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Title: Revealing the time course of signals influencing the generation of secondary saccades using Aalen's additive hazards model

Abbreviated title: Secondary saccades and rate analysis

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Abstract

Saccadic eye movements are frequently followed by smaller secondary saccades which are generally assumed to correct for the error in primary saccade landing position. However, secondary saccades can also occur after accurate primary saccades and they are often as small as microsaccades, therefore raising the need to further scrutinize the processes involved in secondary saccade generation. Following up a previous study, we analyzed secondary saccades using rate analysis which allows us to quantify experimental effects as shifts in distributions, therefore going beyond comparisons of mean differences. We use Aalen's additive hazards model to delineate the time course of key influences on the secondary saccade rate. In addition to the established effect of primary saccade error, we observed a time-varying influence of under- vs. overshooting – with a higher risk of generating secondary saccades following undershoots. Moreover, increasing target eccentricity influenced the programming of secondary saccades, therefore demonstrating that error-unrelated variables co-determine secondary saccade programs. Our results provide new insights into the generative mechanisms of small saccades during postsaccadic fixation that need to be accounted for by secondary saccade models.

Keywords: Eye movements; corrective saccades; secondary saccades; rate analysis; survival analysis

Introduction

Receptor density is highest in the foveal part of the retina. To allow detailed visual processing of a scene, saccadic eye movements shift the center of gaze such that objects of interest fall onto the fovea. Despite the remarkable precision of saccade targeting (Kowler & Blaser, 1995), saccade landing positions are distributed around the saccade target location which is attributed to a combination of uncertainty in the localization of a target and noise in planning and executing the saccade (van Beers, 2007). Moreover, there is a general tendency of primary saccades to undershoot the target (Becker & Fuchs, 1969; Gillen, Weiler, & Heath, 2013). Large primary saccades are frequently followed by a smaller secondary saccade that often reduces the distance between primary saccade landing position and target location (Becker & Fuchs, 1969); therefore secondary saccades are often equated with corrective saccades.

The mechanisms underlying the programming of secondary saccades are far from being understood, but are rarely studied. This is true although secondary saccades constitute a very frequent oculomotor behavior (Hollingworth, Richard, & Luck, 2008). This may be changing. Recently microsaccades have been studied also under more natural conditions (McCamy, Otero-Millan, Di Stasi, Macknik, & Martinez-Conde, 2014) where large saccades precede a fixation including a microsaccade. However, the question arises as to what differentiates such microsaccades from secondary saccades. In contrast to microsaccades, secondary saccades are not defined by an arbitrary amplitude criterion; hence secondary saccades can be both smaller and larger than 1 degree of visual angle. Studying microsaccades and secondary saccades under a common framework offers the possibility to bring together two largely separated fields. As an example, in the present study we identified time-dependent influences on the generation of secondary saccades and test predictions regarding secondary saccades from an adapted model of microsaccade generation.

The strong focus on secondary saccades as corrective eye movements suggests that one can model the latency, amplitude and direction of secondary saccades simply based on the distance between primary saccade landing position and postsaccadic target location. Furthermore, one should be able to predict whether or not a secondary saccade is generated at all. Importantly, secondary saccades are also observed after accurate primary saccades. Moreover, target eccentricity has been identified as independent influence on the latency, amplitude and orientation of secondary saccades (Frost & Pöppel, 1976; Lemij & Collewijn, 1989; Ohl, Brandt, & Kliegl, 2011; 2013). These findings question a simplified relationship of saccadic error and the programming of secondary saccades. Here, we present a new statistical approach to study the time course of saccadic error and error-unrelated variables on the generation of secondary saccades which should further stimulate testing of models underlying the generation of this frequent type of eye movement.

