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The generation of secondary saccades without postsaccadic visual feedback

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Primary saccades are often followed by small secondary saccades, which are generally thought to reduce the distance between the saccade endpoint and target location. Accumulated evidence demonstrates that secondary saccades are subject to various influences, among which retinal feedback during postsaccadic fixation constitutes only one important signal. Recently, we reported that target eccentricity and an orientation bias influence the generation of secondary saccades. In the present study, we examine secondary saccades in the absence of postsaccadic visual feedback. Although extraretinal signals (e.g., efference copy) have received widespread attention in eye-movement studies, it is still unclear whether an extraretinal error signal contributes to the programming of secondary saccades. We have observed that secondary saccade latency and amplitude depend on primary saccade error despite the absence of postsaccadic visual feedback. Strong evidence for an extraretinal error signal influencing secondary saccade programming is given by the observation that secondary saccades are more likely to be oriented in a direction opposite to the primary saccade as primary saccade error shifts from target undershoot to overshoot. We further show how the functional relationship between primary saccade landing position and secondary saccade characteristics varies as a function of target eccentricity. We propose that initial target eccentricity and an extraretinal error signal codetermine the postsaccadic activity distribution in the saccadic motor map when no visual feedback is available.

Introduction

Humans move their eyes two to four times per second in order to bring visual areas of interest onto the fovea and allow visual processing with the highest resolution. Saccades are frequently followed by secondary saccades whose exact triggering mechanisms are not fully understood. In general, secondary saccades are thought to reduce the distance between the saccade landing site and target location (Becker & Fuchs, 1969). Consequently, secondary saccades are often referred to as corrective saccades. Despite the seemingly obvious corrective function of secondary saccades, several lines of evidence suggest that an error-correcting signal constitutes only one source of activation that influences the programming of secondary saccades.

First, even very precise primary saccades can be followed by secondary saccades, which might then increase the distance between the eye and target positions (Lemij & Collewijn, 1989). Second, there is a bias of secondary saccades to follow the direction of the primary saccade (Ohl, Brandt, & Kliegl, 2011). Third, models have been proposed, assuming that target eccentricity significantly modulates the postsaccadic activity distribution in a saccadic motor map and, accordingly, the characteristics (e.g., latency, amplitude, and orientation) of subsequent eye movements (Ohl, Brandt, & Kliegl, 2011; Wang, Satel, Trappenberg, & Klein, 2011). Thus, multiple factors contribute to the programing of secondary saccades, a fact that requires further elaboration of the exact mechanisms producing secondary saccades. Focusing only on the

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process of error correction (e.g., minimizing the distance between the eye and target positions) falls short of providing a comprehensive view on secondary saccades.

In the present study, our aim was to explore the factors that influence secondary saccade programs in the absence of postsaccadic visual feedback. Participants were asked to move their eyes to an upcoming target. During saccade flight, the target was removed, therefore preventing postsaccadic visual feedback. In such a situation, it is typically observed that the number of secondary saccades is strongly reduced as compared to a situation with available postsaccadic visual information (Becker & Fuchs, 1969; Bonnetblanc & Baraduc, 2007; Deubel, Wolf, & Hauske, 1982; Prablanc & Jeannerod, 1975; Shebilske, 1976). This is, of course, strong evidence emphasizing the importance of postsaccadic visual information for the programming of secondary saccades.

The examination of secondary saccade orientation in a paradigm that omits postsaccadic visual information allows us to determine whether an extraretinal error signal influences programming of secondary saccades. The idea that a copy of the saccade motor command, the efference copy, is used as source of information for various brain processes is old (Sperry, 1950; von Helmholtz, 1925; von Holst & Mittelstaedt, 1950) and also very successful, both on a conceptual (Wurtz, 2008) and a neurophysiological level (Sommer & Wurtz, 2008). Nevertheless, whether the copy of the primary saccade motor command also influences the generation of secondary saccades is strongly disputed.

A recent study suggested that the oculomotor error of the primary saccade (e.g., the distance between the saccade landing position and target) might already be included in the efference copy of the saccade (Collins, Rolfs, Deubel, & Cavanagh, 2009). Thus, subtraction of the vector of the efference copy from the target vector could easily determine the postsaccadic target position and, consequently, influence the programming of secondary saccades. It is uncertain whether such a type of extraretinal error signal directly influences the programming of secondary saccades. Interestingly, early studies that prevented postsaccadic visual processing by removing the target during the saccade resulted in opposing conclusions concerning the role of an extraretinal error signal for secondary saccade programs (Becker & Fuchs, 1969; Morel, Deneve, & Baraduc, 2011; Prablanc & Jeannerod, 1975; Shebilske, 1976; Weber & Daroff, 1972). A study by Deubel et al. (1982) demonstrated convincingly that visual feedback is necessary to generate secondary saccades. It should be noted, however, that in their study, the role of visual feedback for the generation of secondary saccades was examined by blanking the target for some time during postsaccadic fixation. The target was lit again subsequently, thus providing visual feedback at a later point in the trial. Given a situation without visual feedback or very large saccadic error, Deubel et al. did not want to rule out that an extraretinal error signal might come into play. Therefore, whether or not an extraretinal error signal directly influences secondary saccades is not clear and needs further elaboration.

Studies supporting the notion that an extraretinal error signal contributes to corrective secondary saccades mainly examined secondary saccades following primary saccades to very distant targets (e.g., larger than 20°; Becker & Fuchs, 1969; Shebilske, 1976). Because saccades to very distant targets are typically undershot, this is a necessary but nevertheless insufficient condition for demonstrating the direct influence of an extraretinal error signal on secondary saccade programs. The subsequent secondary saccade then follows the same direction as the undershooting primary saccade and, consequently, reduces the target undershoot. This reaction can also be explained by usage of a simple strategy in such a way that secondary saccades follow the direction of the primary saccade. Indeed, we recently demonstrated that secondary (micro-) saccades are biased to follow the direction of the primary saccade (Ohl et al., 2011); therefore, secondary saccades that follow the direction of the primary saccade to a very distant target (which is typically undershot by about 10 percent) are not necessarily triggered by an extraretinal error signal but could simply be due to this bias. Strong support for the influence of an extraretinal error signal requires a condition in which the probability of secondary saccades in a direction opposite to the primary saccade increases with increasing overshoot in the absence of postsaccadic visual information.

