



Contribution of Chromatic Mechanisms to the Production of Small-field Optokinetic Nystagmus (OKN) in Normals and Strabismics

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The contribution of chromatic mechanisms to motion processing is currently debated. Although OKN as a measure of motion processing has been employed for chromatic stimuli, the contribution of chromatic mechanisms to the production of OKN has not been assessed directly. We measured voluntary-pursuit and involuntary-stare OKN responses to drifting patterns defined by colors modulated in a cone based color space which isolates luminance and color mechanisms. Results show that OKN responses are reduced for isoluminant stimuli, particularly for the stare conditions. The greatest reduction in responses occur for isoluminance stimuli that isolate the S cones. These results suggest that the chromatic mechanisms may have reduced input to the neural substrate that produces involuntary-stare OKN or that stare OKN has different temporal characteristics when stimulated by chromatic and luminance mechanisms. We also measured OKN asymmetries in several convergent strabismics in response to isoluminant and luminance patterns and compared their response to previous reports of horizontal OKN asymmetries in normal neonate infants. The results question the validity of either the modeling of OKN asymmetries in strabismus as incomplete development or the comparison of adult eye movement records evaluated with criteria for OKN with psychophysical forced choice evaluation of ocular drift in infants. Copyright © 1996 Elsevier Science Ltd.

Color Motion Optokinetic nystagmus (OKN) Strabismus S cone

INTRODUCTION

The degree to which color and motion signals are processed independently is a topic which has enjoyed much attention (e.g. Ramachandran & Gregory, 1978; Cavanagh *et al.*, 1984; Carney *et al.*, 1987; Lindsey & Teller, 1990). The evidence to date suggests that color and motion are partially but not completely segregated in visual processing; the contribution of isoluminant stimuli to motion depends upon the stimulus conditions (e.g. spatial frequency and retinal location).

Optokinetic nystagmus (OKN) has previously been used as a measure of motion processing. Research has shown that certain instructions result in OKN that does not respond equally to all motion stimuli. For example, voluntary OKN resulting from repeated foveal pursuit is the same for continuous target motion stimulated with

1.5 deg displacements presented at 26 Hz and apparent motion stimulated with 6 deg displacements presented at 6.5 Hz (Schor *et al.*, 1984). These two conditions correspond to fast and slow sampling rates of a 40 deg/sec stimulus. In contrast, involuntary OKN, resulting from instructions to stare in the center of the same patterns and not to attempt to follow their individual features, responds to the high frequency continuous motion stimulus but not to the low frequency apparent motion stimulus (Schor *et al.*, 1984). These voluntary and involuntary modes of OKN are distinguished by the fast phase frequency (FPF) of the resulting jerk nystagmus (Cheng & Outerbridge, 1974) which is greater in involuntary-stare than voluntary-pursuit OKN (nominally 3.0 Hz vs 1.0 Hz, respectively).

OKN has also been employed to determine spectral sensitivity (Moreland, 1982) and luminosity (e.g. Teller & Lindsey, 1991). These reports do not specify the class of OKN used as the measure, i.e. voluntary-pursuit or involuntary-stare. Although OKN has been used as an objective measure of motion processing of isoluminant stimuli, the contribution of isoluminant motion to involuntary-stare OKN and voluntary pursuit tracking

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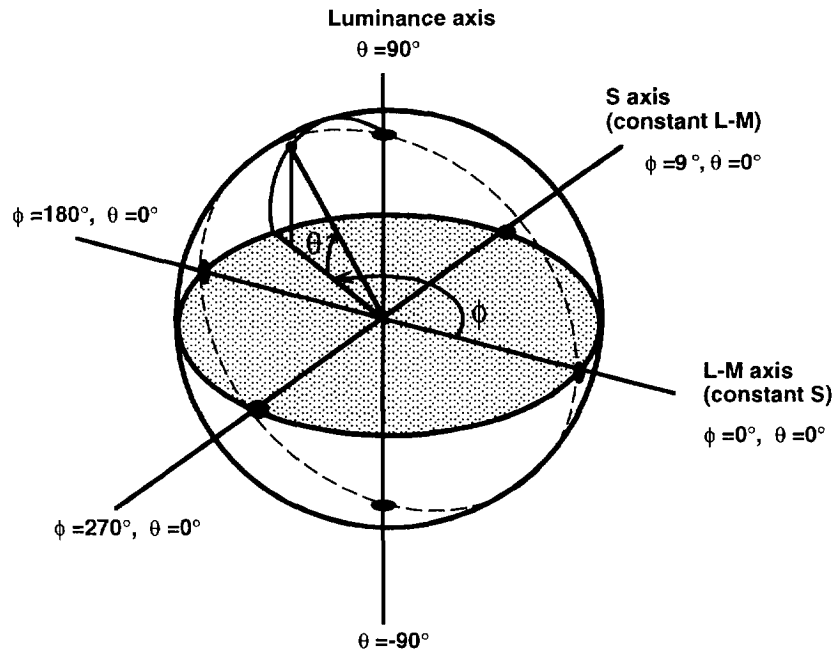


FIGURE 1. Diagram of the MBDKL color space (modified from Derrington *et al.*, 1984). The isoluminant plane is shaded. The S, L-M, and Lum axes are indicated (see text), as are changes in luminance/chromatic ratio (elevation θ) and hue (azimuth ϕ). The dashed curve outlines the plane formed by the Lum axis and the L-M axis.

movements has not been evaluated directly. Previous researchers using isoluminant stimuli for production of OKN have employed psychophysical procedures without the intent of quantifying the type or strength of eye movements produced (e.g. Teller & Lindsey, 1991).

In order to examine the contribution of chromatic and achromatic mechanisms to OKN and motion processing, we measured eye movement responses to monocularly presented, vertical sinusoidal gratings that were drifting horizontally. Patterns were defined by colors that varied along different directions in a cone activation color space. Results indicate that although luminance stimuli can drive both voluntary-pursuit and involuntary-stare OKN, isoluminant patterns are effective stimuli for voluntary-pursuit but not classically defined involuntary-stare OKN. These results suggest that when equated on the basis of detection thresholds, isoluminant stimuli produce quantitatively different OKN than luminance stimuli. A preliminary report of a portion of this work has been published previously in abstract form (Crognale & Schor, 1994).

In an additional experiment, we measured optokinetic eye movement responses to luminance and isoluminance patterns in strabismic subjects to compare with results reported for infants (Epelbaum & Teller, 1995) using a forced-choice psychophysical task. This was done to test the proposal that strabismic eye movement control may be modeled as incomplete or arrested development and thus by infants (e.g. Worth, 1903). Those results indicate that either there are important differences between strabismic and infant subjects for OKN at isoluminance or that there are important discrepancies between the

assessment of eye movements by direct observation and by objective recording.

METHODS

Description of color space

For stimulus color specification we utilized the MacLeod-Boynton-Derrington-Krauskopf-Lennie (MBDKL) color space (Krauskopf *et al.*, 1982; Derrington *et al.*, 1984) which is based upon a cone activation color space described by MacLeod and Boynton (1978). Stimuli composed of colors lying along selective axes in this color space provide activation of isolated cone or color mechanisms without the need for chromatic adaptation.

