Reflexive optokinetic nystagmus in younger and older observers under photopic and mesopic viewing conditions

Trevor J. Hine,1 Guy Wallis,2 Joanne M. Wood,3 and Efty P. Stavrou3

Key Words: age nystagmus mesopic motion perception visual field

Word Count: 4,426

Scientific Section: EY

From the 1Applied Cognitive Neuroscience Research Centre, Griffith University, Mt Gravatt, Queensland, Australia; 2School of Human Movement Studies University of Queensland, St Lucia, Queensland, Australia; and the 3Centre for Health Research (Optometry), Queensland University of Technology, Kelvin Grove, Queensland, Australia.

Supported by an Australian Research Council RIEF Grant R00002734 (GW, JW and TJH) and Griffith University Research Grant (TJH).

Corresponding author: Trevor Hine, School of Psychology, Griffith University Mt Gravatt, Queensland 4111, Australia; t.hine@griffith.edu.au
Abstract

**PURPOSE.** To investigate the effect of age on OKN in response to stimuli designed to preferentially stimulate the M-pathway.

**METHOD.** OKN was recorded in ten younger (32.3±5.98 years old) and ten older (65.6±6.53) visually normal subjects. Vertical gratings of either 0.43 or 1.08 cpd drifting at either 5 or 20°/sec and presented at either 8 or 80% contrast were displayed on a large screen as: full field stimulation, central stimulation within a central Gaussian-blurred window of 15° diameter, or peripheral stimulation outside this window. All conditions apart from the high contrast condition were presented in a random order at two light levels: ‘mesopic’ (1.8 cdm⁻²) and ‘photopic’ (71.5 cdm⁻²).

**RESULTS.** The partial field data indicated that central stimulation, mesopic light levels and lower temporal frequencies each significantly increased slow-phase velocity (SPV). While there was no overall difference between groups for either the partial field stimulation, the full field or low contrast stimulation, a change in illumination revealed a significant interaction with age: there was a larger decrease in SPV going from photopic to mesopic conditions for the older group than the younger group, especially for higher temporal frequency stimulation.

**CONCLUSIONS.** OKN becomes reflexive in conditions conducive to M-pathway stimulation and this rOKN response is significantly diminished in older compared to younger healthy adults indicative of decreased M-pathway sensitivity.
Visual abilities decline as part of the normal aging process due to changes in both central neural pathways and degradation in the optics of the eye.\textsuperscript{1–3} Perception of coherent motion of central stimuli declines significantly with age,\textsuperscript{4–9} particularly at slower speeds ($< 2^\circ/$sec),\textsuperscript{10} with reports of older women undergoing significantly more decline than men.\textsuperscript{11} Peripheral motion processing also declines with age.\textsuperscript{5,12} Conversely, the evidence is not conclusive as to whether there is any significant decline with age in motion sensitivity for small, centrally located stimuli.\textsuperscript{8,13} Most of these findings suggest an age-related decline in the magnocellular neural (M) pathway in vision.\textsuperscript{14} In support of this, there is direct evidence of reduced neural responses to speed and flicker processing within area 17 and 18 of rat cortex in the aged animal.\textsuperscript{15}

In the current study, we examined the decline in the response to motion due to age. Firstly, rather than using direct measures of motion sensitivity like these previous studies, we measured changes in involuntary, reflexive optokinetic nystagmus (rOKN) to explore putative differences in M-pathway functioning in older and younger groups. rOKN, or ‘Stier-nystagmus’, occurs when observers do not actively follow specific features in the moving visual field but rather attempt to stare straight ahead.\textsuperscript{16,17} rOKN is characterised by more frequent and smaller amplitude beats of lower ‘gain’ than those recorded in voluntary, ‘pursuit’ OKN,\textsuperscript{16,18} where gain is slow phase eye movement velocity (SPV) ÷ the velocity of the moving stimulus.

