Dynamic combination of position and motion information when tracking moving targets

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To accurately foveate a moving target, the oculomotor system needs to estimate the position of the target at the saccade end, based on information about its position and ongoing movement, while accounting for neuronal delays and execution time of the saccade. We investigated human interceptive saccades and pursuit responses to moving targets defined by high and low luminance contrast or by chromatic contrast only (isoluminance). We used step-ramps with perpendicular directions between vertical target steps of 10 deg/s and horizontal ramps of 2.5 to 20 deg/s to separate errors with respect to the position step of the target in the vertical dimension, and errors related to target motion in the horizontal dimension. Interceptive saccades to targets of high and low luminance contrast landed close to the actual target positions, suggesting relatively accurate estimates of the amount of target displacement. Interceptive saccades to isoluminant targets were less accurate. They landed at positions the target had on average 100 ms before saccade onset. One account of this finding is that the integration of target motion is compromised for isoluminant targets moving in the periphery. In this case, the oculomotor system can use an accurate, but delayed position component, but cannot account for target movement. This deficit was also present for the postsaccadic pursuit speed. For the two luminance conditions, pursuit direction and speed were adjusted depending on the saccadic landing position. The rapid postsaccadic pursuit adjustments suggest shared position- and motion-related signals of target and eye for saccade and pursuit control.

Introduction

Sudden movements in the periphery of our visual field often elicit immediate goal-directed eye movements (Gellman & Carl, 1991; Dorr, Martinetz, Gegenfurtner, & Barth, 2010). Due to the specific organization of the primate visual system, it is necessary to align the visual axis of our eyes with the moving object to gain highest foveal acuity information (Kowler, 2011; Schütz, Braun, & Gegenfurtner, 2011; Kowler, Aitkin, Ross, Santos, & Zhao, 2014; Gegenfurtner, 2016). Typically, rapid saccadic eye movements with peak velocities up to 500–700 deg/s are first initiated to direct the eyes toward the moving object, so that its retinal projection lands close to the foveal region. Visual tracking responses are then continued with slow eye rotations, called smooth pursuit eye movements. Under optimal conditions pursuit eye movements stabilize the image of a predictably moving target on the fovea after about 200–300 ms. Pursuit minimizes the residual image movement on the retina, the retinal slip and benefits the perception of moving targets (Ludvigh & Miller, 1958; Methling & Wernicke, 1968; Brown, 1972a, 1972b, 1972c; Schütz, Braun, & Gegenfurtner, 2009; Lisberger, 2015). The precision and accuracy of visual tracking responses depends on many factors such as the predictability of the target movement (Barnes & Asselman, 1991; Orban de Xivry & Lefèvre, 2007; Kowler et al., 2014), target contrast (Doma & Hallett, 1988; Ludwig, Gilchrist, & McSorley, 2004; Spering, Kerzel, Braun, Hawken, & Gegenfurtner, 2005; Braun et al., 2008), speed (Carl & Gellman, 1987; Kowler & McKee, 1987; Osborne, Lisberger, & Bialek, 2005; Rasche & Gegenfurtner, 2009), starting position with respect to the fovea (Lisberger & Westbrook, 1985), and its defining motion properties (Hawken & Gegenfurtner, 2001; Lisi & Cavanagh, 2015).

In general, foveating a moving object is not a trivial task for the oculomotor system. Due to inherent delays for processing in the visual and oculomotor systems, some time elapses between the motion of an object in the world and the contractions of the six extra-ocular muscles for the eye movements (Nowak & Bullier,

1997; Schlag & Schlag-Rey, 2002; Van Beers, 2008; Goffart, Bourelly, & Quinet, 2017). Because of this delay, the moving target will be already at another location when either a saccade is initiated, typically after about 200 ms (Guan, Eggert, Bayer, & Büttner, 2005), or smooth pursuit is started after about 100–180 ms (Rashbass, 1961; Gellman & Carl, 1991; Braun et al., 2008; Liston & Stone, 2014). Therefore, a saccade would not land at the actual position of the target at the saccade end, if the time period for signal processing, target movement properties, and durations of the eye movement responses are not taken into account for movement planning (Quinet & Goffart, 2015). Potential errors can be reduced when valid predictions about the target trajectory are available and used for appropriate adjustments of the oculomotor behavior and coordination of intermixed saccadic and pursuit eye movements (Bahill & McDonald, 1983; Orban de Xivry, Bennet, Lefèvre, & Barnes, 2006).

Monkeys and humans are able to make accurate saccades to linearly moving targets (Ron, Vieville, & Droulez, 1989; Keller & Johnsen, 1990; Gellman & Carl, 1991; Guan et al., 2005; Fleuriet, Hugues, Perrinet, & Goffart, 2011; but see Heywood & Churcher, 1981). These interceptive saccades do land close to the actual target position. This indicates that the oculomotor system is capable of generating some representation of the correct target location at saccade end, despite the neuronal delays associated with sensory and motor processing (Robinson, 1973; Engel, Anderson, & Soechting, 1999; Guan et al., 2005; Etchells, Benton, Ludwig, & Gilchrist, 2010; Fleuriet et al., 2011; Daye, Blohm, & Lefèvre, 2014; Braun & Gegenfurtner, 2016). There are two main theories that try to explain how successful saccades to moving targets are achieved.

The "dual drive" theory (Optican, 2009; Optican & Pretegiani, 2017) postulates two independent signals, a representation of the position at the beginning of saccade planning, to which an estimate of target velocity is added to predict the position of the target. Several studies found that it was possible to predict endpoints of interceptive saccades when the position error and the retinal slip measured roughly 100 ms before saccade initiation was combined (Keller & Johnsen, 1990; Gellman & Carl, 1991). This also allowed prediction of endpoints of catch-up saccades correcting for direction and speed changes of the moving target during pursuit (Engel et al., 1999; de Brouwer, Missal, Barnes, & Lefèvre, 2002; Schreiber, Missal, & Lefèvre, 2006). The discrete sampling of position before saccade onset is based on the finding of a saccadic dead-time (Findlay & Harris, 1984). Findlay and Harris reported that only information arriving up to 80 ms before saccade onset affected the saccade

parameters, while information arriving later had no effect on the execution of the saccade.

An alternative explanation is provided by the "continuous drive" theory (Goffart et al., 2017; Goffart, Bourrelly, & Quinton, 2018). Goffart and colleagues argue that due to the structure of the brain, there is no neurophysiological basis for a static snapshot of the position and a mathematical integration of the velocity of the target. They postulate that the oculomotor behavior is driven by a dynamic and continuous visual drive based on a retinal streak caused by the moving the target. Target foveation with saccadic and pursuit eye movements is then achieved by balancing opposing tendencies in the left and the right part of the brain caused by the stimulation. The eyes are then moved to restore the equilibrium.

Here we investigated whether oculomotor behavior to moving targets is affected by target contrast manipulations. These would produce comparable retinal streaks, but have been shown to differentially affect the processing of target position or motion (Thompson, 1982; Anstis & Cavanagh, 1983; Stone & Thompson, 1992; Spering et al., 2005; Braun et al., 2008). We used a two-dimensional (2-D) step-ramp paradigm with orthogonal target directions (see Fleuriet et al., 2011) to separate the errors of the saccade depending on the signals related to the position step or to the target motion. Our main research interest was twofold. First, we wanted to know how interceptive saccades are affected by targets defined either by luminance or chromatic contrast. We used three different contrast manipulations to selectively attenuate processing mechanisms for position and velocity. It is well established that under some conditions color isoluminance attenuates motion and speed perception (Cavanagh, Tyler, & Favreau, 1984; Lu, Lesmes, & Sperling, 1999; for reviews, see Gegenfurtner & Hawken, 1996; Cropper & Wuerger, 2005) and smooth pursuit eye movements (Braun et al., 2008; Spering, Montagnini, & Gegenfurtner, 2008). However, it does not affect positional accuracy (Krauskopf & Farell, 1991), or the accuracy of saccades to static chromatic targets (White, Kerzel, & Gegenfurtner, 2006). A reduction of luminance contrast affects visual processing more generally; the reliability of visual signals is reduced and at slow speeds a wide range of stimuli appear to move slower when presented at low contrast compared to high contrast (Thompson, 1982; Stone & Thompson, 1992; Snowden, Stimpson, & Ruddle, 1998). However, the luminance contrast effects are much smaller compared to isoluminance (Hawken, Gegenfurtner, & Tang, 1994). In agreement with the perceptual findings, contrast reduction of luminance targets also results in longer saccadic latencies (Doma & Hallett, 1988; Ludwig et al., 2004), longer pursuit

onset latencies and reduced pursuit gain (Hawken & Gegenfurtner, 2001; Spering et al., 2005).

We also investigated the postsaccadic oculomotor behavior when the oculomotor system switches from interceptive saccades to smooth pursuit eye movements. Recently, we found that pursuit velocity is modified based on the direction of corrective saccades (Goettker, Braun, Schütz & Gegenfurtner, 2018). Hainque, Apartis, and Daye (2016) demonstrated that saccades and pursuit changed their behavior in a roughly similar time course when the velocity profile of the moving target changed. These results suggest that the pursuit and saccadic system share a common internal representation of the target movement (but see Bourrelly, Quinet, & Goffart 2018b) and interact closely to improve tracking responses rapidly. By analyzing the initial pursuit responses during the first 120-ms time period directly after the end of the initial interceptive saccades, we wanted to gain further insight into the relevant information available for both eye movements before additional visual target or feedback information was available after the saccade to modify the pursuit responses.

As expected, we found that target contrast had strong effects on the oblique interceptive saccades to 2D step-ramps for the three target conditions (high luminance contrast, low luminance contrast, isoluminant color stimuli). Interceptive saccades to low luminance contrast targets had longer latencies compared with saccades to high contrast targets but a comparable accuracy. Interceptive saccades to isoluminant chromatic targets had the longest latencies and lower accuracy. They landed close to positions the targets had on average 100 ms before saccade initiation. The results are in line with an intact but delayed representation of the target position, while the target motion was not considered for saccade programming under isoluminance. This impairment was also visible in a reduced pursuit velocity for the isoluminant targets. The investigation of interactions between saccadic landing position, pursuit direction, and pursuit speed provided further evidence for shared representations of target and eye positions, which are important for the coordination of saccades and pursuit eye movements.

