



Magnocellular and parvocellular visual pathway contributions to visual field anisotropies

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Abstract

It is well established that sensitivity is not necessarily equivalent at isoecentric locations across the visual field. The focus of this study was a psychophysical examination of the spatial sensitivity differences between the upper and lower visual hemifields under conditions biased toward the presumed magnocellular or parvocellular visual pathway. Experiment 1 showed higher contrast sensitivity in the lower visual field when visual sensitivity was biased toward the parvocellular pathway; no visual field anisotropy was found when sensitivity was biased toward the magnocellular pathway. Experiment 2 showed that the magnitude of the contrast sensitivity anisotropy within the presumed parvocellular pathway increased when test targets of higher spatial frequency were used. The results of this study have relevance for the design both of psychophysical paradigms and clinical training programs for patients with heterogeneous visual field loss. © 2007 Published by Elsevier Ltd.

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1. Introduction

The evolution of the human visual system has resulted in arrangements designed to meet the needs of complex environmental demands. Functional differences between different regions of the retina have long been recognized; in many cases the functional differences have clear anatomical or physiological bases. For example, visual acuity, contrast sensitivity, and color perception are best in the fovea. The advantages found in the central field are the result of the increased neural machinery dedicated to information processing in the fovea. Although there is a dramatic over-representation of information processing in the central visual field, information falling in the periphery also plays an important role in perception. The visual periphery is sensitive to stimuli in motion, and several investigations have cited the importance of the visual periphery in the control

of posture, locomotion, reaching, and grasping (reviewed in Danckert & Goodale, 2003).

Although some visual field sensitivity differences have anatomical or physiological bases, other more subtle differences have been reported that lack a clear explanation. For example, many investigations have reported enhanced sensitivity (lower thresholds or reaction times) under specific conditions when stimuli are presented in the lower visual field (LVF) compared to the same stimuli presented in the upper visual field (UVF) at an equal eccentricity (Cameron, 2005; Carrasco, Talgar, & Cameron, 2001; Danckert & Goodale, 2001, 2003; He, Cavanagh, & Intriligator, 1996; Levine & McAnany, 2005a, 2005b; McAnany & Levine, 2004a, 2004b; Previc, 1990; Skrandies, 1987; Talgar & Carrasco, 2003). Some of these studies have shown that significant visual field asymmetries are restricted to the vertical meridian (Carrasco, Giordano, & McElree, 2004; Carrasco et al., 2001; Liu, Heeger, & Carrasco, 2006; Skrandies, 1987; Talgar & Carrasco, 2002); however, other authors have reported a general lower visual field advantage (Cameron, 2005; He et al., 1996; Levine & McAnany,

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2005a, 2005b; McAnany & Levine, 2004a, 2004b; Previc, 1990).

The finding of enhanced sensitivity in the LVF lacks a definitive explanation, and this enhancement has not been obtained consistently. Characteristics of the testing paradigm and target (e.g. target color, spatial frequency, visual field location, eccentricity) appear to play a fundamental role in the magnitude and consistency of the altitudinal visual hemifield anisotropy. Although attention (He et al., 1996), task difficulty (McAnany & Levine, 2004a), and inhomogeneities in ganglion cell density (Carrasco et al., 2001) have been proposed to account for these sensitivity differences, a consensus has not been reached regarding the mechanisms mediating the altitudinal visual field anisotropies. The focus of this study is an examination of the visual pathways mediating sensitivity differences between the upper and lower visual fields.

1.1. Evidence for enhanced sensitivity in the lower visual field

Contrast sensitivity in the upper and lower visual hemifields has been measured with sine wave gratings across a range of spatial frequencies. Skrandies (1987) obtained contrast sensitivity functions (CSFs) with sine wave gratings at an eccentricity of 5° on the vertical meridian in the upper and lower visual fields. Results indicated that contrast sensitivity was greatest in the LVF for all spatial frequencies tested. For low spatial frequency sine wave gratings, the difference between the upper and lower visual field was small; however, for high spatial frequencies, the size of the visual hemifield difference was larger.

Carrasco et al. (2001) obtained performance fields (sensitivity maps showing percent correct performance at particular locations across the visual field) with Gabor patches. Specifically, Carrasco and colleagues obtained the shape of the performance fields while manipulating factors such as spatial frequency, stimulus orientation, presence or absence of a local post-stimulus mask, target eccentricity, and attention. They found a horizontal–vertical anisotropy (better performance on the horizontal than vertical meridian), and a vertical asymmetry (better performance in the lower than upper visual field).

A striking characteristic of the performance fields was that subject performance was particularly poor at the “north” (12 O’clock) position relative to other directions. The magnitude of the vertical asymmetry increased as eccentricity and spatial frequency increased. Manipulating attention did not change the shape of the performance fields (although it did change overall sensitivity). The authors concluded that the performance fields were not due to attentional mechanisms (as was typically assumed); rather, differences in performance across the visual field were determined by visual constraints.

Taken together, the findings described above demonstrate two significant aspects of the sensitivity differences found between the upper and lower visual fields. First, for high spatial frequency test targets, reliable advantages

(lower contrast thresholds or higher sensitivities) have been reported in the LVF compared to identical stimuli presented at the same eccentricity in the UVF. Second, for low spatial frequency test targets, small and less consistent advantages have been reported in the LVF.

1.2. Magnocellular and parvocellular visual pathway contributions to visual field anisotropies

The projection from the retina through the dorsal lateral geniculate nucleus (LGN) to primary visual cortex is of interest because the most convincing differences in anatomy between the upper and lower visual fields have been found at the level of the retina and LGN (anatomical differences between the upper and lower visual fields will be discussed further in the Discussion section). Additionally, the retinogeniculostriate projection, of which the two primary components are the magnocellular (MC) and parvocellular (PC) visual pathways, is believed to be an early stage in the processing stream that leads to conscious visual perception.

