

Saccadic compensation for reflexive optokinetic nystagmus just as good as compensation for volitional pursuit

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The natural viewing behavior of moving observers ideally requires target-selecting saccades to be coordinated with automatic gaze-stabilizing eye movements such as optokinetic nystagmus. However, it is unknown whether saccade plans can compensate for reflexive movement of the eye during the variable saccade latency period, and it is unclear whether reflexive nystagmus is even accompanied by extraretinal signals carrying the eye movement information that could potentially underpin such compensation. We show that saccades do partially compensate for optokinetic nystagmus that displaces the eye during the saccade latency period. Moreover, this compensation is as good as for displacements due to voluntary smooth pursuit. In other words, the saccade system appears to be as well coordinated with reflexive nystagmus as it is with volitional pursuit, which in turn implies that extraretinal signals accompany nystagmus and are just as informative as those accompanying pursuit.

Ilg, 1997; Kowler, 2011). In order to produce effective transitions between foveation and stabilization, these different eye-movement systems need to be able to communicate with one another, exchanging information such as the current position and velocity of the eye so that the next target of interest can be accurately acquired. In this paper, we explored the interplay between foveation and gaze stabilization by investigating the accuracy of saccades made to targets that were flashed during ongoing OKN. In other words, we asked: “To what extent does saccade planning know what the OKN system is currently doing?”

The mechanisms that drive foveation are often considered top down and volitional—a target must be selected from the numerous potential choices available and acted upon in an intentional way. Gaze stabilization, on the other hand, is thought to be more bottom up and reflexive, driven automatically by visual and nonvisual cues to self-motion. By studying the interaction between foveation and stabilization, we therefore inevitably raise questions about the relationship and coordination between intentional and reflexive control systems.

One view is that these different types of control system are very separate from one another, residing in different neural networks (Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977; Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). Indeed, some in the eye-movement literature have proposed that involuntary eye movements like OKN are not accompanied by an essential raw ingredient for coordination with other systems, namely extraretinal information about the eyes' veloc-

Introduction

Active observers alternate between periods of foveation and periods of gaze stabilization as they scan the scene around them (Moeller, Kayser, Knecht, & Konig, 2004). Foveation allows targets of interest to be more closely inspected, while gaze stabilization serves to counteract the whole-field retinal motion associated with self-motion. These distinct goals are thought to be achieved by separate eye movements systems: Saccadic and smooth pursuit systems control foveation, while the vestibular-ocular reflex (VOR) and optokinetic nystagmus (OKN) control stabilization (for reviews see

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ity and/or position (Post & Leibowitz, 1985; Whiteside, Graybiel, & Niven, 1965). This is problematic, because in the absence of extraretinal signals, the saccadic system would be largely ignorant of ongoing OKN and errors would abound when saccades were made during OKN. However, work on the coordination saccades and VOR, on the other hand, shows good coordination between reflexive VOR and intentional eye movement systems. Saccades are as accurate with or without head turn even though there is a rapid transition from VOR suppression during the saccade itself to VOR activation to stabilize the saccade endpoint while the head continues to move after the saccade (Corneil, 2011; Cullen, Huterer, Braidwood, & Sylvestre, 2004). Moreover, accurate saccades can be executed to the remembered location of a head-fixed target after the eyes have been displaced through VOR (Hansen & Skavenski, 1977), implying that VOR activity updates saccadic motor maps.

There are no studies of which we are aware investigating the accuracy of foveating saccades during OKN. However, work by Bedell et al. implies that nystagmus is accompanied by extraretinal signals, since open-loop pointing was reasonably accurate for flashed targets presented in the dark during after-nystagmus (Bedell, Klopstein, & Yuan, 1989) and also during the incessant eye motion accompanying infantile nystagmus syndrome (INS) (Bedell & Currie, 1993). There are therefore a number of reasons to expect effective communication between saccadic and OKN systems, to the point where we might question the traditional view of a dichotomy between reflexive and volitional processes and instead replace it with a more integrated approach (for reviews see McBride, Boy, Husain, & Sumner, 2012; Sumner & Husain, 2008). Such an approach would seem to sit quite comfortably with the idea that intentional behavior like saccades and pursuit emerged from phylogenetically older reflexive control systems like VOR and OKN (Harrison, Freeman, & Sumner, 2014; Post & Leibowitz, 1985; Ron, Robinson, & Skavenski, 1972; Walls, 1962).

Overview of experiments

Our first experiment tested the accuracy of vertical saccades to flashed targets made during horizontal OKN. At the outset, it is important to differentiate between two types of OKN identified in the literature: look OKN and stare OKN (e.g., Freeman & Sumnall, 2005; Fite, 1968). In Experiment 1, we focused on stare OKN, which occurs when participants passively view moving stimuli without trying to track any particular element in the moving display. It is considered fully automatic and characterized by slow phases that are small in amplitude, interspersed with ballistic fast-phases that recenter the eye at a frequency of about 3 Hz (e.g.,

Cheng & Outerbridge, 1974). As shown in Figure 1A, our task required observers to passively view a band of randomly moving dots that elicited a strong horizontal stare OKN, and then make a purposeful saccade to targets flashed briefly above or below the band of OKN dots. Figure 1B outlines two different predictions for how vertical saccades might behave during horizontal stare OKN. If there is no compensation then the retinal location of a briefly flashed target will determine the targeting eye movement and produce substantially inaccurate saccades (solid diagonal line in Figure 1B). However, if compensation for OKN occurs, then saccades will be accurate and arrive at the correct spatial location (dashed line in Figure 1B).

In Experiment 2 we directly compared the accuracy of saccades executed during stare OKN, look OKN, and three conditions of voluntary smooth pursuit, to investigate whether the communication between saccade planning and concurrent reflexive eye movements (stare OKN) is any worse than that between concurrent voluntary eye movements where extraretinal information is fully expected. Look OKN is elicited when participants are asked to purposefully track an element within a moving display and is characterized by slow phases of a longer amplitude and fast phases of a much lower frequency (Knapp, Gottlob, McLean, & Proudlock, 2008). Look OKN, unlike stare OKN, is usually accompanied by cortical activity in areas associated with pursuit and saccades (Freeman & Sumnall, 2005; Kashou et al., 2010; Konen, Kleiser, Seitz, & Bremmer, 2005; Schraa-Tam et al., 2009). Indeed some researchers assume look OKN is identical to alternating pursuit and saccades (Heinen & Keller, 2004).

