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Chromatic temporal integration and retinal eccentricity: Psychophysics, neurometric analysis and cortical pooling

William H. Swanson [a,*], Fei Pan [b], Barry B. Lee [c,d]

[a] Indiana University, School of Optometry, 800 East Atwater Avenue, Bloomington, IN 47405-3680, USA
[b] Glaucoma Institute and Department of Vision Sciences, SUNY State College of Optometry, New York, NY 10036, USA
[c] Department of Biological Sciences, SUNY State College of Optometry, New York, NY 10036, United States
[d] Max Planck Institute for Biological Chemistry, Göttingen, Germany

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ABSTRACT

Psychophysical chromatic sensitivity deteriorates in peripheral retina, even after appropriate size scaling of targets. This decrease is more marked for stimuli targeted at the long- (L) to middle-wavelength (M) cone opponent system than for stimuli targeted at short-wavelength (S) pathways. Foveal chromatic mechanisms integrate over several hundred milliseconds for pulse detection. If the time course for integration were shorter in the periphery, this might account for sensitivity loss. Psychophysical chromatic temporal integration (critical duration) for human observers was estimated as a function of eccentricity. Critical duration decreased by a factor of 2 (from ~200 to ~100 ms) from the fovea to 20° eccentricity. This partly (but not completely) accounts for the decrease in |L–M| sensitivity in the periphery, but almost completely accounts for the decrease in S-cone sensitivity. Some loss of |L–M|I sensitivity thus has a cortical locus.

In a physiological analysis, we consider how the |L–M| cone parvocellular pathway integrates chromatic signals. Neurometric contrast sensitivities of individual retinal ganglion cells decreased with the square-root of stimulus duration (as expected from Poisson statistics of ganglion cell firing). In contrast, psychophysical data followed an inverse linear relationship (Bloch's law). Models of cortical pooling mechanisms incorporating uncertainty as to stimulus onset and duration can at least partially account for this discrepancy.

1. Introduction

It is now well established that the midget ganglion cells of the parvocellular (PC) pathway form the physiological substrate for a long- versus middle-wavelength (|L–M|) cone opponent pathway in the primate visual system (Lee, 1996), sometimes characterized as a 'red–green' system. Human psychophysical contrast sensitivity to L, M chromatic stimuli declines more rapidly with eccentricity than sensitivity to short-wavelength (S) stimuli or luminance stimuli. This difference persists when stimulus size is scaled relative to critical area (Johnson, 1986) or with equiluminant gratings which either modulate the |L–M| or S-cone pathways (Mullen, 1991) and have spatial frequency adjusted so as to compensate for changes in magnification with eccentricity. A study of macaque PC ganglion cells found little effect of eccentricity on |L–M| chromatic sensitivity from the fovea to 40° eccentricity (Martin, Lee, White, Solomon, & Ruttiger, 2001), so the variation in psychophysical chromatic sensitivity from the fovea to the periphery cannot be readily explained at the level of the ganglion cell.

PC cells and S-cone cells give substantial responses to high temporal frequencies that are not perceptible psychophysically, and low-pass temporal filtering at a central (cortical) site has been posited to account for this (Lee, Pokorny, Smith, Martin, & Valberg, 1990; Yeh et al., 1995b). For luminance modulation we had also postulated some filtering of the magnocellular (MC) pathway signal (Lee et al., 1990; Yeh, Lee, & Kremers, 1995a) but most recently (Lee, Sun, & Zucchini, 2007), a reinvestigation of ganglion cell responses using a neurometric approach found little filtering was necessary for the MC pathway and luminance modulation, because MC pathway signals are very noisy at high temporal frequencies. It was confirmed that substantial low-pass filtering occurs with the PC pathway and chromatic modulation. An alternative, but perhaps functionally equivalent, view might be that detection of chromatic modulation is through a detector with a long time constant. This would increase sensitivity at the cost of temporal resolution.

The current study measured human psychophysical chromatic temporal integration in peripheral retina. If temporal integration becomes shorter in the periphery, this might contribute to the loss

* Corresponding author. Fax: +1 812 855 9447.
E-mail addresses: wilswans@indiana.edu (W.H. Swanson), fpan@sunyopt.edu (F. Pan), blee@sunyopt.edu (B.B. Lee).

