Secondary (micro-)saccades: The influence of primary saccade end point and target eccentricity on the process of postsaccadic fixation

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ABSTRACT

We examine how the size of saccadic under-/overshoot and target eccentricity influence the latency, amplitude and orientation of secondary (micro-)saccades. In our experiment a target appeared at an eccentricity of either 6 or 14 degree of visual angle. Subjects were instructed to direct their gaze as quickly as possible to the target and hold fixation at the new location until the end of the trial. Typically, increasing saccadic error is associated with faster and larger secondary saccades. We show that secondary saccades at distant in contrast to close targets have in a specific error range a shorter latency, larger amplitude, and follow more often the direction of the primary saccade. Finally, we demonstrate that an undershooting primary saccade is followed almost exclusively by secondary saccades into the same direction while overshooting primary saccades are followed by secondary saccades into both directions. This supports the notion that under- and overshooting imply different consequences for postsaccadic oculomotor processing. Results are discussed using a model, introduced by Rolfs et al. (2008), to account for the generation of microsaccades. We argue that the dynamic interplay of target eccentricity and the magnitude of the saccadic under-/overshoot can be explained by a different strength of activation in the two hemispheres of the saccadic motor map in this model.

1 Introduction

For optimal processing of our visual environment it is essential to bring areas of interest onto the fovea. This is achieved with rapid shifts of the eyes, so called saccades, which bring the eyes quickly to a new part of the visual scene. Visual information is then processed during fixation following the saccadic eye movement. Consequently, human eye movement behavior is often described as a sequence of alternating periods of saccades and fixation. This ignores at least two additional characteristics of eye movement behavior. First, a saccade towards a target in a visual scene often ends at some distance from the target position. Therefore, primary saccades are frequently followed by secondary saccades bringing the eyes to a position closer to the target location. Second, during the period of fixation the eyes are not motionless but instead show different specific movements which are referred to as fixational eye movements. One type of fixational eye movement which shares similar properties with large saccades are so called microsaccades (Hafed, 2011; Kowler & Steinman, 1980; Martinez-Conde et al., 2009; Rolfs, 2009; Steinman et al., 1973). So far microsaccades have mainly been studied during the initial period of fixation in an experimental trial. This experimental approach lacks insight into a more natural process of fixation which is the fixation following a saccade. Here we report that early (micro-)saccades following saccade execution are strongly influenced by target eccentricity and the magnitude of the saccadic error. Further, we provide new evidence that target under- and overshoot imply different consequences for the programming of secondary (micro-)saccades.

Microsaccades are defined by their amplitude (typically less than 1 degree of visual angle) and their high velocity. Similar to normal saccades, microsaccades fall on the main sequence (Zuber & Stark, 1965) which describes the linear relationship of peak velocity and saccade amplitude. For a number of reasons microsaccades have moved into the focus of eye movement research (see Martinez-Conde et al., 2009; Rolfs, 2009): Microsaccades are a possible index of covert attention (Engbert & Kliegl, 2003; Laubrock et al., 2005), they may play an important role in counteracting visual fading (Engbert & Kliegl, 2004; Martinez-Conde et al., 2006); they afford new perspectives on the dynamics governing saccadic motor programs (Hafed & Krauzlis, 2010; Rolfs et al., 2006; Rolfs & Ohl, 2011).

Despite recent advances in identifying neurophysiological mechanisms underlying the generation and consequences of microsaccades there is a strong need to further explore how microsaccades are embedded in the oculomotor system (Hafed, 2011). Recent models addressing the implementation of microsaccades highlighted the significance of the superior colliculus, a key brain structure for saccade programming (Hafed et al., 2009; Rolfs et al., 2008). Examining secondary (micro-)saccades takes into account that a fixation is preceded by a saccade and therefore allows to examine potential influences related to primary saccade execution on eye movement behavior during postsaccadic fixation. Indeed, identifying the factors that contribute to the overall distribution of postsaccadic activity in the oculomotor system will further improve our understanding of microsaccade generation.

In the current study we determine how (1) the magnitude of the saccadic error, (2) under- or overshoot of the target by the primary saccade, and (3) target eccentricity influence the latency, amplitude and orientation of secondary (micro-)saccades. In the remainder of this study we will refer to the first (micro-)saccade occurring after a goal-directed saccade as secondary saccade. The factors which influence the fixational process conditional on a

previous saccade have received surprisingly little attention in the literature, although they may constitute a crucial source to account for the variance of fixation durations in various tasks studying eye movement behavior. In the present study subjects were instructed to respond immediately with a saccade to an upcoming target and hold fixation after execution of the saccade until the end of a trial. Targets appeared to the left or right of the fixation point at two possible eccentricities resulting in four possible target locations.