Typically, when studying secondary saccades an arbitrary time window during postsaccadic fixation is defined and mean values are reported for that population of secondary saccades. In contrast, we make use of a statistical approach that uncovers time-dependent effects on secondary saccade rate; and therefore overcomes limitations due to reporting mean values. The statistical analyses of secondary saccades must address various challenges that have been largely ignored so far. First, there are trials in which no secondary saccade occurs. Usually such trials are excluded from the analysis when relating experimental variables of interest to the metric of secondary saccades. This procedure is likely to result in biased estimates of experimental effects. Second, even when some variable of interest exerts significant effects on the average secondary saccade latency, the strength of this effect may vary as a function of time. Traditional analyses assume that the effect is of equal strength at all times.

A widely used statistical tool to analyze the dynamics of an event after some time which also takes into account data without an event is survival analysis (see for example (Kleinbaum & Klein, 1996). Survival analyses can be applied in many areas of research and are particularly well suited to address questions in medical research (e.g., time to graft rejection after transplantation). In the following text, we will use the term rate analysis which refers to the family of time-to-event analyses including survival analysis, failure analysis, risk analysis.

In the present study we use the additive hazards model (Aalen, 1980) which allows for estimating time-varying covariate effects. The hazard rate is defined as the instantaneous risk for an event to occur at a specific point in time. The additive hazards model is a nonparametric model which yields estimates about how a baseline hazard rate depends on the included variables in the model. Importantly, the variables included as regression coefficients in the model are allowed to depend on time, thus allowing us to assess the time course of a predictor's influence on secondary saccade rate.

Using the additive hazards model we re-analyze data from a previous study in which we determined the influence of primary saccade landing position and target eccentricity on the latency, amplitude and orientation of secondary saccades – including secondary saccade amplitudes as small as microsaccades (Ohl et al., 2011). Here we complement our previous analyses with an analysis of secondary saccade rate.

We build our hypotheses based on a qualitative model for microsaccade generation (Rolfs, Kliegl, & Engbert, 2008) but see also (Ohl et al., 2011) that assumes a topographically organized motor map in which (micro-)saccades are generated (see Figure 1a). The center of the map codes for the smallest possible saccadic eye movements. Increasingly distant locations in one direction codes for increasing saccade amplitudes into the opposite hemifield. Sites in this map are connected, following the principle that neighboring sites excite and distant areas inhibit each other. In order to account for the generation of small eye movements following large primary saccades we extended this model by assuming (1) a hemispheric bias in the saccadic motor map, meaning a higher level of activation in the hemisphere of the saccadic motor map which also programmed the primary saccade (see Figure 1b) and (2) an even stronger hemispheric bias for larger target eccentricities.

In this study we test these model assumptions when analyzing the hazard rate of secondary saccades using Aalen's additive hazards model. In addition to the well-established influence of absolute primary saccade error on secondary saccades, we observed further evidence for different effects on secondary saccades contingent on under- vs. overshooting and target eccentricity.

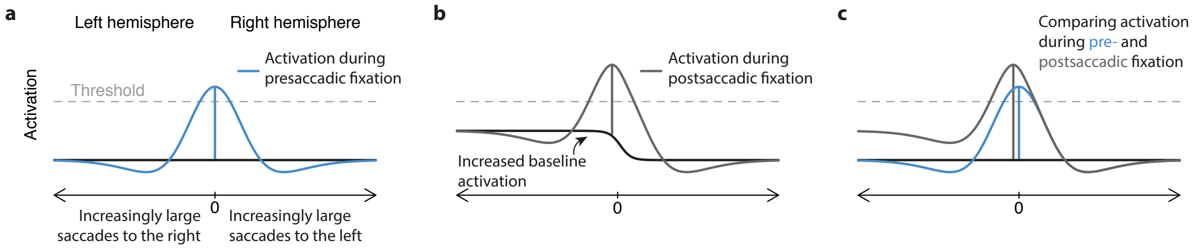

Figure 1. Illustration of activity distribution in an oculomotor map for (micro-)saccade generation. **A,** distribution of activation during presaccadic fixation (adapted from Rolfs, Kliegl, & Engbert, 2008). **B**, distribution of activation during fixation following a saccadic eye movement to the right. Activation is increased in the left hemisphere which programmed the primary saccade to the right. This causes a bias of the overall distribution towards the hemisphere that programmed the primary saccade. The bias increases with increasing target eccentricity. **C**, comparison of activity distribution during pre- and postsaccadic fixation.