Pokorny and Smith (1997) introduced a psychophysical achromatic contrast discrimination technique to assess MC and PC pathway function. Two testing conditions, the steady-pedestal and pulsed-pedestal paradigms, were used to bias sensitivity toward the MC and PC pathways, respectively, (Pokorny & Smith, 1997). These paradigms were modified by Leonova, Pokorny, and Smith (2003) to assess the spatial contrast sensitivity of the presumed MC and PC pathways.

The steady-pedestal paradigm consists of the brief presentation of a test stimulus against a continuously presented luminance pedestal. This paradigm is thought to favor the MC pathway for test targets of low to intermediate spatial frequencies, because the test target is presented briefly. The pulsed-pedestal paradigm consists of the simultaneous brief presentation of a test stimulus and luminance pedestal. The pulsed-pedestal paradigm is thought to bias processing toward the PC pathway because the abrupt onset of the luminance pedestal drives the MC pathway toward saturation.

Psychophysical data acquired using these two paradigms have the contrast response properties and temporal summation characteristics associated with the MC and PC pathways described electrophysiologically (Kaplan & Shapley, 1986; Leonova et al., 2003; Pokorny & Smith, 1997). Additionally, the results obtained under these paradigms have strong parallels with previous work examining pattern versus motion thresholds (Kulikowski, 1978), and sustained versus transient visual mechanisms (Harwerth, Boltz, & Smith, 1980; Kulikowski & Tolhurst, 1973; Legge, 1978). More recently, the steady- and pulsed-pedestal paradigms have been used to examine contrast sensitivity deficits in patients with retinal disease (Alexander, Barnes, Fishman, Pokorny, & Smith, 2004; McKendrick et al., 2004), MC and PC function in schizophrenia (Delord et al., 2006), the visual pathways mediating particular

visual illusions (McAnany & Levine, 2005; Puts, Pokorny, & Smith, 2004), and the equivalency of common optotypes (McAnany & Alexander, 2006). Although these studies had very different goals, the results obtained in each of these studies under the steady- and pulsed-pedestal paradigms are consistent with mediation of visual sensitivity by the MC and PC pathways, respectively.

The goal of the present study was to better understand the altitudinal visual hemifield anisotropies. Visual field sensitivity differences were examined within the framework of MC and PC pathway processing, using a modified version of the steady- and pulsed-pedestal paradigms of Leonova et al. (2003) to bias sensitivity toward either the MC or PC pathway. In Experiment 1, upper and lower visual field sensitivity to a low spatial frequency test target presented under the steady- and pulsed-pedestal paradigms was examined, whereas in Experiment 2, a higher spatial frequency target was used. Some of these data have been published in abstract form (McAnany & Levine, 2006).

2. Methods

2.1. Subjects

Five subjects with normal or corrected to normal visual acuity and normal contrast sensitivity participated in the study. Subjects S1 (male, 26 years) and S2 (male, 62 years) are the authors. Subject S3 (female, 26 years), has participated in previous psychophysical experiments, but was naïve to the intent of this study. Subjects S4 (female, 23 years) and S5 (male 26 years) are untrained psychophysical observers, naïve to the intent of this study. Subject S1 participated in both experiments. Subjects S2 and S3 participated in Experiment 1; S4 and S5 participated in Experiment 2. Institutional Review Board approval was obtained, and subjects gave informed consent before testing.

2.2. Instrumentation

Stimuli were generated by an IBM Pentium III computer and displayed on the screen of an EIZO 19" FlexScan FX-D7 monitor (1024 × 768 pixels, 70 Hz refresh rate), driven by an Appian Graphics video card. The monitor, which was the only significant source of illumination in the room, was viewed binocularly, with natural pupils, from 37 cm. From this distance the display subtended 46.4° by 34.8°. The subject's head was supported with chin and forehead rests. Experiments were written in MATLAB using the Psychophysics Toolbox extensions (Brainard, 1997). The phosphor output of the EIZO display was measured with a Minolta LS-110 luminance meter to allow for the construction of a linearized luminance look-up table. The temporal presentation characteristics of the display were calibrated using an oscilloscope and photocell.

2.3. Stimuli

Sine phase Gabor patches were used as test targets. Each Gabor patch consisted of a sine wave grating multiplied by a circular Gaussian window. The Gaussian had a fixed space constant so that the Gabor patches subtended the same size across different spatial frequencies. Maintaining a constant test target size is desirable when working with stimuli presented outside of fixation; with the space constant of the Gaussian window fixed, the same area of the retina can be examined using different spatial frequencies.

The peak spatial frequency of the Gabor patch was 0.25 cycles per degree (cpd) in Experiment 1, and 2.50 cpd in Experiment 2. Note that the reduced spatial resolution of the peripheral retina shifts these stimuli

to effectively higher spatial frequencies. The effective spatial frequency at 15° eccentricity can be estimated using the M-scaling technique of Virsu and Rovamo (1979). The 0.25 cpd Gabor patch presented at 15° eccentricity was approximately equal to 1.67 cpd in the fovea, and the 2.50 cpd Gabor patch was effectively 16.7 cpd. The width of the corresponding circular Gaussian window subtended approximately 3.5° of visual angle (full width at 1/e).

Gabor patch increment thresholds (ΔL) were obtained at several pedestal luminances. Increment threshold was defined as

$$\Delta L = L_{\max} - L_{\text{ped}}, \quad (1)$$

where L_{\max} is the peak luminance of the Gabor patch, and L_{ped} is the pedestal luminance. Equivalent contrast definitions were used in previous studies that employed D6 patterns (the sixth spatial derivative of a Gaussian in the horizontal dimension, with a Gaussian envelope in the vertical dimension) or Gabor patches as test stimuli (Leonova et al., 2003; McAnany & Alexander, 2006; Swanson & Wilson, 1985). This definition was used here to permit comparison to this previous research. In Experiment 1, the values of L_{ped} ranged from 28 to 71 cd/m^2 in approximately 0.05 log unit steps, and in Experiment 2, the values of L_{ped} covered the same range in approximately 0.10 log unit steps.