Finally, we ran Experiment 3 to check whether differences in fast-phase frequency between oculomotor conditions had an important impact on our results, and to provide a further replication test of the data once this effect, if any, was controlled for.

Experiment 1—Saccadic compensation for OKN displacements

Method

Participants

Four paid observers (AH, GP, JH, ZM, aged 22 to 24, three female, all reporting normal vision) took part in the experiment. GP and JH (an author) had previous experience of eye-tracking experiments. All experimental procedures were approved by the ethics committee of the School of Psychology, Cardiff University, in accordance with the Declaration of Helsinki.

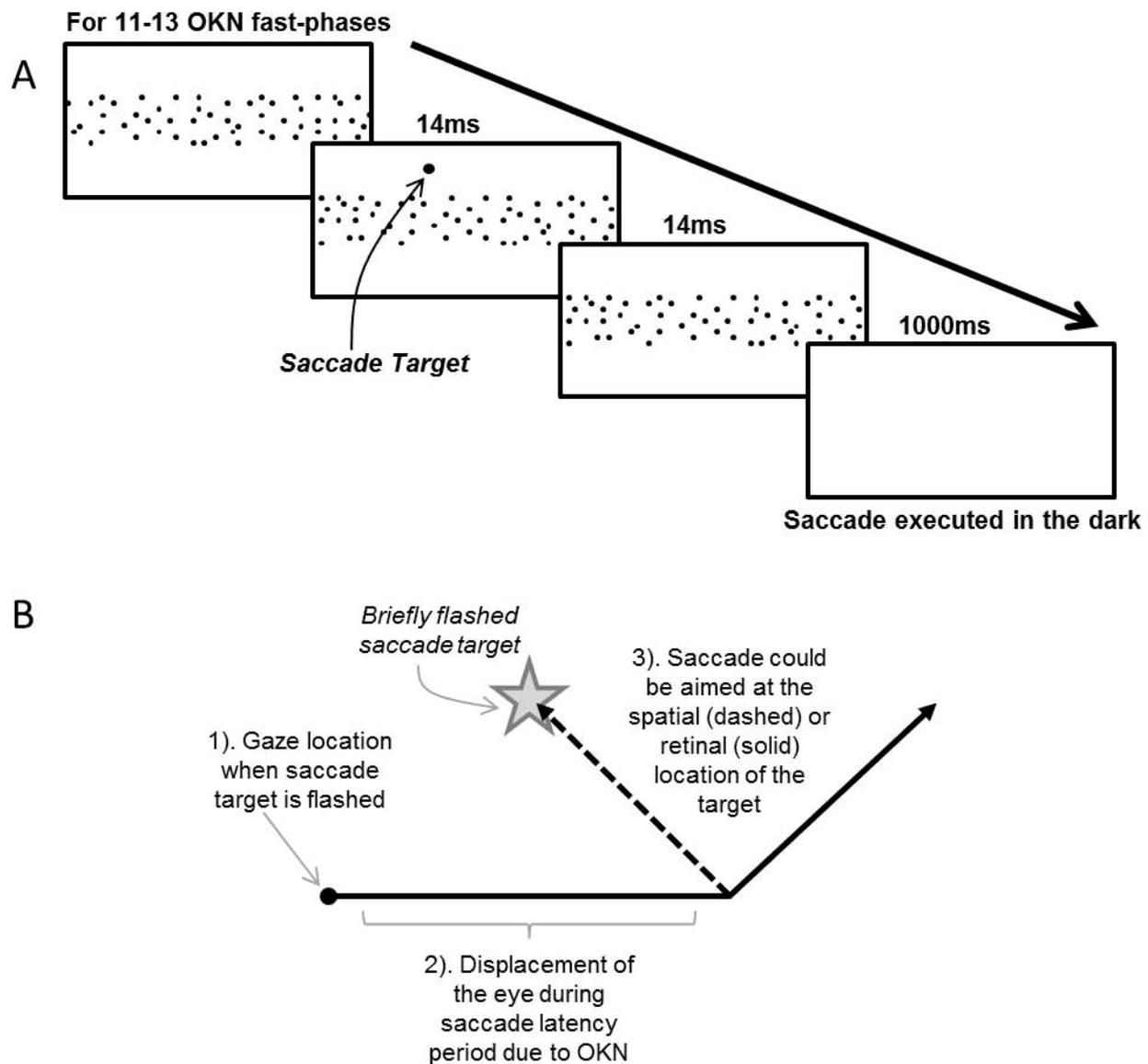


Figure 1. (A) Illustration of the stimuli for Experiment 1. OKN was elicited using a horizontally moving band of random dots. After detecting 11–13 OKN waveforms online, a saccade target was presented for 14 ms. (B) Since gaze will be displaced during the saccade latency period, a retinotopically planned saccade would be inaccurate by the same distance as the eye has traveled (solid diagonal line). If the saccadic system is sensitive to OKN activity, then the saccade may compensate for the displacement and land on the spatial location of the target (dashed line).

Materials

In all experiments stimuli were rendered using OpenGL software running on a Radeon 9800 Pro graphics card. Stimuli were rear projected onto a large screen (2.08×1.56 m, 1024×768 pixels) at a refresh rate of 72 Hz using a Sony Multiscan projector (VPH 1272QM). Only the central green cathode ray tube of the projector was used, and Gamma correction was used throughout. The rest of the lab was completely dark. Participants viewed the stimuli binocularly 140 cm from the screen. Eye movements were recorded using an SR Eyelink 2000 eye tracker mounted on the chin and forehead rest, at a rate of 1000 Hz using

standard video-based technology. To calibrate, participants fixated nine points separated by 10° in a 3×3 square grid. Calibration accuracy was checked by the experimenter and calibration was repeated if necessary (offline drift correction was conducted at analysis).

