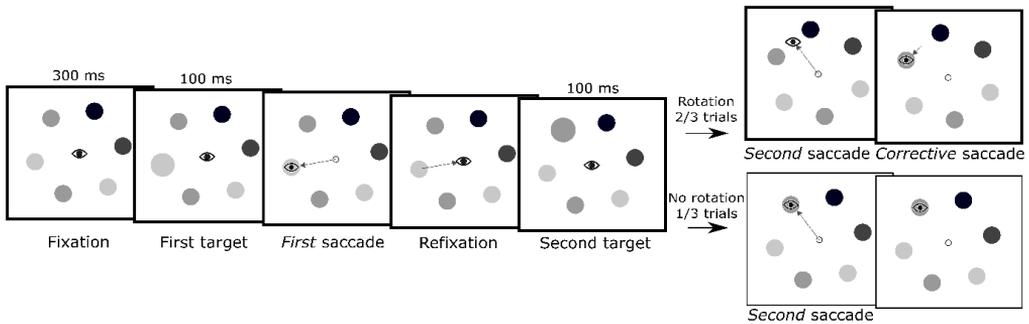


Figure 1. A schematic representation of the procedure used in Experiment 1. The eye icon indicates gaze position and the dashed lines indicate saccades. The procedure for the trials in which the array rotated during the second saccade (experimental trials) is outlined in bold. Note that the background and fixation stimulus were presented with a contrast opposite to that depicted here, as well as that the stimuli were different in color in the experiment.

stimuli to never appear at the exact same location between subsequent trials. One of the six circles was randomly selected as a saccade target and visually expanded in size for 100 milliseconds and was subsequently restored to its original size. This object will be referred to as the *first target*. The participant then initiated, as quickly as possible, a saccade to this first target. After fixating the target, gaze was returned to the fixation point. A new randomly chosen colored circle (*second target*) then expanded for 100 milliseconds after which it returned to its original size. The participant executed a saccade to this second target. When the participant's gaze left a 0.4° area of interest surrounding the fixation point, the array of colored circles rotated either clockwise or counter-clockwise by 30 degrees. Hence, the rotation was such that the participant's gaze would land in between two colored circles, the previously cued circle (the target) and a non-cued circle (a distractor). After a delay of 200 ms after saccade offset a green box (2.0° by 2.0° , line width 1 pixel) was drawn around the target, signaling the end of a trials and providing feedback on target identity. Taking the refresh rate of the monitor and other delays (e.g., monitor response time) into account we retrospectively determined that the maximum onset of the rotation event was 28 milliseconds with respect to saccade offset.

Rotations occurred on two thirds of the trials, with no rotations in the remaining one third of the trials, which prevented participants from making anticipatory corrective saccades. Clock-wise rotation and counter clock-wise rotation were counterbalanced over the remaining trials and target locations.

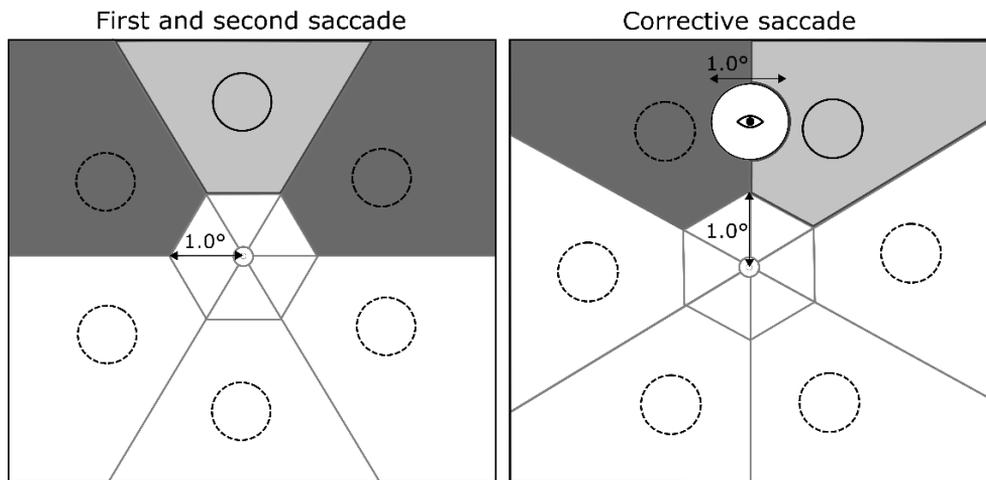


Figure 2. The different regions of interest (ROI) for the exclusion of saccades for an example trial. The left panel shows the saccade exclusion for the first and second saccade. The right panel shows saccade exclusion for the gaze correction saccade. The eye icon in the right panel indicates initial gaze position. The circles with dashed outlines represent distractor stimuli and the circle with a black outline represents the target. The darker shaded area represents the distractor ROI and the light area the target ROI. A trial was excluded if no samples were present in the lighter shaded area or samples were present in the darker shaded area.

Combinations of first and second saccade target were counterbalanced and appeared equally often, in quasi-random order, between participants. Given these constraints the first target and second target were the same circle in one out of six trials.

Data analysis

Trials were excluded based on saccade latency and landing position. Saccade latency for the first and second target was defined by the difference between the onset of each target cue and the following saccade onset. Saccades towards the first and second target were excluded when the latency was higher than 1500 ms (2.1% of trials). Different regions of interest were used to assess whether the saccade to the first or second target was executed appropriately (see Fig. 2). The stimulus array was divided into a hexagon starting at 1° from fixation. The inner area of the hexagon (up to 1° outwards) was designated as a neutral area. If a participant's gaze left this area and a sample was detected in the area of interest surrounding the distractor (Fig. 2, left panel) the trial was excluded (3.2% of trials). Similarly, if no samples were

detected in the area of interest around the target the trial was excluded (0.1% of trials). For the corrective saccade a circular area around the landing position of the *second* saccade (1° diameter) was defined as a neutral area (Fig. 2, right panel). The trial was excluded if the neutral area overlapped with one of the stimuli locations or if the gaze position entered the area of interest around the distractor (5.1% of trials). We chose to exclude the saccades towards distractors because these trials were very infrequent and unsuited for statistical analyses.

Median saccade latencies for three saccades per trial per participant (saccade to first target, second target and gaze correction) were calculated. Only trials in which a rotation occurred during the saccade to the second target were analyzed. Statistical analyses included paired t-tests comparing saccade latencies between condition in which the same stimulus was cued twice, or two different stimuli were cued. Effect sizes are reported as eta squared (η^2). The gaze correction saccade latency was calculated with regards to the offset of the prior saccade as indicated by the saccade detection algorithm. For visualization purposes, grand mean data was plotted with 95% within subject confidence intervals [155,156]. Furthermore, for the corrective saccades we show the data per subject centered around the grand mean and the slope for each individual [156].

Results

In our analyses we examined two saccades: the saccade to the second cued target (second saccade), and the subsequent corrective saccade that was executed if the array had rotated during the second saccade. We first analyzed the saccade latency of the second saccade in two conditions: when the saccade was executed to a previously non-fixated circle, or a previously fixated circle. We expected saccades to a previously fixated object to be affected by IOR and thus executed slower. The latency of the second saccade was significantly higher when a saccade was executed to a previously fixated object ($M = 269.7$ ms, $SD = 26.7$ ms) as compared to saccades to a non-fixated object ($M = 219.4$ ms, $SD = 23.4$ ms), $t(11) = 5.62$, $p < 0.01$, $\eta^2 = 0.41$ (see Fig. 3, left panel). Next, corrective saccades to an object that was previously fixated, but shifted during a saccade, were executed faster ($M = 229.3$ ms, $SD = 26.8$ ms) than corrective saccades to a non-previously fixated object ($M = 238.9$ ms, $SD = 25.2$ ms), $t(11) = -2.64$, $p = 0.02$, $\eta^2 = 0.04$. A visualization of the within-subject effects is shown in the right panel of Fig. 3, which indicates that nine

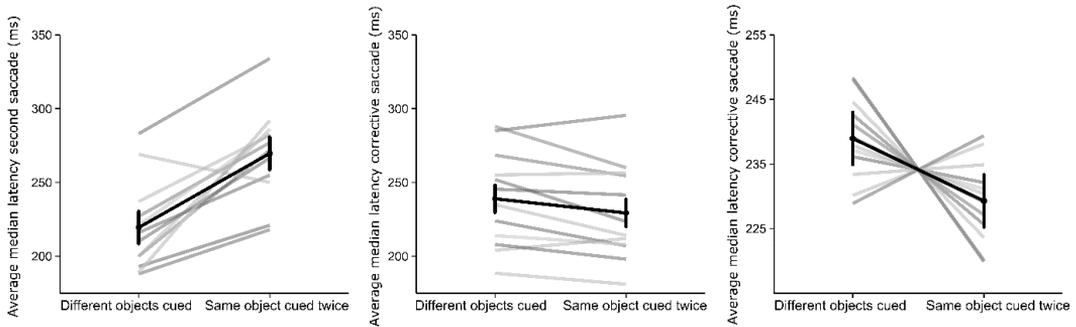


Figure 3. The average of the median saccade latency for saccades to objects that were previously fixated or not. The bold black line shows the group average, with 95% confidence intervals (in the left and middle panel) and within-subject 95% confidence intervals (in the right panel). The grey lines indicate the median latency per participant. The left panel shows the latencies for the second saccade to a target. The middle and right panel show saccade latencies for the corrective saccade. The right panel shows the participant data centered around the grand mean, for visualization of within-subject effects.

out of twelve participants seemed to exhibit a lower latency for the corrective saccade when the first and second target were the same object. There was no difference in latencies of corrective saccades for trials where the array rotated clockwise vs. trials where it rotated counterclockwise $t(11) = 0.36$, $p = 0.73$, $\eta^2 < 0.01$. Together, these analyses suggest that saccades to previously fixated objects are initiated slower, which is in line with IOR effects. In contrast, the initiation of subsequent corrective saccades is facilitated.

We further examined whether surface features alone (here color) could account for facilitation of corrective saccades to previously fixated items. Consider a trial in which a red disc is cued in the top-left of the array, and after refixating the central fixation dot the participant is instructed to make a saccade to a different red disc in the bottom-right of the array. Previous research has shown that congruence between saccade target information and VWM content may increase saccade latency in a gaze correction paradigm [27]. In the current study we observed that saccades to the second target were unaffected by whether an identical color at a different object was previously fixated or non-fixated, $t(11) = 0.89$, $p = 0.38$, $\eta^2 < 0.02$. Similarly, the subsequent corrective saccade did not show an increased or reduced latency for previously fixated as compared to non-fixated stimuli, $t(11) = 0.10$, $p = 0.98$, $\eta^2 < 0.01$. Therefore, surface features of the first cued stimulus do not account

for differences in corrective saccade latency if the surface features were identical to the second target object.

Control analyses

Latency of the second saccade affects latency of the corrective saccade

It is plausible that the corrective saccades were facilitated simply because the preceding saccades were executed slower. To control whether the facilitation observed is not a result of the preceding saccade being slowed, a regression analysis was performed, which included all trials, to estimate the effect of the latency of the second saccade on the latency of the corrective saccade. A t-test was then used to test whether the mean slope was significantly different from null. The results are shown in Fig. 4. Overall, in trials in which the saccade to the second target was slow, the corrective saccade was subsequently faster in its onset, $t(11) = -7.47$, $p < 0.01$. However, comparing the slopes of the trials in which two different objects were cued to the trials in which the same object is cued twice reveals that returning to a previously fixated object alters this relation between saccade latencies. The relation between slowed saccades to the second target and facilitated corrective saccades is stronger when the same object is cued twice, $t(11) = -6.01$, $p < 0.01$. Corrective saccades are faster when prior saccades are slower if the same object is cued twice ($R^2 = 0.061$) as compared to when two different objects are being cued ($R^2 = 0.017$). Therefore, we conclude that the facilitation of corrective saccade onset to a previously fixated target is not just due to the inhibition of the onset of the preceding saccade.

Latency of corrective saccades as a function of landing error

It is plausible that a corrective saccade may be executed faster just because it landed close to the corrective saccade target due to oculomotor variance. To examine whether the observed facilitation of the onset of corrective saccades to previously fixated objects can be accounted for by differences in saccade landing and starting positions, we used linear mixed models. The statistics reported show a comparison of Bayesian Information Criteria (*BIC*s) between one control model and three experimental models. The model with a lower *BIC* is the model that best explains variance in the latency of the corrective saccade, where a difference in *BIC* greater than 10 is generally accepted as strong evidence against the model with

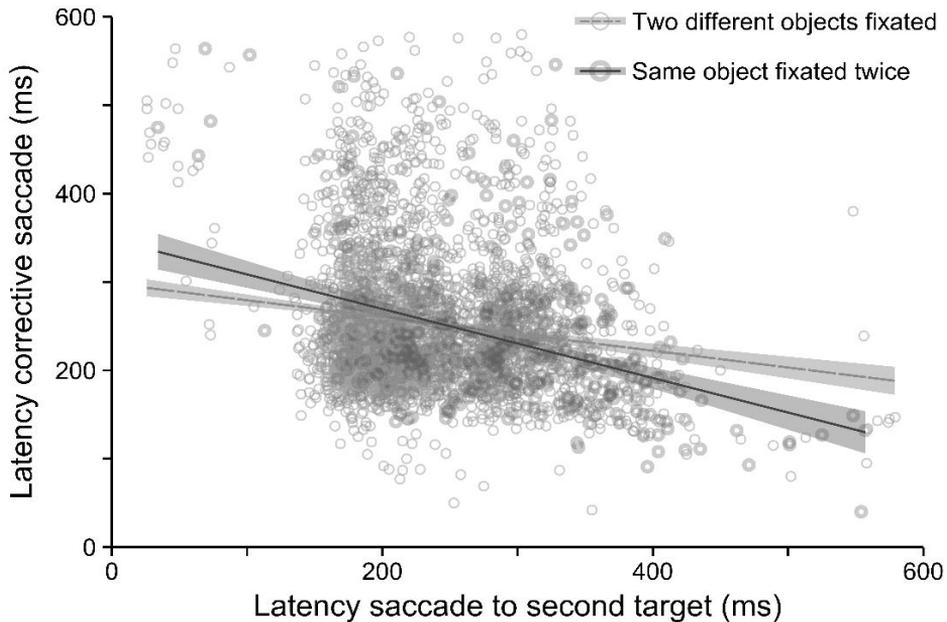


Figure 4. Scatter plot with two regression lines for trials in which two different objects were fixated and trials in which the same object was cued twice. Shaded areas around the regression lines represent SEM.

higher *BIC* [157,158]. The control model was constructed with corrective saccade latency as the dependent measure, whether the object appeared at a previously fixated location as a fixed effect, and a random effect per participant on the intercept. The control models were tested against models that included the second saccade starting position as a fixed effect, the second saccade landing position (same as corrective saccade starting position; barring small gaze shifts) as a fixed effect, or both saccade landing and starting position as fixed effect.

The model including the second saccade starting position as a fixed effect did not outperform the control model, $\chi^2 = 0.30$, $p = 0.86$, nor did the model including a fixed effect for saccade landing position of the second saccade, $\chi^2 = 0.60$, $p = 0.67$. Finally, the model including both saccade landing position and saccade starting position did not account for corrective saccade latency any better than the control model, $\chi^2 = 1.17$, $p = 0.97$. Therefore, saccade landing and starting positions do not seem to contribute to the difference in saccade latency for the corrective saccade between previously fixated objects and novel objects.

Discussion

The aim of Experiment 1 was to study to what extent corrective saccades are influenced by previous fixations. We hypothesized that corrective saccades to previously fixated objects would be affected by either IOR or priming. We found that corrective saccades to a previously fixated object are facilitated. The facilitation in latencies of corrective saccades is in line with object-specific priming, in which previously attended stimuli are responded to quicker than unattended stimuli. This finding indicates that the visual system considers previously fixated objects in saccade corrections and that the visual system recognizes such an object as being previously fixated (despite displacement of the object). Control analyses excluded alternative explanations such as facilitation as the result of the preceding saccade being slowed by IOR, or facilitation as the result of different variance in saccade starting and landing positions.

We also analyzed whether the facilitation of corrective saccade onset could be accounted for by shared surface features between objects, as it has been suggested that tracking a particular surface feature may induce attentional effects for objects sharing that surface feature [159]. However, we did not find a difference in latencies of corrective saccades to objects sharing surface features, as compared to latencies to objects with different surface features. This indicates that the facilitation of a corrective saccade to a previously fixated object is not exclusively explained by shared surface features of a previously fixated object but seems object-specific. Although two objects may share their surface features, the visual system recognizes that these features belong to two different objects, possibly due to contextual cues. These findings provide further evidence that the facilitation of corrective saccade onset is specific to previously fixated objects, rather than surface feature similarity.

To summarize, we observed that if a target object corresponds with a previously fixated object, a corrective saccade is initiated faster. In Experiment 2 we further investigated whether the representation of an object is updated over time and can induce facilitation of corrective saccade onset even when surface features change, or whether maintaining object correspondence requires surface features to remain stable. In other words, we will examine whether spatial updating alone is enough for the facilitation of corrective saccades. To this end, we designed a follow-up experiment that could elucidate whether stability of surface features is necessary for establishing object correspondence. We hypothesized that a representation of an object is acquired and can be subsequently updated despite changes in surface feature

or spatial information. That is, as long as the visual system regards the features as belonging to the same object [160,161]. Additionally, we hypothesized that if the representation of an object can be updated over time, then corrective saccades to a previously fixated object should be facilitated, even when the surface features of the object have changed since fixation of the object. We designed the experiment in such a way that the surface features of the stimuli were ambiguous until the saccade to the first target was executed and the participant had fixated the central fixation point.

Experiment 2

Methods

Participants and Procedure

The methods for Experiment 2 were identical to Experiment 1 with exception of the following changes. Twelve participants (8 female, aged 18 to 28, $M = 20.4$) participated in the experiment and completed 460 trials each. Two participants that participated in Experiment 1 also participated in Experiment 2.

The crucial manipulation in Experiment 2 was that color information of the stimuli was not shown before the first saccade but was only shown after refixating the central point. The stimuli were presented as equiluminant grey circles (10.2 cd/m²) until after refixation (Fig. 5). Thus, participants were cued to make a saccade to one of six grey circles and then fixated the central dot. After detection of gaze within 1° of fixation and a subsequent delay of 100 ms the color of every stimulus changed into one of four colors: red, green, blue and magenta (as described in the methods section of Experiment 1). The experiment then resumed as it did in Experiment 1. One of six locations was cued (with one out of six chance of the same object being cued twice) and the participant executed a saccade towards this target. In two thirds of the trials the array rotated either clockwise or counter-clockwise during the saccade to the second cued target, causing the participant's gaze to land in between the previously cued item and a distractor. After landing, the participants performed a corrective saccade to the cued object's updated position.

Results

To investigate the contribution of fixated surface features in speeding up corrective saccade onset, we masked the color of the discs during fixation, up until

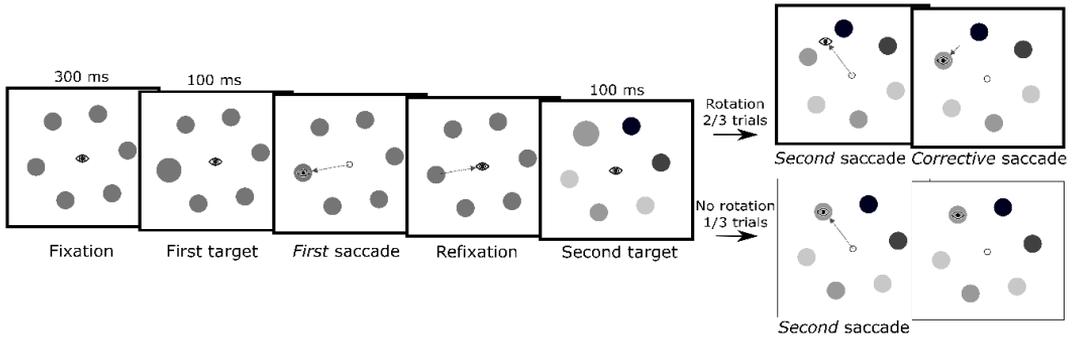


Figure 5. A schematic overview of the paradigm as it was presented in Experiment 2. The eye icon indicates gaze position and the arrows indicate saccades. The panels outlined in bold show the experimental trials. Note that the background and fixation stimulus were presented with a contrast opposite to that depicted here and that the experiment was not presented in greyscale.

the second target was revealed. As shown in the left panel of Fig. 6, we observed a higher latency for the second saccade when it was executed to a previously fixated object ($M = 269.3$ ms, $SD = 41.1$ ms) as compared to a non-fixated object ($M = 238.6$ ms, $SD = 51.5$ ms), $t(11) = 3.79$, $p < 0.01$, $\eta^2 = 0.13$, which indicates that IOR is present. Furthermore, despite the surface features being masked during fixation of the stimulus, we found significantly lowered latencies for corrective saccades when executed to a previously fixated object ($M = 206.3$ ms, $SD = 31.2$ ms) as compared to corrective saccades executed to a non-fixated object ($M = 221.0$ ms, $SD = 28.6$ ms), $t(11) = -2.39$, $p = 0.04$, $\eta^2 = 0.11$.

Control analysis – corrective saccade latency and second saccade latency

Across all conditions we found a significant negative correlation between the latency of the corrective saccade and latency of the saccade to the second target when directed to a novel object, $R^2 = 0.02$. Comparing the baseline correlation for saccades that were executed to a previously fixated object reveals that this relation is strengthened, i.e., corrective saccades to previously fixated objects are even quicker when prior saccades are slowed, $R^2 = 0.09$. The data showed that the slopes (of the relation between corrective saccade and saccades to the second cued object) between targets previously cued and not previously cued objects were significantly

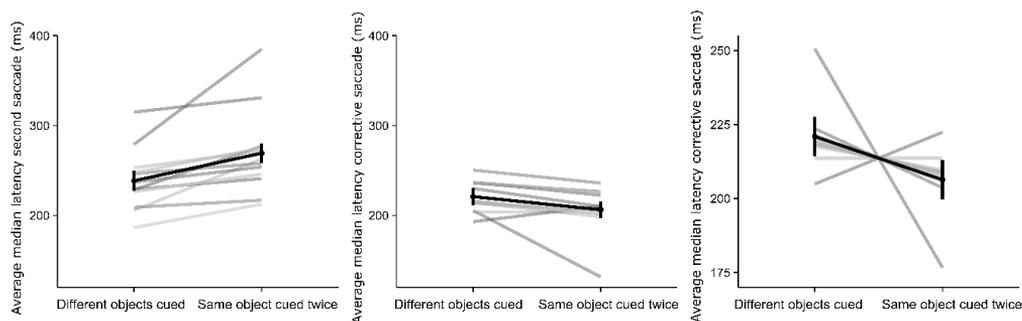


Figure 6. The average of median saccade latencies for saccades to a previously fixated object or a non-previously fixated object. The bold black line shows mean data, with 95% confidence intervals. The grey lines show median latency per participant. In this experiment the fixated object had changed color in between the first and second saccade to the target. The left panel shows the latencies for the second saccade to a target. The middle and right panel show saccade latencies for the corrective saccade. The right panel shows the participant data centered around the mean and within-subject confidence intervals.

different, $t(11) = 1.61$, $p = 0.03$, $\eta^2 = 0.04$. Therefore, we replicated our results from Experiment 1 despite the difference in feature information during the first saccade.

Discussion

In Experiment 2, we examined whether the constancy of surface features is essential in establishing object correspondence. We hypothesized that surface features belonging to an object may be updated over time to establish object correspondence. If a surface feature of an object is updated one might expect that changing color information does not decrease the facilitation of corrective saccades to previously fixated targets. This is indeed what we observed, as well as latencies for first saccades being higher, possibly due to IOR. Importantly, latencies of corrective saccade to previously fixated objects were still facilitated, like what we observed in Experiment 1, even though irrelevant surface feature information was acquired during fixation of that object. Thus, Experiment 2 replicates our result from Experiment 1. Both Experiment 1 and 2 provide support for the notion that the visual system executes a saccade to an integrated object. That is, whereas corrective saccades to previously fixated features at a fixated location were facilitated, previously fixated features at a different spatial location did not affect corrective

saccade latency. We conclude that consistency of surface features is not required for establishing object correspondence and postulate that the process of establishing object correspondence in our paradigm occurs as such: surface features of the object file are updated during the color shift (e.g. from grey disc to red disc, grey disc information is discarded) before the onset of the second saccade and the position of the object in the object file is updated after landing the second saccade (and the target is displaced).

Furthermore, the results showed that the initiation of saccades to a previously fixated object (at a previously fixated location) was again slowed. Inhibition of saccadic return was still present despite changing surface features after attentional withdrawal. These results are inconsistent with previous research, which found that updating surface features of an object associated with IOR may reduce or eliminate IOR [148]. On the other hand, our findings are consistent with macaque studies which show that IOR is more affected by spatial-temporal incongruencies rather than incongruent surface feature information [148]. Possibly, the discrepancies between the data of Tas et al. [148] and our data could be explained by the target locations changing immediately after the refixation in the paradigm by Tas and colleagues, and not changing until the second saccade in our study.

Our results thus far have shown that the effect of previous fixation on saccade latency differs for the second saccade and the corrective saccade. However, both in Experiment 1 and in Experiment 2 we were unable to conclude how this effect is driven by previously fixated location information. The aim of Experiment 3 was to disentangle the effect that previously fixated locations may have on the latency of the second saccade and corrective saccade latency. First, our previous results have shown that corrective saccades executed to previously fixated surface features are facilitated, but the paradigm did not allow the investigation of the effect of previously fixated locations on corrective saccades. The corrective saccades were always executed to a non-fixated location, whereas the second saccade was always performed to either a previously fixated object *and* location, or neither. Research has shown that IOR can be present both at previously attended locations and objects [122,146,147,162]. Moreover, IOR has been proposed to increase fixation efficiency by lowering the fixation probability of previous fixated locations [136]. Considering the difference in spatial information between the second saccade target and corrective saccade target, it is not surprising that the second saccade to a previously fixated object and location in Experiment 1 and Experiment 2 had a higher latency. In contrast, the subsequent corrective saccade was always executed to a non-fixated

location and showed facilitation to previously fixated objects. Currently, it is inconclusive whether facilitation for the corrective saccade and inhibition for the second saccade is confounded by an effect of previously fixated location. We hypothesized that slowed saccade execution for the corrective saccade may also be observed in Experiment 3, but that the second saccade will not show lower latencies when executed to previously fixated targets. Second, it is currently unclear whether the higher latency that was observed for the second saccade to a previously fixated object when compared to a non-fixated object is driven by IOR through oculomotor processes (previously fixated location) or attention (previously fixated surface features). If the IOR effect for the second saccade is not present after the object has moved, we expect oculomotor processes related to IOR to underlie the inhibition [113,126]. Investigating both these effects will allow us to assess attentional processes or oculomotor processes underlie corrective saccade facilitation to previously fixated objects.

Therefore, we altered the design of the paradigm such that we could disentangle the role of previously fixated *locations* (spatial information) and *objects* (feature information) on both the corrective saccade and the second saccade. In experimental trials of Experiment 3 the array was rotated twice, once slowly (after the first saccade) and once quickly (during the second saccade). In two thirds of the trials, the layout of the different stimuli *slowly* rotated after refixating the central fixation point over the course of 500 milliseconds. This rotation was visible to the participant to facilitate object tracking. In the same trials, the array rotated *fast* during the saccade to the *second target* (as in in Experiments 1 and 2). This set-up allowed us to examine corrective saccade latency in three conditions: object congruence, location congruence and object-location congruence.

Object congruence in corrective saccades was determined in the same way as described in Experiments 1 and 2. A corrective saccade is executed to a previously fixated object at an unfixated position. We expect to find similar results to our previous experiments, where corrective saccade latency was facilitated to previously fixated objects.

In *location congruence* the target position of a corrective saccade has been previously fixated but is occupied by an object that was not previously fixated. Previous studies have reported location based IOR to occur in certain spatial memory tasks, dissociable from object-specific IOR [163,164]. Additionally, IOR may be elicited by location more so than object identity [152], which seems supported by

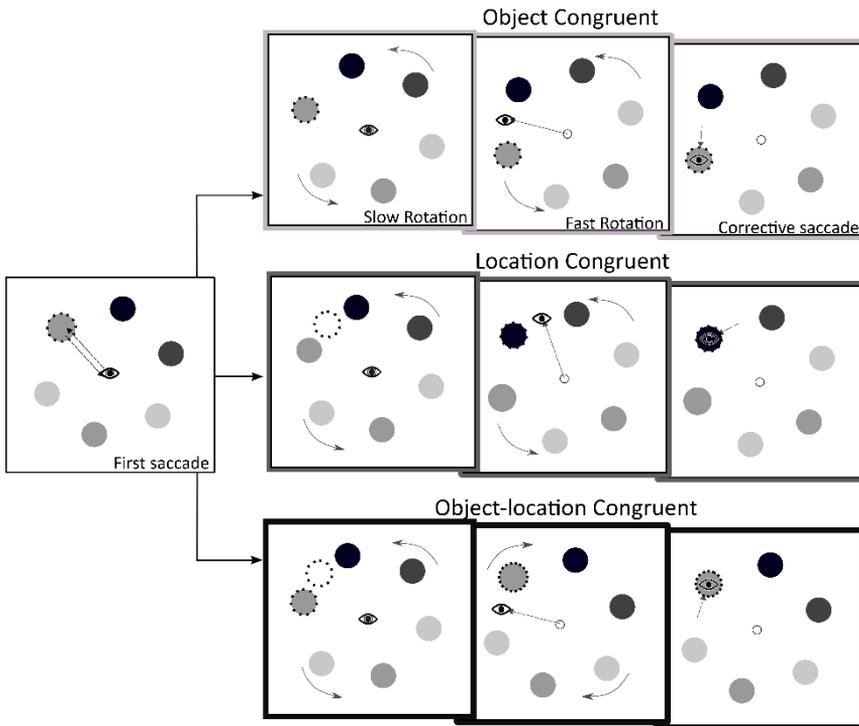


Figure 7. Three example trials in Experiment 3. The first panel shows the experiment up until the rotation during refixation. For illustrative purposes, a dotted line has been drawn around either the fixated object (top panels), location (middle panels) or object and location (bottom panels). The top panels show a situation in which a previously fixated object at a non-previously fixated location is corrected to (object congruent trials). The middle panels show a situation in which a previously fixated location with a non-previously fixated object is corrected to (location congruent trials). The lower panels show the trials in which the corrective saccade was executed to the same object and location as it was previously fixated (object-location congruent trials).

neurophysiological studies. The superior colliculus is critically involved in executing saccades and (disengaging) spatial attention [165–168]. As such, activity in the superior colliculus has been shown to reflect IOR [62,169], which is supported by lesion studies showing that IOR is not generated in patients with a lesioned superior colliculus [165]. In location congruent trials a corrective saccade will be generated to a previously fixated location, which we hypothesize will be slowed by the

previous attending of the target location. Alternatively, corrective saccades to previously fixated locations could be facilitated in onset, as IOR has been implicated as a novelty seeking mechanism [108,170,171]. The novelty, which may elicit facilitation [172], in location congruence is that a new object (not previously fixated) is occupying a previously fixated location.

