

Pre-saccadic orthogonal motion and saccadic suppression of displacement

Utrecht University

Faculty of Social and Behavioural Sciences

Master Neuropsychology

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Name: Lenalin Harskamp

Email: l.harskamp@students.uu.nl

Student number: 4074203

Supervisor

Name: Jasper Fabius

Contact details: j.h.fabius@uu.nl

Abstract

Short disruptions of visual input are caused by saccades. As a consequence, we do not perceive displacements of objects during a saccade, which is known as Saccadic Suppression of Displacement (SSD). When was movement of the retinal image caused by the saccade and when by movement of an object? This question is solved by the process of remapping pre-saccadic object locations to the expected post-saccadic locations. With an error area of remapped coordinates the visual system takes into account that a saccade is subjective to errors. When the post-saccadic object location falls in this area, movement is attributed to the saccade. When it falls out of this area, movement is attributed to the object, a relieve in SSD is seen. Wexler and Collins (2014) found this relieve in SSD by moving out of the error area with an orthogonal step. Unreliable object information after a saccade causes relieve in SSD, but what is the effect prior to a saccade. This study considered this question by having a pre-saccadic orthogonal motion. Furthermore, we aimed to replicate the study of Wexler and Collins. In general, we hypothesize that unreliable information after a saccade can cause relieve in SSD, whereas prior to a saccade it causes high suppression. The orthogonal motion, orthogonal step and orthogonal motion plus step could not relieve SSD. This could be ascribed to greater variability in the saccadic errors. There is a larger chance of the motion being attributed to the saccade when the error area is bigger.

Introduction

A person makes around two to three rapid eye movements per second (Schiller, 1998), which are called saccades. Without consciously perceiving it, the input of visual information is shortly suppressed during this period. Still, the world is seen as stable and detailed. One mechanism that is used to maintain this stability, also plays a role in the verification of movement of the retinal image (Wurtz, 2008).

On top of the actual saccade there can be other causes of retinal movement. Due to these other causes, it is hard for the visual system to verify the origins of the movement (Bridgeman, 1995). Extra shifts of the retinal image can be caused by either a small oculomotor error of the saccade, or movement of the object in the real world. By the process of comparing pre-and post-saccadic coordinates on the retina, also called remapping this problem is made less complicated. Remapping is a process where current locations of objects on the retina, are mapped to the expected future locations of the objects after the saccade (Sperry, 1950; von Holst & Mittelstaedt, 1950). This process of remapping is mediated by the corollary discharge signal (CD). CD is a copy of the motor command that is sent out before the eye movement (Deubel, Schneider & Bridgeman, 1996, 2002). The CD signal conveys the information of the upcoming saccadic vector and this signal is sent to the related neural sensory areas. If the vector of the actual saccade conforms to the pre-and post-saccadic coordinates, retinal motion is attributed to a small oculomotor error of the saccade itself. Movement in the real world is assumed to have taken place when the CD and remapped coordinates do not conform (Deubel, Schneider & Bridgeman, 1996).

Due to small oculomotor errors that can accompany a saccade, the system holds the assumption that the world remains stable unless evidence, given by the remapped coordinates and CD signal, proves otherwise (MacKay, 1972). A consequence of that is that small displacements of objects during a saccade go unnoticed most of the time. This phenomenon is also known as saccadic suppression of image displacement. Bridgeman, Hendry and Stark (1975) were one of the first to describe this inability to see changes of object location during, or shortly after a saccade. In one of the earliest studies Deubel, Schneider and Bridgeman (1996) found that saccadic suppression of displacement can be relieved by introducing a short blanking of the object, just when the eye lands after a saccade. Thus, making people better in noticing small displacements of objects. When an object is present after the saccade but at a slightly different location, the discrepancy between the expected location and the actual location is attributed to a small oculomotor error. However, when an object is not present there is nothing

to compare the expected location to. Therefore, the assumption of a stable world is broken. Retinal movement is then attributed to movement of the object itself. Subsequently making people better in discriminating the direction of displacements.

Investigating what could cause a relieve in saccadic suppression of displacement provides more insight on how the visual system works. Specifically, a better understanding on how the visual system maintains its stability and how the process of remapping is involved in this. Since the study of Deubel, Schneider and Bridgeman (1996), other studies have shown different aspects that can improve this sensitivity. One example is shape change during the saccade (Demeyer, De Graef, Wagemans & Verfaillie, 2010). In this study, the shape of the object changed trans-saccadically which improved sensitivity for direction discrimination. An even better sensitivity was found when they used both shape change and a temporal blank. Discontinuous object properties could thus reject the assumption of visual stability, subsequently improving discrimination ability. The study of Wexler and Collins (2014), investigated a different kind of instability. They used the saccadic suppression of displacement paradigm, but they added an orthogonal step to the displacement. In this case, orthogonal to the saccade direction. They showed that the added orthogonal step improved sensitivity for displacements. In a similar vein, Bansal, Bray, Peterson and Joiner (2015) studied the effect of target displacements that were collinear, orthogonal or diagonal to the initial saccade direction. Their findings were that the detection of the displacement direction (collinear, orthogonal or diagonal), was directly influenced by the initial saccade direction. Specifically, sensitivities for displacements orthogonal to the saccade direction are higher than in collinear or diagonal direction. A possible explanation for this improved sensitivity, is that the endpoint of the object is influenced by manipulating the post-saccadic position of the object relative to the saccade direction. The visual system could not assume that there is an error of the saccade, because the post-saccadic location of the object is out of the error area for remapped coordinates. Overall these studies show that instability of an object, by means of shape change or by giving the displacement an extra step, provides the visual system with sufficient information that something in the world has changed. This object information is seen as unstable because the post-saccadic object location did not fall into the error area of remapped coordinates, or was not even present (temporal blank) and was thus labelled as unreliable. Due to this unreliability, displacement direction discrimination improved, because the system did not ascribe the movement to an error in the saccade itself.

From the previous studies, it could be assumed that the visual system can either label information as reliable or as unreliable. Improvements in sensitivity can be found when information is labelled as unreliable, whilst information is labelled as reliable when movement is attributed to the visual system itself. The previous mentioned studies (Deubel, Schneider & Bridgeman, 1996; Demeyer, De Graef, Wagemans & Verfaillie, 2010; Wexler & Collins, 2014; Bansal, Bray, Peterson & Joiner, 2015) only investigated the effects of unreliable information after a saccade. It would be interesting to investigate the effects of unreliable information prior to a saccade on saccadic suppression of displacement. Since no known studies have investigated this before. Looking at the effects of unreliable information prior to a saccade, could tell us more about how the visual system maintains its stability despite the short disruptions that are caused by an eye movement. Especially it could tell us more about the process of remapping unreliable information to post-saccadic locations on the retina. We hypothesize that the effects of unreliable information prior to a saccade, may have other effects than unreliable information after a saccade. This study will thus focus on pre-saccadic unreliable information and investigate the possible effects on saccadic suppression of displacement.

In the present study, we investigated the effect of unreliable information prior to a saccade, on the sensitivity for object displacements. Motion orthogonal to the saccade direction were added to the displacement, in a displacement task. In the experiment, we aimed to replicate the findings of Wexler and Collins (2014) by adding an orthogonal step in the paradigm. Furthermore, orthogonal motion was added pre-saccadically to test the effects of unreliable information prior to a saccade. We also tested if there was an additive effect of an orthogonal motion and an orthogonal step. There was an orthogonal motion and an extra step either in the same direction as the motion (forward step) or in opposite direction of the motion in these conditions (backward step).

