Human optokinetic nystagmus and spatial frequency

Jonathan Waddington
Christopher M. Harris

Optokinetic nystagmus (OKN) is a fundamental oculomotor response to retinal slip generated during natural movement through the environment. The timing and amplitude of the compensatory slow phases (SPs) alternating with saccadic quick phases (QPs) are remarkably variable, producing a characteristic irregular sawtooth waveform. We have previously found three stochastic processes that underlie OKN: the processes that determine QP and SP amplitude and the update dynamics of SP velocity. SP and QP parameters are interrelated and dependent on SP velocity such that changes in stimulus speed can have a seemingly complex effect on the nystagmus waveform. In this study we investigated the effect of stimulus spatial frequency on the stochastic processes of OKN. We found that increasing the spatial frequency of suprathreshold stimuli resulted in a significant increase in SP velocity with a corresponding reduction in retinal slip. However, retinal slip rarely reached values close to 0, indicating that the OKN system does not or cannot always minimize retinal slip. We deduce that OKN gain must be less than unity if extraretinal gain is lower than unity (as empirically observed), and that the difference between retinal and extraretinal gain determines the Markov properties of SP velocity. As retinal gain is reduced with stimuli of lower spatial frequency, the difference between retinal and extraretinal gain increases and the Markov properties of the system can be observed.

Introduction

Natural movement through the environment causes the image of the visual scene to drift across the retina and disrupt vision. Optokinetic nystagmus (OKN) is an oculomotor response that is believed to compensate for this retinal slip during slow head and body movements. OKN consists of an alternating sequence of compensatory slow phases (SPs) made in the direction of retinal slip and saccadic quick phases (QPs) made predominantly in the opposite direction. Although neural pathways for OKN have been studied for decades, it is a surprisingly complex behavior, and its functional role in humans still remains uncertain.

In birds and lateral-eyed afoveate mammals, the OKN response is generated predominantly by subcortical pathways that produce a slow buildup of eye velocity referred to as the indirect, delayed, or velocity storage component of the optokinetic response (OKNd). OKNd appears to supplement the rotational vestibulo-ocular reflex at low temporal frequencies. It is elicited during prolonged self-rotation in the light by global retinal motion, as the response of the rotational vestibulo-ocular reflex declines (Robinson, 1981; Schweigart, Mergner, Evdokimidis, Morand, & Becker, 1997).

However, in humans and other primates, OKNd is typically dominated by another form of OKN with fast dynamics, referred to as the direct or early optokinetic response. This form shares similarities with the ocular following response and is thought to be driven by local retinal motion involving similar (if not the same) cortical and cerebellar pathways as smooth-pursuit eye movements (Abadi, Howard, Ohmi, & Lee, 2005; Büttner & Büttner-Ennever, 2006; Cohen, Henn, Raphan, & Dennett, 1981; Cohen, Matsuo, & Raphan, 1977; Gellman, Carl, & Miles, 1990; Miles, 1995, 1998; Miles, Kawano, & Optican, 1986; Simons & Büttner, 1985). This has been highlighted in clinical cases where the smooth-pursuit pathway was damaged and the early optokinetic response was lost, while the slow buildup of eye velocity generated from OKNd was preserved (Harris, Walker, Shawkat, Wilson, & Russell-Eggitt, 1993; Yee, Baloh, Honrubia, Lau, & Jenkins, 1979).

Most studies of OKN have ignored QPs and averaged SP velocity over consecutive cycles to obtain a smooth measure of eye velocity. However, when the details of individual cycles are examined, a remarkable degree of variability is observed, even when stimulus velocity is held constant (Anastasio, 1996; Balaban &
The stochastic processes
the previous SP),
autoregressive equation with the update dynamics
i
components (Waddington & Harris, 2012).

evidence for a complex stochastic system of three
using principal-components analysis (PCA) and found
study we analyzed the local correlations between cycles
2002; Waddington & Harris, 2012, 2013). In a recent,
Ariel, 1992; Carpenter, 1993, 1994; Cheng & Outer-
dern variables. The
Figure 1. Geometric representation of OKN and the character-
istic variables. The
constants. The stochastic processes

where

where

and

are uncorrelated. However, because
multiple components, the variables V, S, Q, x, and y are mutually correlated (and autocorrelated) in a complex sequence of cycles (see Figure 1 and Table 1 for a full description of the system).

More recently, we investigated the stochastic nature of the QP switching mechanism (Waddington & Harris, 2013). Previous models of OKN had typically considered QPs to be regular resetting saccades, which are triggered stochastically after a certain period of time. However, our model indicated that QPs were triggered primarily after the eyes had moved a certain distance, with some constraints on timing caused by the dependence of the SP amplitude threshold on SP velocity (Equation 2). This model gives rise to a complex ratio distribution of SP duration (S/V → T) in which the denominator and numerator variables are correlated. We derived the probability density function (pdf) for this model in our previous study and compared it to the pdfs predicted from five other models of the QP trigger to demonstrate its superior fit to the data.

From these studies we concluded that OKN is controlled by a more complicated system than a simple retinal-slip feedback loop with regular resetting saccades. In particular, SP velocity tends to wander in a Markov fashion (see Appendix for an explanation of Markov processes) and does not always maintain low retinal slip, leading us to question the long-held assumption that OKN strives to minimize retinal slip per se.

It is not clear why SP velocity should be so variable, although one possibility is that it is the result of variability in retinal gain, which is dependent on visual contrast and presumably contrast sensitivity, and hence the speed, spatial frequency, and retinal location of the stimulus (Kelly, 1979, 1984). Most previous studies of the effect of spatial frequency on OKN have used stimuli at or near the contrast threshold, with the goal of using eye movements as a behavioral response measure in a detection task. In these studies, OKN eye-movement parameters are typically not investigated, other than to verify whether or not they occur under given stimulus conditions (Cetinkaya, Oto, Akman, & Akova, 2008; Leguire, Zaff, Freeman, Rogers, & Bremer, 1991; Wester, Rizzo, Balkwill, & Wall, 2007). Suprathreshold studies are few and conflicting. Schor and Narayan (1981) demonstrated that at low stimulus speeds, increasing spatial frequency had very little effect, but at moderate speeds, it resulted in a decrease in SP velocity. More recently, Sumnall, Freeman, and Snowden (2003) demonstrated that at low stimulus speeds, increasing spatial frequency actually resulted in an increase in SP velocity.