Finally, *object-location congruence* is a condition under which the corrective saccade is executed to a previously fixated object at a previously fixated location. As mentioned previously, we hypothesize that this may induce inhibition of saccadic return, as this saccade will be executed to a location and object that had been previously fixated, similar how to the second saccade was slowed in Experiment 1 and Experiment 2 when executed to a previously fixated location and object. When the corrective saccade target is both congruent in terms of previously fixated object features and location this should provide evidence to the visual system that this location had been previously attended to elicit object-specific IOR as described by Tipper [146]. These results will provide insight in the interplay between both object and location-specific information by the visual system to establish object correspondence.

Experiment 3

Methods

Participants and Procedure

In Experiment 3 sixteen participants aged between 18 and 27 ($M = 20.1$) completed 648 trials each. The procedure was as follows. A trial in Experiment 3 was the same as Experiment 1 up until refixation of the central fixation point after the first saccade. To reiterate, participants were presented with six colored circles. One of these circles was cued (first saccade target). Participants executed a saccade to this object, after which the participants fixated the central point. The experimental procedure then changed regarding Experiment 1. In two thirds of the trials the array rotated visibly over the course of roughly 500 ms (37 frames; *slow* rotation) whilst the participants fixated the central point. This slow rotation could occur either clockwise or counter-clockwise, which was counterbalanced to occur equally often per participant. During the slow rotation the stimulus array was rotated exactly 30 degrees. After the rotation had concluded, one of the six objects was cued as being the second saccade target. In one out of six trials the same object was cued twice, albeit at a different location between cues due to the slow rotation. Once a saccade

was executed, the stimuli rotated another 30 degrees either clockwise or counter-clockwise (*fast* rotation). The fast rotation, like in Experiment 1 and Experiment 2, occurred during one refresh cycle of the monitor. Finally, the participants executed a corrective saccade to the target's updated position. Rotating the array twice meant that the stimuli could rotate back into a position that was either congruent to when the object was fixated initially or to a position that was occupied by a different object during the saccade to the first target.

The trials in which no slow rotation occurred were added to prevent participants from anticipating the slow rotation. In trials without slow rotation the cue to the second target was delayed by 37 frames (approximately 500 ms), thus keeping the time frame between both types of trials identical. Trials where the array rotated twice were used to investigate corrective saccade latency and will be referred to as the experimental trials.

As mentioned above, this procedure allowed us to examine several situations that may affect corrective saccade latency of which three example experimental trials are shown in Fig. 7. We were interested in studying these conditions for the corrective saccade: object congruent trials in which only the object had been previously fixated, location congruent trials in which only the location was previously fixated with a novel object occupying this location and object-location congruent trials in which the corrective saccade was executed to a location and object which had been previously fixated.

To clarify, object congruent trials (Fig. 7) would be induced by executing the first saccade to one of six objects. In the example shown in Fig. 7, the slow rotation occurred counter-clockwise. The previously fixated object was cued a second time and during the saccade to this object the fast rotation occurred counter-clockwise once more, causing the object to appear at a non-fixated location. After landing the participant therefore executed a corrective saccade to a previously cued object. Object-congruent trials could also occur by cueing the same object twice and rotating the array clockwise both during the slow rotation and fast rotation. In object congruent trials the corrective saccade was therefore executed to a fixated object that was rotated onto a position of a non-fixated neighboring object.

In the location congruent trials, in which only the location was previously fixated, we cued one of six objects. In location congruent trials both fast and slow rotation were congruent (e.g. slow rotation clockwise, fast rotation clockwise), but two neighboring items were cued. For example, the first saccade was executed towards the top left item, and after a counter-clockwise slow rotation the top item

(one item to the right) was cued. During the saccade to this target the array rotated counter-clockwise again. This rotation led to a non-fixated object occupying a location that was previously fixated. Object-location congruent trials occurred if the same object was cued twice. In object-location congruent trials the slow and fast rotation occurred in opposite directions. In the example shown in in Fig. 7, the slow rotation occurred counter-clockwise followed by a clockwise rotation during the second saccade. Therefore, the corrective saccade was executed to the same object and location that had been previously fixated.

These three types of trials (object congruent, location congruent and object-location congruent) were analyzed separately. In all analyses the three trial conditions were compared to situations in which the slow and fast rotations occurred in the same direction, but with different items cued between the first and second saccade.

Results

We analyzed three types of corrective saccade trials: object congruent, location congruent, and object-location congruent trials. The main results are shown in Fig. 8. Individual participant data are shown in Fig. 9.

For object congruent trials we found significant facilitation, $t(15) = -2.22$, $p = 0.04$, $\eta^2 = 0.02$, for corrective saccades to a previously cued object at a novel location ($M = 216.4$ ms, $SD = 49.3$ ms) as compared to a non-previously cued object at a novel location ($M = 227.6$ ms, $SD = 49.0$ ms), left panel Fig. 8. For location congruent trials in which a location was fixated but a novel object occupied it ($M = 235.5$ ms, $SD = 41.0$ ms), we found significant facilitation, $t(15) = -3.04$, $p < 0.01$, $\eta^2 = 0.04$, as compared to a non-previously fixated location with a novel object ($M = 244.3$ ms, $SD = 46.7$ ms). Finally, the analysis for object-location congruent trials indicate that corrective saccades were significantly slowed, $t(15) = 3.09$, $p < 0.01$, $\eta^2 = 0.10$, when corrected to a previously fixated object and location ($M = 237.0$ ms, $SD = 54.4$ ms) as compared to corrective saccades to a non-previously fixated object and location ($M = 216.5$, $SD = 44.8$), as shown in the right panel of Fig. 8.

Lastly, we examined the effects of the slow rotation on saccade latency of the second saccade. In our previous experiments corrective saccade latency was correlated with prior saccade latency. This correlation was stronger when both saccades were executed to a previously fixated object and location in the previous experiments. In Experiment 3, the slow rotation caused the target of the second

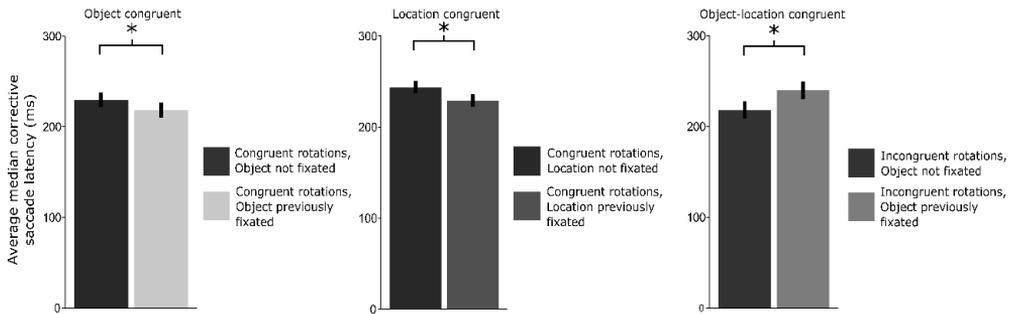


Figure 8. Average median reaction time for corrective saccades. The left panel shows latencies for corrective saccades to an object that was previously fixated versus a non-fixated object, the middle panel shows reaction times for corrective saccade to a previously fixated location occupied by a non-fixated object or corrective saccades to a previously non-fixated location. The right panel shows reaction times for previously fixated objects at a previously fixated location versus trials in which neither object or location were fixated. Congruency refers to the slow and fast rotation occurring in the same direction, e.g. both clockwise. Error bars represent 95% confidence intervals.

saccade to be in a different location than when previously fixated, which may elicit either object-specific facilitation or inhibition. Therefore, we investigated how the latency of the second saccade was affected by the slow rotation we introduced in Experiment 3, as absence of object-specific inhibition for the second saccade may affect saccade latency of the corrective saccade. To analyze the effect of the slow rotation on second saccade latency we performed a repeated measured analysis of variance. The dependent variable was the median saccade latency of the second saccade, with slow rotation (clockwise, counter-clockwise or no rotation) and stimulus fixated previously or not fixated previously as independent variables. We found a main effect of both previously fixating the stimulus, $F(1, 15) = 42.97$, $p < 0.01$, $\eta^2 = 0.13$, and the direction of slow rotation, $F(2, 30) = 11.78$, $p < 0.01$, $\eta^2 = 0.10$, on saccade latency of the second saccade, and an interaction between these two factors, $F(2, 30) = 14.50$, $p < 0.01$, $\eta^2 = 0.03$. We examined the interaction effect in further detail by using Holm-Bonferroni corrected t-tests for post-hoc analyses.

Significant differences are indicated by asterisks in Fig. 10. First, in trials where no slow rotation was present (similar to Experiment 1) we found a significant increase in second saccade latency for saccades to previously fixated objects when

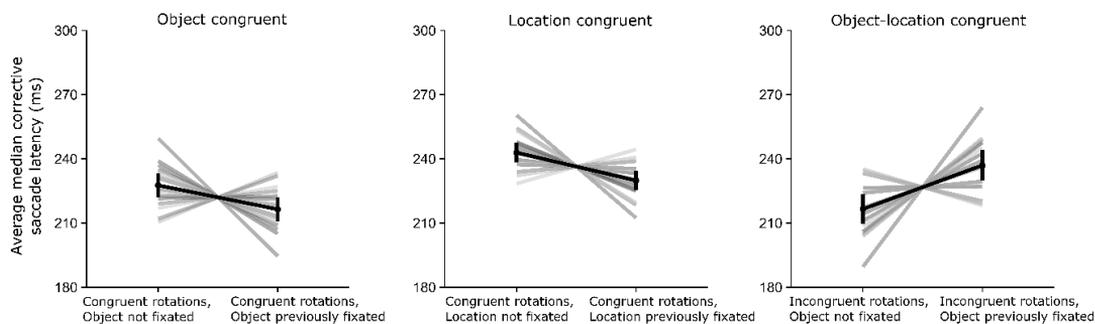


Figure 9. Within subject effects of previous fixations on median saccade latency per participant, centered around the grand mean. The calculated grand mean is shown as a black line with 95% within-subject confidence intervals. The left panel shows reaction times for corrective saccades to a previously fixated object at a novel location, the middle panel shows reaction times for corrective saccade to a previously fixated location and the right panel shows reaction times for previously fixated object and location.

compared to non-previously fixated objects, $t(15) = -6.13$, $p < 0.001$. We also found a significant increase in second saccade latency when a saccade was executed to a previously fixated object which had rotated visibly in both the clockwise and counter-clockwise rotation conditions, $t(15) = -4.90$, $p = 0.01$, and, $t(15) = -4.03$, $p = 0.01$. Comparing when a saccade was executed to a previously fixated object reveals within the condition that the latency for the second saccade in the no slow rotation condition is significantly higher than in the clockwise, $t(15) = -1.88$, $p = 0.04$, or counter-clockwise conditions, $t(15) = -2.26$, $p = 0.02$. Other post-hoc comparisons yielded non-significant results.

We conclude that saccade latency is higher to a previously fixated target, even when the target has moved since fixation, although incongruent spatial information may lessen the magnitude of inhibition.

Discussion

In Experiment 1 and 2, we observed that corrective saccades to previously fixated objects were facilitated in terms of saccade onset latency. However, these corrective saccades were always performed to a location that was not previously

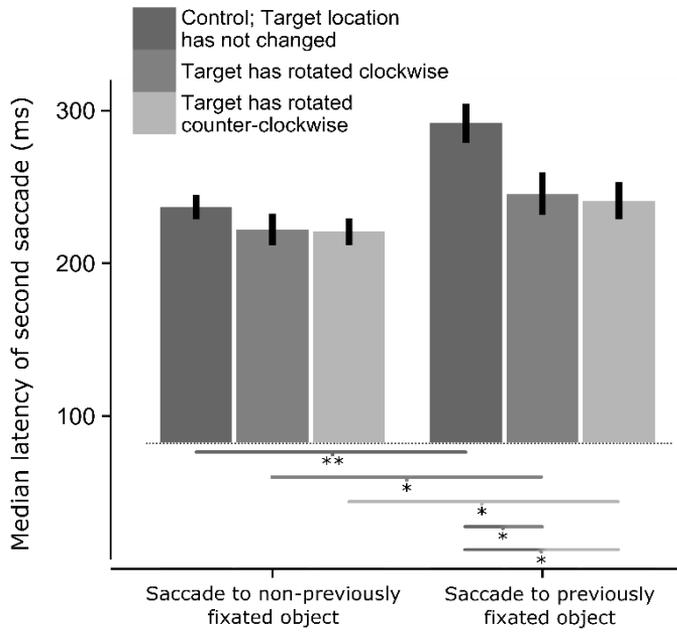


Figure 10. Saccade latencies for the saccade to a second cued target. The bars show trials in which no slow rotation was present and trials in which a slow rotation was present prior to executing the saccade. The bars on the left represent the condition in which a saccade to a non-previously fixated object is executed and the bars on the right show saccade latencies to a previously fixated object. Error bars show 95% confidence intervals.

* $p < 0.05$, ** $p < 0.01$.

fixated. In Experiment 3 we investigated corrective saccade latency to both previously fixated objects and previously fixated locations.

When either the target object or the target location was previously fixated, corrective saccades were facilitated. In contrast, we found inhibition of corrective saccade onset when both the same object *and* location were previously fixated. In Experiment 1 and Experiment 2, corrective saccades to previously fixated objects (at non-fixated locations) were executed faster than to non-fixated objects. The second saccade was executed slower to either a previously fixated object or previously fixated object and location as compared to a non-fixated object at a non-fixated location. Importantly, the second saccade and the corrective saccade are differentially affected by previously fixated locations. This could be taken to suggest that the second saccade and corrective saccade are differentially affected by attention and oculomotor programming. Moreover, our results indicate that saccades to

previously fixated stimuli lead to an increase in subsequent corrective saccade latency (i.e., slower saccades) only when there is both object *and* location congruency. These findings are perhaps explained by some lingering of IOR at the previously fixated location, which is only activated in the absence of novel information (i.e., a new object or a new location).

Our results indicate that corrective saccades were initiated faster when executed to a previously fixated object or location. These results imply that for saccade execution the visual system independently weighs previously fixated surface features (as object correspondence operations) and previously inspected locations.

General discussion

Previous research has indicated that both object-specific IOR [147] as well as object-specific priming [154] can affect the processing of previously viewed stimuli. Here, we conducted a series of gaze correction experiments to investigate how previous fixations may alter corrective saccade onset. More specifically, we investigated whether surface features, such as color and location information would independently affect corrective saccades. To this end, we cued participants to fixate one of the objects in an array prior to performing a corrective saccade task. Our study shows that object-specific priming and IOR may affect corrective saccade latency differently under different circumstances. Corrective saccades were faster when they had to be executed to a new object at a previously fixated location, or when a previously fixated object moved to a new location. In addition, we observed a slowing of corrective saccades to previously fixated objects when they were positioned at the same location as that which was initially inspected (similar to IOR). The mechanisms that underlie these effects are currently unclear. However, the current results suggest that performing a corrective saccade task involves similar processes as performing a visual search task, given that the facilitatory and inhibitory effects occur under highly similar conditions [173]. These observations could be taken to suggest that the visual system compares remembered features to current sensory input and initiates a corrective saccade when surface feature or spatial information is detected that is incongruent with memory content.

Recent studies on transsaccadic integration of object features show that presaccadically acquired peripheral information and subsequent foveal feature information are integrated after a saccade has been completed [30,33,35]. Even more, integration is only present when the visual system considers the pre- and postsaccadic information to belong to the same object [35,43]. The phenomenon of

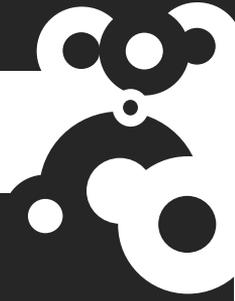
transsaccadic integration implies that VWM representations are not stable over time, but rather are constantly updated by new visual information. Our study extends this hypothesis by showing that object correspondence, despite a mismatch of location, is not driven by template matching of previously viewed features (e.g. matching any red object to another red object establish object correspondence). We suggest that the visual system is either constantly updating object information and integrating remembered and new information into one object representation or replacing information present in VWM between saccades based on task demands.

The current literature seems to agree on the idea that corrective saccades are guided by two kinds of input: visual and motor input. To illustrate the differences, we would like to note that corrective saccades guided by memory content (visual corrective saccades; 200 to 300 milliseconds) are generally slower than corrective saccades in response to variance in motor execution (motor corrective saccade; latency of 50 to 200 milliseconds) [174]. Motor corrective saccades are executed when gaze after a saccade has not reached the intended target coordinates. These motor corrective saccades are likely to be executed quicker than visual corrective saccades since the motor program that has been executed (saccadic corollary discharge) is available to the visual system before the saccade has reached its landing position [50,175]. In other words, the visual system can evaluate the error before the saccade has landed, possibly through a predictive mechanism (a forward model) [40,42,176]. The efference copy of the corollary discharge, which (ultimately) allows a motor corrective saccade to be executed after previous saccade has missed its target, has been shown to contribute to visual stability [49]. In contrast, the implications of visual corrective saccades on visual stability are not as clearly defined. Both motor and visual corrective saccades have been linked to each other in a study that has shown that motor corrective saccades are more accurate when visual information is available upon landing [28]. Additionally, visual corrective saccades are difficult to suppress and are likely to be executed even when not task relevant, suggesting the involvement of lower-level visual processing areas [27]. In our study, participants could not use their copy of the corollary discharge to successfully complete the corrective saccade task (as the displacement of stimuli was artificial), indicating that object correspondence (as indicated by object-specific facilitation of saccade onset to previously fixated objects) can be established by visual information alone. We interpret these results as evidence that both the corollary discharge signal and visual information can guide corrective saccades, depending on the availability of information before saccade onset.

In conclusion, object correspondence is initiated by congruency between remembered surface features and spatial information and promotes visual continuity. Our study adds that previous attended visual information can significantly affect the time course of establishing object correspondence across saccades, as indicated by changes in saccade latency.







Chapter 5

Feature integration is unaffected by saccade landing point, even when saccades land outside of the range of regular oculomotor variance.

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Author contributions

MJS, JHF, NvdS, & SvdS conceptualized and designed the experiment. MJS programmed the experiment, collected the data and performed the analyses. MJS wrote the manuscript, and JHF, NvdS, and SvdS commented on and co-authored the manuscript. SvdS funded the research.

Summary

The experience of our visual surroundings appears continuous, contradicting the erratic nature of visual processing due to saccades. A possible way the visual system can construct a continuous experience is by integrating presaccadic and postsaccadic visual input. However, saccades rarely land exactly at the intended location. Feature integration would therefore need to be robust against variations in saccade execution to facilitate visual continuity. In the current study, observers reported a feature (color) of the saccade target, which occasionally changed slightly during the saccade. In transsaccadic change-trials, observers reported a mixture of the pre- and postsaccadic color, indicating transsaccadic feature integration. Saccade landing distance was not a significant predictor of the reported color. Next, to investigate the influence of more extreme deviations of saccade landing point on color reports, we used a global effect paradigm in a second experiment. In global effect trials, a distractor appeared together with the saccade target, causing most saccades to land in between the saccade target and the distractor. Strikingly, even when saccades land further away (up to 4°) from the saccade target than one would expect under single target conditions, there was no effect of saccade landing point on the reported color. We reason that saccade landing point does not affect feature integration, due to dissociation between the intended saccade target and the actual saccade landing point. Transsaccadic feature integration seems to be a mechanism that is dependent on visual spatial attention, and, as a result, is robust against variance in saccade landing point.

Introduction

We experience that visual perception is continuous, contradicting the disruptions of visual processing due to eye-movements (saccades). This lack of insight into the disruptive nature of saccades [11,12,177], allowing us to perceive the visual world as a continuous whole rather than disparate snapshots, is one of the more complex qualities of the visual system. One of the proposed mechanisms to bridge the gap in visual processing before and after a saccade is transsaccadic feature integration [30]. Transsaccadic feature integration involves storing retinal input of the saccade target before the saccade and *combining* the stored presaccadic information with the retinal image after the saccade [26,33,35,43]. Combining visual feature estimates in this manner allows for more reliable estimates of visual input than when only viewed before or after the saccade, and for presaccadic perception to influence postsaccadic perception. However, the influence of presaccadic perception on postsaccadic feature perception in experiments is quite small [26,33,35,43]. This limited usefulness of transsaccadic feature integration has led to contentiousness about the nature of such a process. For instance, both behavioral and neurophysiological studies range from evidence in favor of feature integration [178,179], evidence for very limited feature integration [180], and evidence against transsaccadic feature integration [181,182]. Proponents of feature integration have suggested that visual continuity may be the product of a match (or lack of conflict) between pre- and postsaccadic retinal input, allowing the visual system to assume that information was present continuously [30]. Although this seems like an elegant solution of how the visual system may establish perceptual continuity across saccades, little is known about how and whether transsaccadic feature integration is affected by the parameters of a saccade. As of yet, no consensus exists whether transsaccadic feature integration is a higher-order process [36] or a lower-order visual process [183]. Therefore, we chose to approach the topic of transsaccadic feature integration in a different manner, to constrain the possible underlying processes. We expect that, if transsaccadic integration is a process that occurs later in the visual processing stream, that transsaccadic integration is saccade landing point invariant, as earlier visual processing areas show a smaller receptive field size, on average [184].

Research into transsaccadic feature integration has shown that the temporal and spatial characteristics of a stimulus may affect how human observers weigh both pre- and postsaccadic visual input. For instance, humans are generally predisposed

to overweighing foveal visual input [35,43]. This is not entirely unsurprising, as postsaccadic visual input is generally foveated, and sampled with higher acuity, than presaccadic visual input. Furthermore, research has shown that the distance between the fovea and an object of interest affects how visual feature representations are weighed both pre- and post-saccadically [33]. In the study by Oostwoud-Wijdenes and colleagues [33] observers were instructed to report the color of one of three objects, after making a saccade. Observers saw the objects before and after the saccade. Unbeknownst to the observers, the objects changed color during the saccade. Observers reported a mixture color (an integrated pre- and postsaccadic color) for all the objects. Crucially, one of the objects was positioned close to the presaccadic point of fixation, another was positioned close to the postsaccadic point of fixation, and the third object was positioned at an intermediate location. The authors found that observers reported a mixture color that was weighed more towards the presaccadic color (before the color change) when the object that had to be reported was the one closest to the presaccadic point of fixation. Additionally, when reporting the color of the object that was closer to the postsaccadic point of fixation observers responded with a mixture color that was weighed more towards the postsaccadic color. Lastly, an intermediate mixture color was reported for the objects at the intermediate location. From this experiment, as well as further experiments by Oostwoud-Wijdenes and colleagues [33], where visual information was manipulated by adding presaccadic or postsaccadic noise, the authors concluded that the weights of pre- and postsaccadic information during transsaccadic feature integration is affected by the reliability of visual input. Furthermore, they show that the reliability of visual input is directly affected by point of fixation.

The observation that distance of visual input relative to the fovea affects the reliability of our estimates of visual input and how we integrate information is interesting, given that saccades show relatively large variance in their landing point. If the distance between the gaze landing point and the target is the only determining factor, it would lead to different weights between pre- and post-saccadic input with every saccade. Especially when using color stimuli, as research has shown that cone (color receptor) density is highest in the central 0.032 degrees² of the surface area of the fovea [185]. Cone density drops off steeply with increasing distance to the fovea, with a factor of 10 with each ~3.5 degree increase in distance from the fovea [185]. Alternatively, transsaccadic feature integration could be robust against within-subject variance in motor execution as visual attention (where visual information is sampled) and point of fixation (the center of gaze) may be dissociated across

saccades. Typically, attention shifts towards the location of the intended saccade target, rather than towards the saccade landing point [4,18,186–188]. In a study by Van der Stigchel & De Vries [18], observers performed an oriented bar discrimination task at the location of their saccade target or at a neighboring location. The bar was presented within an annulus with different timings with respect to saccade onset. In certain trials, a salient distractor was presented, resulting in saccades that landed in between the saccade target and salient distractor due to saccade averaging (global effect). During the distractor present trials, observers were not able to discriminate the target in between the saccade target and the distractor more accurately, even though saccades landed at these positions. Instead, observers remained best at identifying the orientation of the bar at the intended saccade target, regardless of where the saccade landed. The authors concluded that saccades and attentional processes linked to saccade execution can target different spatial locations. This spatial dissociation effect has been expanded by Wollenberg, Deubel, & Szinte [17], who showed that presaccadic attention was equally distributed to both saccade targets. Effectively, these studies rule out a mandatory coupling of attention to the saccade landing point.

In the current study, we will examine whether saccade landing point affects transsaccadic integration of visual features. In the experiments, observers were tasked with reporting the color of a saccade target, which was presented shortly before and after the saccade, similar to the study of Oostwoud-Wijdenes [33]. In our analysis, we contrasted color reports for trials in which saccades landed close to the colored target with color reports for trials in which saccades landed further away from the colored target. We expected that, if deployment of attention can indeed be separated from saccade landing point, then pre- and postsaccadic information is weighed and integrated in the same way regardless of whether saccades land further from the intended saccade landing point. However, since we use color stimuli, and color perception is less accurate further away from the fovea, it also plausible that pre- and post-saccadic visual input is weighed based on saccade landing position. Crucially, we opted to use Bayesian statistics. Whereas traditional/frequentist statistics, which can only reject or lack the evidence to reject the null, Bayesian hypothesis tests can differentiate evidence for the null, evidence for the alternative hypothesis, or inconclusive evidence [67]. We used two measures of transsaccadic integration to investigate this hypothesis in two experiments: reduction of error and changes in bias in reporting the color of the saccade target.

Experiment 1 – Effect of saccade landing point on color reports

Methods

Observers

Observers ($N = 16$, 7 Female, $M_{age} = 20.8$) reported normal or corrected-to-normal vision. The experiment took 90 minutes to complete. Observers signed an informed consent form prior to the start of the experiments. The observers were compensated for their time with €6,- an hour. Both experiments were conducted in accordance with the declaration of Helsinki of 1964 and were approved by the Faculty Ethics committee (FETC) of Utrecht University.

Apparatus

The experiment was conducted in a darkened lab. Observers supported their head with a chin rest at 70 cm distance from an Asus ROG Swift PG278Q monitor (60.1x34.0 cm, 2560x1440 pixels, 100 Hz; pixel response time 1 millisecond; AsusTek Computer Inc., Taipei, TW). To make sure that color mixing did not occur due to persistence of the pixels of the screen, the Ultra-Low Motion Blur setting was turned on, and set to a pulse width of 50. The gamma value was adjusted to linearize luminance within RGB channels prior to the experiment.

To investigate the timing of visual presentation we used a photodiode placed in the bottom-left corner of the screen, connected to the printer port of the EyeLink host-pc, which output the measured luminance in the EyeLink data file. We chose the two hues in the color space used in the experiment with the largest luminance discrepancy (34° and 64° hue values). We set the threshold for detection at 80% luminance of the difference in luminance between the two hues, and dark detection at 20% luminance. We presented 1000 repetitions of 10 frames of the hue at 34°, followed by 10 frames of the hue at 64°. We recorded the luminance of a screen-sized rectangle. Screen settings matched the screen settings in the experiment. The delay between the draw call and response on the screen was around 11 ms ($Mean = 10.8$, $SD = 5.5$, $Median = 10$, $IQR = 9$ to 10). There may be a small portion of trials in which the pixels had not reached the desired values within one frame. In these measurements we found that the desired luminance was only reached after 20 ms. If this proportion holds for our experiment, it would affect 6% of the trials (as shown in Supplementary Fig. 1).

Next, we alternated between 64° in hue in our color space and black. When we set the threshold for brightness detection at 80% luminance, we see that the

luminance is only reached after 20 ms ($Mean = 20.5$, $std = 3.2$, $Median = 20$, $IQR = 20$ to 11 , Supplementary Fig. 1). This indicates that the screen may take an additional frame to update when going from black to one of our colors used in the experiment. It does seem to be an additional frame, as the ‘missing’ frame is followed by 9 subsequent frames. From this we conclude that, when switching between colors, the new color is usually reached within a single frame, whereas in conditions where we transition from color to black, there may be one frame in which the pixels have not reached the desired luminance (a ~ 20 ms delay between the draw call and presentation). Therefore, it seems stimulus presentation was largely as intended and that the screen used is appropriate for stimulus presentation in the experiments.

The left eye was recorded at 1000 Hz with an EyeLink 1000 (SR Research Ltd., Canada), calibrated with the native 9-point calibration procedure. Eye-movement events were detected offline using the native EyeLink saccade and fixation detection algorithms. The experiment was programmed in Python 2.7.3, using the *Pygaze* library for eyetracking research [60]. Colors were generated using the *HSL_{uv}* Python library [189]. The data was analyzed in R using the *BayesFactor* package [69,190].

Stimuli

Stimuli were presented on a black background (1.1 cd/m^2). Observers fixated the center of the screen, indicated by a small annulus of 0.5° (4.2 cd/m^2). The saccade target was a colored circle (radius = 0.5° , luminance = 9.8 cd/m^2), which could appear at one of eight locations. The targets appeared at an eccentricity of 10° and at an angle of 30° or 60° with respect to the cardinal axes (see Fig. 1C). The color space used in the experiment was *HSL_{uv}* [189], a perceptually uniform color space expressed in Hue, Saturation, and Lightness parameters. Saturation and lightness were kept at a value of 50 and hue was randomly selected from a uniform distribution ranging from 0 to 360° . Observers were instructed to report the color of the target on a color wheel. The polar angle of the response on the color wheel corresponded with the angle in hue of the color space. In the Color change condition, the hue of the saccade target shifted by $\pm 30^\circ$ (see Fig. 1B). Lastly, the target could be replaced with a white annulus (with a radius of 0.5° with a border of 0.2° , $\text{cd/m}^2 = 10.4$) either before (Post Only; the condition name refers to when the color was visible) or after a saccade (Pre Only). After the postsaccadic stimulus information was presented, the target was removed from the screen to reduce the influence of corrective saccades.