We expect to see the same improved displacement direction discrimination of the orthogonal step in the current study, as was found in the study of Wexler and Collins (2014) and Bansal, Bray, Peterson and Joiner (2015). Due to the orthogonal step the post-saccadic locations of the object on the retina were moved out of the error area of remapped coordinates (Wexler and Collins, 2014; Bansal, Bray, Peterson & Joiner, 2015). This object is thus seen as unstable and unreliable and improved the discrimination ability (Deubel, Schneider & Bridgeman, 1996; Demeyer, De Graef, Wagemans & Verfaillie, 2010; Wexler & Collins, 2014; Bansal, Bray, Peterson & Joiner, 2015). However, for the orthogonal motion we expect to see the opposite. We predict that the unreliable information (i.e. orthogonal motion) prior to the

saccade will not improve this direction discrimination ability. Due to instable and unreliable information prior to the saccade. The visual system cannot accurately map the post-saccadic locations of the object. More variation in the errors of the saccade are the result. Since more errors are made (resulting in a larger error area), the chance is higher that movement is attributed to the saccade itself. Different things are expected for the orthogonal motion forward step and the backward step condition. In the orthogonal motion forward step we do not expect to see any benefits of the orthogonal step. The step forward is in exactly the same direction as the motion would be. The visual system will also remap the post-saccadic location of the object around the area the actual post-saccadic object is in. So this object actually steps into the error area, which does not cause a relieve in saccadic suppression of displacement. We hypothesize that the performance will not improve following the previous. But in the orthogonal motion and orthogonal step backward however we hypothesize to see an improved performance and a relieve in saccadic suppression of displacement. The step backward, which is in opposite direction of the motion, will cause unreliable object information after the saccade. Due to the step backward, the object is moved out of the error area. Improving the discrimination for displacement direction.

Methods

Participants

A total of 15 healthy participants were recruited for this study. The sample consisted out of 5 males and 10 females between the age of 18-30 years ($M = 23.3$, $sd = 3.24$). Participants had normal or corrected-to-normal vision. See Table 1 for more detailed participant information. Participants were briefed about the experiment through an information letter and an informed consent had to be signed before the start of the experiment.

Table 1.

Descriptives of the participants. The total recruited participants and their average age and standard deviation of age in years for males and females.

| | <i>n</i> | <i>M (years)</i> | <i>SD (years)</i> |
|--------|----------|------------------|-------------------|
| Male | 5 | 21.80 | 2.17 |
| Female | 10 | 24.10 | 3.51 |
| Total | 15 | 23.33 | 3.24 |

Apparatus

Stimuli were displayed on an Asus LED screen (ROG Swift PG278Q) with a resolution of 2560 x 1440 and a refresh rate of 120 Hz. Eye movements were measured with an EyeLink 1000 eye tracker. All the stimuli were presented in Matlab (r2016b), the Psychtoolbox (Brainard, 1997; Kleiner, Brainard & Pelli, 2007) and the EyeLink toolbox (Cornelissen, Peters & Palmer, 2002). Participants were seated in a chair approximately 70 cm from the screen. Head movements were restricted by a head and a chin rest. The room was completely dark apart from the light that was emitted by the computer screens. At the start of each experiment a 9-point calibration and validation was performed. The validation error was always equal to or less than 1°.

Task and procedure

Each trial began with a gray fixation point (0.5° in diameter) with a black centre, targets were presented on a black background (0.06 cd/m²). Participants had to maintain fixation between 750 and 1000 ms before the target onset. The target, a red dot 0.5° in diameter, could appear either on the left or on the right of the fixation point. The participants made a saccade towards the target. The distance between the fixation point and the target was between 7° and 9°. Onset of the saccade was detected once the average horizontal velocity over 4 ms (i.e. 4 samples) had exceeded a velocity threshold of 100°/sec. Displacements followed immediately after saccade onset detection. Targets displaced immediately to one of the four equiprobable locations (0.35°, 0.70°, 1.40°, 2.80°) left or right from the initial target location. After the displacement, the target remained static for 600 ms and was followed by a blank response screen. Participants had to report the direction of the displacement with the arrow keys, either to the left or to the right, two alternative forced choice.

The experiment consisted out of five different conditions. The baseline condition with no orthogonal step or orthogonal motion. A condition with an orthogonal step (but no orthogonal motion) and three conditions with an orthogonal motion. One with only an orthogonal motion, the other with an orthogonal motion and an orthogonal step forward and one with an orthogonal motion and an orthogonal step backward. The conditions were presented in sixteen blocks of eighty trials. The different conditions were taken interleaved with each other. Differences between the manipulations can be divided in pre-saccadic manipulations or post-saccadic manipulations or pre-and post-saccadic manipulations. Prior to the saccade there could be either no orthogonal motion or an orthogonal motion of the target. In the orthogonal

motion conditions, the motion of the target started at 0.7° from the centre of the screen. The motion could either be in an upward or in a downward motion. The target moved at the speed of $4^\circ/\text{sec}$. In the case of a slow saccade, when the target had moved off the screen (after approximately 7 seconds), the participant was given a warning. This warning instructed the participant to initiate the saccade sooner. The manipulation after the saccade consisted out of an orthogonal step. Orthogonal step sizes were 1.2° orthogonal to the saccade direction. In the pre- and post-saccadic manipulations, an orthogonal motion is seen prior to the saccade and an orthogonal step is seen after the saccade. The orthogonal step in these manipulations could be either in the same direction as the orthogonal motion (forward) or in the opposite direction of the orthogonal motion (backward). Figure 1 is an example of a trial in the orthogonal motion condition with no orthogonal step.

A randomized factorial design was used in this experiment, 2 saccade directions (left or right) x 2 displacement directions (left or right) x 4 displacement sizes (0.35° , 0.70° , 1.40° , 2.80°) x 5 conditions (baseline, orthogonal step, orthogonal motion, orthogonal motion and orthogonal step forward, orthogonal motion and orthogonal step backward) x 16 repetitions. Following this, the experiment had 1280 trials that were divided over 16 blocks. After each block feedback was given to the participant on the progression and performance (in percentages) on the task. Each experiment began with 80 practice trials where participants could get accustomed to the task and were given feedback after each trial. The total duration of the experiment was around 1.5 – 2 hours.

