Spatiotopic buildup of saccade target representation depends on target size

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How we maintain spatial stability across saccade eye movements is an open question in visual neuroscience. A phenomenon that has received much attention in the field is our seemingly poor ability to discriminate the direction of transsaccadic target displacements. We have recently shown that discrimination performance increases the longer the saccade target has been previewed before saccade execution (Zimmermann, Morrone, & Burr, 2013). We have argued that the spatial representation of briefly presented stimuli is weak but that a strong representation is needed for transsaccadic, i.e., spatiotopic localization. Another factor that modulates the representation of saccade targets is stimulus size. The representation of spatially extended targets is more noisy than that of point-like targets. Here, I show that the increase in transsaccadic displacement discrimination as a function of saccade target preview duration depends on target size. This effect was found for spatially extended targets—thus replicating the results of Zimmermann et al. (2013)— but not for point-like targets. An analysis of saccade parameters revealed that the constant error for reaching the saccade target was bigger for spatially extended than for point-like targets, consistent with weaker representation of bigger targets. These results show that transsaccadic displacement discrimination becomes accurate when saccade targets are spatially extended and presented longer, thus resembling closer stimuli in real-world environments.

Introduction

How the brain represents visual space is still an open question in neuroscience. This question is complicated by the fact that we move our eye around three times per second, thus producing the need to connect visual input from separate fixations. This linkage enables us to discriminate between motion generated by our own eye movements from motion in external space. Evidence from neurophysiological and behavioral studies suggests the existence of a mechanism that remaps visual coordinates across saccade eye movements (Duhamel, Colby, & Goldberg, 1992; Melcher, 2005; Nakamura & Colby, 2002; Umeno & Goldberg, 1997). Experiments that tried to estimate how well observers perceive transaccadic motion revealed a surprisingly weak ability to detect displacements of the saccade target (Bridgeman, Hendry, & Stark, 1975; Demeyer, Graef, Wagemans, & Verfaillie, 2010; Deubel, Schneider, & Bridgeman, 1996). This phenomenon has been termed saccadic suppression of displacement. We have recently shown that performance in this paradigm drastically improves if the visual system has time to build up a stable representation of the saccade target location (Zimmermann et al., 2013). The longer participants had seen the saccade target before executing the saccade, the better they were able to discriminate the displacement direction. We also measured target displacement discrimination during fixation and found nearly identical performance. This result demonstrated that the proposed remapping mechanism is very precise and creates a stable transsaccadic or spatiotopic representation when given sufficient time to accumulate spatial information. It must be stressed that in real-life situations visual information can easily be accumulated across fixations because targets are mostly stationary and rarely materialize out of the void. A dependence of saccadic localization precision on encoding duration has long been known (Abrams, Meyer, & Kornblum, 1989; Aitsebaomo & Bedell, 1992; Kowler & Blaser, 1995; Lemij & Collewijn, 1989).

Why should spatial localization precision be necessary to discriminate the direction of transsaccadic displacements? Stimuli whose signal strength is degraded either because they are presented at the onset of a saccade or because they are masked, appear compressed toward stimuli with a

high signal strength (Lappe, Awater, & Krekelberg, 2000; Ross, Morrone, & Burr, 1997; Zimmermann, Born, Fink, & Cavanagh, 2014; Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014). We have suggested that compression between the pre- and the post-saccadic stimulus in the displacement paradigm is the reason for the poor discrimination of direction (Zimmermann et al., 2014). We showed that compression strength decreased as probe duration increased (Born, Krüger, Zimmermann, & Cavanagh, 2016). Consistent with that idea, Atsma, Maij, Koppen, Irwin, and Medendorp (2016) created a computational model of transsaccadic displacement performance, in which they modeled viewing time as a factor that changes the precision of the target representation. The shorter the target presentation, the noisier it was, making it more likely for the system to integrate.