Stimuli

OKN was elicited by presenting observers with a band (16° high, 73° wide) of coherently moving random dots (density = $0.5 \text{ dots}/^\circ^2$), as shown in Figure 1A. Each dot had a radius of 0.3° and a brightness of $0.1 \text{ cd}/\text{m}^2$. The whole pattern moved horizontally at a speed of

32°/s in a direction chosen at random on each trial. The luminance of any dot moving into a 4° area at the extreme left or extreme right of the display was faded linearly to reduce the salience of the horizontal edges of the screen and so limit the use of fixed external references. For the same reason, observers were also kept light adapted, which was achieved by showing a blank screen of brightness 0.38 cd/m² for 5 s between each trial. To allow other stimuli to be presented at specific time-points within the OKN waveform, online detection of fast phases was achieved using a simple velocity threshold of 92°/s. Note that this online detection was only used to trigger the target stimuli; the actual analysis of OKN and targeting saccades was carried out offline and based on the recorded eye movements. On 25% of trials the band of dots remained stationary, which allowed measurement of saccadic accuracy in the absence of OKN.

The saccade target consisted of a dot with a radius of 0.6° and brightness of 1.06 cd/m². This was presented for 13.8 ms (equivalent to one frame at the refresh rate of 72 Hz). The target was positioned either 10° above or below the vertical center of the screen (therefore 2° above or below the band of OKN dots) and was randomly presented within 4° to either side of the horizontal center of the screen. Presentation of the saccade target was yoked in time to the participant's nystagmus waveform, appearing after 11 to 13 nystagmus fast phases (randomly selected on each trial) and 110, 160, or 260 ms following the detected fast phase (randomly shuffled). These onset times were chosen to allow the fast phase to be completed (estimated from pilot data at 60 ms) plus a variable time of 50, 100, or 200 ms. This allowed the targeting saccades to be executed early, in the middle, or near the end of the slow phase of the nystagmus. For baseline trials in which the dots were stationary, the target was triggered as though the fast phase frequency was 3 Hz, a reasonable approximation to published values for stare OKN (e.g., Cheng & Outerbridge, 1974; Kolarik, Margrain, & Freeman, 2010).

Procedure

Participants were told to passively view the band of moving dots, and upon appearance of the target, make an eye movement towards its location as quickly and as accurately as possible. Recording was split into 10 blocks, each composed of 40 trials and lasting about 13 min. Each block began with a calibration sequence. The participant initiated each trial with a mouse click, which triggered a small fixation dot of 0.6° at the center of the screen for 300 ms for the purpose of drift correction. The band of random dots then appeared and immediately started to move. The dots disappeared one frame after the saccade target was triggered. Thus

any eye movements that occurred during the saccade latency period were conducted in the dark. Observers had 1000 ms in which to make their saccade, since the eye will continue to move for around a second following cessation of OKN or smooth pursuit stimuli (Gellman & Fletcher, 1992; Leigh & Zee, 1999). Between each block of 40 trials the lights were turned on and participants were given the opportunity to take a break.

Data analysis

All eye-movement recordings were analyzed offline using Matlab. Eye traces were first smoothed with a Gaussian filter ($SD = 16$ Hz) and then velocity and acceleration profiles constructed by temporal differentiation. Fast phases of the OKN waveform were identified using a combination of acceleration (location of zero crossing), eye velocity (mean velocity across the fast-phase of at least 60°/s), local minima and maxima of position, and direction of motion (fast phases nearly always travel against stimulus motion). Detected fast phases had to be more than 40 ms apart to be accepted by the analysis program. To determine the velocity of slow phases, a mean was calculated that disregarded the velocity samples 50 ms immediately before and after a detected fast phase. If this mean was 50% greater than the stimulus velocity the candidate slow phase was flagged as an error. Drift correct was applied at the start of each trial.

Targeting saccades were detected within the appropriate slow phase using a velocity criterion of 100°/s. The start of the saccade was taken to be the time at which the velocity first rose above 20°/s. The endpoint of the saccade was defined as the part of the eye trace that did not deviate by more than 0.3° over a 100 ms period following the detected start of the saccade, and this was used to determine saccade accuracy. All trials were checked visually before being included in the final analysis.

Results and discussion

A typical eye trace is shown in Figure 2, in which the slow phase of OKN was rightward. The trace shows the saccade end point is biased in the direction of the displacement due to OKN, but the horizontal error is less than the displacement distance, demonstrating partial compensation. Since absolute error will depend on both the degree of compensation and the displacement of the eye during the latency period, a normalized error value was computed (Figure 3) by plotting the horizontal error against the displacement distance and calculating the slope. This method is more robust than simply dividing each error by displacement distance or

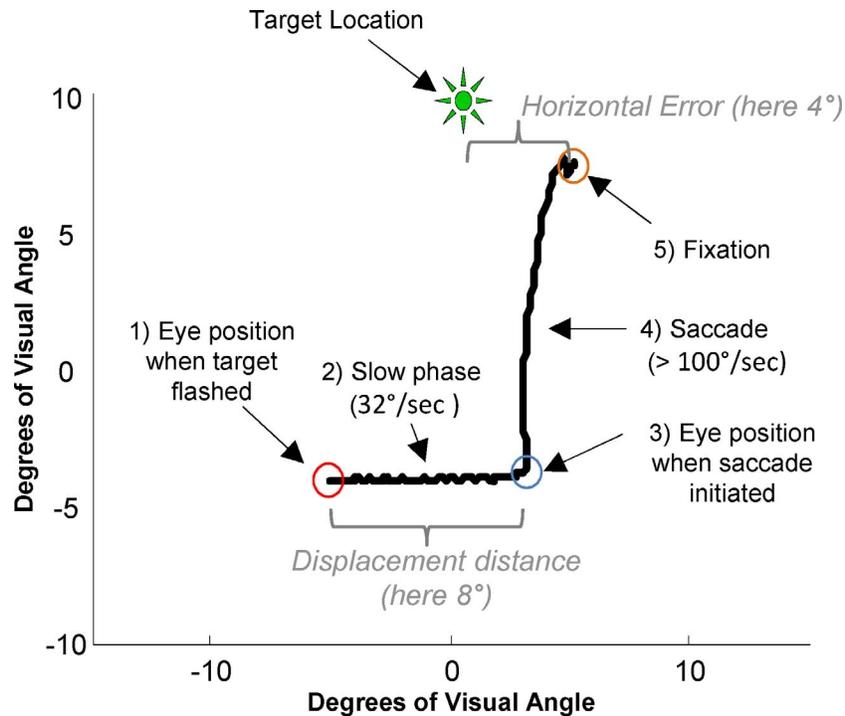


Figure 2. Typical eye trace from this experiment (black line, from JH). In this trial the OKN slow phase was rightward. The displacement distance is the distance the eye travels during the saccade latency period—i.e., between the position of gaze at the time of stimulus onset (red circle) and the position of gaze at the time of saccade onset (blue circle). Horizontal error is the difference on the x axis between target location (green symbol) and the saccade endpoint (orange circle). To obtain measure of normalized error robust against very small displacement distances, we find the slope of the line of best fit when horizontal error is plotted against displacement distance, as in Figure 3.