It is not clear how parameters of the OKN stimulus other than stimulus speed affect the OKN waveform. If the purpose of OKN is simply to minimize retinal slip, then it seems appropriate to assume that the spatial parameters of the stimulus would have no effect. However, there is some evidence to indicate that this is not the case. In this study we decided to investigate the effect of spatial frequency on OKN. We chose three spatial frequencies—0.05, 0.1, and 0.2 c/°—each presented to eight subjects at two speeds: 10°/s and 30°/s. We employed PCA as previously reported in order to quantify how (or whether) spatial frequency changed the stochastic Equations 1 through 3.
Table 1. Dynamic equations for OKN variables.

<table>
<thead>
<tr>
<th>Equation number</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>( V_{i+1} = eV_i + e_q(i) )</td>
</tr>
<tr>
<td>2</td>
<td>( S_i = ax_i + bV_i + e_q(i) )</td>
</tr>
<tr>
<td>3</td>
<td>( Q_i = cy_i + dV_i + e_q(i) )</td>
</tr>
<tr>
<td>4</td>
<td>( y_i = x_i + S_i )</td>
</tr>
<tr>
<td>5</td>
<td>( x_{i+1} = y_i + Q_i )</td>
</tr>
<tr>
<td>6</td>
<td>( T_i = S_i/V_i )</td>
</tr>
<tr>
<td>7</td>
<td>( x_{i+1} = (1 + a)(1 + c)x_i + \left( (1 + c)b + d \right)V_i + (1 + c) \left( e_q(i) \right) )</td>
</tr>
<tr>
<td>8</td>
<td>( y_{i+1} = (1 + a)(1 + c)y_i + \left( (1 + a)d + be \right)V_i + b \left( e_q(i) \right) )</td>
</tr>
<tr>
<td>9</td>
<td>( S_{i+1} = (1 + a)(1 + c)S_i + \left( - b(1 + c - e) + ad \right)V_i + b \left( e_q(i) \right) + e_s(i + 1) )</td>
</tr>
<tr>
<td>10</td>
<td>( Q_{i+1} = (1 + a)(1 + c)Q_i + \left( - d(1 + c - e) + cbe \right)V_i + (cb + d) \left( e_s(i) \right) + (1 + a) \left( e_q(i) \right) + c \left( e_s(i + 1) \right) + e_q(i + 1) )</td>
</tr>
<tr>
<td>11</td>
<td>( T_{i+1} = \frac{(1 + a)(1 + c)T_i}{e + e_q(i)} + \frac{- b(1 + c - e) + ad}{e + e_q(i)} \frac{1}{eV_i + e_q(i)} + \frac{b}{eV_i + 1} )</td>
</tr>
</tbody>
</table>

**Materials and methods**

**Participants**

Eight healthy adults (six male, two female), with a mean age of 26 (SD = 4) years, participated in the study and had no self-reported neurological, ophthalmological, or vestibular impairments. The visual acuity of each participant was measured using a Snellen chart before consent to participate was elicited, and only participants with uncorrected binocular visual acuity of 6/6 or higher on the Snellen scale were included in this study. All protocols were approved by the Plymouth University Faculty of Science Human Research Ethics Committee. Participants gave informed written consent and were made aware of their right to withdraw at any time.

**Procedure**

Participants sat in a chair 1 m from the middle of a flat white screen (1.57 × 1.17 m landscape, subtending 76° × 61°) with the tangent error uncorrected. The OKN stimulus was rear projected (Epson EMP-500; Seiko Epson Corporation, Suwa, Japan) onto the screen at a frame rate of 60 Hz. During the procedure, the room was kept completely dark except for the luminance of the projection onto the screen. The participant’s head was constrained using a chin rest. Eye movements were measured using a binocular head-mounted eye tracker (Skalar IRIS Infrared Light Eye Tracker; Skalar Medical BV, Breda, Netherlands) that recorded horizontal eye movements with a maximum resolution of 3 arcmin at a sampling rate of 1 kHz. Measurements were recorded on a computer (vsgEye-trace v. 3.0.beta software for Windows; Cambridge Research Systems, Cambridge, UK) and stored for offline analysis.

The eye tracker was calibrated for each participant at the start of each procedure and again halfway through the procedure, after participants had a break. Calibration was performed by recording the voltage output of the eye tracker during fixation of 40 targets placed at different positions on the horizontal midline of the screen. The voltage was linearly proportional to eye position within ±20° of the center of the display, and linear regression was used to generate a calibration scale and offset.

Translational OKN was elicited with a flat vertical square-wave grating, composed of alternating black and white vertical stripes moving horizontally at a fixed tangential speed. Each recording session comprised a
pseudorandom sequence of 12 trials, each with a different spatial frequency (0.05, 0.1, or 0.2 c/°), stimulus speed (10°/s or 30°/s), or direction (leftward or rightward).

For our analysis we required a relatively long time series of OKN data, so each stimulus presentation was recorded for 100 s. To alleviate discomfort from long periods of OKN stimulation we chose to use stimuli with comparatively low spatial frequency and speed. Participants were instructed to stare at the center of the screen rather than follow the moving lines, to evoke “stare” OKN rather than “look” OKN (Honrubia, Downey, Mitchell & Ward, 1968), and attention was maintained by giving brief verbal feedback about the amount of time lapsed during the stimulus presentation approximately every 10 s. Participants were given a break for 1 min after each trial to alleviate discomfort and tiredness and to minimize the effects of any optokinetic after-nystagmus. Participants were given an additional 5-min break after the sixth presentation, after which the eye tracker was recalibrated.

Data analysis

Movement in the direction of the stimulus motion was defined as positive, and movement in the opposite direction as negative. Position was defined as positive on the side that the stimulus is drifting towards relative to the center of the stimulus display, and negative on the opposite side.

All programs and algorithms for analyzing data were developed and created in MATLAB (MathWorks, Natick, MA). Each eye was calibrated separately, and the average was computed to yield a cyclopean eye position. Eye velocity was derived from the eye position using a central difference algorithm and an 80-Hz Butterworth filter with zero phase. Eye acceleration was derived from the filtered eye-velocity data using a central difference algorithm.