Our application of this color space to the spatio-chromatic visual evoked potential has been described in detail previously (Crognale *et al.*, 1993; Rabin *et al.*, 1994). Briefly, colors can be specified by vectors with an azimuth (ϕ) and an elevation (θ) (Fig. 1). Changes in azimuth correspond to changes in hue ($\phi = 0$, reddish; $\phi = 90$, violet/blue; $\phi = 180$, bluish-green; $\phi = 270$, greenish-yellow) while changes in elevation correspond to changes in the luminance/chrominance ratio (e.g. for a grating along an axis where $\theta = 45$, the reddish component will be brighter but less saturated than at $\theta = 0$, and the bluish-green component will be darker and less saturated; the relative brightness of the two colored components will be reversed for $-90 < \theta < 0$). Purely achromatic (black/white) stimuli are produced by modulation along the luminance axis ($\theta = 90$ or -90). Changes along the luminance axis produce equal,

TABLE 1. CIE coordinates of the monitor phosphors and the endpoints of the major axes in the MBDKL color space

Phosphors	CIE coordinates (x, y)	
R	(0.602, 0.352)	
G	(0.263, 0.591)	
B	(0.124, 0.051)	
Colour axes	$[\phi, \theta]$	
S	+s	[90,0] (0.273, 0.230)
	-s	[270,0] (0.389, 0.501)
LM	+l-m	[0,0] (0.391, 0.278)
	-l+m	[180,0] (0.205, 0.365)
Lum	+l+m+s	[°,90] (0.310, 0.316)
	-l-m-s	[°, -90] (0.310, 0.316)

*Undefined.

simultaneous modulation of all three cone types. Stimulus modulations in the plane $\theta = 0$ (shaded in Fig. 1) are all isoluminant (purely chromatic). Within this plane, stimulus variations along the axis where $\theta = 0$ and 180 (LM axis) inversely modulate the long wavelength sensitive (L) and middle wavelength sensitive (M) cones but not the short wavelength sensitive (S) cones, whereas variations along the axis where $\theta = 90$ and 270 (S axis) modulate only the S cones.

Table 1 provides the CIE (International Commission on Illumination) coordinates of the endpoints of the major axes and our monitor phosphors. The achromatic origin of the color space was chosen to be illuminant C ($x = 0.310$; $y = 0.316$). Cone activations were calculated from the Smith and Pokorny (1975) fundamentals.

Stimuli

Stimuli were generated on a Sony monitor with a Sun-TAAC color graphics system. The stimulus patterns were 0.5 c/deg sine wave gratings in a circular patch subtending 18 deg, drifting at 10 deg/sec and viewed from 57 cm. The edges of the pattern were Gaussian tapered to remove high frequencies. Drifting patterns were created by sinusoidally modulating two interlaced patterns in temporal and spatial quadrature (separated in space and time by 90 deg). Stimulus patterns were composed of colors that varied symmetrically around white along various directions (axes) in the color space, keeping the mean space-averaged chromaticity and luminance (37 cd/m^2) constant throughout the experiments.

Procedure

Psychophysics—Isoluminance and Thresholds. Individual isoluminance was determined psychophysically using a motion nulling paradigm (Cavanagh *et al.*, 1987) for colors lying along the two major axes which isolate either the S cones (S axis) or the L and M cones (LM axis). For measurements of isoluminance, we interleaved two counterphasing sinusoidal patterns in temporal and spatial quadrature. One pattern was a low contrast, horizontal, achromatic grating which was fixed in chromaticity and contrast and the other pattern was a

horizontal chromatic grating composed of colors lying in either the plane of the LM and luminance axes or the plane formed by the S and luminance axes. The luminance/chromatic ratio of these patterns was adjusted by changing the elevation (θ) of the color axis. Motion is perceived by forming a correspondence between the luminance components of the achromatic grating with any luminance component in the colored grating. The direction of perceived motion is either up or down, depending upon the relative luminosity of the colors in the grating and the spatial phase of the quadrature ($+90^\circ$ or -90°). At isoluminance, there is no luminance correspondence between the achromatic and chromatic patterns and therefore unambiguous motion is not perceived (e.g. the pattern may appear as a stationary counterphasing grating). Isoluminance determination along the LM and S axes in this manner defines the location of an individual's isoluminant plane relative to that of the CIE standard observer in the MBDKL color space.

Thresholds for detection of stationary 0.5 c/deg luminance and isoluminance (LM and S axis) gratings were also measured. To measure luminance thresholds, we utilized an auxiliary optical system which superimposed the two halves of the CRT display. One half of the display contained the patterned test and the other half contained an unpatterned field. Superposition of the two fields served to reduce the contrast of the patterned image. The combined stimulus had the same mean chromaticity and luminance as used elsewhere in this study. The contrast of the drifting gratings for measurement of OKN was subsequently set to 12 times the detection threshold for both luminance and isoluminant conditions. The average cone contrasts at 12 times detection threshold for modulations along the major axes were: S axis-S cones = 0.74; LM axis-L cones = 0.04, M cones = 0.09; Lum axis-L cones = 0.10; M cones = 0.10, S cones = 0.10.

OKN Stimuli. Vertical sinusoidal gratings (0.5 c/deg) were drifted at a rate of 10 deg/sec. Subjects performed two tracking tasks; they were instructed either to pursue individual bars in the drifting grating (pursuit) or to stare in the center of the field and keep the moving bars visible (stare) (Ter Braak, 1936; Honrubia *et al.*, 1968). The pursuit and stare modes of tracking are believed to produce two classes of OKN responses, voluntary-pursuit OKN and involuntary-stare OKN respectively (Honrubia *et al.*, 1968). Involuntary-stare and voluntary-pursuit OKN are distinguished by their fast phase frequencies (Cheng & Outerbridge, 1974). OKN was stimulated for 10 sec durations for two to three trials of each condition. Eye movements were recorded using an IR limbal eye tracking system (G+W eye-trac, Applied Science Laboratories).

Horizontal OKN was measured in the nasal and temporal directions for different axes within the individual's isoluminant plane and along the achromatic axis. Directions of OKN stimulation (nasal/temporal) were interleaved to avoid optokinetic aftereffects (Cohen *et al.*,

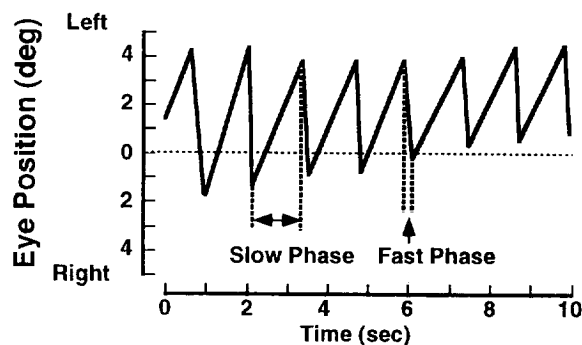


FIGURE 2. Characteristic sawtooth eye movement trace obtained from stimuli drifting from right to left. Slow and fast phases are indicated.

1977). In one experiment, the luminance/chrominance ratio of the gratings was varied in small increments bracketing the isoluminant plane near the LM axis.*

Analysis

Figure 2 is a drawing of a prototypical recording of eye position vs time during the production of voluntary-pursuit OKN. Typical OKN is characterized by a sawtooth pattern with slow and fast phases (indicated) (Honrubia *et al.*, 1968; Schor *et al.*, 1984). OKN was evaluated with several parameters including FPF, slow phase velocity (SPV) and percent duration of OKN (PD). FPF is a measure of the number of saccades (jerk nystagmus) occurring during intervals when eye movements exceeded a criterion SPV level (1.2 deg/sec). FPF provides a classification of the type of OKN [nominal voluntary-pursuit OKN = 1.0 Hz; nominal involuntary-stare OKN = 3.0 Hz; Cheng & Outerbridge (1974)]. SPV is the average speed of slow following eye movements

(nonsaccadic). SPV provides a measure of the strength of OKN. PD is the percentage of the stimulus duration during which eye movements greater than 0.5 deg/sec occur. PD provides an additional measure of the strength of OKN. During strong OKN, eye movements occur almost continuously and PD is high. Weak OKN is often sporadic, producing a lower PD.

Subjects

Three normal subjects (RC, CS and PB) had normal visual acuity and binocular vision. All exhibited normal stereopsis (thresholds < 20 sec arc) as measured by the Wirt test and no strabismus. None had a history of strabismus, amblyopia or any eye movement disorder including latent nystagmus. One subject was emmetropic (RC) and the other two subjects were one diopter (PB) and two diopters (CS) myopic and wore spectacle corrections. Ages were 25, 28, and 52 yr, respectively.