angle, which creates some very large values where displacement distance or angle is small; these would need to be filtered out by using an arbitrary criterion. To calculate slopes we use Deming regression, which assumes noise in both X and Y observations, such that the slope of Y on X is the exact inverse of the slope of X on Y . In simple linear regression the predictor X is assumed to be accompanied by no noise. Hence only the error in one axis is minimized, with the result that the slope of X on Y is not the inverse of Y on X .

If compensation were complete, we would expect no systematic relationship between the distance traveled during the latency period and the horizontal error. On the other hand, a complete lack of compensation would mean that the distance traveled becomes the horizontal error, giving a strong correlation with a slope of one. Figure 3 shows clear correlations for all observers but the slopes are less than one. This means that the error at fixation is systematically related to the amount of displacement due to stare OKN, but the magnitude of the error is less than the size of the displacement. Thus targeting saccades executed during stare OKN appear to partially compensate for the ongoing stare OKN eye movement. We checked whether the time since last fast phase influenced saccade accuracy, and found no

evidence for this (AH: $r = -0.068$, $p = 0.3$; GP: $r = 0.093$, $p = 0.14$; JH: $r = -0.001$, $p = 0.99$; ZM: $r = 0.16$, $p = 0.04$).

The results of Experiment 1 suggest that the saccadic system receives information about eye displacement during stare-OKN. However systematic errors in saccadic accuracy were still apparent. One possibility is that saccade planning is less well integrated with reflexive OKN than with more voluntary, pursuit-like eye movements. We test this possibility in Experiment 2, comparing the accuracy of saccades executed during concurrent stare OKN, look OKN, and smooth pursuit to a small target moving in three different viewing contexts.

Experiment 2—Saccade accuracy during stare OKN, look OKN, and pursuit

Saccadic accuracy during look OKN remains unknown, although some authors consider the slow phase to be identical to pursuit (Heinen & Keller, 2004). There are mixed reports of saccade accuracy during displacement due to pursuit. Some studies report good compensation (Hansen, 1979; Ohtsuka, 1994; Schlag,

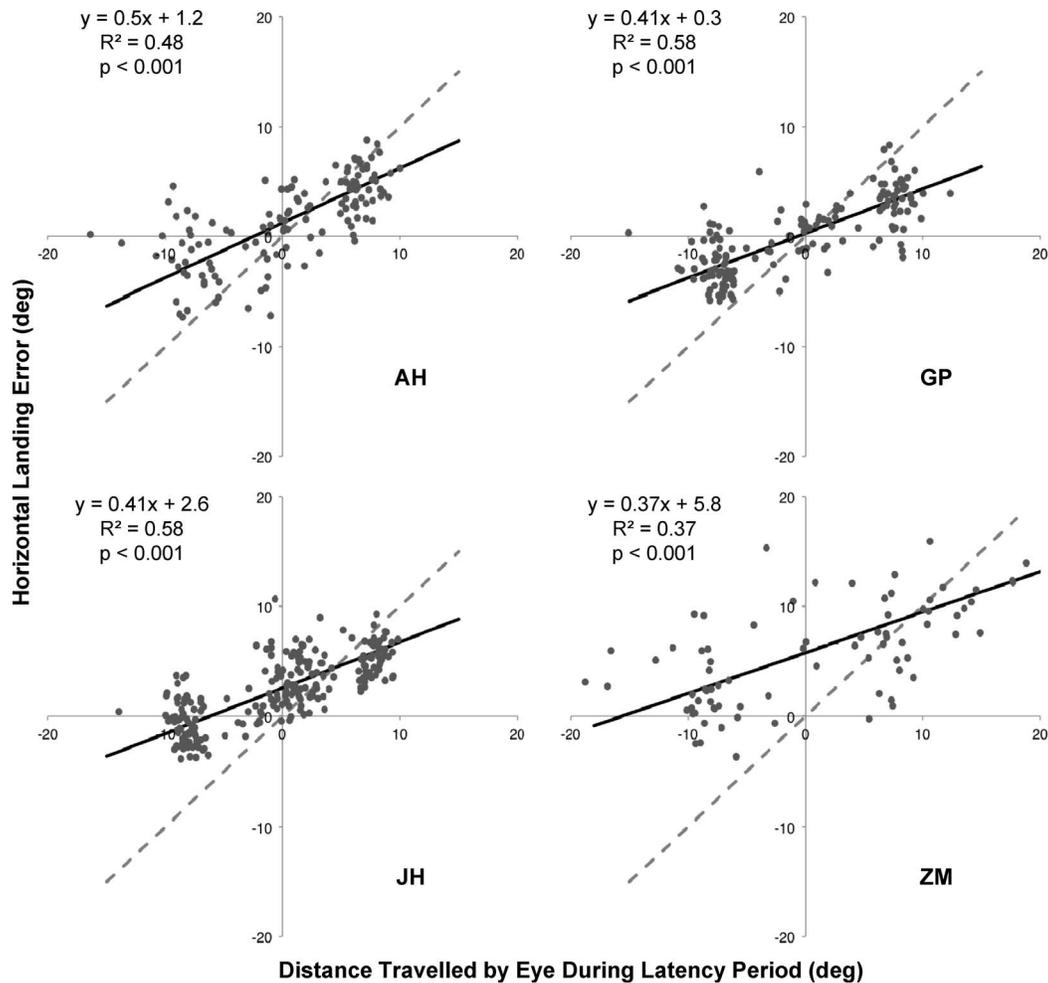


Figure 3. Correlation between the distance the eye travels during the saccade latency period and the horizontal error at fixation, for each observer. Dashed lines show a slope of one, solid lines show the Deming regression lines of best fit (which, unlike standard regression, assume error in both X and Y observations). Note that the relative absence of distance-travelled values of about 5° is due to the timing of saccades relative to when fast phases occurred. Values over 5° generally occurred when no fast phase intervened between target presentation and vertical saccade, while values under 5° generally occurred when there was a resetting fast phase before the vertical saccade.