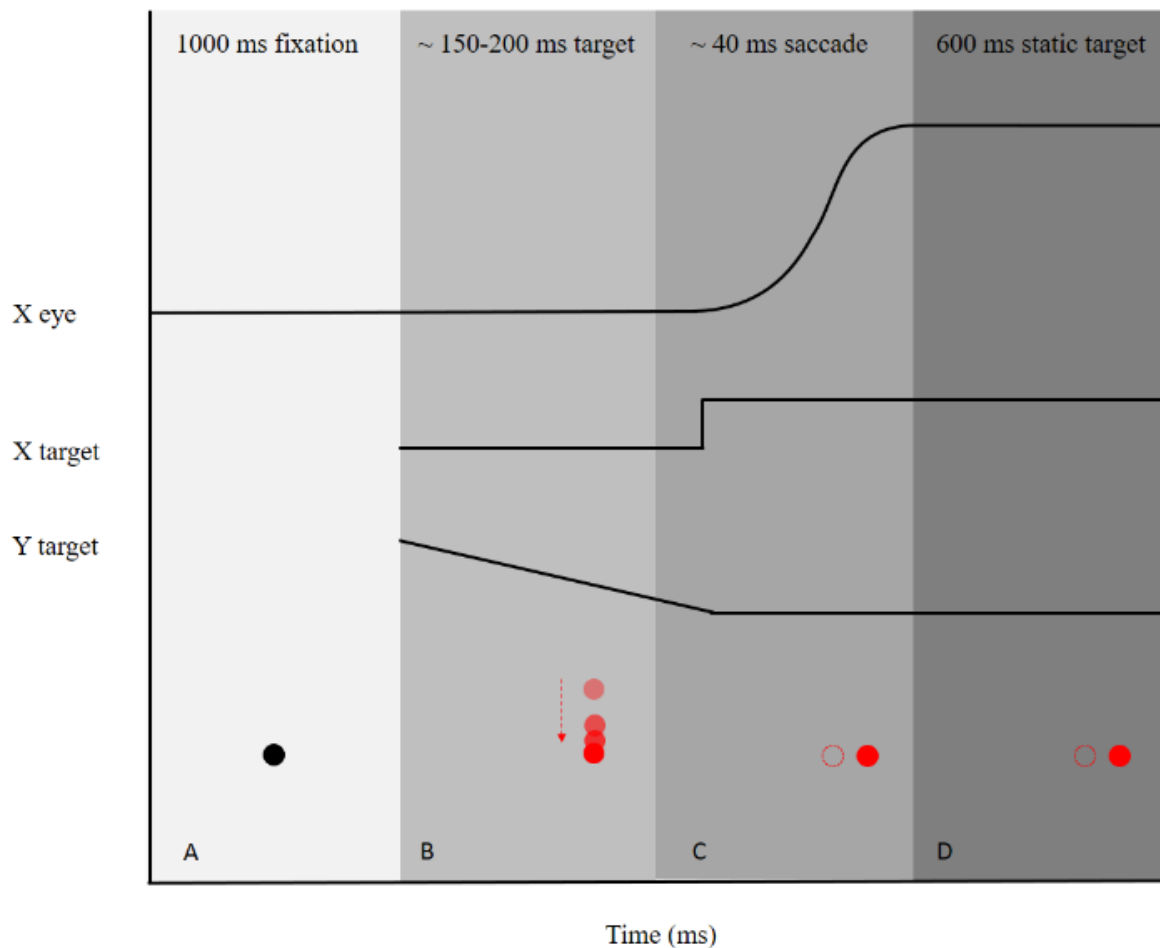


Figure 1. Target and eye position over time, in the orthogonal motion condition (downward motion) without an orthogonal step and a displacement to the right. Trial starts with 1000 ms fixation (A) followed by the onset of a moving target (which can be in an upward or downward motion) with a saccade latency around 150-200ms (B). Displacement of the target follows when onset of the saccade is detected (C). Solid dot indicates new target location and the dashed dot indicates the old location. The displaced target will remain static for another 600 ms on the screen (D). After, a response screen is shown.

Data reduction

Trials were only included for further statistical analysis if they met the following seven criteria. First of all, the saccade length to the initial target had to be bigger than 5° . The target had to be displaced 10 ms before the ending of the saccade. Moreover, the minimal duration of the saccade before displacement of the target took place had to be 80 ms and the landing of the saccade had to be within 4° of the actual target. The saccade should be initiated within 1000 ms after the target onset. Trials in which the displacement took place during a blink or in which the displacement took place after the end of the saccade, were also eliminated. Trials in which the saccade latencies and the saccade durations were in the 95% quantile were included, the remaining 5% of the trials were excluded. This exclusion was done for each participant separately. A total of 20.2% of the trials were excluded following these criteria.

Statistical analysis

Psychometric curves were plotted with on the x-axis target displacements varying from -2.80° to 2.80° and the proportion forward responses on the y-axis. Responses in the task were coded as plus 1 for forward perception and 0 for backward perceptions (with respect to the saccade direction). The slope of each psychometric curve was determined with a generalized linear model regression. We used the function `glmfit` with a binomial distribution in Matlab (r2016b) to fit the curve to our data and to determine the corresponding slopes. The generalized linear regression made a prediction from our data on the probability of a person making a forward response depending on the displacement size. The slopes were transformed to thresholds, which was the distance from the point of subjective stationarity (PSS) to performance at 75% correct. A Wilcoxon signed rank test was used to calculate if there were significant differences between the thresholds of the different manipulations. We specifically looked if there were significant differences in the following conditions: baseline and orthogonal step, baseline and orthogonal motion, orthogonal motion and orthogonal motion orthogonal step forward, orthogonal motion and orthogonal motion orthogonal step backward. A holm Bonferroni correction was used to correct for the multiple comparisons. All statistical analyses were performed in MATLAB (r2016b).

Results

In the analysis, we fitted the curves to the corresponding data points. The slopes of the curves were determined and then transformed to thresholds (distance from the PSS to performance at 75% correct). See Figure 2a for the mean transformed thresholds for each participant separately and the overall mean for all the participants. Figure 2b shows the same but only for the baseline and orthogonal step condition. We included Figure 2b to be able to have a clearer comparison with the study of Wexler and Collins (2014). See Figure 3 for the curves fitted to the data points for all the participants on each condition.