During a forward pass of the data, possible QPs were detected when eye acceleration became greater than ±1000°/s². Peak velocity was then recorded from the time 1 ms before velocity first decreased, if velocity remained at a lower magnitude for more than 4 ms. The starting and ending point of each QP was determined by respective backward and forward passes of the data from the time of peak velocity to the time when eye velocity returned to a value between 0°/s and the stimulus speed for a period of 2 ms or more. This procedure allowed us to collect QPs that were made in the direction of optic flow as well as QPs made in the opposite direction.

All eye movements were reviewed in a customized interactive graphical interface. Blinks were detected manually, and cycles containing blinks were marked and removed from the analysis. After blinks were extracted, each recorded trial contained m SP–QP cycles, where m ranged from 63 to 342. Six measurements were taken from each OKN cycle: xᵢ, Sᵢ, Vᵢ, Tᵢ, yᵢ, and Qᵢ (i = 1, . . . , m), according to the scheme in Figure 1 (where x is the SP start position and y is the QP start position). When calculating the mean, median, and standard deviation of variables from each trial, the first 5 s was removed from the analysis to ignore early OKN behavior.

Linearity of slow phases

There are three constraints to consider on the OKN variables we have selected (Equations 4–6). Equations 4 and 5 must be true by definition, and Equation 6 is true if SPs have constant SP velocity. We observed that SPs were grossly linear when plotted as position against time, although individual SPs could be nonlinear. We performed linear regression of eye position against time on all 19,120 recorded SPs and collected the residuals of each linear fit, sampled every 1 ms from the start to the end of each SP. If SPs were grossly nonlinear, we would expect residuals to depend on when they were sampled from each SP (e.g., performing a linear fit on an accelerating SP would produce predominantly positive residuals at the start and end of each SP, and negative residuals in the middle).

We plotted the mean value of residuals against the time at which they were sampled during each SP, as a fraction of the total duration of the SP on a scale from 0 (the start of each SP) to 1 (the end of each SP). We observed a very slight but significant trend in the mean value of residuals (Figure 2) that indicated that SPs tended to start slightly faster than the average SP velocity and decelerate over the course of the SP. However, the deviation from expected position was typically less than 3 arcmin (0.05°), indicating that SPs were still grossly linear.

Distribution fitting

In our model of OKN, we expect the distribution of SP duration to be determined by the ratio of two variables: SP amplitude and SP velocity. In a previous study we derived the pdf for the ratio of two correlated and zero-truncated normal variables (Waddington & Harris, 2013). We considered the goodness of fit of six different distributions (including the ratio distribution) to the histogram of SP duration from each trial to determine whether the ratio distribution gave the best fit to the data.

The distributions we tested were predicted from models of the QP trigger that we and others had
We found the maximum-likelihood estimates of the pdf parameters for each distribution, and tested the goodness of fit of all six distributions to the SP duration histogram from each trial using the chi-square criterion. Maximum-likelihood estimates were obtained using the MATLAB statistics toolbox function mle with the exception of the correlation coefficient, which was estimated using the sample Pearson’s correlation coefficient between SP amplitude and SP velocity from the respective trial. The chi-square test statistic was calculated using the MATLAB function chi2gof, using the fitted pdf to give the expected frequency and the SP duration histogram to give the observed frequency. Each SP duration histogram was originally covered by 45 bins of equal size, and the expected and observed frequencies were determined from the midpoint of each bin. When the expected frequency from a bin in either tail of a histogram was less than 5, the chi2gof function automatically merged neighboring bins until there was a minimum expected frequency of 5 or more in every bin, to maintain the reliability of the test.

Principal-components analysis

Variables from adjacent OKN cycles were grouped to create a vector that was used to generate a correlation matrix for each trial. We defined an OKN cycle as one SP followed by one QP. Each vector contained the variables $x_i$, $i = 1, \ldots, 5$, and $S_i$, $V_i$, $T_i$, $y_i$, and $Q_i$, $i = 1, \ldots, 4$, to generate a $25 \times 25$ element correlation matrix. Cycles separated by blinks were not included in generating the correlation matrix. During one trial, blinks were so frequent that a correlation matrix could not be created, so only 95 of 96 correlation matrices were analyzed using PCA.

We performed PCA using the MATLAB function pca to diagonalize the correlation matrices and yield the underlying eigenvectors and eigenvalues. We discarded the eight components with the smallest eigenvalues from each trial to retain 13 principal components. The remaining eigenvectors explained over 99.3% of the variability in the data, indicating that the data were well explained by the (linear and stochastic) components. After discarding redundant components, we performed factor rotation using the varimax strategy to obtain orthogonal rotated components using the MATLAB function rotatefactors. After factor rotation, similar loading patterns were observed across trials but expressed in a different eigenvalue order. The 13 principal components from each trial were sorted into categories according to their loading pattern using numerical heuristics. As eigenvectors can be rotated to face in the opposite direction, it was necessary to flip the sign of all loadings in these mirrored components so that they could be sorted correctly. Each loading pattern was then displayed as a line plot of loading value against OKN variable, where components placed in the same category were averaged across trials and error bars were used to show the variability between trials. This sorting was exhaustive, and we found that all loading patterns clearly fell into only three qualitatively different categories (see Results).
Results

Stimulus effects on OKN variables

OKN waveforms were grossly similar to those previously reported in the literature, although we noted that SP velocity was remarkably variable across cycles, as we had observed in our previous investigation (Waddington & Harris, 2012). The variability was particularly noticeable at the higher stimulus speed (see Figure 3 for an example waveform).

We performed a three-way analysis of variance on the mean value of OKN variables, using stimulus spatial frequency, speed, and direction as factors. Increasing spatial frequency resulted in a significant increase in mean SP velocity, $F = 6.8, p = 0.009$, and consequently a decrease in retinal slip (Figure 4A), although retinal slip did not fall to zero. Increasing stimulus speed also resulted in a significant increase in mean SP velocity as expected, $F = 14.5, p = 0.007$.

Remarkably, we found that at stimulus speeds of 10°/s and 30°/s, retinal slip reached values greater than 3°/s in over 30% and 87% of SPs, respectively.