Schlag-Rey, & Dassonville, 1990; Van Beers, Wolpert, & Haggard, 2001), while others report little or partial compensation (Daye, Blohm, & Lefèvre, 2010; Gellman & Fletcher, 1992; McKenzie & Lisberger, 1986). These differences may be due to target duration (Schlag et al., 1990) and whether saccades were required quickly or after a delay—accuracy was improved for delayed saccades even if pursuit continued during that delay (Blohm, Missal, & Lefèvre, 2005).

The objective in Experiment 2 was to compare reflexive stare OKN with voluntary look OKN and pursuit under closely matched conditions. Stare and look OKN conditions use identical stimuli and just a difference in task instructions (we check that instructions were followed below). In the pursuit conditions, by definition, a specified pursuit target is needed, so the stimuli cannot be exactly matched to the OKN

conditions. Therefore we used three types of pursuit condition to cover both traditional pursuit (a single stimulus) and closer stimulus matches to the OKN conditions. The latter used either background dots moving with the pursuit stimuli, which are expected to facilitate pursuit, presumably making it even closer to look OKN (Heinen & Watamaniuk, 1998; Niemann & Hoffmann, 1997; van den Berg & Collewijn, 1986), or background dots that were stationary, which could hamper pursuit by driving OKN in the opposite direction to the pursuit movement (Lindner & Ilg, 2006; Lindner, Schwarz & Ilg, 2001). Moreover, because these two pursuit conditions provide the same scene structure as in the two OKN conditions, saccadic accuracy might be improved over pursuit to an isolated target. We refer to these three conditions as: single-target pursuit, full-field pursuit, and static-background pursuit.

Method

Participants

This experiment was conducted on five participants (CR, GP, JH, LH, ZM, aged 22 to 25 years; all reported normal vision; three female).

Stimuli

The stimuli used to elicit stare and look OKN were identical to those in Experiment 1, except for the timings of saccade target presentation, due to the different fast-phase frequencies in stare and look OKN (any effect of fast-phase frequency is investigated in Experiment 3). We kept the stimuli as similar as possible and only changed the instructions to the participant, in order to enable the most direct comparison. For stare-OKN saccade targets were presented 50, 100, or 200 ms into the slow phase, as in Experiment 1. For look OKN they were presented randomly between 50 and 500 ms into the slow phase and classified as early (50–200 ms), middle (201–350 ms,) or late (351–500 ms). Saccade targets were triggered between five and 13 fast phases after the onset of OKN and the target was presented at a random position within 4° either side of the horizontal location of gaze at the time of target presentation.

The pursuit target consisted of a single dot of 0.3° radius and 0.38 cd/m² (the same size as the dots used to elicit OKN, but brighter). During pursuit the target moved at 32°/s for 30°. In single-target pursuit it was presented alone, in full-field pursuit it moved coherently with the OKN-dot display (which was identical to that for the OKN conditions), and during static-background pursuit the band of OKN dots did not move. The pursuit target's horizontal location at the start of the trial was up to 3° either side of the center of the screen (randomly determined on each trial) and the 30° amplitude of the pursuit target's motion was centered on the screen, with a random shift by up to ±3°. The pursuit target's vertical location was always in the middle of the screen. The saccade target's location and onset during the pursuit condition was determined in exactly the same way as described in the look-OKN condition.

Procedure

For stare OKN, participants were asked not to track any particular dot in the display, but not to allow the band of dots to become blurred. For look OKN, participants were asked to pick any particular dot and follow it across the screen for as long as they liked and then return their gaze to the other side of the screen to track another dot. For pursuit, participants were asked to follow the single bright dot only, regardless of whether it appeared superimposed upon a moving or

static background. In all conditions participants were asked to saccade to the vertically presented saccade target as quickly as they could. Standardized written instructions were given. Each condition was divided up into five blocks; each block consisted of 40 trials. The order of conditions (stare OKN, look OKN, single-target pursuit, full-field pursuit, or static-background pursuit) was randomized for each participant.

Results

In order to check that the manipulation to elicit either stare or look OKN was successful, the amplitudes and frequencies of nystagmus in these two conditions were compared (mean number of slow phases analyzed = 353 per participant for look, and 1,127 for stare, due to its higher frequency). Figure 4 shows example eye traces. There were clear differences between the two nystagmus waveforms: stare OKN showed high frequency (mean = 2.59 Hz, $SD = 0.52$ Hz), and small amplitude (mean = 11.29°, $SD = 7.30$ °) nystagmus that is characteristic of this type of eye movement (Freeman & Sumnall, 2005), whereas look OKN was lower frequency (mean = 1.22 Hz, $SD = 0.48$ Hz) and larger amplitude (mean = 29.41°, $SD = 5.64$ °). These differences were significant, $t(4) = 4.26$, $p = 0.013$, $r = 0.91$; $t(4) = -4.97$, $p = 0.008$; $r = 0.93$. We therefore concluded that the standardized instructions were successful in eliciting the reflexive or the volitional types of OKN as appropriate (Cheng & Outerbridge, 1974). As expected, pursuit gains were higher, $F(2, 8) = 51$, $p < 0.001$, $\eta^2 = 0.93$, with a moving background (mean = 0.89, $SD = 0.05$) than with a static background (mean = 0.70, $SD = 0.10$) or no background (mean = 0.69, $SD = 0.07$). There was no difference in gain between look OKN and full-field pursuit, $t(4) = -0.62$, $p = 0.568$, $r = 0.30$. We also checked for any consistent differences in saccade latency between conditions and found none (Table 1), $F(4, 16) = 1.3$, $p = 0.314$, $\eta^2 = 0.24$.