A second feature of our study is that we recorded OKN under different ambient light levels as evidence suggests that vision under low light conditions is likely to favour M-pathway over P-pathway functioning. Purpura and colleagues\textsuperscript{19,20} have shown in monkey that the M-pathway is the predominant conveyor of contrast
information under mesopic/scotopic illumination, and this is supported by human data from simultaneous psychophysical and electrophysiological recording. At scotopic light levels, these low spatial frequencies accentuate a significant diminution in average sensitivity with age. In the current study, we tested our subjects at mesopic light levels, where differences in sensitivity at the low spatial frequencies between the old and young groups were smaller and the effect of senile miosis was minimised. We also compared the rOKN with peripheral vs central stimulation: the absence of cones in the periphery ensures predominant M-pathway response there even though the central visual field is more important in generating OKN.

Finally, we studied rOKN in young and old groups as a recent review of the literature on the effects of ageing on eye movements has revealed a lack of data on rOKN and age. There is clear evidence that the SPV in pursuit OKN decreases with increasing age from the age of 30 years, but these differences only become marked with stimuli velocities above 50º/sec and may not exist at slower speeds. Such declines have tended to follow similar losses in smooth pursuit accuracy and may be due to the fact that SPV in older people ‘saturates’. Older people with ocular disease also show reduced OKN responses compared to their healthy controls. The current study measured OKN in older and younger people, and compared the results under photopic and mesopic light levels contrasting high gain OKN data with low gain rOKN.

METHODS

Participants
Participants were recruited from staff and students at Queensland University of Technology (QUT) and the University of Queensland, as well as from the wider community. The ‘young’ group (five males, five females) had a mean age 32.3 years (SD = 5.98, range 26 to 42) and the ‘old’ group (four males, six females) a mean age of 65.6 years (SD = 6.53, range 53 to 75). All had normal or corrected-to-normal vision and were free of ocular disease. All participants were screened at the School of Optometry clinic at QUT, except for one 67-year-old female in the old group who was tested by a private optometrist.

A clinical examination and brief screening battery of tests were administered to ensure that all participants fulfilled the inclusion criteria of having normal ocular health. These assessments consisted of biomicroscopy and ophthalmoscopic examination and measurement of intraocular pressure (Goldmann applanation tonometry), Bailey-Lovie MAR, Pelli-Robson contrast sensitivity and perimetry with the Humphrey Field Analyser program 24-2 tested in each eye of each participant. Only those participants with normal ocular health and visual acuity, as well as contrast sensitivity and visual fields within the normal range, were included in the study. Our research adhered to the tenets of the Declaration of Helsinki. Informed consent was obtained from the subjects after explanation of the nature and possible consequences of the research. The QUT Human Research Ethics committee approved the research.

**Stimuli**

Achromatic vertical sinewave gratings were projected onto one wall of a darkened laboratory via a ceiling mounted Barco 808S digital projector (Kortrijk, Belgium) and
a SGI Onyx 300 graphics computer (Mountain View, California) generated all stimuli. The observers viewed the stimuli binocularly at a viewing distance of 1.5 m and the centre of the image was indicated by a small fixation cross. The image size was 2.33 m high and 3.12 m wide and subtended 75.7° × 92.2°. Two light levels were employed: a ‘photopic’ light level of 71.5 cdm⁻² and a ‘mesopic’ light level of 1.8 cdm⁻², where levels were measured at the centre of the image and represent the mean luminance of the grating. To ensure that the mean luminance for the photopic condition was at an appropriate level (>60 cdm⁻²), two arc lamps with diffusers (to avoid any ‘hotspots’) were positioned 4 m apart and illuminated the wall at a distance of 3.5 m.

The gratings drifted from left or right at either ‘slow’ (5°/sec) or ‘fast’ (20°/sec) velocities, with a spatial frequency of either 0.43 or 1.08 cycles per degree of visual angle (cpd). They were presented at two levels of Michelson contrast under mesopic conditions: ‘low’ (8%) and ‘high’ (80%), with only the low contrast level being possible under photopic conditions as the augmented background light level prevented sufficient modulation in the projected image to attain the high contrast. To ensure the visibility of our spatially coarse gratings for all participants in both age groups, the ‘low contrast’ condition was set at 8% contrast. This is, at the very least, five times threshold for our older group and most probably greater than this given that slow movement at these spatial frequencies enhances contrast sensitivity.