Materials and Methods

The present study is a re-analysis of data from a previously published experiment. For detailed information on the experimental setup, eye movement recordings and procedure, the reader is referred to our previous publication (Ohl et al., 2011).

Participants and procedure

Ten undergraduate students (19-28 years old) participated in our study. For participation, they received study credit or were paid seven Euros. In an experimental trial, subjects had to fixate a central fixation point (diameter of 0.67°). Participants had to fixate that point for 200 ms with a maximum allowed distance of 1° from the center of the screen in order to start the trial. After a random interval between 1000 - 1500 ms the fixation point was removed and a target (diameter of 0.67°) appeared at an eccentricity of 6° or 14° to the left or right of the fixation point. Subjects had to move their eyes immediately to the target and hold fixation at the target location for at least 1100 ms. Each observer performed eight training and 300 test trials. We obtained written informed consent from all subjects before beginning of the experiment. The study was performed in accordance with the declaration of Helsinki from 1964.

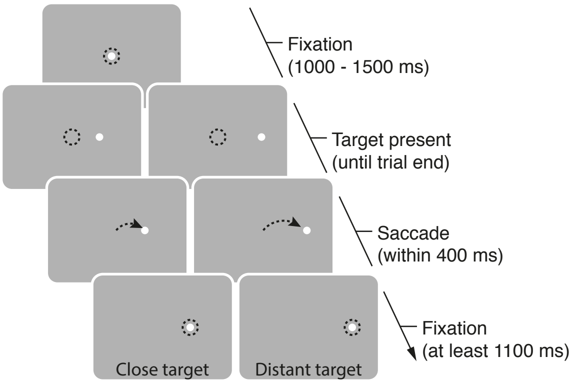

Figure 2. Illustration of trial sequence.

Data preparation and analysis

Eye positions of the left and right eye were recorded with a sampling rate of 500 Hz using an EyeLink-II system (SR, Research, Ontario, Canada). For detection of microsaccades and saccades we transformed the eye trajectory in 2D velocity space and classified epochs passing the peak velocity criterion (6 SD) for a minimum duration of 4 samples (8 ms) as saccadic events, with saccade onset defined as the first sample above the velocity criterion (Engbert & Kliegl, 2003; Engbert & Mergenthaler, 2006).

In order to be included for further analysis a trial had to meet three criteria: (1) primary saccadic reaction times were slower than 80 ms and faster than 400 ms, (2) the distance between primary saccade end point and center of the target was smaller than 2.5°; (3) no eye blinks occurred during the trial. For data analysis we considered an interval of 1100 ms after execution of the primary saccade. In total 88.78% of the trials entered the final analyses (2635 of 3000 trials). We observed 2249 trials including at least one secondary (micro-)saccade and 386 trials without any secondary saccade within an interval of 1100 ms.

Statistical analyses were performed using the timereg package (Scheike, Martinussen, & Silver, 2010) in the R environment (R Core Team, 2013). In order to account for interindividual differences in the rate-analysis we specified participants as clusters in a marginal additive model. Primary goal for specifying the clusters was to increase the validity when estimating standard errors for effects on the population level. As an alternative, frailty models can provide estimates for subject specific effects within a cluster akin to random effects in linear mixed models (for details on clustering see Martinussen & Scheike, 2007). Given the small number of observers in the study, a detailed analysis of inter-individual differences using frailty models (and its comparison to marginal models) is left for future studies.

P-values and tests for time-varying effects were derived from resampling (n = 10,000). After running the analysis we carefully checked that the continuous covariate met the assumption of additivity. This was accomplished by computing the residuals in the Aalen analysis and subsequent resampling (n = 10,000) of cumulative residuals. Violation of the additivity assumption is indicated when the confidence interval of simulated cumulative residuals significantly deviates from zero.