SPs and QPs tended to compensate for each other over time, so the mean magnitude of SPs and QPs for each trial were typically identical. Spatial frequency and stimulus speed had an interaction effect on the mean SP magnitude, $F = 4.8, p = 0.025$, and mean QP magnitude, $F = 6.4, p = 0.01$. Essentially, increasing spatial frequency resulted in an increase in both mean SP and QP magnitude, but the effect of increasing spatial frequency was greater at 30°/s than at 10°/s (Figure 4B). We did not find an effect of spatial frequency or stimulus speed on the mean angle of contraversion, which was held at $-3.9°$ when averaged across all trials.

Increasing spatial frequency did not have a significant effect on the median SP duration, but increasing stimulus speed resulted in a significant decrease, $F = 12.5, p = 0.009$ (Figure 4C).

Distribution of SP duration

Histograms of SP duration were usually positively skewed, as expected (e.g., Cheng & Outerbridge, 1974), and 89% were significantly different from Gaussian (Holm–Bonferroni-corrected Lilliefors test, $p < 0.004$ for 85 trials; Holm, 1979). Histograms of reciprocal SP duration (QP rate) were also usually positively skewed, and 85% were significantly different from Gaussian.
We found the maximum-likelihood estimates of pdf parameters from each trial and tested the goodness of fit of six defined pdfs to each SP duration histogram using the chi-square criterion (see Materials and methods). The ratio distribution (RATIO) gave the best fit to the data and was able to fit 90% of SP duration histograms (Table 2). This appeared to verify our model of QPs as saccades triggered after the eyes had moved a certain distance, with the complex distribution of SP duration determined by the ratio of an SP amplitude threshold and SP velocity that varied between cycles. The other pdfs that were tested were based on models of QPs as regular resetting saccades that are triggered stochastically after a certain period of time (see Materials and methods). The reciprocal normal mixture model (mixRN), the gamma (GAM), and the lognormal (LN) did give reasonably good fits to the data, fitting between 79% and 86% of individual histograms. The inverse Gaussian (IG) and the reciprocal zero-truncated normal (rectrN) were relatively poor models, as they were only able to give a good fit to 69% and 49% of histograms, respectively.

**Autocorrelation of SP velocity**

To replicate the observation from our previous investigation (Waddington & Harris, 2012) that the update dynamics of SP velocity could be explained as a first-order Markov process, we found the sample autocorrelation and partial autocorrelation functions of SP velocity from each trial, using (respectively) the MATLAB functions autocorr and parcorr. We plotted the mean autocorrelogram of SP velocity across all trials and found that autocorrelation of SP velocity extended back as far as five or six cycles (Figure 5A). However, the mean partial autocorrelogram of SP velocity showed a distinct cutoff at a lag of 1 (Figure 5B), implying that the correlation between SP velocity in one cycle and the cycle before could explain all the higher order autocorrelation observed in the autocorrelogram, identifying the time series as a first-order autoregressive process.

**PCA results**

We performed PCA on the correlation matrices of OKN variables recorded over four cycles in series (see Materials and methods). The analysis revealed that eigenvalues of components varied between trials, but eigenvectors remained predominantly the same and could be sorted into 13 distinct categories, which represented three groups of similar loading patterns shifted by one, two, or three cycles (Figure 6). This indicated that each cycle of OKN constituted three uncorrelated stochastic processes.

These loading patterns appeared to be almost identical to the loading patterns found in our previous study (Waddington & Harris, 2012). We tested the significance of the linear relationships between OKN variables predicted by our model (Equations 1–3) with ordinary least-squares multiple linear regression using the MATLAB function regress and Holm–Bonferroni correction for multiple comparisons. We found that regression of $S_i$ against $x_i$ and $V_i$ gave a mean $R^2 = 0.34$ ($p < 0.006$ for 91 trials), $Q_i$ against $y_i$ and $V_i$ gave a mean $R^2 = 0.28$ ($p < 0.005$ for 95 trials), and $V_{i+1}$ against $V_i$ gave a mean $R^2 = 0.27$ ($p < 0.003$ for 78 trials). The similarity of these results to the results from our previous study indicated that our model could extend to account for spatial-frequency effects on the OKN waveform.

**Spatial-frequency and stimulus-speed effects on stochastic processes**

We estimated the parameters of the proposed stochastic processes for each trial with weighted least-
squares multiple linear regression using the MATLAB function *robustfit*, and assessed their dependency on stimulus spatial frequency and stimulus speed using repeated-measures analysis of variance.

We found no significant effect of spatial frequency or stimulus speed on the parameters a, b, c, or d; the mean values of these parameters were −0.25, 0.12, −0.38, and −0.18, respectively. We noted that these were approximately the same values as found in our previous study (−0.25, 0.16, −0.48 and −0.17; Waddington and Harris, 2012)—see Table 3—which indicated that these parameters may represent fundamentally invariant relationships between OKN variables.

Interestingly, increasing spatial frequency from 0.05 to 0.1 and 0.2 c/° did result in a significant increase in $\hat{v}$, from 4.6 to 6.1 and 7.7, $F = 4.2$, $p = 0.037$, but did not have a significant effect on $e$ or $\sigma_v$. Conversely, increasing stimulus speed from 10°/s to 30°/s resulted in a significant increase in $e$ from 0.38 to 0.60, $F = 19.5$, $p = 0.003$, and an increase in $\sigma_v$ from 1.6 to 3.8, $F = 95.4$, $p < 0.001$, but did not have a significant effect on $\hat{v}$. Effectively, increasing the stimulus spatial frequency resulted in the mean SP velocity being shifted by a constant value to be more positive, without having any other effects on the update dynamics of SP velocity.

Spatial frequency and stimulus speed had a significant interaction effect on $\hat{q}$, $F = 4.2$, $p = 0.037$, but not $\sigma_q$. When the stimulus speed was 30°/s, increasing spatial frequency resulted in $\hat{q}$ becoming more negative, from −1.9 to −2.4 and −3.4, but there was no clear trend at 10°/s. This may reflect the interaction effect observed between stimulus speed and spatial frequency on the mean SP and QP amplitude in our initial analysis of the stimulus effects on OKN variables. Spatial frequency did not have a significant effect on $\hat{s}$ or $\sigma_s$. However, increasing stimulus speed did cause an increase in both $\sigma_s$, $F = 18.2$, $p = 0.004$, and $\sigma_q$, $F = 26.2$, $p = 0.001$.