The gratings were presented as ‘full-field’ stimulation across the entire image, or as either ‘central’ or ‘peripheral’ stimulation, called ‘partial field’ here. In central stimulation, a software mask was used such that the drifting gratings with full contrast
modulation appeared just in a central circular region of 6º radius around the fixation cross. From 6º to 9º radius, the contrast modulation of the gratings diminished to zero following a Gaussian function and the image was a uniform background grey beyond the central region of 18º diameter. Peripheral stimulation was the inverse of this: the central region was filled with uniform grey and the periphery was filled with drifting gratings of full contrast modulation.

**Eye Movement Recording and OKN Analysis**

Eye movements were recorded with a SensoMotoric Instruments GmbH (Berlin, Germany) Eye-Link I system, which recorded horizontal and vertical movement using video-oculography with infrared illumination of the eye. This head-mounted system consists of binocular miniature cameras (with built-in infrared illuminators) attached to a lightweight padded headband. Both eye position and relative pupil size data were recorded. Eye position data was acquired from each eye at a rate of 250 Hz with gaze accuracy of less than 0.5º with eye rotation precision of 0.01º as claimed by the manufacturer. Van der Geest and Frens\(^3^7\) have compared the Eye-Link performance with a scleral coil system, and the former has been found to be remarkably accurate and precise, with average position discrepancy between the systems of <1º over a range of 40º × 40º for saccadic velocities up to 300 º/sec. In some cases, heavy anti-reflection coatings on spectacles prevented recording of reliable, accurate eye position and those participants were not included in this study. Our system consisted of a host computer containing the Eye-Link card that acquired and stored the eye movement data and controlled the presentation of stimuli generated by the SGI graphics computer (see above).
Calibration of the eye movement record was done automatically at the beginning of each session using software provided with the Eye-Link system. The raw data files of horizontal and vertical eye position for each trial were analysed in the following way. Only one eye’s signal was used given that the eyes were ‘yoked’. The horizontal signal was displayed graphically on a position vs. time x–y plot. A highly trained operator, blind to both the condition and the participant’s identity, positioned a cursor at the beginning and end of the slow-phase of each ‘candidate’ OKN beat as well as the end of the fast-phase. The operator’s scoring was highly reliable when tested against re-scoring of a sample of the same data by another operator. A computer program then determined: (i) the slow phase velocity (SPV) of each beat which corresponded to the slope of a linear regression through all data points constituting the slow phase, (ii) the duration of that slow phase and (iii) the amplitude of the fast-phase in each beat. The program also discarded ‘suspect’ beats if they failed to meet one of the following criteria: slow-phase duration > 150 msec, SPV of > 0.5°/sec, fast phase amplitude > 1°, SPV within 3 standard deviations of the average SPV within a particular trial.

**Procedure**

Participants were fitted with the Eye-Link headpiece and their horizontal and vertical eye movements were calibrated. Trials were blocked by each of the two light levels: twenty-four trials were presented in random order under mesopic lighting conditions and twelve under photopic conditions. Each combination was tested: either fast or slow drifting gratings, presented as full-field, peripheral or central stimuli, at low or high contrast (if possible) at each of the two spatial frequencies. A ten-minute rest period was taken between the mesopic and photopic trial blocks and the order of these
blocks was randomised. All participants were dark adapted before viewing under mesopic conditions.

There was a 25 sec OKN rest period between trials where the participant viewed a uniform grey field. A trial began with the participant fixating the cross for five seconds. This was replaced with the drifting gratings that lasted for twenty seconds. During this period, participants were instructed to keep their gaze straight ahead where the fixation cross had been and not to track specific ‘stripes’. Eye movement data was acquired during the 20 seconds of the trial when the stimulus was visible and then for an additional ten seconds immediately following the removal of the stimulus. The entire experimental session lasted no more than 50 minutes.

RESULTS

The average pupil sizes for each older and younger participant were obtained under the mesopic and photopic conditions. A precise calibration of these sizes for each participant in mm$^2$ was not possible due to differences in the working distance from the miniature camera to the pupil for each observer. However, a ratio of the pupil sizes: mesopic vs. photopic was calculated for each participant and analyses of variance (ANOVAs) were performed on these data for the two groups. Mesopic pupil size was clearly larger than photopic (ratio > 1, $F(1, 18) = 96.15, P < 0.0001$), however, there was no effect of age group on the ratios ($F(1, 18) = 0.172, ns$).