The statistical model included the following covariates. First, saccadic error is defined as the absolute horizontal distance from saccade end point to the center of the target in degree of visual angle. Second, the variable under/ overshoot indicates whether the primary saccade was either undershooting (hypometric) or overshooting (hypermetric). Each saccade landing between the fixation point and the center of the target was classified as undershoot (coded as -1 in the variable under/ overshoot) while all other saccades were classified as overshoots (coded as 1 in the variable under/ overshoot). In 44% of trials, the saccade undershot the target (with 59% off target and 41% on target); and correspondingly the target was overshot in 56% of the trials (with 61% off target and 39% on target). The final variable is target eccentricity (coded close target as -1 and distant targets as 1 in the variable eccentricity) which denotes whether the target was presented at a distance of 6 or 14°. We visualized results with a smoothed version of the first derivative for all resulting cumulative coefficients (smoothing spline with df = 12).

Results

In this study we determined the influence of absolute saccadic error, under- vs. overshoot, target eccentricity and the interaction of under/overshoot x eccentricity on the risk to generate a secondary saccade. All three main effects and the interaction significantly influenced the rate of secondary saccades (see Table 1; test for non-significant effects). Most importantly, all of the effects were time-dependent, meaning that their influence was significantly different at different times during postsaccadic fixation (see Table 1, test for time-invariant effects).

The time-varying effects need to be interpreted with respect to the baseline rate–which reflects secondary saccade rate independent of primary saccade error (magnitude of error, under/overshooting) and target eccentricity–for which we observed a steep increase until 174 ms followed by a flat decrease until the end of the observed time interval at 1100 ms (see Figure 3; the rates are displayed as a) the cumulative coefficients and b) the first derivative of the resulting cumulative coefficients over time). The additional predictors now tell us whether a covariate increases or decreases the baseline rate of secondary saccades at a given point in time.

A classic finding relates the occurrence of secondary saccades to increasing saccadic error. In our analysis this result translates into a significant effect of absolute saccadic error on the generation of secondary saccades ($p < 0.001$). In addition, the analysis reveals the time course of this effect which peaked at 148 ms following the onset of postsaccadic fixation (the rate evolvement is shown for an absolute error of one degree of visual angle). Thus, the higher the absolute primary saccade error, the more is the overall risk increased at an earlier interval as compared to the baseline rate which peaked at 174 ms. This finding replicates the reliable observation that secondary saccade latencies are much shorter than the average latency of primary saccades which has often been put forward to argue for an extra-retinal influence on the programming of secondary saccades (Becker & Fuchs, 1969; Weber & Daroff, 1972). However, a peak influence after 148 ms is also in accordance with visual feedback being the driving corrective signal on the programming of secondary saccades in our study. Follow-up analysis of the residuals for this continuous covariate confirmed the additivity assumption of the additive hazards model ($p = 0.276$).

The influence of primary saccade landing position on secondary saccades may not only be expressed in terms of absolute saccadic error but also as a difference between under- and overshooting. Indeed, undershooting may be advantageous in terms of visual processing time, as the postsaccadic visual target will be processed in the same hemisphere as the presaccadic target (Robinson, 1973). Increasing secondary saccade latency following primary saccade overshoot as compared to undershoot supports this claim (Deubel, Wolf, & Hauske, 1982; Henson, 1978; Ohl et al., 2011). On the other hand, latency differences following under- and overshoots have been argued to result from the overall smaller amplitude of secondary saccades following overshoots (Kapoula & Robinson, 1986) that are known to have longer latencies (Kalesnykas & Hallett, 1994). However, recent evidence suggests that the latency benefit after undershoots persisted even when controlling statistically for secondary saccade amplitude (Ohl et al., 2011).