In a recent report, Collins (2016) claimed a failure to replicate the effect of preview duration on discrimination performance of transsacadic displacements (Zimmermann et al., 2013). This study however was not an exact replication of our experiment. The size of the saccade target, i.e., the probe stimulus, did not match our experimental protocol. Collins used small, point-like saccade targets (0.2° diameter) whereas we used spatially extended targets (0.75° diameter). It is known that size influences the representation of the saccade target when no priority is given to either accuracy or reaction time (Dick, Ostendorf, Kraft, & Ploner, 2004; Ploner, Ostendorf, & Dick, 2004). Saccades to larger targets are less precise and less accurate and have higher latencies. This influence of size on the saccade target representation allows a clear prediction: Large targets, due to their noisier representation, should lead to poorer discrimination performance compared to small, point-like targets. The latter, being represented more precisely, should lead to better displacement discrimination performance. Bigger targets should benefit more strongly from an increase in the target preview duration because their representation is noisier than that of small targets. I tested whether the buildup of spatial position information across saccades depends on saccade target size. Subjects discriminated the direction of transsaccadic target displacements for various preview durations of the saccade target. Saccades were performed to targets either with a small (0.2° diameter) or with a bigger size (0.75° diameter). Although target sizes in both conditions differ only by a factor of 3.75, they change from point-like to spatially extended. Spatially extended targets induce large errors in saccade landing, resulting in a hypometry of saccades (Ploner et al., 2004).

Methods

Participants

Eleven subjects (one male author and one male and nine female naive subjects; mean age: 27 years) participated in all tasks of the main experiment. All subjects had normal or corrected-to-normal vision. Subjects gave informed consent. The experiments were carried out along the principles laid down in the Declaration of Helsinki. All experiments were approved by the local ethics committee of the psychological department of the Heinrich-Heine University Düsseldorf.

Apparatus

Subjects were seated 57 cm from an Eizo FlexScan T57S. The visible screen diagonal was 20 in., resulting in a visual field of 40° × 30°. Stimuli were presented on the monitor with a vertical frequency of 120 Hz on a homogeneously gray background.

Procedure

Figure 1 shows the general experimental procedure. A black fixation point appeared at 10° to the left of screen center at the horizontal meridian to which the subject directed gaze. The size of the fixation point and saccade target varied according to condition. In the big target condition, the size of the fixation point and saccade target was 0.75° × 0.75°. In the small target condition, the size of the fixation point and saccade target was 0.2° × 0.2°. After 1000 ms, a target appeared 10° to the right of screen center at the horizontal meridian. The go-signal to perform the saccade to the target was the disappearance of the fixation point. The fixation point disappeared either 100, 250, or 500 ms after saccade target onset. The time between onset of the saccade target and initiation of the saccade will be called saccade target preview duration. With this method, I could vary systematically the preview duration of the saccade target before saccade execution. As soon as the eyes had moved 2.5° in the direction of the target, the target was displaced either leftward or rightward. Seven different displacement sizes between ±2° (including zero) were drawn pseudorandomly with equal probability. The subject responded by key press whether the target was displaced to the left or to the right (two-alternative forced choice task). Then the next trial began with the presentation of a fixation point.
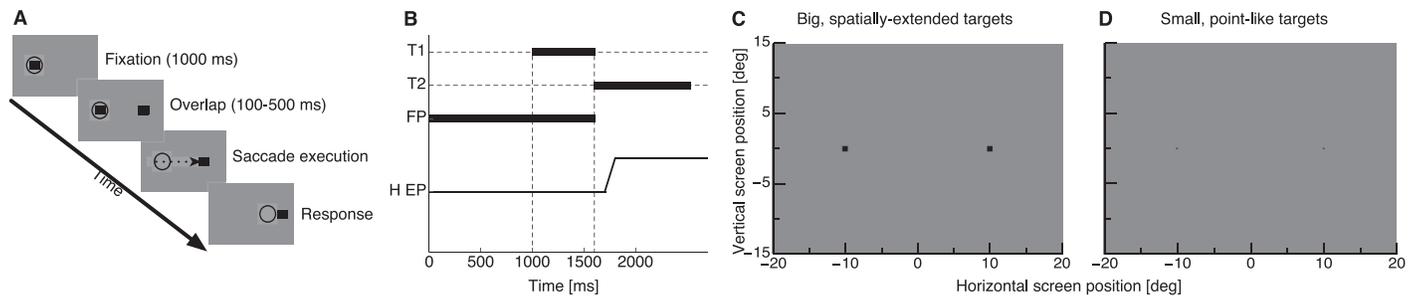
Figure 1. (A) Experimental setup for saccade trials. The black circles indicate eye position. The black squares indicate targets for fixation or saccades. A trial started with the presentation of a fixation point. The saccade target T1 appeared 1000 ms later. The fixation point disappeared either 100, 250, or 500 ms later. Fixation point offset was the go-signal for the subjects to perform a saccade. As soon as the saccade (H EP) was detected, the saccade target was displaced either leftward or rightward (T2). At the end of the trial, the subject indicated the direction of the target displacement by pressing the left or right arrow key. (B) Time course of events. (C) Positions of the fixation point (FP) and the saccade target (T1) in trials with big targets. (D) Positions of the FP and the saccade target (T1) in trials with small targets.