2.4. Testing paradigms and procedure

As shown in Fig. 1, Gabor patches were presented according to the two paradigms of Leonova et al. (2003). Under both paradigms, a Gabor patch was presented on a large uniform luminance pedestal that subtended 45.5° horizontally and 33.9° vertically. The pedestal, in turn, was presented in the center of a surround whose outer edges subtended 46.4° horizontally and 34.8° vertically. The surround was maintained at 45 cd/m^2 throughout all experiments. For the steady-pedestal paradigm (Fig. 1, top), the luminance pedestal was presented continuously. During the test period, the Gabor patch was presented. For the pulsed-pedestal paradigm (Fig. 1, bottom), the luminance pedestal was only present during the test period; the pedestal luminance was an increment or decrement from the surround, and the Gabor patch was presented simultaneously with the luminance pedestal. The stimulus duration was 28.6 ms (2 video refreshes at 70 Hz) for both testing paradigms.

Each block of trials was preceded by a 30 s period of adaptation to the surround (under the pulsed-pedestal paradigm), or to the appropriate luminance pedestal and surround combination (under the steady-pedestal paradigm). During and following the 30 s adaptation period,

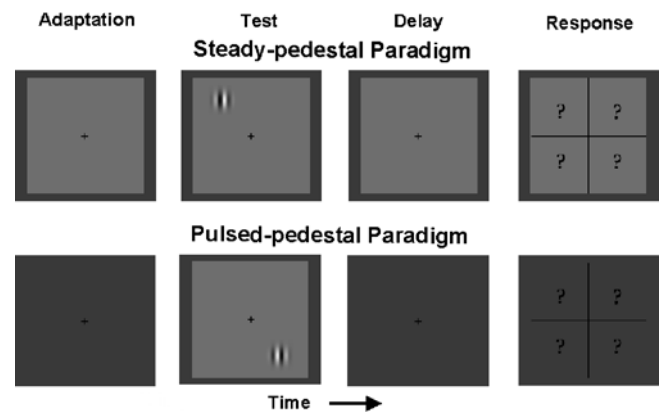


Fig. 1. The steady- and pulsed-pedestal paradigms. For the steady-pedestal paradigm (top row), a large uniform luminance pedestal was presented continuously in the center of a constant surround. During the test interval, a Gabor patch was presented briefly in one quadrant of the luminance pedestal. For the pulsed-pedestal paradigm (bottom row), the subject first adapted to the surround luminance, then during the test period a luminance pedestal and Gabor patch were presented simultaneously. For both paradigms, a fixation mark was shown continuously.

the subject fixated on a centrally located mark. Each trial proceeded as follows: First, the subject viewed the surround, or the combination of the pedestal and surround. The subject indicated readiness for the trial to begin with a mouse click. Following the click, the cursor disappeared, a tone sounded, and the stimulus was presented. The stimulus consisted of a Gabor patch whose mean luminance was equal to that of the pedestal. The Gabor patch was presented in one of four possible isoeccentric screen locations (15° eccentricity above or below fixation, to the left or right). The visual field quadrant in which the stimulus appeared was randomized; eye movements were precluded by the brief stimulus presentation duration. After a 500 ms delay the cursor reappeared to allow the subject to identify the quadrant of the screen in which the Gabor patch appeared (four alternative forced choice; 4AFC). The minimum difference between the peak luminance of the Gabor patch and the pedestal (threshold ΔL) at which the subject could detect the target was obtained at each of the four possible locations using the QUEST psychometric procedure (Watson and Pelli, 1983). Pilot testing determined that the staircase typically reached an asymptote within approximately 25 trials, so the number of trials was set to 30.

For each subject, initial testing in each experiment employed four randomly interlaced staircases (corresponding to the upper right, upper left, lower right, and lower left visual field quadrants). Analysis of variance (ANOVA; repeated measures design with subjects, pedestal luminance level, and field included as factors) showed that there were no significant differences between the left and right visual fields for either experiment under either paradigm.

To expedite data collection in Experiment 1, only two interlaced staircases corresponding to the UVF and LVF were used in replications. Although only two interlaced staircases were used, the task was still 4AFC since a Gabor patch appeared in one of four quadrants; the Gabor patch contrast changed in tandem in the left and right visual fields. In Experiment 2, two subjects showed a slight, but inconsistent, trend for lower thresholds in the left visual field. Consequently, replications were made with all four interleaved staircases to allow independent measurement of threshold in each visual field quadrant to ensure potential differences between the left and right visual fields were not missed. However, when differences between the left and right visual fields were examined across subjects, the differences were not greater than would be expected by chance. Data points in the figures represent the average of a minimum of three threshold measurements (the number of staircase threshold measurements comprising each data point is given in the appropriate sections below). Error bars represent one standard error of the mean (SEM).

3. Results

3.1. Experiment 1: Sensitivity for low spatial frequency Gabor patches

The purpose of Experiment 1 was to examine visual field sensitivity differences within the presumed MC and PC pathways using a low spatial frequency Gabor patch. Increment thresholds (ΔL) for briefly presented low frequency Gabor patches were obtained under the steady- and pulsed-pedestal paradigms in the four quadrants of the visual field.