Methods

Participants

Eleven volunteers ($M = 24.7$ years old, $SD = 3.2$; eight females) participated in the main and first control experiment. Six volunteers (one of them author AG) participated in the second control experiment. All participants, except the author, were naive to the purpose of the study and received money as compensation. They had normal or corrected-to-normal vision. Before the start of the experiments they gave informed consent (Declaration of Helsinki) and all experiments were approved by the local ethics committee (Giessen University LEK 2017-0029) and were conducted in accordance with those guidelines.

Experimental setup and condition

During experimental sessions participants sat at a table in a dark room facing a gray monitor screen (Display ++, LDC; Cambridge Research Systems, Ltd., Rochester, UK) with their head stabilized on a chin and forehead rest to minimize head movements. The body position was adjusted so that the participant's eyes were approximately at the height of the screen center at a distance of 90 cm. A desk mount video-based eye tracker (EyeLink 1000 Plus, SR Research Ltd., Mississauga, Canada) with a sampling frequency of 1000 Hz was used to record eye movements from the right eye. Before each experimental block a 9-point grid calibration was run until the average validation error of the measured versus the predicted eye position was below 0.35 deg. When the validation error was higher the camera images of the pupil area were closely inspected for all target positions, and corneal and pupil threshold levels and the height of the head position were fine-tuned. Then the calibration procedure was repeated. Each experimental block consisted of 120 single eye movement trials, which the participant initiated separately by pressing the space bar. The trial interval was thus determined by the participant's key pressing. In a single block the target contrast was kept constant while target ramp speeds were randomly selected from a set of three speeds. Two to three experimental blocks of 15–20 min were separated by breaks and were run on a single day for each participant.

In Experiment 1, the ramp speed was randomly selected to be either 10, 15, or 20 deg/s and in Experiment 2 to be either 2.5, 5, or 7.5 deg/s. Experiment 1 was always performed before Experiment 2. Overall each participant completed four blocks of the 2-D step-ramp experiments on different days for each of the three contrast conditions and the two target speed experiments, leading to a total of 2,880 trials (two sets of 3 Speeds × 3 Contrast Conditions × 4 Blocks × 120 Trials). Experiments were controlled by MATLAB using the Psychtoolbox (Kleiner et al., 2007).

Step-ramp experiments

We used an orthogonal step-ramp paradigm with a vertical target step followed by a ramp motion in one of
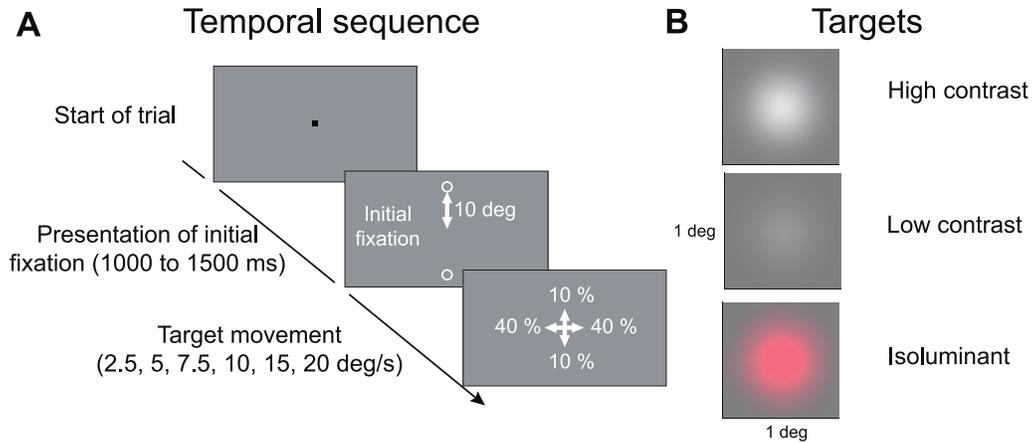
Figure 1. Illustration of the step-ramp paradigm and the three contrast conditions of the targets. (A) Temporal sequence. After offset of the central fixation spot, a Gaussian target appears for a random time either 10 deg above or below the screen center. It is displaced to the center and moves immediately with different probabilities into one of the four cardinal directions. The ramp speed is chosen randomly from a set of three speeds (10, 15, or 20 deg/s in Experiment 1, and 2.5, 5, or 7.5 deg/s in Experiment 2). (B) Illustration of the eye movement targets: Gaussian blobs of high or low luminance contrast or red chromatic contrast only.

the four cardinal directions (Figure 1). This allows us to separate the errors to the position step in the vertical dimension, from errors related to the motion of the stimulus in the horizontal dimension. Since we were interested in the orthogonal configuration only, targets moved horizontally with an 80% probability. In 40% of the cases it moved to the left and in 40% it moved to the right. In the remaining 20% of the trials, the target moved along the vertical axis (10% up; 10% down), to make the motion trajectory less predictable. This resulted in the absence of a presaccadic pursuit response. We did not analyze the 20% vertical trials. At the beginning of each trial, a small, black fixation cross appeared in the center of a gray monitor screen with a background luminance of 104 cd/m^2. When the participant had pressed the space bar, the initial target, a Gaussian blob with a standard deviation of 0.2 deg appeared on one half of the trials 10 deg above and in the other half of trials 10 deg below the center of the screen. After a random time between 1 and 1.5 s, the target was displaced to the screen center and immediately started to move into one of the four cardinal directions for 1,000 ms. The luminance contrast (high/low) or the color of the Gaussian target differed in the three contrast conditions as described below. Participants were instructed to keep their eyes on the Gaussian target blob or the fixation cross as accurately as possible. To make sure that participants kept fixating the eccentric target, we monitored the position of their right eyes online. When the gaze deviated more than 2° horizontally or vertically from the center of the initial fixation target, a red warning message appeared and the trial was restarted.

We used six ramp speeds in two separate experiments. In the first experiment (Experiment 1), the three

ramp speeds of 10, 15, and 20 deg/s were randomly intermixed with equal probability, and in the second (Experiment 2) the ramp speeds were 2.5, 5, and 7.5 deg/s. We tested eye movements at lower ramp speeds in the second experiment to cover tracking behavior over a larger range of speeds. Recently, Agtzidis, Startsev, and Dorr (2016) analyzed eye movement behavior of observers watching short video clips of dynamic natural outdoor scenes, e.g., moving pedestrians or animals in streets or parks or cars in traffic (see Dorr et al., 2010). The analysis of eye movement patterns of participants revealed that under free viewing conditions, 12% of the viewing time contained pure smooth pursuit episodes and that pursuit to track dynamic objects in natural videos occurred most frequently at lower speeds, with an median of around 5 deg/s.

Targets contrasts

Three target contrast conditions (Figure 1) were chosen to manipulate the processing of visual signals, as described in the Introduction (Thompson, 1982; Doma & Hallett, 1988; Stone & Thompson, 1992; Hawken & Gegenfurtner, 2001; Ludwig et al., 2004; Spering et al., 2005; Braun et al., 2008; Spering et al., 2008). For the high luminance contrast condition the peak luminance contrast of the white Gaussian target blob was set to 0.8. For the low luminance contrast condition peak luminance contrast was 0.1. In the isoluminant chromatic condition the Gaussian blob was reddish with a peak root-mean-squared cone contrast of 0.1 on the red-green axis in the color space proposed by Derrington, Krauskopf, & Lennie (1984).

Its luminance was identical to that of the gray background (Krauskopf, Williams, & Heeley, 1982; for calibration details, see Hansen & Gegenfurtner, 2017).

Control Experiment 1 to test position- and motion-related components separately

We conducted this experiment to separately measure saccades correcting for only the position error caused by the 10° vertical target step, or for the motion component caused by the ramp. The paradigm was similar to the orthogonal step-ramp experiments with the exception that a delay of 1 s was introduced after the eccentric target was displaced to the screen center and before the ramp movement started. Because of the delay, subjects made two separate saccades before pursuing the target. The first saccade was initiated in response to the vertical step and the second one in response to the horizontal ramp. We used the same variations in target contrasts and ramp speeds as described above; i.e., the target moved in one of the four cardinal directions with one of three ramp speeds; either 10, 15, or 20 deg/s as in Experiment 1 or 2.5, 5, or 7.5 deg/s as in Experiment 2. Overall each participant completed two blocks for each contrast conditions and the two sets of target speeds, leading to a total of 1,440 trials.

Control Experiment 2 to measure metrics of saccades to static targets

We conducted a second control experiment, using the same conditions as in the main experiments, but with static targets. The targets appeared at the physical locations that the 2-D step-ramp targets had when the interceptive saccade landed. We performed this experiment for the high luminance contrast and isoluminance condition to compare the saccade trajectories and measurements of curvature of saccades with moving and static targets. In the high contrast condition, we chose the average target position at saccade end for each of the six different velocities. Based on our results and to create saccades with comparable amplitudes as in the isoluminant condition, we chose the position of the target 100 ms before saccade onset for each of the six velocities. Participants completed three blocks in each condition, in which we randomized the initial starting direction (up, down), the side of the static target (left, right), and the horizontal eccentricity (based on the six different velocities). In each block, participants completed five repetitions of each combination, thus 120 trials per block and a total of 720 trials combined for both conditions per subject.