Eye movements and data analysis

Eye movements were monitored by the EyeLink 1000 system (SR Research), which samples gaze positions with a frequency of 2000 Hz. Viewing was binocular, but only the dominant eye was recorded. The system detected start and end of a saccade when eye velocity exceeded or fell below 22°/s and acceleration was above or below 4000°/s^2.

The saccade target preview duration was defined as the duration between target onset and saccade initiation. This duration thus depended on the go-signal, i.e., the disappearance of the fixation point plus the saccade reaction time of the subjects. For each subject, data were binned according to preview duration into five equal intervals of 133 ms. On average, 62 trials were measured per psychometric function. The psychophysical data were expressed as proportion rightward as a function of displacement. Gaussian error functions were fit to the raw data and the variance of these functions taken as a measure of displacement sensitivity. Mean and standard error of the mean were estimated across subjects.

Results

Figure 2 shows psychometric functions for transsaccadic target displacement discrimination from one subject. Data are binned into five different preview duration bins. Results from trials with big saccade targets are shown in Figure 2A. For preview durations smaller than or equal to 300 ms, the displacement discrimination threshold was 0.99°. The threshold lowered as a function of preview duration. For preview durations higher than 700 ms, the displacement discrimination threshold was only 0.30°. Results from

trials with small saccade targets are shown in Figure 2B. Discrimination in these trials was generally better. For preview durations smaller than or equal to 300 ms, the threshold was 0.59°. Thresholds changed unsystematically with higher preview durations. For preview durations higher than 700 ms, the threshold was 0.40°.

Average thresholds for displacement discrimination of big targets for the five average saccade target preview durations are shown in Figure 3A. For short preview durations, performance is poor. For a 245-ms mean preview duration, the average threshold is 1.24° (*SEM* 0.09). However, with a longer mean saccade target preview duration of 715 ms, the average threshold decreases to 0.64° (*SEM* 0.19). As can be seen in Figure 3B, the average performance differed when saccade targets were small. For a 255-ms mean saccade target preview duration, displacement discrimination was 1.08° (*SEM* 0.13) and therefore as good as performance for big targets with a long target preview. For the longest mean preview duration of 766 ms, average thresholds were 1.25° (*SEM* 0.27). Therefore, no decrease of thresholds as a function of preview duration occurred when targets were small. I calculated a 2 × 5 repeated-measures ANOVA with the factors target size (big/small) and preview duration (five bins). The significant interaction effect, $F(4, 40) = 3.548$, $p < 0.05$, revealed a stronger decrease in discrimination thresholds as a function of preview duration for big than for small saccade targets.