In our model we suggested an increased activation in the hemisphere of a saccadic motor map that also programmed the primary saccade. We reasoned that the incoming visually evoked activation during postsaccadic fixation can add to the already increased level of activation in the one hemisphere of the saccadic motor map and is therefore more likely to cross the threshold for saccade execution. Consequently, we hypothesized an increased rate of secondary saccades following primary saccade undershoot as compared to saccadic overshoot. Indeed the rate analysis revealed a very strong effect of the covariate under/ overshoot on the generation of secondary saccades ($p < 0.001$). As predicted, overshooting the saccade target resulted in fewer secondary saccades than a corresponding undershoot. The time course shows a peak at 158 ms after beginning of postsaccadic fixation and declines slower than other rate effects in Figure 3. Again, this effect is time-varying, showing the necessity to study the dynamics during postsaccadic fixation in such a motor map.

A possible effect of target eccentricity on secondary saccades is of theoretical importance as it constitutes an error-unrelated influence on the programming of secondary saccades. Based on the model assumption that a hemispheric bias increases for more eccentric targets, we hypothesized a higher rate of secondary saccades with increasing target eccentricity. Again, the rate analysis confirmed our model prediction. Target eccentricity significantly influenced secondary saccade rate with more secondary saccades following primary saccades to distant targets ($p < 0.001$), peaking at 148 ms. This finding adds to previous studies that report a significant influence of target eccentricity on secondary saccades (Lemij & Collewijn, 1989; Ohl et al., 2011; 2013) and is compatible with the original report for these data (Ohl et al., 2011).

There was also a significant interaction between target eccentricity and under/ overshoot (p < 0.001). Undershooting a distant target (as opposed to a close target) further increased secondary saccade rate. The interaction reached its maximum influence after 142 ms. This finding is in line with our model prediction of an increased hemispheric bias (i.e. increased activation in the hemisphere of the motor map that programmed the primary saccade) with increasing target eccentricity.

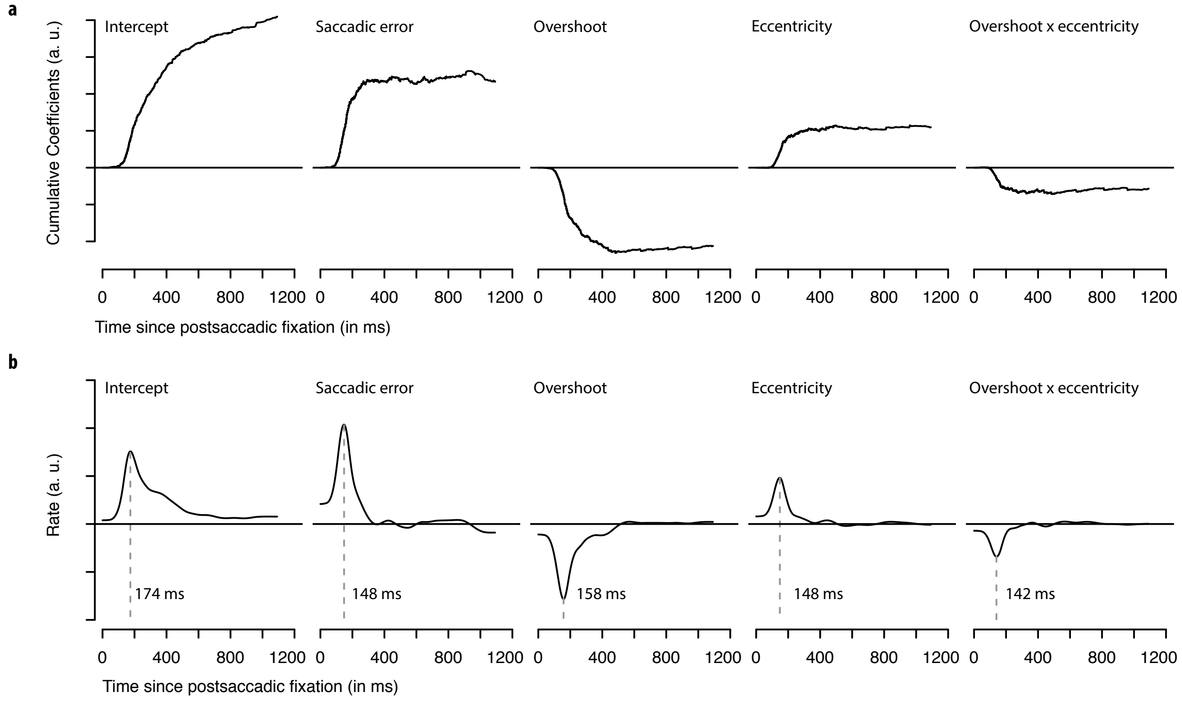

Figure 3. Displayed rates represent the **a)** cumulative coefficients and **b)** estimated first derivative of the obtained cumulative coefficients for each term in the Aalen's additive hazards model; that is the instantaneous risk to generate a secondary saccade.