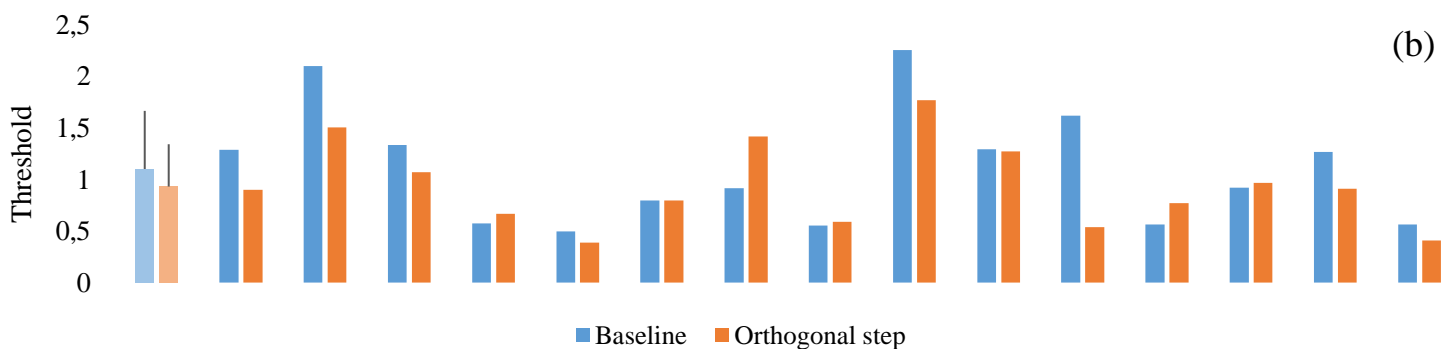
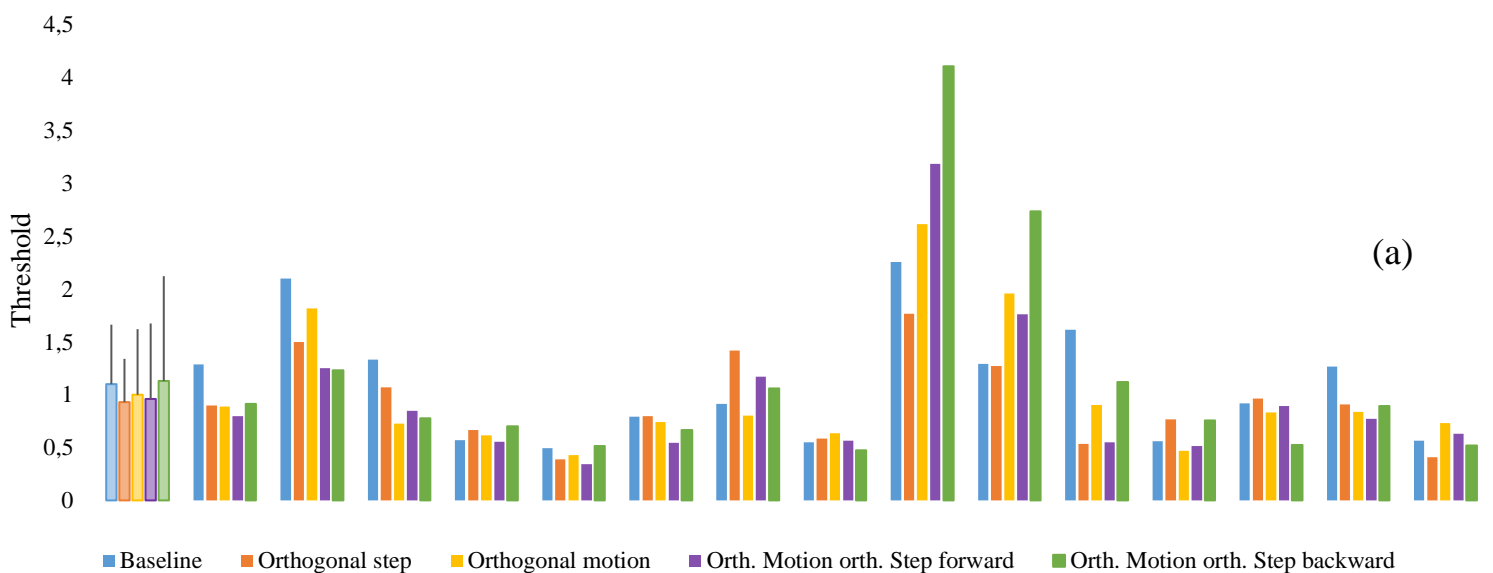


Figure 2. (a) Mean threshold of each participant on each condition (bright bars) and the mean of all participants and the standard deviation (dim bars). (b) Mean threshold of each participant in the baseline condition and the orthogonal step condition (bright bars) and mean for all the participants and the standard deviation (dim bars) in the baseline and orthogonal step condition. Thresholds are the distance between the Point of Subjective Stationarity (PSS) and performance at 75% correct.

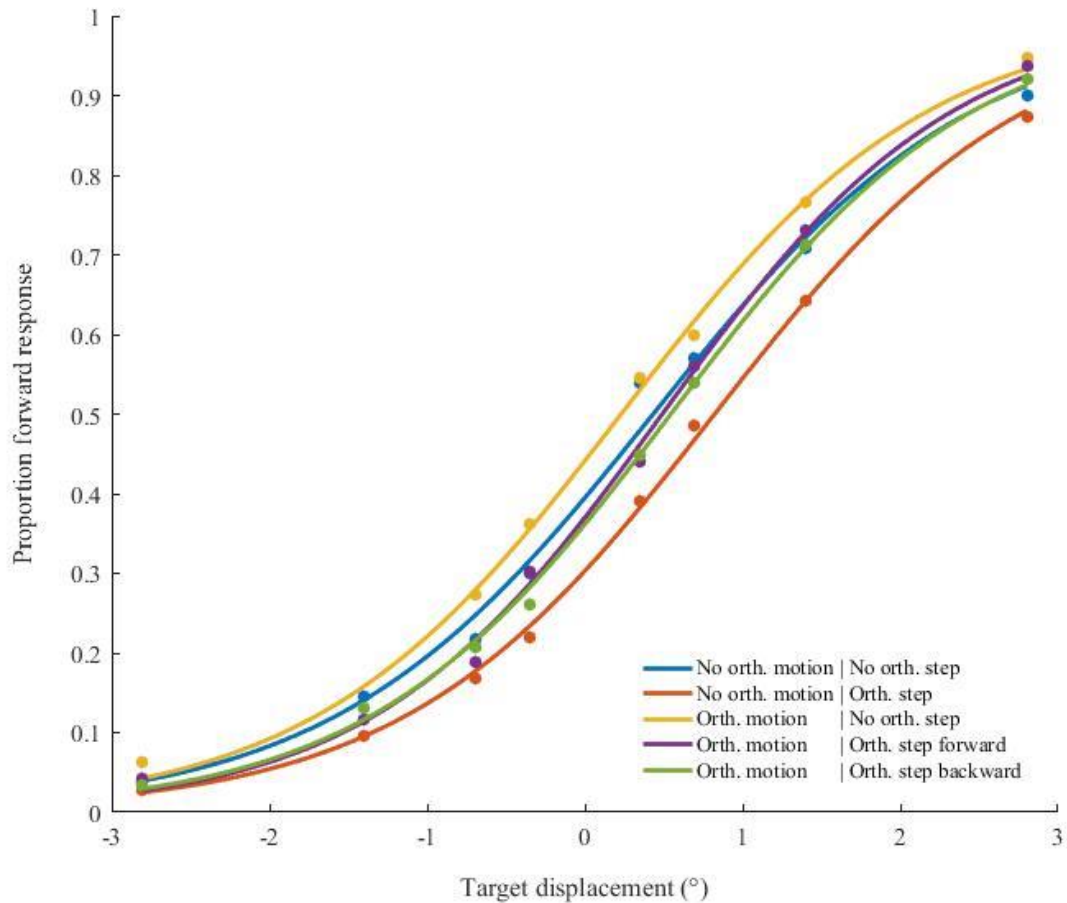


Figure 3. Data of all participants on all conditions. Points show average response forward (with respect to the saccade direction) as a function of displacement. The lines represent the logistic model fit to these data points. Displacements were coded as 1 for displacements in the same direction as the saccade and 0 for displacements in the opposite direction as the saccade. The lines represent the following conditions: no orthogonal motion and no step (baseline) (blue), no orthogonal motion and orthogonal step (red), orthogonal motion and no orthogonal step (yellow), orthogonal motion and orthogonal step forward (purple) and last orthogonal motion and orthogonal step backward (green).

The Shapiro-Wilk test of normality was performed on the thresholds. The test of normality was found to be significant in three of the five conditions. Normality was found not to be violated in the no orthogonal step no orthogonal motion (baseline) condition ($p = 0.06$) and in the orthogonal step condition ($p = 0.54$). However, in the orthogonal motion ($p < .001$), the orthogonal motion orthogonal step forward ($p < .001$) and orthogonal motion orthogonal step backward conditions ($p < .001$) this assumption was violated. Therefore, we continued our analysis with the non-parametric version of a paired samples t-test, a Wilcoxon signed rank test. We compared the thresholds of the following conditions with each other in a Wilcoxon signed rank test: baseline and orthogonal step, baseline and orthogonal motion, orthogonal motion and orthogonal motion orthogonal step forward and orthogonal motion and orthogonal motion orthogonal step backward. Level of significance was .05 and the Holm-Bonferroni correction was used to correct for multiple comparisons.