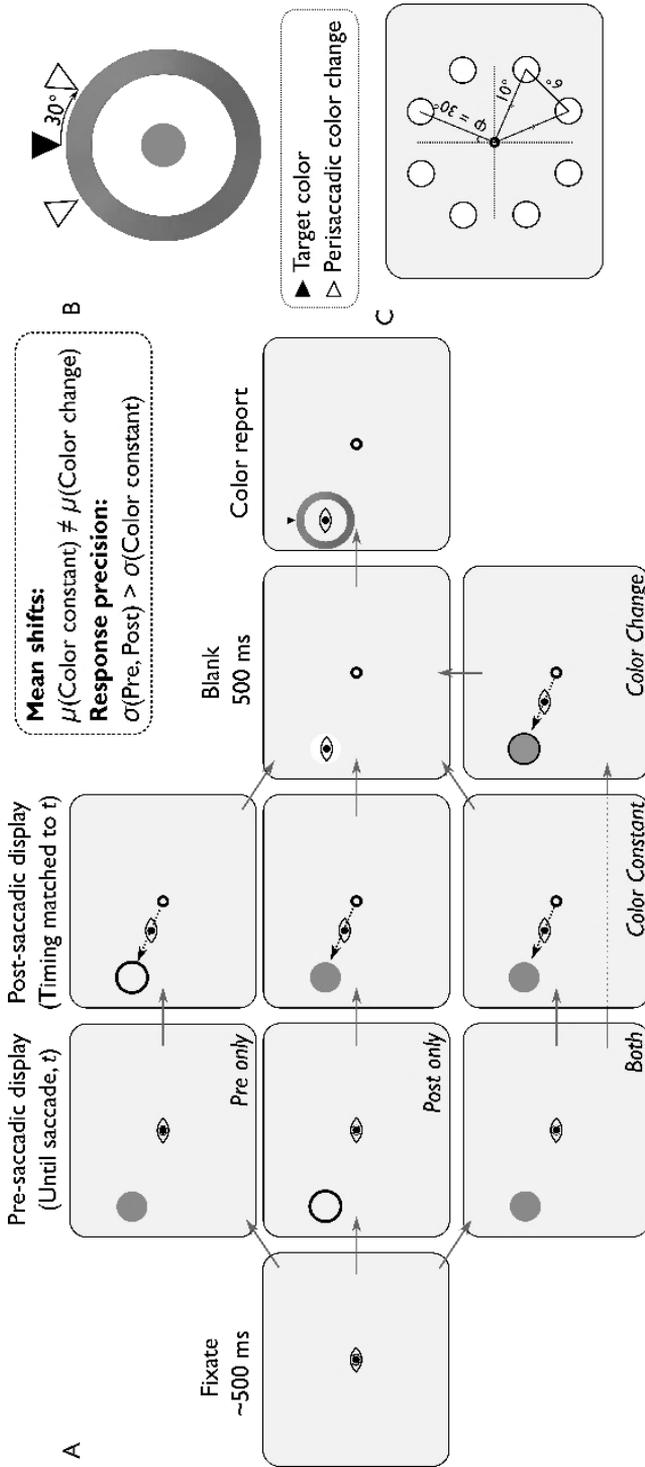


Figure 1. The procedure of Experiment 1. Note that the experiment was presented in inverted contrast (background was black, annulus was white). B) The color wheel used in all experiments, the distance between the white and the black arrows indicate the magnitude of the color change in the experiment. C) Stimuli were presented at one of eight locations relative to the fixation point, as indicated by the circles. A black circle was added to make the color change visible in greyscale.

Procedure

Each observer ($N = 16$) completed 448 trials evenly distributed across all conditions. Trials were counterbalanced across the experimental conditions (Pre Only, Post Only, Color Constant and Color Change), as well as the target location (1 out of 8 locations), resulting in 14 trials per observer per condition. For the analyses, target location was collapsed (thus resulting in a maximum of 112 trials per observer per condition). Observers were instructed to make a saccade to the target and to report the color of the saccade target. There were four experimental conditions, which relate to when the color of the target was visible, and whether the color changed (see Fig. 1A). The stimulus either turned into an annulus after a saccade was made (Pre Only; 25% of trials), started as a white annulus and became colored after a saccade was made (Post Only; 25% of trials) or was colored before and after the saccade (Both; 50% of trials). Trials in the Both condition were divided into Color Constant (25% of total trials) and Color Change trials (25% of total trials). In the Color Change trials, the hue of the target shifted by $+30^\circ$ or -30° . As a measure of feature integration, we: 1) investigated whether responses in the Color Change trials were a mixture of presaccadic and postsaccadic hue, when compared to the Color Constant trials, and 2) investigated whether observers were more precise in reporting the color in the Color Constant (both Pre *and* Postsaccadic color) trials as compared to the Pre Only and Post Only trials.

A typical trial occurred as follows: observers fixated a point in the center of the screen until a saccade target appeared (a circular object). Observers were instructed to execute a saccade as quickly as possible to the saccade target. The (online determined) saccadic reaction time was calculated as the difference between saccade target onset and the recorded gaze position leaving a 1.5° area of interest around fixation. We matched the duration that the stimulus remained on screen postsaccadically to the saccadic reaction time (SRT; the amount of time the stimulus was visible presaccadically). Then, all stimuli were removed from the screen for 500 ms. Finally, observers reported the color of the saccade target by clicking on a color wheel. The selected color was shown in a small circle at the center of the color wheel, observers confirmed their answer by pressing the space bar. Observers were aware that the saccade target was either colored before the eye-movement, after the eye-movement, or both. Unbeknownst to the observer, we included trials in which the color of the saccade target changed during the saccade (a hue change of $\pm 30^\circ$).

Observers first completed twenty practice trials to familiarize themselves with the task, where conditions were randomly assigned. Observers were encouraged to make fast saccades (SRT shorter than 250 ms) and received feedback on their saccade latency after each trial in the practice block through an onscreen message. Furthermore, participants were instructed to not make any additional saccades after directing their gaze toward the target. If, during the practice block, mean SRT was higher than 250 ms, another twenty practice trials were completed. Observers completed 448 trials in 14 blocks, with short breaks between the blocks, and were debriefed at the end of the experiment. At the end of each block, observers received feedback on their mean SRT, and were encouraged to execute saccades faster if their latency was higher than 250 ms. Debriefing consisted of a digitized questionnaire where observers were asked whether they had perceived the color change. None of the observers reported seeing the color change in either the questionnaire or when questioned at the end of the experiment by the experiment leader.

Data Preprocessing

Data preprocessing consisted of two main steps. First, we recalculated the saccade latency and amplitude using offline saccade detection. Then we recoded the target and distractor locations to one quadrant. Saccades were detected offline with the default Eyelink saccade detection algorithm. For all analyses on saccade metrics, we chose the first saccade after the target had been presented, but only if the saccade was started before the postsaccadic probe presentation.

To be able to compare saccade landing distance we recoded all target locations to the same location. We converted the Euclidian coordinates of targets, and saccade landing points to polar coordinates. In polar coordinates, ϕ is the counter-clockwise angle from the horizontal meridian (in degrees) and ρ is the saccade amplitude (in degrees visual angle). Then, we recoded the target locations by collapsing all the target quadrants into one quadrant (see Fig. 1C). This was accomplished by calculating $\phi = \phi - 0^\circ$ from trials in quadrant 1, $\phi = \phi - 90^\circ$ in quadrant 2, $\phi = \phi - 180^\circ$ in quadrant 3, and $\phi = \phi - 270^\circ$ quadrant 4. By subtracting a set amount of degrees from ϕ based on the quadrant, we ended up with all targets represented in one quadrant.

Next, once all targets were recoded to the same quadrant, we recoded the location once more so that the target stimulus was always presented at $\rho = 10^\circ$ and $\phi = 30^\circ$ from the vertical meridian. We did so by calculating $\phi = 90^\circ - \phi$ in trials where the target was presented at 60° degrees. After this final preprocessing step,

each trial was recoded in the same way so that the saccade landing points were represented in the same way (e.g. a saccade with a vector of $\rho = 10^\circ$, $\phi = 30^\circ$ landed exactly on target).

Lastly, we recoded the dependent variable for our analyses. For all our main analyses we entered the difference between the given answer and the presaccadic color as the dependent variable. Where 0° indicates the presaccadic color on the color wheel, positive values indicate answers with clockwise deviations from 0° and negative values counter-clockwise deviations from 0° in the color wheel. In the Color Change trials, the postsaccadic color was either 30° (clockwise) or -30° (counter-clockwise) from the presaccadic color. For the counter-clockwise color change trials, we recoded the direction of the color space by multiplying the reported color by -1 , so that for every trial the postsaccadic color was at 30 degrees (clockwise) from the presaccadic color.

Data Exclusion

From the 7407 trials where a saccade was recorded we excluded 285 trials where a gaze sample was recorded further than 2° from fixation before the target was presented. We excluded 63 trials where a saccade landing point was detected in the wrong quadrant. Furthermore, 198 trials were excluded where the saccade amplitude was lower than 6° or higher than 14° , and 73 trials where the saccade latency was higher than 250 ms. Lastly, we excluded 161 trials in which a corrective saccade was detected, as defined by a saccade that was initiated after the first saccade, which landed before the stimulus was removed from the screen. Some trials did not meet several of these criteria. After exclusion, one participant had less than 50% of the trials left (119 out of 448 trials), this participant was excluded from further analysis. After excluding the participant, 6493 trials were left across all participants. The average amount of trials left per observer was 404 trials (SD = 44, range 256 to 434 trials).

Statistical analyses

Because of the nature of the design, the hypotheses suggesting that saccade landing point does and does not influence transsaccadic integration are equally valid. Therefore, we opted for Bayesian statistics. Bayesian statistics allow us to differentiate between two hypotheses, rather than only rejecting one hypothesis, as in frequentist testing [67]. The outcome of a Bayesian analysis is a Bayes Factors

(BF) which is the ratio of evidence for one hypothesis over another. For example, a test which shows $BF = 100$ for one model indicates that this model is 100 times more likely than the model it is tested against. To interpret the strength of evidence, Kass & Raftery [44] have provided guidelines. A BF of between 1 and 3 is described as providing evidence that is ‘not worth more than a bare mention’. A BF of 3 to 20 provides ‘positive’ evidence, 20 to 100 ‘strong’ evidence and above 100 ‘very strong’ evidence [68]. In the manuscript, we report all BF s in favor of one model over the other, where BF_{10} is the evidence for the alternative hypothesis over the null hypothesis and BF_{01} is the evidence for the null hypothesis over the alternative hypothesis (since BF_{10} is equal to BF_{01}^{-1}). In our design, BF_{10} indicates evidence for the alternative hypothesis (gaze position affecting color reports), whereas BF_{01} is evidence for the gaze position invariance hypothesis. First, we divided the data into two halves using a median split on saccade landing distance. Then, using Bayesian modeling averaging we investigated whether observers reported a different color between saccades that landed closer (lower or equal to the median) or further from the target (higher than the median). The model included three fixed effects: a fixed effect for Condition (Pre Only, Post Only, Color Constant, or Color Change), and a fixed effect for Landing Distance (close vs. far), and an interaction effect between Condition and Landing Distance. Furthermore, a random intercept was added per observer. We compared models that included the fixed effects to models that did not, as evidence for inclusion of the parameter (Bayesian Model Averaging) [70,71]. All reported statistics are within-subject statistics. All priors for Bayesian tests were set to a Cauchy distribution centered at 0° (or 30°) with a width of 0.707 [67,69].

To investigate whether observers integrated information across saccades we used Bayesian t-tests. Our criterion for integration in Experiment 1 was, in the Color Constant condition, a response similar to 0° . For the Color change condition, we tested for a response in between 0° (presaccadic color) and 30° (postsaccadic color). With a Bayesian t-test, we examined whether we collected sufficient evidence for either the hypothesis that that the difference between two (scaled) conditions is more likely to be zero (BF_{01} : $\delta = 0$), or different from zero (BF_{10} : $\delta \neq 0$). Similarly, we used Bayesian t-tests to compare the standard deviation of the responses in the Pre Only and Post Only condition to the standard deviation of the responses in the Color Constant condition. For Bayesian tests, we report the Bayes Factor (BF_{10} or BF_{01}) and the 95% credible intervals (95% CI).

Additionally, we used an optimal observer model as described by Ganmor and colleagues [43]. We calculated the bias in the Color Change condition

($\hat{\mu}_{ColorChange}^*$) and estimated the standard deviation in the Color Constant condition ($\hat{\sigma}_{ColorConstant}^*$). First, we calculated the weighted sum of observer estimates using the following formula: $\hat{\theta}_{ColorConstant}^* = w_{post}^* \hat{\theta}_{post} + w_{pre}^* \hat{\theta}_{pre}$, where $w_{post}^* = \frac{\sigma_{post}^{-2}}{\sigma_{post}^{-2} + \sigma_{pre}^{-2}}$, and $w_{pre}^* = 1 - w_{post}^*$. Next, we calculated the expected response (according to the optimal observer model) in the Color Change condition given the calculated weights for each observer, where $\hat{\mu}_{ColorChange}^* = w_{post}^* (\theta * \mu_{post}) + w_{pre}^* (\theta * \mu_{pre})$. We also calculated the optimal standard deviation with, $\hat{\sigma}_{ColorConstant}^* = (\sigma_{post}^{-2} + \sigma_{pre}^{-2})^{-2}$. We compared the calculated estimates to the observed means in the color change condition using a paired Bayesian t-test. The maximal reduction of variance, given the model, would occur when the standard deviation of the Post only and Pre only conditions are equal. However, since we matched the time of the presaccadic presentation to the postsaccadic presentation, and foveal processing is of higher resolution, we expect that $\sigma_{post} < \sigma_{pre}$, thus resulting in a higher weight of postsaccadic information and a smaller reduction in variance due to optimal integration. In addition, we expect that $\sigma_{both} < \sigma_{post}$, but that this difference will be minimal, as the largest reduction in error is expected when the reliability of presaccadic and postsaccadic visual input is roughly similar ($\sigma_{post} = \sigma_{pre}$, which can be accomplished by e.g. lowering the contrast of the target during the saccade [35,43]). In our design the stimuli were of equal strength before and after the saccade.

Results

To investigate the effect of saccade landing point on transsaccadic perception we compared color reports across saccades that landed close to the target to color reports after saccades that landed far from the target. There were four conditions in our experiment, relating to when the color of the target was visible (Pre Only, Post Only, Color Constant, and Color Change). We observed that observers reported the color of the saccade target in the Pre Only condition, i.e. we found evidence that the difference between the color of the saccade target and response was 0, $BF_{01} = 7.08$, $95\%CI = -3.39^\circ$ to 0.17° . Similarly, observers reported the target

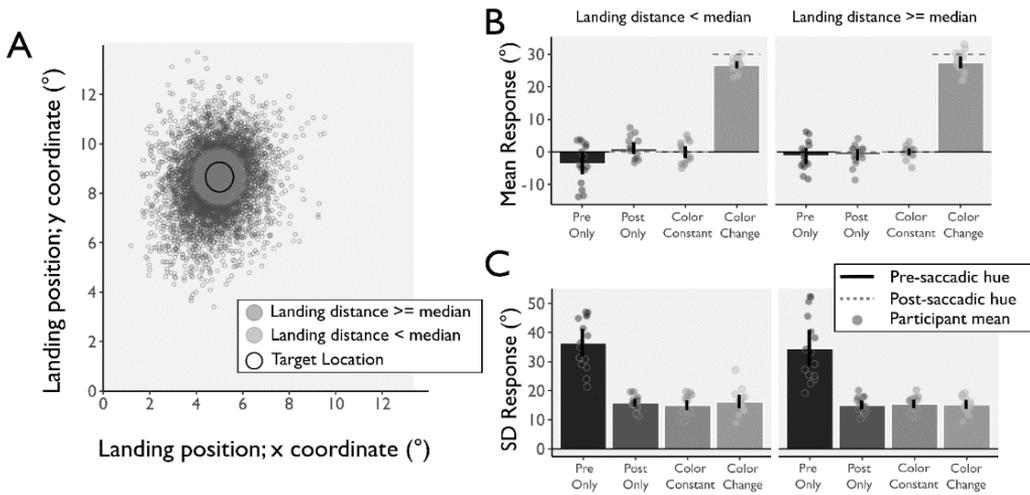


Figure 2. Main results Experiment 1.

A) Observers made saccades to a target (here the black circle). Each dot represents the landing point of one saccade. The two colors represent the median split, close vs. far saccades. B & C) Average responded color per condition and standard deviation of responses per condition, respectively. The bars show the grand mean, the black dots the observer means, the error bars the 95% confidence intervals. The horizontal black lines indicate the Presaccadic color in each condition (if present) and the horizontal red dashed lines indicate the Postsaccadic color in each condition.

color in the Post Only condition, $BF_{01} = 34.7$, $95\%CI = -0.87^\circ$ to 0.70° , and the Color Constant condition, $BF_{01} = 22.49$, $95\%CI = -1.12^\circ$ to 0.38° .

We validated the timing of the color transitions revealing that the screen update happens around 20 ms after saccade onset (Median = 20 ms, IQR = 17 – 24 ms, shown in Supplementary Fig. 2). Here, the draw call is corrected to account for the extra 10ms it takes for the screen to update. The screen update happens around 20 ms before the saccade ends (Median = -23 ms, IQR = -30 – -17ms). In trials in which the stimulus is transitioning into black, another 10 milliseconds should be added to these numbers.

Color reports

We expected that observers in the Color Change condition reported a color that is a mixture (in between) of the presaccadic and the postsaccadic color. In these

trials, a response of 0° would indicate the presaccadic color whereas a reported hue of 30° would indicate the postsaccadic color was reported. We observed that observers indeed neither reported the presaccadic, $BF_{10} = 1.15 * 10^{468}$, nor the postsaccadic color, $BF_{10} = 4.91 * 10^9$ but a color in between, $95\%CI = 26.27^\circ$ to 27.86° .

Second, we compared the standard deviation of the responses in the Pre Only and Post Only condition to the Color Constant condition. The standard deviation was higher in the Pre Only condition (*Average SD* = 36.5°) than in: 1) the Post Only condition, *Average SD* = 15.9° , $BF_{10} = 12638$, $95\%CI = 13.36^\circ$ to 24.73° , 2), and the Color Constant condition, *Average SD* = 15.5° , $BF_{10} = 57254$, $95\%CI = 14.53^\circ$ to 24.60° . We found evidence for no difference between the Post Only condition and the Color Constant condition, $BF_{01} = 2.83$, $95\%CI = -0.57^\circ$ to 1.28° . Thus, observers integrated pre-and postsaccadic information in terms of mean shifts, but this did not reduce the absolute error. All participants had a smaller standard deviation in their responses in the Post Only condition (*Mean difference* = 19.8° , *min* = 7.01, *max* = 36.62).

Effect of landing distance on color reports

Next, we investigated the effect of saccade landing distance on reported color. We divided landing distance into two distances (close, far) using a median split (median distance = 1.18° , *IQR* = 0.75° to 1.80°). The saccade landing points are shown in Fig. 2A. For each condition (Pre/Post Only, Color Constant/Change) we calculated the mean response and standard deviation of the responses per observer, per landing distance. We constructed a Bayesian linear mixed model with mean reported color as dependent variable, and fixed effects for Condition, and Landing distance (median split), as well as an interaction between Condition and Landing distance. The results of the analysis are shown in Fig. 2B, and the Bayesian Modeling Averaging statistics are shown in Table 1. The analysis reveals a main effect of Condition, $BF_{10} = 5.10 * 10^{61}$, no main effect for Landing distance on reported color, $BF_{01} = 2.06$, and evidence against an interaction between Landing distance and Condition, $BF_{01} = 45.87$. Similarly, for the standard deviation of the responses (Fig. 2C) we observed a main effect for Condition, $BF_{10} = 3.84 * 10^{32}$, no evidence for a

Table 1. Parameter estimates for Bayesian Model Averaging analysis investigating how saccade landing distance (median split) affects mean error and standard deviation of errors.

Model parameters	Mean error		Standard deviation	
	<i>BF</i> ₁₀	Error	<i>BF</i> ₁₀	Error
Condition + Observer	3.06 * 10 ⁶¹	0.79%	8.70 * 10 ³²	1.16%
Landing Distance + Observer	1.96 * 10 ⁻¹	2.63%	5.65 * 10 ⁻¹	0.93%
Condition + Landing Distance + Observer	6.22 * 10 ⁶⁰	2.61%	6.42 * 10 ³¹	0.91%
Condition * Landing Distance + Observer ^[1]	3.55 * 10 ⁶⁰	15.2%	3.92 * 10 ³⁰	9.32%
Observer ^[2]	1.00	<0.01%	1.00	<0.01%

[1] The * symbol denotes a model with both main effects and interaction effects.

[2] Bayes Factors have been rescaled to the random effects model (Observer only) for readability.

main effect for Landing distance, $BF_{01} = 2.35$, and evidence against an interaction effect, $BF_{01} = 310.84$. When saccades landed further away from the saccade target, and postsaccadic visual input is presumably sampled at a lower resolution, yet the reported color remains the same.

Optimal observer model

Next, we investigated color reports across saccades in an optimal observer model. Such models provide insights into how observers could theoretically combine both presaccadic and postsaccadic information in a way that utilizes both sources of information in a way that combines the information in a statistically optimal manner. We calculated the weights that observers attributed to pre- and postsaccadic information based on the variance of the color reports in the Pre Only and Post Only condition. These weights were used to calculate the optimal combination of pre- and post-information in the Color Constant and Color Change condition and compared this to the observed standard deviation in the Color Constant condition and the observed mixture colors in the Color Change condition.

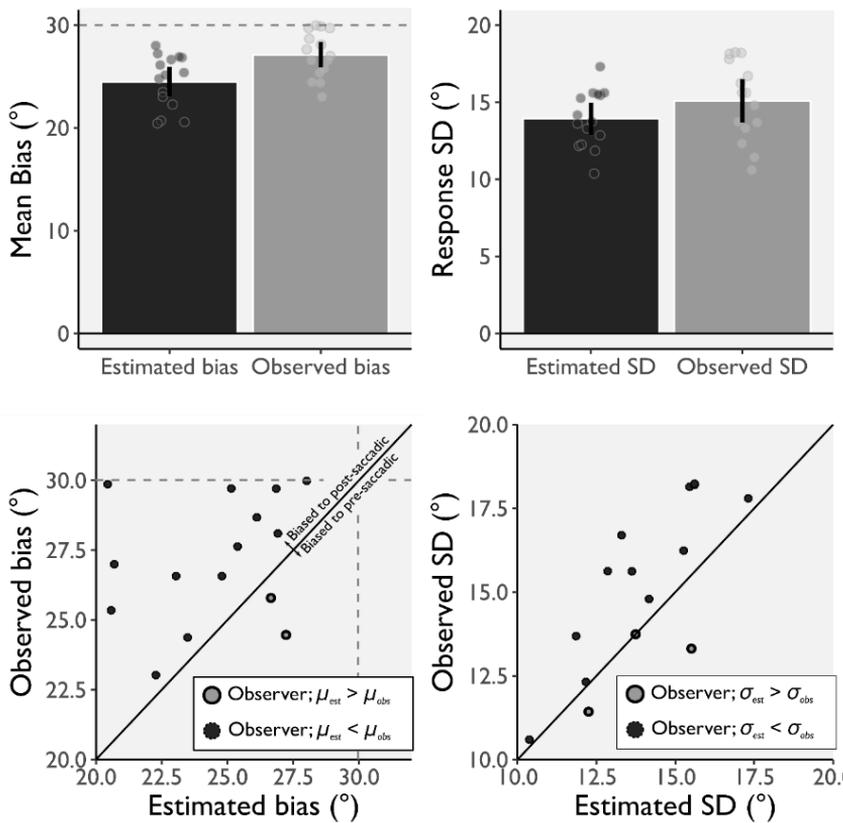


Figure 3. Results from optimal observer model analysis in Experiment 1. In the top panels, the dark bars indicate the estimated bias according to the optimal observer model, whereas the lighter bars indicate the observed bias, i.e. the response in the Color Change condition. The right figure shows the estimate standard deviation versus the observed standard deviation, i.e. the standard deviation in the Color Constant condition. The bias (left plot) indicates that observers are biased towards postsaccadic visual information, whereas the standard deviation (right plot) indicates that participants do not reach optimal performance. In the bottom panels, the dots indicate observer means, the bars indicate 95% confidence intervals. Observer averages for both the bias and standard deviation. The reference line indicates an optimal trade-off between pre- and postsaccadic visual input. Most observers overweigh the postsaccadic (foveal) input. The dashed lines in both left-hand graphs indicate the postsaccadic color of the target.

We investigated two measures within the optimal observer model: 1) bias, which is reflected in the mean reported color in the Color Change and Color Constant condition, and 2) precision, which is reflected by the response error variability. Note that in prior analyses we only observed shifts in the mean (differences in bias) and did not find a reduction in variability. The analysis will provide insight into whether observers could (theoretically) combine presaccadic and postsaccadic information in a more efficient manner. Lastly, we investigated the effect of saccade landing point (close vs. far) on presaccadic and postsaccadic weights.

The estimated values, as compared to the observed (mean) values are shown in Fig. 3. The observed standard deviation in the Color Constant condition was 15.1° ($SD = 2.52$). The optimal standard deviation for the Color Constant condition, based on the responses given in the Pre Only and Post Only condition was 13.94° ($SD = 1.86$), which indicates that it was possible for participants to improve further (respond more precisely). The observed standard deviation in the Color Constant condition was higher than the optimal standard deviation, $BF_{10} = 4.55$, $95\%CI = -1.85$ to -0.16 . The grand mean observed bias was 27.11° ($SD = 2.22$), whereas the estimated bias in the optimal observer model was 24.51° ($SD = 2.59$). We found that the observed bias was more weighed towards to postsaccadic visual input (the observed response is closer to 30° than the optimal response), $BF_{10} = 12.29$, $95\%CI = -3.90$ to -0.76 . In line with prior studies, observers are integrating presaccadic and postsaccadic information close to optimality.

Lastly, we investigated the effect of saccade landing distance on bias and precision. In particular, we were interested to see whether observers weighed presaccadic and postsaccadic information differently if saccades landed further from the saccade target. Using a paired Bayesian t-test we compared the estimated weights for saccades that landed close and saccades that landed further away. The average weight of presaccadic input, w_{pre} (where the postsaccadic weight is given by $w_{post} = 1 - w_{pre}$), for saccades that land nearby was 0.176 , $IQR = 0.069$ to 0.336 . The average w_{pre} for saccades that landed further away from the saccade target was 0.187 , $IQR = 0.062$ to 0.32 . There was no difference in estimated weights for saccades that landed closer or further away, $BF_{01} = 3.36$, $95\%CI = -0.03$ to 0.02 . Consistent with our prior findings, the color reports did not change as the saccade landing point deviated more from the saccade target.

Experiment 2 - Larger landing point deviations

In the previous experiment, we found no effect of saccade landing point on reported hue. The saccade landing point variability in Experiment 1 was relatively small, however. To test our hypothesis in a more extreme situation, we set out to investigate transsaccadic color reports, under deviations that exceed the ones found in everyday situations (e.g. regular oculomotor error such as in Experiment 1). We removed the Pre Only and Post Only conditions from the experiment, as we found no effect of reduction of error when compared to the Color Constant condition. We replaced these conditions with Distractor Present trials. In these trials a salient distractor is presented at the same time as the saccade target. Prior research has shown that by presenting a salient object near a saccade target, cause saccades to land at the geometric mean of these objects [191–193]. We placed the distractor object at 6° from the target. Based on the observation that global effect saccades land (on average) on the geometric mean between the target and distractor, we expect an average deviation of the saccade of 3° . Through this method, saccade landing points will deviate further from the saccade target than in Experiment 1 (where the median deviation of saccade landing point was 1.18°).

Methods

Observers, Stimuli, & Procedure

Given that we debriefed observers at the end of Experiment 1, none of the observers that participated in Experiment 1 participated in Experiment 2 ($N = 16$, 10 Female, $M_{age} = 22.3$). In Experiment 2, a white distractor object could be presented simultaneously with the saccade target (Fig. 4, radius = 0.5° , 31.2 cd/m^2). The saccade target and the distractor were presented at an eccentricity of 10° visual angle from fixation (Fig. 1C). The distractor was always presented within the same quadrant as the saccade target, at a distance of 6° visual angle from the target. The size of the stimuli and distance between distractor and saccade target were chosen to favor a strong global effect, based on prior research [194].

Data Preprocessing & Exclusion

The number of recorded trials was identical to Experiment 1. Observers completed 448 trials, counterbalanced across the experimental conditions (Color Constant/Change and Distractor Absent/Present). Thus, a maximum of 112 trials was recorded per observer per condition after collapsing across target locations (8

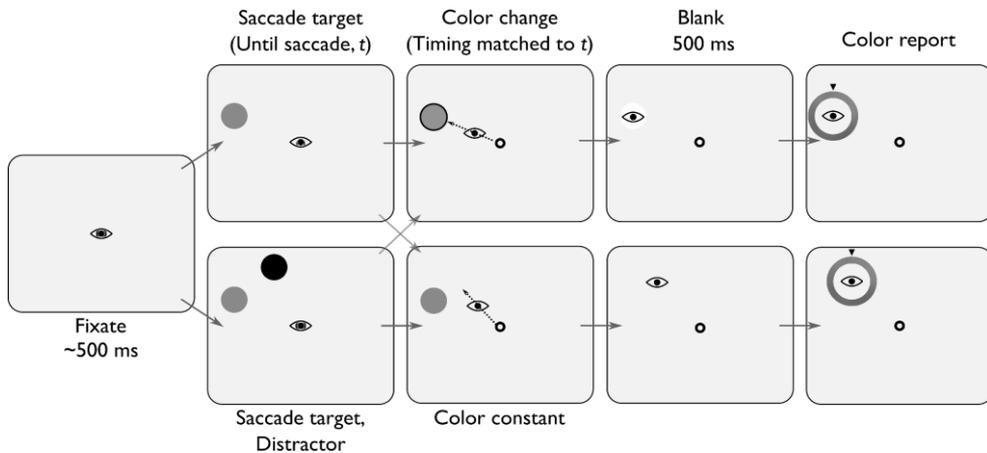


Figure 4. Procedure Experiment 2. A salient distractor object could appear at the same time as the saccade target (colored circle). Note that the figure is presented in inverted contrast, in the experiment the background was black, and the distractor was white. A black outline was added to make the color change visible in greyscale.

possible locations). We excluded trials (from a total of 6990 trials in which a saccade was detected) based on the same criteria as in Experiment 1. First, we excluded a trial if a gaze sample was recorded further than 2° from the fixation point before the target was presented (0 trials). Second, a trial was excluded if a saccade landing point was detected in a quadrant where no target was present (10 trials). Third, if a saccade had an amplitude lower than 6° or higher than 14° (606 trials). Fourth, if a saccade had a latency of higher than 250 ms (32 trials), and lastly, if a corrective saccade was made (180 trials). After exclusion, one participant had less than 50% of trials left, this participant was excluded (159 trials left of 448). Thus, after exclusion, 5989 trials were left for analysis (Mean trials per observer = 399, $SD = 38$, range 310 to 440 trials).

Statistical analyses

The analyses of Experiment 2 were largely similar to the analyses in Experiment 1. All reported statistics are within-subject statistics. First, we examined whether our saccade landing point manipulation (presenting a distractor) was successful in increasing saccade landing point deviations (i.e. whether there was a global effect). We compared the Euclidian saccade landing distance from the target

in the Distractor Absent trials to the Distractor Present trials. To quantify this, we chose to use a Bayesian t-test. To quantify the difference in color reports between Distractor Present and Distractor Absent trials we ran a full factorial linear mixed model that predicted the difference between the reported hue and the presaccadic hue. The model included three fixed effects: a fixed effect for Color (change vs. constant), a fixed effect for Distractor Presence (present vs. absent), and an interaction effect between Color and Distractor Presence. Furthermore, a random intercept was added per observer. The rest of the statistics largely follow the procedure of Experiment 1.

Results

We investigated the effect of saccade landing point on color reports when saccades deviate far from the saccade target by making use of the global effect. We manipulated the landing points of saccades by showing a salient distractor in half of the trials (Distractor Present/Absent) at the same time as a colored saccade target. Observers were tasked with indicating the color of the saccade target on a color wheel. In half of the trials the color of the saccade target changed during the saccade (Color Change/Constant).