In the present study, subjects were asked to move their eyes from a central fixation point to a peripheral target (located at 6° or 14° of visual angle on the horizontal meridian) and hold fixation at the new target location despite the target being removed immediately after saccade onset. Our experimental paradigm allows us to determine the functional relationship between the primary saccade landing site and the characteristics of secondary saccades (e.g., latency, amplitude, and orientation) for two different target eccentricities. Assuming that the latency, amplitude, or orientation of secondary saccades depends on the saccade landing site would strongly support the notion that an extraretinal error signal can indeed influence secondary saccade programming. We also explore whether the bias of secondary saccades to follow the direction of the primary saccade might also be observed in a condition without postsaccadic visual information. Moreover, we test whether these relationships between primary saccade error and secondary saccade latency, between primary saccade error and secondary saccade amplitude, and between primary saccade error and secondary saccade orientation vary as a function of target eccentricity.

In summary, we examine the influence of saccadic error on subsequent secondary saccade latency, amplitude, and orientation. This should add valuable information for the solution of the debate on whether an extraretinal error signal influences secondary saccade programs. Furthermore, we test whether an orientation bias and modulation by target eccentricity are also observed when no postsaccadic visual information is available.

Method

Participants

Twenty-four subjects, 19–44 years old ($M = 24.4$), participated in the study. The experimental session involved eight practice trials and 300 test trials. Participants were paid seven euros or received study credit. The experiment was conducted in accordance with the declaration of Helsinki (1964), and written informed consent was obtained from all participants prior to the experiment.

Materials and procedure

Participants sat in a dark, silent room with their head positioned on a chin rest. Stimuli were presented at a viewing distance of 50 cm on a 19-inch EYE-Q 650 CRT monitor at a spatial resolution of 1024 × 768 pixels and a refresh rate of 100 Hz. Stimulus presentation was controlled by an Apple Power Macintosh G4 computer. Eye movements were recorded with the EyeLink-II system (SR Research, Osgoode, Ontario, Canada) with a sampling rate of 500 Hz. The experiment was implemented in MATLAB (MathWorks, Natick, MA) using the EyeLink (Cornelissen, Peters, & Palmer, 2002) and Psychophysics (Brainard, 1997; Pelli, 1997) toolboxes.

Each trial started with the subject fixating a white point (0.67° diameter) presented on a gray background in the center of the monitor. After a uniformly distributed random interval (1–1.5 s), the fixation point was removed, and a white circle target (0.67° diameter) was presented at a distance of 6° or 14° to the left or right of the fixation point. The order of target locations was randomly chosen, and each target had the same probability of being presented. The subject's task was to move the eyes immediately to the target. After the subject's eyes crossed an invisible boundary located at a distance of 2° from the initial fixation point, the target was removed, resulting in a completely gray background. Subjects were instructed to hold fixation after the end of the goal-directed saccade (for at least 1100 ms). The next trial started after an interval of 500 ms, given that the eyes were within a defined area around the fixation point. When fixation failed, a drift correction was carried out (e.g., presentation of a fixation symbol and correction of small drifts in the computation of eye position). At the beginning of the experiment and after blocks of 30 trials, eye-tracker calibration and validation procedures were run. Blinks occurring during a trial were detected online and led to trial abortion. These trials were presented again before the end of the experiment in randomized order.

Data preparation and analysis

For detection of microsaccades, we used an improved version (Engbert & Mergenthaler, 2006) of the original algorithm developed by Engbert and Kliegl (2003). For microsaccade detection, eye positions were transformed in two-dimensional velocity space, and thresholds for peak velocity (6 *SD*) and minimum duration (8 ms) were applied. Primary saccades were defined as the first saccadic eye movement landing within a distance of 2.5° around the target location. Primary saccadic reaction times faster than 80 ms or slower than 500 ms and trials with eye movements larger than 1.5° prior to target onset were discarded from further analysis. We analyzed the first secondary (micro-) saccade occurring within an interval of 600 ms after the end of the primary saccade. Secondary saccade latency was defined as the interval between the end of the primary saccade and the beginning of the secondary saccade. Trials including a secondary saccade with an amplitude larger than 3.5° were also removed in order to exclude trials in which subjects wrongly directed their gaze back to the center of the screen in anticipation of the next trial. Overall, 2,880 secondary (micro-) saccades were detected ($M = 120$ events per subject). In a second step, based on the angular orientation, we determined whether secondary (micro-) saccades (a) followed the direction of the primary saccade, (b) followed the opposite direction of the primary saccade, or (c) were vertically oriented. For analysis of secondary saccade orientation, we excluded vertically oriented secondary (micro-) saccades. This resulted in 2,619 events (of the original 2,880 events; 90.9%).

For data analysis, we used the R Environment (R Development Core Team, 2010) and, more specifically, the *lme4* package (Bates & Maechler, 2010). The *lme4* package allows specification of a linear mixed model (LMM) and also generalized LMMs (GLMMs) for binary responses. The statistical advantages of LMMs over the classical ANOVA have been repeatedly addressed. They include the specification of random effects, tests of covariates, and the robustness of LMMs in not fully balanced designs as a result of missing data (Kliegl, Wei, Dambacher, Yan, & Zhou, 2010). Typically, t values are reported when using LMMs. We considered absolute t values larger than 2 as significant. Note, negative t values indicate a coefficient of a model predictor with a negative sign. Graphics were created using the *ggplot2* package (Wickham, 2009).

Results

General characteristics

The characteristics of primary saccades are displayed in Table 1. Primary saccades to close targets were very precise on average (Kowler & Blaser, 1995) while there was a tendency to undershoot distant targets (Becker & Fuchs, 1969; Henson, 1978; Kapoula, 1985). Within a time interval of 600 ms, secondary saccades occurred slightly more often in the distant target condition in comparison to those in the close target condition. In Figure 1, distributions of saccadic error, secondary saccade latency, and amplitude are shown separately for the close and distant target conditions. Importantly, undershoots and overshoots were observed for both target eccentricities. Moreover, many of the observed secondary saccades were smaller than 1° of visual angle and thus met the criterion for microsaccades.