In order to check the dependence of displacement discrimination performance on preview duration for big and small targets more directly, I compared the slopes of the linear fits within each subject. Average slopes from fits are shown in Figure 4 for big (shown in orange) and small (shown in purple) saccade targets. As can be seen, for big saccade targets, all subjects showed a negative slope, thus indicating a decrease in performance scaling with preview duration. Slopes for
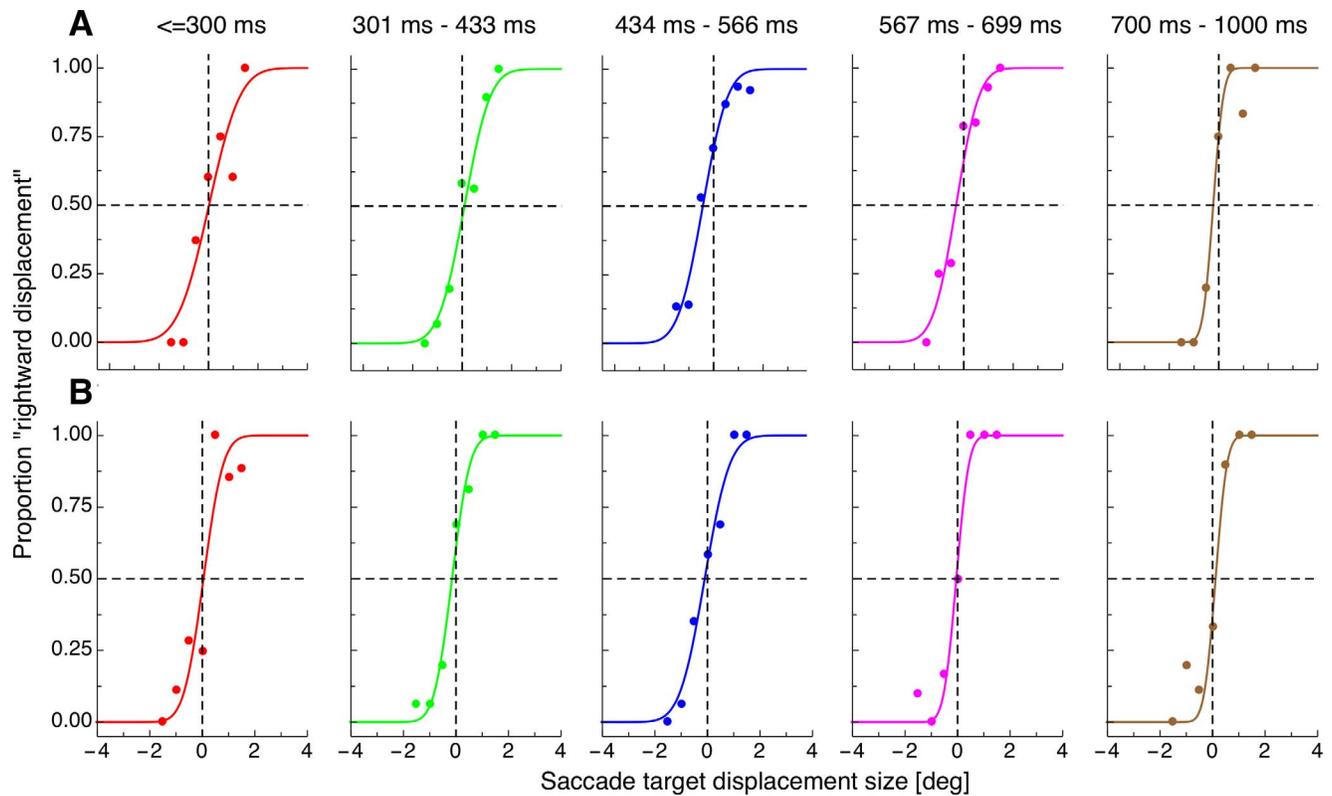
Figure 2. (A) Example psychometric functions for all preview bins for one subject from trials with big saccade targets. The data are fitted with a Gaussian error function whose variance is taken as an estimate of threshold (just noticeable difference). (B) Psychometric functions from trials with small saccade targets. Same conventions as in panel A.
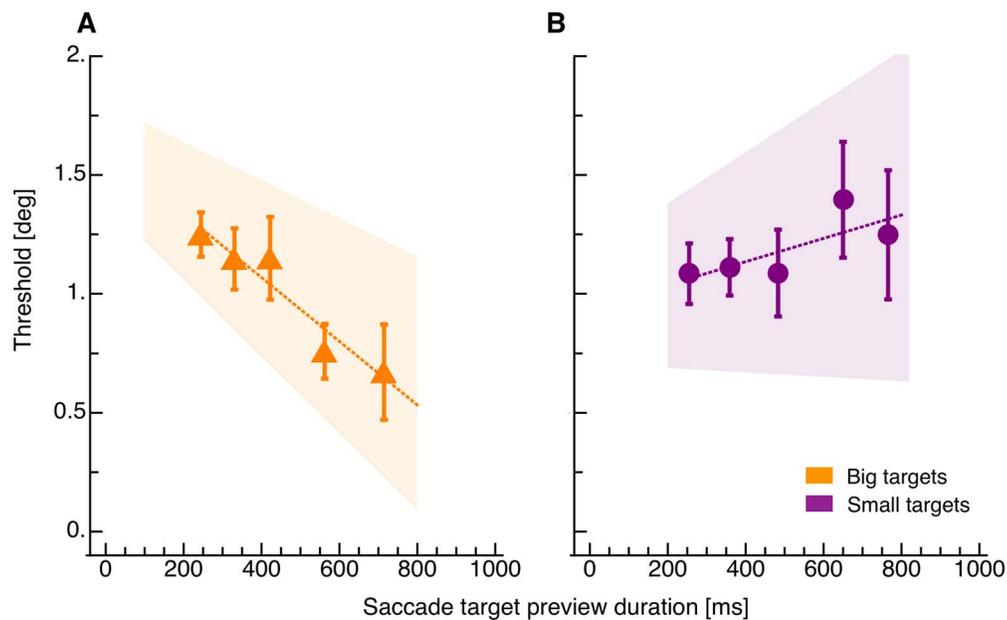