No significant results were found in the compared conditions. Participants were not better in discriminating the direction of the displacement in the orthogonal step ($Mdn = 0.90$) compared to the baseline (no orthogonal step and no orthogonal motion) ($Mdn = 0.92$), $p = 0.15$, $r = 86$. Furthermore, no benefits were found in discrimination ability due to the orthogonal motion ($Mdn = 0.80$) compared to the baseline ($Mdn = 0.92$), $p = 0.21$, $r = 83$. This was also the case for the orthogonal motion ($Mdn = 0.80$) compared to the orthogonal motion step forward ($Mdn = 0.77$) and the orthogonal motion step backward ($Mdn = 0.79$). No significant results were found between these comparisons, orthogonal motion and orthogonal motion forward step $p = 0.28$, $r = 80$ and orthogonal motion and orthogonal motion backward step $p = 0.39$, $r = 44$.

Table 2 shows the saccade parameters on the different conditions. Statistical analyses were performed to see if there were significant differences between the different conditions and the saccade parameters. For the comparisons of the latency of the saccade and duration of the saccade a Friedman Two-Way ANOVA was used since the assumption of normality was violated. The Friedman Two-Way ANOVA indicated a significant difference between the latencies across the conditions, $\chi^2_F = 54.03$, $df = 4$, $p < .001$. Furthermore, a significant difference was also found for the saccade durations across the different conditions, $\chi^2_F = 44.53$, $df = 4$, $p < .001$. Afterwards, follow-up pairwise comparisons were done with a Wilcoxon Signed rank test. For the amplitude of the saccade and saccadic errors in endpoints, a repeated measures ANOVA was used. The analyses indicated that there were significant differences

between the saccade parameters across the conditions. A Holm Bonferroni correction was used to correct for multiple comparisons. See Table 3 for an overview of the compared conditions, the level of significance and the mean difference.

Table 2.

Saccade parameters of the participants. Standard deviations are between the brackets.

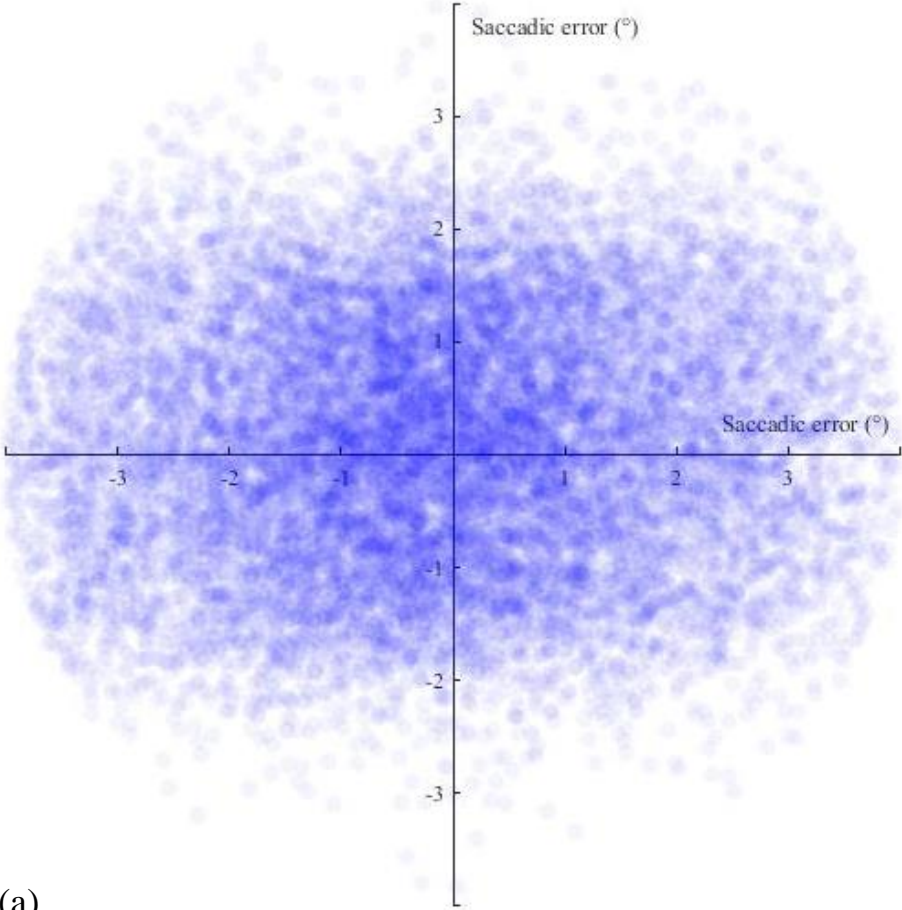
| | Baseline | Orthogonal step | Orthogonal motion | Orthogonal motion + orthogonal step forward | Orthogonal motion + orthogonal step backward | Overall |
|------------------------------|-------------------|------------------------|--------------------------|--|---|-------------------|
| Latency (ms) | 170.51 (39.32) | 170.89 (38.71) | 172.00 (42.84) | 172.70 (43.20) | 173.05 (44.37) | 171.82 (41.75) |
| Saccade duration (ms) | 39.87 (4.78) | 40.09 (4.60) | 39.80 (4.53) | 39.94 (4.52) | 39.75 (4.55) | 39.89 (4.60) |
| Amplitude (°) | 7.64 (1.06) | 7.69 (1.03) | 7.64 (1.01) | 7.68 (1.02) | 7.64 (1.03) | 7.66 (1.03) |
| Saccadic error (°) | 1.61 (0.97) | 1.98 (0.85) | 1.61 (0.95) | 1.87 (0.86) | 2.14 (0.81) | 1.84 (0.91) |

Table 3.

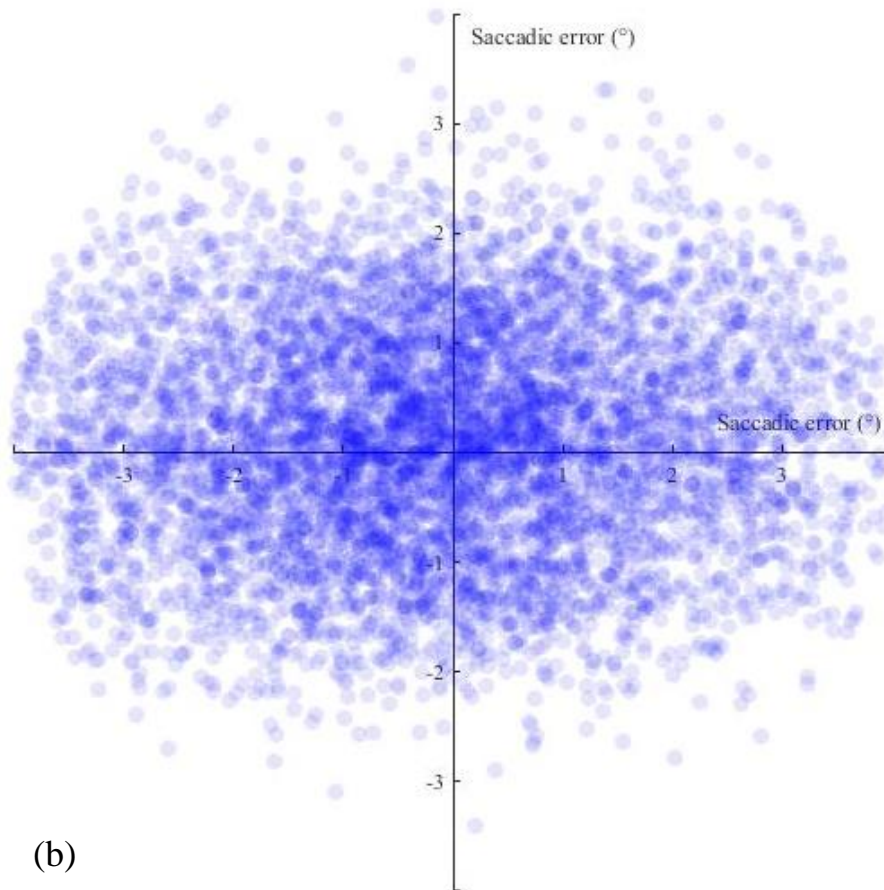
The level of significance of the different saccade parameters compared between different conditions. Bold values flag the significant differences. Mean difference is shown between the bracket (the first column minus the second column). Mean difference for latency and duration are in milliseconds. Mean difference for the amplitude and the saccadic error are in degrees visual angle.