Secondary saccade latency

For tasks with postsaccadic visual information available, it is typically reported that larger primary saccade errors are associated with larger secondary saccade amplitudes and shorter secondary saccade latencies (Kapoula & Robinson, 1986). This result can be explained by different mechanisms. First, an error signal (either retinal, extraretinal, or both) is computed and is present as additional activity in a saccadic motor map. This additional activation increases with an increasing magnitude of primary saccade error and, consequently, speeds up the generation of a secondary saccade. Second, the latency of saccadic eye movements is known to be influenced by target eccentricity (Kalesnykas & Hallett, 1994); increasing eccentricity is associated with increasing latency while for very small eccentricities the latency is increased, too. Thus, decreasing secondary saccade latency with increasing error could simply reflect the general eccentricity-dependent modulation of saccade latency.

	Close target	Distant target
SRT in ms	167.3 (25.6)	183.5 (31.1)
Accuracy in degrees	0.057 (0.374)	−0.419 (0.406)
% secondary saccades	42 (25.2)	50 (26.8)

Table 1. Characteristics of primary saccades. Mean (*SD*) is displayed for primary saccadic reaction times (SRT), saccadic error (accuracy), and the percentage of secondary saccades. A negative (positive) value for accuracy indicates undershooting (overshooting).

In the present study, postsaccadic visual feedback was not available. In this situation, secondary saccade latency can only vary with primary saccade error when the oculomotor system is informed about primary saccade error by an extraretinal signal. Consequently, a significant modulation of secondary saccade latency by primary saccade error is a first hint of extraretinal influence on the generation of secondary saccades.

In Figure 2, secondary saccade latency is shown as a function of saccadic error and target eccentricity. Overall, secondary saccade latency is not strongly modulated by the primary saccade landing site. Nevertheless, increasing undershoot as well as increasing overshoot (even if only slightly) appear to result in shorter secondary saccade latency while target eccentricity does not affect the functional relationship between saccadic error and latency.

We tested the influence of linear and square saccadic error and target eccentricity as well as interactions between saccadic error and target eccentricity on the latency of secondary saccades with a LMM. In addition to these fixed effects, we included the intercept, saccadic error (linear and square), and target eccentricity as random effects in the LMM (see Table 2). Thus, besides the analysis of fixed effects, we estimate variance components associated with the fixed effects as well as correlation parameters between them (Kliegl et al., 2010).

Indeed, in agreement with Figure 2, square saccadic error was the only fixed effect that significantly influenced secondary saccade latency ($t = -3.72$). The modulation of secondary saccade latency by primary saccade error supports the notion of an extraretinal error signal influencing secondary saccade programming. The observed influence was in the expected direction with increasing error being associated with shorter secondary saccade latency. Target eccentricity had no significant influence on the latency of secondary saccades ($t = -1.34$).

Secondary saccade orientation

The main goal of our present study was to determine the functional relationship between the primary saccade landing position and the orientation of secondary

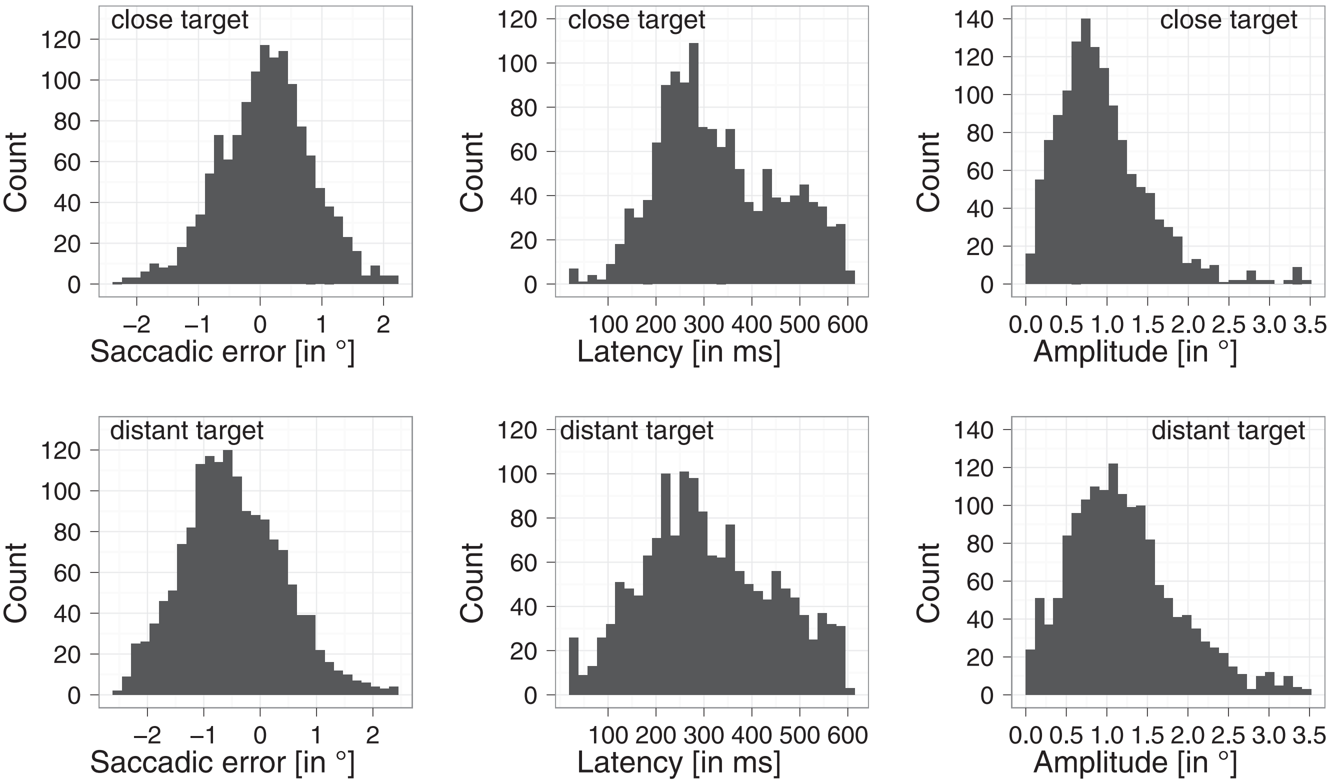

Figure 1. Distribution of primary saccade error, secondary saccade latency, and secondary saccade amplitude for close and distant target conditions.

saccades. In the absence of any information about primary saccade error for programs of secondary saccades, the orientation of secondary saccades should be independent of primary saccade error. In contrast, a significant influence of primary saccade error on secondary saccade orientation in the absence of post-saccadic visual feedback (i.e., secondary saccades in the direction of an undershooting primary saccade and opposite to the direction of an overshooting primary saccade) strongly supports the hypothesis that an extraretinal error signal influences the generation of secondary saccades.