Figure 3. (A) Displacement discrimination thresholds as a function of saccade target preview duration from trials with big targets. Saccade target preview duration was calculated as the time between saccade target onset and saccade initiation. Error bars represent standard error across subjects. The dashed line shows the linear fits to the data (1.59–0.12×) and the shaded area its standard error. (B) Displacement discrimination thresholds as a function of saccade target preview duration from trials with small targets. Same conventions as in panel A. The dashed line shows the linear fits to the data (0.94 + 0.05×).
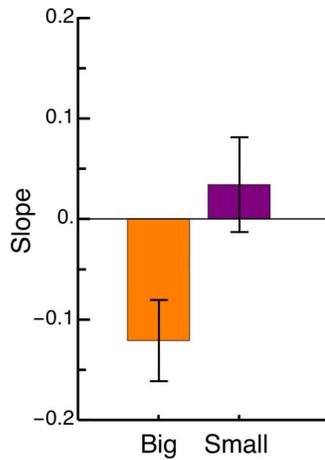
Figure 4. Average slopes of individual fits to the threshold data shown in Figure 3A and B for big saccade targets (shown in orange) and for small saccade targets (shown in purple). Error bars represent *SEM*.

small saccade targets, however, were positive on average. A paired *t* test revealed a significant difference between the slopes for big and small targets ($p < 0.05$).