These results indicated that the spatial frequency of the OKN stimulus had two primary effects on the stochastic processes described in Equations 1–3. Firstly, increasing spatial frequency resulted in an increase in SP velocity by shifting $\hat{v}$ to be more positive. Additionally, increasing spatial frequency increased the magnitude of QPs and SPs (dependent on stimulus speed) by shifting $\hat{q}$ to be more negative.

**Figure 6.** PCA Results. Loading patterns of 13 principal components extracted from four cycles of OKN data in series. Each data point represents the mean loading value averaged across 95 trials analyzed; error bars represent standard deviation between trials. The loading patterns can be classified as one of three broad categories representing components that are shifted by one or more cycles. We defined these three broad categories as Q (loading patterns 1–5), S (loading patterns 6–9), and V (loading patterns 10–13).

**Discussion**

We have found that the spatial frequency of suprathreshold OKN stimuli has a significant effect on eye movements during OKN. Mean values of SP velocity, SP amplitude, and QP amplitude all increased
Table 3. Estimates of OKN parameters. Notes: *Significant main effect of stimulus speed ($p < 0.01$). **Significant interaction effect between spatial frequency and stimulus speed ($p < 0.05$). †Significant main effect of spatial frequency ($p < 0.05$).

<table>
<thead>
<tr>
<th>Stimulus speed ($^\circ$/s)</th>
<th>Spatial frequency (c/°)</th>
<th>$a$</th>
<th>$b$</th>
<th>$c$</th>
<th>$d$</th>
<th>$e^*$</th>
<th>$s$</th>
<th>$q^{**}$</th>
<th>$q_g$†</th>
<th>$q_s$†</th>
<th>$q_v$†</th>
<th>$g_s$†</th>
<th>$g_v$†</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.05</td>
<td>-0.23</td>
<td>-0.09</td>
<td>-0.40</td>
<td>-0.25</td>
<td>0.38</td>
<td>0.75</td>
<td>-1.71</td>
<td>4.43</td>
<td>1.15</td>
<td>1.90</td>
<td>1.73</td>
<td>0.44</td>
</tr>
<tr>
<td></td>
<td>0.10</td>
<td>-0.21</td>
<td>-0.13</td>
<td>-0.37</td>
<td>-0.13</td>
<td>0.39</td>
<td>0.96</td>
<td>-2.94</td>
<td>5.08</td>
<td>1.26</td>
<td>1.86</td>
<td>1.72</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>0.20</td>
<td>-0.25</td>
<td>0.10</td>
<td>-0.40</td>
<td>-0.18</td>
<td>0.38</td>
<td>1.28</td>
<td>-2.22</td>
<td>5.43</td>
<td>1.23</td>
<td>1.75</td>
<td>1.42</td>
<td>0.54</td>
</tr>
<tr>
<td></td>
<td>0.05</td>
<td>-0.22</td>
<td>-0.18</td>
<td>-0.39</td>
<td>-0.21</td>
<td>0.65</td>
<td>-0.17</td>
<td>-1.92</td>
<td>4.80</td>
<td>1.53</td>
<td>2.26</td>
<td>4.15</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>0.10</td>
<td>-0.25</td>
<td>0.13</td>
<td>-0.30</td>
<td>-0.17</td>
<td>0.62</td>
<td>0.70</td>
<td>-2.41</td>
<td>7.16</td>
<td>1.69</td>
<td>2.17</td>
<td>3.74</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td>0.20</td>
<td>-0.32</td>
<td>0.11</td>
<td>-0.39</td>
<td>-0.15</td>
<td>0.53</td>
<td>1.78</td>
<td>-3.37</td>
<td>10.00</td>
<td>1.89</td>
<td>2.47</td>
<td>3.52</td>
<td>0.33</td>
</tr>
<tr>
<td>Global (current study)</td>
<td></td>
<td>-0.25</td>
<td>0.12</td>
<td>-0.38</td>
<td>-0.18</td>
<td>0.49</td>
<td>0.89</td>
<td>-2.43</td>
<td>6.15</td>
<td>1.46</td>
<td>2.07</td>
<td>2.71</td>
<td>0.37</td>
</tr>
<tr>
<td>Global (previous study)</td>
<td></td>
<td>-0.25</td>
<td>0.16</td>
<td>-0.48</td>
<td>-0.17</td>
<td>0.52</td>
<td>1.1</td>
<td>-2.7</td>
<td>7.1</td>
<td>1.7</td>
<td>2.2</td>
<td>3.2</td>
<td></td>
</tr>
</tbody>
</table>

with increasing spatial frequency, and these effects became more pronounced at the higher stimulus velocity (Figure 4). There was also a decrease in SP duration (increase in nystagmus frequency) with stimulus speed. Although increasing spatial frequency resulted in a significant decrease in retinal slip, it did not fall to zero.

Sequential analysis of OKN cycles using PCA revealed three underlying components, as found in our previous study (Waddington & Harris, 2012). The $V$ component described how SP velocity is updated on every cycle (Equation 1). We found that it is independent of the other processes but dependent on stimulus velocity and spatial frequency (Equation 12). We also found that the process that determines QP amplitude (the $Q$ component) is dependent on stimulus velocity and spatial frequency (Equation 14), and confirmed that both SP and QP amplitudes depend on SP velocity and each other (Equations 1 and 2). The three underlying stochastic processes that drive the system are uncorrelated, but because individual OKN variables load onto multiple components (and multiple variables load onto each component), many variables are dependent on more than one of the underlying sources of variance. This shared variance gives rise to a complex sequence of cycles in which OKN variables are mutually correlated and autocorrelated (Equations 1 and 7–11).

The most important findings to discuss from this investigation are that spatial frequency has a significant effect on steady-state SP velocity (and hence retinal slip) and that the OKN system does not reduce retinal slip to zero even when stimulus parameters are kept constant and participants are given a substantial period of time (100 s) to adapt.

### Spatial frequency and contrast have a significant effect on the OKN waveform

A previous study by Sumnall et al. (2003) found a small increase in SP velocity with spatial frequency, although their stimulus differed from ours (drifting Gaussian blobs with differing densities of 1.4 elements/$^\circ^2$ and 0.16 elements/$^\circ^2$, at a speed of 4.6$c/°$/s). However, they also noted that Schor and Narayan (1981) had found a decrease in SP velocity at high spatial frequencies and high speeds (drifting gratings with a spatial frequency of 0.5–8$c/°$ and speeds of 38$s/°$–48$s/°$).