In Figure 3, secondary saccade orientation is shown as a function of primary saccade error and target eccentricity. Saccadic undershoot was associated with secondary saccades in the same direction as the primary saccade. Moving from undershoot to overshoot resulted in an increasing probability of observing secondary saccades in a direction opposite to the primary saccade. Furthermore, secondary saccade orientation was influenced by target eccentricity.

Secondary saccade orientation was modeled with a GLMM for binomial data. The following covariates were included in the model: (a) magnitude of saccadic error, (b) target eccentricity, and (c) the interaction between saccadic error and target eccentricity (see Table 3).

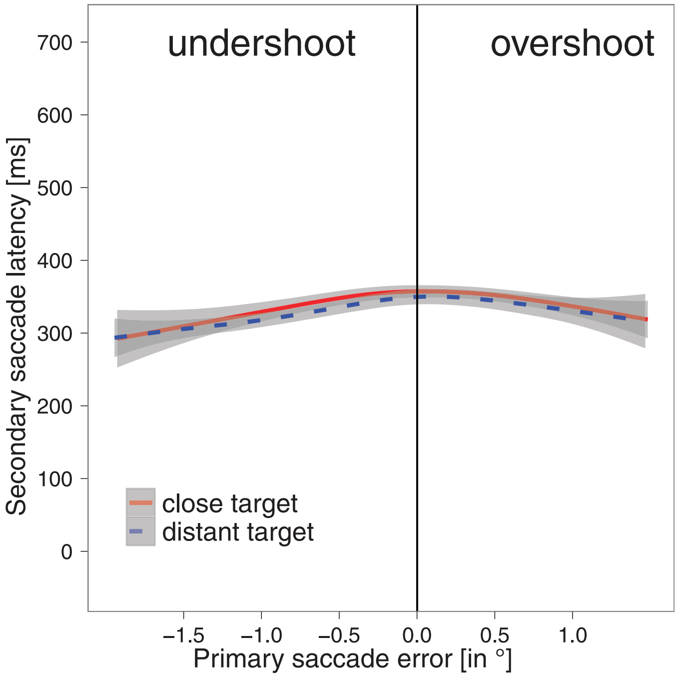

Figure 2. Secondary saccade latency as a function of primary saccade error and target eccentricity (red solid = close target; blue dashed = distant target) after removing between-subject variance. Gray bands show 95% confidence intervals.

				Random effects			
	Estimate	SD	*t* value	SD	Correlation parameters		
Intercept	356	12.3	28.89	56.3			
Eccentricity (ecc)	−11.8	8.8	−1.34	30.9	0.54		
Error	6	6.3	0.96	14.4	0.34	0.51	
Square error	−21	5.6	−3.72	13.4	−0.32	−0.16	0.54
Error x ecc	−7.7	7.1	−1.08				
Square error x ecc	1.4	5.8	0.24				

Table 2. LMM statistics for secondary saccade latency.

Again, we also estimated variance components and correlation parameters for intercept, saccadic error, and eccentricity with this model.

The GLMM confirms our inspection of Figure 3, showing a significant effect of saccadic error ($p < 0.001$) on secondary saccade orientation. The more the primary saccade landing site shifted from undershoot to overshoot, the higher was the probability of secondary saccades to be oriented in a direction opposite to the primary saccade. This result strongly supports the hypothesis that secondary saccades are directly influenced by an extraretinal error signal. The strength of this effect was significantly smaller in the distant target condition ($p < 0.001$). Also, we observed a significant orientation bias after primary saccades to distant targets ($p < 0.001$). Secondary saccades in the distant target condition mainly followed the direction of the primary saccade for precise saccades, therefore providing additional support for the hypothesis that both an extraretinal error signal and target eccentricity contribute to the programming of secondary saccades.

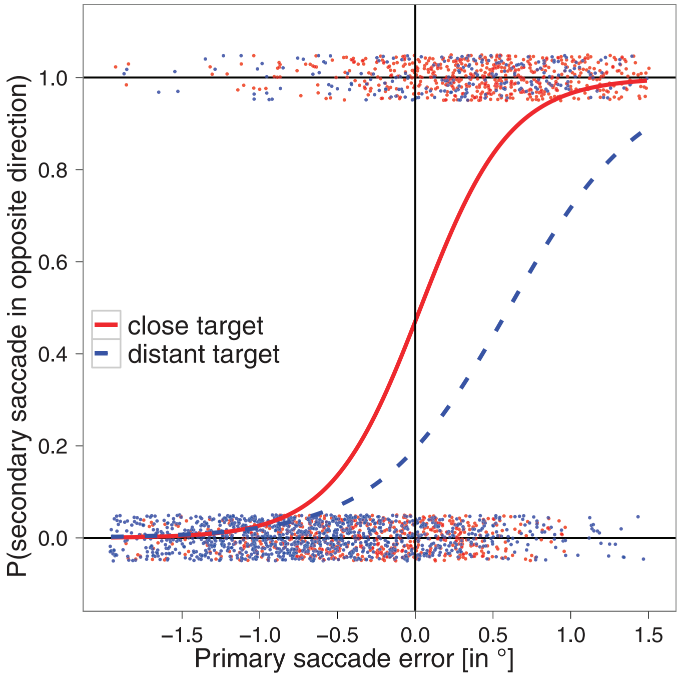

Figure 3. Probability of secondary saccades in the direction opposite to primary saccade direction as a function of saccadic error and target eccentricity. Data points are jittered (vertical jitter = 0.05) around $p = 1$ for secondary saccades in a direction opposite to the primary saccade. When secondary saccades follow the direction of the primary saccade, they are jittered around $p = 0$. Data points are colored in red (close target) or blue (distant target). Predictions derived from the GLMM are shown for the close (red, solid) and distant (blue, dashed) target condition.

Secondary saccade amplitude

In the previous section, we demonstrated that the direction of secondary saccades depends on primary saccade error even in the absence of postsaccadic visual feedback. Most notably, increasing the magnitude of primary saccade overshoot increased the probability that secondary saccades were in a direction opposite to the primary saccade. In the next step, we were interested in examining secondary saccade amplitude as a function of primary saccade landing position and target eccentricity. We hypothesized that increasing primary saccade error should elicit secondary saccades with increasing absolute amplitude.