Data analysis

Eye movement data were digitized online and analyzed offline using our own software programmed in MATLAB. For each trial, we stored the horizontal and vertical eye position of the right eye measured during the whole trial. To combine the data for both vertical starting positions, we inverted the vertical positions of the eye movement traces starting from the top position. Then we filtered the eye positions using a second-order Butterworth filter with a cutoff frequency of 30 Hz and calculated the horizontal and vertical eye velocity by taking the difference between consecutive samples of the filtered position traces and multiplying it by the sampling frequency to represent it in degrees per second. Saccades were detected using a speed and acceleration threshold of 30 deg/s and 4,000 deg/s^2, respectively. In addition to the initial interceptive saccade, we analyzed the early phase of postsaccadic smooth pursuit during a time period of 120 ms after the estimated saccade offset. The upper boundary of our analysis window was chosen to investigate pursuit behavior with relatively limited influence of new incoming retinal information (but see Buonocore, Skinner, & Hafed, 2019).

Saccade analysis

We calculated saccadic latencies with respect to the onset of the ramp motion. Position errors were defined as Euclidean distance between saccade end position and the actual target position, as illustrated in Figure 2. Note that we calculated all errors with respect to the center of the Gaussian stimulus. We do not assume that only the center of the stimulus is the saccade goal, and it is possible that participants are not aiming directly at its center. However, such a bias would be visible in a constant offset of the saccade endpoints, which we did not observe. For each saccade to an orthogonal step-ramp we calculated the horizontal and vertical error. These two types of error are very informative in our paradigm, as the vertical error should be mainly related to the position step of the target, whereas the horizontal error should be mainly related to the target movement. For horizontal errors, negative values indicate a saccade landing position behind the moving target; for vertical errors, negative values indicate a saccade landing below the target. As we focused our analysis on the accuracy of saccadic interception, saccade performance was quantified based on the comparison of the horizontal endpoint of each saccade and the target position at different moments in time with respect to each saccade. For comparison we calculated the average target positions at three points in time: (a) 100 ms before saccade onset, (b) at saccade
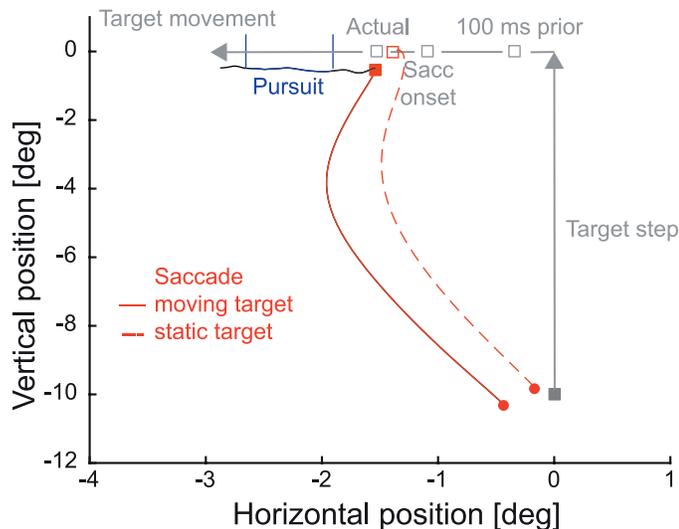
Figure 2. Eye position over a single trial and illustration of the analysis. This trial starts with a 10 deg upward target step (gray square) to the screen center, followed by a horizontal ramp movement of 7.5 deg/s to the left. The trajectory of the initial interceptive saccade is shown in the continuous red line; its landing position is indicated by the red square. The starting position of the saccade can differ from the target position because of unsystematic drift movements during the fixation period. Open squares mark target positions at different points in time: 100 ms before saccade onset, at saccade onset, and at saccade end. Note that inward saccade curvatures, such as in this illustrative trial, were found in about two-thirds of all trials. The same curvature pattern was present for saccades to static targets (red dashed line) presented at the average actual target position at saccade end. The postsaccadic pursuit analysis was done in the interval from 50 to 120 ms after saccade end as indicated by the blue lines.

onset, and (c) for the actual target position at saccade end. Saccade curvature was measured using the algorithm of Ludwig and Gilchrist (2002). In brief, the algorithm rotates the saccade principal axis to be horizontal and normalizes its length. Then a second-degree polynomial is fitted and the second-order term is used as the estimate of curvature. The sign is based on the direction of the target, so that a negative value indicates an inward saccade curvature.

Pursuit analysis

To investigate the transition from saccades to pursuit we analyzed the pursuit responses during a time window of 120 ms after the saccade end. This interval corresponds roughly to the open-loop phase of the pursuit during which pursuit responses are influenced relatively little by new incoming retinal information due to processing delays (e.g., Lisberger & Westbrook, 1985; Tychsen & Lisberger, 1986; Rasche & Gegen-

furtner, 2009; Tavassoli & Ringach, 2009). We omitted the pursuit response for the initial 50 ms after the saccade end from this analysis to reduce the influence of motor noise and high velocity residuals of interceptive saccades during landing on our direction measurements.

To analyze the postsaccadic pursuit direction, we aligned all trials in a way that the target movement direction was always to the right, by multiplying the horizontal component of targets moving to the left by −1. Additionally, we also made sure that the direction the eye had to move to reduce the vertical error was always upwards, by adjusting the vertical component of trials in which the saccade landed above the target. In this way we were able to plot the pursuit direction of all trials in a single plot. For comparison we additionally defined a hypothetical optimal pursuit direction as the direction that would immediately correct for the position error within the postsaccadic period of 120 ms. To investigate how the saccade landing position influenced the pursuit direction, we looked at the difference in the vertical velocity component depending on a median split of the vertical saccade landing position.

For pursuit speed, we also computed the average horizontal and vertical eye velocity in the interval between 50 and 120 ms after saccade offset. We also averaged the horizontal velocity during the first 50 ms after saccade offset over all trials for each target speed, condition, and subject. We took the minimum of the resulting velocity profiles as an estimate of the early pursuit response. To investigate whether pursuit velocity was affected by saccade landing position, we performed a median split based on the horizontal landing position of the saccade and compared the minimum velocity between these two groups of trials.

Statistical analysis

We collapsed the data across the two sets of target speeds and averaged the results for each target contrast condition and all six ramp speeds for each participant. We ran repeated measurement analyses of variance (ANOVAs) with the factors target contrast (high, low, isoluminant) and target speed (2.5, 5, 7.5, 10, 15, 20 deg/s) to test for differences between target contrast conditions and speeds effects. We used independent-sample t tests to compare the curvature of saccades to moving and static targets for each target speed. Due to the multiple tests we used the Bonferroni correction and set the p value to 0.008 (0.05/6 target speeds). For comparisons of the saccade landing position with the target position as well as the pursuit measurements, we always computed the 95% confidence interval (CI) for each data point ($M \pm 1.96 \times SEM$).
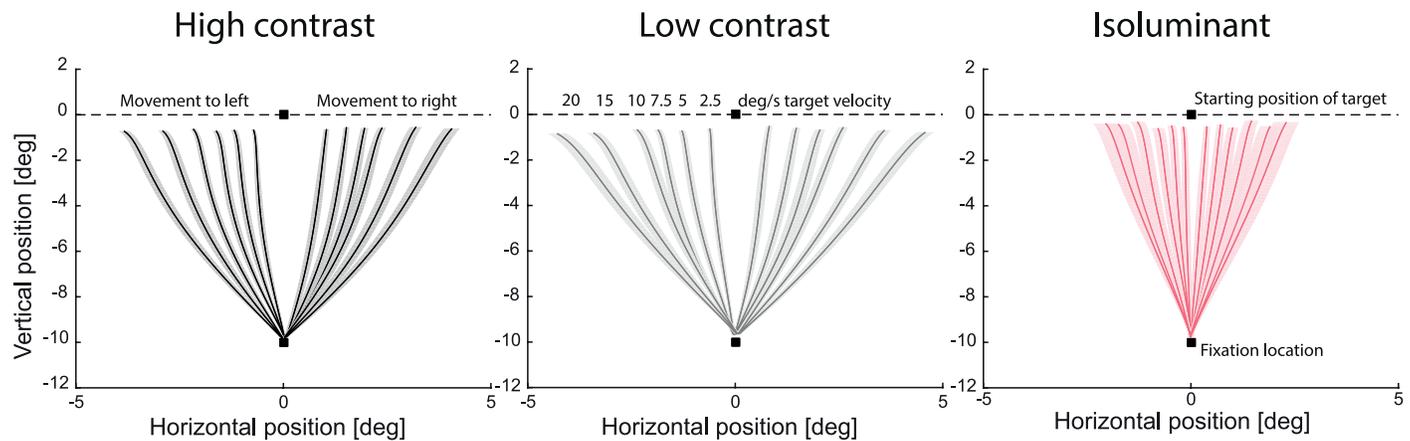
Figure 3. Average normalized saccade trajectories across all 11 subjects for the three target contrast conditions and the six target speeds. The black squares show the averaged eye positions before saccades at −10 deg along the y-axis and the starting positions of the ramp movements at 0 deg in the screen center. The black dotted line indicates the trajectories of the target ramp movements to the left or right. For all target contrasts, average saccade trajectories are clearly separated for the left- or rightward moving targets and all ramp speeds (2.5 to 20 deg/s). Shaded areas around the averaged saccade trajectories indicate ± 1 SEM.

Exclusion criteria

We excluded trials for several reasons. For the main experiments we excluded trials for five reasons from the saccade analysis: (a) if a blink was detected during the target movement, (b) if the first saccade had a latency smaller than 100 ms, (c) if the saccadic amplitude was smaller than 4 deg, (d) if the saccade duration was shorter than 20 ms or longer than 100 ms, and (e) if the initial saccade direction deviated more than 90° from the optimal direction. Based on our exclusion criteria we used 22,613 trials (or 89%) out of a total of 25,344 trials (2,731 trials excluded) in the 2-D step-ramp experiments. The additional 6,336 trials to vertically moving targets were not included in our analysis. The percentage of excluded trials was comparable across the different conditions and varied between 9% and 13%. For the both control experiments the same exclusion criteria for saccades were applied. For the first control experiment 14,144 (89%) were included out of 15,840 trials (1,705 excluded trials) and for the second control experiment 4,136 (96%) out of 4,320 trials (184 excluded trials). For the pursuit analysis in the main experiment we used only trials without corrective saccades in the relevant 120 ms after the saccade offset. For the pursuit analysis we found 19,494 trials, which fulfilled our criteria.