1.1 Saccadic error

Saccades towards a target do not exactly land on the target. Indeed, there is a general tendency to undershoot a target by 10% of the target distance (Becker & Fuchs, 1969; Henson, 1978). Nevertheless, the overall accuracy of saccades strongly depends on the experimental procedure (Lemij & Collewijn, 1989). Saccades that miss the target position are usually followed by a secondary saccade bringing the target closer to the center of the fovea thereby reducing initial saccadic error (Becker & Fuchs, 1969; Becker, 1972; Hallett, 1978; Prablanc & Jeannerod, 1975; Weber & Daroff, 1972). These secondary saccades can occur shortly after the end of the primary saccade and it is argued that such error correction must rely to some degree on an internal signal (e.g., efference copy) as visual feedback is not available so quickly. The latency of secondary saccades with respect to their error-correcting amplitude is shorter for larger amplitudes of secondary saccades (Becker, 1972; Prablanc & Jeanerod, 1975). Kapoula and Robinson (1986) also reported such a negative relationship between amplitude and latency for secondary saccades, including also eye movements with amplitudes well below one degree of visual angle; hence in the range of microsaccades. Therefore it is reasonable to expect that early secondary saccades

(including microsaccades and large saccades) in our experiment will also be influenced by the magnitude of the saccadic error.

1.2 Under-/overshoot

Goal-directed saccades can either undershoot or overshoot a target. Hypometric and hypermetric saccades may trigger different processes. It is found that secondary saccades in the same direction as the primary saccade are on average faster than secondary saccades in opposite direction to the primary saccade (Deubel et al., 1982; Henson, 1978). Following a functional explanation first put forward by Robinson (1973), programming of secondary saccades is facilitated after undershooting as the undershot target object is kept in the same hemisphere of the cortex. Nevertheless, longer latencies in correcting overshoots could be also due to the in general smaller error for over- compared to undershoots (Henson, 1978; Kapoula & Robinson, 1986). Considering the relationship of amplitude and latency for corrective saccades (Becker, 1972; Kapoula & Robinson, 1986; Weber & Daroff, 1972), hence longer latencies for overshoots could be explained by the smaller amplitude of the subsequent corrective saccades. Given the conflicting results of previous research, the question whether undershooting and overshooting imply different consequences for postsaccadic processing needs further clarification. In the present study we provide new insights into this issue by determining the functional relationship between the magnitude of the saccadic under-/overshoot and the dependent variables latency, amplitude and orientation of secondary saccade.

1.3 Target eccentricity

The aim of our study is to examine the influence of primary saccades on small eye move-

ments during postsaccadic fixation. In natural vision, fixations are preceded by saccades of different amplitudes. Recently, Wang et al. (2011) introduced a dynamic neural field model of the superior colliculus that explores the effect of primary saccades on the latency of subsequent saccades. Simulations predict a strong influence of primary saccade amplitude on the postsaccadic neuronal activity within their dynamic neural field model of the superior colliculus. Assuming that primary saccade amplitude significantly modulates the distribution of postsaccadic activity in the superior colliculus we would also expect a significant influence of target eccentricity on the characteristics of secondary saccades in our study.

Increasing target eccentricity is typically associated with an increasing number of secondary saccades (Frost & Pöppel, 1976; Lemij & Collewijn, 1989). Lemij and Collewijn (1989) also examined the latency of secondary saccades with respect to target eccentricity and found shorter secondary saccade latencies for larger target eccentricities which they thought to be independent of the magnitude of the saccadic error. Here we test the influence of target eccentricity on secondary saccade latency (amplitude and orientation) after statistical control of the magnitude of the saccadic error. In summary, the goal of the present study is to investigate how the process of postsaccadic fixation depends on the previously executed primary saccade. Therefore we examine the influence of (1) saccadic error, (2) under-/overshoot, and (3) target eccentricity on the latency, amplitude and orientation of secondary saccades.

2 Materials and methods

2.1 Participants

Ten undergraduate students from the University of Potsdam were paid seven Euros or received study credit for their participation.

They were 19 - 28 years old ($M = 23.4$) and had normal or corrected-to-normal vision. A session involved 300 test and 8 training trials and lasted for approximately 45 minutes. This experiment was performed in accordance with the declaration of Helsinki (1964). Written informed consent was obtained from all participants.