A difference in the representation of big and small targets should be apparent in the size of errors in saccade landing. Figure 5A shows the average constant error of saccades executed to big targets on the ordinate against the mean constant error of saccades executed to small targets on the abscissa. Constant error refers to the average spatial distance that saccades landed from the target, and positive values indicate hypometry. Data were first averaged within subjects, then averaged across subjects. Average data are shown for all five preview duration bins. If constant error is equal for big and small saccade targets, data points should lie on the identity line. For short preview, however, it can be seen that the average is shifted to the left of the identity line, indicating a stronger constant error for big but a smaller constant error for small targets. For long preview, the average is closer to the identity line. I calculated a 2×5 ANOVA with the factors target size (big/small) and preview duration (five bins). A significant main effect target size, $F(1, 10) = 5.602$, $p < 0.05$, confirmed that the constant error was higher for big targets. The main effect of preview duration, $F(4, 40) = 3.255$, $p = 0.052$, and the interaction effect, $F(4, 40) = 2.471$, $p = 0.07$, marginally failed to reach significance. Figure 5B shows the average variable error of saccades executed to big targets on the abscissa against the average variable error of saccades executed to small targets on the ordinate. Variable error refers to the standard deviation of saccade landing. First, I calculated the standard deviation of saccade landing within subjects and then averaged these results across subjects. A 2×5 ANOVA with the factors target size (big/small) and preview duration (five bins) did not reveal any significant effect. Table 1 shows average durations and peak velocities for big and small targets from all five preview duration bins. I calculated a 2×5 ANOVA separately for durations and peak velocities. No significant difference was found for peak velocities or duration. A change in saccade landing positions would have predicted either a change in peak velocities or in saccade duration. The absence of any significant difference here might be due to variability in the data given that the differences in saccade landing are rather small. There is thus no evidence that changes in these saccade dynamics are related to the differences in perceptual thresholds.
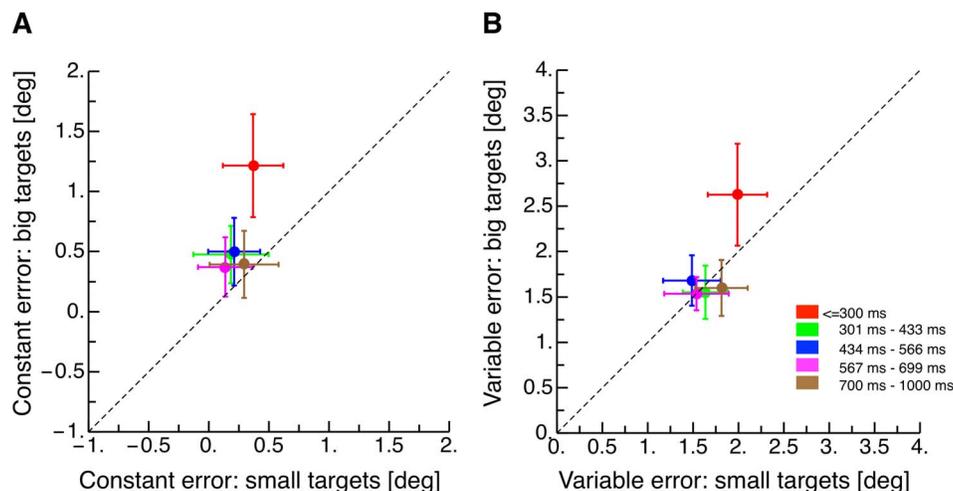

Figure 5. (A) Constant saccade error from trials with big saccade targets on the ordinate against constant saccade error from trials with small saccade targets on the abscissa. Data from the five different bins are color coded. Error bars represent *SEM*. (B) Variable saccade error from trials with big saccade targets on the ordinate against variable saccade error from trials with small saccade targets on the abscissa. Same conventions as in panel A.

Small saccade targets		Big saccade targets	
Saccade duration	Peak velocity	Saccade duration	Peak velocity
68.35 ± 5.26 ms	452.1 ± 9.29°/s	71.69 ± 5.85 ms	452.4 ± 13.3°/s
69.31 ± 4.66 ms	454.3 ± 10.70°/s	72.39 ± 4.85 ms	480.0 ± 34.0°/s
66.80 ± 4.00 ms	448.6 ± 11.40°/s	70.87 ± 3.64 ms	438.3 ± 12.0°/s
68.49 ± 3.04 ms	451.7 ± 10.10°/s	74.08 ± 5.16 ms	457.8 ± 30.7°/s
75.81 ± 12.10 ms	448.8 ± 9.63°/s	75.03 ± 5.90 ms	418.5 ± 19.3°/s

Table 1. Analysis of saccade dynamics. *Notes*: Saccade durations and peak velocities for big and small saccade targets. Errors represent *SEM*.

Discussion

The main finding of this study is that saccade target size interacts with the buildup of a spatiotopic saccade target representation. When spatially extended targets were used, transsaccadic displacement discrimination was poor when saccades were performed directly to the targets. Discrimination performance increased as a function of saccade target preview duration. The longer the target was seen before saccade execution, the better transsaccadic displacements could be judged. For small, point-like targets, no such dependence on preview duration was found.