Results

We will first present the results for the latency and the landing positions of saccades to orthogonal 2-D step-ramps for varying target contrasts. Then we will

analyze the postsaccadic slow eye movement behavior and investigate the relationship between the saccade and postsaccadic eye movements.

Interceptive saccades
Moving targets of different contrasts and speeds

Figure 3 shows average saccade trajectories for all 2-D step-ramps in separate graphs for the three different target contrast conditions for visual comparison. The increase in target speed spreads saccade trajectories left- and rightward to different horizontal landing positions, whose range is determined by the target contrast. Compared with the high luminance condition, low luminance contrast leads to a slightly larger spread of saccade trajectories, while for the pure chromatic contrast condition without any luminance contrast, all saccade trajectories for the different target speeds are still separate but lie much closer together.

We tested target contrast effects on saccades by performing repeated measurement ANOVAs for saccadic latency and landing position error with the factors target contrast and speed. Saccadic latency differed significantly depending on the target contrast, $F(2, 20) = 101.03$, $p < 0.001$, but not with respect to target speed, $F(5, 50) = 1.3$, $p = 0.28$. As expected and shown before (Braun et al., 2008), saccades had the shortest latencies of 173 ms (grand mean value) in the high contrast luminance condition, significant longer latencies of 212 ms in the low luminance contrast condition, and even longer latencies of 227 ms in the isoluminant chromatic condition (see Figure 4A). For the position error, the influence of both, target contrast, $F(2, 20) = 71.34$, $p < 0.001$, and target speed, $F(5, 50) = 98.82$, $p < 0.001$, was significant. As
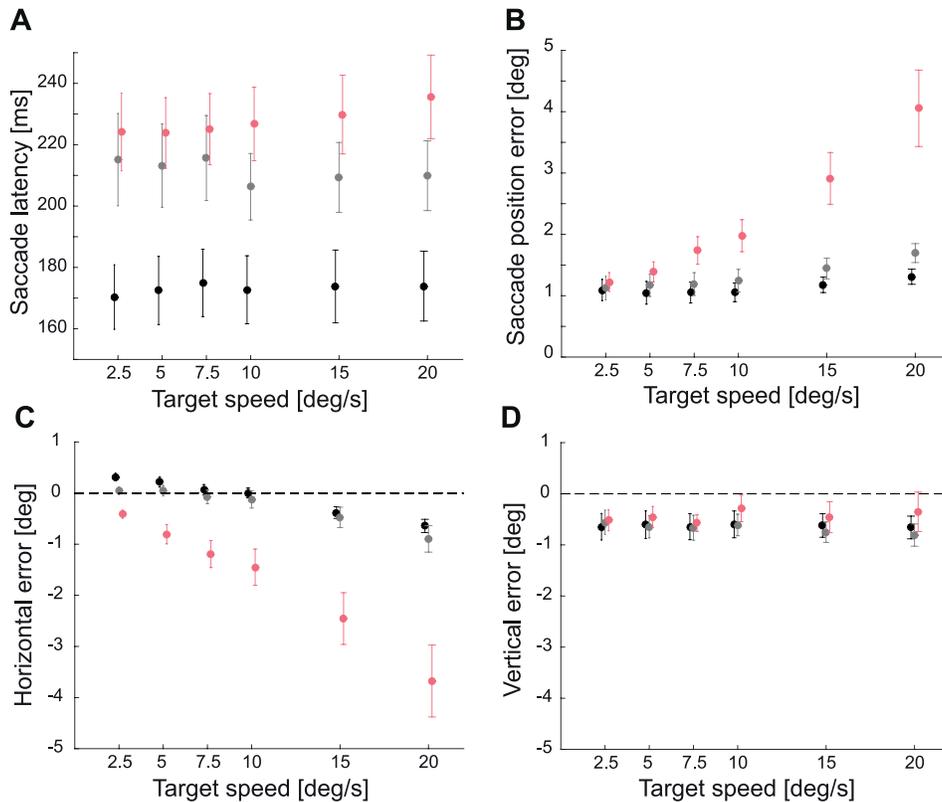
Figure 4. Saccadic latencies and endpoint errors. (A) Average saccade latencies of the three contrast conditions for the six target speeds (*x*-axis). Black symbols denote latencies for the high luminance contrast targets, gray symbols for low luminance contrast, and red symbols for isoluminant red targets. (B) Average Euclidean position errors of saccade endpoints for the three contrast conditions and all target velocities. Error bars always show the 95% CI around the mean. (C–D) Horizontal (C) and vertical (D) components of the saccade position errors depicted in (B). Negative values indicate saccades landing behind (for horizontal error) or below (for vertical error) the target.

expected, saccadic accuracy was best for high contrast luminance targets with an average position error 1.12 deg. The error was just slightly higher at 1.31 deg for saccades to low luminance targets. In general, the position error increased for faster target speeds. The interaction between contrast and speed, $F(10, 100) = 66.05$, $p < 0.001$, was driven by the strong influence of target speed in the isoluminant condition (see Figure 4B). While for the slowest target speed of 2.5 deg/s, position errors were comparable across all three target contrasts, the position error of the isoluminant condition was about 4 times as big for the fastest target (20 deg/s). Our experimental design allowed us to look at this effect in more detail. Due to the orthogonal orientation of the position step and target movement, the vertical error of the saccade should be mainly related to the position step, whereas the horizontal error should be mainly related to the target movement. When we analyzed the horizontal and vertical error separately, we found a systematic difference for the horizontal error in the isoluminant condition (see Figure 4C), but not for the vertical error (see Figure 4D). Taken together, these results show that saccade

landing positions differ depending on the target contrast. Interceptive saccades to isoluminant targets are less accurate when the targets move.

Contributions of position and motion information

To investigate how visual signals are converted into saccadic commands for the three conditions, we compared the horizontal eye position at the saccade end with the target position at three points before saccade end. We calculated the average target positions (a) for the target position 100 ms before saccade onset, (b) at saccade onset, and (c) at saccade end (see the three lines in Figure 5). The target position 100 ms before saccade onset was available to the visuomotor system at the start of the saccadic deadtime. The target position at saccade onset and at saccade end has to be extrapolated to overcome the change in target position during saccade deadtime and saccade execution. We found that saccades landed closest to the actual target positions at saccade end for the high and low luminance contrast conditions (Figure 5A and B). For slow target velocities (<5 deg/s), saccades landed
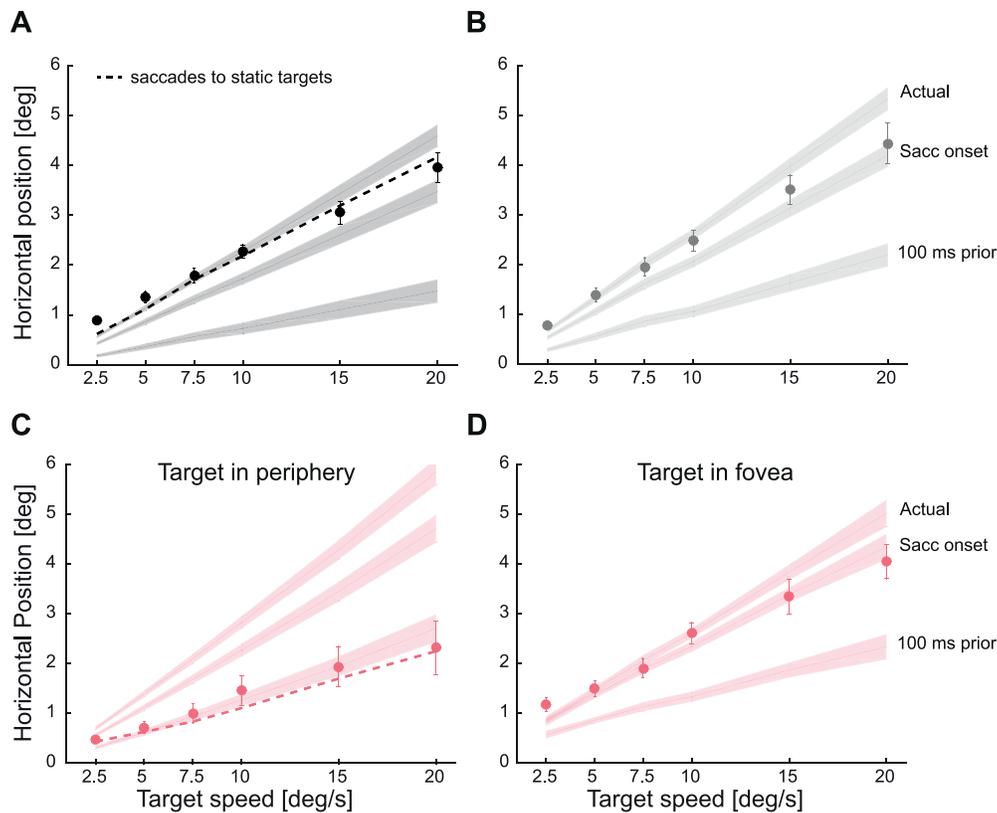
Figure 5. Compensation for target movements during saccades. Average horizontal positions of saccade endpoints (circles) are plotted with respect to target positions at three points in time: The lowest line stands for the average target position 100 ms before saccade onset, the intermediate one for the target position at saccade onset (time 0), and the top line for the actual target position at the end of saccades. The dashed lines in (A) and (C) indicate the horizontal component of control saccades made to static targets presented at the average actual position of the target for the high contrast target and at the position 100 ms before saccade onset in the isoluminant case. (A–B) In the two luminance contrast conditions (A, high contrast, and B, low contrast) saccade endpoints are quite close to the actual target positions. (C–D) Horizontal positions of saccades to isoluminant chromatic targets. (C) In the isoluminant condition, saccades landed close to the target position at 100 ms before saccade initiation when the target was moving at 10 deg in the periphery. (D) In the first control experiment saccades to isoluminant ramp targets starting from fixation landed close to the actual target position. Error bars and shaded areas symbolize the 95% CI around the mean.

slightly ahead of the moving target, while saccades for high target velocities (>15 deg/s) landed slightly behind the target. This could indicate an underestimation of the high target velocities, but we did find a similar undershoot to static targets presented at the corresponding eccentricities in the second control experiment (see dashed line in Figure 5A). Thus, saccades to moving targets defined by luminance have comparable accuracy as saccades to static targets presented at the actual position of the moving target (highest of the three diagonals in Figure 5A). To achieve this, the oculomotor system has to take the amount of target displacement into account. The saccadic undershoot for higher ramp speeds seems to be related to the larger retinal eccentricity of these fast-moving targets and was independent of the starting position and target movement direction.