Fig. 2 presents the increment threshold versus pedestal luminance data obtained under the steady- and pulsed-pedestal paradigms for subjects S1 (left), S2 (middle), and S3 (right). As noted above, significant differences were not observed between the left and right visual fields, so data from the left and right visual fields were averaged. For subject 1, each data point in Fig. 2 consists of four staircase measurements of threshold. For subjects 2 and 3, each data point consists of three staircase measurements of threshold.

In Fig. 2, log increment threshold ($\log \Delta L$) is plotted as a function of log pedestal luminance. Linear scale equivalents are presented on the top and right axes. The arrows on the x -axes indicate the surround luminance (decrement pedestals are to the left of the arrow and increment pedestals are to the right). The pulsed-pedestal UVF data are represented by the filled triangles and dashed line, and the pulsed-pedestal LVF data are represented by the filled squares and solid line. Data obtained under the steady-pedestal paradigm are also presented in Fig. 2, with the UVF represented by open triangles and a dashed line, and the LVF represented by open squares and a solid line.

Under the steady-pedestal paradigm, log increment threshold for the Gabor patches increased linearly as the log pedestal luminance increased. The slope of the least-squares linear regression lines fit to the steady-pedestal

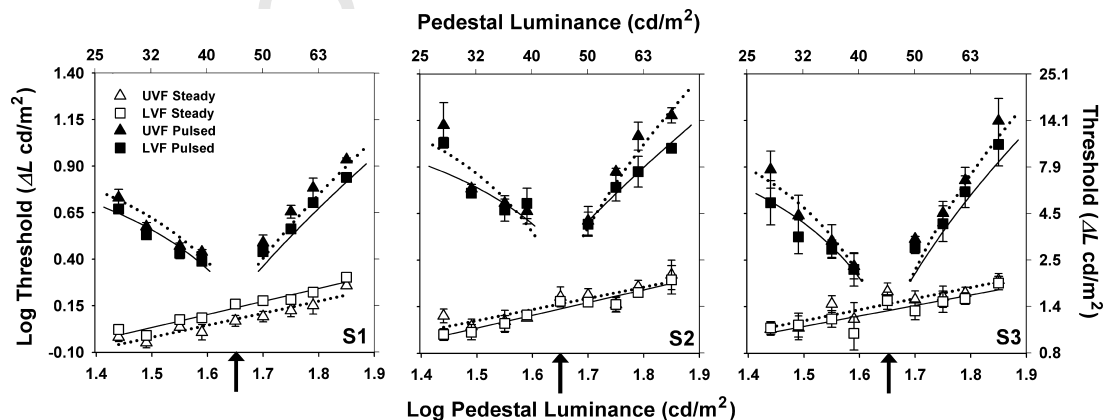


Fig. 2. Threshold versus pedestal luminance functions for the 0.25 cpd Gabor patch stimuli. Log increment threshold is plotted as a function of the log pedestal luminance for S1 (left), S2 (middle), and S3 (right). Linear scale equivalents are presented on the top x -axis and right y -axis. The arrows on the x -axes indicate the surround luminance value. Data for the steady-pedestal paradigm (open symbols) were fit with a least-squares regression line; data for the pulsed-pedestal paradigm (filled symbols) were fit with Eq. (2), as described in the text. Data for the UVF are indicated by triangles and dashed lines, and data for the LVF are indicated by squares and solid lines. Error bars are ± 1 SEM.

increment threshold data are given in Table 1 (R^2 values for the fits are also listed in Table 1). Repeated measures ANOVA (3 subjects \times 9 pedestal luminance levels \times 2 fields) indicated that threshold depended upon the pedestal luminance ($F(8, 45) = 52.06$, $p < .01$), but threshold values in the upper and lower visual fields were not significantly different, $F(1, 52) = 0.0001$, $p > .01$. Subject S1 showed consistently lower thresholds in the UVF under the steady-pedestal paradigm. However, S2 and S3 did not display this difference. When examined across subjects, the size of the UVF advantage was not greater than would be expected by chance.

For the pulsed-pedestal paradigm (filled symbols), log increment threshold increased as the pedestal luminance was either increased or decreased from the surround luminance, so that the threshold function formed a V-shaped pattern, consistent with previous results for sine phase Gabor patches (McAnany & Alexander, 2006), D6 patterns (Leonova et al., 2003), and luminance increments and decrements (Pokorny & Smith, 1997). Data from the pulsed-pedestal paradigm were fit with the following equation from Smith, Sun, and Pokorny (2001):

$$\log \Delta L = \log \left[(C_{\text{sat}} + |C|)^2 / \{C_{\text{sat}} - (K_c)(C_{\text{sat}} + |C|)\} \right] + \log(K_p L_s), \quad (2)$$

where $|C|$ is the absolute value of the contrast of the pulse, C_{sat} is the contrast at which the pathway reaches saturation, K_c is the criterion response magnitude of the pathway, L_s is the surround luminance, and K_p is a scaling constant. The data for positive and negative pedestal contrasts were fit with a single function. The value of C_{sat} , which governs the steepness of the function, is indicative of the visual pathway mediating sensitivity. Results from previous psychophysical work have shown that the presumed PC pathway saturates at contrast values from approximately 0.40–1.5, whereas the presumed MC pathway saturates at a low-

er contrast level, approximately 0.1–0.15 (Pokorny & Smith, 1997; Puts et al., 2004; Smith et al., 2001). Kaplan and Shapley (1986) recorded electrophysiological responses from the MC and PC laminae of the LGN, and reported that MC cells saturate at a contrast value of approximately 0.13, whereas PC cells saturate at a contrast value of approximately 1.74. Thus, psychophysical and electrophysiological contrast saturation measurements are similar. Eq. (2) provided an excellent fit to the data in both the upper and lower visual fields for each subject; R^2 values for the fits are listed in Table 1.