Effect of distractor presence on saccade landing error

We examined whether saccade landing points were different in Distractor Present trials as compared to Distractor Absent trials. Observers landed, on average, 1.17° ($SD = 0.72$) from the saccade target in the Distractor Absent condition. In the Distractor Present condition, we observed an average landing error of 2.89° ($SD = 1.50$). The landing error was higher in the Distractor Present trials as compared to the Distractor Absent trials, $BF_{10} = 4.24 * 10^{10}$, $95\%CI = 1.57$ to 1.85 (Fig. 5A). Next, we investigated whether saccades landed in-between the target and the distractor in the Distractor Present trials, or saccades got less precise overall in the Distractor Present condition. To this end, we compared the mean polar angle of saccades in the Distractor Present and Distractor Absent conditions, where the target is presented at a polar angle of 30° and the distractor at a polar angle of 60° . In the Distractor Absent condition, observers made saccades with an average polar angle of 30.1° ($SD = 4.97$). In the Distractor Present condition, this average was 44.8° ($SD = 10.28$). A Bayesian t-test revealed that saccades in the Distractor Present condition were angled more towards the distractor as compared to the Distractor Absent

Table 2. Parameter estimates for Bayesian Model Averaging analysis investigating how saccade landing distance affects reported color across Color Change/Constant conditions. In the left column landing distance is the comparison between distractor present vs. distractor absent trials, in the right column landing distance is a continuous measure of saccade deviation relative to the center of the saccade target.

Model parameters	Landing distance as Distractor present vs. Distractor Absent		Landing distance as a continuous measure	
	<i>BF₁₀</i>	<i>Error</i>	<i>BF₁₀</i>	<i>Error</i>
Color Change + Observer	1.01 * 10 ⁶⁷³	1.35%	1.01 * 10 ⁶⁷³	1.07%
Distractor Present / Landing Distance + Observer	0.028	1.14%	0.18	1.23%
Color Change + Distractor Present / Landing Distance + Observer	3.02 * 10 ⁶⁷¹	2.92%	5.02 * 10 ⁶⁷¹	4.49%
Condition * Distractor Present / Landing Distance + Observer ^[1]	3.89 * 10 ⁶⁷⁰	5.92%	5.22 * 10 ⁶⁷⁰	1.62%
Observer ^[2]	1.00	<0.01%	1.00	<0.01%

*[1] The * symbol denotes a model with both main effects and interaction effects between the parameters.*

[2] Bayes Factors have been rescaled to the random effects model for readability.

condition, $BF_{10} = 8.45 * 10^{14}$, 95% $CI = 14.12$ to 15.23 . These findings are indicative of a global effect, confirming the successful manipulation of saccade landing point by presenting a distractor, and increasing the average distance to the target from 1.17° to 2.89° .

Effect of saccade landing point on color reports

Next, we examined the reported hue across the different conditions. To recapitulate, a response of 0° would mean an observer reported the target hue exactly. In the Color Change condition, a reported hue of 30° represents the target hue of the postsaccadic color. The mean reported hue, with respect to the presented hue, in the Distractor Absent/Color Constant trials was -0.86° ($SD = 2.66$). In the Distractor

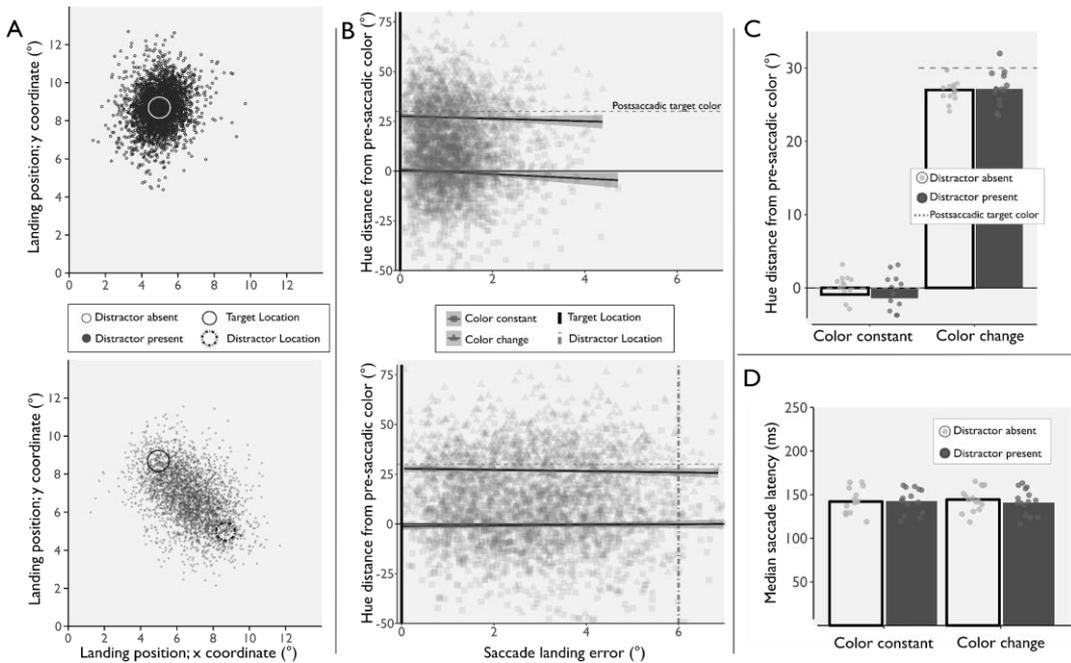


Figure 5. Results from Experiment 2.

A) Saccade landing points in the Distractor Absent (upper panel)/Present (lower panel) conditions. On average, saccades landed farther away from the saccade target in the Distractor Present condition than in the Distractor Absent condition. B) Linear fit to saccade landing error and reported color in the Distractor Absent (upper panel)/Present (lower panel) conditions. None of the slopes were different from 0, indicating no effect of saccade landing distance. Shaded regions indicate the standard error of the fit, the transparent points are individual responses. C) Average reported color per condition. D) Median saccade latency across conditions.

Present/Color Constant condition observers reported a hue of -1.54° ($SD = 3.44$). Lastly, on average, observers reported a hue of 26.87° ($SD = 1.75$) in the Distractor Absent/Color Change condition, and a hue of 27.5° ($SD = 2.3$) in the Distractor Present/Color Change condition (see Fig. 5C). A Bayesian model averaging analysis (parameter estimates are shown in Table 2) shows evidence for the inclusion of the factor Color Change to predict reported hue, $BF_{10} = 1.52 \times 10^{73}$. We observed no main effect of Distractor Presence on reported color, $BF_{01} = 19.78$. Lastly, we observed evidence against inclusion of interaction effect between Distractor Presence and Color Change, $BF_{01} = 1067$. These results indicate that observers

reported a different color in the Color Change condition, but this response was not affected by the presence of a distractor.

To examine the effect of landing position in more detail we analyzed color performance in relation to Landing Error (as a continuous measure), rather than Distractor Presence (dichotomous). Landing Error was defined as the Euclidian distance between saccade landing point and midpoint of the target (x-axis in Fig. 5B). With a Bayesian Model Averaging analysis, we found evidence that models including Color Change as a fixed effect outperformed models that did not $BF_{10} = 1.35 \times 10^{73}$. We observed that models that included the factor Landing Error performed worse, $BF_{01} = 12.12$. Lastly, the interaction between Color Change and Landing error was not significantly predictive of the reported color, $BF_{01} = 814.83$. Together, these analyses show that observers did not respond differently in the presence of a distractor that caused the eye to land far from the saccade target.

Control analysis – Reporting color mixtures

Next, we examined whether observers were reporting a mix of the pre- and postsaccadic colors in the Color Change condition, rather than only the postsaccadic color. In the Color Change condition observers were answering significantly different from both the postsaccadic color, $BF_{10} = 16.9$, 95% CI = 24.5 to 29.5, and the presaccadic color $BF_{10} = 2.1 \times 10^{702}$. Participants are responding accurately, as in the Color Constant condition, we find that observers are reporting the target hue, $BF_{01} = 3.1$, 95% CI = -3.54 to 1.46. Lastly, because we observed a slight counter-clockwise bias in the Color Constant condition (reports $< 0^\circ$), we directly compared the Color Constant and the Color Change conditions. A comparison between conditions showed that the reported color in the Color Change condition deviated more from the post saccadic color than the reported color in the Color Constant condition deviation from the pre- saccadic target color, $BF_{10} = 3233$, 95% CI = 1.09 to 2.71. We conclude that changing the color of the saccade target during the saccade significantly affects the reported color, to a color that is in-between the presaccadic and postsaccadic color.

Control Analysis – Saccadic latency

We examined whether saccade latencies differed across conditions, as differences in presaccadic exposure to the stimulus may affect the weights of the reported mixture color. The median saccade latency across conditions was 159 ms

(IQR 142 – 175; see Fig. 5D). We ran a Bayesian Model Averaging analysis, with Color Change and Distractor Presence as fixed effects and Saccade Latency as dependent variable. We found no main effect for Color Change, $BF_{01} = 13.41$, no main effect for Distractor Presence, $BF_{01} = 22.43$, and no interaction effect between Color Change and Distractor Presence, $BF_{01} = 4920867$. Thus, saccade latencies were the same across conditions.

Discussion

In the current study, we set out to investigate whether and how trial-by-trial deviations in saccade landing point affect transsaccadic feature perception. Saccade landing points naturally slightly deviate from the intended target location. Observers remain unaware of these deviations, allowing for continuous visual perception. From prior research it is clear that the position of visual information with respect to the eye affects the reliability of perceptual information [33]. Therefore, one could reason that deviations in saccade landing point would cause similar alterations in reliability of visual input. In Experiment 1, we investigated how saccade landing point affected integration of feature information across saccades (i.e. combining pre and post saccadic visual input) in terms of shifts in the mean reported color and a reduction of variance [33,35,43]. Saccade landing point did not affect bias and precision of the reported color. Even when landing far away from a saccade target, observers did not report a different color, presumably because these deviations were not affecting the postsaccadic reliability of the visual input.

We investigated color reports with an optimal observer model. We calculated the (statistically) optimal weights in combining presaccadic and postsaccadic information, to utilize both pre- and postsaccadic visual input to its fullest extent [35,43,195]. In line with prior research, we found that observers were generally overweighing the foveal/postsaccadic visual input [35,43]. We replicated the finding that observers' behavior is close to, but not quite, statistically optimal. However, whether transsaccadic feature integration really is a process that follows optimal Bayesian cue integration is difficult to say given that we could not compare observed percepts with optimal percepts for different stimulus reliabilities as we did not use degraded postsaccadic stimuli in the current study. In general, it seems that observers are somewhat predisposed to weigh foveal input more strongly than what would be predicted from the reliability. This is similar to multisensory perception in which the (more spatially reliable) visual input is overweighed relative to the auditory (less reliable) input [195–197]. Importantly, the optimal observer models

allowed us to investigate whether observers weigh pre- and postsaccadic information differently across larger deviations in saccade landing point. These analyses showed that observers did not weigh presaccadic and postsaccadic information differently across saccadic landing positions, even when landing further away from the saccade target.

In Experiment 2 we set out to increase deviations in saccade landing point beyond the deviations that are observed when making a saccade to a single target (like in Experiment 1). To this end, we presented a distractor at the same time as the colored target. As expected, saccades in trials in which both a distractor and a target were present landed in between the target and the distractor. We investigated the effect of saccade landing point on color reports in distractor present trials. Even under the relatively large saccade landing point deviations in Experiment 2, we found that color reports did not differ between saccades that landed closer to as compared to further away from to the saccade target. This finding is striking as, cone density drops off steeply with increasing distance to the fovea [185]. Behavioral studies have shown that color perception declines steadily with increasing distance from the fovea, although color can still be perceived to some extent up to 50 degrees in the periphery [1]. However, in our experiments, even though the color information of the (relatively small) target stimulus is located up to 6 degrees from the high cone density area of the retina, it does not alter how observers weigh presaccadic and postsaccadic visual input.

The finding that color reports are unaffected by saccade landing point raises the question as to how the visual system can accomplish such stability. Prior studies have found behavioral evidence supporting a separation of intended and actual saccade landing point, showing that visual attention is not mandatorily coupled to the saccade landing point [17,18]. This may be especially useful when visual information needs to be sampled specifically at the intended saccade landing point, rather than the actual saccade landing point. In line with this proposed mechanism, one notable study has found that by redirecting attention by presenting a salient presaccadic distractor both saccade motor performance and integration of pre- and postsaccadic feature information was impaired [37]. The authors conclude that attention may be a mechanism which facilitates or allows for transsaccadic feature integration. The critical difference with our study and the Stewart & Schütz [37] study is that the distractor was presented at an unpredictable moment, thus involuntarily redirecting attentional resources to the distractor. In our experiment, it is likely that attentional resources are distributed across the target and distractor, and

not necessarily redirected away from the saccade target. Our study adds that disparity between intended and actual saccade landing point can be as large as 6 degrees visual angle without affecting transsaccadic perception, if attentional processes are not disrupted, underlining the remarkable stability of visual perception in the face of motor variance.

The current results complement the prior hypothesis that the distance to fixation affects the reliability of visual input. In the series of experiments by Oostwoud-Wijdenes and colleagues [33] observers fixated further away from the colored targets, and fully intended to do so, causing no dissociation between point of fixation and visual attention. Therefore, in the previous study, attention (*and* the point of fixation) was deployed further away from the color targets, causing a decrease in the reliability of visual input. In the current set of experiments, the saccade deviations were relatively unnoticed by the observers, as attention was still deployed to the saccade target, even when the saccade landing point differed from the position in space where attention was deployed. The combined results from Oostwoud-Wijdenes' study [33] and the current study raise important implications when investigating transsaccadic perception: both the actual and intended saccade landing point need to be taken into consideration when considering an experimental design.

In Experiment 1, we found a shift in bias, but no increased precision of color reports. Further investigating the optimal observer model revealed that observers could have, theoretically, combined pre- and postsaccadic information more optimally to reduce their error beyond the standard deviation that we measured. First, this may be due to a design limitation, where participants are reporting the color of the object on a color wheel. Here, we introduced some motor error on top of the existing sensory error, whereas prior studies implementing the optimal-observer model to study feature integration used a binary (unsped) response [35,43]. We somewhat expected these results, as they are related to a necessary trade-off in experiment design when studying transsaccadic integration. To elaborate, studies that found higher precision due to combining pre- and postsaccadic visual input used degraded postsaccadic stimuli [35,43]. Likely, foveal visual perception is so rapid and accurate that reduction of error due to combining extra-foveal (presaccadic information) and foveal input does not typically occur outside of a controlled (psychophysical) environment where foveal visual input can be degraded (see [198]). In the current study, we opted to *not* use degraded foveal stimuli. Degrading a visual stimulus necessitates a particularly large change in the stimulus content during the

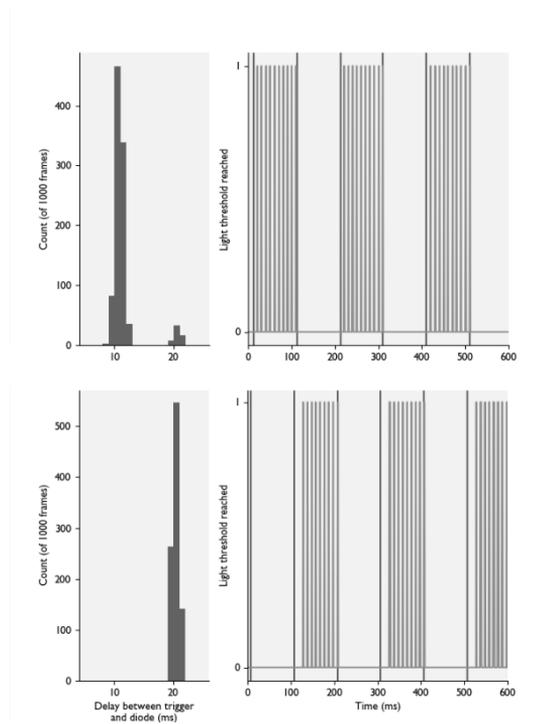
saccade. Therefore, when using degraded visual stimuli observers will be aware that something is changing when they are making a saccade. We were concerned that degrading the postsaccadic color in Color Constant trials would affect awareness of the changing color in these trials. Prior studies have shown that observers are more likely to notice multiple changes, (e.g. location and feature) than single changes, and crucially, that these changes can affect object recognition [102,199]. Reducing the amount of time the stimulus is shown on screen postsaccadically would likely not influence the pre- and postsaccadic weights much, as postsaccadic visual input is weighed and processed immediately after the saccade [35]. Furthermore, we were similarly restricted in not being able to change the position of the target, as it would (likely) break object correspondence. Here, we opted to use an experiment in which we were more likely to find integration in terms of mean shifts, than in terms of error reduction, while ensuring a lack of awareness of the changes in colors across conditions.

Lastly, we note that transsaccadic feature integration is a contentious topic, where many studies find limited or non-existent transsaccadic feature integration [181,200]. This contentiousness within the literature of transsaccadic feature integration is especially striking when compared to the strong body of literature supporting the transfer of *spatial* information (attentional pointers) across saccades [175,200,201]. At current, whether transsaccadic feature integration is indeed a literal transfer and mixing of features, or some other higher-order process remains debated. It seems that feature integration may require congruence between signals, as shown in multisensory integration [202,203]. Similar conclusions on the stimulus specificity of transsaccadic feature integration are drawn from a study which shows that presaccadic (visual) motion integration across the currently attended and predictively remapped locations, but only for congruent motion signals [188]. Importantly, earlier studies largely disproved the existence of transsaccadic fusion, using highly dissimilar spatial arrays [181], whereas more recent studies seem to examine transsaccadic memory processes, using similar pre- and postsaccadic visual input [33,35,43]. Regarding memory-based transsaccadic feature integration, our study adds that is likely a process which is saccade landing point invariant and is possibly facilitated or modulated by visual attentional processes. Lower order visual processes are typically more spatially selective, due to overall smaller receptive field sizes in earlier parts of the visual processing hierarchy [184]. The lack of spatial selectivity in our study, and the requirement of congruence of the signal across saccades, can be seen as (moderate) support that transsaccadic feature integration is

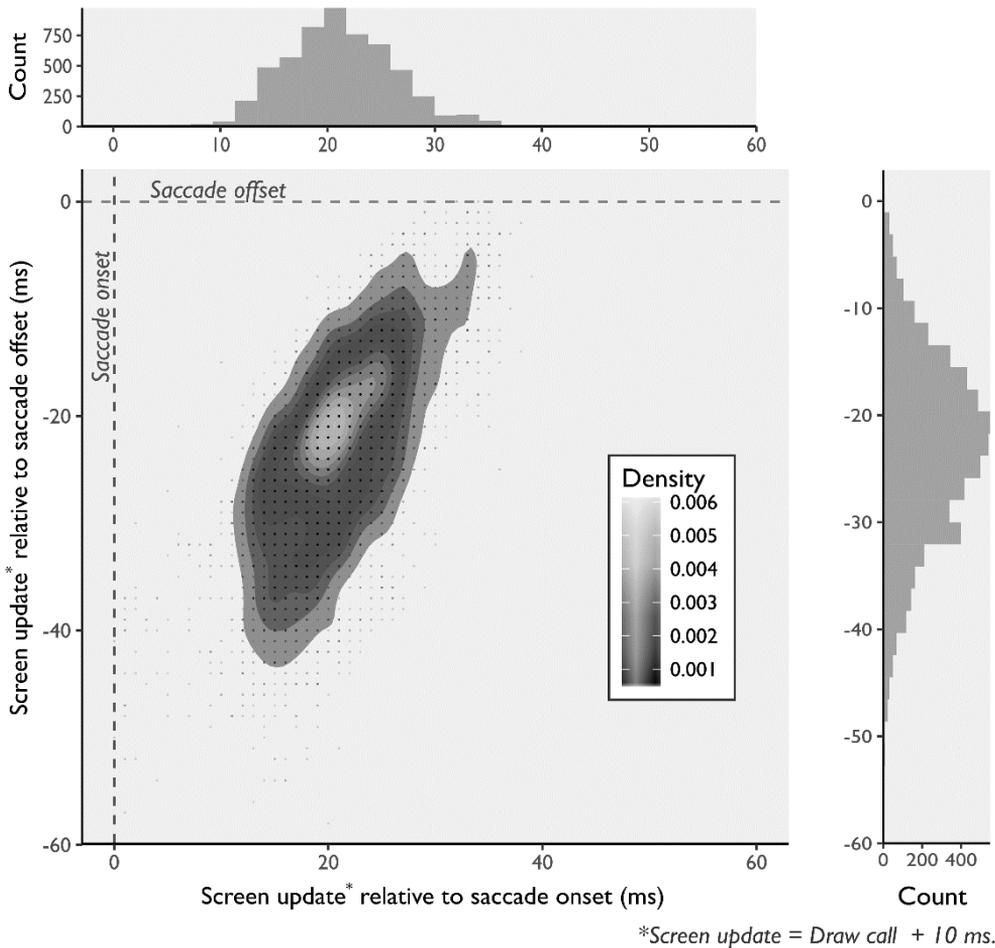
a higher order process [36]. Furthermore, several studies report that spatial judgement tasks may rely on saccade execution [175,204]. From our findings that saccade landing point does not affect feature integration we suggest that, transsaccadic feature integration may be a separate process from transsaccadic spatial judgements, where spatial information needs to be transferred across saccades.

In conclusion, in the current study we set out to investigate the effect of saccade landing point deviations on transsaccadic integration. As transsaccadic feature integration remains a somewhat contentious topic, we aimed to investigate how the parameters of a saccade may affect this process. We hypothesized that, if attentional deployment is separate from saccade landing point, then pre- and postsaccadic information is weighed and integrated similarly even when saccades deviate away from the saccade target. In line with this hypothesis, we found no indication that deviations in saccade landing point affected transsaccadic integration. The deviations induced were as large as 6 degrees visual angle, but we presume that with much larger deviations in saccade landing point transsaccadic integration would be affected at some point. However, deviations of this magnitude would likely not occur under everyday viewing circumstances in healthy observers. Taken together, this study provides compelling evidence for the disparity between the intended saccade target (locus of attention) and the actual saccade landing point. Based on prior research, we speculate that this disparity is the results of two flexible remapping systems, one based on memory/attentional pointers and another which predicts motor execution. These mechanisms, separating attentional deployment from saccade execution, may very well underlie our stable representation of the visual world, despite frequent deviations in saccade landing point due to oculomotor variation. It seems that these systems are so efficient in their interaction that stable perception can be facilitated outside the range of regular oculomotor variance, offsetting the lower acuity of postsaccadic visual input when a saccade deviates away from its intended target.

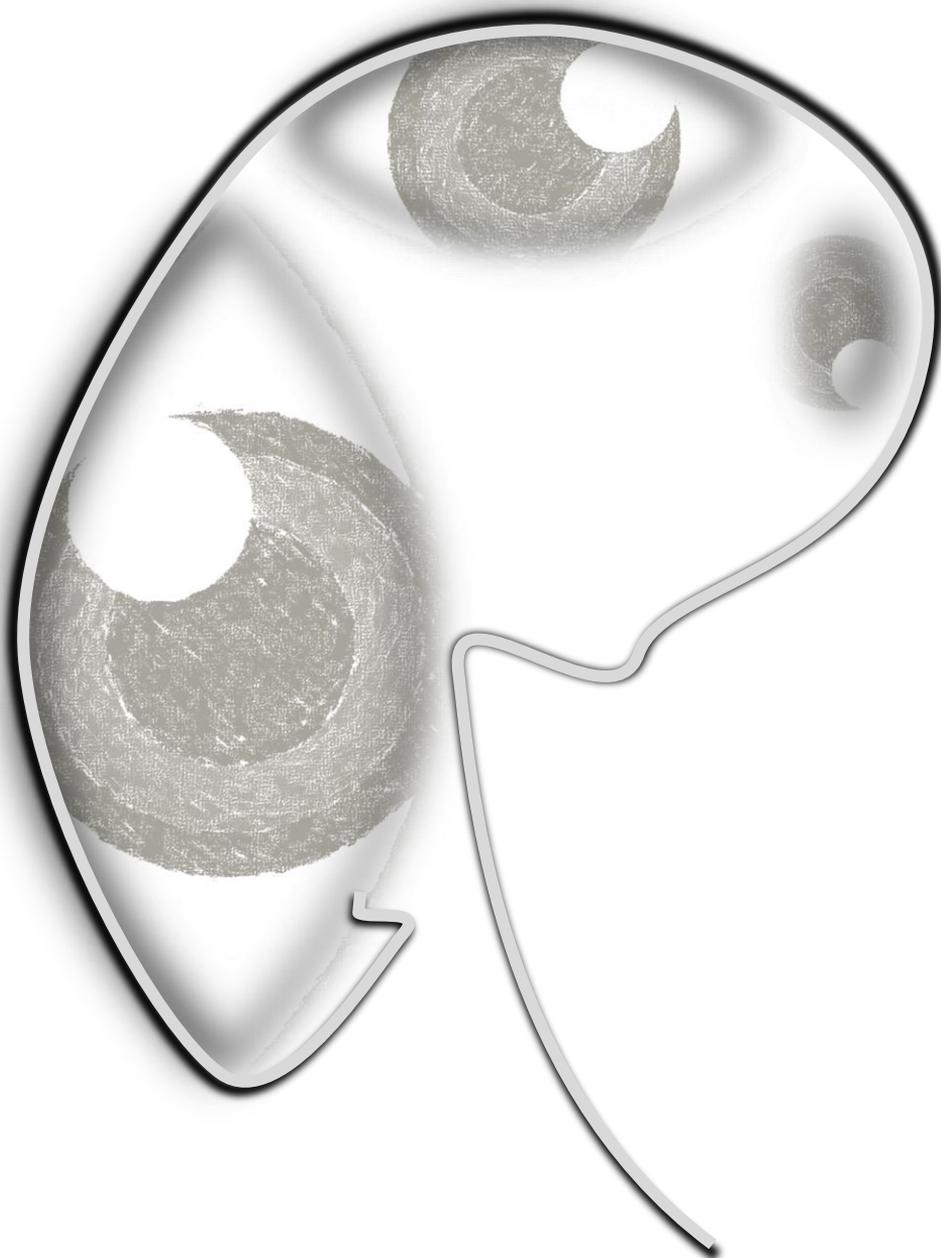


Supplemental Material

Supplementary Figure 1. A histogram of the measured delays and a timeseries plot of the photodiode and draw calls. The histogram shows the delay between draw calls for 1000 repetitions. In the top figure we measured response time between the most luminant and least luminant color in our experiment. In the bottom figure we switch between the most luminant color and black. The line in the right figure represents the status of the photodiode. The vertical lines represent the draw calls.



Supplementary Figure 2. Timing of the stimulus onset, relative to the saccade onset and offset. The contour plot shows the joint distribution of stimulus onset relative to both the saccade onset and the saccade offset. In the contour plot, each point represents a screen update in Experiment 1. A density plot is overlaid, where the highest density corresponds with the medians of the two single distributions (~20 ms to saccade onset/offset). The two histograms show the distribution of the saccade offset/onset. Note that the screen update is a corrected number, by retrieving the timing of the draw call and adding the median screen response time as measured by a photodiode.



Chapter 6

Auditory spatial attention is encoded in a retinotopic reference frame across eye-movements.

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Author contributions

MJS, NvdS, & SvdS conceptualized and designed the experiment. MJS programmed the experiment, collected the data and performed the analyses. MJS wrote the manuscript, and NvdS, and SvdS commented on and co-authored the manuscript. SvdS funded the research.

Summary

The retinal location of visual information changes each time we move our eyes. Although it is now known that visual information is remapped in retinotopic coordinates across eye-movements (saccades), it is currently unclear how head-centered auditory information is remapped across saccades. Keeping track of the location of a sound source in retinotopic coordinates requires a rapid multi-modal reference frame transformation when making saccades. To reveal this reference frame transformation, we designed an experiment where participants attended an auditory or visual cue and executed a saccade. After the saccade had landed, an auditory or visual target could be presented either at the prior retinotopic location or at an uncued location. We observed that both auditory and visual targets presented at prior retinotopic locations were reacted to faster than targets at other locations. In a second experiment, we observed that spatial attention pointers obtained via audition are available in retinotopic coordinates immediately after an eye-movement is made. In a third experiment, we found evidence for an asymmetric cross-modal facilitation of information that is presented at the retinotopic location. In line with prior single cell recording studies, this study provides the first behavioral evidence for immediate auditory and cross-modal transsaccadic updating of spatial attention. These results indicate that our brain has efficient solutions for solving the challenges in localizing sensory input that arise in a dynamic context.

Introduction

Introspectively, determining that visual input matches auditory input appears trivial. Yet, comparing the location of sensory input between senses is complicated, because locations are encoded in different reference frames, native to their sensory modality. Within midbrain structures, the locations of visual input are encoded relative to the retina (retinotopic, also oculocentric), whereas auditory locations are initially encoded relative to the head [45,205–209]. Additionally, animal studies have shown that auditory coordinates are also (partially) converted into the dominant visual reference frame (i.e. a retinotopic coordinate space map), in structures such as the superior colliculus [210–215]. Adding to this complexity, each eye-movement shifts the retinotopic location of visual input [11,25]. Humans make several eye-movements per second, requiring auditory spatial information to be represented in retinotopic coordinates immediately after an eye-movement to allow for comparison of auditory and visual locations. Key papers have shown that gaze/eye position affects auditory localization: 1) by shifting the localization of auditory stimuli towards the gaze position, and 2) improving localization of auditory stimuli at the gaze position [216–219]. Yet, how eye-movements, and the introduction of disparity between the retinotopic and craniotopic reference frame, may cause auditory spatial attentional pointers to update is less clear.

Previous studies have shown that observers continue to transiently sample visual information at previous retinotopic locations (retinotopic trace) for a brief period after an eye-movement has been made, due to retinotopic encoding and lingering of visual attention [220,221]. Compared to stimuli at non-retinotopically matched locations, stimuli at the location of the retinotopic trace (1) are responded to faster [220,222], (2) elicit an enhanced P1 and anterior N1 event related potential component [223,224], and (3) correlate with differential blood oxygen level-dependent response patterns in primary visual cortex (V1) and further in the visual processing hierarchy (V4) [224]. These findings (both behavioral and neurophysiological) show that visual attention is retinotopically encoded, and that visual attention lingers in retinotopic coordinates after an eye-movement.

The behavioral effects of the retinotopic lingering of visual attention can be observed in a task originally described by Golomb and colleagues [220]. In this paradigm, participants are instructed to remember the exact location of a stimulus (the memory cue). After this, participants are cued to make a saccade. After the saccade is executed, an oriented bar (probe) is presented at either the previous

retinotopic location, the spatiotopic location, or a different (neutral) location after a short or a long delay between saccade offset and probe (target) onset. The authors observed shorter reaction times to the probe when presented at the previous retinotopic location shortly after the saccade, compared to probes presented at other locations shortly after the saccade. The authors attribute this facilitation effect to lingering of visual attention at the location of the retinotopic trace. This attentional lingering at previous retinotopic locations diminished for probes presented later after the saccade, reflecting the decay of the retinotopic trace. In contrast, reaction times to probes at spatiotopic locations are facilitated at longer delays. The authors argue that spatiotopic attentional facilitation with longer delays is the result of attentional updating from the prior retinotopic location to the new spatiotopic location. In conclusion, visual spatial attention is natively encoded in a retinotopic reference frame.