OKN was analysed from the last 15 seconds of each trial. The first five seconds of recording were discarded to ensure that only steady state OKN SPV was used. Only eleven of the 960 trials analysed did not produce OKN as defined by our criteria and most of these trials were from younger participants spread across the mesopic, partial field conditions. These data were excluded from further analysis.
The eye movement record was also analysed for optokinetic afternystagmus (OKAN) in the ten seconds after extinction of the stimulus. Few OKAN beats fulfilled our criteria (see above) and this precluded statistical analyses of these data. Clearly, the short duration of the OKN stimulation as well as the small size of the OKN beats were unable to sufficiently ‘charge’ the brainstem velocity storage mechanism to yield OKAN.\(^{39}\)

ANOVAs were performed on the OKN SPV data that were log-transformed due to the high level of positive skew in their distributions. Because of our inability to test high contrast gratings under photopic conditions (see Methods), our experimental design was not completely balanced. For this reason, separate ANOVAs were performed on high and low contrast data, and an additional ANOVA performed to test the interaction of contrast with the other factors. For ease of interpretation, analysis of partial field data was conducted separately from the analysis of full field data.

**Partial Field Analysis**

An age group (older vs. younger) × ‘stimulation’ (central vs. peripheral) × light level (mesopic vs. photopic) × spatial frequency (0.43 vs. 1.08 cpd) × drift velocity (slow vs. fast) mixed ANOVA was conducted on each of the low contrast and high contrast SPV partial field data, dropping the factor ‘light level’ in the latter case. These ANOVAs revealed significant main effects (all \( P < 0.01 \) or greater) for light level (just for the low contrast data: mesopic > photopic), for spatial frequency (0.43 > 1.08 cpd), for drift velocity (slow > fast) and for stimulation (central > peripheral).
means with standard errors representing these main effects collapsed across all levels of the other factors are presented in Table 1.

Full Field Analysis

Full field stimulation clearly produced faster SPVs in all conditions compared to their partial field equivalents (see Table 1). Again the ANOVAs revealed significant main effects (all $P < 0.005$ or greater) for light level (just for the low contrast data: mesopic < photopic) and for spatial frequency ($0.43 > 1.08 \text{ cpd}$). There was no main effect for drift velocity resulting from the low contrast data analysis, however, this main effect did reach significance for high contrast data (fast > slow, $F(1, 18) = 5.93, P = 0.026$). The means with standard errors representing these main effects collapsed across all levels of the other factors are also presented in Table 1.

Interactions with Contrast at Mesopic Light Levels

To test the interaction of contrast with the other factors, an age group × stimulation × contrast × spatial frequency × drift velocity mixed ANOVA was conducted on just the mesopic SPV data for each of the partial field and full field data, dropping the factor ‘stimulation’ in the latter case. In both analyses, high contrast conditions produced consistently higher SPVs than similar low contrast conditions ($P < 0.0001$, see Table 1). These analyses produced only one significant three-way interaction with contrast that is discussed in the next section.

Interactions with Temporal Frequency
In consideration of interactions among factors, the spatial frequency × drift velocity interaction reached significance ($P < 0.005$ or greater) in every ANOVA, and this interaction is plotted for each of the high and low contrast, full and partial field conditions in Fig. 1. Since temporal frequency is the product of spatial frequency and drift velocity, is it clear that the interaction is due to SPV being much reduced in the highest temporal frequency conditions (that is, 1.08 cpd drifting at the fast velocity).

For the ANOVA conducted on the mesopic, full-field data, there was a significant three-way interaction: contrast × spatial frequency × drift velocity ($F(1, 18) = 4.86, P = 0.041$) that subsumed significant interactions between each of frequency and contrast, and velocity and contrast. Even though Fig 1c includes photopic data, mesopic and photopic SPV means are very similar here, so the nature of this three-way interaction emerges in the comparison of Fig 1c with Fig 1d. Here the highest temporal frequency stimulus causes a large diminution in SPV, however this diminution is much greater (almost to the extinction of OKN) for low contrast gratings compared to high contrast.