2.2 Experimental setup and eye movement recordings

Participants were seated in a silent and dark room with the head positioned on a chin rest, 50 cm in front of the computer screen. Eye movements were recorded with the Eyelink-II system (SR Research, Osgoode, Ontario, Canada) with a high spatial resolution of less than 0.01°and a sampling rate of 500 Hz. Stimuli were displayed on a 19-in. EYE-Q 650 CRT monitor at a resolution of 1024 x 768 and a refresh rate of 100 Hz. The experiment was controlled by an Apple Power Macintosh G4 computer. The experimental software controlling stimulus display and response collection was implemented in Matlab (Mathworks, Natick, MA, USA) using the Psychophysics (Brainard 1997, Pelli 1997) and Eyelink (Cornelissen et al. 2002) toolboxes.

2.3 Procedure

A nine-point calibration was conducted to align eye and screen coordinate systems. At the beginning of a trial subjects were fixating a white point (0.67 diameter of visual angle) on a grey background at the center of the computer screen. After a uniform random interval of 1 to 1.5 seconds, the fixation point was removed and a white circle target (0.67 diameter of visual angle) appeared in the periphery at one of four possible positions (6°to the left or right of the fixation point, 14°to the left or right of the fixation point, respectively). Each of the four

target locations occurred with the same probability in a randomized order. Subjects were instructed to move their eyes as quickly as possible to the target and keep their eyes on the target until the end of a trial. A trial was terminated 1500 ms after target presentation. After an inter-trial interval of 500 ms the next trial started. Before the first and every 30 trials, the eye tracker was calibrated and the calibration was validated. Before a new trial started, fixation was checked and the stimuli were only presented when the gaze of the subjects was in the specified fixation area. A drift correction was carried out when fixation check failed. If fixation check failed after drift correction a new calibration and validation was initialized.

2.4 Data preparation

2.4.1 Preprocessing

Trials with eye blinks and saccadic reaction times (SRT) of primary saccades faster than 80 ms or longer than 400 ms were discarded. Primary saccades had to end within a distance of 2.5°around the center of the target in order to be included for further analysis. (Micro-)saccades were determined using an improved version (Engbert & Mergenthaler, 2006) of the algorithm reported by Engbert and Kliegl (2003). (Micro-)saccades were detected in 2D velocity space using thresholds for peak velocity (6 SD) and a minimum duration of 8 ms (4 data samples). Similar to Mergenthaler and Engbert (2010) we defined a 30 ms interval as minimum duration which separated two (micro-)saccades from each other. For further analysis we considered the first secondary (micro-)saccade occurring in an interval of 350 ms after the end of the primary saccade. Subjects contributed 137 - 251 (M = 178) secondary saccades, resulting in a total of 1778 secondary saccades within this interval. For analysis of secondary saccade orientation we as-

signed each postsaccadic eye movement to one of four categories according to their angular orientation. Secondary saccades with an angular orientation between 45°and 135°(upward) or between -45°and -135°(downward) were removed for analysis of secondary saccade orientation. Leftward and rightward secondary saccades were classified as either following the direction of the primary saccade or as in opposite direction to the primary saccade. Analysis of secondary saccade orientation comprises 1611 of the initial 1778 (90.6%) secondary saccades.

2.4.2 Data analysis

For statistical analyses of secondary saccade latency and amplitude we use linear mixed models (LMM) with subjects as random factor. Effects with a t-value larger than ± 2 are considered as significant (i.e. there is a strong correspondence between the t-statistic and the z-statistic given that the number of subjects and observations per subject is sufficiently large). We carefully checked that reported significant results are also significant (95% confidence interval) when drawing samples (n = 1000) from the posterior distribution of parameters of the given LMM. Secondary saccade orientation is analyzed as bivariate dependent variable (coding: 0 = same direction as primary saccade; 1 = opposite direction to primary saccade). Therefore we use a generalized linear mixed model (GLMM) for binomial data, again including subjects as random factor. Functions for LMMs (and GLMMs) are provided by the lme4 package (Bates & Maechler, 2010) in the R environment (R Development Core Team, 2010). Graphics were obtained with the ggplot2 package (Wickham, 2009).