Repeated measures ANOVA (3 subjects \times 8 pedestal luminance levels \times 2 fields) indicated that under the pulsed-pedestal paradigm, threshold in the LVF was significantly lower than that in the UVF ($F(1, 46) = 149.36$, $p < .01$), and that threshold depended on the pedestal luminance, $F(7, 40) = 26.60$, $p < .01$. The mean difference between the log increment thresholds obtained in the upper and lower visual fields was 0.06 for subject S1, 0.08 for S2, and 0.07 for S3. Bonferroni corrected follow-up comparisons indicated that the threshold differences between the upper and lower visual fields exceeded the criterion for significance at only the two lowest pedestal luminances (28 and 31 cd/m^2), and the three highest pedestal luminances (56, 62, and 71 cd/m^2). This finding indicates that the shape of the log increment threshold function obtained in the UVF was not identical to the LVF function with a simple vertical shift. Rather, for all three subjects the UVF function tended to be steeper than the LVF function, which was also evident from the lower values of C_{sat} obtained in the upper visual field. The values of C_{sat} from the fits to the data obtained in the upper and lower visual field are given in Table 1.

In summary, the results of Experiment 1 showed that contrast sensitivity was higher in the lower visual field when visual sensitivity was mediated by the presumed PC pathway. No visual field anisotropy was found when sensitivity was mediated by the presumed MC pathway. Additionally, for the V-shaped function fit to the data under the pulsed-pedestal paradigm, the UVF function tended to be steeper than the LVF function. The general patterns of data obtained under the steady- and pulsed-pedestal paradigms were similar across subjects. The primary difference among subjects was an overall sensitivity difference, particularly for the data obtained under the pulsed-pedestal paradigm.

3.2. Experiment 2: Sensitivity for higher spatial frequency Gabor patches

The purpose of Experiment 2 was to examine visual field sensitivity differences within the presumed MC and PC pathways using a higher spatial frequency Gabor patch than the 0.25 cpd Gabor patch used in Experiment 1. Previous reports have indicated that altitudinal hemifield sensitivity differences increase as the spatial frequency of the test target is increased (Carrasco et al., 2001; Levine &

Table 1
Slope, C_{sat} , and R^2 values from the fits to the increment threshold functions

Subject	Slope		C_{sat}		R^2 fits	
	UVF	LVF	UVF	LVF	UVF	LVF
<i>Experiment 1</i>						
1	0.65	0.70	0.50	0.58	0.94	0.95
2	0.59	0.56	0.26	0.36	0.94	0.95
3	0.60	0.68	0.33	0.64	0.96	0.92
Mean	0.61	0.65	0.36	0.53	0.95	0.94
<i>Experiment 2</i>						
1	0.53	0.45	1.75	2.06	0.76	0.39
4	0.43	0.34	0.93	0.97	0.37	0.55
5	1.09	0.74	1.12	0.86	0.67	0.92
Mean	0.68	0.51	1.27	1.30	0.60	0.62

For Experiments 1 and 2, the values of the slopes from the data obtained under the steady-pedestal paradigm, and the values of C_{sat} obtained from Eq. (2) are given for each subject. Additionally, the R^2 values for the fits to the data are given in the last two columns.

McAnany, 2005b; Liu et al., 2006). Thus, it is of interest to examine visual hemifield sensitivity differences with stimuli of different spatial frequency. In Experiment 2, increment thresholds for briefly presented 2.50 cpd Gabor patches were obtained under the steady- and pulsed-pedestal paradigms in the four quadrants of the visual field.

Fig. 3 presents the increment threshold data obtained in the upper and lower visual fields under the steady- and pulsed-pedestal paradigms for subjects S1 (left), S4 (middle), and S5 (right). In Fig. 3, each data point is the mean of four staircase measurements of threshold. As in Experiment 1, data from the left and right visual fields were combined. The conventions of Fig. 3 are as in Fig. 2.

For the steady-pedestal paradigm, log increment threshold for Gabor patches increased linearly with the log pedestal luminance. The slopes of the least-squares linear regression lines fit to the steady-pedestal increment threshold data are given in Table 1. ANOVA (3 subjects \times 5 pedestal luminance levels \times 2 fields) indicated that thresholds obtained under the steady-pedestal paradigm were significantly different at the different pedestal luminances ($F(4, 25) = 128.13$, $p < .01$), and that threshold was significantly lower in the LVF than in the UVF ($F(1, 28) = 609.29$, $p < .01$). The mean difference between the log increment thresholds obtained under the steady-pedestal paradigm in the upper and lower visual fields was 0.30 for subject S1, 0.11 for S4, and 0.15 for S5. Bonferroni corrected follow-up comparisons for each subject indicated that threshold was significantly lower in the LVF than in the UVF (for each subject $t > 5.32$, $p < .05$). These differences in the mean threshold between the upper and lower visual fields were significantly greater than those observed for the low spatial frequency Gabor patch under the pulsed-pedestal paradigm in Experiment 1 ($t = 2.62$, $p < .05$).

Under the pulsed-pedestal paradigm (filled symbols), log increment threshold in both the upper and lower visual fields increased as the pedestal luminance was either increased or decreased from the surround luminance, so that the threshold function produced a shallow V-shaped pattern. As in Experiment 1, data from the pulsed-pedestal

paradigm were fit with Eq. (2), and the R^2 values of these fits are given in Table 1. These fits were generally poorer than those for Experiment 1, but the curves still provided a reasonable fit to the increment threshold data obtained in both the upper and lower visual fields. We attempted to separately fit the data obtained in the upper and lower visual field with linear regression; however, the R^2 values for these fits were lower than those obtained with the fits from Eq. (2). Specifically, pooled across subjects and visual fields, the average R^2 for the fit to Eq. (2) was 0.61, whereas the average R^2 for the fit to the linear function was 0.04.