Three adults with a history of infantile esotropia were also examined. Age of onset for esotropia was under 2 yr for two subjects (DR and EL) and between 2 and 4 yr for the third (FL). This subject also had a 4.5 D anisometropia. One of the other subjects had amblyopia of 20/80 with dissociated vertical deviation (DVD) and the other was a recovered amblyope with 20/27 in the treated eye. Both of them had patching therapy of the left eye between 2 and 4 yr of age. None of the subjects had latent nystagmus. Two of the subjects had attempted surgical correction for their esotropia between 2 and 4 yr and the third at 5 and 8 yr. All subjects were unilateral left esotropes and only the right fixating eye was tested in this study. All subjects wore current refractive spectacle corrections. The age of two subjects was 38 yr and the third was 39 yr.

RESULTS

Eye movement records of OKN in response to temporal-to-nasalward (TN) motion and to nasal-temporalward (NT) motion for three normal subjects are seen in Fig. 3. Shown are records obtained with drifting patterns defined by modulations along the luminance (Lum), S-(L+M) chromatic axis (S), and L-M chromatic axis (LM). Records from the pursuit condition are shown on the left side of each figure and those from the stare condition are shown on the right. The numbers to the right of the waveforms indicate FPF, SPV and PD (from top to bottom). Both stare and pursuit eye movement records for the luminance condition show the classic sawtoothed pattern for all subjects. Lower amplitudes for stare relative to pursuit are clearly discernible. Although the general pattern of OKN measures were the same for all three normal subjects, subject RC showed an asymmetric bias for TN stimuli, producing more robust OKN at isoluminance (i.e. using S and L-M stimuli) than either of the other subjects under these conditions. The topic of OKN asymmetries and directional biases will be discussed below.

Several interesting characteristics of the OKN are apparent in the individual records of Fig. 3.

*Changing the elevation (θ) from 0 to 90 deg is equivalent to changing from a purely chromatic grating to an achromatic grating or changing the luminance/chrominance component ratio from 0 to 1. Note that this is not equivalent to changing the relative brightness of red and green stripes, as is often done for comparison of luminance and chrominance. The major differences are: (1) we are modulating along an LM axis at isoluminance which is not the same as a red-green phosphor line. (2) Unlike the LM axis, the red-green phosphor line has an average chromaticity that is yellow and not achromatic. (3) The phosphor axis may provide some modulation of the S cones at isoluminance. (4) In our application, as one moves from the isoluminant plane to the luminance axis, the chromatic content of the grating decreases from one to zero while the luminance contrast increases from 0 to 1. In studies which change the relative intensity of the red and green stripes of a grating, only the luminance component is varied. Thus the "luminance" conditions are not achromatic and are either red/black or green/black. These patterns are powerful stimuli for the color opponent mechanisms as well as the luminance mechanism and thus do not isolate the luminance system. (5) The same problems arise in other studies which add a red/black and a green/black grating in phase to produce luminance, 180 deg out of phase to produce purely chromatic stimuli. In these studies, the "luminance" gratings are yellow/black and strongly modulate the S-(L+M) (blue-yellow) opponent mechanism in addition to the luminance system.

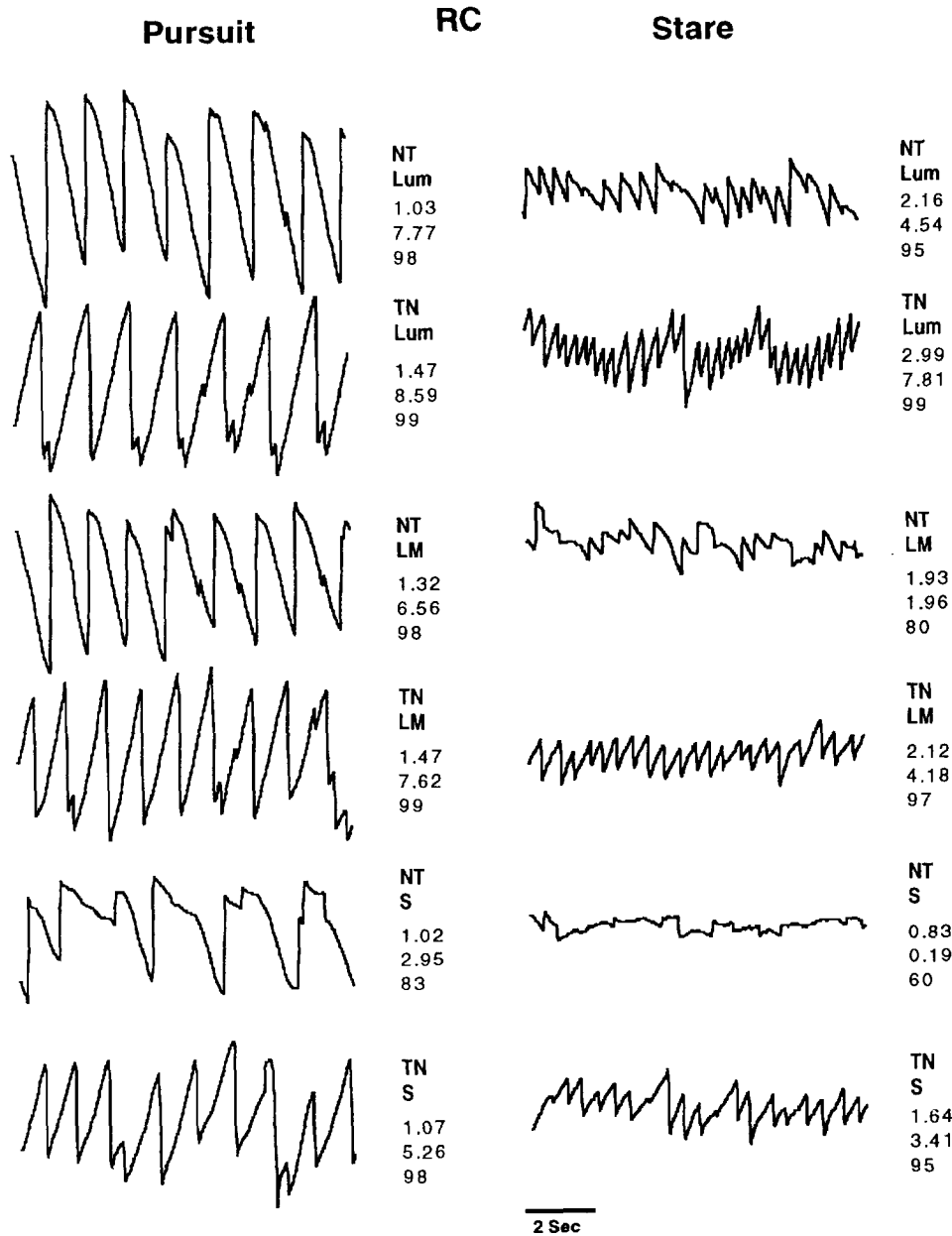


FIGURE 3. (a-c) OKN eye movement records obtained from normal subjects (CS, PB, and RC) for temporal-to-nasal (TN) and nasal-to-temporal (NT) motion of two chromatic gratings (S and LM) and one achromatic grating (Lum). Pursuit condition is shown on the left and stare condition on the right. Associated measures of FPF, SPV, and percentage of directional eye movements (top to bottom) are indicated to the right of the waveforms.

1. For the luminance stimuli, stare and pursuit conditions produced predominantly classic OKN as reported previously.
2. For the pursuit condition in both the luminance and isoluminant stimuli, fast reflexive OKN often occurred at the end of a saccade back to the center, before the resumption of pursuit tracking. Inter-saccadic interval analysis of the waveforms for subject PB who showed the most pronounced intrusions indicate a bimodal distribution of response frequencies with mean values of 0.93 and 2.90 Hz for the NT direction and 0.84 and 2.41 Hz for the TN direction.
3. Except for the TN direction for subject RC, the stare condition produced remarkably different OKN for

isoluminant stimuli than for luminance stimuli. Isoluminant stare OKN was often sporadic, low amplitude, and lacking in distinct slow and fast phases.

4. Subject RC showed a strong TN bias while subject CS showed a less pronounced bias.

Figure 4 summarizes the data of all three normal subjects' pursuit and stare responses to luminance and isoluminance gratings, respectively. The figure provides means for FPF, SPV and PD. Error bars indicate +1 standard error of the mean (SEM) for each measure. For these data TN and NT eye movements were averaged together for each subject.