2.4.3 Covariates

The following variables are used to setup our statistical models. To quantify the magnitude

	Close target	Distant target
SRT (in ms)	159.9 (16.3)	168.6 (16.2)
Accuracy (in °)	0.198 (0.26)	-0.177 (0.36)
Secondary saccades (in %)	55 (0.19)	82.7 (0.08)

Table 1: Mean (SD) are shown for saccadic reaction times (SRT), saccadic error (accuracy) and the percentage of secondary saccades. Negative accuracy indicates undershooting

of the saccadic error we determined the absolute horizontal distance from the end point of the primary saccade to the center of the target in degree of visual angle. This magnitude of the saccadic error is coded contingent on whether the primary saccade under- or overshot the target. Specifically, the covariate undershoot contains the absolute size of the saccadic error in case of undershoot and zero for overshoots. Respectively, the covariate overshoot contains the size of the saccadic error when the target is overshot and zero for undershoots. Further we use the square for both variables (undershoot2, overshoot2). Target eccentricity (eccentricity) is coded as 0 (close target at 6°) and 1 (distant target at 14°).

3 Results

In Table 1 the overall characteristics (saccadic reaction time, accuracy) of the primary saccades and the proportion of secondary saccades depending on target eccentricity are shown. In general, primary saccades are very precise in our study. Interestingly, the number of secondary saccades is much higher after saccades to distant as opposed to close targets.

In Figure 1 the distribution for latency (upper panel) and amplitude (lower panel) of secondary saccades occurring within the first 350 ms is displayed. The peak of the latency distribution is reached 135 ms after the end of the primary saccade. The distribution of secondary saccade amplitude shows a large proportion of secondary saccades with an amplitude smaller
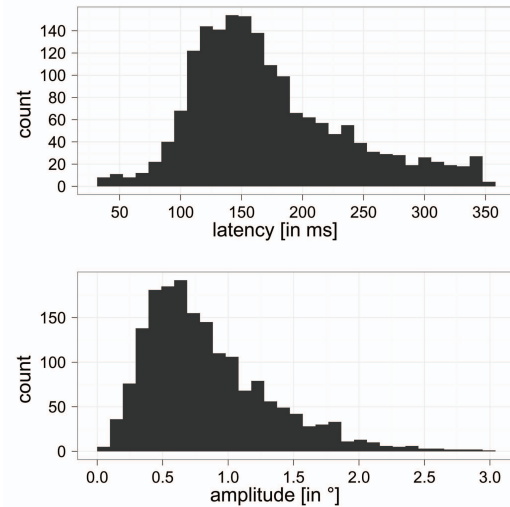

Figure 1: Distribution of secondary saccade latency (upper panel, binwidth = 10 ms) and secondary saccade amplitude (lower panel, binwidth = 0.1°).

than one degree of visual angle, hence meeting the criterion for microsaccades. In Figure 2 the distribution of saccadic error (for the 1778 events which are followed by a secondary saccade) is shown for close (left panel) and distant (right panel) targets. Note, we observe under- and overshoots for both target eccentricities.

3.1 Secondary saccade latency

Figure 3 shows two important results. First, secondary saccade latency is longer for close (red solid line) than distant (blue solid line) targets. This difference decreases with the magnitude of the saccadic error. Second, secondary saccade latency is longer for small than large saccadic error. The peak of secondary saccade latency is shifted to small overshoot with an even further shift in the distant target condition.

The LMM specified in order to model secondary saccade latency includes the covariates undershoot, overshoot, target eccentricity as well as the interactions undershoot x eccen-
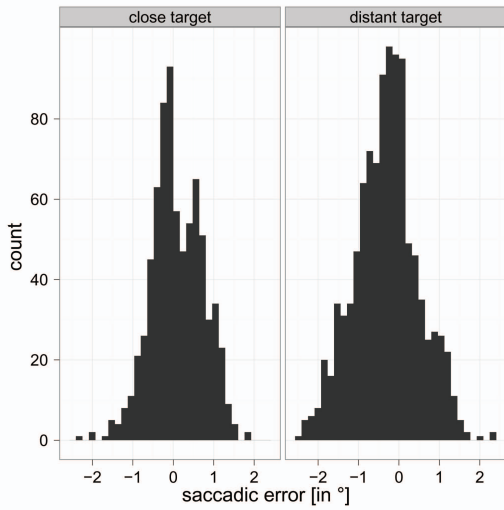
Figure 2: Distribution of saccadic error (binwidth=0.15°) by target eccentricity. Negative values indicate undershooting, positive values indicate overshooting.