The slopes of the upper and lower visual field functions obtained under the pulsed-pedestal paradigm in Experiment 2 were clearly shallower than those obtained with the low spatial frequency Gabor patches in Experiment 1. The shallower functions obtained in Experiment 2 are also evident from the higher values of C_{sat} obtained from the fits to the pulsed-pedestal data. The values of C_{sat} for the fits to the 2.50 cpd Gabor patch targets are given in Table 1. In contrast to results of Experiment 1, the shape of the log increment threshold functions obtained in the upper and lower visual fields were similar (i.e. C_{sat} values were not consistently lower in the UVF). Implications of this result are discussed in Section 4.2.

ANOVA (3 subjects \times 4 pedestal luminance levels \times 2 fields) indicated that under the pulsed-pedestal paradigm, threshold in the LVF was significantly lower than that in the UVF ($F(1, 22) = 210.79$, $p < .01$), and that threshold depended on the pedestal luminance ($F(3, 20) = 55.85$, $p < .01$). Bonferroni corrected follow-up comparisons for each subject indicated that threshold was significantly lower in the LVF than in the UVF (for each subject $t > 4.78$, $p < .05$). The mean difference between the log increment thresholds obtained under the pulsed-pedestal paradigm in the upper and lower visual fields was 0.29 for subject S1, 0.07 for S4, and 0.15 for S5. Bonferroni corrected follow-up comparisons indicated that the magnitude of the threshold difference between the upper and lower visual fields exceeded the criterion for significance obtained at all pedestal luminances.

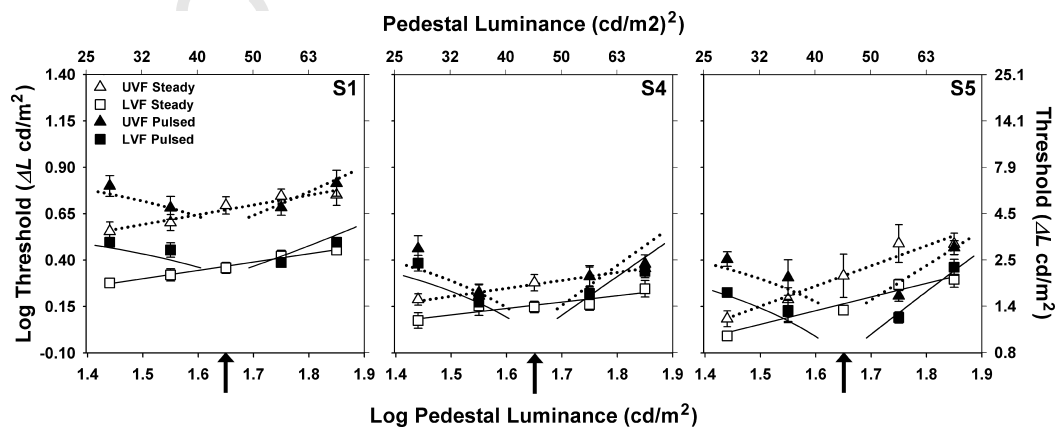


Fig. 3. Threshold versus pedestal luminance functions for the 2.50 cpd Gabor patch stimuli. Log increment threshold is plotted as a function of the log pedestal luminance for S1 (left), S4 (middle), and S5 (right). Other conventions are as in Fig. 2.

In general, little difference was observed between the threshold values obtained under the steady- and pulsed-pedestal paradigms for the 2.50 cpd Gabor patches. Because of the similarity of the data obtained under the two paradigms, the same pathway (which was inferred to be the PC pathway because of its better sensitivity to high spatial frequencies, and the high C_{sat} values obtained under the pulsed-pedestal paradigm) was interpreted to have mediated sensitivity under both paradigms for the 2.50 cpd Gabor patches. With the exception of the lowest luminance pedestal, the data obtained in the upper and lower visual fields under the steady- and pulsed-pedestal paradigms were nearly coincident (in the respective visual fields). As discussed further in Section 4.2 below, previous work has shown that the presumed PC pathway mediates sensitivity under the steady- and pulsed-pedestal paradigms for high spatial frequency test targets (Leonova et al., 2003; McAnany & Alexander, 2006), and the results of Experiment 2 are consistent with these previously reported results.

It is interesting to note that for some conditions under which the PC pathway presumably mediates contrast sensitivity (e.g. high spatial frequency test targets examined under the pulsed-pedestal paradigm) the patterns of data do not always conform to the typical V-shaped function, rather the data can be fit nearly as well with a single positively sloped function. Leonova (2003) also reported very shallow V-shaped functions for high spatial frequency test targets measured under the pulsed-pedestal paradigm, which could have been fit with straight lines. For the data reported here, however, Eq. (2) provided a better fit than a linear function, as noted above.

4. Discussion

These results provide new information regarding altitudinal visual hemifield anisotropies. Experiment 1 provided evidence that sensitivity differences between the upper and lower visual fields were only evident when the presumed PC pathway mediated visual sensitivity. Experiment 2 showed that the magnitude of the visual field asymmetry in the presumed PC pathway increased as the spatial frequency of the test target increased, consistent with previous work (Carrasco et al., 2001; Levine & McAnany, 2005b; Liu et al., 2006). In contrast to some previous work (Carrasco et al., 2001, 2004; Cameron et al., 2002; Liu et al., 2006), visual field anisotropies were not restricted to the vertical meridian. However, this is not the first study to report visual field asymmetries at locations other than the vertical meridian (Cameron, 2005; He et al., 1996; Levine & McAnany, 2005a, 2005b; McAnany & Levine, 2004a, 2004b).