If auditory locations are also encoded in retinotopic coordinates, attentional lingering at the location of the retinotopic trace after a saccade should be observed after both auditory and visual stimulation. Furthermore, it is currently unclear whether the time course of the decay of attention at the location of the retinotopic trace is similar for audition and vision. If the magnitude and the time course of attentional facilitation of the retinotopic trace is similar across modalities, it would suggest that visual and auditory attention are affected by a shared attentional updating process.

The experiments by Golomb and colleagues provide evidence for a dual-process model of attentional updating [220,225]. In this model, visual attention lingers in retinotopic coordinates immediately after a saccade, and visual attention is simultaneously updated to the new spatiotopic location. The observed attentional facilitation at spatiotopic locations increases with longer delays, whilst attentional facilitation decreases at the retinotopic location with longer delays. Interestingly, spatiotopic updating is slower when less visual information is available, whereas retinotopic lingering is unaffected by the amount of visual input [226]. In the current study, the visual-only task will have the fixation point, memory cues, and probes as visual anchors. The auditory-only task will only have the fixation point as a visual anchor. We expected this reduction of visual anchors to slow spatiotopic updating relative to the visual-only condition, perhaps halting it altogether.

In sum, we expected spatiotopic updating for visual stimuli, and slower spatiotopic updating for auditory stimuli. We expect both auditory and visual information to be represented in retinotopic coordinates immediately after the

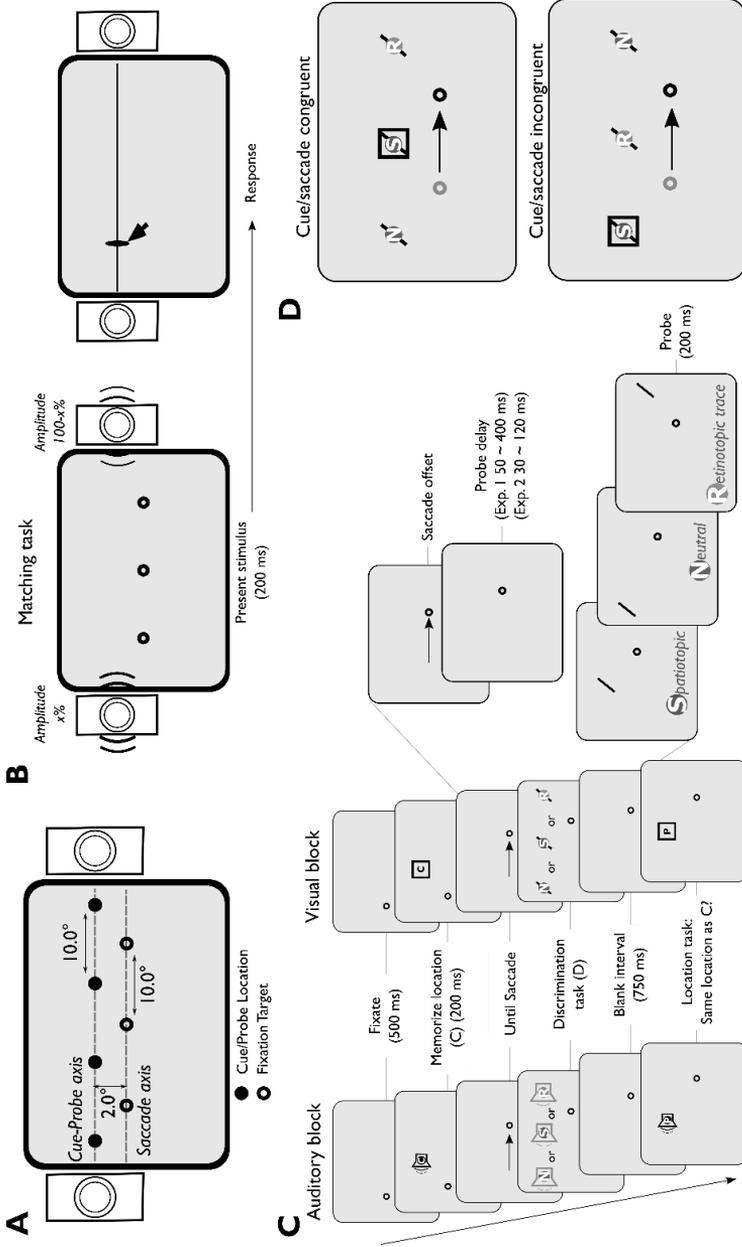


Figure 1. Experimental procedure for Experiment 1 and 2. A) An illustration of the set-up. Stimuli could appear on two axes on the screen. Fixation targets were presented on the bottom axis, cues and probes on the upper axis. B) A trial in the matching task. White noise was presented for 200 ms, participants clicked where they heard the sound originating from. C) Experimental procedure during the auditory and visual blocks. The discrimination task portion of the trial is shown in further detail on the right. There were different probe locations and probe delays. D) An example of congruent and incongruent probe and memory locations with respect to saccade direction. Square = visual cue location, diagonal line = visual probe location.

saccade. To investigate whether auditory spatial attention is immediately available in retinotopic coordinates across eye-movements, we adapted the design used by Golomb [220], and created an auditory analogue to the visual task (see Fig. 1).

Methods

Subjects

Subjects reported normal or corrected-to-normal vision and hearing (Experiment 1: $N = 17$, 12 Female, $M_{age} = 23.4$ years, Experiment 2: $N = 17$, 9 Female, $M_{age} = 22.2$ years). Participants were compensated with €14,- for two hours. Written informed consent was obtained from all participants. All experiments were approved by the faculty ethics committee of Utrecht University (FETC) and in accordance with the Declaration of Helsinki.

Setup

The experiment was conducted in a darkened, sound-attenuated lab. Participants were seated with their head supported in a chin rest 70 cm from an Asus ROG Swift PG278Q monitor (60.1x34.0 cm, 2560x1440 pixels, 100 Hz). Auditory stimuli were presented with two speakers (Harman/Kardon HK206, frequency response: 90–20,000 Hz), placed along the vertical edges of the screen. The speaker cones were placed 2° above the horizontal meridian of the screen (i.e. at the cue-probe axis), 60° apart horizontally (see Fig. 1A). Eye-movements were recorded with an EyeLink 1000 (SR Research Ltd., Canada), calibrated with the native 9-point calibration procedure, recording the left eye at 1000 Hz.

Procedure

The experiments were divided into a matching task (100 trials; Fig. 1B), a visual block, and an auditory block (each 240 trials, Fig. 1C). The matching task was completed first. Half of the participants completed the visual block before the auditory block, for the remaining participants this order was reversed. Participants completed 25 practice trials before starting each block.

Matching task

In the matching task, participants were shown three placeholder stimuli while fixating the center. After a 200 ms delay, white noise was played for 200 ms.

The stimuli were linearly panned in amplitude in 100 equal steps (from -1; amplitude left = 100%, amplitude right = 0%; to 1), one step per trial in random order (counter-balanced). After the stimulus was presented, participants positioned the mouse cursor where they perceived the sound originating from using a computer mouse. Each participant completed 100 trials in the Matching task. The data for the matching task was used to fit a sigmoid relation between the recorded horizontal location of the reticule (in visual angle, -30° to 30°) and the panning values (-1 to 1). This was done to match stimulus locations in the visual block and the auditory block. In a pilot study, we found that the mapping of panning values with blue noise and pink noise into degrees of visual angle matched the mapping of white noise. For this reason, we only mapped out white noise in the current set of experiments.

Visual/Auditory block

The visual and auditory block were kept similar. Participants were instructed to perform two tasks within a trial. To direct spatial attention to a location, participants were tasked with remembering a location of a square (memory cue) presented 5° to the left or right of fixation. The first memory cue was presented for 200 ms, followed by a 200 ms blank. The first memory cue was either a white box (visual) or a white noise burst (auditory). Next, the fixation point moved from the center of the screen 10° to the left or right. Participants were instructed to make an eye-movement to this location. The memory cue location was non-predictive with respect to saccade direction (Fig. 1D). Crucially, after saccade landing a probe was shown. We manipulated (1) the time between saccade offset and probe onset (determined online, Experiment 1: 50 to 400 ms in steps of 50 ms, Experiment 2: 30 to 120 ms in steps of 30 ms), and (2) the location of the probe for the discrimination task. The probe was presented at one of three locations: the same location as the memory cue (Spatiotopic), the presaccadic retinotopic location of the memory cue (Retinotopic trace), or an uncued location (Neutral). Participants were instructed to report the identity of the probe as quickly as possible (visual: left/right tilt, auditory: blue noise/pink noise) using the up and down arrow keys. After 1000 ms had passed, a second memory cue was presented at either the same location (as the first cue) or a different location (first cue location \pm horizontal offset). Other stimulus parameters of the second memory cue were identical to the first memory cue. Participants responded whether the second memory cue was presented at the same or different location as the first memory cue ('S' or 'D' key, unspeeded response). During the experiment, the horizontal offset was adapted with a three up, one down staircase to

keep the task challenging. This task was implemented to keep the location of the memory cue relevant across eye-movements.

Stimuli

In all blocks, small white annuli of 0.5° (4.2 cd/m^2) were used as fixation stimuli. Fixation stimuli were always presented on an imaginary horizontal axis (the Saccade axis, see Fig. 1A) on the vertical center of the screen. In the visual block, probes were grey bars (12.1 cd/m^2 , $0.1^\circ \times 1.0^\circ$) that were tilted 45 degrees to the left or right and memory cues were grey squares of $1.0^\circ \times 1.0^\circ$ (7.6 cd/m^2). Auditory stimuli were panned in amplitude between the two speakers, varying from -1 (left speaker amplitude = amplitude \times 1, right speaker amplitude = amplitude \times 0) to 1, to create the perception of different sound sources in between the speakers. The auditory stimuli consisted of different types of noise: the probe was a pink noise stimulus [1/f noise: 55 dB(A)] or blue noise stimulus [f noise: 53 dB(A)] and the memory cue was a white noise stimulus [58 dB(A)]. The white noise stimuli that were used in the matching task and the auditory block were the same. The response stimulus in the matching task was a grey horizontal line spanning the width of the screen with a height of 0.1° , with a rectangle (12.2 cd/m^2 , $0.1^\circ \times 1.0^\circ$) as mouse cursor that could only be moved in the horizontal plane.

Data analysis

Pre-processing and exclusion

All experiments used the same analysis procedure. The eye-movement data was pre-processed with Python 2.7 (the data and analyses are registered on the Open Science Framework website [227]). For each trial, we determined several exclusion criteria. First, we determined whether fixation was established appropriately up until the saccade cue. We excluded a trial if a sample was recorded more than 2.5° away from the fixation point between the onset of the memory cue and the saccade cue (half of the distance between the fixation point and memory cue, see Fig. 1C; Experiment 1: 6.2% of all trials, Experiment 2: 4.9% of all trials). This is important, because additional saccades may elicit additional remapping processes, which could affect retinotopic lingering. We also excluded trials based on saccade metrics. Saccades were excluded if not performed within 80 to 1000 ms after the onset of the saccade cue (Experiment 1: 5.3% of all trials, Experiment 2: 4.7% of all trials), or if the amplitude was lower than 8° or higher than 12° , i.e. if the participants overshoot

or undershot the saccade target (Experiment 1: 7.5% of all trials, Experiment 2: 8.0% of all trials). Lastly, we excluded trials in which the probe was presented during the saccade (Experiment 1: 3.3% of all trials, Experiment 2: 3.3% of all trials). One participant reversed their response during the probe discrimination in the Auditory Remapping block in Experiment 1 (e.g. consistently pressed the key corresponding with ‘Left’ when the answer was ‘Right’). We discovered this during the experiment, and rather than correcting the observer during the experiment (and slowing reaction times), the participant maintained this mapping and we inverted the responses afterwards. In total on average 390 (out of 460, range: 203 to 439) trials remained per participant for analysis in Experiment 1, and 391 trials (out of 480, range: 261 to 463) per participant remained in Experiment 2.

Statistical analyses

We first determined whether there was an effect of memory cue location (Fig. 1D) with a Bayesian t-test [67]. If not, the left/right cue conditions were collapsed into three probe location conditions (Spatiotopic, Retinotopic, or Neutral). A Bayes Factor (BF) of 3 or higher indicates positive evidence in favor of the alternative model (BF_{10}) or in favor of the null-model (BF_{01}) [68]. We analyzed the data with full-factorial linear mixed models. These models predicted reaction time to the probe and included fixed effects for Probe location (3 levels; Spatiotopic, Retinotopic trace, or Neutral), Probe delay (continuous; Experiment 1: ~50 to ~400 ms, Experiment 2: ~30 to ~120 ms) and Task modality (auditory, or visual). Note that we included the offline calculated Probe delay to the analysis, although we specified bins after which the probe was presented, we calculated a more accurate (and continuous) measure of Probe delay for statistical analyses based on offline saccade detection algorithms. A random intercept was added per participant. We compared the full-factorial model to a null model, using a Chi-square test, with a significance criterion of $\alpha = 0.05$. For each parameter in the model, we report the β -estimates, standard errors, and t -values, using a significance criterion of $\alpha < 0.05$. We used Bayesian t-tests to further describe null-effects of interest (e.g. absence of differences of effects between the auditory and visual task). Note, that the linear mixed effects models are relative to a reference model, which is the Auditory modality, Neutral probe condition with a delay of 0 ms. The figures in the results section reflect that the statistics are based on comparisons to this reference model.

We analyzed the proportion correct answers to the probe with a full-factorial generalized linear mixed model. This is the same analysis as used for the reaction

times, but with a logit link function to better account for ceiling/floor effects. For this analysis, we had to bin the data, due to convergence issues. As the experiment was designed with 50ms (online registered) delay bins in mind, we divided the offline registered (actual) delays into 50 ms bins. For Experiment 2 we binned the data into 30ms bins. This solved convergence issues for both analyses. Note that for the reaction time analyses, we used a continuous measure, and therefore did not need to use bins.

Results

To investigate whether auditory spatial attention lingers in retinotopic coordinates, thus revealing retinotopic encoding of auditory spatial attention, we ran a similar procedure in both Experiment 1 and Experiment 2. In Experiment 1 we investigated the presence and long-term decay of the auditory spatial attention across an eye-movement. We designed Experiment 2 to investigate whether auditory spatial attention is available in retinotopic coordinates *immediately* after a saccade. We only expect to find spatiotopic updating in the visual task, as the lack of visual stimuli in the auditory task may slow spatiotopic updating [226].

Experiment 1

To recapitulate, we replicated the visual experiment by Golomb and colleagues [220], and further tested an auditory variant of the task. If reference frame transformations occur between visual and auditory spatial input, auditory locations perceived before a saccade should be available in retinotopic coordinates after a saccade. If auditory locations are encoded into retinotopic coordinates, we expected participants to react faster to probes presented after the saccade at the location of the retinotopic trace, regardless of sensory modality.

Matching task

To match the perceived visual and auditory locations, we ran a matching task (see Fig. 1B) for each participant. Each trial, a white-noise stimulus was presented with different panning values between the speakers (see Fig. 1A), the participant then clicked the location on the screen that matched the perceived origin of the sound. We fitted a sigmoid relation between speaker panning values and degrees of visual angle on the screen (Fig. 2 for an exemplary participant, Supplementary Fig. 1 for all participant fits). Participants were excluded from further

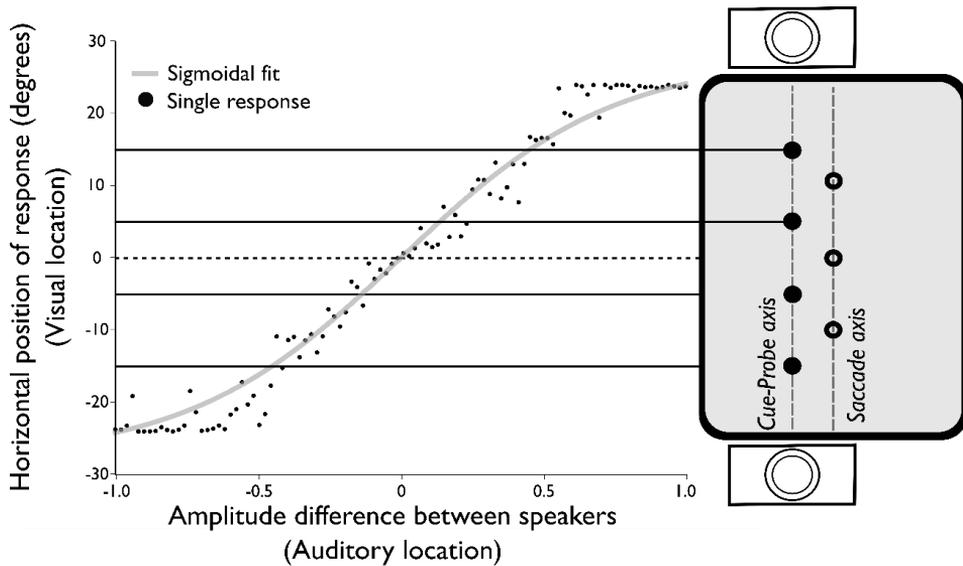


Figure 2. Sigmoid fit of pointing responses to auditory locations of a single participant in the matching task. The black dots show the participant's localization response to a panned white-noise stimulus. The line shows the sigmoid fit to the responses. The locations of the probes used in the auditory block are superimposed on the right side and are connected via a black line. Note that the illustration of the screen is rotated by 90 degrees here, with respect to Fig. 1, to align the stimulus location with the vertical axis in the graph.

analysis if they did not perceive the most extreme panning values coming from the locations used in the subsequent auditory task (15° from central fixation, Experiment 2: 2 participants). For example, one of the excluded participants in Experiment 2 perceived a panning value of 1 (right speaker full volume) at a location of 5 degrees visual angle, which prohibited us from presenting an auditory probe at 15 degrees visual angle for this participant.

Cue/saccade direction congruency

Before collapsing the probe locations across the levels of the factor Cue location (Fig. 1D) we performed a Bayesian t-test. The results show that saccade/cue location congruent trials (e.g. cue right/saccade right, *Med.* = 535.8 ms, *SD* = 179.4 ms) or saccade/cue location incongruent trials (e.g. cue right/saccade left, *Med.* =

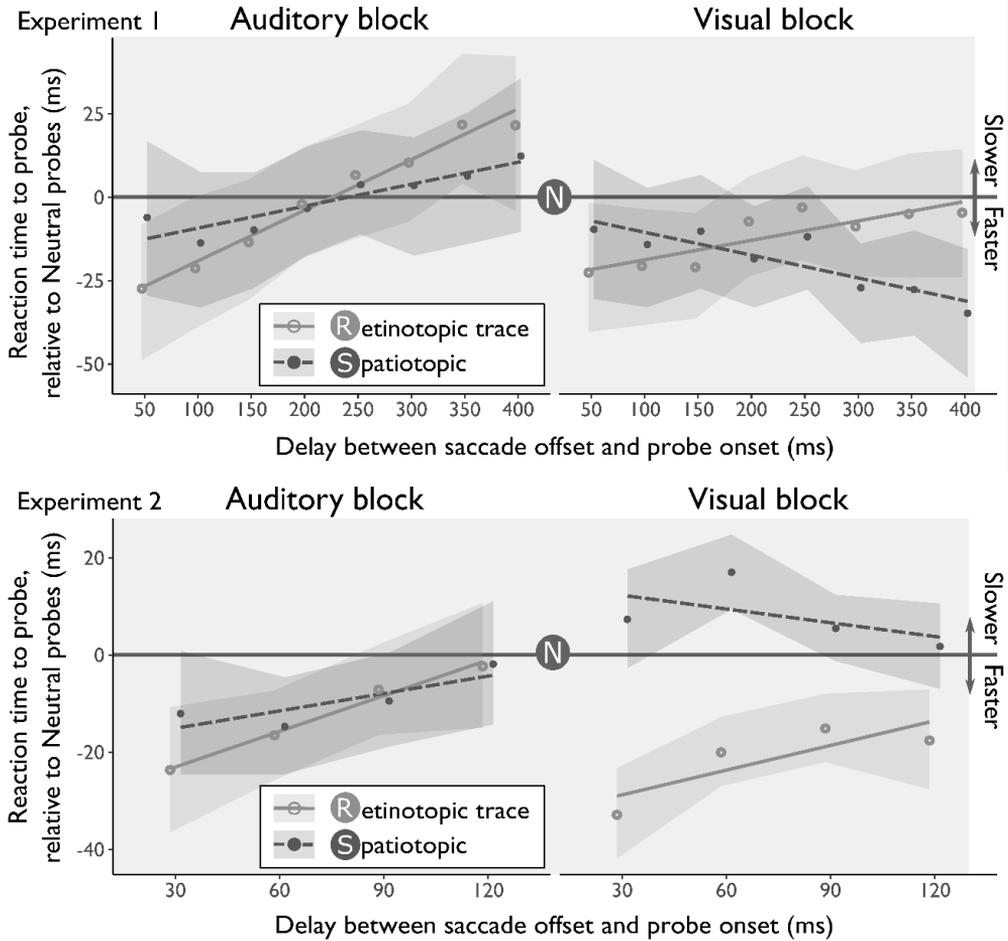


Figure 3. Results from the linear mixed effects models in Experiment 1 and Experiment 2. The horizontal line represents the fit of the linear mixed model of reaction times to probes shown at the neutral location, all other lines are drawn relative to the neutral condition. The lines represented the fits from the linear mixed models, the points indicate the binned average data, after correcting for online saccade detection. Shaded regions represent bootstrapped 95% CI's. To reduce visual overlap, lines have been offset slightly in the horizontal direction.

531.37 ms, $SD = 179.6$ ms) were not significantly different from one another, $BF_{01} = 32.3$, $95\%CI = [-11.48, 11.70]$. We collapsed the saccade/cue location conditions, resulting in three main conditions for probe location: Spatiotopic, Retinotopic trace, and Neutral (Fig. 1C). The design in the current experiment is somewhat limited in

the sense that the retinotopic location is always at a closer eccentricity than the Spatiotopic and Neutral probes, with respect to postsaccadic fixation point, both when participants made a saccade to the left and right. However, we found no effect of saccade direction on reaction time to the Spatiotopic or Neutral probes. Therefore, we assumed that the eccentricity of the probe did not affect reaction times. Lastly, as an additional test we repeated the main linear mixed models without collapsing the probe direction, but instead added probe direction as a random effect to the linear mixed model. Including probe direction in the model did not significantly affect the results. Thus, here we report the models in which we collapsed over cue location below.

Response times

To test whether participants ($N = 17$) reacted significantly faster to probes presented at the location of the Retinotopic trace, we constructed a linear mixed model. The full-factorial model included reaction time to probe as the dependent variable, a random intercept per participant and three fixed effects. The fixed effects were: Task Modality (Auditory or Visual), Probe Location (Spatiotopic, Retinotopic trace or Neutral) and Probe Delay (continuous from 50 ms to 400 ms delay between saccade offset and probe onset). The full-factorial linear mixed model outperformed a null model, which only included a random intercept per participant, $\Delta BIC = 384$, $X^2(11) = 499.67$, $p < 0.001$.

Responses to retinotopic probes

The full-factorial model (Fig. 3, top panels) revealed an offset difference for Probe Location, where participants reacted significantly faster to probes presented at the location of the Retinotopic trace at the earliest delay relative to probes at the Neutral location, $\beta = -29.37$, $SE = 14.13$, $t = -2.08$, $p = 0.04$. Furthermore, the model showed that the relative facilitation in reaction times to probes presented at the location of the Retinotopic trace diminished over time, $\beta = 0.15$, $SE = 0.059$, $t = 2.52$, $p = 0.01$. The mean RTs in Experiment 1 across conditions are shown in Supplementary Table 1. A comparison between the raw data and the linear mixed effects model is shown in Supplementary Fig. 2.

Responses to spatiotopic probes

The analysis did not provide evidence that probes presented at the Spatiotopic location were reacted to differently compared to the Neutral location, $\beta = -8.45$, $SE = 14.02$, $t = -0.60$, $p = 0.54$. We also found no evidence that the facilitation at the Spatiotopic location changes with longer delays, $\beta = 0.04$, $SE = 0.059$, $t = 0.68$, $p = 0.49$. All beta-estimates for the full-factorial model are shown in Supplementary Table 2.

Comparison effects of visual and auditory retinotopic trace

Averaged across delays, we found no difference in the amount of facilitation of responses to probes presented at the location of the retinotopic trace between the Visual task ($Med. = -47.6$ ms, $SD = 146.4$ ms) and the Auditory task ($Med. = -49.8$ ms, $SD = 196.50$ ms), $BF_{01} = 7.62$, $95\%CI = [-4.5, 25.9]$. Together, these results indicate that observers reacted faster to probes that were presented at the location of the Retinotopic trace, regardless of their sensory modality.

Proportion of answers correct

Lastly, we investigated whether response accuracy differed across locations and/or delays. We used a similar analysis as the analysis used for the reaction times, but with response to the probe (correct/incorrect) as dependent variable. Overall, the accuracy was high ($M_{correct} = 0.96$). The analysis showed a significant effect only for Probe delay, where probes presented later after saccade landing were responded to more accurately than earlier delays, $\beta = 0.54$, $SE = 0.27$, $z = 2.033$, $p = 0.04$. However, this should be interpreted with caution, as the full-factorial model ($BIC = 2679$, $df = 13$) did not outperform a null-model ($BIC = 2600$, $df = 2$, $X^2(11) = 16.66$, $p = 0.12$). This is a sign of overfitting, possibly due to many participants performing at ceiling (56 out of 204 proportions correct per condition per participant are at 1.0). In conclusion, we found no evidence of changes in accuracy across different probe locations and task modality.

Experiment 2

In Experiment 2 ($N = 17$), we set out to replicate Experiment 1, and investigated whether reaction times to probes at the location of the Retinotopic trace are reacted to faster immediately after the saccade. We designed Experiment 2 so that the offset (i.e. the intercept) of the linear mixed model reflects the first moment

after the saccade. After offline encoding of saccades in Experiment 1, we noticed that probes were presented ± 30 ms relative to the online definition of a saccade offset. Therefore, we presented the probes 30, 60, 90, or 120 ms after saccade offset (defined online) in Experiment 2 (Fig. 1C). After offline saccade detection in Experiment 2, we found that 30 to 42 trials (out of ~ 990 trials) per condition were trials in which the probe was presented immediately (the first screen update) after the saccade had landed.

Reaction times at retinotopic & spatiotopic location

As in Experiment 1, the full-factorial linear mixed model outperformed a null-model, $\Delta BIC = 415$, $X^2(11) = 510.41$, $p < 0.001$. The beta estimates of the full-factorial model are shown in Supplementary Table 4. Participants reacted significantly faster to probes presented at the location of the Retinotopic trace at the earliest delay relative to probes at the Neutral location, $\beta = -30.21$, $SE = 13.61$, $t = -2.20$, $p = 0.03$ (Fig. 1, bottom panels). The reduction of the retinotopic trace over time was not significant (likely due to the smaller timescale of the experiment), $\beta = 0.20$, $SE = 0.13$, $t = 1.50$, $p = 0.13$. We found no significant evidence for relative facilitation at the Spatiotopic location, $\beta = -13.04$, $SE = 13.75$, $t = -0.95$, $p = 0.34$, or that facilitation at the Spatiotopic location changed over time, $\beta = 0.06$, $SE = 0.13$, $t = 0.48$, $p = 0.63$. The means across conditions are shown in Supplementary Table 3. The raw data, and the model are shown in Supplementary Fig. 3.

Comparison effects of visual and auditory retinotopic trace

Like Experiment 1, the amount of response facilitation of probes presented at the location of the retinotopic trace was similar for Auditory ($Med. = -47.4$ ms, $SD = 127.3$ ms) and Visual probes ($Med. = -58.8$ ms, $SD = 177.4$ ms), $BF_{01} = 8.66$, $95\%CI = [-5.1, 23.3]$. These results suggest that attention is present in retinotopic coordinates immediately after a saccade for both auditory and visual stimuli. The magnitude of the attentional benefit is similar for both auditory and visual input.

Proportion of answers correct

In Experiment 2, participants gave the correct answer for a large proportion of the trials ($M_{correct} = 0.962$). A generalized linear mixed model analysis revealed no effects of Probe delay, Task (A or V), or Probe location. Importantly, the full-factorial model ($BIC = 1925$, $df = 13$) did not outperform a null model ($BIC = 1844$,

$df = 2$, $X^2(11) = 14.37$, $p = 0.21$), which fits only a random intercept per participant. From this we can conclude that there is no significant difference in accuracy between conditions.

Combined Analyses Experiment 1 and 2

In Experiment 1 and Experiment 2, we found attentional facilitation at retinotopic locations for visual and auditory probes. However, we found no support for spatiotopic updating relative to the control condition (which was observed in prior studies). However, in both experiments a trend was visible in the expected direction: responses to probes at the Visual Spatiotopic location became faster with longer delays relative to the other conditions. As Experiment 1 and Experiment 2 had no overlapping participants and were essentially the same experiment, but with a different range of probe delays, we performed the same analyses on the combined datasets of Experiment 1 and 2. Lastly, in our prior experiments we lacked the power to show differences between retinotopic and spatiotopic conditions, as the difference between these conditions is much lower, and thus requires more power to detect. In the combined dataset we can investigate, exploratively, the difference in facilitation between the spatiotopic and retinotopically presented probes using a sequential analysis. The results from the exploratory analyses were as follows.

Response times

Overall, participants reacted faster to probes in the Visual task, $\beta = -104.58$, $SE = 8.46$, $t = -12.36$, $p < 0.01$, and responses became faster as the delay between saccade offset and probe onset increased, $\beta = -0.18$, $SE = 0.03$, $t = -5.57$, $p < 0.01$. The decrease in reaction time with increasing delay was more pronounced in the Auditory task, $\beta = 0.13$, $SE = 0.05$, $t = 2.91$, $p < 0.01$. The retinotopic results from the analysis are consistent with the results described in Experiment 1 and Experiment 2. The participants reacted faster to probes that were presented at the Retinotopic trace when shown directly after the eye-movement, $\beta = -25.65$, $SE = 8.21$, $t = -3.13$, $p < 0.01$, and this retinotopic benefit decayed over time, $\beta = 0.14$, $SE = 0.05$, $t = 3.11$, $p < 0.01$, both with respect to the neutral condition. Lastly, the analysis indicated a 3-way interaction effect (Modality x Delay x Location), where the slope in the Spatiotopic-Visual condition is different relative to the other conditions, $\beta = -0.17$, $SE = 0.07$, $t = -2.55$, $p = 0.01$. This indicates that over time, responses to Visual-Spatiotopically presented probes get faster over time, providing some (anecdotal)

evidence for spatiotopic updating within this paradigm. The Beta estimates for the model are shown in Supplementary Table 6. This result provides some evidence for spatiotopic updating, consistent with prior findings, but *only* for the visual modality.