[Insert Fig. 2 about here]

In each of the partial field analyses, there was a significant stimulation × drift velocity interaction (low contrast: $F(1, 18) = 23.64, P < 0.0001$, see Fig 2, left-hand plot; high contrast: $(F(1, 18) = 8.49, P = 0.009$, see Fig 2, right-hand plot) where diminution in SPV for the faster velocity was greater with the central field stimulation as opposed to peripheral field stimulation$.^1$ Finally, in the low contrast, full field data analysis, there was a significant three-way interaction light level × spatial frequency ×

---

$^1$ Some of this diminution may be due to the fact that the image of the stimulus was projected onto a flat wall so spatial frequency and velocity are geometrically distorted as a function of eccentricity especially in the far periphery (for example, at 30°, velocity is about 0.75× the value at 0° and spatial frequency is 1.33× the value). No correction for this was made in the software. Note that counteracting this artefact is the result from the partial field data analysis: slower drift velocity produced higher OKN gains but the finer spatial frequencies generated lower OKN gains.
drift velocity interaction \( F(1, 18) = 7.458, P = 0.014, \) Fig 3). From Fig. 3, the OKN for the highest temporal frequency was virtually non-existent under mesopic conditions but was restored by an increase in light level, whereas the 0.43 cpd grating data are not affected by light level.

[Insert Fig. 3 about here]

**Interactions with age**

While age group did not emerge as a significant main effect, some interesting interaction effects with age did emerge. For the low contrast, partial field analysis, there was a significant three-way interaction of age group \( \times \) spatial frequency \( \times \) drift velocity \( F(1, 18) = 7.460, P = 0.014 \). An examination of the mean data revealed that this interaction was caused by the older group having a significantly lower mean SPV than the younger group just for the highest temporal frequency condition, while there were no between-group differences in the 0.43 cpd, slow or fast velocity conditions.

[Insert Fig. 4 about here]

Turning to the full field analyses, there was a significant interaction for the low contrast data, age \( \times \) light level \( F(1, 18) = 6.76, p = 0.018 \): there was a larger drop-off in SPV for the older group for photopic vs. mesopic than for the young group. This interaction was particular prominent in the 1.08 cpd condition and an ANOVA on this condition alone revealed a main effect for light level \( F(1, 18) = 12.07, p = 0.003 \) and a significant age group \( \times \) light level interaction \( F(1, 18) = 6.87, p = 0.017 \) as shown in Fig. 4. This last result also is seen in the raw eye movement traces presented in Fig. 5 and it should be noted that among the old group, the high velocity, 1.08 cpd stimulation under mesopic conditions produced by far the lowest mean SPV of the entire experiment (0.85 °/sec).

[Insert Fig. 5 about here]
DISCUSSION

It was clear from the eye movement records that participants in both age groups were performing rOKN rather than pursuit OKN in most of our stimulation conditions. The OKN beats were rapid and there were no long, tracking slow phases or any large excursions of gaze from the straight-ahead position where participants were instructed to stare (see Fig. 5). In addition, except for the slow velocity, full field conditions where OKN gain was near unity (Fig 1c and 1d), gains were below 0.7 which is indicative of rOKN. In fact, the fastest SPVs for the entire experiment were recorded in the full field, high contrast, mesopic, 0.43 cpd condition at the fast velocity with mean SPVs (±1 SEM) for the older group of 10.02±2.15º/sec and 13.59±1.70º/sec for the younger group: gains here are still below about 0.7.