4.1. Interpretation of Experiment 1

Under the pulsed-pedestal paradigm in Experiment 1, sensitivity was interpreted to be mediated by the PC pathway. Threshold in the upper and lower visual fields was

approximately equal at pedestal luminances near the surround luminance, but as the pedestal luminance diverged from the surround luminance (with pulses of greater contrast) threshold rose faster in the UVF than in the LVF. This trend for a steeper V-shaped UVF function was found for all three subjects.

The differences in the shapes of the functions obtained in the upper and lower visual fields under the pulsed-pedestal paradigm indicated that differences in visual field sensitivity were most likely a result of PC pathway processing, and were not likely due to an extraneous factor such as cortical magnification differences (e.g. both the MC and PC pathways could simply be more sensitive in the LVF than in the UVF). We interpret these shape differences to reflect the transition from mediation of sensitivity by the MC pathway (for the low contrast pulses) to mediation by the PC pathway for the higher contrast pulses, and these differences are consistent with the steady- and pulsed-pedestal paradigms targeting the MC and PC pathways. When the transition from MC to PC pathway processing occurs, a visual hemifield sensitivity difference becomes apparent. The anisotropy is absent for the lowest contrast pulses where sensitivity is mediated by the MC pathway, small for pulses of intermediate contrast, and larger for high contrast pulses for which sensitivity is dominated by the PC pathway.

Under the steady-pedestal paradigm, sensitivity was interpreted to be mediated by the MC pathway. No consistent differences were found between the slopes or intercepts of the functions obtained in the upper and lower visual fields under the steady-pedestal paradigm.

Taken together, the most parsimonious interpretation of the results is that there is an altitudinal visual hemifield contrast sensitivity anisotropy in the PC pathway, which yields greater sensitivity in the lower than upper visual field. Additionally, the visual field anisotropies are not limited to the vertical meridian, as our data show differences that extend at least several degrees from the vertical meridian. When visual sensitivity was biased toward the MC pathway, a consistent anisotropy was not found.

4.2. Interpretation of Experiment 2

The purpose of Experiment 2 was to examine visual field sensitivity differences using higher spatial frequency Gabor patches, because previous reports have shown that the magnitude of the visual hemifield sensitivity differences increase as the spatial frequency of the test target is increased (Carrasco et al., 2001; Levine & McAnany, 2005b; Skrandies, 1987). However, interpretation of the visual pathway mediating sensitivity under the steady- and pulsed-pedestal paradigms becomes somewhat difficult for test targets of high spatial frequency. Leonova et al. (2003) and McAnany and Alexander (2006) measured CSFs with D6 patterns and Gabor patches, respectively, over a range of spatial frequencies, under the steady- and pulsed-pedestal paradigms. Both studies found that the

steady- and pulsed-pedestal CSFs were well separated at low spatial frequencies but merged at high spatial frequencies, and concluded that the PC pathway likely mediated sensitivity for high spatial frequency test targets. The 2.50 cpd Gabor patch presented at 15° of eccentricity used in Experiment 2 can be assumed to be beyond the point at which the CSFs obtained under the steady- and pulsed-pedestal paradigms merge. The data Leonova and colleagues (2003) obtained at spatial frequencies from 4 to 16 cpd closely resembled the data obtained in Experiment 2. Specifically, the data of Experiment 2 and the data of Leonova (2003) showed only a small difference between the steady- and pulsed-pedestal paradigms for the decrement pedestals, and the functions obtained under the two paradigms merged for the increment pedestals. Thus, due to the similarity of the data obtained in Experiment 2 and the data obtained by Leonova et al. (2003), it seems reasonable to assume, as Leonova et al. did, that sensitivity was mediated by the PC pathway for the high spatial frequency Gabor patch test targets under both the steady- and pulsed-pedestal paradigms. Furthermore, temporal integration functions obtained under these paradigms with 2.5 cpd Gabor patches at this retinal eccentricity were very similar, and had relatively long critical durations for integration consistent with sensitivity being mediated by the PC pathway under both the steady- and pulsed-pedestal paradigms (McAnany, 2006).

In Experiment 2, the shapes of the functions obtained under the pulsed-pedestal paradigm in the upper and lower visual fields were similar; log increment threshold values were not consistently steeper in the upper than lower visual field, as was found in Experiment 1. This result is likely due to mediation of sensitivity by the same visual pathway for all pedestal luminance levels, which is assumed to be the PC pathway due to the better sensitivity of the PC than MC pathway for high spatial frequencies. Moreover, the high value of C_{sat} obtained from the fits to the pulsed-pedestal paradigm data is consistent with mediation of sensitivity by the PC pathway (Leonova et al., 2003). In contrast to the patterns observed with the low spatial frequency Gabor patches, there was no transition from MC to PC pathway processing as the magnitude of the pulse increased.

The assumption that the PC pathway mediated sensitivity under both paradigms for 2.50 cpd Gabor patches at all pedestal luminance levels provides a simple explanation for the clear LVF advantage. The lower thresholds found in the LVF are due to the anisotropy found in the PC pathway, consistent with the observations in Experiment 1. The magnitude of the LVF advantage was similar for the steady- and pulsed-pedestal paradigms, again consistent with mediation by the same visual pathway.

One possible reason for the difference in the magnitude of the LVF advantage between Experiments 1 and 2 may be the method used to bias sensitivity toward the PC pathway. In Experiment 1, a luminance pulse was used to saturate the MC pathway, leaving only the PC pathway for

detection of the Gabor patch. In Experiment 2, the 2.50 cpd Gabor patch that was used was better matched to the spatial frequency tuning of the PC pathway, and the luminance pulse had relatively little effect on threshold under the pulsed-pedestal paradigm. Consistent with previous work (Leonova et al., 2003), the use of a high spatial frequency Gabor patch (even in the absence of an MC pathway saturating pulse) was sufficient to bias processing toward the PC pathway. These results suggest that within the PC pathway, there is greater sensitivity to high spatial frequencies in the LVF than in the UVF. Alternatively, the smaller difference between the upper and lower visual fields for low spatial frequencies may be due to incomplete saturation of the MC pathway when low spatial frequency targets were used. If pulses of greater contrast had been used in Experiment 1, the difference between the upper and lower visual fields might have been greater. (Due to hardware limitations, the contrast of the largest pulse was $\pm 58\%$.)