In contrast, for the isoluminant chromatic condition, saccades landed closest to the position of the target 100 ms before saccade onset (see lowest line in Figure 5C). This result indicates that for pure chromatic targets appearing in the visual periphery, no appropriate predictions about the target movement trajectories were available, even though the latency of on average 227 ms was the longest of all three conditions. This pattern of responses could arise from an accurate, but delayed representation of the position of the target and the complete absence of a velocity signal. It could also result from the combination of a weak velocity signal and a weak position signal, but certainly the processing of target speed is impaired. In our first control experiment, we presented the vertical step and the motion-related component separated by a temporal break. In this case, the target started to move while it was viewed foveally, and interceptive saccades to isoluminant moving targets landed accurately at the actual target position (see Figure 5D). This result agrees well with psychophysical findings that for pure
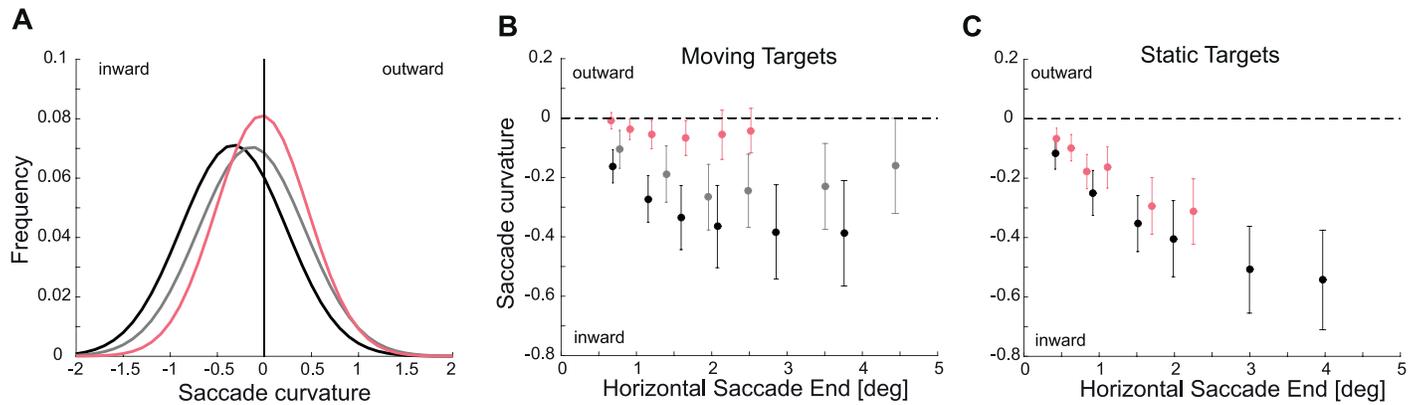
Goettker, Braun, & Gegenfurtner

Figure 6. Saccade curvature of saccades to moving and static targets for the three contrast conditions. (A) Distribution of saccadic curvature in all trials for targets moving at 20 deg/s. Colors denote the different contrast conditions. Positive values indicate an outward curvature, negative values an inward curvature. (B–C) Average curvature of saccades for the six different target speeds to moving (B) and static (C) targets with matched amplitudes plotted against the average horizontal saccade landing position. Positive curvature values indicate an outward curvature, negative values an inward curvature. Error bars represent the 95% CI around the mean.

chromatic targets, motion-related information is available in or near the foveal visual field, but not in the periphery (e.g., Gegenfurtner & Hawken, 1996).

Saccadic curvature

Curvature is often used to measure the balance of competing saccade programs and their dynamics (Viviani, Berthoz, & Tracey, 1977; Becker & Jürgens, 1979; Smit & Van Gisbergen, 1990; Ludwig & Gilchrist, 2002; Schreiber et al., 2006). Despite the large overall variability in curvature (see Figure 6A), interceptive saccades landed on average quite accurately and reliably either at the actual target position in both luminance conditions or at the position of the target 100 ms before saccade onset in the isoluminance condition. We compared the curvatures of single interceptive saccades for the three conditions. In general, we found a continuum of different trajectories with varying curvatures. About two thirds of saccades to luminance targets had inward curvatures, and the average curvature for these targets was inward as well (see example trace in Figure 2 and negative values in Figure 6B and C). Since our paradigm did not allow to dissociate position and velocity from vertical and horizontal, we performed a control experiment. We used static targets to disentangle whether the target motion was responsible for the inward curvature, or whether this effect depended on the oblique nature of the saccade only (see Viviani, Berthoz & Tracey, 1977; Smit & Van Gisbergen, 1990). Figure 6 shows that the inward curvature was present both for static and moving luminance targets with matched endpoints. There was no significant difference between moving and static targets for the high contrast luminance condition for any of the velocities (all ps > 0.30). Thus, the curvature of saccades does not seem to be directly

related to the integration of the velocity of the moving target.

However, for the isoluminance condition, saccadic curvatures differed between the dynamic and the static conditions. Saccades to isoluminant targets had an on average inward curvature for static targets, while they were on average quite straight for moving targets at all speeds. This indicates, as before, a deviation in the pattern of results for isoluminant moving targets. Why this leads to an absence of curvature is puzzling, though.

Interactions between pursuit and saccades

So far we have focused on the interceptive saccades of the tracking responses. In the following we present results concerning the oculomotor behavior at the transition from the interceptive saccade to pursuit. We limited our analysis on the pursuit responses to a 120-ms time window starting directly after the end of the interceptive saccade. As mentioned earlier, in this early phase after saccade offset there should be relatively little influence of new retinal information on the pursuit response due to sensorimotor processing delays. We were particularly interested in the question whether and how the pursuit direction and speed would be influenced by the saccade landing position. Any such effect would suggest shared representations of eye and target position for saccadic and pursuit eye movements.

Pursuit direction

We investigated whether the pursuit direction was influenced by the saccade landing position. If the pursuit response was determined only by the target
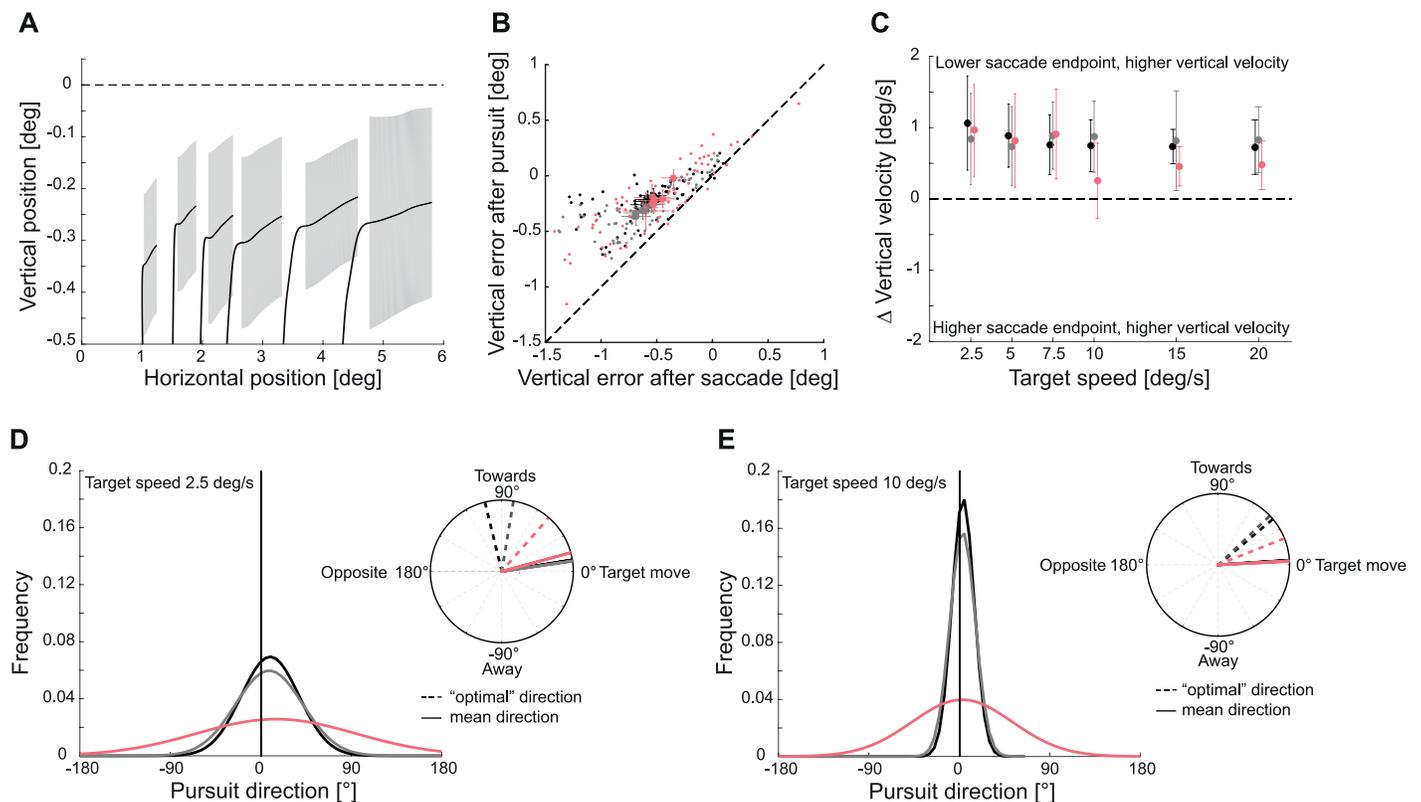
Figure 7. Adjustment of postsaccadic pursuit direction. (A) Average pursuit trajectories during the 120-ms time interval after saccades offset for high contrast luminance targets moving left- and rightward at six different speeds. For all ramp movements the directions of the 120-ms pursuit segments are slanted. The shaded area shows the 95% CI around the vertical mean. The thin gray lines represent interceptive saccades before pursuit onset. (B) Scatter plot of vertical errors at saccade offset and after the 120-ms pursuit segment. Individual data points show the average of each participant for each target speed. Note that nearly all data points are above the diagonal, indicating a reduction of vertical error by pursuit. (C) Difference in vertical pursuit velocity based on a median split of the vertical position errors at saccade offset. Positive values indicate that the vertical velocity was higher upwards when the eye landed further below the target. (D) Distribution of pursuit directions for all trials for targets moving at 2.5 deg/s. The inset serves as a legend for the pursuit direction; trials are aligned such that the target always moved toward the right and that trials in the upper half of the circle represent a deflection of pursuit direction toward the position of the target. The lines represent the mean of the pursuit direction shown in the histograms. The dashed lines originating from the center of the circle indicate the hypothetical pursuit direction that would reduce the position error completely at the end of the pursuit interval. Colors denote the three contrast conditions. (E) Same depiction as in (D), but here for a target moving at 10 deg/s.