Why would target size influence the buildup of a spatiotopic saccade target representation? In our previous report (Zimmermann, Morrone, & Burr, 2013), we argued that spatial position information has to accumulate in order to be precise enough for a transsaccadic comparison of spatial positions. Although it seems as if we perceive spatial location instantly, the dependence of apparent spatial location on viewing duration is known for perceptual and saccade localization (Aitsebaomo & Bedell, 1992). Another factor that influences saccadic localization is saccade target size (Ploner et al., 2004): Although saccades to point-like targets are very precise and accurate, saccades to larger targets show a higher scatter of landing positions and a stronger undershoot. Only when subjects are instructed to prioritize accuracy over reaction time, can saccades be really precise for larger targets as well (Kowler & Blaser, 1995). The loss of accuracy and precision can be explained by the need to compute a saccade goal from a spatially extended target based on pooling or integration of the spatial information within the target (McGowan et al., 1998). It has been suggested that the averaging was carried out by detectors with such large receptive fields that sensitivity to local structure within the stimulus would be lost (Findlay, 1982; Ottes, Van Gisbergen, & Eggermont, 1985). The imprecision in the saccade target representation for large targets might be counterbalanced by the beneficial influence of prolonged presentation duration. In this view, spatial position is a visual feature that, like other features,

takes time to be processed. It might be argued that the buildup effects are simply artifacts of choosing larger saccade targets as stimuli. However, neither point-like nor suddenly appearing stimuli exist often in the real world.

Collins (2016) argued that target size would not produce systematic differences because saccadic suppression of displacement magnitudes in the literature are not systematically related to saccade target size. However, when comparing saccade target sizes, eccentricity must be considered that differs in most studies. Here, I compared two different saccade target sizes matched for eccentricity and tested within the same pool of subjects. This finding reinforces the importance of matching experimental details exactly.

We have argued in an earlier report (Zimmermann et al., 2014) that saccadic suppression of displacement occurs because visual space is compressed during saccades (Lappe et al., 2000; Ross et al., 1997; Zirnsak et al., 2014). In this view, suppression of displacement is not a signature of a poor transsaccadic resolution of space, but rather a constant bias due to spatial attraction of two stimuli. In the displacement paradigm, the first stimulus, which usually is shown only briefly before saccade initiation, would become attracted by the postsaccadic stimulus, usually shown until the subject responds. In perisaccadic compression experiments, the probe stimulus is flashed, mostly for one frame only. If the presentation duration of the stimulus is increased, compression drastically weakens (Born et al., 2016). The absence of compression might explain why the long overlap duration in this and an earlier study (Zimmermann et al., 2013) supports transsaccadic displacement discrimination. We have shown that suppression of displacement occurs with similar magnitude also during fixation if the suppressive effects of the saccade are mimicked by a mask (Zimmermann et al., 2013). Thus, I suggest that the mechanism behind the poor performance in transsaccadic displacement paradigms is spatial attraction between targets rather than a loss of spatial sensitivity across the execution of saccades. Accumulating spatial information over time increases the representation strength of stimuli, thus making it possible to localize

them precisely (Abrams et al., 1989; Aitsebaomo & Bedell, 1992; Kowler & Blaser, 1995; Lemij & Collewijn, 1989). Stimuli that are represented only weakly, however, become susceptible to attractive influences by stimuli with a strong signal strength. Such a mechanism might minimize the variance in spatial localization for weak stimuli (Ernst & Banks, 2002).

It has to be stressed that neither the present data nor that of Zimmermann et al. (2013) were collected in a dark environment. Thus, it cannot be excluded that visual references, such as the screen border, contributed to the increase in discrimination performance. To test the role of the screen border, Deubel (2004) presented a target on a gray area that was inside a large black frame. Intrasaccadic displacements of the frame had only a very weak influence on the localization of the target. However, the influence of the frame was measured only for saccades without an artificial preview duration of the saccade target. It could thus be that the preview duration supports an estimation of the relative distance between target and screen border.

In conclusion, saccade target size modulates performance in the saccadic suppression of displacement paradigm. Displacement discrimination of spatially extended targets is poor with short saccade target preview duration and increases with longer preview duration. The preview duration might counterbalance the weak representation of spatially extended targets.

Keywords: saccade target size, suppression of displacement, visual stability

Acknowledgments

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