We believe our partial field rOKN data provide new insights into the reflexive response of the M-pathway to motion. rOKN seems to be similar to pursuit OKN with partial field stimulation, except that the OKN response is much weaker and the gains are considerably lower. There are very modest increases in SPVs as contrast increases, and larger increases as stimulation is changed from the peripheral field (where the area of stimulation is much larger) to central field stimulation. Unlike previous work, we found that when we increased the velocity of the drifting gratings from 5 to 20º/sec (which is only a modest increase in the context of usual OKN stimulus velocities) there was a small decrease in SPV for central stimulation (Fig 2). Previous work on so-called ‘passive’ OKN with partial field stimulation at stimulus velocities of 20º/sec and greater has shown only modest increases in SPV with increasing velocity. However these researchers used very low spatial frequency gratings of 0.25 cpd, and hence the temporal modulation of most of their
stimuli was lower than in the present experiment. Our SPVs and hence OKN gains seem to be limited by the temporal modulation of the stimulus even though the temporal frequency of the stimulus with the highest modulation (21.6 Hz) is less the limit (24 Hz) for ‘optimal’ OKN, but this limit may be less in low light or low contrast conditions.

The interaction effects in our eye movement data among the different stimulus parameters: contrast, temporal frequency and light level strongly suggest rOKN is being driven by the M-pathway and hence is indicative of the level of functioning of that system. A recent fMRI study in humans has shown that unlike pursuit OKN, rOKN does not activate cortical oculomotor structures associated with planned eye movements, but rather, strongly activates the ‘traditional’ motion processing cells in the medial temporal (MT) area of both the macaque and human cortex. In addition, Crognale and Schor have shown that the gain of rOKN in human observers is severely reduced compared to pursuit OKN, but only when the drifting patterns inducing the OKN are isoluminant (to which the M pathways are unresponsive), as opposed to being luminance modulated. In macaques, lesions interrupting M-pathway functioning have been shown to reduce the response to low contrast gratings at high temporal frequencies and this in turn is linked to deficits in motion perception. These reductions and deficits become more prominent in low contrast stimulation and M-pathway functioning predominates over P-pathway at low light levels. In a similar way, our mean SPVs and gains are reduced, that is, the OKN is more clearly reflexive with higher temporal frequency stimulation, but more so in the low contrast than high contrast conditions (Fig 1c vs Fig 1d for full field stimulation). SPVs are actually slightly higher with mesopic compared to photopic light levels with low gain OKN in partial field stimulation.
The three-way interaction between light level and temporal frequency with full field stimulation at low contrast shown in Fig 3 could also be due to M-pathway functioning. Note that the lowest SPVs occur with high temporal, mesopic stimulation, and increasing the light level reduces the differences produced by high temporal vs low temporal stimulation (right hand graph). Conversely, there is no effect of temporal frequency or light level for OKN gains over 0.7 (left hand graph) corresponding to pursuit OKN. This connection between M-pathway and rOKN seems to be stronger using central rather than peripheral stimulation, but best tested using full field stimulation.

These interactions in the rOKN data are greater in the older group than the younger group. In the partial field, low contrast conditions, the older group differed in their mean SPV from the younger group but only with high temporal frequency stimulation. Such differences were even clearer with full-field, low contrast stimulation. In Figs 4 and 5, the low contrast, higher temporal frequency stimulation reveals differences between the groups but only with mesopic (vs photopic) light levels. However, a potential problem may exist when comparing visual functions in young and old groups at low light levels due to the reduction in retinal illumination in older individuals caused by senile miosis as well as increased intraocular light scatter. Such optical factors do not affect the contrast thresholds at high levels of illumination and low spatial frequencies (below about 1.5 cpd), which are similar for subjects in their twenties and seventies. We believe the age differences in our data cannot be attributed to reduced contrast sensitivity at low light levels in the old group given the light levels and contrast levels we have chosen. Nor can it be attributed to differences in retinal illuminance due to senile miosis: there was no difference in the ratio of pupil sizes between different light levels for the old and
young groups. Clearly, our mesopic light level was not dark enough to reveal the
limitations in pupil dilation due to age.

A motivation for doing this work was to record changing visual function in
older people who have normal scores on traditional clinical tests, yet often complain
of visual difficulties in day-to-day life. For example, as light levels decline and
contrast decreases, there is research indicating that older drivers have much greater
difficulty with moving hazards than younger drivers.\textsuperscript{52–54} That our rOKN age group
differences are occurring at low light levels, low contrast and at higher temporal
frequencies suggest a reduction in M-pathway functioning in the older group
compared to the younger. This decline is exaggerated under mesopic light levels, a
decline that may begin with reduced rod numbers and sensitivity in the healthy, but
aging macula.\textsuperscript{55} However, one must be cautious in interpreting these results as a
decline in all motion perception, as it has recently been shown that for high contrast
stimulation (independent of light level), an old group performed better on a motion
direction discrimination task than a young group.\textsuperscript{56}
Acknowledgment

The authors thank John Stephens for writing the OKN eye movement record analysis program.
References


54. Wood JM, Tyrrell RA, Carberry TP. Limitations in the drivers' ability to recognise pedestrians at night. *Hum Factors*. 2005;47:644-653.