movement, then the postsaccadic pursuit direction should primarily be parallel to the horizontal ramp. Any vertical component of pursuit presumably should be related to a postsaccadic position error (see Figure 7A). To quantify the vertical component, we compared the vertical error at the saccade end (see Figure 4D) with the vertical error after the first 120 ms of pursuit. We found a significant reduction of the postsaccadic vertical error by pursuit. The reduction took place for all contrast conditions: from −0.62 to −0.28 for high luminance contrast, from −0.65 to −0.32 for low luminance contrast, and from −0.44 to −0.14 for isoluminance (all $ts > 3.46$, all $ps < 0.006$). This reduction indicates that pursuit was not only driven by the horizontal ramp motion, but that it also corrected

for the vertical position error, so that the eye got closer to the moving target (see Figure 7B).

The reduction of the vertical position error suggested that the pursuit direction was adapted based on the saccadic landing position. Accordingly, the pursuit direction should be slightly upwards to correct the position error when the preceding interceptive saccade landed below the target, and it should be slightly downwards for saccades landed above the target. For each participant we performed a median split based on the vertical landing position of saccades and calculated the mean velocity for these groups. Note that interceptive saccades of all participants generally undershot the targets (see Figure 4D) so that the two groups not directly corresponded to saccades landing above or below the target. However, if the vertical

pursuit velocity was influenced by the vertical position errors of saccades, the vertical velocity should be smaller or even in the opposite direction for landing positions closer to the target. To quantify the effect we took the difference between both groups, thus a positive value indicated a higher vertical velocity for trials that landed further below the target (Figure 7C). Across all conditions we found a consistent pattern that indeed the vertical pursuit velocity, and thus the direction of the pursuit response was adjusted according to the saccade landing position,

To analyze how the pursuit direction was influenced by the position- and the velocity-related component in more detail, we aligned all trials so that the target was always in the upper half of the representation and moved to the right (see Figure 7D). We computed for all trials the direction of pursuit responses that would reduce all position errors at the end of the 120 ms pursuit interval. This hypothetical optimal pursuit direction depended on two factors: the saccadic landing position and the ramp speed. In general, hypothetical optimal pursuit directions for higher ramp speeds resulted in shallower pursuit directions, whereas for lower speeds optimal pursuit direction could sometimes even be in the opposite direction of the target movement when the saccade landed ahead of the target (see Figure 7D). For all three contrast conditions the average hypothetical optimal directions are represented by straight dashed lines originating from the center of the circles in in the insets of Figure 7D. By looking at the distributions of pursuit direction one can learn two things. First, for the two luminance conditions, pursuit responses were following mainly the ramp directions and showed a small shift toward the target, which explained the reduction of the vertical position error. However, pursuit directions were always more similar to the ramp directions than to the hypothetical optimal directions for fast corrections of the position errors (compare mean and "optimal" pursuit direction in the insets). Therefore, pursuit was mainly responding to the horizontal ramps, and vertical position errors were corrected by a small additional vertical velocity component. Second, in the isoluminant condition, pursuit responses were reduced (see also next section about pursuit speed) and more variable (see Figure 7D and E), since the motion-related representations of ramp targets were impaired. These findings are in line with the results of the interceptive saccade to isoluminant targets and suggest an impaired representation of the target velocity in the isoluminant condition.

Pursuit speed

In addition to pursuit direction, we also compared the average eye speeds after saccade offset. For the luminance targets, a difference between the velocity

profiles for the six target speeds was already present during the first 50 ms after saccade offset (see Figure 8A). This separation was reduced for the isoluminance condition (see Figure 8B). To analyze the pursuit speed in more detail, we took a closer look at the average horizontal eye velocity in the interval directly after the saccade. We computed the average minimum horizontal eye velocity in the first 50 ms after saccade offset. We expect that this measurement will scale with the target velocity if a speed-dependent pursuit command overlapping with the saccade dynamics controls the eye movements. If no target speed-related pursuit command is processed in parallel with the interceptive saccade, this measurement should be independent of the target speed. We observed that the minimal horizontal eye velocity closely followed the ramp speeds for luminance targets (Figure 8C). For isoluminant targets the horizontal velocity was much reduced, indicating again an impaired velocity representation for isoluminant targets moving in the periphery.

To test whether pursuit velocity was influenced by the landing position of the preceding saccade, we performed a median split based on the horizontal saccadic landing positions relative to the target. For the luminance contrasts the two groups roughly encompassed saccades landing in front or behind the target. For the isoluminant condition all saccades landed behind the target. If saccades and pursuit share only velocity-related information, but not the saccadic landing position, the minimum horizontal eye velocity should be higher for saccades that landed ahead of the target, as these estimated the target to move further than it actually did. Interestingly, for the luminance conditions we found that minimum horizontal eye velocity of pursuit was lower for saccades landing ahead of the target, and faster for saccades landing behind the target. This shows that the initial pursuit response is not only based on shared estimates of the ongoing target movements. It might also be based on the estimated (predicted) saccadic landing positions to reduce potential errors of tracking and catch-up saccades. These adjustments of the pursuit speed were stronger for the high luminance contrast conditions, suggesting that more reliable target information allows stronger adjustments of the oculomotor responses. For isoluminant targets the pattern of minimum eye velocities of pursuit was more diverse, and there was no adjustment of the velocity, neither for target speed nor for saccade landing position.

Discussion

We investigated saccade and pursuit responses to orthogonal step-ramps under three target contrast
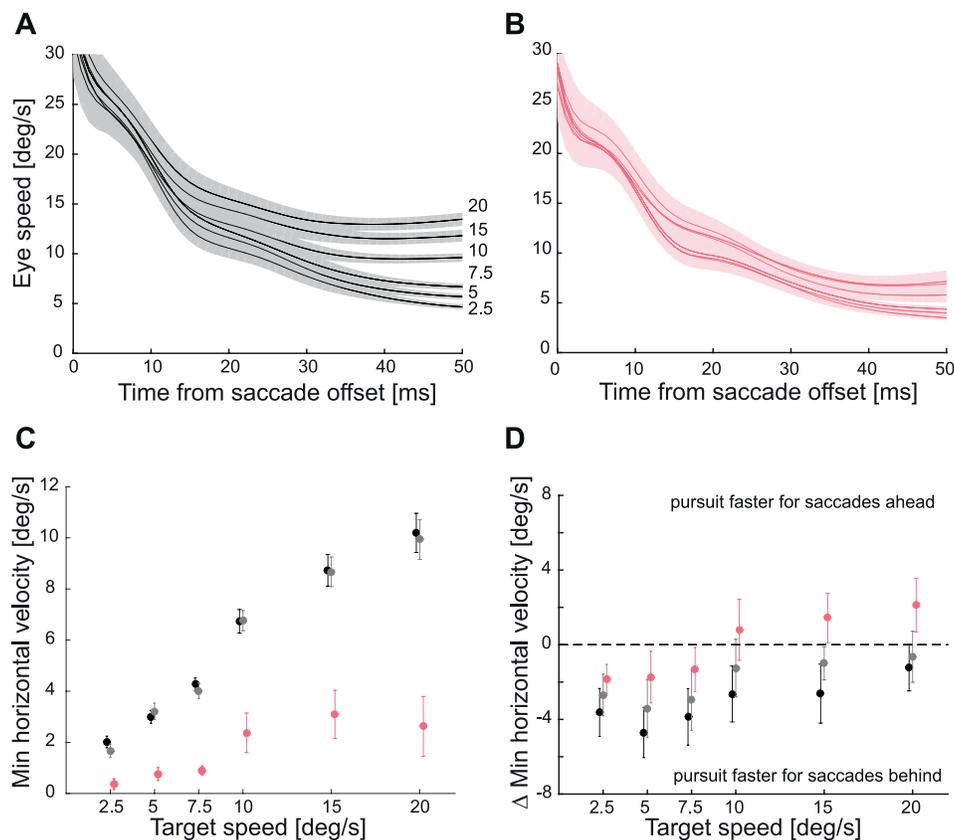
Figure 8. Adjustment of postsaccadic eye speed. (A–B) Average eye speed across subjects for the high luminance (A) and isoluminance (B) contrast condition during a 50-ms interval after the calculated saccade offset. Each velocity profile is for one of the six target velocities. The shaded areas represent the standard error of the mean. (C) Average minimal horizontal eye velocity during the 50 ms after saccade offset for the six target speeds. (D) Differences between the minimal horizontal eye velocities based on a median split with respect to the horizontal saccade landing position. Negative values indicate a higher minimum eye velocity of pursuit for trials with a saccade landing further behind the target. The error bars show the 95% CI for the differences. Colors denote the three contrast conditions.