Following from the analysis described in Experiment 1, normalized error was obtained as the slope of the Deming regression between horizontal saccade error and the distance traveled by the eye during the saccade latency period for each condition for each participant. Recall that no compensation predicts a slope of one, while full compensation predicts no correlation between horizontal error and displacement distance. All correlations between distance and error were significant ($p < 0.001$) except for that of Participant 4's data in the look-OKN and static background pursuit conditions, which appeared to be influenced by a number of outliers. Since the regression slope is undefined when a correlation does not exist, we set the slope in these two cases to zero (which would bias the results towards better compensation for look OKN and pursuit than for stare OKN, which is opposite to our conclusions). As shown in

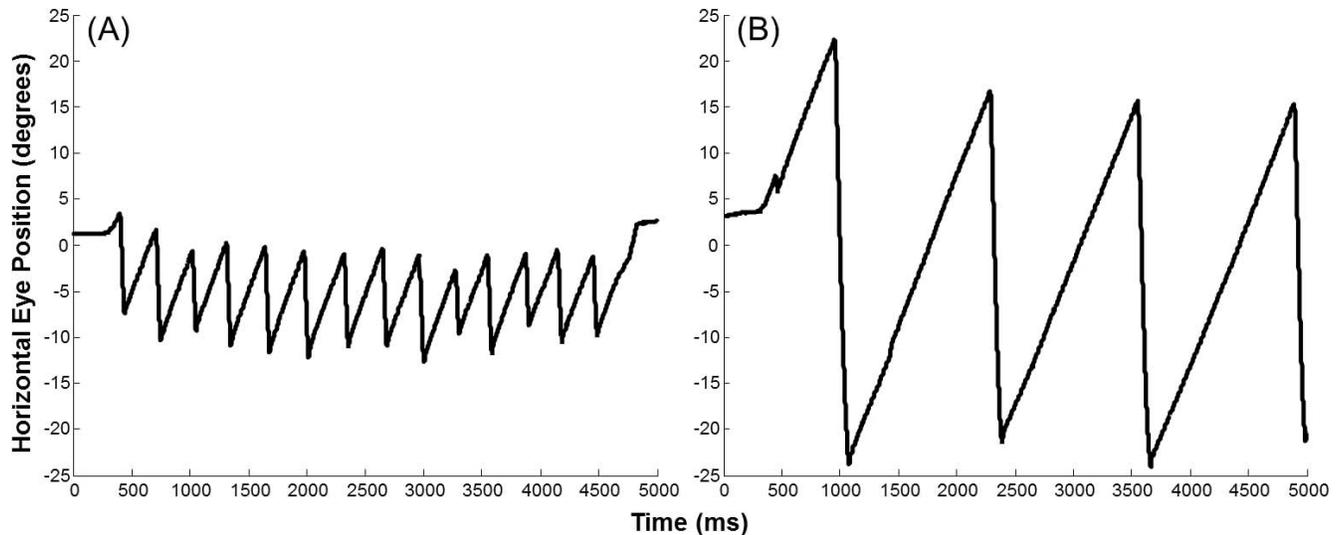


Figure 4. Example eye traces from one participant (JH). (A) shows a stare-OKN trial, whilst (B) shows a look-OKN trial. Note the characteristic small amplitude, but high frequency waveform of stare OKN.

Figure 5, the stare-OKN condition replicates the partial compensation found in Experiment 1 and there is no indication that normalized saccade error is greater during stare OKN than during look OKN or pursuit, $F(4, 16) = 1.3$, $p = 0.3$, $\eta^2 = 0.25$. Indeed, stare OKN was never the condition with the largest amount of error for any of our participants. Therefore there is no indication that saccadic planning is better able to compensate when the displacement during the saccade latency period is due to a volitional eye movement.

Previous researchers found that saccadic accuracy following pursuit displacements was improved at longer delays (Blohm et al., 2005; Blohm, Optican, & Lefèvre, 2006; Schlag et al., 1990). However, there was no evidence of a consistent relationship between saccade latency and normalized error in any of our conditions (Table 2). In some previous studies (Schlag et al., 1990) the extra delay was externally imposed by requiring saccade execution only after the smooth pursuit target extinguished (130–300 ms after the saccade target was displayed). Although the smooth pursuit target was moving throughout the imposed

delay, this may not be equivalent to extra delay from spontaneous variance in saccadic latency (Sumner, 2011).

Experiment 3—The effect of fast-phase frequency

By definition, stare OKN has a higher frequency of resetting fast phases than look OKN or pursuit, and a recent study on saccade curvature and saccadic inhibition has established that activity relating to fast phases can interact with saccade planning (Harrison et al., 2014). The results reported above contain no sign that any interaction from frequent fast phases makes compensation worse. However, there remained the possibility that fast phase interaction could enhance measured compensation if the resultant saccade vector was biased in the direction of an impending fast phase—which would often also be the directional bias needed for compensation to acquire the target position (if no other fast phase has yet taken place since target presentation). Therefore, Experiment 3 investigated whether fast-phase frequency might have affected the results reported above; specifically, whether compensation during stare OKN was not as good as during look OKN and pursuit once any effects of frequency are accounted for.

It is not possible to directly specify fast-phase frequency in either type of OKN, since by definition the participant is free to make the return saccade at any time. Frequency differences can be encouraged by different stimulus speeds, though only to a limited extent (Cheng & Outerbridge, 1974). With pursuit, both speed and frequency can be directly specified and unconfounded. We used the full-field pursuit condition

Participant	OKN		Pursuit		
	Stare	Look	Single target	Full field	Static background
CR	466.1	487.7	436.4	426.0	540.6
GP	296.8	268.0	265.1	263.6	285.9
JH	292.7	292.0	299.5	272.0	284.5
LH	433.8	410.2	450.7	390.6	383.6
ZM	339.6	416.9	341.2	333.7	352.0
Mean	365.8	375.0	358.6	337.2	369.3

Table 1. Saccade latencies (in ms) for each observer and each condition.