	Test for non-significance		Test for time-invariance	
	Test-statistic	*p*-value	Test-statistic	*p*-value
Baseline	12.70	<0.001	0.66	<0.001
Saccadic error	6.73	<0.001	0.89	<0.001
Under/ overshoot	20.70	<0.001	0.70	<0.001
Eccentricity (ecc)	10.70	<0.001	0.37	<0.001
Ecc x Under/Overshoot	11.20	<0.001	0.27	<0.001

Table 1. Parameter estimates in Aalen's additive hazards model.

Secondary saccades and rate analysis

Finally, we computed predicted survival curves based on the outcome of the additive hazards model. Here, survival curves $S(t) = P(T > t)$ denote the probability P that a trial at time t will be without secondary saccade, where T is a random variable denoting the time of the event (i.e., secondary saccade onset). We derived predictions for different sizes of absolute primary saccade error for four different landing scenarios (undershot vs. overshoot of close vs. distant targets). Undershooting a distant target shows a quickly decaying survival curve irrespective of absolute primary saccade error (see second panel in Figure 4a)– meaning that secondary saccades are generated quickly when undershooting a distant target. A similar, but weaker, pattern is observed for undershooting a close target. This is in stark contrast to overshooting a target. There, we observe a strong variability of survival curves depending on absolute error. Following small overshoots, the curves are still far from converging at zero even after 1100 ms of postsaccadic fixation. This means that a large proportion of trials is without secondary saccades in the examined time window after a small overshoot of the distant target.

In Figure 4b, we also show empirical densities and median latencies to facilitate a comparison of the different analysis techniques. Comparing medians with densities clearly reveals that a single descriptive value is too simple. Although densities provide much clearer evidence at what time an effect takes place as compared to reports of medians, they both fall short of showing an error-related influence on secondary saccade generation in a subsample of the population. As an example we show the influence of absolute primary saccade error on secondary saccade latency (when splitting the data in large vs. small error) in Figure 4b. In the distant target condition, densities and medians are largely identical which would be interpreted as absence of an error-related influence on the generation of secondary saccades for distant targets. However, using rate analysis (Figure 4a) we observed a strong effect of primary saccade error on secondary saccade rate after overshooting a distant target–an effect that is concealed when reporting densities and median values.