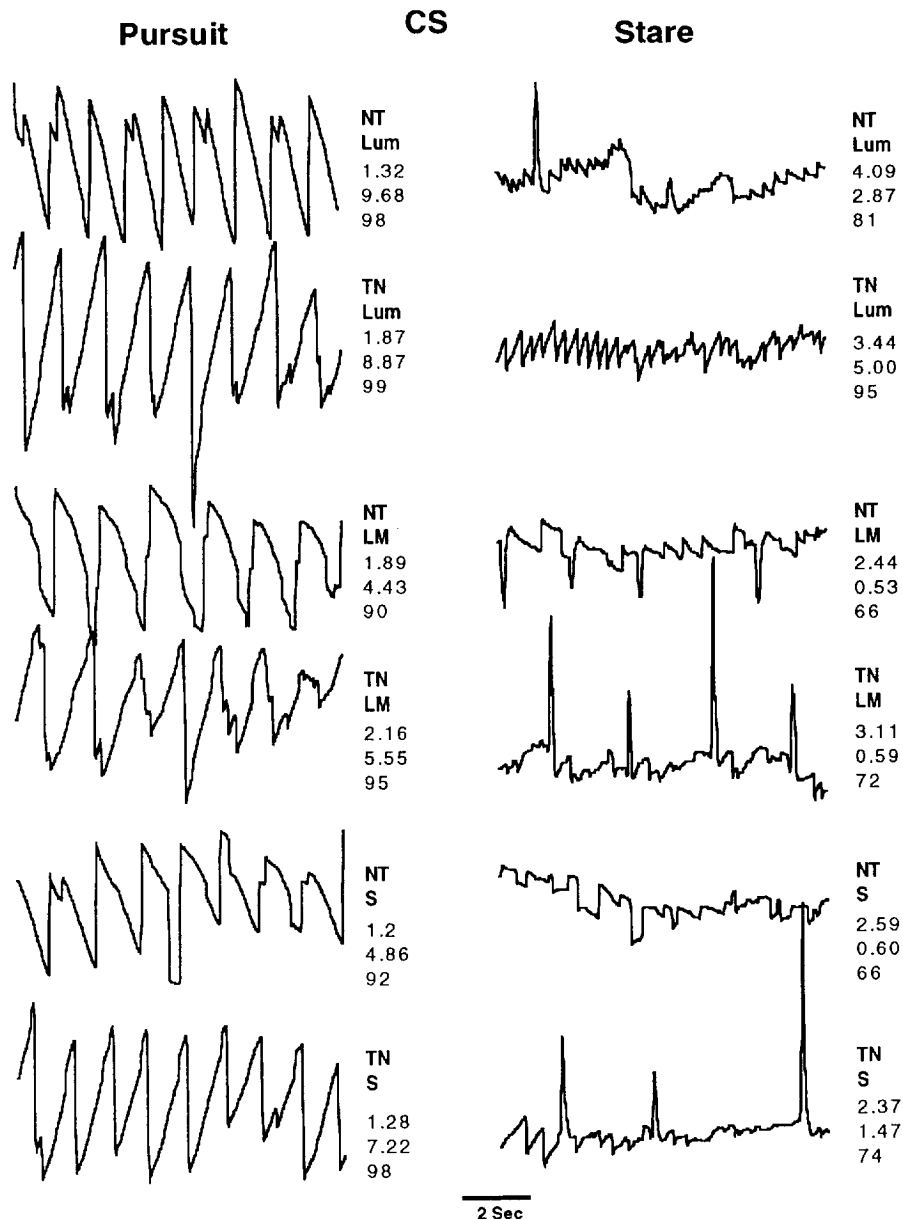


FIGURE 3(b).

Luminance OKN

Figure 4 shows the results of measurements of pursuit and stare responses to drifting luminance gratings as well as measurements for a control condition using a blank screen. The averaged fast phase frequencies for the pursuit condition are higher than 1 Hz reflecting the intrusion of reflexive (stare) OKN as noted above. These low contrast stare responses also display a slightly lower FPF than previously reported for high contrast stimuli. Average SPV [Fig. 4(b)] indicates a clear difference between stare and pursuit conditions for the luminance stimuli. Percent duration [Fig. 4(c)] measures show that the production of luminance OKN was continuous for both stare and pursuit conditions.

Isoluminant OKN

Figure 4 also shows the averaged results of measurements of stare and pursuit responses to drifting

isoluminant (chromatic) gratings. The trends for the S and the LM axis were similar. FPF [Fig. 4(a)] indicates that the differences between pursuit and stare responses elicited by isoluminant stimuli were less than those for luminance stimuli, largely reflecting weak stare OKN as seen in the individual records. The reduction in FPFs for pursuit and stare conditions was particularly evident along the S axis.

Pursuit SPV [Fig. 4(b)] shows that the subjects could pursue isoluminant patterns but not quite as well as luminance patterns. SPV for stare responses was diminished for isoluminant stimuli along the LM axis and particularly along the S axis. PD measures [Fig. 4(c)] for isoluminant stimuli indicate that stare eye movements were not produced as consistently as pursuit eye movements along the S axis or along the LM axis or as well as for luminance stimuli, reflecting the sporadic nature of the OKN for the chromatic conditions (Fig. 3).

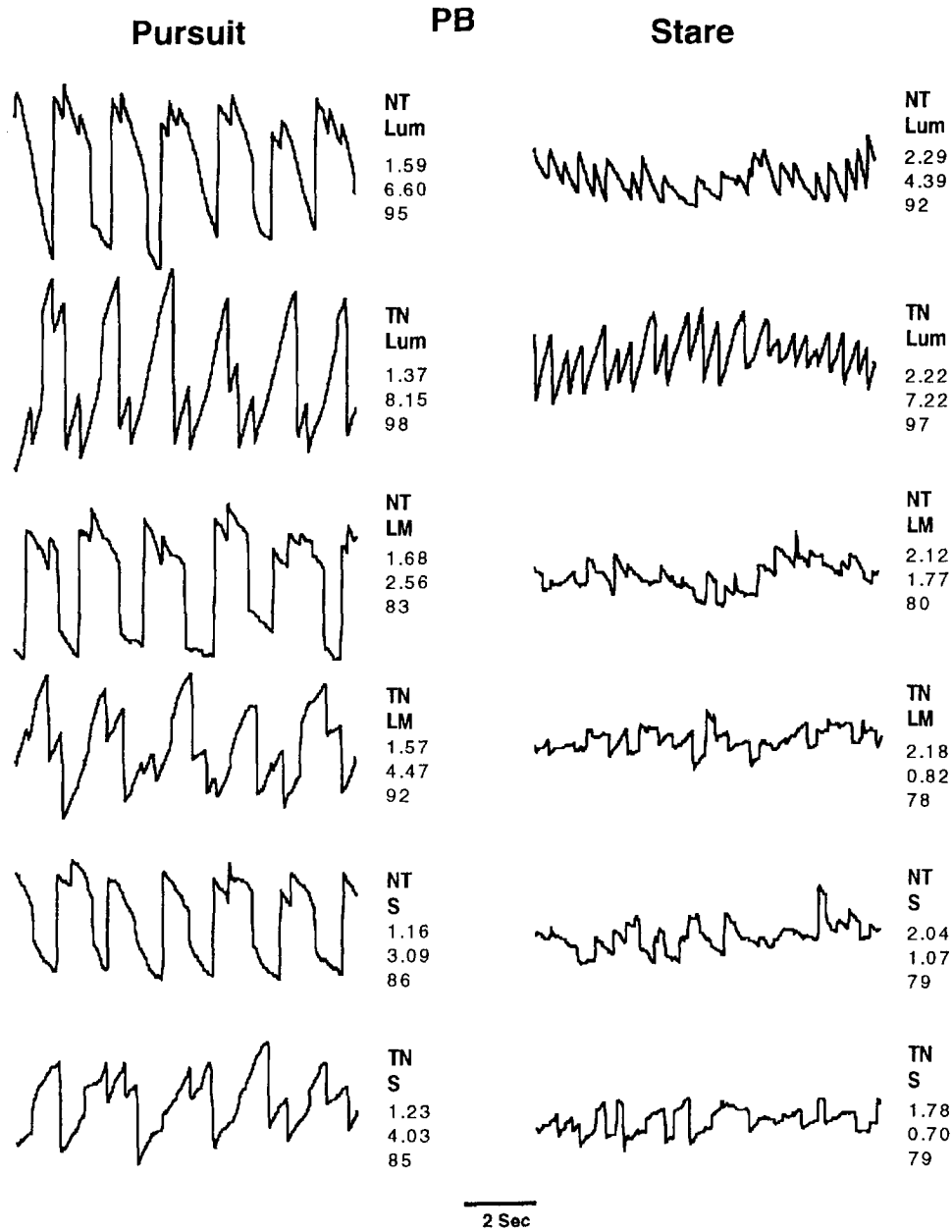


FIGURE 3(c).