Proportion correct

Analyzing the proportion of answers correct for the combined dataset did not yield any different results from prior analyses. Comparing a full-factorial linear mixed model ($BIC = 4481$, $df = 13$) to a null-model reveals that the null-model outperforms the full-factorial model ($BIC = 4403$, $df = 2$, $X^2(11) = 24.97$, $p < 0.01$). Thus, the accuracy did not differ between the various conditions.

Sequential analysis – Retinotopic/Spatiotopic differences

Lastly, we ran a sequential analysis on the combined dataset, as it can provide information on whether effects were not found due to a lack of power. Here, we investigate whether retinotopically presented probes have a different offset, and slope, than spatiotopically presented probes. Rerunning the linear mixed model with the Retinotopic trace condition as the reference indicates that there is a difference in offset between retinotopic and spatiotopic probes, $\beta = -15.84$, $SE = 8.00$, $t = -1.98$, $p = 0.04$, as well as a slope difference, $\beta = -0.09$, $SE = 0.04$, $t = -2.08$, $p = 0.03$.

The results of the sequential analysis are shown in Supplementary Fig. 4 (with the Neutral condition as the baseline) and Supplementary Fig. 5 (with the Retinotopic condition as the baseline). It seems that our assertion that we lacked power in the single dataset was correct, as differences between Retinotopic and Spatiotopic conditions are only statistically significant at $N = 27$ (for a difference in offset) and at $N = 26$ (for a difference in slope) and remain significant with further inclusion. Note that these results are tenuous, as we did not design the experiment or our analyses to (initially) test for a difference between spatiotopically and retinotopically presented probes.

Experiment 3

In Experiment 1 and 2 we have demonstrated that both auditory and visually evoked spatial attention lingers at the retinotopic coordinates after a saccade, facilitating responses to auditory and visual probes presented at that location. We reasoned that retinotopic encoding of non-visual (e.g. auditory) locations may

contribute to multisensory perceptual stability in the face of frequent disruptions of visual processing due to saccades.

First, it is unclear whether retinotopic encoding of spatial attention is specific to one modality (i.e. intra-modal) or shared between modalities (i.e. cross-modal). That is, visual and auditory spatial attention could be independently encoded into retinotopic coordinates or retinotopic encoding of spatial attention could be cross-modal. We expected some form of peri-saccadic cross-modal attentional orienting to occur, as cross-modal cueing effects have been readily observed in many cross-modal cueing tasks [24–28]. Studies on cross-modal cueing have shown that without spatial relevance, auditory information can be processed tonotopically, resulting in a lack of spatial cueing effects [24-27]. This is in contrast with visual spatial cueing effects, which are inherently spatial due to the retinotopic organization of the visual processing hierarchy. Prior research has shown that cross-modal spatial attentional cueing can be asymmetric (A-V cueing, but not V-A cueing) under certain circumstances [24-27], and that cross-modal cueing effects are only present in both directions across sensory modalities when the spatial location of auditory stimuli is task-relevant [97,228,230]. Running a cross-modal variant of our paradigm allows us (1) to investigate whether retinotopic encoding is modality specific, and (2) to investigate the role of spatial relevance for responses to auditory stimuli at prior retinotopic coordinates.

In Experiment 3, we have run a cross-modal variant of the task used in Experiment 1 and Experiment 2. To elaborate, the paradigm used in all experiments consisted of two tasks, a spatially relevant memory cue task, and a spatially irrelevant probe discrimination task. In Experiment 1 and Experiment 2, participants completed a fully unimodal Auditory cue/Auditory probe and a unimodal Visual cue/Visual probe task. In Experiment 3, participants completed an Auditory cue/Visual probe task and a Visual cue/Auditory probe task. If retinotopic deployment of attention occurs separately for auditorily evoked and visually evoked spatial attention, then there would be no retinotopic effects in either cross-modal task. That is, auditory evoked retinotopic attention only effects auditory processing of stimuli at that location and the same for visual evoked retinotopic attention. Next, if retinotopic deployment of auditory spatial attention requires spatial relevance, an asymmetry between the two cross-modal cueing tasks would be observed. In Experiment 3, auditory information was only spatially relevant in the Auditory cue/Visual probe condition, as participants remembered and reported the location of the auditory memory cue, whereas the visual probe is implicitly spatially relevant. In the Visual

cue/Auditory probe condition the auditory task was a spatially irrelevant frequency discrimination task. Given the large body of literature on cross-modal cueing effects, we expected to find evidence of cross-modal retinotopic attentional facilitation in at least the task with auditory spatial relevance (Auditory cue/Visual probe) [24-27].

Methods

Subjects and procedure

The subjects ($N = 20$, 18 Female, $M_{age} = 20.2$) completed 252 trials in the Auditory cue/Visual Probe task and 252 trials in the Visual cue/Auditory probe task. Half of the participants completed the Auditory cue/Visual probe before completing the Visual cue/Auditory probe task. This order was reversed for the remaining half. Participants found the task noticeably harder than the task in Experiment 1 and Experiment 2. We found a higher rate of exclusion in this experiment, as compared to Experiment 1 and Experiment 2, after examining the quality of the data when we tested 12 participants. Therefore, after testing 12 of the subjects in Experiment 3, we chose to test up to 20 subjects.

Importantly, in Experiment 3 the modalities of the cue and the probe differ (cross-modal cueing). To recapitulate, the cue task required observers to maintain a location in memory across saccades, which creates a framework for spatial relevance. The probe task requires observers to react to the identity of the probe as quickly as possible (and the location is incidental). Although tasks are the same in task demands, we expect an asymmetric cueing effect driven by the differences in the spatial properties of the task. We expect cueing effects even when the visual spatial locations are not relevant (Auditory cue/Visual probe task). If retinotopic encoding of auditory spatial attention only occurs with spatial relevance we expected to replicate retinotopic attentional facilitation only for the Auditory cue/Visual probe task, but not for the Visual cue/Auditory probe.

Based on the results from Experiment 1 and Experiment 2 we changed the timing of the probe presentation. In Experiment 3 the probe was presented either 30 ms, 120 ms or 210 ms after saccade offset. We determined that this would give a good estimate of the attentional facilitation both directly after the saccade (at ~30 ms) as well as the decay of retinotopic lingering at longer delays (at >200 ms).

Data exclusion

The exclusion criteria were identical to the criteria in Experiment 1 and Experiment 2. We excluded a trial if a sample was recorded more than 2.5° away from the fixation point between the onset of the memory cue and the saccade cue (12% of all trials). Trials were excluded if saccades were not performed within 80 to 1000 ms after the onset of the saccade cue (8% of all trials), or if the saccade amplitude was not between 8° and 12° (20% of all trials). Lastly, we excluded trials in which the probe was presented during the saccade (5% of all trials). After exclusion 6914 trials were left in total (69% of all trials), on average 345 trials per participant (out of 504 trials, range 110 to 465). The statistical analyses were identical to the previous experiments.

Results

Reaction times at retinotopic/spatiotopic location

The full-factorial linear mixed model, containing the independent variables for Task modality (A cue/V probe or V cue/A probe) and Probe Location (Neutral, Spatiotopic, or Retinotopic) and a random intercept per participant ($BIC = -159$, $df = 14$), outperformed a null model with only a random intercept per participant ($BIC = 88441$, $df = 3$, $X^2(11) = 88698$, $p < 0.01$). The full-factorial linear mixed model analysis (Fig. 4) again showed evidence for facilitation at the location of the retinotopic trace relative to neutral probes, $\beta = -49.7$, $SE = 20.1$, $t = -2.48$, $p = 0.01$. Like Experiment 1 and Experiment 2, if the delay increased between saccade onset and probe onset, participants responded faster, $\beta = 0.346$, $SE = 0.092$, $t = -3.46$, $p < 0.01$. We found the participants responded slower in the Visual cue/Auditory probe task relative to the Auditory Cue/Visual Probe task, $\beta = 164$, $SE = 19.9$, $t = 8.23$, $p < 0.01$. All other fixed effects were not statistically significant, $t < 1.12$, $p > 0.26$, indicating no evidence for (slowed) spatiotopic updating. Condition means are shown in Supplementary Table 5. The raw data, and the bootstrapped estimates from the linear mixed effects model are shown in Supplementary Fig. 6.

In Experiment 1 and Experiment 2, the magnitude of attentional facilitation at the location of the retinotopic trace was similar for the auditory and visual sensory modality. In Experiment 3, however, there was a clear difference in the magnitude of retinotopic attentional facilitation between tasks (A-V vs. V-A), $BF_{10} = 157$, 95%CI = 12.1 to 36. A Bayesian t-test (one for each task), indicated a null effect of attentional facilitation at the Retinotopic trace location in the Visual cue/Auditory

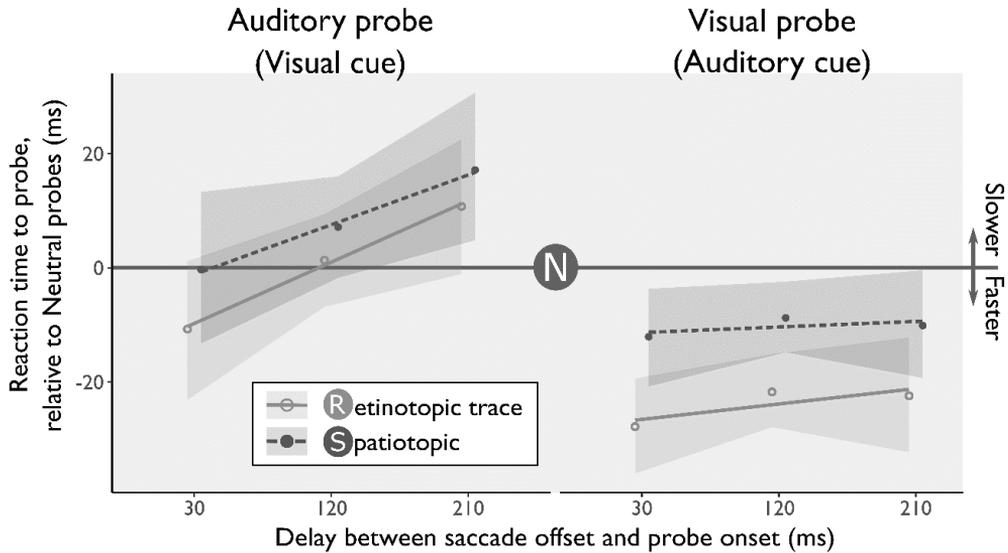


Figure 4. Results from the linear mixed effects model in Experiment 3. The horizontal line represents reaction times to probes shown at the neutral location, all other lines are drawn relative to the neutral condition. The lines represented the fits from the linear mixed models, the points indicate the binned average data, after correcting for online saccade detection. In both the visual and auditory experimental block, probes at the location of the retinotopic trace are reacted to significantly faster. Shaded regions represent bootstrapped 95% CI's.

probe condition, $BF_{01} = 30.7$, $95\%CI = -11.4$ to 12.6 . In contrast, in the Auditory Cue/Visual Probe condition we found strong evidence for attentional facilitation at the Retinotopic trace location, $BF_{10} = 801223$, $95\%CI = -31.0$ to -16.7 .

In sum, we observed cross-modal attentional facilitation at the location of the retinotopic trace in the Auditory Cue/Visual Probe condition, but not in the Visual cue/Auditory probe condition. Thus, in line with previous research on cross-modal spatial attention, cross-modal attentional facilitation at the location of the retinotopic trace is only present when auditory spatial information is task-relevant.

Accuracy at retinotopic/spatiotopic location

Overall, the accuracy was very high ($M_{correct} = 0.92$). Analyzing the accuracy yielded similar results to prior accuracy analyses. Comparing a full-factorial linear mixed model ($BIC = 3782$, $df = 13$) to a null-model reveals that the null-model outperforms the full-factorial model ($BIC = 3739$, $df = 2$, $X^2 = 54.48$, $p < 0.01$). We

conclude that, in Experiment 3 there was no difference in the proportion of correct answers.

General Discussion

In the current study, we demonstrated that auditory spatial attention is encoded in a retinotopic reference frame across eye-movements. Retinotopic encoding of spatial attention facilitates both auditory and visual information processing at the location of the retinotopic trace. Our findings are in line with the studies by Golomb and colleagues who showed that after a saccade visual spatial attention lingers in retinotopic coordinates, and that visual attention slowly updates to the spatiotopic location [220,226,231]. Our study expands these findings by revealing the multisensory/cross-modal nature of retinotopic lingering of spatial attention across eye-movements.

Prior studies have shown that visual attention is retinotopically encoded and lingers in retinotopic coordinates after a saccade [220,226,231]. We hypothesized that auditory spatial attention may be retinotopically encoded around the time of a saccade as well. We found that spatial pointers obtained via both vision and audition elicit a retinotopic trace, immediately after a saccade. The retinotopic lingering of auditory evoked spatial attention directly after a saccade indicates that auditory information is encoded in retinotopic coordinates around the time of a saccade. Interestingly, we found that the attentional benefit at the location of the retinotopic trace (shorter reaction time) was similar across modalities. This similarity of attentional benefits across modalities suggests a common attentional updating mechanism shared between modalities (around the time of a saccade).

Furthermore, we observed that auditory evoked spatial attention elicited visual retinotopic effects, but not the other way around. This asymmetry suggests that auditory spatial attention does not mandatorily linger in retinotopic coordinates around the time of a saccade. Asymmetries in cross-modal cueing effects were found in prior studies as well, where cross-modal spatial attentional effects are only present when auditory spatial locations are made task-relevant [6,97,232]. When responses to auditory targets rely on frequency discrimination, responses can be based on tonotopic representations of the auditory target, which lack spatial specificity (although spatial information is processed as well) [6,97,232]. This is in contrast with visual representations, which are inherently spatial due to the retinotopic organization of the early visual processing areas. In studies by Ward and colleagues [228,230], cross-modal cueing effects were only present in an auditory cue-visual

probe task, but not in a visual cue-auditory probe task. This asymmetry was not observed when auditory spatial information was made task-relevant [228,233]. Our study also demonstrates that auditory spatial attention is likely only deployed when auditory space is task-relevant.

For auditory information to be retinotopically encoded, a reference frame transformation is required from craniotopic auditory coordinates to retinotopic auditory coordinates. Studies using animal models have provided insight into the neurophysiological underpinnings of reference frame transformations in the midbrain. Broadly speaking, the location of visual input is represented in a retinotopic reference frame within the superior colliculus [234,235], whereas auditory input is represented in a head-centered reference frame in the inferior colliculus [236–238]. Auditory localization is based on multiple binaural and monaural cues, including differences in intensity and arrival time between the ears (binaural cues) for horizontal sound localization [239]. The binaural cues for horizontal localization are amplitude differences of the sound wave when it reaches each ear (interaural level differences), and phase differences of sound waves due to differences in arrival times to the ears (interaural time differences). Binaural cues are processed in parallel in brain stem pathways, converging in frequency tuned maps in the central nucleus of the inferior colliculus [236,237]. The information across the frequency tuned maps for vertical and horizontal localization are integrated into a single, three-dimensional, auditory map in the external nucleus of the inferior colliculus [236,237,240]. This auditory map is consequently relayed and integrated with a retinotopic visual map in the superior colliculus, resulting in a multimodal, retinotopic map of space [213,237]. Additionally, gaze control circuitry in the forebrain has been identified to modulate auditory responses in the midbrain, showing direct connectivity between higher order visual areas and structures such as the inferior colliculus [241]. These processes have been studied extensively in animal models and have been corroborated by results from studies with human subjects, for example, by measuring auditory brainstem responses to auditory stimuli [242–244]. The role of the superior colliculus has therefore been described as unifying attentive and orienting behavior between senses, as sensory maps in the superior colliculus share a similar axis system [207]. It seems that the pathways between the brain stem, inferior colliculus, and superior colliculus may play a critical role in the subjective experience of sensory unity by integrating audiovisual location information in shared (retinotopic) reference frames. Our results reveal that reference frame transformations are relevant to human perception around the time of a saccade.

Likely, reference frame transformations allow humans to quickly compare locations of sensory input regardless of differences in coordinate systems native to the modality.

In addition to retinotopic facilitation effects, we observed spatiotopic updating in the visual condition. However, we did not find support for spatiotopic updating in the auditory condition in Experiment 1 and 2. We designed Experiment 3 only with retinotopic effects in mind, not expecting to find cross-modal spatiotopic updating, which limits the conclusions that can be drawn about spatiotopic updating based on the results in that experiment. As previously shown [226], spatiotopic updating may be affected both by the amount of visual stimuli (being slowed by less visual stimulation), and task instruction (being attenuated when participants are instructed to disregard spatiotopic coordinates).

In Experiment 1 of the current study, auditory spatial attention did not update faster to spatiotopically presented probes when compared to auditory neutral probes. When investigating the results from the visual task, we did observe attentional updating at spatiotopic locations when we combined the data from both Experiment 1 and Experiment 2. This discrepancy between visual and auditory spatiotopic updating is unsurprising. First, spatiotopic updating of attentional facilitation becomes less apparent if participants remember locations in retinotopic coordinates, whereas retinotopic facilitation is present without explicit task-relevance [220]. We explicitly chose not to instruct participants which coordinate system they should use, to not bias participants to remember auditory probes in retinotopic coordinates only. We postulate that by not instructing participants to update auditory probes in spatiotopic coordinates they were not focusing on spatiotopic locations. Secondly, work by Golomb and colleagues has shown that spatiotopic updating is facilitated (sped up) by providing more visual input (a grid overlaying the background [226]). Conversely, removing visual input may slow spatiotopic updating. In the current study, in the visual conditions, cues and probes may have provided a spatial framework, allowing for spatiotopic updating. Therefore, the lack of spatiotopic updating in the auditory task in the current study is inherently confounded by the lower amount of visual stimulation in the auditory block, which in turn may further slow the spatiotopic updating of auditory spatial attention.

Finally, we note that auditory information is not actually represented in retinotopic coordinates, but rather in *oculocentric* coordinates. This distinction is important, as auditory stimuli are not projected onto the retina. However, we chose to keep the terminology consistent with the studies of Golomb and colleagues [220],

as we consider this study to be an extension of the literature on the retinotopic trace, and spatiotopic updating.

The current series of experiments shows that auditory information is, likely, presaccadically encoded into retinotopic coordinates, causing postsaccadic lingering of the retinotopic trace for auditory input. Encoding auditory spatial attention in a retinotopic reference frame may facilitate comparing auditory and visual spatial information, allowing for spatial alignment of these sensory systems, and intramodal and cross-modal attentional facilitation in humans.



*Supplementary Material**Supplementary Table 1. Table of grand means for Experiment 1.*

Probe Location	Modality	Online Delay *	# of Trials*	Mean RT (ms)	SD RT (ms)	95% CI
Neutral	Auditory	50	139	656.80	184.87	31.00
		100	138	643.31	192.80	32.45
		150	141	622.80	196.16	32.66
		200	136	632.94	201.94	34.25
		250	137	608.92	183.69	31.03
		300	135	587.42	188.97	32.17
		350	128	584.46	166.05	29.04
		400	96	590.36	170.38	34.52
	Visual	50	124	556.06	114.02	20.27
		100	125	539.37	151.42	26.81
		150	127	546.67	149.78	26.30
		200	139	524.73	137.29	23.03
		250	121	532.06	169.69	30.54
		300	124	510.34	138.47	24.61
350		114	543.75	149.88	27.81	
400		93	546.23	128.82	26.53	
Retinotopic	Auditory	50	133	637.55	169.24	29.03
		100	149	638.00	210.77	34.12
		150	144	622.96	171.67	28.28
		200	145	618.09	200.32	32.88
		250	136	615.20	207.31	35.16
		300	140	603.12	204.40	34.16
		350	129	599.70	171.87	29.94
		400	92	615.23	204.42	42.33

	Visual	50	109	537.64	124.88	23.71
		100	123	535.54	128.41	22.92
		150	124	502.35	139.51	24.80
		200	135	533.01	146.70	24.97
		250	126	508.52	140.04	24.69
		300	134	516.05	130.34	22.27
		350	116	528.95	160.93	29.60
		400	91	548.97	164.53	34.27
Spatiotopic	Auditory	50	141	662.61	188.92	31.45
		100	138	658.07	217.47	36.61
		150	140	622.21	201.49	33.67
		200	133	581.93	177.88	30.51
		250	142	621.78	179.26	29.74
		300	141	591.80	169.06	28.15
		350	131	611.96	195.84	33.85
		400	98	568.09	178.85	35.86
	Visual	50	130	542.93	146.49	25.42
		100	126	537.91	170.04	29.98
		150	129	512.68	145.23	25.30
		200	124	511.28	150.47	26.75
		250	122	511.75	163.31	29.27
		300	129	515.73	132.46	23.08
		350	118	503.17	136.13	24.82
		400	87	506.80	128.18	27.32

* We calculated the offline delay, which differed from the online delay. For analyses we used the offline delay. For purposes of this table, we rebinned the offline determined delays back into 50 ms bins. The number of trials reflects the amount of trials after rebinning the conditions, thus the mean RTs approximate the values used in the analyses.

Supplementary Table 2. Beta estimates, standard error and t-values per factor of the full-factorial model specified in Experiment 1. Statistically significant results are indicated by an asterisk ().*

Factor name	β-estimate	Standard error	t-value
Intercept	658.63	19.88	33.12 *
Location – Retinotopic trace	-29.37	14.13	-2.08 *
Location – Spatiotopic	-8.45	14.02	-0.60
Task – Visual	-110.21	14.44	-7.63 *
Probe delay	-0.19	0.04	-4.51 *
Location – Retinotopic trace *	13.42	20.55	0.65
Task – Visual			
Location – Spatiotopic * Task – Visual	3.42	20.27	0.86
Location – Retinotopic trace *	0.15	0.06	2.53 *
Probe delay			
Location – Spatiotopic * Probe delay	0.04	0.06	0.68
Task – Visual * Probe delay	0.16	0.06	2.59 *
Location – Retinotopic trace *	-0.13	0.09	-1.48
Task – Visual * Probe delay			
Location – Spatiotopic * Task – Visual * Probe delay	-0.11	0.09	-1.29

Supplementary Table 3. Table of grand means for Experiment 2.

Probe Location	Modality	Online Delay*	# of Trials*	Mean RT (ms)	SD RT (ms)	95% CI
Neutral	Auditory	30	288	579.81	176.14	20.43
		60	291	609.10	199.09	22.97
		90	271	582.64	180.19	21.55
		120	298	578.27	192.30	21.92
	Visual	30	259	525.55	143.97	17.62
		60	250	491.56	118.39	14.75
		90	263	496.82	147.10	17.86
		120	249	480.31	134.71	16.81
Retinotopic	Auditory	30	271	586.41	168.70	20.18
		60	274	586.36	188.51	22.42
		90	285	563.94	161.67	18.85
		120	286	574.40	186.02	21.65
	Visual	30	244	480.05	111.44	14.05
		60	252	477.47	136.18	16.89
		90	242	476.46	147.25	18.64
		120	252	469.75	142.68	17.70
Spatiotopic	Auditory	30	278	588.91	180.28	21.28
		60	293	571.03	166.37	19.12
		90	290	577.91	192.08	22.20
		120	296	576.23	181.16	20.72
	Visual	30	248	515.73	137.65	17.2
		60	255	511.20	145.80	17.98
		90	256	497.05	132.70	16.33
		120	245	487.29	137.56	17.31

* We calculated the offline delay, which differed from the online delay. For analyses we used the offline delay. For purposes of this table, we rebinned the offline determined delays back into 30 ms bins. The number of trials reflects the amount of trials after rebinning the conditions, thus the mean RTs approximate the values used in the analyses.

Supplementary Table 4. Beta estimates, standard error and t-values per factor of the full-factorial model specified in Experiment 2. Significant results are indicated by an asterisk ().*

Factor name	β-estimate	Standard error	t-value
Intercept	630.27	25.6	24.5 *
Location – Retinotopic trace	-30.21	13.61	-2.20 *
Location – Spatiotopic	-13.05	13.74	-0.95
Task – Visual	-97.13	14.32	-6.78 *
Probe delay	-0.25	0.09	-2.72 *
Location – Retinotopic trace *	-5.97	20.49	-0.29
Task – Visual			
Location – Spatiotopic * Task – Visual	31.81	20.34	1.56
Location – Retinotopic trace *	0.20	0.13	1.50
Probe delay			
Location – Spatiotopic * Probe delay	0.06	0.13	1.50
Task – Visual * Probe delay	0.06	0.14	0.48
Location – Retinotopic trace *	-0.06	0.19	-0.30
Task – Visual * Probe delay			
Location – Spatiotopic * Task – Visual * Probe delay	-0.21	0.19	-1.07

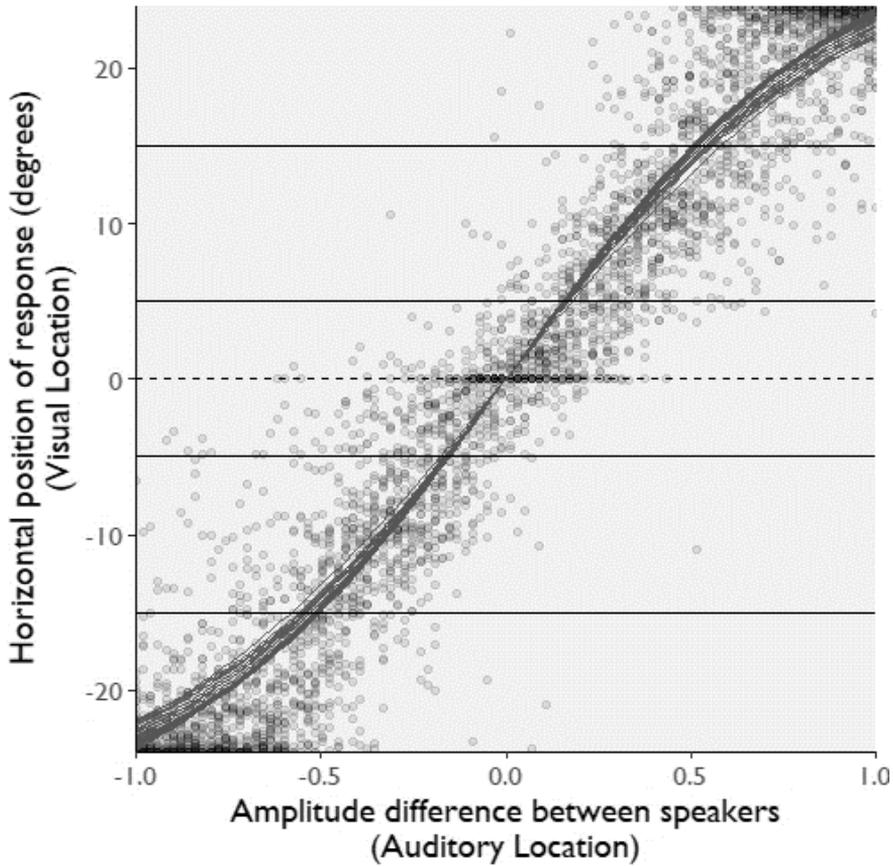
Supplementary Table 5. Table of grand means for Experiment 3.

Probe Location	Modality	Online Delay*	# of Trials*	Mean RT (ms)	SD RT (ms)	95% CI
Neutral	Auditory	30	388	598.82	168.01	16.77
		120	414	557.43	156.59	15.13
		210	405	545.22	165.07	16.12
	Visual	30	344	516.58	121.67	12.90
		120	373	493.63	125.60	12.79
		210	352	483.29	126.97	13.31
Retinotopic	Auditory	30	400	585.12	148.80	14.63
		120	405	570.26	179.57	17.54
		210	413	547.07	160.18	15.49
	Visual	30	365	490.01	109.50	11.27
		120	350	471.37	125.38	13.18
		210	370	460.65	120.67	12.34
Spatiotopic	Auditory	30	391	604.41	171.40	17.04
		120	410	564.23	152.62	14.82
		210	406	557.75	162.36	15.84
	Visual	30	362	501.81	105.25	10.88
		120	379	482.42	127.23	12.85
		210	387	478.77	121.94	12.19

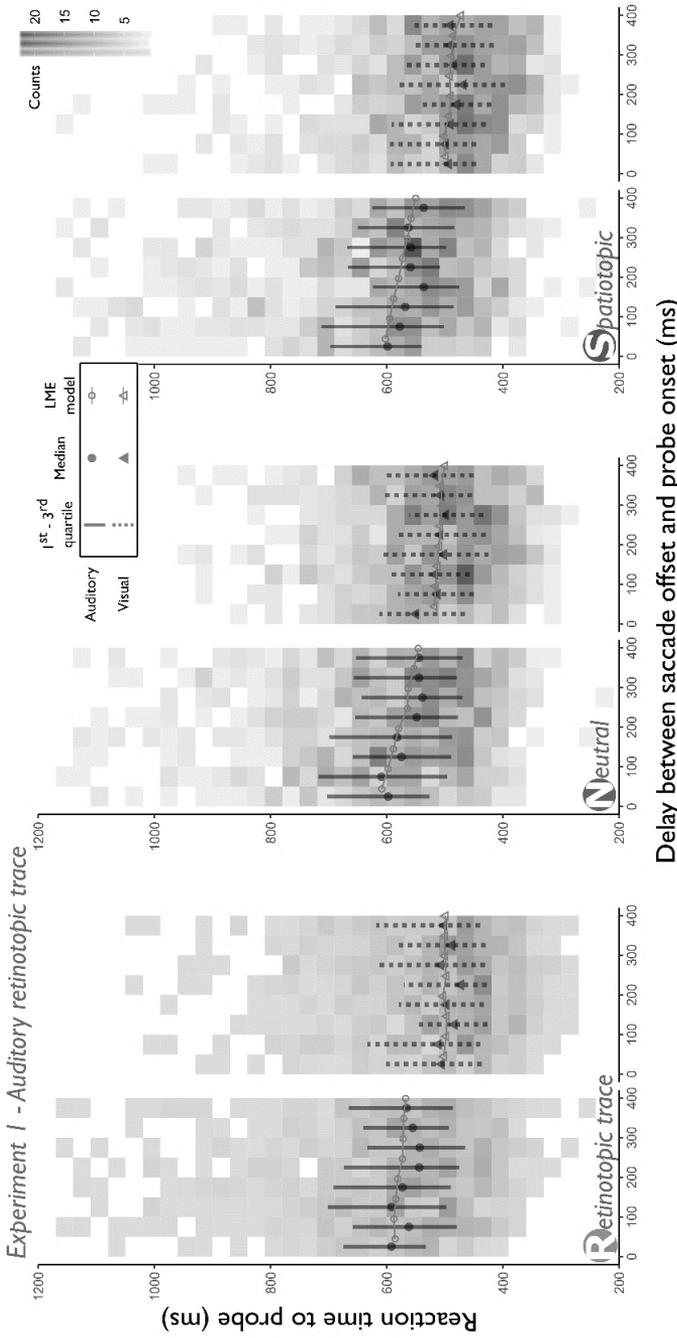
* We calculated the offline delay, which differed from the online delay. For analyses we used the offline delay. For purposes of this table, we rebinned the offline determined delays back into 50 ms bins. The number of trials reflects the amount of trials after rebinning the conditions, thus the mean RTs approximate the values used in the analyses.