	Estimate	SE	*t*-Value
Intercept	222.8	5.8	38.50
Eccentricity (ecc)	-42.1	5.6	-7.52
Undershoot	-132.6	16.0	-8.31
Undershoot2	43.4	10.5	4.15
Overshoot	55.6	16.6	3.35
Overshoot2	-81.1	13.0	-6.26
ecc x undershoot	31.6	18.7	1.69
ecc x undershoot2	-9.5	11.7	-0.81
ecc x overshoot	10.3	21.2	0.48
ecc x overshoot2	32.3	15.9	2.04
Variance components		SD	
Subjects		12.02	
Residuals		51.28	

Table 2: LMM statistics for secondary saccade latency

tricity and overshoot x eccentricity. Furthermore we include the square of undershoot (undershoot2) and the square of overshoot (overshoot2) along with their interactions with target eccentricity (see Table 2). We find a significant main effect of target eccentricity (t=-7.52). Thus in the case of minimal saccadic error we still observe a significant decrease of secondary saccade latency in the distant target condition. Moreover, the linear and quadratic saccadic error is necessary to account for secondary saccade latency after under- and overshooting a close target. The prediction of the LMM (Figure 3, dashed lines) is in line with the notion of shorter latencies for a large saccadic error. The only significant interaction is overshoot2 x eccentricity (t=2.04); meaning that overshoot2 is the only covariate associated with saccadic error which is modulated by target eccentricity.

3.2 Secondary saccade amplitude

Figure 4 illustrates the relationship of secondary saccade amplitude and saccadic error depending on target eccentricity. Four important characteristics are evident. First, increasing undershoot is associated with increasing secondary saccade amplitude. Second, irrespective of the size of saccadic undershoot amplitudes are larger in the distant target condition. Third, the minimum of secondary saccade amplitudes is shifted towards a small overshoot. Alike for latencies, the shift is more pronounced in the distant target condition. Fourth, for both target eccentricities a further increase in saccadic overshoot is associated with increasing amplitudes.

In order to model secondary saccade amplitude we use the same main factors and interactions as described in the LMM to account for secondary saccade latency (see Table 3). Again we find a significant main effect of target eccentricity (t=5.84). Thus even in the case of minimal saccadic error, secondary saccade amplitude is significantly larger in the distant than in the close target condition. Furthermore we find a significant main effect of undershoot (t=5.83). Importantly, neither quadratic
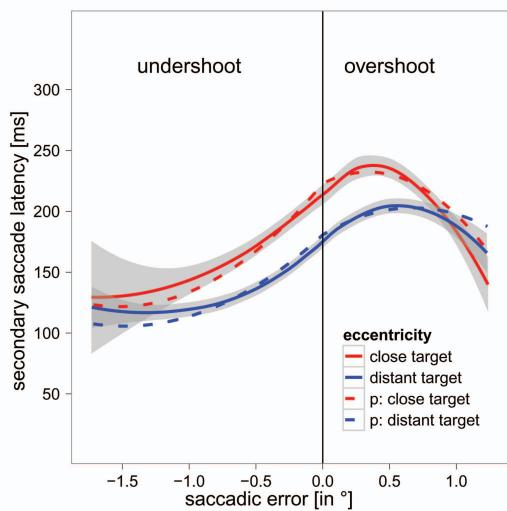
Figure 3: Secondary saccade latency as function of saccadic error by target eccentricity. Smoothing (solid line) is based on loess method (degree=2). For smoothing we used saccadic error values ranging from the 2.5 to 97.5 percentile. Grey bands represent the 95% confidence interval. Prediction (p: close target, p: distant target) of the LMM (dashed line) after removal of between-subject variance.

	Estimate	SE	t-Value
Intercept	0.549	0.055	10.00
Eccentricity (ecc)	0.177	0.030	5.83
Undershoot	0.513	0.087	5.93
Undershoot2	0.068	0.057	1.20
Overshoot	-0.197	0.090	-2.19
Overshoot2	0.239	0.070	3.39
ecc x undershoot	-0.062	0.101	-0.61
ecc x undershoot2	0.058	0.063	0.91
ecc x overshoot	-0.285	0.115	-2.47
ecc x overshoot2	0.147	0.086	1.71
Variance components		SD	
Subjects		0.157	
Residuals		0.278	

Table 3: LMM statistics for secondary saccade amplitude

undershoot (undershoot2; t=1.2) nor the interactions undershoot x eccentricity (t=-0.61) and undershoot2 x eccentricity (t=0.91) significantly influence secondary saccade amplitude. These results confirm our observations from Figure 4 and we can conclude that increasing saccadic undershoot is associated with increasing secondary saccade amplitude. Secondary saccade amplitude is significantly larger after undershooting distant than close targets as the significant main effects of undershoot and eccentricity are not further influenced by a significant interaction.

The pattern is more complex when studying the consequences of overshooting. Both, the linear (t=-2.19) and quadratic (t=3.39) magnitude of saccadic overshoot significantly influence secondary saccade amplitude. Further, the effect of overshoot is modulated by target eccentricity (t=-2.47). These effects lead to the prediction of the LMM (Figure 4, dashed lines) that larger overshoot is associated with increasing amplitudes. An amplitude modulation by target eccentricity is not present anymore.