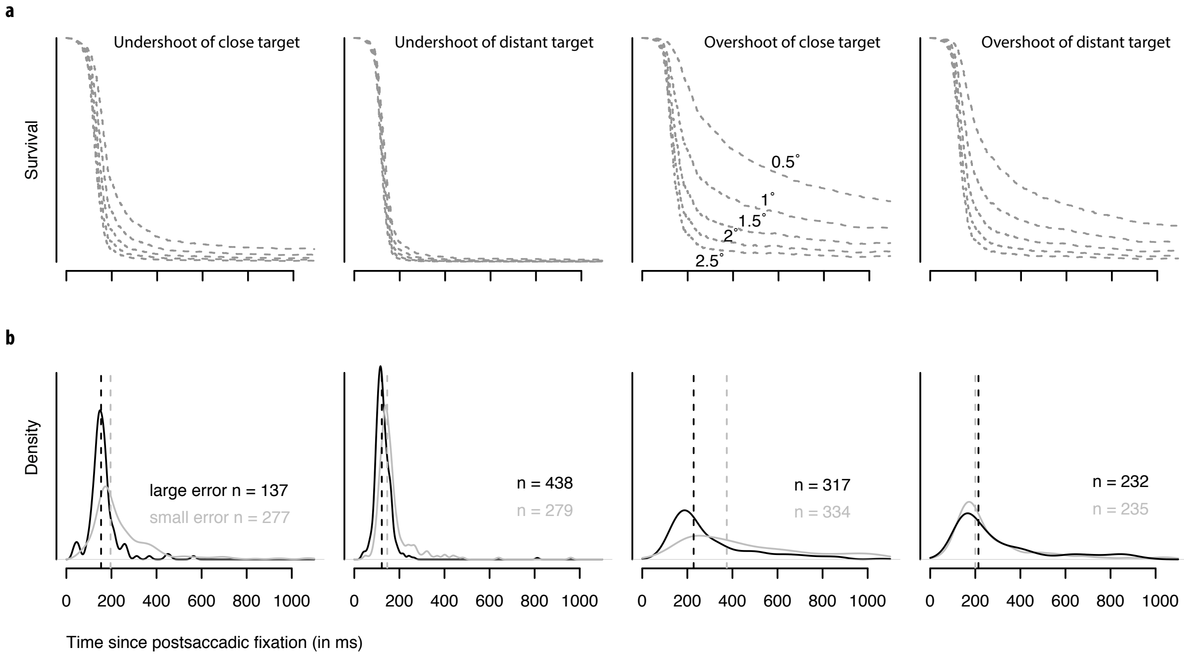

Figure 4. **A),** predicted survival curves as a function of absolute saccadic error (0.5, 1, 1.5, 2, and 2.5°; depicted as dashed lines in each panel). **B),** densities (solid lines) and medians (dashed lines) shown for secondary saccades following primary saccades with a small (in grey) or large primary saccade error (in black). We computed median split (at 0.45°) of absolute primary saccade error to construct the groups for small and large error.

Discussion

In the present study we applied Aalen's additive hazards model in order to examine the time-dependent influences of primary saccade landing error and target eccentricity on the generation of secondary saccades. In addition to the absolute magnitude of the saccadic error, we observed significant and time-dependent influences of under- vs. overshooting, target eccentricity and their interaction on the risk to generate a secondary saccade. These results were predicted from our qualitative model of (micro-)saccade generation during postsaccadic fixation.

We replicate the well-established effect that primary saccade error largely shapes the occurrence of secondary saccades (Becker & Fuchs, 1969) which has recently been extended for eye movements in 3-D (Pérez Zapata, Aznar-Casanova, & Supèr, 2013; Pérez Zapata, Solé Puig, Aznar-Casanova, & Super, 2014). Our analysis yielded estimates of the time course underlying the error-related influence, showing a peak influence 148 ms after fixation onset which is in line with visual feedback as a driving influence on secondary saccades. A recent study investigated in detail the role of visual feedback on secondary saccade programming and suggested a conceptual model for corrective saccades in which forward motor control allows prediction of the saccadic error (Tian, Ying, & Zee, 2013). This approach could also account for the existence of fast corrective saccades in our study.

Under vs. overshooting further influenced programming of secondary saccades with a higher rate to generate a secondary saccade following primary saccade undershoot. Robinson (1973) already suggested an advantage in programming secondary saccades following saccadic undershoot. This explanation is based on the reasoning that the undershot target can be kept in the same hemisphere; thus avoiding the extra-cost of interhemispheric transfer. Alternatively, a bias for saccades to undershoot a target has been shown to be in line with a model that minimizes saccadic flight time as opposed to minimization of retinal error (Harris, 1995). In contrast, our model predicted an effect of under- vs. overshooting based on the dynamics in a saccade motor map around saccade execution. So far, a benefit in programming of secondary saccades following saccadic undershoot has been observed in terms of shorter secondary saccade latencies (Deubel et al., 1982; Henson, 1978; Ohl et al., 2011). The result of an increased secondary saccade rate following saccadic undershoot lends further support to the differences between primary saccade undershoot and overshoot.