Interestingly, Sumnall et al. (2003) found a more pronounced increase in SP velocity with increasing stimulus contrast (for a given speed). Similarly, Sperling, Kerzel, Braun, Hawken, and Gegenfurtner (2005) have shown a systematic increase in the gain of smooth-pursuit eye movements (SPEM) with increasing contrast. Perceived contrast depends not only on physical contrast but also on contrast sensitivity to different spatial frequencies, retinal image velocities, and retinal location as determined by the bandpass spatiotemporal contrast sensitivity function (Kelly, 1979, 1984). For central retinal stimulation and very low spatial frequencies (as we have used), we would expect contrast to increase with image velocity, but for high spatial frequencies contrast would decrease with image velocity. Of course, image velocity and image position are in turn controlled by the oculomotor system, leading to a highly complex nonlinear system (Harris & Waddington, 2013) that is not fully understood.

It appears that global visual contrast is not being maximized either. Based on the contrast sensitivity curves observed by Burr and Ross (1982), when using drifting sinusoidal gratings with very low spatial
frequency (0.05 c/°), contrast would be maximized by very high image velocity (≈100°/s). Higher spatial frequencies (0.5 c/°) require more moderate values of retinal slip (>10°/s) to maximize contrast. We might expect these speeds to be overestimates of our own results because we have used square-wave gratings, which have Fourier energy at higher harmonics. However, if we treat each of our grating cycles as two bars with widths 10°, 5°, and 2.5°, respectively, then we still expect contrast to be maximized at high image velocities (>10°/s; Burr & Ross, 1982). To achieve such retinal slip could even require OKN SPs in the opposite direction of stimulus motion, which we have not observed.

The OKN waveform is clearly dependent on the spatial frequency of the visual stimulus, and the gain of both OKN SPs and SPEM are dependent on visual contrast. It is now well established that retinal slip alone does not necessarily drive SPEM (Beutter & Stone, 2000; Stone & Krauzlis, 2003). Likewise, the traditional view that OKN simply minimizes retinal slip does not seem tenable.

**Internal estimates of stimulus speed must be reconstructed from prior retinal and extraretinal signals**

Consider the problem of choosing an SP velocity during OKN. We know that SP velocity \( V_i \) depends on stimulus velocity \( V_S \), but \( V_S \) is not known directly and can only be estimated from retinal information and extraretinal information (efference copy and other proprioceptive cues). At the start of each SP, retinal information can only arise from previous SPs: \( R_j = V_S - V_j \) for \( j < i \). Thus the current estimate of stimulus velocity \( \hat{V}_{S,i} \) must depend somehow on actual previous SP velocities \( V_{j<i} \) and hence must be intrinsically Markov when estimates are stochastic. In principle, dependencies on previous SPs could stretch far back, but our empirical findings indicate a dependency on only the last SP \( (j = i - 1) \).

In Figure 7 we present a simple scheme where we assume that the estimate of stimulus velocity is given by the sum of the estimates of retinal slip and eye velocity: \( \hat{V}_{S,i} = \hat{R}_{i-1} + \hat{V}_{j-1} \). Psychophysical evidence suggests that the gains of \( R_{i-1} \) and \( V_{j-1} \) are different (Freeman, 2001; Freeman & Banks, 1998) and possibly less than unity (Pola & Wyatt, 1989), which would lead to an underestimate of stimulus velocity. We denote the retinal slip estimate by the nonlinear equation

\[
\hat{R}_i = g_r(V_S - V_i) + \sigma_r n_r(i)
\]

where \( g_r \) is a nonconstant gain that depends on the spatiotemporal contrast sensitivity of the retina (and hence spatial frequency and retinal slip), \( n_r \) is a standard normal noise process, and \( \sigma_r \) is the standard deviation of the noise. We denote the SP velocity estimate by the nonlinear equation

\[
\hat{V}_i = g_r V_i + \sigma_r n_e
\]

where \( g_e \) is extraretinal gain and may also depend on eye velocity \( V_e \), \( n_e \) is a standard normal noise process, and \( \sigma_e \) is the standard deviation of the noise. If we assume that current SP velocity attempts to match the internal estimate of the current stimulus speed, then \( \hat{V}_{i+1} = (\hat{R}_i + \hat{V}_i) \); and substituting Equations 12 and 13, we obtain the first-order Markov relationship

\[

V_{i+1} = (g_e - g_r)V_i + (g_r V_S + \sigma_r n_r + \sigma_e n_e)\]

In this study \( g_r \) and \( g_e \) are not directly observable, but comparing Equation 14 to Equation 1, we have \( e = g_e - g_r \), \( v = g_r V_S \), and \( \sigma_v = \sqrt{\sigma_r^2 + \sigma_e^2} \). Freeman, Champion, and Warren (2010) have proposed that the perceived speed of visual stimuli during SPEM is based on Bayesian estimates of retinal slip velocity and extraretinal eye velocity. Their key assumption is that prior expectation of stimulus speed is zero, causing shifts to lower velocities for the posterior estimates. Further, because the combined signal is less certain than the retinal signal alone (\( \sigma_v = \sqrt{\sigma_r^2 + \sigma_e^2} > \sigma_r \)), the perceptual estimates of pursued stimuli will be lowered by prior expectations more than moving stimuli observed during fixation, which they use to explain a number of perceptual illusions. However, it is not clear whether priors could be updated over time, eventually
leading to an unbiased asymptote if OKN stimulus parameters remain constant. We will thus explore some alternative explanations for reduced SP gain.

The effect of retinal and extraretinal gains less than unity on SP gain

We have found that \( e = g_r - g_e \) and \( \hat{v} = g_r V_s \). This indicates a relationship between \( \hat{v} \) and \( e \) that is linear if extraretinal gain remains constant: \( \hat{v}/V_s = g_r - e \). Plotting \( \hat{v}/V_s \) against \( e \) (Figure 8) revealed an intercept of 0.82 and a slope of \(-0.92\). The nearly (negative) unity slope supports the scheme in Figure 7, although we should exercise some caution, as it is slightly lower than expected.