Chromatic/luminance ratio

To investigate how OKN changes as a function of the degree to which we are isolating the chromatic vs luminance mechanisms, we measured eye movements to drifting gratings at 20 different axes in the plane formed by the LM axis and the Lum axis (dashed plane in Fig. 1). Recall that as elevation (θ) is raised or lowered from the isoluminant plane ($= 0$ deg), the chromatic content of the pattern decreases and the luminance content increases. Elevations of $\theta = 90$ and $\theta = -90$ indicate achromatic gratings which are spatially 180 deg out of phase with each other (i.e. black is white and white is black).

Figure 5 shows how the stare responses varied as a function of elevation out of the isoluminant plane for individual trials for subject RC for both TN (open squares) and NT (solid circles) directions. The subject

was tested twice for each direction. NT measures were consistently lower than TN measures for this subject. All measures except the TN condition for PD, show a trend towards a minimum near the isoluminant plane ($\theta = 0$). Although somewhat variable, these measures do not change appreciably in a range of ± 20 – 30 deg around the isoluminant plane. The dip near isoluminance is most pronounced for NT directions, consistent with the records shown in Fig. 3(a).

OKN vs direction within the isoluminant plane

Figure 6 shows polar plots of OKN measures for three subjects as a function of direction within the isoluminant plane (shaded in Fig. 1) in 15 deg increments of θ . The S axis ($\phi = 90$ deg) is shown as vertical while the LM axis ($\phi = 0$ deg) is horizontal. The shaded region outlines

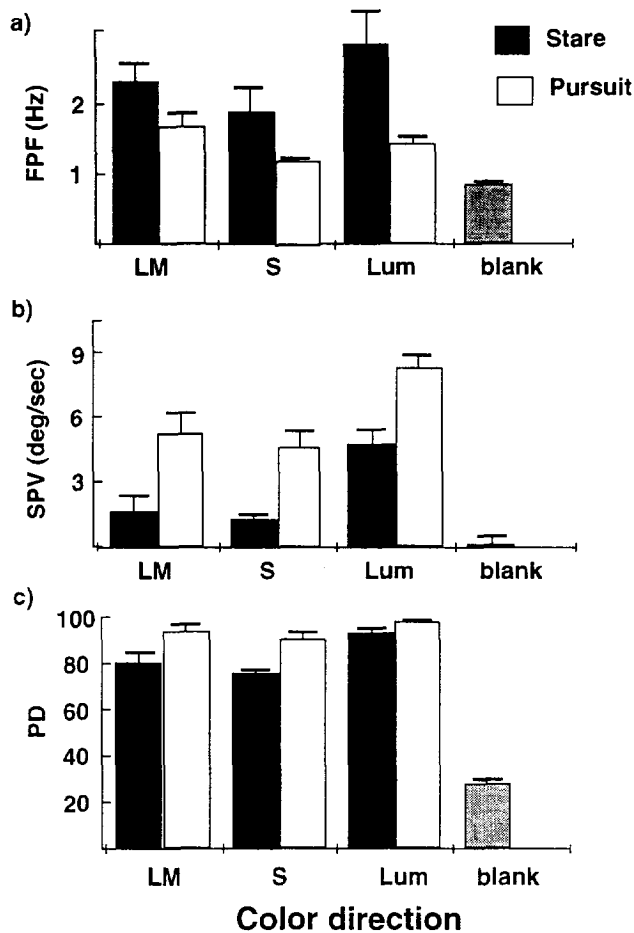


FIGURE 4. a) Comparison of average pursuit and stare fast phase frequencies (FPF) of OKN obtained for drifting patterns for chromatic stimuli (S axis and LM axis) and achromatic (Lum) stimuli. A blank control stimulus is included. Error bars indicate 1 SEM ($n=3$). (b) Measurements of OKN SPVs. (c) Measurements of the proportion of stimulus time spent making directional eye movements (PD).

± 1 SEM around the average values ($n=3$) for stare OKN. The values for each of the three subjects was the average of one TN measure and one NT measure. Pursuit responses along the S and LM axis were included for comparison (center of filled squares = ± 1 SEM). Luminance measures (± 1 SEM) are plotted arbitrarily along the 45 deg line (solid circles—pursuit; open circles—stare).

FPF measures are shown in Fig. 6(a). Stare FPF was highest along the LM axis and decreased systematically towards the S axis (see also Fig. 4). Isoluminant stare FPFs were consistently lower than luminance stare measures and higher than pursuit measures. Stare SPV measures [Fig. 6(b)] also show a systematic decrease towards the S axis. SPV was maximal near the LM axis (15 deg). The isoluminant stare SPVs were consistently lower than luminance stare SPVs and all pursuit measurements. Isoluminant stare PD measures [Fig. 6(c)] agree with FPF and SPV and exhibited a minimum along the S axis (see also Fig. 4) and are lower than all other conditions.

Directional biases

Normal subjects. Large directional biases for the

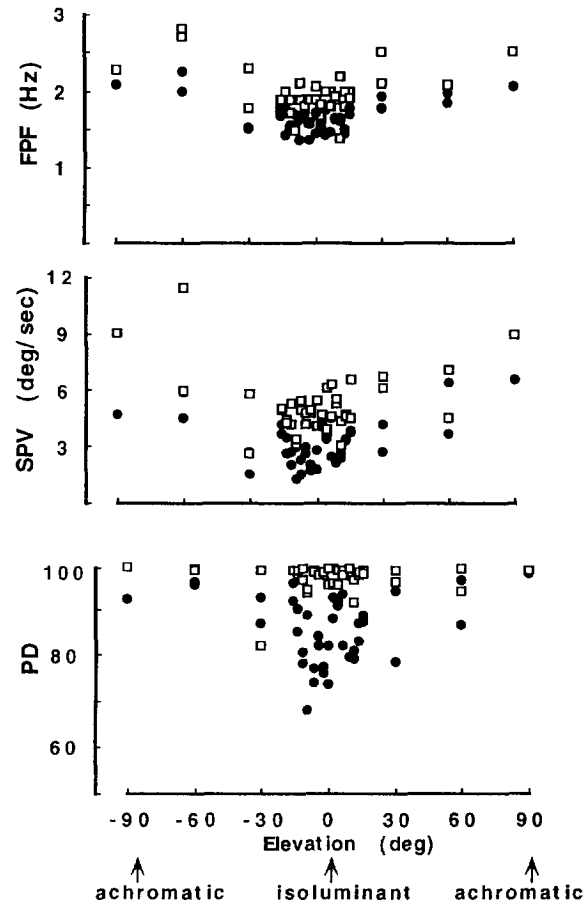


FIGURE 5. Stare OKN measures at different elevations in the MBDKL color space (\bullet , NT; \square , TN) for subject RC. The isoluminant plane is at $\theta=0$. Purely achromatic stimuli are at $\theta=90$ and $\theta=-90$. (a) FPF. (b) SPV. (c) Proportional time of eye movements (PD).

production of monocular horizontal OKN are rare in normal adults. However, for luminance patterns, normal subjects sometimes exhibit small biases which take all possible forms: TN, NT, rightward, or leftward (Schor & Narayan, 1981; Schor & Westall, 1984). On the other hand, infants and strabismic subjects typically display strong TN biases (Atkinson & Braddick, 1981; Naegele & Held, 1982; Schor, 1993; Schor & Levi, 1980). The degree to which asymmetries exist for isoluminant stimuli in normal adults has not been reported. However recently, Epelbaum and Teller (1995) have provided evidence using a psychophysical forced choice procedure, that infants exhibit a paradoxical NT bias rather than a TN bias for isoluminant patterns.