Supplementary Table 6. Beta estimates, standard error and t-values per factor of the full-factorial model specified for the combined analysis of Experiment 1 and Experiment 2. This analysis was exploratory in nature, to investigate whether we replicated results found previously. Significant results are indicated by an asterisk ().*

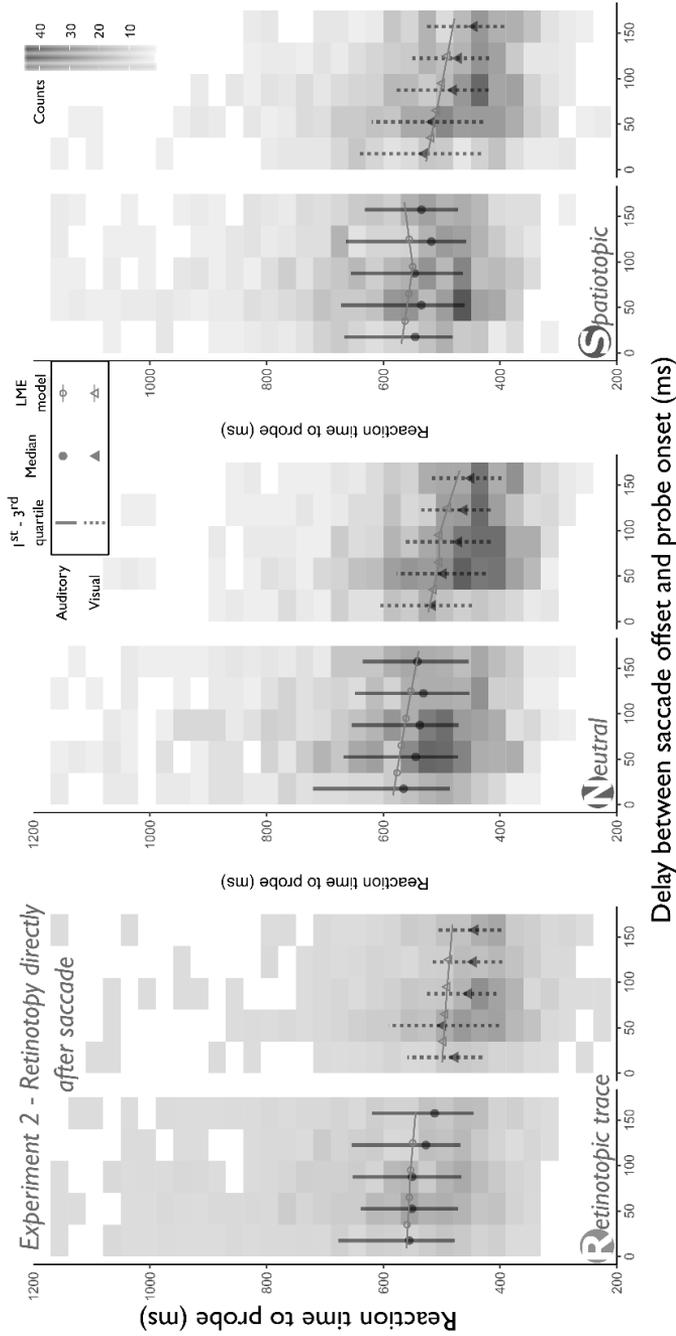
Factor name	β-estimate	Standard error	t-value
Intercept	642.61	16.03	40.09*
Location – Retinotopic trace	-25.65	8.21	-3.13*
Location – Spatiotopic	-9.35	8.18	-1.14
Task – Visual	-104.58	8.46	-12.36*
Probe delay	-0.18	0.03	-5.57*
Location – Retinotopic trace *	-0.96	12.04	-0.08
Task – Visual			
Location – Spatiotopic * Task – Visual	20.74	11.96	1.74
Location – Retinotopic trace * Probe delay	0.14	0.05	3.11*
Location – Spatiotopic * Probe delay	0.04	0.04	0.94
Task – Visual * Probe delay	0.13	0.05	2.91*
Location – Retinotopic trace * Task – Visual * Probe delay	-0.07	0.07	-1.22
Location – Spatiotopic * Task – Visual * Probe delay	-0.17	0.07	-2.55*



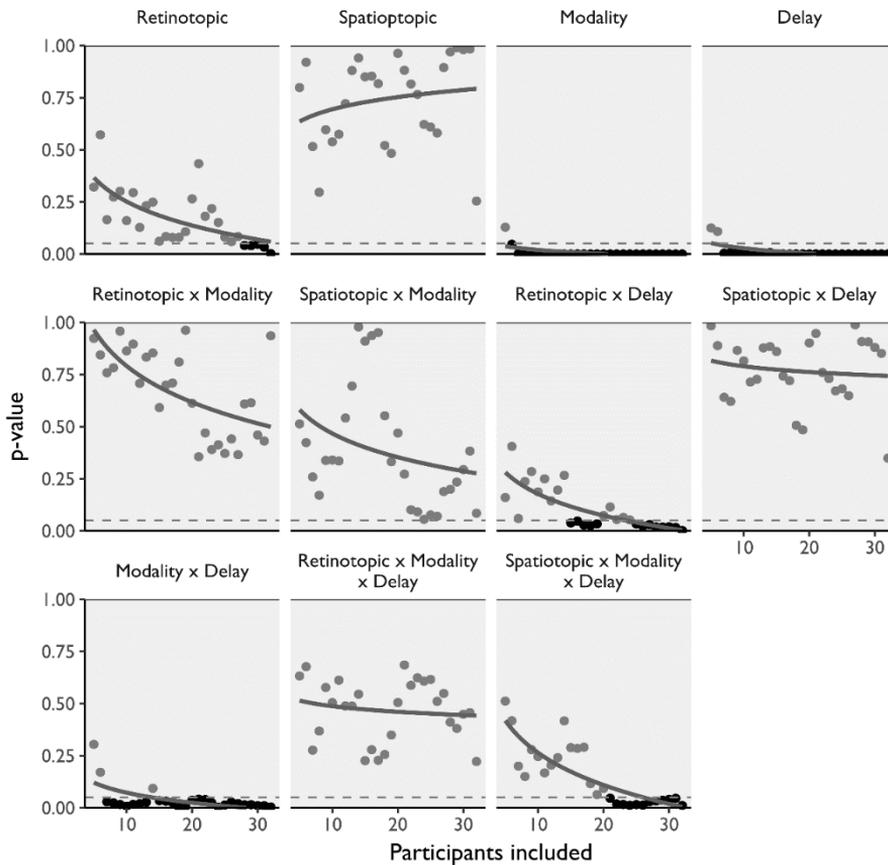
Supplementary Figure 1. Sigmoid fit of pointing responses to auditory locations of all participants in the matching task. The black dots show individual responses. The cyan colored lines represent the sigmoid fit used to match visual and auditory location.



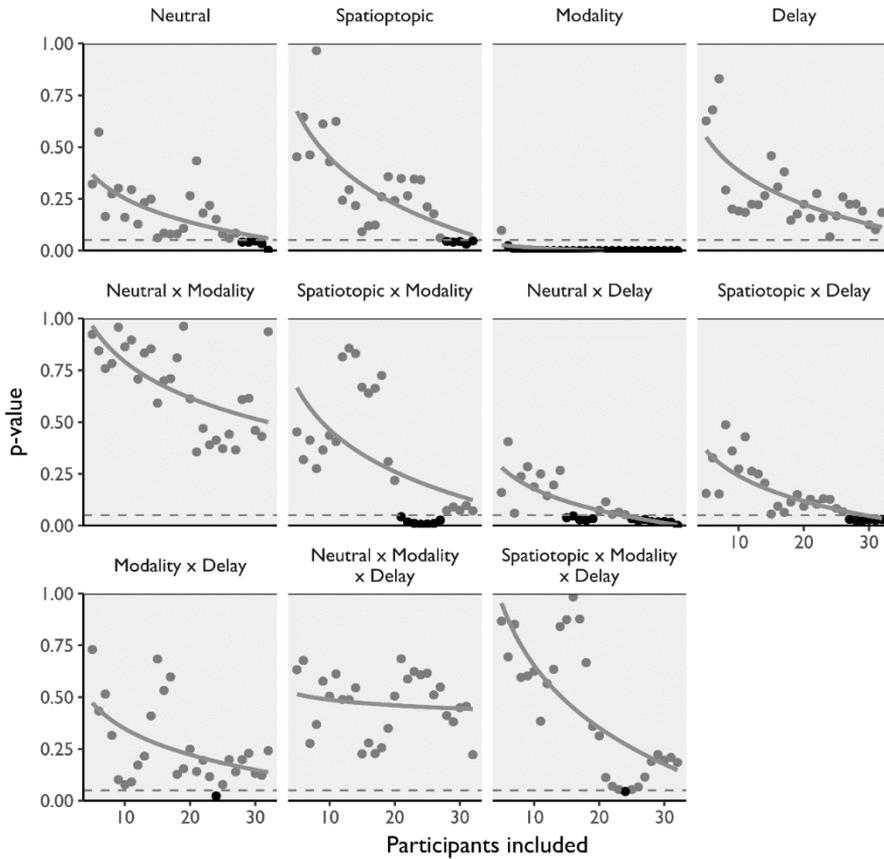
Supplementary Figure 2. Overview of all data in Experiment 1. The colored squares are counts in a 2D histogram. The horizontal bins in the histogram are 50 ms wide, the vertical bins are 30 ms wide. The median, 1st and 3rd quartile and estimates from the linear mixed model are plotted per condition.



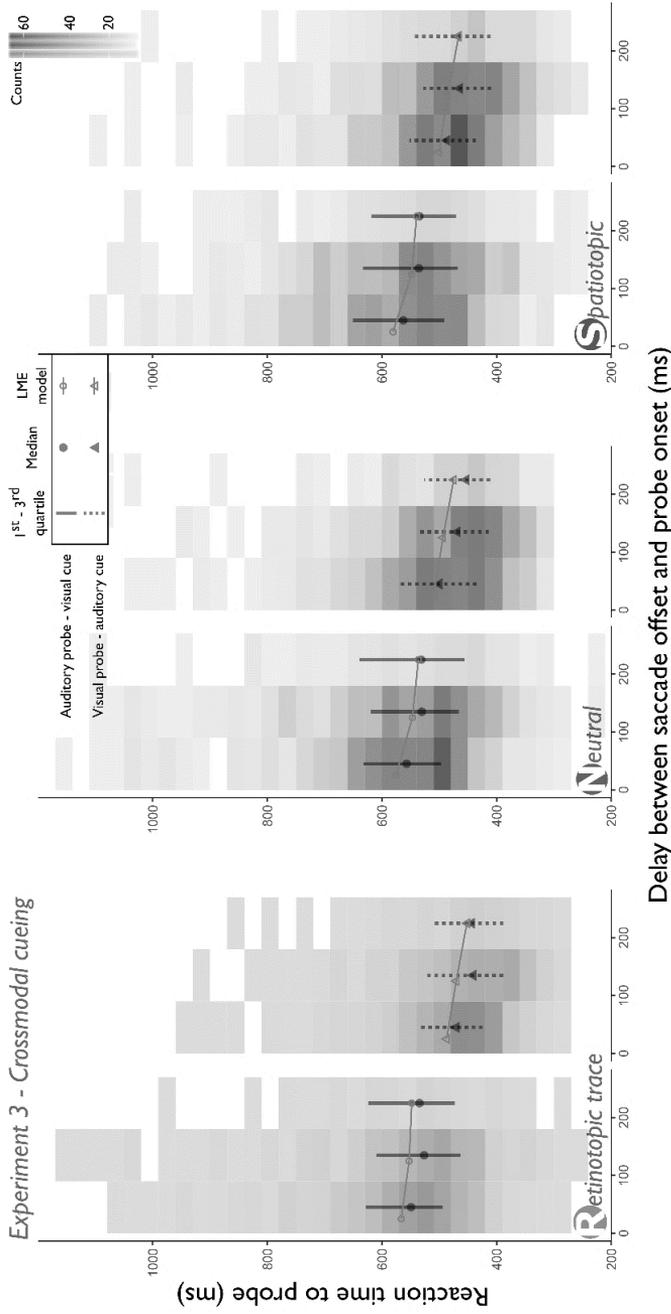
Supplementary Figure 3. Overview of all data in Experiment 2. The colored squares are counts in a 2D histogram. The horizontal and vertical bins in the histogram are 30 ms wide. The median, 1st and 3rd quartile and estimates from the linear mixed model are plotted per condition.



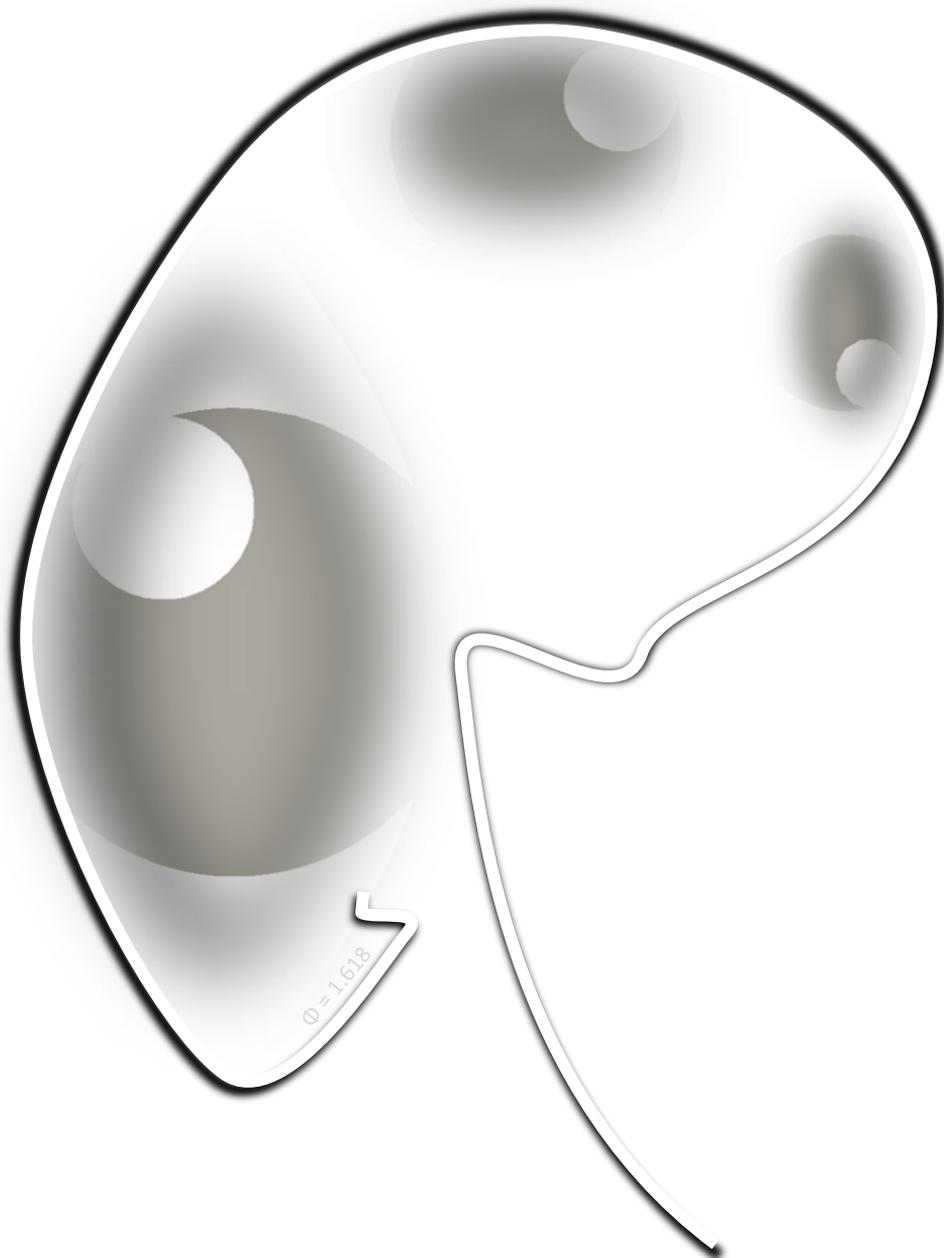
Supplementary Figure 4. Sequential analysis using Neutral locations as reference. Each dot represents one linear mixed model analysis, the x-axis shows the number of participants included in the analysis (in no order) and the y-axis shows the p value for the parameter. Black dots indicate a value of $p < 0.05$. The line is a log-linear fit to the data and only serves as visual reference. Note that under the null-hypothesis, the p-value is expected to do a random walk.



Supplementary Figure 5. Sequential analysis using Retinotopic trace locations as reference. Each dot represents one linear mixed model analysis, the x-axis shows the number of participants included in the analysis (in no order) and the y-axis shows the p value for the parameter. Black dots indicate a value of $p < 0.05$. The line is a log-linear fit to the data and only serves as visual reference. Note that under the null-hypothesis, the p-value is expected to do a random walk.



Supplementary Figure 6. Overview of all data in Experiment 3. The colored squares are counts in a 2D histogram. The horizontal bins in the histogram are 90 ms wide, the vertical bins are 30 ms wide. The median, 1st and 3rd quartile and estimates from the linear mixed model are plotted per condition.



Chapter 7

General Discussion

Martijn J. Schut

In the introduction of this dissertation I argued that continuity of visual perception across saccades may be interpreted within a forward model. Typically, forward models have been used to explain learning from motor errors [41,42]. Within the context of this theory, motor systems use efference copies of the motor command that is sent to the muscles to increase motor accuracy over time. Subsequently, the efference copy is used to predict the outcome of the motor command, by an abstract process known as a forward model. After the motor command is completed, a comparison can be made to determine whether the forward model correctly predicted the outcome, or whether the forward model needs to be updated. Predicting the future state of the world in this manner is invaluable, as it allows humans to make increasingly precise motor movements as they age from infancy to adulthood. Without a predictive process for motor movements, the wealth of complex and precise motions that humans can execute would not exist.

Many studies on visual perception start with the notion that somehow, the visual system can combine discrete snapshots of visual information into a continuous perceptual experience. Recently, a theory has been proposed that the human visual system may be able to establish continuity by predicting future retinal input, and integrating the prediction with the postsaccadic visual input [30]. I add to this model that the prediction needs to account for variance in saccade landing point, to facilitate stable perception, and that it probably uses an efference copy of the motor signal sent to the eye-muscles (as the corollary discharge is an essential component of stable visual perception [49]). The notions that 1) future retinal input is predicted, and 2) that this prediction may be based on an efference copy of the corollary discharge, intersect within a forward model for visual perception.

In my view, the integration of presaccadic prediction and postsaccadic visual input may occur as follows. Before a saccade is made, the visual information at and surrounding the saccade target is processed in high detail due to the presaccadic shift of attention [14,19,20,47]. The presaccadic shift of attention is deployed at the intended landing point of the saccade [17,18]. Based on the processed information, a prediction of the postsaccadic state of the visual world is made [29,32]. This prediction is then stored into visual working memory (VWM) to retain it during the saccade [23,245,246]. After the saccade is completed, postsaccadic visual input is immediately processed and integrated with the presaccadic prediction [35–37,43]. Lastly, the most speculative part of the model as it stands, integrating pre- and postsaccadic information may allow for the visual system to assume that visual information was always present, thus establishing visual continuity (as hypothesized

in the paper by Herwig [30]). In the following sections I will discuss the different elements of the forward model, and which chapters relate to those aspects. I will discuss some open questions within the chapters and tie the results back into implications for the forward model.

Attentional selection

In Chapter 3 we investigated attentional selection coupled to saccade execution. We hypothesized that other attentional processes would interact with the presaccadic shift of attention. Here, we found that participants were less accurate when reporting an item close to a saccade target that was previously fixated, than items that were not previously fixated. We interpreted these results as follows; that inhibition of return (IOR), an inhibitory attentional effect, interacts with the presaccadic shift of attention.

There are several things to note about this study. One thing that has piqued my curiosity in this study is that performance is better close to the saccade target, but also close to the anti-saccade target. When discussing the increase of performance at both tail ends with a colleague at a conference, he jokingly dubbed it the ‘spoon effect’ *<citation needed>*. Apparently, where effects in opposite directions are observed are somewhat common. My view is that it was probably related to participants having both saccade targets attended, yet, after contemplating the spoon effect for a while I am still uncertain why we would observe this pattern of results. Especially as the ‘spoon attentional trace’ does not seem to be affected by IOR nor can it be explained due to crowding effects. As it stands, it is a somewhat peculiar overall pattern of results, and have yet to come up with a completely satisfactory explanation.

On a personal note, I would probably approach the data analysis somewhat differently at this point (as this was the first paper I wrote to this capacity). The main problem, I think, lies in the participant analysis, where we have done t-tests on participant data to give an indication of similarity of effects within participants. Although I commend my 4-year younger self on the effort, the purpose of these statistics is to make some sort of statement on a group level. At this moment, I think comparing bootstrapped confidence intervals would have sufficed and would have probably delivered a clearer message, as psychophysics effects using the methods we used are usually not significant at the participant level (hence the multiple participants).

Our other study focusing on attentional selection is discussed in Chapter 4. We studied gaze corrections, where saccade targets are selected, and are reselected if necessary. Such reselection processes were shown to be affected by the content of VWM, but the relationship between reselection and other attentional processes were unclear. We studied the effect of previous fixations on corrective saccades and found that corrective saccades to previously fixated objects and locations were executed faster. Only when both the object as well as the location was previously fixated did we observe inhibition. These results show that attentional selection, and further use of the selected information for corrective saccades are subject to previous fixations. Based on these results we conclude that corrective saccades are not merely executed to locations or features, but fully bound object files that include all relevant information about the corrective saccade target.

On the topic of analyses, I would choose a slightly different approach once again. A study, which was published after I finished writing the chapter, has shown that an additive hazard model is a great way to investigate corrective saccades [247]. Typically, these models are used to predict the odds that an event (usually something bad) that varies in its occurrence across time has occurred. For example, it can be used to model the odds of contracting lung cancer after x amount of years of smoking, or odds of a disease contracted after being in contact with a disease vector for a variable amount of time (hence the *hazard* part of the name). Coincidentally, due to the variability in saccade latencies and occurrences, a hazard model is a great way to analyze corrective saccades. For example, it allows you to investigate at what point a saccade is most affected by previous fixations, or previously fixated objects, or the interaction between the two. Similarly, just like lung cancer is not contracted in 100% of smokers after a lifetime of smoking, not every inaccurate saccade is followed by a corrective saccade (this may be the most bizarre simile I have ever written). Lastly, this model allows the researcher to investigate influences on corrective saccade execution over time, as you would expect certain influences on saccade execution to enact their effects at different time points. For example, previously fixated locations will probably affect saccade latency at an earlier timepoint than feature information, as feature information needs to be processed first. I would replace the correlation between first saccade latency and second saccade latency analysis from Experiment 1 with this model, but I think the model would be more appropriate overall.

As a final note on visual attention, the studies in both Chapter 3 and Chapter 4 show that attentional selection is not exclusively affected by saccade execution. In

terms of our proposed forward model, Chapter 3 shows that, most likely, integration across saccades is not only limited to information mandatorily selected by executing the saccade. Rather, integrative processes take fixation history and other knowledge about the visual world into account as a sort of prior. Chapter 4 shows a behaviorally relevant outcome of integrating location and feature information, as corrective saccades are a necessity to foveate visual information after motor variance inevitably occurs.

Prior studies have shown that transsaccadic integrative processes are affected by attentional selection [37], showing a tight coupling between attention, and integration. However, I think the functional implications of such integrative processes are still vague. I think it either serves to execute corrective saccades, or to establish visual continuity. Of course, it is possible that, integrative processes do not serve any meaningful behavioral influence, and are merely an artifact of the way the visual system processes information. Currently, there is no decisive evidence for either direction. To strengthen how attention relates to integration of presaccadic and postsaccadic information, a strong theoretical framework must exist about the possible functionality of this relationship.

Storing the prediction in VWM

Previous research has showed that VWM content affects saccades. In these studies, participants more often make saccades to objects that share features to those held in VWM [23]. In Chapter 2, we investigated the inverse relationship. In this study we asked participants to remember several objects, then initiate an eye-movement. We hypothesized that before the eye-movement the saccade target is mandatorily encoded into VWM. We find that participants lose one item worth of VWM capacity when making an eye-movement when compared to trials in which they do not make an eye-movement. We also show that this loss of information is selective for visual information. We interpret this as evidence for the notion that the saccade target, or a presaccadic prediction, is mandatorily stored into VWM, likely to allow for a postsaccadic comparison between the presaccadic (stored) state of the world and the postsaccadic visual input.

I think that the relation between VWM and corrective saccade target selection is more tightly coupled than described in Chapter 2. I postulate that, just as saccades are more likely to be made to objects in VWM, if an object is mandatorily loaded in VWM participants are more likely to make a saccade towards this object. This circular relationship had not occurred to me prior but seems plausible. Rather

than the object loaded into VWM being some sort of ‘special’ object that you make a saccade to, it makes more sense that in general you make more corrective saccades to objects in VWM *and* that the saccade target is mandatorily loaded into VWM to facilitate this mechanism. Note, that this is post-hoc speculation after re-reading the chapter and I would very much encourage any emboldened scientist to investigate my hypothesis.

Although I am happy with the methodology and the analysis in Chapter 2, my niggling irritation with it is that Experiment 1 and 2 are somewhat dissimilar from each other. Although the piece is fine as it stands, I would have liked to have a replication experiment for Experiment 1 using the methodology for Experiment 2. For the analysis, I think Bayesian statistics were the right choice to make (you might want to strap in, as you’re going to read this point of view a few more times). Having this very informative continuous measure in Experiment 1, and not modeling the response profiles was a bit of a missed opportunity. Many studies have shown how you could investigate such continuous data, e.g. separating out random guesses, non-target responses, and responses to the target [52,54]. However, for a Bayesian approach the manner to do this is not very straightforward. You would have to construct the model yourself and parse it to a (MCMC) sampler. We had built such a model, for a reviewer’s comment, but decided not to use it as: the results were similar, but the approach was too different with respect to the other analyses. In retrospect, I think it would have been better to only use the mixture model and drop all the linear mixed effects models, but the current manuscript gives a fine, but slightly more limited, interpretation of the data as well.

Furthermore, this continuous measure could have allowed us to investigate something even more intriguing. We have shown that saccades cost about one item worth of VWM, but we were not able to show with the current analyses what this exactly means for the items in VWM. To illustrate, it seems likely that the least represented object is removed from VWM. However, whether this means that the saccade target is overriding the least represented object in VWM, or just diminishes all representations equally is still unclear. I especially wonder on what basis information is selected to be overridden. However, if all representations in VWM are equally diminished by a saccade selection this may be a moot point.

I think the storage of items in VWM is the least contentious part of the proposed *forward model*, but there are still some crucial questions to be explored. According to our study, the prediction that is made about the saccade target takes up one item worth of VWM capacity. For a follow-up experiment I would suggest that,

the prediction altering paradigm from Herwig and colleagues [32] could prove essential in providing evidence whether the prediction or the actual visual information is mandatorily encoded into VWM. Using this paradigm, one can dissociate the prediction (by altering it) from the physical presaccadic properties in VWM. Perhaps then in combination with a corrective saccade paradigm, one could observe whether participants are more likely to make an eye-movement to the predicted/manipulated stimulus or the unaltered stimulus. In my perspective, especially this prediction/perception delineation experiment is crucial in establishing the role of corrective saccades for visual stability.

Transsaccadic integration

In Chapter 5, we discussed transsaccadic feature integration. Here, we set out to investigate how the visual system deals with motor variance when integrating pre- and postsaccadic visual input. Here, we hypothesized that color integration across saccades is affected by saccade landing distance, due to color perception being poorer in the periphery than in the fovea. Alternatively, by deploying attention to the intended saccade landing point, and keeping it there, the visual system may be able to offset motor variance. It seems that visual attention is deployed at the intended saccade target, rather than being affected by variance [17,18], and may therefore be able to account for unaffected feature integration across saccade landing point variance. We found that both for regular motor variance, and extreme variance due to global effect saccades, participants did not integrate color information differently when landing further away from the saccade target. This shows that, transsaccadic feature integration is (at least in part) driven by visual attention before the saccade [36,37], and after the saccade [Chapter 5].

Interestingly, transsaccadic feature integration is a somewhat contentious process. Although behaviorally, there seems to be some form of integration, it is currently unclear whether this is a form of perceptual integration or response integration. If feature integration is indeed perceptual, participants perceive a mixture of the pre- and postsaccadic state of the world and report this mixture. If feature integration is motor integration, it means participants are combining their responses to the presaccadic and postsaccadic state of the world into a single response. Although the evidence for feature integration being (at least in part) a perceptual process is mounting, the literature remains divided [36,37]. This becomes more complicated, as feature integration is often convolved with perceptual fusion [183], which I think are two distinct processes. Perceptual fusion involves fusing

spatially dissimilar information, whereas integration involves integrating information at the exact same spatiotopic location. This is important, as perceptual fusion investigates fusing two disparate objects, whereas the second shows how the visual system establishes continuity of a single object. Further adding to the contentiousness of transsaccadic feature integration, some studies have used methodology which caused fusion of the state of the world to occur physically, due to pixel persistence [181]. In this study, the monitors used in the experiment showed a physical mixture of the before and after change state, as the pixels of the screen were too slow to update. Despite these challenges, it is essential for the field of feature integration to continue to separate itself from integration based on motor integration as well as use appropriate methodology. Currently, the field remains too contentious for wide adoption of transsaccadic feature integration as a perceptual phenomenon.

As for the methodology in Chapter 5, the only logical choice was Bayesian statistics. Here, I had two equally valid hypotheses, and if I specified a prior distribution appropriately, Bayesian hypothesis testing could provide evidence for either. I would argue that frequentist statistics would have been conceptually inappropriate for this chapter, as it assumes the null-hypothesis to be true a priori and would not allow us to find evidence for the null. Again, I would have liked to construct a hierarchical Bayesian model to model the response distribution to our continuous data. In retrospect, the optimal observer model analyses were not very informative, as the results were so similar to the rest of the results in the chapter. I think a replacement with a hierarchical Bayesian modelling approach would have been more informative and would have allowed us to model e.g. random guesses, or participant effects in more detail.

As a last note, it was quite informative (and fun!) to measure the screen properties for this experiment. Unfortunately, I only had the presence of mind to do so after receiving reviews. Especially since this was the last experiment I conducted for my dissertation, I would very strongly recommend that other vision scientists validate their screen response time before starting. Rather than do what I did and only validate the timing (using a photodiode, see supplementary material Chapter 5) after everything was done and opening the potential of all the work being invalid.