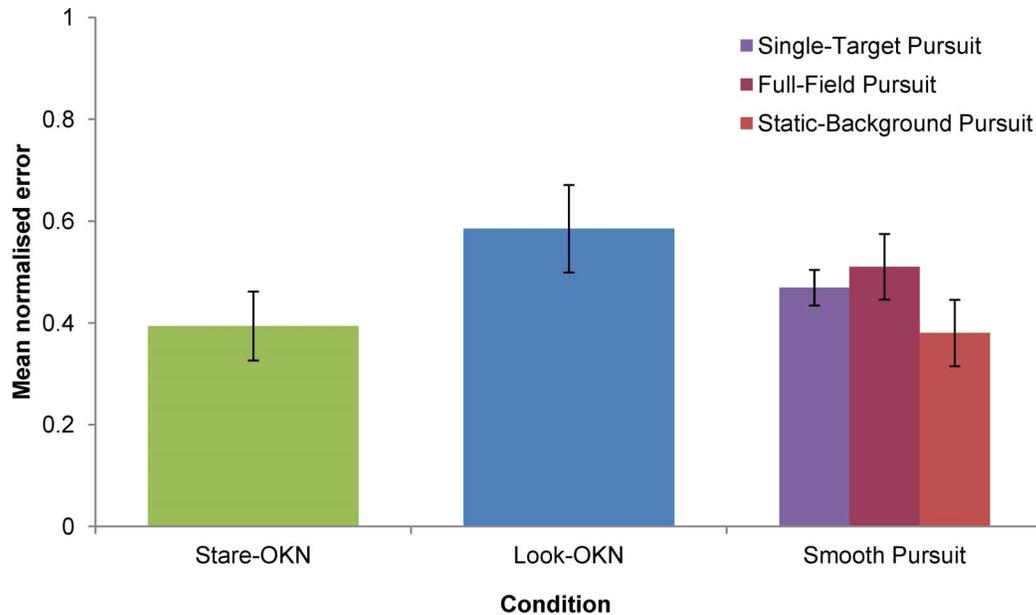


Figure 5. Mean normalised error (Deming regression slope) across all condition types. Error bars show ± 1 standard error with variance attributable to between-subject differences partialled out in line with Cousineau’s (2005) method.

of Experiment 2 to as far as possible equate the stimuli in pursuit and OKN conditions.

Method

Participants

There were five participants (AS, BD, GP, JH, LM, aged 23–35, three male, all reported normal vision). Two participants (GP and JH) participated in Experiments 1 and 2; three were naïve to this paradigm.

Stimuli

The stimuli displayed for stare OKN, look OKN, and full-field pursuit were as described in Experiment 2, except now there were two possible stimulus speeds ($32^\circ/s$ and $40^\circ/s$), and two specified frequencies for pursuit at each speed (1.067 Hz and 1.6 Hz). This meant there were

four pursuit conditions, requiring different amplitudes to meet the specified frequencies (low speed, low frequency, requiring an amplitude of 30° ; low speed, high frequency, amplitude 20° ; high speed, low frequency, amplitude 37.5° ; high speed, high frequency, amplitude 25°). The saccade stimulus occurred randomly in a specified temporal window following fast phase detections, in order to spread them through the waveform. The windows for stare OKN and look OKN at $32^\circ/s$ were identical to Experiment 2. For look-OKN at $40^\circ/s$, the saccade target window was 110–560 ms following fast-phase detection, owing to the shorter duration of slow phases. For the high and low frequency pursuit conditions the windows were, respectively, 110–460 ms and 110–760 ms following resetting saccade detection.

Procedure

The order in which each participant completed the eight conditions (four pursuit conditions and two conditions each for stare OKN and look OKN) was randomized. There were five blocks of 40 trials for each condition.

Results

For OKN, stimulus speed successfully changed fast-phase frequency, with mean frequencies increasing with the faster speed, 2.69 to 2.97 Hz for stare OKN; 0.95 to 1.14 Hz for look OKN, $F(1, 4) = 8.20$, $p = 0.046$, $\eta_p^2 = 0.67$. For pursuit, frequency closely followed the stimulus resetting frequency, and was not statistically affected by stimulus speed, as we hoped. The results

Participant	OKN		Pursuit		
	Stare	Look	Single target	Full field	Static background
CR	0.10	-0.34	0.19	0.02	-0.29
GP	0.15	0.42**	0.05	-0.19*	0.20*
JH	-0.05	-0.00	0.23	0.08	0.24*
LH	-0.03	0.17	0.24	-0.09	-0.10
ZM	-0.19	-0.02	0.11	-0.48**	0.20

Table 2. Correlation coefficients between saccade latency and normalized error. Normalized error was here calculated on a trial by trial basis by dividing absolute error by distance traveled in saccade latency period. * $p < 0.05$; ** $p < 0.005$.

	<i>B</i>	<i>SE B</i>	β
Saccade latency	−0.001	<0.001	−0.149**
Frequency	−0.036	0.02	−0.052
Stare-OKN vs. look-OKN	0.151	0.047	0.112**
Stare-OKN vs. pursuit	0.070	0.037	0.059

Table 3. Results from second step of multiple regression model. *B* = unstandardized beta coefficient; *SE B* = standard error of coefficient; β = standardized beta; * denotes $p < 0.01$; ** denotes $p < 0.001$. The variance accounted for using participant as a predictor ($R^2 = 0.014$) has been left out of the table for clarity. For Step 2, $\Delta R^2 = 0.031$ ($p < 0.001$).

also replicated Experiment 2 when collapsing the results within each eye-movement type and applying the same analysis: There was no hint that normalized error was greatest for stare OKN, means of 0.52, 0.55, 0.47, for stare OKN, look OKN, and pursuit, respectively; $F(2, 8) = 0.35$, $p = 0.7$, $\eta^2 = 0.08$.

We performed a multiple regression analysis to test for any effect of frequency on normalized error, and at the same time test for any effect of eye-movement condition once frequency is accounted for. Normalized error on each trial was the dependent variable, and since this was required on a trial-by-trial basis for the analysis, it was here calculated simply by dividing absolute error by distance traveled in saccade latency period. The problem of small divisors was avoided by rejecting outliers where normalized error was greater than three or less than minus three. Following Lorch and Myers (1990), “participant” was entered into the regression model as the first independent variable using four ($N - 1$) dummy variables, which removed any significant between-subjects variance, $R^2 = 0.014$, $F(4, 2976) = 10.45$, $p < 0.001$ prior to investigating the influence of the other independent variables (see also Field, 2005). In the second step, eye-movement condition, fast-phase frequency, and saccade latency were added as independent variables. Eye-movement condition was coded with two dummy variables such that stare OKN formed the baseline category (Davis, 2010; Howell, 2007). Frequency (the mean frequency on each trial in the 5–13 cycles before target presentation) and saccade latency were treated as continuous variables.