Figure 3(a) shows eye movement traces obtained from normal subject RC in response to S, LM and Lum patterns drifting in the NT direction. Voluntary-pursuit OKN (left) shows robust following responses for all the stimuli. However, for stimuli modulated along the S axis, the eye movements were produced less consistently as evidenced by the lower PD measure. The pursuit OKN responses to NT stimuli appear as strong as those to TN stimuli except along the S axis. In contrast to the robust NT pursuit eye movements for the LM axis, the stare eye movement traces (right) indicate much weaker OKN for LM (and S) axis gratings moving in the NT direction than

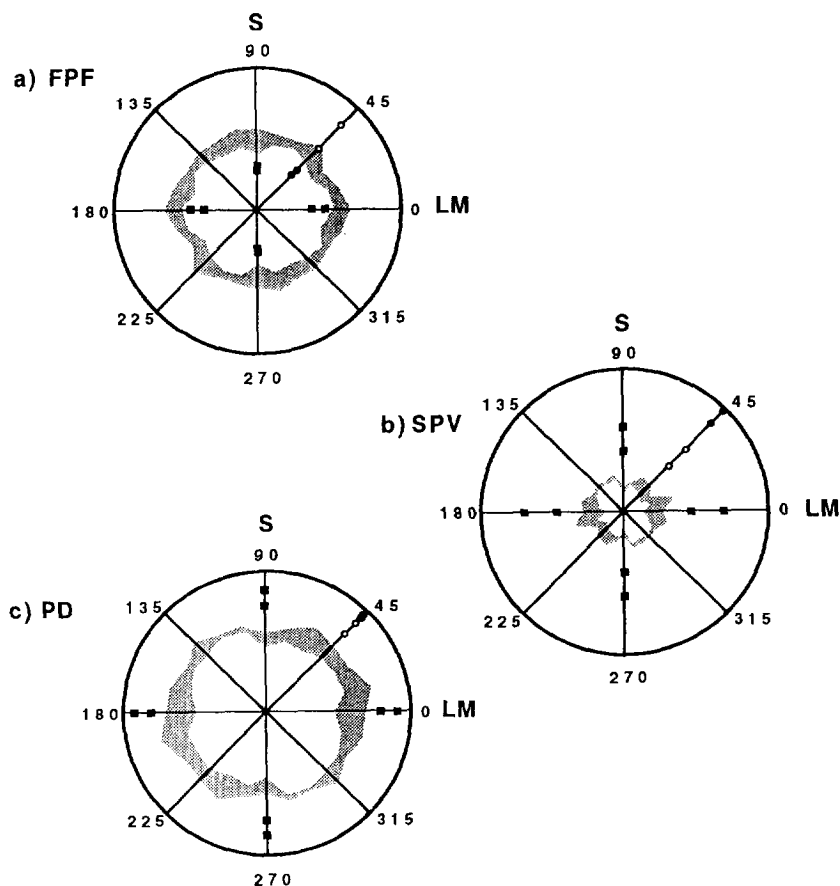


FIGURE 6. Polar plots of OKN measures for stimuli in 15 deg increments of θ within the isoluminant plane. The S axis is vertical and the LM axis is horizontal. The data are plotted twice and are reflected about the origin. The shaded region outlines ± 1 SEM around the mean stare OKN values ($n = 3$). The center of the solid squares bound ± 1 SEM for the pursuit conditions. For purposes of comparison, ± 1 SEM bounds for the luminance conditions are arbitrarily plotted on the isoluminant 45 deg line (\circ , stare; \bullet , pursuit). (a) Plot of fast phase frequencies (outer ring = 4.0 Hz). (b) SPVs (outer ring 9.0 deg/sec). (c) Percent time of directional eye movements (origin = 50; outer ring = 100).

in the TN direction. The luminance NT OKN measures were also reduced slightly compared to TN measures. The S axis stimuli show the greatest asymmetry. Recall that the data of Fig. 5 also showed a consistent TN bias. Measurements using the subject's other eye (not shown) revealed a rightward bias confirming that the bias was indeed TN and not leftward.

Figure 7 shows how the TN (open circles) and NT (solid circles) OKN measures in normal subject RC varied as a function of direction within the isoluminant plane. The figure plots the stare measures for 15 deg increments in the isoluminant plane. Isoluminant pursuit and stare FPFs (a) were consistently higher in the TN direction than in the NT direction as in the example shown in Fig. 3. In addition, the difference between NT and TN FPFs were greatest along the S axis. The SPVs (b) and PD measures (c) reveal a similar bias for TN OKN. Both NT and TN SPVs show a systematic decrease towards the S axis. However, the NT velocities were always slower than the TN velocities with the greatest difference lying along the S axis. Pursuit responses along the S axis were also similarly biased as mentioned above and a small bias for luminance OKN was in the TN direction (Fig. 3).

One other normal observer showed a similar but less pronounced pattern of bias. The third normal observer showed little evidence of a bias. Although the strength of bias was an idiosyncratic property of each observer, the direction of the bias was highly consistent within each subject, based upon multiple measurements, interocular comparison, and measurements for different axes in color space (e.g. Figs 5 and 7). In addition, isoluminant biases were consistently in the same direction as the smaller luminance biases (Figs 3 and 5).

Subjects. Observations of three strabismic subjects indicate that a TN bias existed for both luminance and isoluminant stimuli for all measures of pursuit and stare responses. Figure 8 shows the SPVs of the three strabismic subjects to modulations along the LM, S and Lum axes under both pursuit and stare conditions. All three subjects show a similar pattern of asymmetry. Voluntary-pursuit SPVs were greater than comparable stare SPVs and TN SPVs were faster than comparable NT SPVs. FPF and PD measures showed a similar pattern of results. Since errors in the estimation of an individual's isoluminant plane might fail to reveal a reverse asymmetry at isoluminance, we conducted a careful exploration of OKN near the isoluminant plane as was

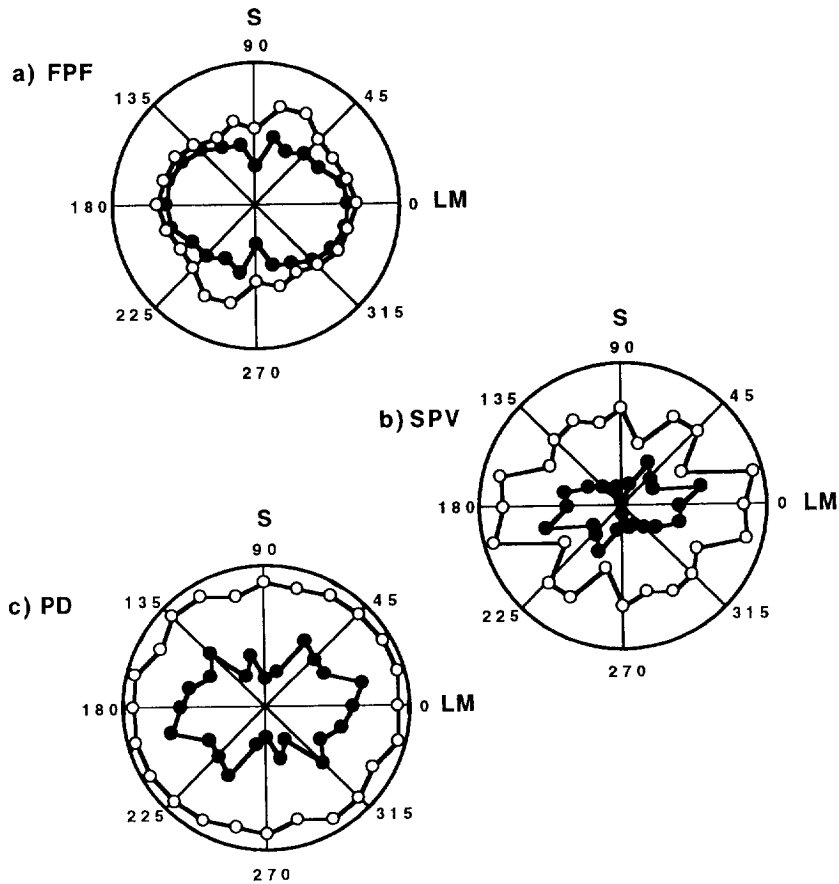


FIGURE 7. (a) Polar plot of FPFs for different directions within the isoluminant plane for subject RC. Both TN and NT conditions are shown (outer ring = 3 Hz). (b) SPVs plotted as in (a) (outer ring = 5 deg/sec). (c) Percentage of time of directional eye movements plotted as in (a) (origin = 50%, outer ring = 100%).