Figure Legends

**FIGURE 1** Mean SPVs for interactions due to temporal frequency in both partial and full field conditions. (a) Low contrast, partial field conditions. (b) High contrast, partial field conditions. (c) Low contrast, full field conditions. (d) High contrast, full field conditions. Error bars are ± 1 SEM.

**FIGURE 2** Mean SPVs for interactions between stimulation location and drift velocity for partial field conditions. Plot on the left illustrates the interaction for low contrast conditions and plot on the right illustrates the interaction for high contrast conditions. Error bars are ± 1 SEM.

**FIGURE 3** Mean SPV for full field conditions, low contrast gratings. Plots illustrate the interaction between light level × spatial frequency × drift velocity (see text). Data for slow (5º/sec) gratings are plotted with solid lines and data for fast (20º/sec) gratings plotted with broken lines. Error bars are ± 1 SEM.

**FIGURE 4** Mean SPV for full field, low contrast gratings, demonstrating interactions with age group and light level. Error bars are ± 1 SEM.

**FIGURE 5** Typical raw eye movement data from the last 15 sec of a trial: full field, low contrast, mesopic conditions, 1.08 cpd gratings drifting at the fast velocity of 20º/sec. Darker trace is horizontal left eye movement and lighter trace is vertical left eye movement. The residual ‘vertical’ OKN seen during vigorous horizontal OKN (left hand column) is probably an artefact due to a slight misalignment between the horizontal direction of stimulus movement and the putative horizontal axis of eye
movement recording. Participant AX (upper traces) is a 42-year-old male; participant DY (lower traces) is a 74-year-old female.
Table

**TABLE 1** Mean SPVs (with ± 1 SEM) for main effects collapsed across all other factors in each of the partial field stimulation analyses and the full field stimulation analyses.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Levels</th>
<th>Partial Field Low Contrast</th>
<th>Partial Field High Contrast</th>
<th>Full Field Low Contrast</th>
<th>Full Field High Contrast</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light level</td>
<td>Mesopic</td>
<td>2.51±0.16</td>
<td>2.52±0.25</td>
<td>4.03±0.47</td>
<td>7.15±0.59</td>
</tr>
<tr>
<td></td>
<td>Photopic</td>
<td>2.42±0.14</td>
<td>*</td>
<td>4.76±0.41</td>
<td>*</td>
</tr>
<tr>
<td>Spatial Frequency</td>
<td>0.43 cpd</td>
<td>2.79±0.17</td>
<td>2.92±0.25</td>
<td>5.59±0.52</td>
<td>8.42±0.89</td>
</tr>
<tr>
<td></td>
<td>1.08 cpd</td>
<td>2.13±0.14</td>
<td>2.10±0.20</td>
<td>3.21±0.30</td>
<td>5.89±0.73</td>
</tr>
<tr>
<td>Drift velocity</td>
<td>slow</td>
<td>2.63±0.14</td>
<td>2.68±0.21</td>
<td>3.88±0.20</td>
<td>5.00±0.19</td>
</tr>
<tr>
<td></td>
<td>fast</td>
<td>2.13±0.14</td>
<td>2.34±0.26</td>
<td>4.91±0.56</td>
<td>9.31±1.06</td>
</tr>
<tr>
<td>Stimulation</td>
<td>central</td>
<td>3.06±0.17</td>
<td>3.13±0.25</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>peripheral</td>
<td>1.87±0.12</td>
<td>1.89±0.19</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

* high contrast, photopic stimulus not able to be tested (see Methods)
Fig 1.
Fig 2
Fig 3
Fig. 4
Fig. 5