It is possible that extraretinal gain varies or depends on stimulus parameters such as spatial frequency. Extraretinal signals for eye movements are mostly in the form of efference copy, where a copy of the motor command is used to predict the behavior (Bridgeman, 1995; Sperry, 1950). Efference copy cannot be intrinsically veridical, and it must be learned or adapted from its sensory consequences, namely retinal slip (Haarmeier, Bunjes, Lindner, Berret, & Thier, 2001). If retinal slip is perturbed by noise, sensory consequences cannot be certain. Thus extraretinal gain would be attempting to adapt to a noisy reference, and hence would become noisy itself. Therefore, noise in the extraretinal pathway is unlikely to be independent of noise in the retinal pathway.

We computed \( g_r = \hat{v}/V_s \) (see Table 3), which showed a significant decrease with stimulus speed and a significant increase with spatial frequency, whereas \( g_e = g_e + e \) only showed a slight decrease with speed and a slight increase with spatial frequency. These results mirror the findings that perceived retinal speed is dependent on spatial frequency (Campbell & Maffei, 1981; Diener, Wist, Dichigans, & Brandt, 1976; Ferrera & Wilson, 1991; Freeman & Banks, 1998; Smith & Edgar, 1990) and support the findings of Sumnall et al. (2003) that extraretinal signals do not appear to be significantly affected by spatial frequency.

From the traditional viewpoint of minimizing retinal slip, having an extraretinal gain close to unity seems highly advantageous. From Equations 14 and A6, the steady-state mean gain for SP velocity is

\[
\frac{\hat{V}}{V_s} = \frac{g_r}{1 - (g_e - g_r)}
\]

As can be seen, when \( g_e = 1 \) the mean OKN gain becomes unity regardless of retinal gain. Thus, in principle, it is possible to track the stimulus perfectly at steady state. Indeed, efference copy was introduced implicitly by Young, Förster, and van Houtte (1968) for a discrete-time smooth-pursuit model and explicitly by Robinson, Gordon, and Gordon (1986) for a continuous-time smooth-pursuit model to explain how the smooth-pursuit system could track a moving target with large open-loop gain and long loop delays.

However, \( g_e \) has been shown to be considerably less than unity (Pola & Wyatt, 1989), and we surmise that the report by Spering et al. (2005) of low SPEM gain to low contrast stimuli could only occur if \( g_e < 1 \). Our deduction that \( g_e \) is less than unity for discrete-time OKN is consistent with these results (see Table 3), although we perhaps find a higher extraretinal gain for OKN SPs than some SPEM estimates.

The difference between retinal and extraretinal gains affects the variance of all OKN variables

An important property of Markov systems is the evolution of variance towards an asymptotic steady state (see Appendix). From Equations 14 and A7, steady-state variance of SP velocity is given by

\[
\sigma^2_{VEL} = \frac{\sigma^2_v}{1 - (g_r - g_e)^2}.
\]

Thus, the noise on the estimate of SP velocity \( \sigma^2_v \) is generally amplified by the Markov process in a way that depends only on the difference between retinal and extraretinal gains. When \( g_e = g_r \), variance is at a minimum \( (\sigma^2_{VEL} = \sigma^2_v) \) and the system becomes zero order.

The term \( e = g_e - g_r \) affects the steady-state mean and variance of most OKN variables that we have measured, including QP and SP amplitude, duration, and position (see Table 4). It is possible that variance constraints or costs on OKN variables other than SP velocity could lower the optimal \( g_e \) to reduce the difference \( e = g_e - g_r \) and hence reduce \( \sigma^2_{VEL} \). For example, increasing \( \sigma^2_{VEL} \) will lead to more extremely long SP durations (a property of reciprocal and ratio.
 distributions; Harris & Waddington, 2012; also see Equation 27 in Table 4) and more variability in the end position of QPs (Equations 23 and 26). Too much variability in the end position of QPs could be extremely costly to the visual system, as contrast sensitivity is dependent on the retinal location of the visual stimulus and visual acuity decreases rapidly outside the central 2° of foveal vision. It is not difficult to imagine a situation where a compromise needs to be made between minimizing positional variance on QPs and minimizing retinal slip.

The difference between extraretinal and retinal gains also determines the response speed of the velocity update dynamics. Consider a reference cycle labeled as \( i = 0 \) with velocity \( V(0) \), then from Equation A3, the velocity of the \( i \)th cycle is

\[
V_i = (g_e - g_r)^i V_0 + \left( 1 - (g_e - g_r)^i \right) \bar{V} + \sum_{k=0}^{i-1} (g_e - g_r)^{i-k} n(k)
\]

which clearly takes time to reach mean velocity \( \bar{V} \). That is, any deviation from the mean takes time to recover depending on \( g_e - g_r \). In natural OKN, stimulus velocity may change rapidly when gaze is shifted from one region of optic flow to another, so it seems plausible that responding quickly to any changes could be important. If \( g_e - g_r \rightarrow 1 \), response time becomes infinite (a random walk) and the system would be trapped by its history and unable to change. On the other hand, when \( g_e = g_r \), response is instantaneous, but \( V \) would never reach \( V_S \) if \( g_r < 1 \). Presumably some compromise is needed, but how speed and accuracy trade off is unknown.

Of course, lowering \( g_e \) to reduce the difference \( g_e - g_r \) will also have visual consequences that cannot be directly inferred from Equations 17–28. Recently, Harrison, Freeman, and Sumner (2015) have shown that the horizontal component of saccades made to visual targets flashed during ongoing OKN falls well short of the target. That is, the saccades do not compensate for the excursion of the current SP. This undershoot error was proportional to the distance traveled by the eye during the saccade latency period, which is expected if the error was due to extraretinal underestimation. Therefore, if we assume that QPs are visually guided, lower extraretinal gain will lead to QPs that undershoot (or overshoot, depending on location) their target, as well as lower SP gain. We should also
recognize that the SP amplitude threshold is likely to be estimated by an extraretinal signal of eye position. If this signal is also an underestimate, then QPs will tend to be triggered before they reach the target threshold, and any variance in the end position of QPs could not be fully compensated for during the SP. Indeed, this would lead to a partial negative correlation between the amplitude and start position of SPs (and QPs), and to the first-order Markov properties that we have observed.

It is plausible, therefore, that adapting or optimizing OKN requires controlling \( g_e - g_r \) (or \( g_e \), if \( g_r \) is unknown). The overall process is complex, however, and at present we have no specific model of adaptive control of OKN. Indeed, it is even possible that there are three separate adaptive mechanisms each attempting to optimize some visual consequence of OKN, with competing and nonintuitive effects.