3.3 Secondary saccade orientation

In Figure 5, we show whether the orientation of secondary saccades follows the same (dots scattered around 0) or opposite (dots scattered around 1) direction of the primary saccade depending on the size of the saccadic error and target eccentricity. Moreover, the prediction of the GLMM is included for both target eccentricities (solid lines). Note, the GLMM models the probability that secondary saccade direction is opposite to the primary saccade's direction. Importantly, when a target is undershot almost all secondary saccades are in the same direction as the primary saccade. In contrast, after an overshoot secondary saccades in both directions are observed. With increasing overshoot secondary saccades are more likely to be executed in opposite direction to the primary saccade. This effect is modulated by target eccentricity. In the distant target condition an
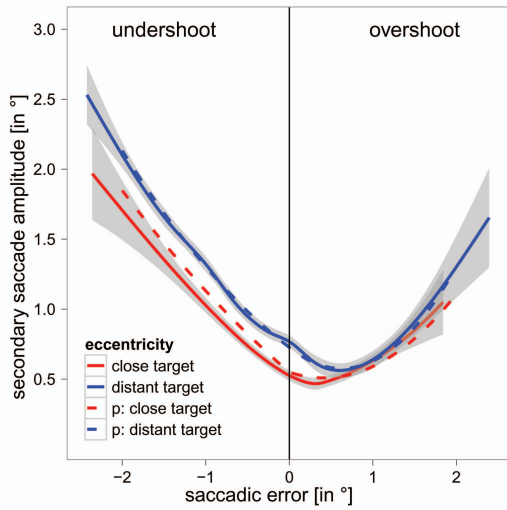
Figure 4: Secondary saccade amplitude as function of saccadic error by target eccentricity. Smoothing (solid line) is based on loess method (degree=2). Grey bands represent the 95% confidence interval. Prediction (p: close target, p: distant target) of the LMM (dashed line) after removal of between-subject variance.

	Estimate	SE	t-Value
Intercept	-1.97	0.274	0
Eccentricity (ecc)	-1.51	0.434	0.0005
Undershoot	-7.09	2.094	0.0007
Overshoot	2.60	0.349	0
ecc x undershoot	-0.04	4.145	0.992
ecc x overshoot	1.11	0.549	0.044
Variance components		SD	
Subjects		0.37	

Table 4: LMM statistics for secondary saccade orientation

cade's direction.

3.4 Control analyses

In control analyses we carefully ruled out the possibility that the observed results are due to expectation drift during the initial period of fixation.

Following a reviewer's suggestion we checked for the possibility that the relationship between saccadic error and secondary saccade latency may arise from a correlation between primary and secondary saccade latency as observed in tasks examining sequences of saccades (Zingale & Kowler, 1987). Given that fast primary saccades are less precise, the inverse relationship between saccadic error and secondary saccade latency could indirectly result from the saccadic system's tendency to execute saccades in a specific rhythm (e.g. fast saccades are also followed by saccades with short latency). Indeed, in control analyses (see Online supplementary material) we find a small decrease of the absolute saccadic error with increasing primary saccade latency. Furthermore, we find a small increase of secondary saccade latency with increasing primary saccade latency. Nevertheless, this explanation can neither account for the overall differences between close and distant targets nor for the shift of minimum amplitude and maximum latency to a small overshoot. Furthermore, it cannot account for the

even larger saccadic overshoot is necessary in order to be followed by secondary saccades to the opposite direction.

The GLMM includes the same main factors and interactions like the above introduced LMMs but spares main effects and interactions including a quadratic term (see Table 4). The significant negative influence of the intercept (p<0.001) tells us that secondary saccades are significantly more often executed into the direction of the primary saccade when landing in the center of a close target. While undershooting (p<0.001) significantly increases the probability to follow primary saccade direction, overshooting (p<0.001) significantly increases the probability to go into the opposite direction of the primary saccade. Again, we find a significant main effect of target eccentricity (p<0.001). At minimal saccadic error, significantly more secondary saccades at the distant than close target location follow primary sac-
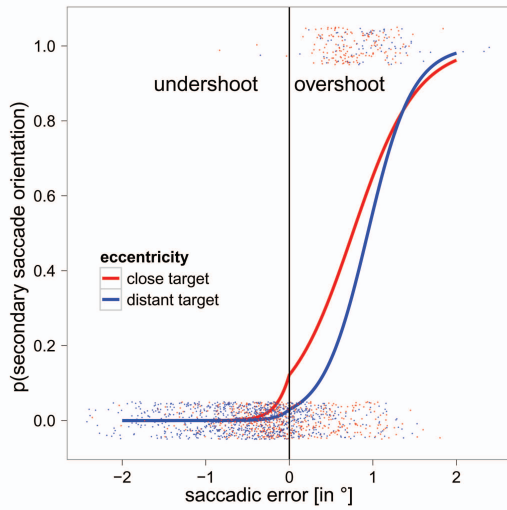
Figure 5: Probability of secondary saccade orientation as function of saccadic error by target eccentricity. Individual data points are jittered (vertical jitter=0.05) around 1 for secondary saccades in opposite direction of the primary saccade. Secondary saccades following primary saccade direction are jittered around 0. Depending on target eccentricity data points are red (close target) and blue (distant target). Predictions of the GLMM (solid line) are displayed after removal of between-subject variance.