In Figure 4, secondary saccade amplitude is displayed as a function of primary saccade error and target eccentricity. Again, saccadic error appears to influence the amplitude of secondary saccades. This time, we also observed a large difference between close and distant targets. In the LMM for modeling secondary saccade amplitude (see Table 4), we used primary saccade error and target eccentricity as predictors to account for signed secondary saccade amplitude (Collins, 2010; Joiner, Fitzgibbon, & Wurtz, 2010). Primary saccade error in the close target condition significantly influenced secondary saccade amplitude ($t = -14.42$), thus providing additional support for the idea that an extraretinal error signal contributes to secondary saccade motor programs. As expected from such a perspective, increasing undershoot was associated with an increase in amplitude of the secondary saccades that followed the primary

				Random effects		
	Estimate	SD	*p* value	SD	Correlation parameters	
Intercept	−0.118	0.403	0.77	1.83		
Eccentricity (ecc)	−1.305	0.331	<0.001	1.33	−0.72	
Error	3.463	0.342	<0.001	1.11	−0.21	−0.31
Error x ecc	−1.109	0.275	<0.001			

Table 3. GLMM statistics for secondary saccade direction.

saccade direction. Also, increasing overshoot resulted in an increase of absolute amplitude of the secondary saccades in a direction opposite to the primary saccade. The relationship between primary saccade error and secondary saccade amplitude was significantly weaker in the distant as compared to the close target condition ($t = 2.14$). In addition, we observed a significant effect of target eccentricity ($t = 4.12$) with a shift away from optimal corrective behavior in the distant target condition. Following precise primary saccades, secondary saccade amplitude was significantly increased in the distant as compared to the close target condition. This result implies that, in addition to an extraretinal error signal, there is also an effect of target eccentricity. Obviously, more than one factor influences the programming of secondary saccades.

In additional analyses, we determined the correlation between our dependent variables in order to examine the degree of overlap in information represented in our analyses of secondary saccade latency, amplitude, and orientation. It is noteworthy that the correlation between secondary saccade amplitude and latency was not significantly different from zero ($r = -0.01$, $p = 0.61$). This holds for both secondary saccades in the same direction as the primary saccade ($r = -0.02$, $p = 0.47$) and for secondary saccades in a direction opposite to the primary saccade ($r = 0.04$, $p = 0.27$). Thus, the reported results represent complementary rather than redundant information on secondary saccade programming.

Secondary saccade error

In the previous sections, we found support for the hypothesis that an extraretinal error signal and target eccentricity significantly influence the generation of secondary saccades. Next, we examined whether secondary saccades decrease primary saccade error. Two important aspects need to be kept in mind about secondary saccade error.

First, the observation of secondary saccades that do not decrease primary saccade error is not an argument against the existence of the usage of an extraretinal error signal. Indeed, a secondary saccade in a direction opposite to an overshooting primary saccade is evidence for an extraretinal signal, but an undershooting secondary saccade may have a larger absolute error than the initial primary saccade overshoot. Second, a large proportion of primary saccades landed precisely on the target. Obviously, secondary saccades following precise primary saccades are likely to increase the distance between the eye and target positions.

Figure 5 displays secondary saccade error as a function of primary saccade error. Obviously, large distances between the eye and target locations persist even after secondary saccades. This result can also be

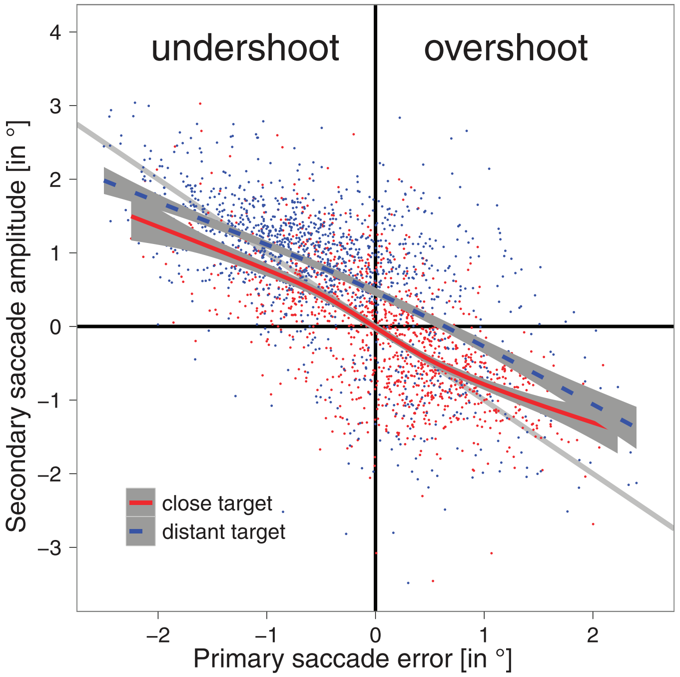

Figure 4. Secondary saccade amplitude as a function of primary saccade error and target eccentricity (red solid = close target; blue dashed = distant target) after removing between-subject variance. Negative values of primary saccade error indicate an undershooting primary saccade; positive values are overshoots. Negative values of secondary saccade amplitude indicate secondary saccades in the direction opposite to the primary saccade. Data points include data within a 95% interval of primary saccade error after removing between-subject variance. Gray bands show 95% confidence intervals. The light gray diagonal indicates saccade amplitude that corrects perfectly for primary saccade error.

				Random effects		
	Estimate	SD	*t* value	SD	Correlation parameters	
Intercept	−0.009	0.165	−0.06	0.793		
Eccentricity (ecc)	0.442	0.107	4.12	0.482	−0.14	
Error	−0.765	0.053	−14.42	0.178	0.23	−0.44
Error x ecc	0.094	0.044	2.137			

Table 4. LMM statistics for secondary saccade amplitude.

visualized by distributions of primary and secondary saccade error next to each other (see Figure 6). In the close target condition, primary and secondary saccade errors have similar distributions. In the distant target condition, the peaks differ for the two distributions: the peak of the primary saccade error distribution indicates many undershooting primary saccades; the distribution of secondary saccade error peaks around zero.

As mentioned above, we did not expect to observe a decreasing error after each secondary saccade simply because many primary saccades were already quite precise. In Figure 7, we plot distributions of primary and secondary saccade error after removal of precise primary saccades; only primary saccades were included with an absolute error larger than 1°. Evidently, secondary saccades strongly reduced the error resulting from an imprecise primary saccade.