**Markov properties may be modified at high spatial frequencies**

In this study we have used stimuli with very low spatial frequency, and it is interesting to speculate what would happen with more naturalistic high-contrast and high-spatial-frequency stimuli. Clearly, we expect retinal gain to increase. Thus the difference \( g_e - g_r \) would decrease, leading to an overall increase in SP gain and also a decrease in SP velocity variance and a general reduction in cyclic variability. Should \( g_e = g_r \), the Markov properties would disappear and zero-order statistics would set in.

However, visual contrast depends on retinal slip, particularly at high spatial frequencies, due to the spatiotemporal contrast sensitivity of the visual system (Kelly, 1979, 1984). There must therefore also be a nonlinearity in the time course of OKN. To illustrate, consider a random fluctuation that happens to reduce SP velocity on the \( i \)th cycle. This will increase retinal slip, and hence reduce retinal gain \( g_r(i) \). This in turn will reduce SP velocity on the next cycle, causing a further increase in retinal slip, and so on in a positive-feedback fashion. Although a steady state may occur, it is also possible that OKN will simply cease if the random fluctuation is large enough. The opposite effect could occur with a fluctuation that increases SP velocity. A moving high-spatial-frequency grating may have minimal contrast for a stationary eye and generate no OKN. However, if the eye happened to move spontaneously in the direction of the stimulus, retinal slip would decrease, increasing contrast and potentially sustaining OKN for a while. This nonlinearity leads to a nonstationary Markov process, but whether it can be detected remains to be explored, although we expect it to be stronger for high-spatial-frequency stimuli because of the sharp dependency on retinal slip.

**Conclusion**

Clearly, the OKN system does not simply minimize retinal slip and generate regular resetting saccades. The influx of QPs and SPs of OKN are remarkably variable and must depend on preceding extraretinal and retinal signals encoding velocity and position, such that they vary in a Markov fashion. In principle, an OKN gain of unity could be maintained if extraretinal gain were also unity, but empirical studies have demonstrated that it is typically significantly lower. We have deduced that the Markov properties of SP velocity depend only on the difference between retinal and extraretinal gain: When retinal gain is much lower than extraretinal gain (e.g., when viewing low-spatial-frequency stimuli), the Markov properties of the system can be observed and variability in the whole system increases. Any noise on the internal estimates of SP velocity (and position) will be amplified by a Markov process. It is therefore possible that extraretinal gain (or the difference between retinal and extraretinal gain) adapts to control a trade-off between perfect tracking and minimizing the variability of OKN parameters, but this remains to be investigated.

**Keywords:** optokinetic nystagmus, spatial frequency, Markov process, retinal gain, extraretinal gain

**Acknowledgments**

This research was funded with an Engineering and Physical Sciences Research Council Standard Research Student Award (DTG: EP/P02675/1), and a Knowledge Transfer Partnership associate development grant provided by the UK Technology Strategy Board, Medical Research Council, and WESC Foundation (KTP008989).

Commercial relationships: none.
Corresponding author: Jonathan Waddington.
Email: jwaddington@wescfoundation.ac.uk.
Address: WESC Foundation, Countess Wear, Exeter, Devon, UK.

**References**


Appendix

We consider a sequence of random variables $w_i, i \geq 0$, where each $w_i \in \mathbb{R}^1$ is continuous. The simplest stochastic process is the zero-order process, where all $w_i$ are mutually independent. If the probability distribution of $w_i$ depends explicitly on the outcome of the previous random variable $w_{i-1}$ but not explicitly on the
outcome of earlier random variables, the system is said to be a first-order Markov process. To describe $w_i$ requires the specification of the infinite dimensional probability transition matrix $\Pr(w_i|w_{i-1})$. A special case is given by the stationary Gauss–Markov first-order autoregressive system

$$w_{i+1} = \alpha w_i + \varepsilon_i$$  \hfill (A1)

where $w_0$ is the initial value and may be a random variable, $\alpha$ is a constant, and $\varepsilon(i)$ is a sample from a continuous white-noise process that is normally distributed with a nonzero mean $\mu$ and variance $\sigma^2$: $\varepsilon(i) \sim N(\mu, \sigma^2)$. Samples are mutually independent so that $\text{cov}(\varepsilon(i), \varepsilon(j)) = 0$ for $i \neq j$. Equations 1 and 7–11 can be written in this form. Expanding Equation A1 gives

$$w_{i+1} = \alpha w_i + \mu + \sigma n(i)$$  \hfill (A2)

where $n(i)$ is a standard normal random variable $n(i) \sim N(0, 1)$. From Equation A2, we have $w_1 = \alpha w_0 + \mu + \sigma n(0)$; $w_2 = \alpha^2 w_0 + \alpha \mu + \mu + \alpha n(1) + n(2)$; $w_3 = \alpha^3 w_0 + \alpha^2 \mu + \alpha \mu + \mu + \alpha^2 n(1) + \alpha n(2) + n(3)$; etc. Summing the power series yields the $i$th term

$$w_i = \alpha^iw_0 + \mu(1 - \alpha^i)/(1 - \alpha) + \sum_{k=0}^{i-1} \alpha^{i-k} n(k)$$  \hfill (A3)

with mean

$$\bar{w}_i = \alpha^i \bar{w}_0 + \mu(1 - \alpha^i)/(1 - \alpha)$$  \hfill (A4)

and variance

$$\sigma^2_w = \alpha^{2i} \sigma^2_w + (1 - \alpha^{2i}) \sigma^2 / (1 - \alpha^2)$$  \hfill (A5)

where $\sigma_w^2$ is the variance associated with the initial value $w_0$. Provided $|\alpha| < 1$, this series converges with an initial transient that depends on $w_0$, followed asymptotically by a steady-state behavior that is independent of $w_0$. Thus the steady-state mean is given by $\bar{w}_\infty = \alpha \bar{w}_\infty + \mu$ and hence

$$\bar{w}_\infty = \frac{\mu}{1 - \alpha}$$  \hfill (A6)

Similarly, the steady-state variance is

$$\sigma^2_w = \frac{\sigma^2}{1 - \alpha^2}$$  \hfill (A7)