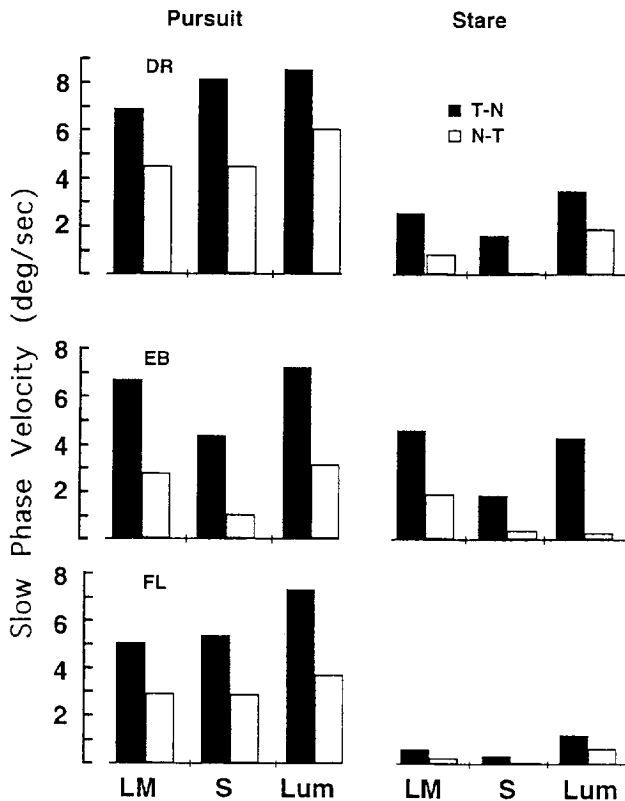


FIGURE 8. Pursuit (left) and stare (right) SPVs obtained from three strabismic subjects in response to S, LM and Lum patterns drifting in the TN and NT directions. The values are the average of two measurements for each condition.

done for the normal subjects shown in Fig. 5. These results revealed a consistent picture of bias; there was no point at which the TN bias was reversed.

DISCUSSION

The results shown in Figs 3 and 4 are in agreement with previous luminance OKN studies and indicate that the subjects were performing the tasks required to produce voluntary-pursuit and involuntary-stare OKN (Honrubia *et al.*, 1968; Schor *et al.*, 1984).

The reduction in SPVs FPF and PD measures for isoluminant conditions suggest that under these conditions, the chromatic pathways may not provide a good stimulus for the neural substrate that produces classic involuntary-stare luminance OKN. It is conceivable that isoluminant input to the pathways or neural level which produces classic involuntary-stare OKN is lacking entirely, and small unavoidable luminance cues from retinal inhomogeneity and errors in estimation of individual isoluminance contribute to the residual production of involuntary-stare-like OKN at isoluminance in the present study. One other possible interpretation is that the lower FPFs and smaller SPVs of the stare condition reflect differences between the characteristics of the isoluminant and luminance involuntary-stare OKN mechanisms.

The data of Fig. 5 demonstrate that OKN measures

decrease systematically as the stimuli change from achromatic to chromatic. In addition, there is a range around an individual's isoluminant plane wherein the responses show a minimum. It would be interesting to compare this range to the size of the region bracketing the isoluminant plane where motion is difficult to discern under some conditions ("motion dead zones", Teller & Lindsey, 1993b), providing that such ranges could be determined for the stimulus parameters of the present study.

The stare FPF, SPV and PD data of Fig. 6 suggest that stare responses vary as a function of color being minimal along the S axis (see also Fig. 4), and are reduced compared to luminance stimuli. Both achromatic and isoluminant gratings produced classic voluntary-pursuit OKN under pursuit conditions with achromatic stimuli being a more powerful stimulus. Achromatic gratings produced classic involuntary-stare OKN under stare conditions while chromatic gratings, particularly S axis stimuli, produced stare OKN that was much less powerful and showed lower FPFs than classic involuntary-stare OKN when stimulated by achromatic gratings. The results shown in Figs 4 and 6 suggest that at equal multiples of detection threshold, isoluminant patterns are not as powerful a stimulus for motion as luminance patterns (Lindsey & Teller, 1990), and the S cones have minimal contribution to the luminance system (e.g. Cavanagh *et al.*, 1987).

Extraretinal motion signals may also influence the optokinetic response to drifting gratings. Correlates of transient eye movements can produce apparent motion of a stabilized image such as a floater or afterimage, and this apparent motion can stimulate additional ocular pursuits (von Helmholtz, 1866). Perceived motion produced by slow eye movements can also evoke continuous optokinetic nystagmus (Sigma OKN) in response to a string of stationary spots illuminated stroboscopically (Adler *et al.*, 1981). Motor correlates of the initial acceleration phase of voluntary-pursuit OKN (smooth pursuit) (Lisberger *et al.*, 1987) could interact with small retinal image displacements of the drifting isoluminance gratings and enhance the percept of continuous motion and the subsequent voluntary following response. In this way, residual luminance cues or the isoluminant patterns themselves may provide the triggering stimulus for the production of stare OKN by extra-retinal motion signals associated with smooth pursuit responses to small target displacements.

Another explanation for the difference in responses of involuntary stare OKN to luminance and isoluminant patterns is that the parameters chosen for this study might have favored OKN production by the luminance system over that of the chromatic pathways. There is a large body of evidence (e.g. Kelly, 1974) indicating that the luminance pathways are tuned to relatively higher spatial and temporal frequencies than the chromatic pathways. This is particularly evident for S cone pathways. However, it is unlikely that the choice of a 0.5 c/deg stimuli, near the maximum of the chromatic spatial tuning function, would provide a strong advantage for the

luminance pathways. Similarly, the choice of a 10 deg/sec drift rate (corresponding to a temporal frequency of 5 Hz) is well within the capacity of the color mechanisms, as further supported by the facility with which subjects produced pursuit responses. Nonetheless, slower drift rates may produce improved stare responses at isoluminance.

An additional explanation for the relatively poor production of involuntary-stare OKN at isoluminance, particularly along the S axis, is that scaling the contrasts as a multiple of detection threshold is an inappropriate metric for the comparison of OKN to stimuli modulated along the different axes. For example, one may want to equate the stimuli on the basis of cone contrast or discrimination thresholds for motion. It would be valuable for future research to determine exactly what (if any) relative contrasts are required to equate involuntary-stare OKN measures along the S, LM and luminance axes and to quantify the extent to which these relative contrasts depend upon temporal and spatial parameters.

If we consider the possibility that involuntary-stare OKN occurs when foveal pursuits are suppressed then we would predict that the reported relative paucity of the short wavelength sensitive cones in the central foveola (e.g. Ahnelt *et al.*, 1987) might produce a weak foveal pursuit that is more easily suppressed. In such a case, it should be relatively easy to produce involuntary-stare OKN with S axis stimuli. The present results are contrary to this prediction and it is likely that either suppression of foveal pursuit or the regional differences in the S vs L and M cone numerosity in the central foveola play little role in the production of involuntary-stare OKN to low spatial frequency (0.5 c/deg) stimuli.