bias to follow primary saccade direction.

4 Discussion

The main objective of the present study is to extend the focus on fixational eye movements by studying the fixational process following saccade execution. To this end we tested how (1) the magnitude of the saccadic error, (2) saccadic under-/overshoot, and (3) target eccentricity influence the latency, amplitude and orientation of secondary saccades. All factors contribute to motor programs of secondary saccades. Previous studies concerning the programming of secondary saccades were focusing on the magnitude of the saccadic error and a potentially different influence between under-

and overshooting on secondary saccade latency. Our results demonstrate that these influences are strongly modulated by target eccentricity, which sheds new light on the postsaccadic oculomotor activity triggering secondary saccades.

When the primary saccade ends in the center of a target, we observed significant effects of target eccentricity with respect to the latency, amplitude and orientation of secondary saccades. Secondary saccades following precise primary saccades to distant targets are on average faster, have a larger amplitude and are more likely to follow primary saccade direction. This result is very surprising if one assumes the saccadic error to be the driving source to perform a secondary saccade. Our results support the initial observation by Lemij and Collewijn (1989) who reported also shorter secondary saccade latencies for increasing target eccentricities; a result they already thought to be independent of the saccadic error.

Increasing saccadic undershoot is associated with decreasing secondary saccade latency and increasing amplitude. Examining the orientation of secondary saccades after undershooting reveals that almost all secondary saccades follow the direction of an undershooting primary saccade. Importantly, maximum latency and minimum amplitude of secondary saccade are shifted to a small overshoot (with an even further shift in the distant target condition). This supports the idea of different consequences for the programming of secondary saccades depending on whether the target is under- or overshot. A further increase in saccadic overshoot is associated with shorter saccade latency and larger amplitude.

Examining the orientation of secondary saccades reveals an additional important difference between under- and overshooting. As reported above, almost all secondary saccades after undershooting follow the direction of the primary saccade (they are corrective secondary saccades). Increasing saccadic overshoot also

results in a higher probability of corrective secondary saccades (they are in opposite direction to primary saccade direction). Nevertheless, after overshooting it is still very likely that secondary saccades follow the direction of the primary saccade; therefore increasing the saccadic overshoot. We have shown a significant effect of target eccentricity on the orientation of secondary saccades following an overshoot. As illustrated in Figure 5, in the distant target condition a larger saccadic overshoot is necessary in order to elicit a corrective secondary saccade.

4.1 Secondary (micro-)saccades during postsaccadic fixation

A large proportion of the observed secondary saccades were in the range of microsaccades. Recently, two models of microsaccade generation have been put forward. Rolfs et al. (2008) introduced a conceptual model which assumes the rostral pole of the superior colliculus to be directly involved in microsaccade generation. Hafed et al. (2009) demonstrated a causal involvement of the superior colliculus in the control of microsaccades. As the model of Rolfs et al. (2008) successfully accounted for various effects concerning small saccades we will use this framework to discuss the observed results of our study. In the model of Rolfs et al. a motor map is assumed coding eye movements of very small amplitudes (microsaccades) in the center of the map (around the amplitude of 0°) and increasing amplitudes in increasingly peripheral sites of the map (topographical organization). Rightward eye movements are programmed in the left hemisphere and leftward eye movements in the right hemisphere of the motor map. Activation in one site of the map will also cause excitation of neighboring locations (local excitation) while at the same time distant locations will be inhibited (global inhibition). When activation crosses a certain

threshold in this model a saccadic eye movement of the corresponding amplitude and orientation will be executed.

Postsaccadic visual information is processed and will cause activity to build up within the motor map. Considering this model to account for secondary saccade characteristics we claim (1) the visually evoked postsaccadic activation within the hemisphere in which the primary saccade has been programmed is enhanced and (2) the enhancement is stronger for distant as opposed to close targets.