As a statistical test of this result, we specified an LMM for the effect of primary versus secondary saccades and close versus distant target conditions on the absolute error, including only trials with imprecise primary saccades with an absolute error larger than 1° (see Table 5). As expected, absolute secondary saccade error was significantly smaller than absolute primary saccade error ($t = -23.68$). Initial absolute primary saccade error was larger in the distant as compared to the close target condition ($t = 2.69$). The interaction was not significant ($t = 1.45$).

Discussion

In the present study, we demonstrated two important influences on the generation of secondary saccades when postsaccadic visual feedback is not available: (a) an extraretinal error signal and (b) target eccentricity.

Our analyses show that the latency, amplitude, and orientation of secondary saccades vary with the primary saccade landing position. Increasing error results in faster and larger secondary saccades. The strongest evidence for an extraretinal influence is found for secondary saccade orientation. A shift in the primary saccade landing site from undershoot to

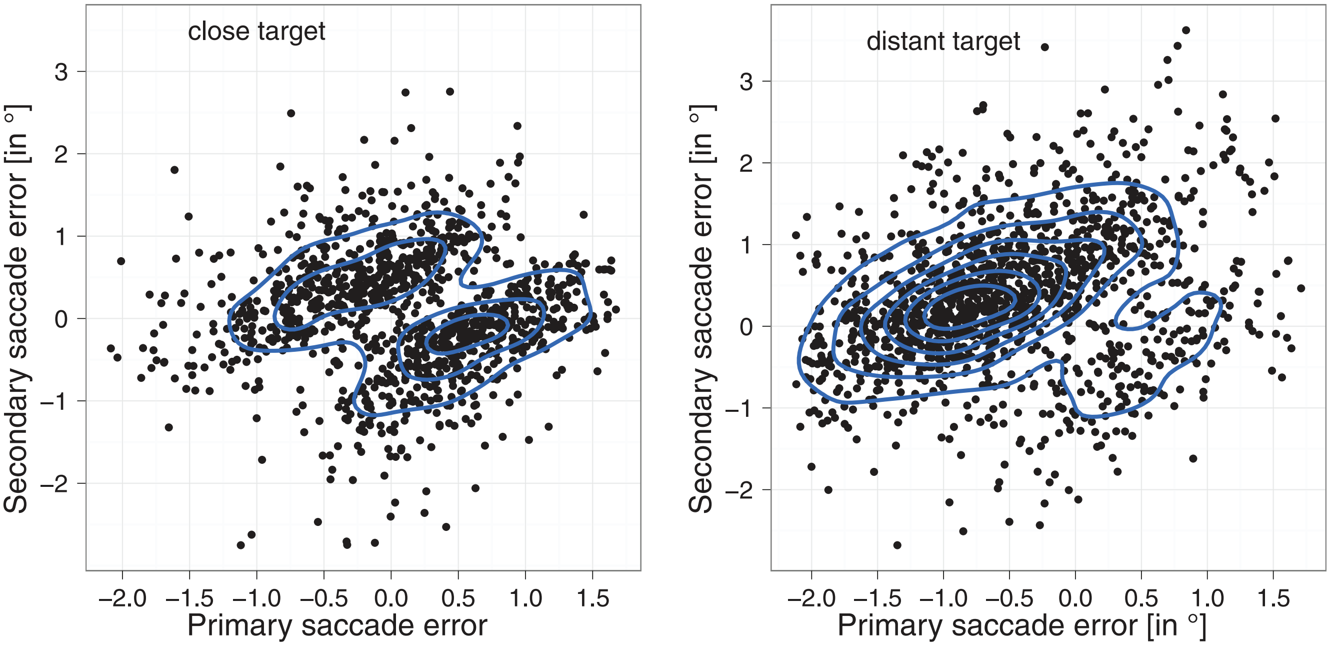

Figure 5. Secondary saccade error as a function of primary saccade error and target eccentricity. Individual data points are from within a 99% interval of primary and secondary saccade error. Contour lines (blue, solid) reflect increments of 10%.

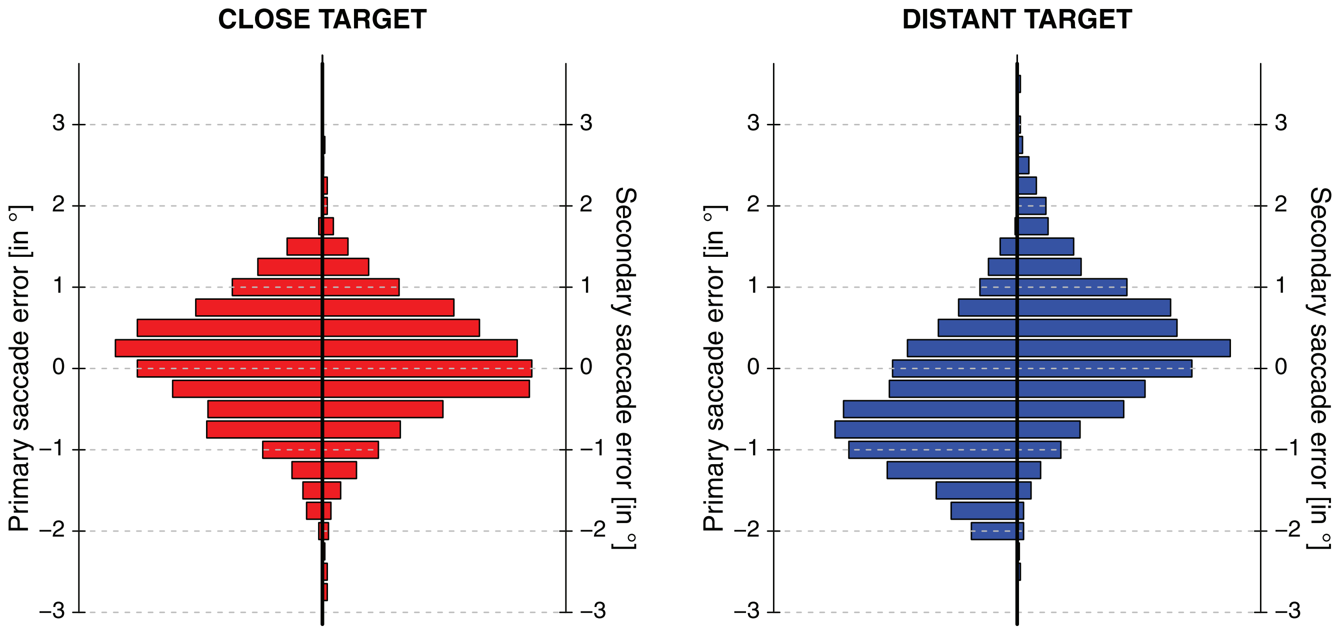

Figure 6. Distributions of primary and secondary saccade error for close (red) and distant target (blue) conditions.

overshoot increases the probability that a secondary saccade is generated in a direction opposite to the primary saccade. Previous studies that argued for an extraretinal influence on secondary saccade programming mainly studied very large eccentricities that were accompanied by a large undershoot. Thus, it was not possible to exclude the possibility that a secondary saccade in the same direction as the primary saccade was only due to a bias in such a way that secondary saccades always follow the primary saccade direction. We can now show that increasing overshoot results in secondary saccades of the opposite direction.