| Comparisons | | Latency | Duration | Amplitude | Saccadic error |
|-----------------------------------|--------------------------------------|------------------------|------------------------|------------------------|------------------------|
| Baseline | - Orth. step | $p = .083$ (.471) | $p < .001$ (- .183) | $p < .001$ (- .050) | $p < .001$ (- .374) |
| Baseline | - Orth. motion | $p < .001$ (-1.198) | $p = .135$ (.035) | $p = .527$ (.008) | $p < .001$ (- .021) |
| Baseline | - Orth. motion + Orth. step forward | $p < .001$ (-2.742) | $p < .001$ (- .167) | $p < .001$ (- .056) | $p < .001$ (- .271) |
| Baseline | - Orth. motion + Orth. step backward | $p < .001$ (-3.356) | $p = .041$ (.065) | $p = 1.00$ (.007) | $p < .001$ (- .567) |
| Orth. step | - Orth. motion | $p < .001$ (-1.669) | $p < .001$ (.218) | $p < .001$ (.058) | $p < .001$ (.353) |
| Orth. step | - Orth. motion + Orth. step forward | $p < .001$ (-3.214) | $p = .303$ (.017) | $p = .011$ (- .007) | $p < .001$ (.103) |
| Orth. step | - Orth. motion + Orth. step backward | $p < .001$ (-3.471) | $p < .001$ (.249) | $p = .005$ (.056) | $p < .001$ (- .193) |
| Orth. motion | - Orth. motion + Orth. step forward | $p < .001$ (-1.545) | $p < .001$ (- .201) | $p = .006$ (- .065) | $p < .001$ (- .250) |
| Orth. motion | - Orth. motion + Orth. step backward | $p < .001$ (-2.178) | $p = .252$ (.031) | $p = 1.00$ (- .001) | $p < .001$ (- .546) |
| Orth. motion + Orth. step forward | - Orth. motion + Orth. step backward | $p = .073$ (- .633) | $p < .001$ (.232) | $p = .011$ (.063) | $p < .001$ (- .296) |

Furthermore, a spread diagram of the saccade endpoint variability is plotted to check the accuracy and variability of the saccade. See Figure 4a for the variability across all conditions and all participants and Figure 4b for all participants in the baseline and orthogonal step condition. Figure 4b is included for a better comparison of the current study and the study of Wexler and Collins (2014).



(a)



(b)

Figure 4. Saccadic endpoint variability across all conditions and subjects (a) and saccadic endpoint variability across all participants in the baseline and orthogonal step condition (b). The transparent dots indicate the errors in saccadic endpoints relative to the target and are expressed in degrees visual angle. Errors bigger than 4° are excluded from this plot and the rest of the analyses.

We further analysed the correlation between the saccade error and the thresholds to see if there was a relation between these two variables. We tested the relation between the spread in vertical errors and the threshold in the orthogonal motion condition. The assumption of normality was not violated in the orthogonal step condition. Shapiro Wilk was found to be not significant $p = .478$ for the spread of the vertical error and for the threshold in the orthogonal step condition $p = .542$. We performed a correlation. No relationship was found between the threshold of the orthogonal step condition and the spread of the vertical error in the orthogonal step condition, $p = 0.494$, $r(13) = -.191$

Discussion

With each saccade, the visual system is left with the question: Was movement on the retina caused by the saccade itself (accompanied by a small oculomotor error), or did an object in the real world move? In general, the visual system holds the assumption that the outside world remains stable (MacKay, 1972) and ascribes motion most often to the errors of the saccade itself. When this stability assumption is broken, other processes are used to make a more accurate judgment on what happened. To verify the cause of movement, remapping and the corollary discharge signal are used to compare pre-and post-saccadic locations on the retina (Sperry, 1950; von Holst & Mittelstaedt, 1950). The study of Wexler and Collins (2014) showed that an extra orthogonal step to the displacement (orthogonal to the saccade direction), can relieve saccadic suppression of displacement. They presume that there is a motor error area of remapped coordinates. When the object after the saccade falls within this area, strong saccadic suppression of displacement is seen and we do not perceive the changed location. But when the object falls out of this error area, saccadic suppression of displacement is relieved and improved sensitivity for displacement direction is seen. With the orthogonal step, the post-saccadic location of the object now falls out of this error area. Improving the discrimination ability for direction. The orthogonal step, but also the orthogonal displacement (Bansal, Bray, Peterson and Joiner, 2015), temporal blanking of the target (Deubel, Schneider and Bridgeman, 1996), and shape change (Demeyer, De Graef, Wagemans and Verfaillie, 2010) all showed that unreliable objects relieve saccadic suppression of displacement. All of these studies however, looked at the effects of unreliable information after a saccade. This study was the first to look into the effects of unreliable information prior to a saccade, on saccadic suppression of displacement. Furthermore, we also tried to replicate the findings of an improved discrimination for the direction of the displacement due to the orthogonal step (Wexler and Collins). Last, we investigated if there was an additive effect of the orthogonal step, when there was an orthogonal motion pre-saccadically. We hypothesized that unreliable information prior to a saccade actually makes it harder for the visual system to remap this motion, resulting in more errors. Due to more errors, there is a larger chance that movement is attributed to the saccade than to the object. Indeed, we did not find any differences between the orthogonal motion and the baseline. For the orthogonal step condition, we expected to see an improved performance for the direction discrimination ability. Interestingly we could not replicate the findings of Wexler and Collins since we did not find any differences between the orthogonal step and baseline condition. For the additive effects of the pre-saccadic orthogonal motion and post-saccadic

orthogonal step, we expected different things. For the orthogonal step forward in the orthogonal motion condition we expected to see high saccadic suppression of displacement. Our results indeed show no difference between the orthogonal motion and the orthogonal motion plus orthogonal motion orthogonal step forward condition. For orthogonal motion orthogonal step backward we actually did expect to see an improved performance compared to the orthogonal motion condition. Though no differences were found between these two manipulations.