Strong support for these claims is given by studying the orientation of secondary saccades. When a target is undershot almost all secondary saccades follow the direction of the primary saccade. Note, even at minimal saccadic error secondary saccades still follow almost exclusively the direction of the primary saccade. Under the assumption of equal postsaccadic activation in both hemispheres of the motor map one would expect secondary saccades after minimal error to be executed in both directions with same probability. As shown, this is clearly not the case. The second claim is supported by the finding that primary saccades to distant in contrast to close targets have to overshoot the target even more in order to be followed by a corrective secondary saccade. Thus, the activation in the hemisphere which programmed the primary saccade is even more enhanced in the distant target condition as there is a stronger tendency of secondary saccades to follow primary saccade direction.

Interestingly the assumption of different levels of postsaccadic activation in the two hemispheres of the motor map predicts a shift of maximum latency and minimum amplitude from zero saccadic error to a small overshoot. After exact primary saccades the incoming visual signal of the fixated target will cause activation to build up around the center of the motor map. This visually evoked response will be stronger in the hemisphere which programmed

the initial primary saccade, causing the building up activation to be biased towards this hemisphere. Further, this bias will be stronger after saccades to distant as opposed to close targets. Consequently after saccades to distant targets maximum latency and minimum amplitude is even further shifted in the direction of overshooting. Revealing the sources for different activations in the two hemispheres of the motor map and their modulation by target eccentricity is beyond the scope of this study. We argue that at least three possible sources have to be considered in future investigations. First, execution of saccades with an amplitude of 6°(close target) and 14°(distant target) might result in a different distribution of activation within the oculomotor network (e.g. superior colliculus; Wang et al., 2011). Second, the strength of the incoming visual information might be modulated by the previous saccade amplitude. It has been shown that saccade execution causes a postsaccadic enhancement of neural firing in the lateral geniculate nucleus (Reppas et al., 2002; Royal et al., 2006). Nevertheless, examining the influence of saccade amplitude on postsaccadic enhancement of neural firing in the lateral geniculate nucleus, Reppas et al. (2002) conclude that the effect of saccade amplitude is rather small. Third, the generation of microsaccades is known to be influenced by the allocation of attention (Engbert & Kliegl, 2003; Hafed & Clark, 2002). Importantly, directly after the end of a saccade attention resides in retinotopic coordinates for some time, which is referred to as the retinotopic attentional trace (Golomb et al., 2008; Golomb et al., 2010). With increasing time attentional facilitation decays at the retinotopic and increases at the spatiotopic location. Given the close link of microsaccades and attention we suspect the retinotopic attentional trace to be an important phenomenon when studying secondary saccades and the process of postsaccadic fixation.

So far we have not addressed how our model accounts for the inverse relationship between the magnitude of saccadic error and secondary saccade latency. There are two possible mechanisms. First, an error signal is computed which impinges on the saccadic motor map. A larger saccadic error would be associated with a stronger error signal and consequently, cause faster secondary saccades. Second, it has been shown that primary saccade latency decreases with decreasing eccentricity but increases again for very small eccentricities (Kalesnykas & Hallett, 1994). The same latency-eccentricity function could be present for secondary saccades in our study. Thus, the inverse relationship between saccadic error and subsequent latency could simply result from the fact that very small eye movements in general need more time to be executed. Importantly, this explanation would not need an additional computation of an (extra-retinal) error signal.

5 Conclusion

The present study demonstrates that secondary saccades are strongly influenced by characteristics of the previous goal-directed saccade. We replicate that subsequent, postsaccadic eye movements are largely determined by the initial landing error. Importantly, we provide new evidence for a different postsaccadic fixational state depending on whether the target has been under- or overshot. We extend these results with an additional modulation by target eccentricity. All of them constitute important influences on the generation of secondary saccades during postsaccadic fixation. Our experimental task and the proposed mechanisms for a model of postsaccadic fixation strongly rely on postsaccadic visual processing of the target. Future experiments will examine how postsaccadic fixation depends on the quality of incoming visual information and

a possible role of extra-retinal error correction.

Microsaccades constitute a large proportion of postsaccadic eye movements in our experiment. Much current research is devoted to understand how microsaccades contribute to perception: that is to their role in functions such as counteracting visual fading, maintaining visual stability, and as an index of covert attention. The present study constitutes an important step to examine small eye movements in a more natural situation which is examining (micro-)saccades being embedded in a sequence of saccades and fixations.

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