conditions: high luminance, low luminance, and isoluminant color contrast. In line with earlier studies, we found that interceptive saccades to 2-D step-ramps targets of high and low luminance contrast landed close to the actual target position. However, we found a differential effect for isoluminant chromatic stimuli. Interceptive saccades to such targets moving at 10 deg in the periphery landed at positions the targets had passed 100 ms before saccade initiation (Figure 5). This was not the case for isoluminant targets close to the fovea, for which saccades landed close to the actual target location. This suggests that for peripheral pure chromatic targets, a reliable, although delayed, estimate of the target position before saccade onset was present, but that the motion-related information about the ramp speed was impaired. Differences in the processing of the motion-related signals was not only present in the errors of the saccadic end position, but also in the saccade trajectories (Figure 6). Additionally, we found that for the luminance contrast conditions, the initial pursuit direction (Figure 7) and speed

(Figure 8) were adjusted based on the saccadic landing position. This suggests that saccade-pursuit interactions are based on shared information about ongoing target movements, e.g., shared (predicted) eye position signals. In line with the impaired motion-related signal of peripheral targets for the interceptive saccade in the isoluminant condition, subsequent pursuit was reduced and more variable, especially the horizontal velocity component directly related to the target motion (Figure 8). This presents strong evidence that the signals related to the position and motion of the target are to some degree separated for sensorimotor processing.

Combination of position and motion signals

In line with other studies we found that saccades to 2-D step-ramp targets of high luminance contrast landed close to the actual target position (Robinson, 1973; Ron et al., 1989; Keller & Johnsen, 1990; Gellman & Carl, 1991; Engel et al., 1999; Etchells et al.,

2010; Fleuriet et al., 2011). Saccades were accurate even when the luminance contrast was reduced to 10%, indicating that information about target speed was used for saccade programming. The high accuracy of interceptive saccades to moving low luminance targets is remarkable since motion perception is strongly influenced by luminance contrast and for low contrast targets a substantial perceptual slowing is described (Thompson, 1982; Stone & Thompson, 1992). However, our findings suggest that with sufficient processing time (Gellman & Carl, 1991) due to the longer latencies (Figure 4), the integration of the velocity-related signals is also successful for the stimuli of low luminance contrast.

These results can be explained by both the dual drive as well as the continuous drive theory. According to the dual drive hypothesis, programming of interceptive saccades is based on a static position error determined some time before saccade onset, and on information or predictions about the target speed (Rashbass, 1961; Robinson, 1973; Keller & Johnsen, 1990; Keller, Gandhi, & Weir, 1996; Optican & Pretegiani, 2017). The endpoints of saccades to moving targets are then based on a combination of the two (de Brouwer et al. 2002; Guan et al., 2005; Schreiber et al., 2006). In contrast to the dual drive theory with its discrete measurements of position and velocity, Goffart and colleagues (Fleuriet & Goffart, 2012; Quinet & Goffart, 2015; Goffart et al., 2018) proposed that a single, continuous, and robust estimate of the expected spatiotemporal coordinates of a moving target is represented in the brain by the spread of neuronal activity. It is then used to synchronize the tracking eye movements with the motion of the visual target (Goffart et al., 2017). Both theories would predict that saccades to moving targets should land close to the correct position of the target: either due to a combination of a discrete position estimate with a velocity signal, or due to a continuous drive based on the streak of retinal activity steering the saccade toward the actual position of the target. The interesting new result is the observed oculomotor behavior to saccade isoluminant targets. In contrast to luminance stimuli, interceptive saccades to peripheral isoluminant targets were less accurate. They landed at positions the targets passed about 100 ms before saccade onset.

In the framework of the continuous drive theory (see Goffart et al., 2017, 2018), this behavior could indicate a simple underestimation of the target displacement, which leads to the saccade lagging behind the target. However, this seems unlikely to us due to several reasons. First, in contrast to a simple underestimation, the errors of the saccades are highly systematic. The error increased with target speed in a way that the saccades always landed to the position the target had roughly 100 ms before saccade onset (see Figure 5).

Second, saccades to isoluminant static targets have comparable accuracy to saccades to static luminance targets (White et al., 2006). Therefore, the difference can also not be explained by the retinal response to the stimulus itself, but seems to be directly related to the movement of the stimulus. Third and most crucially, the retinal streak that in theory elicits the steering of the saccade toward the moving target should be comparable in location and strength for the isoluminant and our low luminance contrast condition. However, the behavior is drastically different.

In the framework of the dual drive theory, the results of the isoluminant condition would indicate an impairment in the prediction of the target position at saccade end. The pattern of responses to isoluminant peripheral moving targets could arise from an accurate, but delayed representation of the position of the target and the complete absence of a velocity signal. It could also result from the combination of a weak velocity signal and a weak position signal determined at some point after target appearance, but this seems unlikely to us for two reasons. First, for the luminance contrast conditions, there was a strong postsaccadic pursuit response that depended on the target speed. This dependence was much weaker for the isoluminant targets (Figure 8), indicating an impaired velocity representation. This fits well with the literature on motion perception. Psychophysically, the existence of (at least) two pathways for visual motion is well established: a position-based system and a motion energy-based system (Braddick, 1974; Cavanagh, 1992). While for isoluminant targets the motion energy-based system is severely impaired, the position-based system is attenuated in the periphery (e.g., Gegenfurtner & Hawken, 1996; Lu & Sperling, 2001). Second, instead of a discrete measurement of position and velocity at one moment in time, the oculomotor system seems to have access to continuous estimates of the current target position (Becker & Jürgens, 1979; Goffart et al., 2017). Therefore, the oculomotor system should have access to the position of the target up until the time the execution of the saccade can no longer be changed, about 100 ms before saccade onset. This interval, 100 ms before saccade onset, is often used to characterize the information available for saccade programming in a variety of paradigms, such as double-steps (Becker & Jürgens, 1979; Ron et al., 1989), catch-up saccades in response to position and velocity changes (Engel et al., 1999; de Brouwer et al., 2002, Schreiber et al., 2006), or neuronal responses in neurophysiology (Keller et al., 1996). Thus, the interpretation of our results based on the dual drive theory would be that the saccade is based on an intact, but delayed position estimate as it is sampled before the saccadic dead time, while the motion integration is impaired.

A possible impairment of the motion-related component was also visible in the saccade trajectories. Interceptive saccades to luminance targets landed close to the target, but the saccadic curvatures showed considerable variability (Erkelens & Vogel, 1995). Most saccades curved inwards, and we found the same inward curvature to static targets with matched amplitudes (see Figure 6). Therefore, curvature is presumably based on the early horizontal dominance of eye velocity (Smit & van Gisbergen, 1990), rather than on the integration of the velocity component of the ramp target. Unfortunately, our paradigm did not allow us to disentangle the early horizontal dominance from potential velocity-related effects on the saccade trajectory (Guan et al. 2005; Schreiber et al., 2006; but see Fleuriet et al., 2011), because the interceptive saccade always had to compensate for a vertical step. This issue, and potential differences between the upper and lower visual field (Hafed & Chen, 2016) or target movement to left and right, require further investigation. Despite this, it is particularly puzzling in this context that the early horizontal dominance was not present for interceptive saccades to isoluminant moving targets.

It was postulated by Goffart and colleagues in their continous drive theory that a representation of a static position signal and the mathematical integration of a velocity signal is unlikely (Goffart et al., 2018). As mentioned above we agree with this view as there is indeed evidence for a continuous processing of the target (Cassanello, Nihalani, & Ferrera, 2008; Orban de Xivry, Missal, & Lefèvre, 2008; Daye et al., 2014; Quinet & Goffart, 2015). There are also factors that can influence the saccade trajectory after the initially proposed discrete measurements of the target position 100 ms before saccade onset: the estimated retinal slip of a target (Schreiber et al., 2006), target steps during the saccade (Gaveau et al., 2003), or even micro-stimulation, which displaces the eyes shortly before saccade onset (Fleuriet & Goffart, 2012). This provides evidence that oculomotor behavior is driven by continuous signals instead of discrete and static measurements 100 ms before saccade onset. However, our results suggest that there are two quite independent representations of position and motion, interacting to allow for accurate saccades to moving targets. If the motion information is impaired, saccades land close to the position representation, which is lagging behind the physical location of the moving target due to neuronal processing delays. In this case, there is still a systematic change in position over time, but the brain seems to be unable to extrapolate the moving stimulus based on a continuous representation of target position. Instead it uses different signals for processing position and motion (Smeets & Brenner, 1995).

Our interpretation seems to be in disagreement with the continuous drive theory. However, as noticed by Goffart et al. (2018), there might be different imbalances for driving saccadic or pursuit eye movements, based on different sets of neurons that steer the eye movements. It could be assumed that saccadic as well as pursuit eye movements are affected by position as well as motion information (see Orban de Xivry & Lefèvre, 2007). Then, instead of imbalances for saccade and pursuit, the imbalances would reflect the position or the motion of the target. Our results could then be interpreted as an intact representation of the position imbalance, which is lagging behind the target due to neuronal delays, while the motion imbalance is distorted due to the impaired motion processing of isoluminant stimuli in the periphery.