Importantly, we observed additional support for an independent influence of target eccentricity on the generation of secondary saccades. Secondary saccade rate was higher for distant than close targets, therefore replicating results from previous studies (Frost & Pöppel, 1976; Lemij & Collewijn, 1989; Ohl et al., 2011). Target eccentricity is unrelated to saccadic error and consequently demonstrates the need to develop models of secondary saccade generation that go beyond a simple error-correction mechanism. In the present model, we hypothesized an increasing hemispheric bias with increasing eccentricity. This assumption might be an oversimplification as we tested only two eccentricities. A future study needs to map visual space in a continuous metric in order to unveil the possibly nonlinear influence of eccentricity on the generation of secondary saccades.

The present findings are based on a well-controlled prolonged postsaccadic fixation paradigm. This allowed us to identify the full time course of hypothesized variables that influence secondary saccade programming, with influences being present up to ~300 ms after postsaccadic fixation onset and peaking in a range of 140 ms to 175 ms after saccade offset. Regarding the model of secondary saccade generation presented here, one could ask about the duration of the hemispheric bias in a dynamic saccadic motor map. Although, in the present framework we did not assume a time-dependent decay of the increased baseline activation it would make sense to include such a time-dependent decay–in particular in a computational model. Similar concepts of a hemispheric bias were formulated in a dynamic neural field model of the superior colliculus, exploring the aftereffects of saccades on the programming of forward vs. return saccades (Wang, Satel, Trappenberg, & Klein, 2011; for challenges of a neural field account see Casteau & Vitu, 2012). A critical difference to that study is our aim to model secondary saccades as small as microsaccades which was not simulated in this model.

Our model assumption of a hemispheric bias that increases with primary saccade amplitude should be regarded as a general term that encompasses mechanisms that favor the generation of forward over return saccades. One such mechanism is *inhibition of return* which underlies the reduced probability of re-visiting an inspected site during visual search (Klein & MacInnes, 1999). A second mechanism is the retinotopic attentional trace which refers to the finding that the initial pre-saccadic distribution of attention is still lingering in retinotopic coordinates after saccade execution (Golomb, Chun, & Mazer, 2008). Thus, the distance of this lingering attentional trace from the center of current fixation depends on primary saccade amplitude. Attention-related shifts in the activity distribution of a push-pull network as the superior colliculus (Munoz & Wurtz, 1995; Munoz & Fecteau, 2002) will also affect the generation of microsaccades (Engbert & Kliegl, 2003; Hafed & Clark, 2002) by favoring a small eye movement in the same direction as the primary saccade.

A second important goal of our study was to introduce Aalen's additive hazards model as a promising tool for eye movement research. This statistical model allowed us to include the information from trials in which we did not observe any secondary saccade. Importantly, this analysis not only shows main effects and interactions of covariates on secondary saccade rate (i.e., the equivalent of the mean differences in ANOVA), but also the time-dependencies of these influences. Thus, the results from the present rate analysis go beyond our recent observation concerning secondary saccades in a paradigm with visual feedback (Ohl et al., 2011). The hypotheses for secondary saccade rates were based on a model introduced to account for the latency, amplitude and orientation of secondary saccades. The additional analysis of secondary saccade rates is useful in order to falsify models of secondary saccade generation; here, however, the model predictions were in line with the results from the rate analysis.

It is noteworthy that the present study is not the first time rate analysis has been used for the analysis of eye movements. In particular, rate analyses have been used in reading to determine influences on fixation duration (Reingold, Reichle, Glaholt, & Sheridan, 2012; Risse & Kliegl, 2014; Schad, Risse, Slattery, & Rayner, 2014; Sheridan, Rayner, & Reingold, 2013). In our study, applying Aalen's additive hazards model was fruitful because all variables exerted a time-varying influence and Aalen's additive hazards model does not depend on a constant influence of the terms in the statistical model (as opposed to the Cox proportional hazards model). Our analysis also explicitly checked assumptions that must be met for valid inference. Such time-dependent effects provide important tests for falsification of models of eye movement control that aim to account for the generation of large and small saccades.

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