Two related mechanisms could produce greater sensitivity to high spatial frequencies in the LVF (in the PC pathway). The LVF may have a greater density of PC cells than the UVF. Additionally, the receptive fields of PC cells may be smaller in the LVF. If there were a greater density of PC cells in the LVF (or if the receptive fields of these cells were smaller), threshold would be expected to be lower in the LVF, particularly for high spatial frequency patterns, under conditions favoring the PC pathway. For low spatial frequency patterns, a smaller difference between the upper and lower visual field would be expected. A greater density of PC cells in the LVF would provide a greater ability to sample the stimulus (sensitivity differences would be greatest for the high spatial frequency Gabor patches where sampling density is of greater importance). In the MC pathway, contrast sensitivity was found to be equivalent between the upper and lower visual fields, which suggests the absence of large differences in MC ganglion cell density across the peripheral retina at this eccentricity.

A greater density of both ganglion cells and cone photoreceptors has been reported in the superior hemiretina (Curcio & Allen, 1990; Curcio, Sloan, Packer, Hendrickson, & Kalina, 1987; Curcio, Sloan, Kalina, & Hendrickson, 1990). In the non-human primate, the LGN may also have a slightly greater density of cells corresponding to the lower visual field, though differences in cell density seem to be less apparent at the level of the cortex (Connolly & Van Essen, 1984). Although ganglion cell density has been reported to be approximately 40% greater in the superior hemiretina (corresponding to the LVF), the density estimates did not examine the distribution of MC and PC cells across the retina (Curcio et al., 1990). These anatomical studies merit replication, and need to be extended to examine MC and PC cell densities across the retina. It is important to note that these anatomical studies do not reveal how information is encoded, or the sensitivity of cells corresponding to the upper or lower visual field representation.

735 4.3. Implications of the findings

736 The results of this study are of importance to basic
737 research, particularly in the design of psychophysical para-
738 digms. These results confirm previous findings that showed
739 that sensitivity is not identical at isoeccentric locations across
740 the visual field, but extend previous findings to show that the
741 altitudinal anisotropies are features of the PC pathway, and
742 seem to be absent or minimal in the MC pathway. Conse-
743 quently, when sensitivity of the visual periphery is assessed,
744 the visual pathway mediating sensitivity should be taken into
745 account. Larger differences across the visual field may be
746 found when high spatial frequency test targets are used, or
747 when processing is biased toward the PC pathway by other
748 means (e.g. color discriminations).

749 The results of the current study are consistent with previ-
750 ous clinical work showing sensitivity differences across the
751 visual field in both normal and patient populations, and
752 may have application in clinical research. Seiple, Holopi-
753 gian, Szlyk, and Wu (2004) used a variety of standard clinical
754 measures to examine visual field sensitivity. Grating acuity,
755 contrast sensitivity, duration for letter identification, multi-
756 focal electroretinograms, and Humphrey visual field thresh-
757 olds (a strategy in which several points in the central retina
758 are tested with a small luminance spot to map visual field sen-
759 sitivity) were measured at isoeccentric locations throughout
760 the visual field. They found that the rate of sensitivity loss as
761 a function of eccentricity from the fovea was not equivalent
762 for the different psychophysical measures. Additionally, they
763 found that the pattern of sensitivity loss for each measure
764 was dependent upon the meridian of the visual field tested.
765 Sensitivity loss as a function of eccentricity was greater along
766 vertical than horizontal meridian, consistent with Carr-
767 asco et al. (2001). For most of the sensitivity measures, no
768 altitudinal visual hemifield anisotropies were found. How-
769 ever, a relatively large LVF advantage was found for Hum-
770 phrey visual field thresholds measured with high luminance
771 test targets. The differences in visual field sensitivity, and
772 the different patterns of data produced by the various clinical
773 psychophysical measures may be related to the visual path-
774 way mediating sensitivity.

775 Studies like that of Seiple et al. (2004) and the current
776 study yield a better understanding of the functional differ-
777 ences between the upper and lower visual fields, which
778 could benefit rehabilitation training for patients who have
779 lost central vision. In low-vision therapy, patients with cen-
780 tral vision loss due to diseases such as macular degenera-
781 tion are trained to use an eccentric retinal location as a
782 surrogate fovea. The preferred retinal location for use as
783 a surrogate fovea is often established either above or to
784 the left (on the retina) of the scotoma (Guez et al., 1993;
785 Q6 Seiple, Szlyk, McMahon, Pulido, & Fishman, 2005). It is
786 of interest to note that patients with central field loss seem
787 to have a tendency to naturally adopt a preferred retinal
788 location in the LVF. The tendency to choose a preferred
789 retinal location in the LVF may be driven, in part, by the
790 enhanced sensitivity of the LVF.

4.4. Conclusions 791

792 The existence of altitudinal visual hemifield sensitivity
793 differences is clear from the literature. However, the magni-
794 tude, consistency, and source of these differences have been
795 debated. The empirical data provided here show that con-
796 trast sensitivity was greater in the LVF when sensitivity
797 was mediated by the presumed PC pathway; no differences
798 were present when sensitivity was mediated by the pre-
799 sumed MC pathway. The results of this study have rele-
800 vance in both the design of psychophysical paradigms, as
801 well as the design of training programs for patients with
802 heterogeneous visual field loss.

5. Uncited references Q9 803

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805 and Pokorny (2003); Perry, Oehler, and Cowey (1984).

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