Neural correlates of the position and motion signal

The visuomotor circuits for saccades and pursuit are well studied and their cortical and subcortical networks show more overlap and interactions than previously thought (see Krauzlis, 2004, 2005; Orban de Xivry & Lefèvre, 2007; Leigh & Zee, 2015). An important subcortical structure for the potential position signal or imbalance is the multilayered superior colliculus (SC; for review see Sparks, 1986; Gandhi & Katnani, 2011, White & Munoz, 2011). The distribution of activity across the SC motor map appears to provide an estimate of the retinal location of the eye motor goal for fixation, saccades, and pursuit (Basso, Krauzlis, & Wurtz, 2000; Krauzlis, Basso, & Wurtz; 2000; Krauzlis, 2005). In line with our interpretation of a position-related effect of distortions, unilateral deactivation of the SC leads to a constant offset of the gaze with respect to the target even during pursuit (Hafed, Goffart, & Krauzlis, 2008). Importantly, neurons in the SC are sensitive to luminance and isoluminant chromatic stimuli (White, Boehnke, Marino, Itti, & Munoz, 2009) leading to a good match between the properties of the SC and the behavioral results of our study.

The most prominent structure as the origin for the proposed motion signal/imbalance is the middle temporal area (MT or area V5) with its high percentage (80%–90%) of motion-direction sensitive neurons (Dubner & Zeki, 1971; Pack & Born, 2001). Area MT has been directly linked to encode estimates of the velocity of visual targets, which are important for pursuit initiation and interceptive saccades, since MT lesions compromised the accuracy of saccades to moving but not to stationary targets (Newsome, Wurtz, Dursteler, & Mikami, 1985; Newsome & Pare, 1988). In the monkey MT neurons respond with high sensitivity to moving luminance-defined stimuli but rarely to pure

chromatic stimuli (Saito, Tanaka, Isono, Yasuda, & Mikami, 1989; Dobkins & Albright, 1994; Gegenfurtner et al., 1994; Seidemann, Poirson, Wandell, & Newsome, 1999; Thiele, Dobkins, & Albright, 1999; Riečanský, Thiele, Distler, & Hoffmann, 2005). Motion processing of pure chromatic stimuli seems not to include area MT, but to be realized by a different pathway via V3 and V4 (Gegenfurtner & Hawken, 1996) and to work best for foveal targets (Gegenfurtner & Hawken, 1995). Thus, while MT seems to be the main candidate as the origin for the computation of motion signals of luminance stimuli, it does not seem to process the motion of pure chromatic targets in the periphery. This lack of motion processing could lead to changes (or to be precise, no changes) in the activity of adjacent areas such as the nuclei of the optic tract (NOT; Hoffmann, Bremmer, Thiele, & Distler, 2002; Krauzlis, 2004) Unilateral lesions of the NOT do lead to an irrepressible drift of the eye to the contralateral side (Inoue, Takemura, Kawano, & Mustari, 2000), suggesting some motion-related effects. Another crucial area might be the caudal fastigial nuclei (CFN). Lesions to the CFN impair saccades and pursuit made to moving targets (Bourrelly et al., 2018a, 2018b). Thus, the impaired motion processing in MT for isoluminant peripheral targets could be the origin for our behavioral results.

It is still an open question if these potentially different signals are integrated into one continuous signal, and where these potential signals converge onto the motor neurons. However, the impairment of oculomotor behavior for isoluminant stimuli moving in the periphery should allow a closer look at these questions. A recent study investigating saccades to moving targets demonstrated that the spread of activity in the SC reflects a continuous representation of the target position (Goffart, Cecala, & Gandhi, 2017), but only for previous and not for future target positions. This could indicate that the motion-related signals influence the target representation already in SC to code for the correct target position. The question that arises based on our results is whether the SC is providing the actual target position corrected for target motion, or whether the SC provides the delayed position signal. The answer may be found by recording neuronal responses in the SC to moving luminance and isoluminant stimuli in the periphery. If SC responses are similar for moving luminance and isoluminant stimuli, then SC presumably provides position signals of the past, the end position of saccades to isoluminant targets. If SC responses are different, then some integration of motion information takes place in the SC. A similar logic can be used to investigate the contributions of the NOT or the CFN regarding the motion signal. Both should show less activity or imbalance for isoluminant targets moving in the

periphery. Thus, our results for isoluminant stimuli open new possibilities for electrophysiology to separate the contributions of position and motion processing in the brain.

Saccade-pursuit interactions

The second focus of our study was whether signals are shared at the transition from interceptive saccades to pursuit. We investigated pursuit behavior immediately after the offset of saccades (0–120 ms) since we expected little influence of new retinal information due to sensorimotor processing delays during this interval.

In line with our findings for interceptive saccades to isoluminant ramp targets, the postsaccadic pursuit was also compromised (see Figure 8). This indicates that for both types of eye movements the integration of the target velocity was impaired. The common deficit can be explained either by a shared velocity representation used by both subsystems (Hainque et al., 2016) or by separate but similarly reduced velocity signals used by each subsystem (Bourrelly et al., 2018b). At the neural level, Bourrelly et al. (2018b) inactivated the CFN unilaterally. They found that interceptive saccades were hypometric and the postsaccadic pursuit velocity was reduced for contralesional tracking. However, on a trial-by-trial basis no correlation was present between the contralesional saccadic undershoots and the reduced postsaccadic pursuit gain. In contrast, Hainque et al. (2016) showed that catch-up saccades and pursuit eye movements were adjusted toward a new target movement along a similar time course, leading them to propose a shared velocity signal. A crucial idea resolving these conflicting findings might be that the oculomotor responses use different time windows of the same continuous signal. In Hainque et al. (2016) both eye movements, pursuit as well as corrective saccades, were directed toward the new target movement at comparable times after the change in target movements. Consecutive saccadic and pursuit eye movements to the same target, such as in our study and the study of Bourrelly et al. (2018b), could also be based on readouts of the same continuous signal, but with different integration time windows. An effect of different integration time windows was recently shown by Goettker, Brenner, Gegenfurtner, and de la Malla (2019). They found that interceptive hand movements were only affected by information roughly 100 ms before movement execution, but not by earlier information. Similarly, the window of integration of information for the initial interceptive saccade might be earlier than for the following pursuit eye movement. Along these lines, we hypothesize that Bourrelly et al. (2018a) observed common lesion effects due to a shared signal, but did not find trial-by-trial correlations

because the crucial intervals for the relevant signals for saccade and pursuit execution differ. Thus, we propose that the pathways for saccades and pursuit share a continuous target motion signal (or imbalance), but sequential eye movements can differ due to the temporal dynamics of their readout.

Regarding a shared estimate of eye and target position, we found two different types of adjustments in pursuit behavior with respect to saccadic landing positions. First, we observed that the early postsaccadic pursuit direction did not match the target movement direction, but deviated depending on the vertical position error between the saccadic landing position and the target position. Despite the deflection of the pursuit direction toward the target, we did not observe an immediate reduction of the error. Pursuit movements adjusted continuously for the vertical error, but they were dominated by the horizontal pursuit component, which roughly matched the target velocity. This behavior suggests that in addition to the velocity related horizontal component, an additional vertical velocity component was added that was based on a position error (Segraves & Goldberg, 1994; Blohm, Missal, & Lefevre, 2005). This component was influenced by the saccadic landing position. Interestingly, the adjustment of the vertical pursuit component based on the saccadic landing position looks comparable between the luminance and isoluminant targets (see Figure 7C), possibly indicating again that the mismatch or imbalance with respect to the position of the target was estimated correctly. Such an effect in this early pursuit interval suggests that the position mismatch was presumably derived from a comparison between the predicted target and the predicted eye position through some kind of forward model. A different source for this rapid adjustment could be an extremely fast processing of the retinal error signal. Interestingly, recent studies have indicated a possibility for adjustments as fast as 50–80 ms during pursuit (Tavassoli & Ringach, 2009; Buonocore et al., 2019).

Second, there was not only an adjustment of the pursuit direction, but also of the pursuit velocity depending on the saccadic landing position (Lisi & Cavanagh, 2017; Goettker et al., 2018). Intuitively, if target representations are shared in the oculomotor system, saccades that land ahead of the target would be based on an overestimation of the target velocity or the target displacement. If that same overestimation is then used to drive pursuit, postsaccadic pursuit velocity should also be higher. Our results showed the opposite effect for the luminance conditions. The minimal horizontal eye velocity in the first 50 ms after saccade end was slower for saccades landing in front of the target than for saccades landing behind the target (Figure 8). This result allows two important insights. On the one hand, pursuit velocity is adjusted based on

the relative saccadic landing position, either slower to wait for the moving target or faster to catch the target when it is ahead (Segraves & Goldberg, 1994; Lisi & Cavanagh, 2017; Goettker et al., 2018). On the other hand, this adjustment is presumably based on the comparison of predictions about future target and eye position at the end of the interceptive saccade. Since these effects already occur in the first 50 ms after saccade offset, we are quite confident that effects of retinal position error described in Buonocore et al. (2019) do not play a major role for this result. For the isoluminant targets, the pattern of results looked much more diverse (see Figure 8D). Here, the large effect on the endpoints of the saccade and the related high horizontal position error could potentially lead to an even stronger adjustment of the pursuit response. However, as mentioned earlier, gaze lagging behind the target should lead to an increase in pursuit velocity (Segraves & Goldberg, 1994). This is the opposite of the impaired pursuit we observed. Overall, these adjustments suggest a shared position-related signal of target and eye that affects the ongoing pursuit.

These early dynamic saccade-pursuit interactions support the current view of a tight coupling and shared information within the oculomotor system (Krauzlis, 2004; Orban de Xivry & Lefevre, 2007). Saccades and pursuit seem to be both driven by the same underlying position- and motion-related signals and also use a shared representation eye position and velocity (Orban de Xivry et al., 2006; Morris, Bremmer, & Krekelberg, 2016; Orban Deravet, Blohm, Orban de Xivry, & Lefèvre, 2018; Goettker et al., 2018; Goettker et al., 2019).

Keywords: saccades, moving targets, saccade curvature, target contrast, integration of position and motion information, saccade-pursuit interaction

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