No replication of the study of Wexler and Collins (2014)

One aim of this study is to replicate the findings from the study of Wexler and Collins (2014). In their study, they showed that a step orthogonal to the saccade direction could improve displacement direction discrimination. They explained that this improved sensitivity is due to the manipulation of the post-saccadic position of the object by means of the orthogonal step. This step would cause the object to be out of the error area of remapped coordinates, thus improving the sensitivity. However, we did not find any benefits of the orthogonal step for the displacement direction detection in our study. No significant differences are found between the baseline (no orthogonal motion no orthogonal step) and orthogonal step condition. How can we explain the fact that we could not replicate this study? This could possibly be explained by the fact that the variability of saccadic errors was smaller in the study of Wexler and Collins than in ours. The error area of remapped coordinates is bigger in the current study, than it was in the study we were trying to replicate. Our errors have more spread in the vertical direction (around -2 to 2 visual angle) in the no step and step condition (see figure 3) whereas Wexler and Collins show a spread of around -1 to 1 in vertical direction. Since our error area of remapped coordinates is bigger, it means that our orthogonal step needs to be bigger. Whereas a step of 1.2° was enough in their study, a step of at least 2° seems to be needed in our study to see a benefit of the orthogonal step. The larger error area for remapped coordinates could thus possibly explain the fact that we did not find any effects of the orthogonal step. However, we should keep in mind that we did not find a relationship between the saccadic endpoint errors in the vertical direction and the performance on the task. Which indicates that the performance on the task not seems to be influenced by the size of the error. For future research, it would be interesting to look at the effects of a larger orthogonal step (relative to the error area) and to further check the relation between the errors in the saccade and the performance on the task.

The current study had a mixed design with five different manipulations that were taken interleaved with each other. This can be an explanation for the bigger variety in the saccadic endpoints. The current study also consisted out almost three times as much trials in the same conditions as Wexler and Collins. Furthermore, we considered the design differences (e.g. amplitude, target size, luminance) between the studies, however these differences are minor. We think that the mixed design and the larger amount of trials are the main reason that there is a larger variety in endpoints.

No effect of pre-saccadic orthogonal motion.

No effect of the orthogonal motion prior to a saccade is found. We hypothesized that the pre-saccadic unreliable information would cause the visual system to mainly attribute errors to itself and not to the object. Due to the unreliable information prior to the saccade, it is harder to accurately remap the coordinates to the post-saccadic locations. The chance that errors are ascribed to the saccade are considerably larger. It is still speculative that unreliable information makes it harder for the visual system to remap coordinates because no differences between the baseline and the orthogonal motion condition were found. But no relieve in saccadic suppression of displacement is seen because of the orthogonal motion.

Furthermore, we made a distinction in the orthogonal motion condition between orthogonal steps forward and backward. Our expectation was that with forward steps the direction discrimination ability was low and high in the backward condition. We hypothesised that the forward step would exactly step in the remapped error area of the orthogonal motion. Since the motion and the step were in the same direction, the visual system also maps the object to be around that place. We did not find any differences between the orthogonal motion condition and orthogonal motion plus forward orthogonal step condition. When a motion is seen, you would expect the visual system to map the post-saccadic location of the object to be somewhere in the movement direction. So, we could indeed speculate that the step forward steps exactly to where the object was expected to be seen. This now falls right into the error area or remapped coordinates. No relieve in suppression of displacement is seen and it thus hard to see the direction of the displacement.

In the backward condition, we expected the direction discrimination ability to improve. To see a better ability in the step backward condition compared to the baseline. The saccade starts with unreliable information, but because of the step in the opposite direction of the

saccade there again is the unreliable information after the saccade. Due to the step that was taken opposite to the motion, we expected the object to now fall out of the error area. Thus, relieving saccadic suppression of displacement. This hypothesis was not confirmed, no improved performance was found in this condition. We can speculate again that maybe the object after the saccade was not seen as reliable. That the object still fell into the error area after the saccade. Due to the bigger error area that this study has this could be a possibility.

We could also speculate that the orthogonal motion is actually not seen as unreliable information. That the visual system is better in remapping this motion than we think it is. For future research, it could be interesting to investigate what the effect is of a faster motion. Since the motion we used was possibly still quite easy to remap for the visual system. A faster motion could perhaps make the process of remapping harder.

Conclusion

In this study, we tested the effects of unreliable information prior to a saccade on saccadic suppression of displacement. There was no effect of unreliable information (i.e. orthogonal motion) compared to the baseline condition. We could speculate that indeed unreliable information influences the process that is important for verifying the cause of movement. Possibly making it harder for the visual system to accurately remap the motion. Furthermore, we tried to replicate the improved displacement direction discrimination that was found in the study of Wexler and Collins. Interestingly, no improvements of the orthogonal step were found. A possible explanation could be the larger error area in the current study than in the study of Wexler and Collins (2014). We also looked at the additive effects of unreliable information prior as well as after the saccade (pre-saccadic orthogonal motion and post-saccadic orthogonal step). No additive effects of the motion and step were seen in comparison to the motion condition. For future research, it would be interesting to see if a larger orthogonal step (relative to the error area) could again improve the sensitivity. It would also be interesting to see what the effect of a faster motion would be on saccadic suppression of displacement.

References

- Bansal, S., Bray, L. C. J., Peterson, M. S., & Joiner, W. M. (2015). The effect of saccade metrics on the corollary discharge contribution to perceived eye location. *Journal of neurophysiology*, *113*(9), 3312-3322.
- Brainard, D. H. (1997) The Psychophysics Toolbox, *Spatial Vision* *10*:433-436.
- Bridgeman, B. (1995). A review of the role of efference copy in sensory and oculomotor control systems. *Annals of Biomedical Engineering*, *23*, 409–422.
- Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during saccadic eye movements. *Vision research*, *15*(6), 719-722.
- Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The EyeLink Toolbox: eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers*, *34*(4), 613-617.
- Demeyer, M., De Graef, P., Wagemans, J., & Verfaillie, K. (2010). Object form discontinuity facilitates displacement discrimination across saccades. *Journal of Vision*, *10*(6): 17, 1–14, <http://www.journalofvision.org/content/10/6/17>, doi:10.1167/ 10.6.17.
- Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision research*, *36*(7), 985-996.

- Deubel, H., Schneider, W. X., & Bridgeman, B. (2002). Transsaccadic memory of position and form. *Progress in brain research*, 140, 165-180.
- Kleiner M, Brainard D, Pelli D, 2007, "What's new in Psychtoolbox-3?" Perception 36 ECVF Abstract Supplement
- MacKay, D. M. (1972). Voluntary eye movements as questions. *Bibliotheca ophthalmologica: supplementa ad ophthalmologica*, 82, 369-376.
- Schiller, P. H. (1998). The neural control of visually guided eye movements. In J. Richards (Ed.), *Cognitive neuroscience of attention: A developmental perspective* (pp. 3–50). New Jersey: Lawrence Erlbaum Associates.
- Sperry, R. W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *Journal of Comparative and Physiological Psychology*, 43, 482–489.
- von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip [Translation: The reafference principle]. *Naturwissenschaften*, 37, 464–476.
- Wexler, M., & Collins, T. (2014). Orthogonal steps relieve saccadic suppression. *Journal of vision*, 14(2), 13-13.
- Wurtz, R. H. (2008). Neuronal mechanisms of visual stability. *Vision research*, 48(20), 2070-2089.

Appendix A

Table with extended information about the data reduction. The different criteria and how many trials were excluded following these criteria. The total of erased trials for each participant and the percentage of erased trials. Under the table more extended descriptions of the criteria are given.