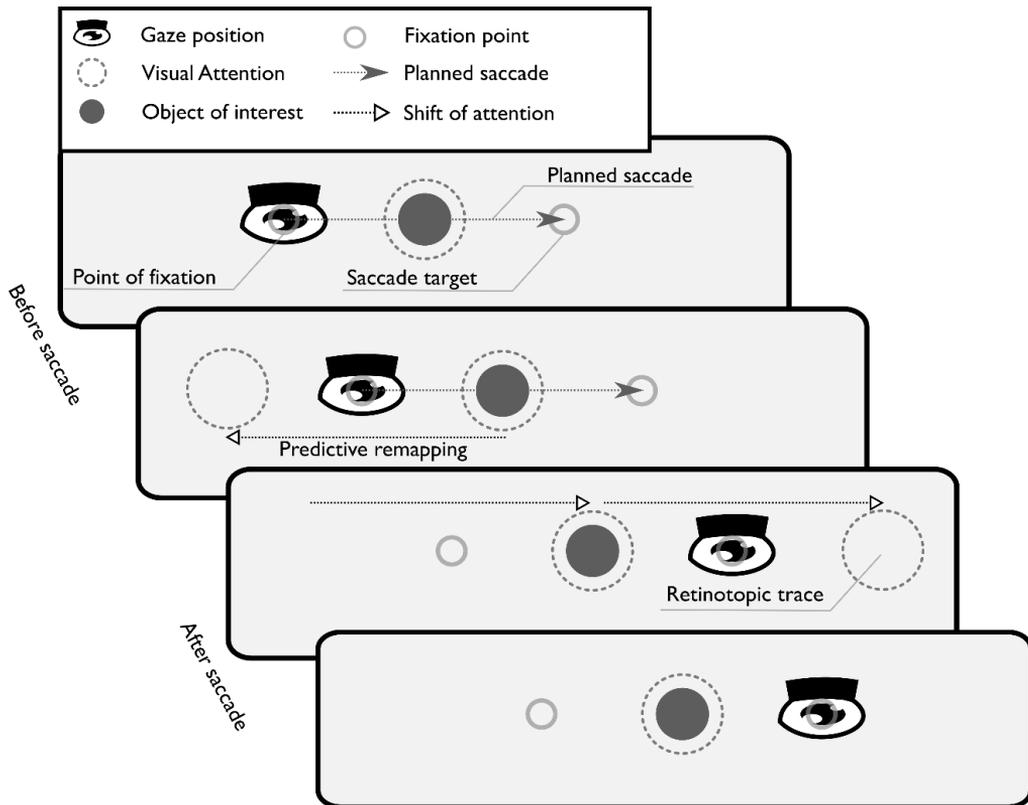


Figure 1. Remapping visual attention across saccades.

The four panels illustrate four timepoints across a saccade. First, a saccade is planned to a saccade target. Then, attention updates to the future postsaccadic position of the object. Next, the saccade is executed, and finally the old presaccadic locus of attention is extinguished. Not that this illustration only includes one locus of attention that updates and does not show the updating of attention at the saccade target. Also note that, for simplicity's sake, the saccade is 100% accurate.

Crossmodal attentional updating

In the final chapter, we investigated whether the forward model for visual perception across saccades could be extended outside of the visual modality. Visual attention is encoded relative to the retina (retinotopic), this is useful, since when a saccade is made visual attention needs to update in the opposite direction to the saccade vector to be positioned at the correct postsaccadic location (Fig. 1). Broadly

speaking, if I make an eye-movement to the *right*, the visual information is going to shift *leftward* relative to the retina, thus visual attention needs to shift *leftward* relative to the retina. An artifact of attentional updating can be observed, whenever a saccade is made. After a saccade is made, attention continues to linger at the previous retinotopic location for a short while [220,225,226]. In Chapter 6 we hypothesized that this retinotopic trace may be observable for auditory stimuli as well. Although auditory stimuli are encoded relative to the head, it is essential for the interaction between vision (encoded relative to the retina) and auditory that the visual system has some notion of the retinotopic location of an auditory stimulus after a saccade. Based on neurophysiological studies, it seemed plausible that sensory systems use similarly updating attention across saccades [63,235,248,249]. Conform our hypothesis, we found that a retinotopic trace was present for auditorily presented stimuli. The results suggest that the retinotopic trace declines similarly across modalities, possibly due to some sort of common updating mechanism. To conclude, this chapter implicates that the forwards model for visual perception could, possibly, be extended beyond the visual domain (although I make this claim very carefully, as it is based on a single study).

To exemplify what work remains, Fig.1 illustrates the updating of visual attention across a saccade. We have shown that, at least partially, cross-modal attention updates in a similar manner with respect to the retinotopic trace. However, many studies have shown the predictive updating of spatial visual attention before a saccade is made [179,250–253]. It is still unclear whether the entire peri-saccadic attentional updating period is reflected across multiple sensory systems. To further strengthen the notion that attentional resources may be updated in a similar manner across sensory systems when a saccade is made, the predictive remapping processes need to be investigated for auditory stimuli. As a note of warning to any prospective researchers on this topic, we have attempted such a predictive remapping paradigm with audition. However, we found it extremely difficult to find performance that was consistent enough to detect such an effect. Combining the timing of the auditory presentation, the response, as well as the saccade was quite difficult. If anyone does decide to investigate multisensory attentional updating in this manner, know that such updating may take well-trained participants to be detected (if it exists at all). I would personally recommend that prospective researchers evaluate saccade latency of a participant and exclude participants that generally make saccades too quickly or too slowly to reliably present auditory information at the time the predictively remapped attentional trace is present.

For the next paragraph I am going to get on my soapbox, so to speak. Although I like the Chapter 6 as it stands, it is somewhat of a Frankenstein's monster of parts that were added on. Initially, only Experiment 1 and Experiment 2 were part of the paper. We have submitted the paper multiple times and found that reviewers took a particularly strong stance against Experiment 2, an almost direct replication of Experiment 1. The stance was, typically, to remove Experiment 2 as it did not add anything new. I find that attitude somewhat grating, as the field of psychology has been under scrutiny, exactly due to non-replicable results. In the end we solved the issue by adding an additional experiment, to sandwich the "not-novel" Experiment 2 between the novelty of Experiment 1 and 3 (primacy and recency effect are your friends here) and resubmitted it to a new journal. As I have engaged with more people that have found difficulties in publishing an internal replication, I hope my approach could provide a solution. Furthermore, I would like to encourage anyone who reads this section to stand by your replication, and not yield a replication to the pursuit of novelty. Out of the chapters in dissertation, I think Chapter 6 is the most convincing, exactly due to this replication. The only price that we had to pay is a slightly less succinct manuscript, which is relatively small in the grand scheme of things.

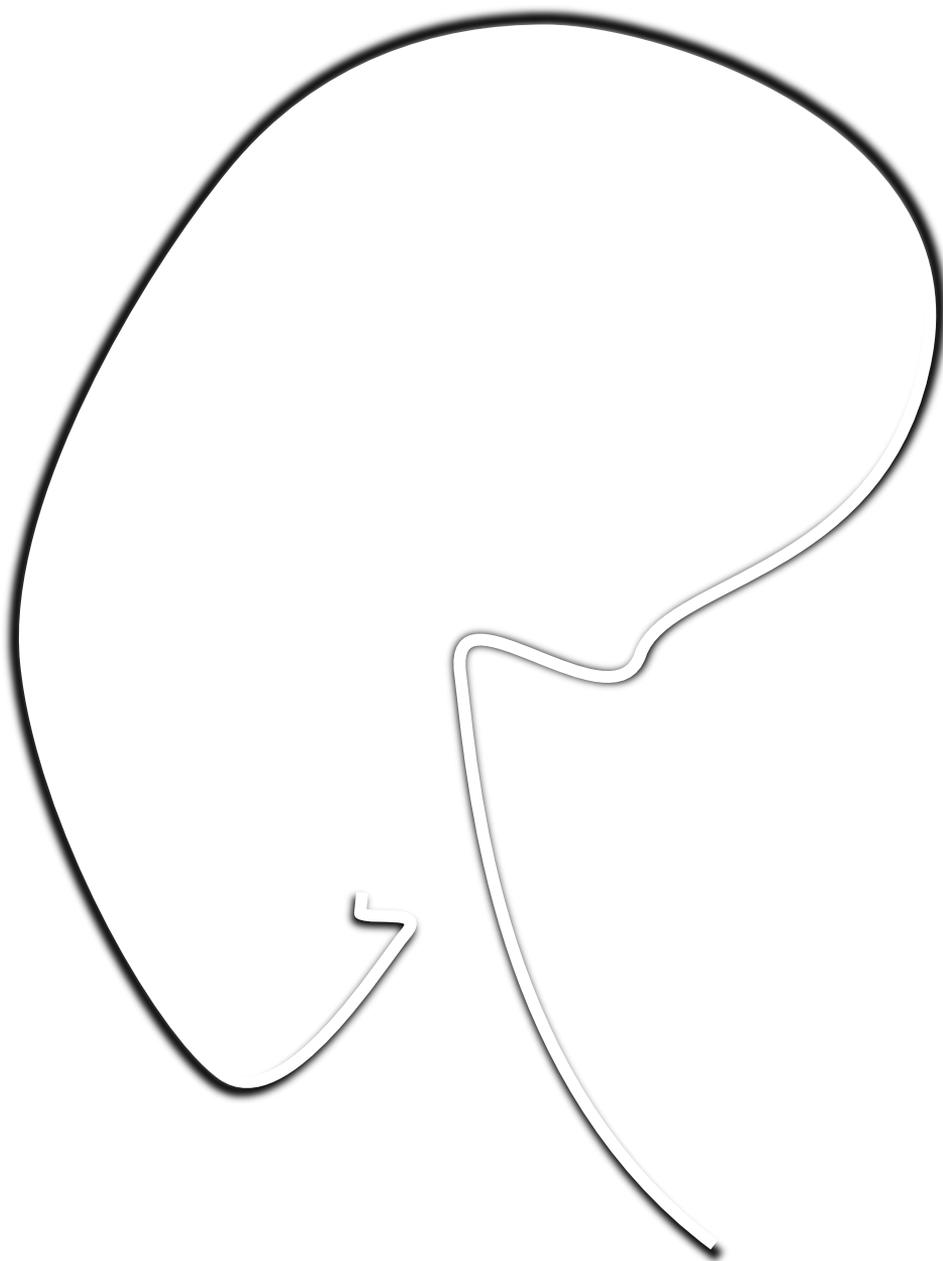
I think our difficulties with getting the project published stem from the fact that this study sits at the intersection of vision and multisensory research. Often, the auditory element was not too interesting for visual researchers, and the saccade elements were confusing to multisensory researchers. Although I think it is interesting to break open vision research to the other modalities, I believe this transition is still very much in its infancy. There are several researchers who are, slowly but surely, extending their work across modalities. I encourage any reader that researches some intra-modality sensory process to consider their projects in a broader scope, across modalities, as (in my view) it seems likely that the visual system reuses solutions to common perceptual problems across sensory modalities.

Lastly, regarding the analyses in this chapter, the one thing I would do differently is remove the assumption of linearity across the analyses. Alternatively, we could have fit a generalized additive mixture model (GAMM) to this sort of data, which makes no assumptions about the underlying function. I have used GAMMs for a side project not included in this dissertation, and I can very much recommend them for any time-series analysis (see Ohl's article for a great example on GAMMs and saccadic updating [254]).

Conclusion

Before an eye-movement is made, attention is used to select information about the saccade target. Then, this information is stored into a memory buffer, VWM. Lastly, the information is compared, after the eye-movement, to the presaccadically stored information. If the postsaccadic information matches the presaccadic prediction, observers integrate the features of objects and assume that these features had been present all along, eliminating our need to process the information during the saccade. Interestingly, many of these terms have previously been combined into a model that is known as the forward model. However, this forward model is rarely applied to the study of visual perception. Here, we showed that the forward model may be an excellent point for future research into visual perception, as many of the processes linked to saccade execution and visual continuity fit within this theoretical model. Through prediction and integration, the visual system may be able to establish visual continuity, even though visual processing is discrete.





Appendix – Reference list

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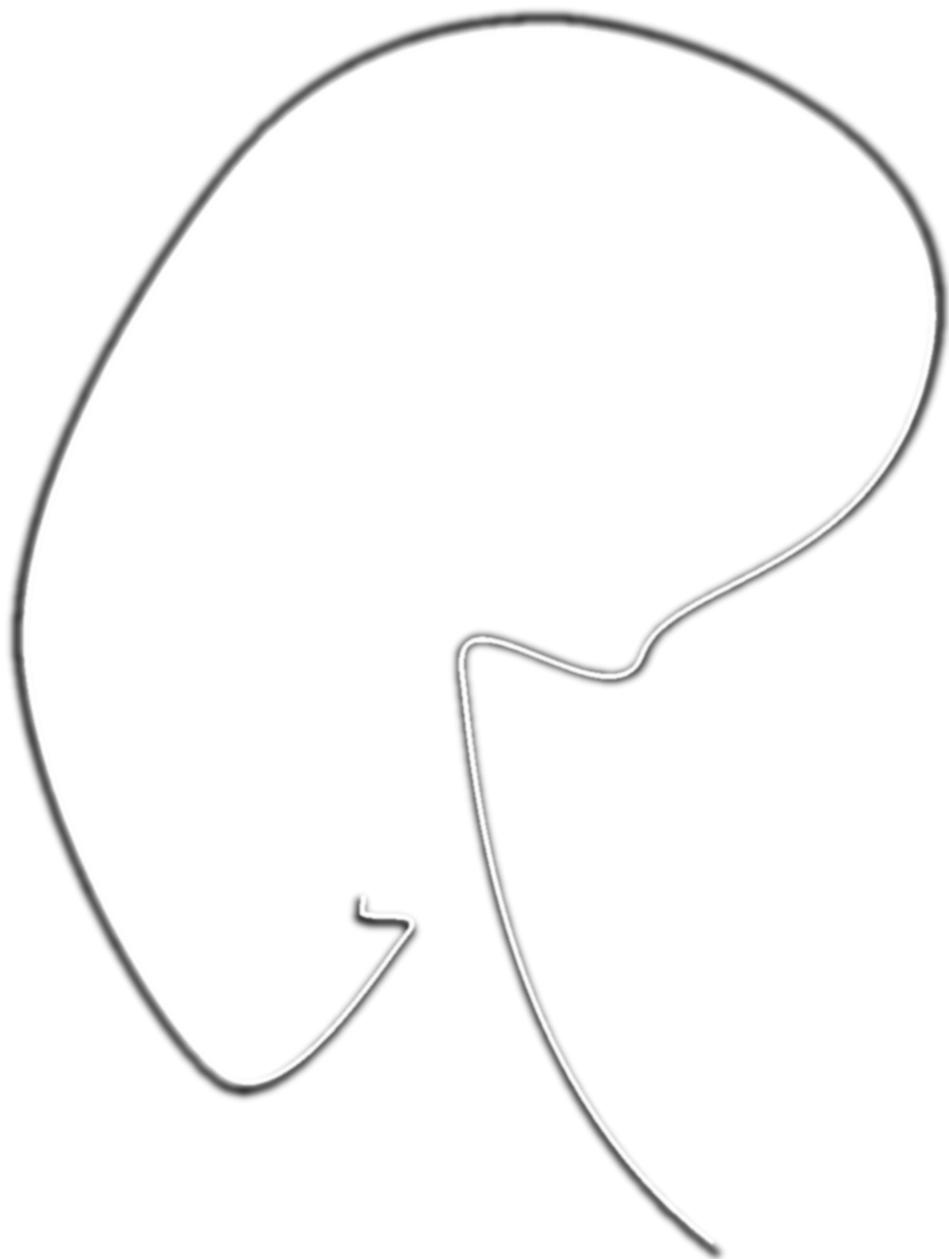
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Appendix – Dutch summary

Het zicht is het belangrijkste zintuig van mensen, de hele samenleving is ingericht op het vermogen om te kunnen zien. De meeste activiteiten gebruiken ons gezichtsvermogen als uitgangspunt, bijvoorbeeld: autorijden, het gebruik van smartphones, en het spelen van videogames. De nadruk op zicht is logisch, want ons zicht stelt ons in staat om objecten die ver én dichtbij zijn waar te nemen, en dat met een accuratesse waar de andere zintuigen niet tegenop kunnen. Ons wereldbeeld is echter niet zo nauwkeurig als onze ervaring ons zou doen geloven, en we leven alleen maar in de illusie van perfect zicht. Hoewel we naar de hele wereld aan het *kijken* zijn, *zien* we maar een heel klein deel van de wereld. Het kunnen verwerken van visuele informatie is gekoppeld aan visuele aandacht. Visuele aandacht fungeert als een selectiemechanisme voor visuele informatie, zodat niet alle visuele informatie verwerkt wordt, maar alleen dat wat relevant voor ons is.

Het visuele systeem verwerkt niet alle informatie in het hele visuele veld, en het verwerkt ook niet aldoor visuele informatie. Het visuele systeem is genoodzaakt om oogbewegingen te maken (saccades). Mensen maken saccades om de hoge resolutie fovea (het deel van het netvlies met de meeste fotoreceptoren) te verplaatsen richting relevante visuele informatie. Tijdens saccades stoppen we grotendeels met het verwerken van visuele informatie. Visuele verwerking wordt opzettelijk stopgezet, omdat het verwerken van het visuele beeld zou leiden tot het uitsmeren van het beeld op het netvlies. Dit is vergelijkbaar met het soort uitsmeren dat je ziet wanneer je een foto maakt met een bewegende camera. Waarschijnlijk lost het visuele systeem het probleem van het uitsmeren van het visuele beeld op door de visuele verwerking aan het begin van een saccade stop te zetten, en weer te beginnen zodra het oog weer stil staat. Het opvallende verschil tussen onze continue subjectieve ervaring en onze discrete visuele informatieverwerking wordt vaak het visuele continuïteit probleem genoemd.

Om de pauzes in visuele informatieverwerking om te zetten naar een continue subjectieve ervaring, moet informatie worden geselecteerd, opgeslagen en vergeleken met de visuele informatie na de oogbeweging. In dit proefschrift betoog ik dat het visuele systeem de continuïteit van visuele waarneming over oogbewegingen kan bereiken via verschillende koppelingsmechanismen: 1) pre-saccadische verschuivingen van aandacht, 2) visueel werkgeheugen, en 3) transsaccadische integratie. Deze begrippen komen samen in één gemeenschappelijk model: een *forward model* van visuele waarneming.

Vele studies hebben aangetoond dat processen van visuele aandacht nauw gekoppeld aan het maken van oogbewegingen. Onderzoek heeft aangetoond dat

visuele aandacht verschuift naar het doelwit van een oogbeweging. Dit staat bekend als de pre-saccadische verschuiving van aandacht. Dit gebeurt waarschijnlijk om het doelwit van de saccade gedetailleerder te verwerken, zodat het visuele systeem de visuele kenmerken en de locatie van het object kan evalueren voordat een oogbeweging wordt gemaakt.

Als pre-saccadische informatie inderdaad wordt vergeleken met post-saccadische informatie, moet de pre-saccadische informatie worden opgeslagen gedurende de saccade. Pre-saccadische informatie wordt opgeslagen in visueel werkgeheugen (*visual working memory*, VWM). Met VWM kunnen mensen tijdelijk visuele informatie opslaan en manipuleren. Voordat een saccade wordt uitgevoerd, heeft visuele informatie meestal een lage resolutie, omdat het ver van de fovea af staat. Op basis van pre-saccadische visuele informatie maken we een voorspelling van hoe de wereld er na de oogbeweging uit gaat zien. Het is mogelijk dat het visuele systeem de pauzes in visuele verwerking tussen saccades kan overbruggen door pre-saccadische en post-saccadische visuele informatie te combineren tot één perceptuele ervaring. Dit fenomeen staat bekend als transsaccadische integratie. Door visuele informatie over saccades te integreren, kan het visuele systeem aannemen dat visuele informatie altijd aanwezig was. Deze aanname van het visuele systeem kan je zelf ervaren door oogbewegingen te maken naar een klok met een secondewijzer. Als je dit een aantal keer doet, merk je misschien dat het even duurt voordat de secondewijzer verder loopt. Dit komt omdat je visuele systeem, nadat je de oogbeweging hebt gemaakt, het gebrek aan visuele informatieverwerking tijdens de oogbeweging maskeert met de post-saccadische visuele informatie. Hierdoor lijkt het moment tot het bewegen van de secondewijzer iets langer te duren.

Ik denk dat deze fenomenen binnen een theoretisch model passen, een *forward model*. Doorgaans wordt de theorie van het *forward model* gebruikt om bewegingen te bestuderen. De essentie van een *forward model* is dat een kopie van het motorcommando dat naar de spieren wordt gestuurd gebruikt kan worden om de uitkomst van het motorcommando te voorspellen. De kopie wordt vaak een efferentekopie genoemd. Het voorspellende mechanisme dat een efferentekopie als invoer gebruikt, en een voorspelling als uitvoer geeft heet een *forward model*. Nadat de beweging is voltooid, wordt de voorspelling van het *forward model* vergeleken met de nieuwe staat van de wereld. Als de voorspelling niet overeenkomt, kan het systeem leren van de fout door het *forward model* bij te werken om nieuwe voorspellingen te doen. We stellen dat visuele waarneming in een vergelijkbaar theoretisch model past. Wanneer een saccade wordt gemaakt, voorspelt het visuele

systeem de uitkomst van de oogbeweging op basis van de efferentekopie dat naar de oogspieren gestuurd wordt. Vervolgens wordt de pre-saccadische visuele invoer geïntegreerd met de post-saccadische visuele invoer. Tijdsintegratie zou kunnen verklaren waarom we tijdens een saccade ons gebrek aan visuele verwerking niet merken. Zo zou visuele continuïteit tussen saccades kunnen worden vastgesteld.

Binnen dit proefschrift onderzoeken we een aantal elementen van het *forward model*. Ten eerste, eerder onderzoek heeft aangetoond dat de inhoud van VWM van invloed is op saccades. Mensen maken vaker saccades naar objecten die eigenschappen hebben die opgeslagen zijn in VWM. Bijvoorbeeld, als je een rood voorwerp onthoudt, maak je vaker oogbewegingen naar rode objecten. In Hoofdstuk 2 hebben we de omgekeerde relatie tussen VWM en oogbewegingen onderzocht. In deze studie vroegen we proefpersonen om verschillende objecten te onthouden en vervolgens een oogbeweging te maken. We veronderstelden dat vóór de oogbeweging het doel van de oogbeweging in VWM opgeslagen wordt. De resultaten toonden aan dat deelnemers één visueel object aan VWM-capaciteit verliezen bij het maken van een oogbeweging. We laten ook zien dat dit informatieverlies selectief is voor visuele informatie. We interpreteren dit als een bewijs dat het doel van de oogbeweging, of een pre-saccadische voorspelling, wordt opgeslagen in VWM.

In Hoofdstuk 3 onderzochten we de aandachtselectie gekoppeld aan saccade-uitvoering. We veronderstelden dat andere aandachtsprocessen zouden interacteren met de pre-saccadische verschuiving van aandacht. De resultaten toonden aan proefpersonen minder nauwkeurig waren bij het rapporteren van een object dat dichtbij het doel van een oogbeweging staat, als proefpersonen eerder naar de locatie hadden gekeken. We interpretererden deze resultaten als volgt; dat inhibitie van terugkeer (inhibition of return; IOR), de pre-saccadische verschuiving van aandacht remt. Deze resultaten suggereren dat de koppeling tussen oogbewegingen en aandacht verschuivingen beïnvloed wordt door andere aandachtsprocessen.

In Hoofdstuk 4 bestudeerden we correctieve oogbewegingen. Correctieve oogbewegingen zijn nodig, omdat saccades niet altijd accuraat zijn. We onderzochten het effect van eerdere bekeken locaties op correctieve oogbewegingen. We ontdekten dat correctieve oogbewegingen naar eerder bekeken objecten en locaties sneller werden uitgevoerd. Alleen als zowel het object als de locatie eerder waren gefixeerd, observeerden we een vertraging. Op basis van deze resultaten concluderen we dat correctieve saccades worden uitgevoerd op basis van volledig

gebonden objectbestanden die alle relevante informatie bevatten over het doel van de correctieve oogbeweging.

In Hoofdstuk 5 bespreken we transsaccadische-integratie van visuele eigenschappen. Hier bestuderen we hoe het visuele systeem omgaat met onnauwkeurige oogbewegingen bij het integreren van pre- en post-saccadische visuele informatie. Eerder onderzoek toont aan dat het visuele systeem kan compenseren voor onnauwkeurigheden van oogbewegingen door aandacht te plaatsen op het doel van de oogbeweging en het daar te houden. Het lijkt erop dat visuele aandacht wordt geplaatst op het beoogde doelwit van de saccade, in plaats van het daadwerkelijke eindpunt van de saccade. We vonden dat zowel voor alledaagse motorische afwijkingen, en extreme afwijkingen, deelnemers visuele eigenschappen niet op een andere manier integreerden. Dit toont aan dat transsaccadische integratie van visuele eigenschappen wordt gestuurd door visuele aandacht vóór de saccade en na de saccade.

In Hoofdstuk 6 hebben we onderzocht of het *forward model* voor visuele waarneming kon worden uitgebreid naar andere zintuigen. Visuele aandacht is gecodeerd ten opzichte van het netvlies (retinotopisch). Wanneer een saccade wordt gemaakt, wordt visuele aandacht bijgewerkt in de tegenovergestelde richting van de oogbewegingen. Als ik een oogbeweging naar rechts maak, zal de visuele informatie naar links gaan ten opzichte van het netvlies, dus visuele aandacht moet naar links verschuiven ten opzichte van het netvlies om op het doelwit te blijven. Een artefact van het verplaatsen van aandacht kan worden waargenomen, na iedere saccade, waarbij visuele aandacht even blijft hangen op de vorige retinotopische locatie (bekend als het retinotopisch spoor van visuele aandacht). In Hoofdstuk 6 hebben we onderzocht of dit retinotopische spoor ook waarneembaar is voor auditieve stimuli. Auditieve stimuli worden verwerkt worden ten opzichte van het hoofd, omdat de oren aan het hoofd vast zitten. Echter, is het essentieel voor de interactie tussen het zicht en gehoor (dat verwerkt wordt ten opzichte van het netvlies) dat het auditieve systeem een idee heeft van de locatie van een visuele prikkel na een saccade. Het leek aannemelijk dat alle sensorische systemen dezelfde manier gebruiken om de aandacht over saccades te verplaatsen. Conform onze hypothese, vonden we dat het retinotopische spoor aanwezig was voor auditief gepresenteerde stimuli. De resultaten suggereren dat auditieve informatie ook relatief aan het netvlies verwerkt worden, en dat het verplaatsen van aandacht na een oogbeweging op eenzelfde manier gebeurt tussen modaliteiten.

Ter conclusie, voordat een oogbeweging wordt gemaakt, wordt aandacht verplaatst zodat het doelwit van de saccade verwerkt wordt. Vervolgens wordt deze informatie opgeslagen in een geheugenbuffer, VWM. Tot slot wordt de informatie na de oogbeweging vergeleken met de pre-saccadische opgeslagen informatie. Als de post-saccadische informatie overeenkomt met de pre-saccadische voorspelling, integreert het visuele systeem de kenmerken van objecten en kan aangenomen worden dat deze visuele informatie altijd aanwezig was. Hierdoor is het niet noodzakelijk om visuele informatie te verwerken tijdens de oogbeweging. In deze dissertatie hebben we laten zien dat het *forward model* een uitstekend uitgangspunt is voor toekomstig onderzoek naar visuele perceptie, omdat veel van de processen die verband houden met oogbewegingen en visuele continuïteit binnen dit theoretische model passen. Door voorspelling en integratie kan het visuele systeem in staat zijn om visuele continuïteit te bewerkstelligen, ondanks het feit dat visuele verwerking discreet is.





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Members of the perception group, thank you for your input. I feel like the perception meeting has pushed me to improve as a public speaker. I am nowhere near as nervous for presenting, or for negative feedback. This meeting has been hugely relevant for me personally and professionally and I thank you all for your efforts and your time.

All first Reviewers, your kind, critical, yet fair words have improved my published work immensely.

All second Reviewers, thank you for your great input on why my work was not interesting to you¹. I hope the scientific review process continues to be a great outlet for your frustration.

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En tot slot...

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Chloe, at this time you can't read this yet. Nor can you realize just how important you are to me. You have made my life complete. I will love you forever and will always be proud of you. I hope that, with enough work and dedication me and your mom can build you a home that you always feel safe and loved in. You mean the world to us, and you are an inspiration to us both.

¹ *Actual quote from one Reviewer #2: "In general, it is rather clear that the authors are not willing to collect any new data in support of their null effect [...] I can understand that and will not insist as indeed this goes against my main point that their effects are simply not interesting."*

And thus, my final paragraph written as a scientist ends. I cannot help but feel slightly melancholic at my departure, as I will be leaving many great colleagues behind. Yet, I am content with my contribution of science, and if I had to go back knowing what I know now, would make the choice to start this journey a hundred times over.

“Thus we never see the true state of our condition till it is illustrated to us by its contraries, nor know how to value what we enjoy, but by the want of it.”

— Daniel Defoe



Appendix - Information on author

Curriculum Vitae

Martijn Jan Schut werd geboren op 26 juni 1990 te Amsterdam. Na het behalen van zijn vwo-diploma in 2008 aan het Alfrink College te Zoetermeer is hij naar Leiden gegaan voor zijn studie. Vier jaar studie later heeft hij een bachelor in psychologie behaald, en een master of science in klinische neuropsychologie behaald. Hij volgde stages bij het Sophia kindziekenhuis binnen het *Generation R* project en bij Parnassia binnen het *Virtual Reality bij Psychose* project. Vervolgens is hij bij Experimentele Functieleer bij de Universiteit Utrecht aangenomen als promovendus onder het VIDI-project van Dr. van der Stigchel. Dit project werd mede begeleid door Prof. Dr. Postma en Dr. van der Stoep, en heeft na drie en een half jaar geresulteerd tot het proefschrift over visuele perceptie en oogbewegingen. Door zijn affiniteit met programmeren en analyses, heeft hij de stap gezet weg van de academische wereld om verder te gaan als onderzoeker, bij Tessella als Associate Analyst Programmer.

List of published work

Peer-reviewed publications

Schut, M.J., Van der Stoep, N. & Van der Stigchel S. (2018) Auditory spatial attention is encoded in a retinotopic reference frame across eye-movements. *PLOS ONE*, 13(8), e0202414.

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Conference talks

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Schut, M.J., Maarseveen, J., Fabius, J.H., Wittenberg, A.C.W., Van der Stoep, N., & Van der Stigchel S. The location of covert spatial attention is continuously reflected by pupil size. Presented at *NVP 2017*, Egmond aan Zee, The Netherlands.

Schut, M.J., Van der Stoep, N., Fabius, J.H., & Van der Stigchel S. Feature integration is unaffected by saccade landing point, even when saccades land outside of the range of regular oculomotor variance. Presented at *ECEM 2017*, Wuppertal, Germany.

Poster presentations

Schut, M.J., Fabius, J.H., Van der Stoep, N., & Van der Stigchel S. Maintaining a stable world across eye-movements: Object and location information can operate independently in corrective saccades. Presented at VSS 2016, St. Pete's Beach, Florida.

Schut, M.J., Fabius, J.H., & Van der Stigchel S. Investigating the parameters of transsaccadic memory: inhibition of return impedes information acquisition near a saccade target. Presented at The Bernstein Spark's workshop for working memory, 2015. Berlin, Germany.