Although we demonstrated that an extraretinal signal influences the orientation of secondary saccades, this does not necessarily imply that secondary saccades always reduce absolute primary saccade error. Indeed, we show that secondary saccades mainly correct for large primary saccade error. This also means that secondary saccades following rather precise primary saccades can also increase the distance between the eye

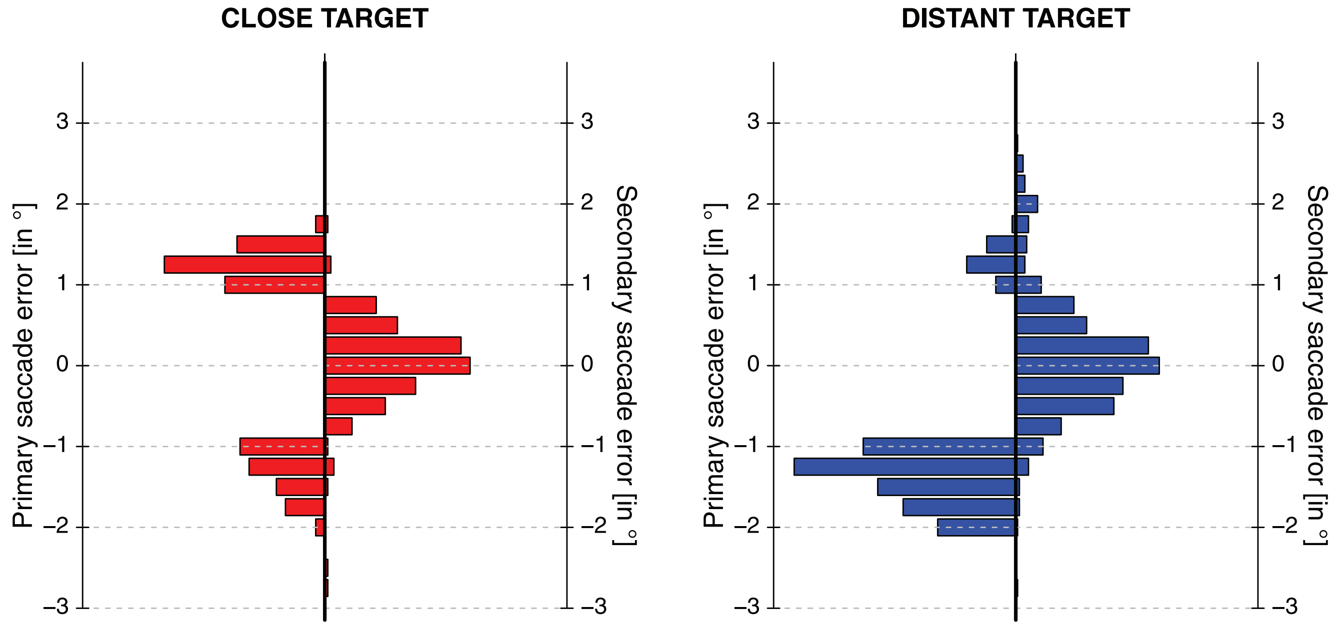

Figure 7. Distributions of primary and secondary saccade error after removal of precise primary saccades are shown for close (red) and distant target (blue) conditions.

	Estimate	SD	*t* value
Intercept	1.34	0.044	30.6
Eccentricity (ecc)	0.09	0.034	2.69
Secondary saccade	−0.91	0.038	−23.68
Ecc x secondary saccade	0.07	0.046	1.45
Variance components			
Intercept		0.156	
Residual		0.387	

Table 5. LMM statistics for error after primary versus secondary saccades and close versus distant targets.

and target positions. Nevertheless, the orientation of these eye movements is still influenced by an extraretinal signal. These results further support the idea that secondary saccades are the result of an activity distribution in a saccadic motor map that can be influenced by multiple factors (e.g., extraretinal signal, target eccentricity, noise, attention).

So far, we strongly argued for an extraretinal influence on the generation of secondary saccades. Nevertheless, it could also be argued that secondary saccades are preprogrammed along with the primary saccade. Thus, an extraretinal error signal would not be necessary in order to explain the results in our experiment. But, there exist several findings in the literature that are difficult to reconcile with a preprogramming account. Importantly, fewer secondary saccades are observed when postsaccadic visual feedback is not available (Bonnetblanc & Baraduc, 2007; Prablanc & Jeannerod, 1975), highlighting the importance of a visual signal for secondary saccade programming. A strong preprogramming account would predict that the generation of secondary saccades should be independent of postsaccadic visual feedback. Also, a brief presentation of a postsaccadic visual stimulus can easily elicit secondary saccades (Deubel et al., 1982), which again demonstrates the importance of the postsaccadic visual stimulus. In addition, a strong preprogramming account would predict that secondary saccade latency should exhibit small variability. In the present experiment, we observed a broad distribution of secondary saccade latency, which provides further support against a strong preprogramming account. Nevertheless, we cannot completely rule out the possibility that a subset of secondary saccades in our experiment was preprogrammed, but, in general, we think preprogramming of secondary saccades in a single target step experiment is unlikely.

Apart from the extraretinal signal, we found evidence for an additional influence on the programming of secondary saccades, namely target eccentricity. Secondary saccade amplitude and orientation were significantly different in the close and distant target conditions. Secondary saccades to distant targets were more likely to follow the direction of the primary saccade than secondary saccades in the close target condition. This finding was also present in our earlier study with postsaccadic visual feedback (Ohl et al., 2011). In contrast to our previous study, target eccentricity did not influence secondary saccade latency.