The results of the second step of the regression analysis are shown in Table 3. Frequency had no significant effect on the magnitude of normalized error. There was a significant effect of latency ($t = 7.2$, $p < 0.001$), such that longer latencies were associated with a decrease in normalized error, but this effect was very slight (beta = 0.001). Whilst controlling for any effects of frequency and latency, errors were actually larger during look OKN than stare OKN ($t = 3.24$, $p = 0.001$). The regression analysis also reported that errors were possibly larger during pursuit than during stare OKN ($t = 1.89$, $p = 0.06$). Therefore, as in Experiment 2 we

again find no evidence for improvement in saccade accuracy when the displacement was due to a volitional eye movement (either look OKN or pursuit); surprisingly, we found slight effects in the opposite direction.

General discussion

Some authors have questioned whether reflexive OKN is accompanied by extraretinal information that informs voluntary foveation systems about ongoing stabilization eye movement (Post & Leibowitz, 1985; Whiteside et al., 1965); in other words, whether systems considered reflexive are as well integrated with volitional control systems as volitional systems are with each other. In each of three experiments, we found that volitional saccades made in the dark to brief targets partially compensated for displacements due to stare OKN. Hence saccadic-planning centers seem to know—at least to some extent—what the reflexive OKN system is doing. In each experiment mean errors were a third to a half the size of those predicted if there were no compensation. Most interestingly, compensation during reflexive stare OKN was at least as good as compensation during volitional look OKN and smooth pursuit under comparable conditions, as shown in both Experiments 2 and 3. Therefore we conclude that stare OKN is accompanied by an extraretinal signal that is just as informative as that accompanying look OKN or pursuit, and this enables saccades to be just as well coordinated with each type of tracking movement. This conclusion is consistent with the exquisite coordination reported between saccade and VOR systems (e.g., Corneil, 2011).

Why only partial compensation?

Efficient saccade behavior by moving observers might be expected to demand complete compensation for OKN and pursuit. The degree of compensation measured here for both types of OKN as well as pursuit sits within the (wide) range reported previously for saccade-pursuit interaction (Daye et al., 2010; Gellman & Fletcher, 1992; Hansen, 1979; McKenzie & Lisberger, 1986; Ohtsuka, 1994; Schlag et al., 1990; Van Beers et al., 2001). Nevertheless, the remaining error demands some discussion, given that it is around a third to a half of the distance traveled by the eye. We believe there are two critical factors limiting compensation in our design compared to normal viewing environments, and one factor that limits compensation whenever saccades are required as soon as possible. The first two factors are brief target duration and the use of a dark room with no visible external references, which we purposely employed in order not to provide ongoing visual information

during saccade planning. In normal viewing, of course, visual information about target and background is continuously available and it is known that retinal feedback can modify saccadic plans up until about 80 ms before the saccade is initiated (Becker & Jürgens, 1979; Bompas & Sumner, 2011; Reingold & Stampe, 2002).

More interesting, perhaps, is how the effect of intrinsic variability in saccade latency is taken into account whenever saccades are required as soon as possible. Even with perfect extraretinal and retinal information about eye displacement, the system cannot plan for the exact displacement that will have occurred at the moment of saccade initiation unless it knows when that moment will be. But given the wide distribution of saccade latencies, even for the most basic tasks, it is unlikely that the saccade planning system can know exactly when the upcoming saccade is going to be initiated. Instead the system has to continuously update a spatiotopic reference frame during the saccade latency period, which is then translated back into the retinotopic coordinates of the superior colliculus, presumably creating a moving hill of retinotopic activity. In other words, the limitations we have measured may not be imperfect communication between nystagmus, pursuit, and saccade systems, but rather the consequence of unpredictability of saccade latency within the saccade system itself and the effect of this on translation between reference frames. In contrast, paradigms such as double-step saccades, where the eye is static during the latency period, will be unaffected by variable time delays. In these cases, perhaps it is unsurprising that the updating and compensation subsequently measured is seemingly more accurate than found here (e.g., Becker & Jürgens, 1979; Vliegen, Van Grootel, & Van Opstal, 2005).

OKN fast phases and saccades

Our results showing a degree of integration between saccades and the slow phases of OKN are consistent with previous research showing integration and similarities between saccades and the fast phases of OKN. Saccades and fast phases have a very similar main sequence (Guitton & Mandl, 1980) and latency distributions (Carpenter, 1993; Carpenter, 1994; Roos, Calandrini, & Carpenter, 2008) and can be modeled by accumulator models that were originally designed for saccades (Carpenter & Williams, 1995; Roos et al., 2008). Saccades and fast phases both suffer the saccadic inhibition effect produced by irrelevant visual stimuli, and interact to produce targeting saccades that are curved (Harrison et al., 2014). In real viewing, fast phases of OKN appear to take on object-targeting properties just like saccades (Moeller et al., 2004), and to do so they would have to accommodate the displace-

ment occurring during the slow phase. Taken together, the evidence suggests that saccades and OKN are better considered as one integrated system rather than separate reflexive and volitional systems. This parallels the view that pursuit and saccadic systems also share common neural machinery (Krauzlis, 2004).

Summary

We found that saccades are partially compensated for displacements of the eye due to optokinetic nystagmus. Furthermore saccades were no more sensitive to look OKN or smooth pursuit displacements than they were to stare OKN. Our results therefore suggest that automatic eye movements are accompanied by extraretinal signals that are just as informative as those accompanying volitional eye movements. We conclude that saccade planning is closely coordinated with all types of foveating and stabilizing eye movements, allowing a moving observer to most efficiently act when viewing natural stimuli, with no evidence for any categorical divide between eye movements that appear volitionally willed and those that appear reflexively elicited.

Keywords: automatic, control, exogenous, endogenous, oculomotor

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