The temporal to nasal bias observed in two normal subjects, although less pronounced, was in the same direction as that seen for luminance gratings in infants and strabismic subjects (Schor, 1993) but opposite to that recently reported for infant OKN at isoluminance (Epelbaum & Teller, 1995). That the third normal subject showed a small but consistent nasal to temporal bias for all stimulus conditions suggests that both the direction and strength of bias is idiosyncratic for the observer but that the individual's bias was not reversed at isoluminance.

The observation that infants, but none of our childhood esotropic subjects, showed a reverse (NT) asymmetry at isoluminance suggests that the mechanisms which produce the TN biases for luminance OKN in infants and strabismics may have different physiological bases. Another interpretation of these results is that there are real differences between the results obtained with a psychophysical paradigm to detect ocular drift bias, as in Epelbaum and Teller (1995) and objective measures of eye movements which employ several criteria for defining OKN (i.e. jerk nystagmus, FPF and minimum SPV). Future measurements of isoluminant OKN in infants using an eye tracking method would address this issue.

CONCLUSIONS

Based upon the PPF analysis, voluntary-pursuit OKN responds to both luminance and isoluminant gratings. The same analysis indicates that classic involuntary-stare OKN responds to luminance stimuli more strongly than to LM and S axis patterns. Stare OKN has a greater SPV response to luminance than isoluminance stimuli. Isoluminant patterns which only stimulate the S cones are the weakest stimuli for classic involuntary-stare OKN. Finally, measures of directional biases for OKN revealed similar biases for luminance and isoluminance conditions. The horizontal directional biases for individual normals were idiosyncratic (i.e. nasal or temporal) and they were larger in response to the chromatic than luminance conditions. A similar concordance between directional bias in luminance and chromatic conditions was observed in the larger horizontal asymmetries of both pursuit and stare OKN of three strabismic subjects, contrasting with prior reports of reverse asymmetries (NT bias) at isoluminance observed in infants.

REFERENCES

- Adler, B., Collewijn, H., Curio, G., Grüsser, O. J., Pause, M., Schreier, U. & Weiss, L. (1981). Sigma movement and sigma nystagmus: A new tool to investigate the gaze-pursuit system and visual-movement perception in man and monkey. *Annals of the New York Academy of Science*, 374, 284–302.
- Ahnelt, P. K., Kolb, H. & Pflug, R. (1987). Identification of a subtype of cone photoreceptors likely to be blue sensitive in the human retina. *Journal of Comparative Neurology*, 255, 18–34.
- Atkinson, J., Braddick, O., Fisher, D. F., Monty, R. A. & Senders, J. W. (1981). *Cognition and visual perception*. New Jersey: Lawrence Erlbaum and Assoc.
- Carney, T., Shadlen, M. & Switkes, E. (1987). Parallel processing of motion and color information. *Nature*, 328, 647–649.
- Cavanagh, P., MacLeod, D. I. A. & Anstis, S. M. (1987). Equiluminance: Spatial and temporal factors and the contribution of blue sensitive cones. *Journal of the Optical Society of America A*, 4, 1428–1438.
- Cavanagh, P., Tyler, C. W. & Favreau, O. E. (1984). Perceived velocity of moving chromatic gratings. *Journal of the Optical Society of America A*, 1, 893–899.
- Cheng, M. & Outerbridge, J. S. (1974). Inter-saccadic interval analysis of optokinetic nystagmus. *Vision Research*, 14, 1053–1058.
- Cohen, G., Matsuo, B. & Raphan, T. (1977). Quantitative analysis of the velocity characteristics of optokinetic nystagmus and optokinetic after-nystagmus. *Journal of Physiology, London*, 270, 321–344.
- Crognale, M. A. & Schor, C. M. (1994) Vision science and it's applications. *Technical Digest Series*, 2, 148–150. Optical Society of America Washington DC.
- Crognale, M. A., Switkes, E., Rabin, J., Schneck, M. E., Hægerström-Portnoy, G. & Adams, A. J. (1993). Application of the spatio-chromatic visual evoked potential to detection of congenital and acquired color deficiencies. *Journal of the Optical Society of America*, 10, 1818–1825.
- Derrington, A. M., Krauskopf, J. & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology*, 357, 241–265.
- Epelbaum, M. & Teller, D. Y. (1995). Infant eye movement asymmetries: Temporal-nasal OKN asymmetry is reversed at isoluminance in 2-month-olds. *Vision Research*, 35, 1889–1895.
- von Helmholtz, H. (1866) *Handbuch der physiologischen Optik*, Viss Leipzig.
- Honrubia, V., Downey, W. L., Mitchell, D. P. & Ward, P. H. (1968). Experimental studies on optokinetic nystagmus: Normal humans. *Acta Otolaryngologica* 64, 441–448.
- Kelly, D. H. (1974). Spatiotemporal frequency characteristics of color vision mechanisms. *Journal of the Optical Society of America*, 64, 983–990.
- Krauskopf, J., Williams, D. R. & Heeley, D. W. (1982). Cardinal directions of color space. *Vision Research*, 22, 1123–1131.
- Lindsey, D. T. & Teller, D. Y. (1990). Motion at isoluminance: Discrimination/detection ratios for moving isoluminance gratings. *Vision Research*, 30, 11, 1751–1761.
- Lisberger, S. G., Morris, E. J. & Tychsen, L. (1987). Visual motion processing and sensory-motor integration form smooth pursuit eye movements. *Annual Reviews in Neuroscience*, 10, 97–129.
- MacLeod, D. I. A. & Boynton, R. M. (1978). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America*, 69, 1183–1186.
- Moreland, J. D. (1982). Spectral sensitivity measured by motion photometry. In: Verriest, G. (Ed.), *Documenta Ophthalmologica Proceedings Series 33*. The Hague: Dr. Junk.
- Naegele, J. R. & Held, R. (1982). The postnatal development of monocular optokinetic nystagmus in infants. *Vision Research*, 22, 341–346.
- Rabin, J., Switkes, E., Crognale, M. A., Schneck, M. E. & Adams, A. J. (1994). Visual evoked potentials in three-dimensional color space: Correlates of spatio-chromatic processing. *Vision Research*, 34, 2657–2671.
- Ramachandran, V. S. & Gregory, R. L. (1978). Does colour provide an input to human motion perception? *Nature*, 275, 55–56.
- Schor, C. M., Lakshminarayanan, V. & Narayan, V. (1984). Optokinetic and vection responses to apparent motion in man. *Vision Research*, 24, 1181–1187.
- Schor, C. M. & Levi, D. M. (1980). Direction selectivity for perceived motion in strabismic and anisometropic amblyopia. *Investigative Ophthalmology and Visual Science*, 19, 1094–1104.
- Schor, C. M., Miles, F. A. & Wallman, J. (1993). Visual motion and its role in the stabilization of gaze, Elsevier London.
- Schor, C. M. & Narayan, V. (1981). The influence of field size upon the spatial frequency response of optokinetic nystagmus. *Vision Research*, 21, 985–994.
- Schor, C. M. & Westall, C. (1984). Visual and vestibular sources of fixation instability in amblyopia. *Investigative Ophthalmology and Visual Science*, 25, 729–738.
- Smith, V. C. & Pokorny, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400–500 nm. *Vision Research*, 15, 161–171.
- Teller, D. Y. & Lindsey, D. T. (1991). Motion nulls for white versus isochromatic gratings in infants and adults. *Journal of the Optical Society of America A*, 6, 1945–1954.
- Teller, D. Y. & Lindsey, D. T. (1993a). Infant colour vision: OKN techniques and null plane analysis. In: Simons, K. (Ed.), *Early Visual Development: Normal and abnormal*. New York: Oxford University Press.
- Teller, D. Y. & Lindsey, D. T. (1993b). Motion at isoluminance: Motion dead zones in three-dimensional color space. *Journal of the Optical Society of America A*, 10, 1324–1331.
- Ter Braak, J. W. G. (1936). Untersuchungen über optokinetischen Nystagmus. *Archives of Neurology and Physiology*, 21, 309–376.
- Worth, C. A. (1903). *Reviews of Oculomotor Research*, Vol. 5, Blakiston, Philadelphia.

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