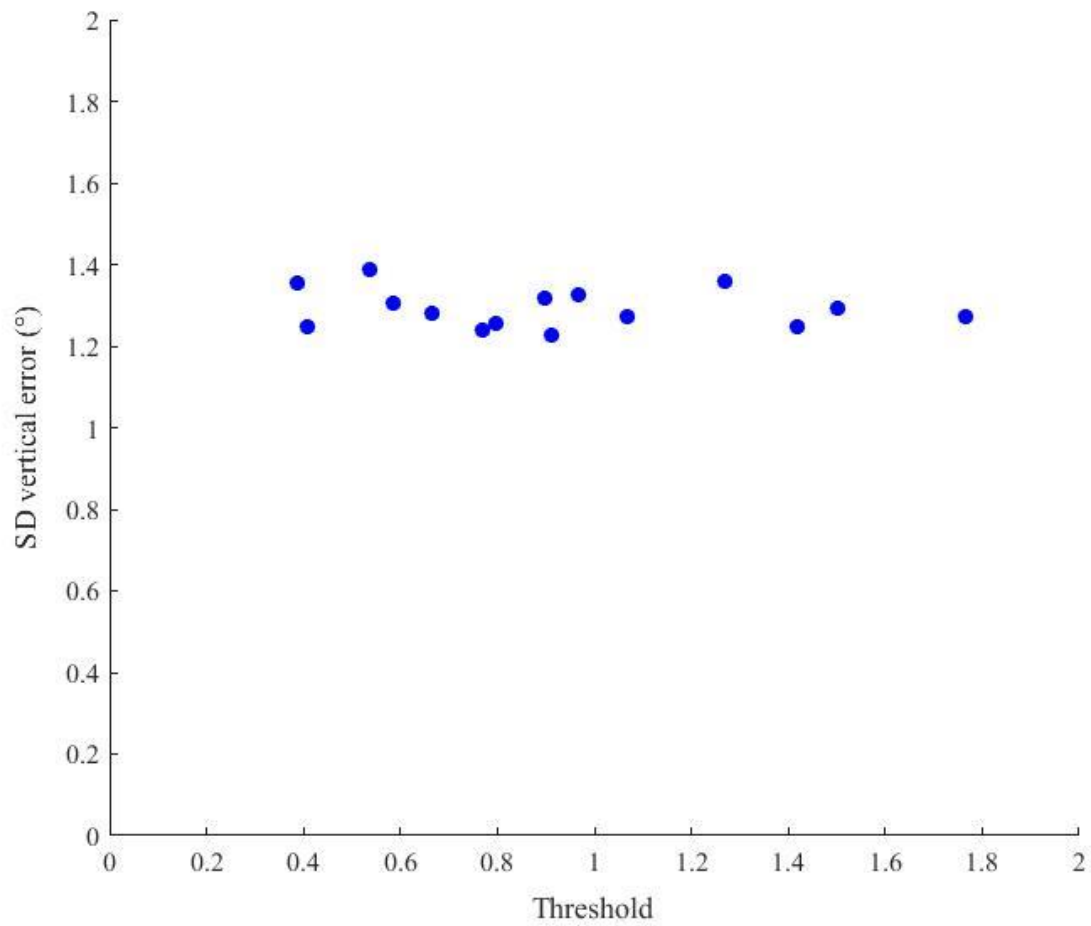
| Participant | 1 T2 in blink | 2 Amplitude | 3 Displacement | 4 Latency | 5 Endpoint | 6 Sacc onset | 7 Double sacc | 8 Latency > quantile 0.95 | 9 Duration > quantile 0.95 | Total erased trials | Total correct trials | Percentage erased trials |
|-------------------------------|---------------|-------------|----------------|-----------|------------|--------------|---------------|---------------------------|----------------------------|---------------------|----------------------|--------------------------|
| AB | 0 | 0 | 12 | 2 | 86 | 0 | 45 | 44 | 50 | 239 | 1041 | 18.7% |
| AC | 0 | 0 | 2 | 0 | 41 | 9 | 10 | 60 | 34 | 156 | 1124 | 12.2% |
| AD | 0 | 0 | 0 | 0 | 71 | 19 | 6 | 57 | 58 | 211 | 1069 | 16.5% |
| AE | 0 | 0 | 2 | 9 | 52 | 0 | 17 | 54 | 49 | 183 | 1097 | 14.3% |
| AF | 0 | 0 | 23 | 4 | 91 | 0 | 34 | 53 | 53 | 258 | 1022 | 20.2% |
| AH | 0 | 0 | 19 | 2 | 84 | 1 | 12 | 54 | 52 | 224 | 1056 | 17.5% |
| AI | 0 | 0 | 1 | 2 | 31 | 0 | 2 | 60 | 38 | 134 | 1146 | 10.5% |
| AK | 0 | 0 | 12 | 1 | 61 | 0 | 13 | 51 | 55 | 193 | 1087 | 15.1% |
| AL | 0 | 0 | 0 | 3 | 94 | 0 | 4 | 58 | 33 | 192 | 1088 | 15.0% |
| AM | 0 | 0 | 22 | 7 | 134 | 7 | 131 | 46 | 44 | 391 | 889 | 30.5% |
| AN | 0 | 0 | 3 | 0 | 79 | 3 | 20 | 47 | 49 | 201 | 1079 | 15.7% |
| AO | 0 | 0 | 1 | 0 | 34 | 1 | 9 | 51 | 60 | 156 | 1124 | 12.2% |
| AP | 0 | 0 | 2 | 0 | 49 | 1 | 3 | 58 | 51 | 164 | 1116 | 12.8% |
| AR | 0 | 0 | 145 | 3 | 70 | 0 | 16 | 50 | 43 | 327 | 953 | 255% |
| ZZ | 0 | 0 | 34 | 1 | 45 | 1 | 11 | 54 | 45 | 191 | 1089 | 14.9% |
| Total | 0 | 0 | 278 | 34 | 1022 | 42 | 333 | 797 | 714 | 3220 | 15980 | 20.2% |
| Percentage from erased trials | 0% | 0% | 8.6% | 1.1% | 31.7% | 1.3% | 10.3% | 24.8% | 22.2% | | | |

Criteria:

1. T2 in blink: when the onset of T2 was during a blink
2. Amplitude: when the amplitude was shorter than 5°
3. Displacement: when the displacement of the target was within the last 10ms before the end of the saccade
4. Latency: saccade latencies that were shorter than 80ms
5. End point: all saccade endpoints were not in 4° of the target
6. Saccade onset: long saccade onsets that were 1000ms after the first target onset
7. Double saccades: saccade was finished and new saccade was initiated before displacement took place
8. Latency quantile: all latencies that fell in the 5% quantile
9. Duration quantile: all saccade durations that fell in the 5% quantile

Appendix B

Visual representation of the relationship between the spread (standard deviation) of the errors in the vertical direction and the thresholds in the orthogonal step condition. No significant relation was found $p = .494$, $r(13) = -.191$.



Appendix C

Results of the Shapiro Wilk test of normality of the saccade parameters across different conditions.

| | Latency | Saccade duration | Amplitude | Saccadic error |
|---|----------------|-----------------------------|------------------|---------------------------|
| Baseline | $p < .001$ | $p = .006$ | $p = .466$ | $p = .074$ |
| Orthogonal step | $p < .001$ | $p = .008$ | $p = .898$ | $p = .240$ |
| Orthogonal motion | $p < .001$ | $p = .014$ | $p = .123$ | $p = .589$ |
| Orthogonal motion + Orthogonal step forward | $p < .001$ | $p = .007$ | $p = .005$ | $p = .241$ |
| Orthogonal motion + Orthogonal step backward | $p < .001$ | $p = .022$ | $p = .970$ | $p = .913$ |