We recently introduced a modified version of the model by Rolfs, Kliegl, and Engbert (2008) to account for the generation of secondary (micro-) saccades. This model represents a one-dimensional, topographically organized motor map. Very small saccades are generated when activation crosses a certain threshold in the center of the motor map. Increasingly distant locations from the center code for increasingly large saccade amplitude. The left hemisphere programs saccades to the right while the right hemisphere codes for saccades to the left. We proposed that activation in the hemisphere programing the primary saccade is enhanced compared to the opposite hemisphere. Moreover, this hemispheric bias in activation increases with increasing target eccentricity. This model was able to account for our findings that secondary saccades to distant targets were faster, larger, and more likely to follow primary saccade direction. With this mechanism, we provided an explanation for eccentricity-specific modulations of the latency, amplitude, and orientation of secondary saccades.

In the present study, we observed a less coherent picture concerning the results on latency, amplitude, and orientation. Still, the eccentricity-dependent hemispheric bias in activation after primary saccade execution can account for larger secondary saccade amplitude and the bias in secondary saccade orientation with increasing target eccentricity. We proposed that the hemispheric bias could be the consequence of the retinotopic attentional trace (Golomb, Chun, & Mazer, 2008). The retinotopic attentional trace refers to the phenomenon that immediately after a saccade attention persists at retinotopic coordinates. Attentional facilitation at the retinotopic location might pull secondary saccades in the direction of the primary saccade, resulting in a bias of secondary saccades to follow the primary saccade direction.

So far, we discussed that both an extraretinal error signal and target eccentricity have a direct influence on the generation of secondary saccades. Nevertheless, the influence of target eccentricity may still be rather indirect, and the accuracy of the extraretinal signal may decrease with increasing target eccentricity (e.g., a systematic underestimation of the extraretinal signal). Consequently, after a precise primary saccade to a distant target, the underestimated extraretinal signal would inform the system about a saccadic undershoot and favor secondary saccades in the same direction as the primary saccade. Such a mechanism is in line with our results concerning secondary saccade amplitude and orientation. Secondary saccades in the same direction as the undershooting primary saccade had larger amplitudes in the distant as compared to the close target condition. In addition, we observed an orientation bias for secondary saccades following precise primary saccades to distant targets. Finally, another possible indirect influence of target eccentricity concerns the usage of an extraretinal signal. Increasing eccentricity could result in decreasing influence of the extraretinal signal. Consequently, a general tendency of secondary saccades to follow the primary saccade direction would become increasingly dominant with increasing eccentricity.

Obviously, the relationship between the saccade landing position and characteristics of secondary saccades as a function of target eccentricity in the present experiment is weaker than previously reported in an experiment with visual feedback (Ohl et al., 2011). This can be explained by the missing postsaccadic visual stimulation. The lack of visual stimuli during postsaccadic fixation results in reduced activity in a saccadic motor map, and consequently, the activity often remained below the critical threshold for saccade triggering. With fewer observations of secondary saccades, it is, of course, more difficult to detect additional factors that contribute to secondary saccade motor programs.

Now, what might be the role of the extraretinal signal in our experiment? Generally, in response to target onset a saccade is launched. A copy of the saccade command (efference copy) is available in the oculomotor system (Wurtz, 2008) that includes information about the oculomotor error (Collins et al., 2009). This copy can now be used to predict the location where the target should be found during postsaccadic fixation. We propose that activation is increased at the predicted target location in a retinotopic motor map for saccades (e.g., superior colliculus). In a paradigm with postsaccadic visual feedback, the visually evoked response in this saccadic motor map can then add to this prebuilt activation, causing a rapid triggering of the secondary saccade. This could explain the existence of very short-latency secondary saccades as reported earlier (Bahill, Clark, & Stark, 1975; Becker & Fuchs, 1969). These authors already reasoned that the short-latency secondary saccades were too fast to be triggered by postsaccadic retinal feedback alone.

We want to highlight the potential use of our experimental paradigm for studying nonretinal signals around saccadic eye movements. Visual feedback is not available during postsaccadic fixation; therefore, systematic influences on the generation of secondary saccades cannot be traced back to postsaccadic visual processing. In future studies, secondary saccades may serve as dependent variables to study the influence of nonretinal signals on a postsaccadic motor map. Thus, studying secondary saccades can go beyond a pure interest in their underlying generating mechanisms.

A large proportion of secondary saccades in our study were smaller than 1° of visual angle, therefore meeting the criterion for microsaccades (for recent reviews on microsaccades, see Hafed, 2011; Martinez-Conde, Macknik, Troncoso, & Hubel, 2009; Rolfs, 2009). We recently argued that studying microsaccades requires also studying them in a more natural situation, that is, the fixation following a large saccade. We suggest that both microsaccades and the classical secondary saccades share a similar implementation in the oculomotor system, which produces small-scale saccades.

The study of microsaccades and secondary saccades has been tackled from very different perspectives. Microsaccades have been shown to counteract visual fading (Engbert & Kliegl, 2004; Martinez-Conde, Macknik, Troncoso, & Dyar, 2006); they are an index of covert attention shifts (Hafed & Clark, 2002; Hafed, Lovejoy, & Krauzlis, 2011; Engbert & Kliegl, 2003; Laubrock, Engbert, & Kliegl, 2005), and visual suppression occurs in the superior colliculus around the time of microsaccades (Hafed & Krauzlis, 2010; see also Rolfs & Ohl, 2011). In contrast, secondary saccades are classically thought to exclusively fulfill a corrective function. We have shown that referring to secondary saccades as corrective saccades is only one part of the story as these small postsaccadic eye movements are the result of error-correcting and non-error-correcting factors (e.g., target eccentricity) that influence their generation. It is critical to identify the factors (e.g., saccadic error, target eccentricity) that contribute to the overall activity distribution in a motor map in which saccadic eye movements are generated. Studying both microsaccades (during prolonged fixation) and secondary saccades (during postsaccadic fixation) can help to understand how small-amplitude eye movements are implemented in the oculomotor system.

Conclusion

We provide strong support for the idea that an extraretinal signal influences motor programs of secondary saccades. Moreover, we demonstrate that target eccentricity can significantly influence the generation of secondary saccades. For future research, it will be important to address whether and how these systematic influences in the oculomotor system affect postsaccadic visual perception.

Keywords: saccades, eye movements, efference copy, postsaccadic feedback, secondary saccades, microsaccades

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