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in psychophysical sensitivity. We measured thresholds for |L–M| chromatic perturbations as a function of duration at different eccentricities, and compared the result with chromatic perturbations specifically targeted at the S-cone pathway. Responses of macaque PC cells were recorded for similar stimuli, and we attempted to relate psychophysical and physiological data with a quantitative neurometric model of central low-pass chromatic temporal filtering.

2. Methods

2.1. Psychophysics

2.1.1. Observers

Two of the authors (WS and FP) served as psychophysical observers. Both are experienced psychophysical observers who are normal trichromats with good acuity and moderate refractive error (myopia < −5 diopters), and recent comprehensive eye exams found no evidence of ocular disorders (other than corrected presbyopic myopia in observer WS). This study complied with the Declaration of Helsinki and was approved by the Institutional Review Board of SUNY State College of Optometry.

2.1.2. Apparatus and stimuli

Stimuli were presented on a 21" color monitor (PressView, Radius) driven by a 10-bit/phosphor video board (ThunderScan, Radius) controlled by a Macintosh G3 computer using the Psychophysics Toolbox (Brainard, 1997) with Yi-Zhong Wang's interface in MATLAB (The MathWorks). This provides high-level access to the C-language VideoToolbox (Pelli, 1997). The resolution of the monitor was 832 by 624 pixels. Dithering was used to further extend the contrast range: within each 10 by 10 pixel array, for each phosphor adjacent DAC values were interleaved to obtain luminances intermediate between those for the two DAC values.

The tests were conducted at a one-meter viewing distance, for which the monitor subtended 21° × 16°. The background luminance of the monitor was set to 3 cd/m^2, and a 2° square pedestal in the center was set to 20 cd/m^2; for both background and pedestal the chromaticity was set to equal-energy white. Each stimulus was a rectangular temporal pulse created by changing either the chromaticity or the luminance of the square pedestal. Previous studies have shown that use of a contiguous pedestal improves isolation of chromatic responses by suppressing the response to luminance increments (Snelgar, Foster, & Scase, 1987).

Pulse duration was defined in terms of the number of frames in which the stimulus was displayed, from 1 frame to 64 frames, in octave steps. Calibration with a storage oscilloscope (Hitachi Densai VC-6025) found that each frame lasted 5 ms, with 12.5 ms between frames. Since critical duration for human observers is typically greater than 25 ms (Swanson, Ueno, Smith, & Pokorny, 1987), stimulus duration was considered equivalent to the number of frames times 12.5 ms. The equivalent durations were 1.1–2.9 log ms.

A spectroradiometer (Photo Research Spectra Scan PR704) was used to calibrate the spectral properties of the phosphors, and a luminance meter (Minolta LS-100) was used to measure the gamma function for each phosphor. The Smith-Pokorny cone fundamentals (DeMarco, Pokorny, & Smith, 1992) were used to compute modulations of the long-wavelength-sensitive (L-), middle-wavelength-sensitive (M-) and short-wavelength-sensitive (S-) cones; for eccentricities of 9° and 21° macular pigment was removed from the cone fundamentals for these calculations.

Chromatic pulses were created by modulating chromaticity in one of two directions in an equiluminant color plane (Smith & Pokorny, 1996): one direction was an increment in excitation of the S-cones with no change in excitation of the L- and M-cones; the second direction was an increment in L-cone excitation and decrement in M-cone excitation, with no change in S-cone excitation. For control experiments, luminance pulses were used in which luminance incremented with no change in chromaticity. In this cone excitation space, the effects of individual differences (photopigment polymorphisms, lenticular density, photopigment optical density, cone numerosity) would have minimal effect on the degree of chromatic isolation or the depth of chromatic modulation (Smith & Pokorny, 1995). Control experiments with luminance pulses showed that, at all three eccentricities, contrast sensitivity for a 25 ms pulse was within 0.1 log unit of asymptotic contrast sensitivity for long pulses. By comparison, for both chromatic stimuli at all three eccentricities, contrast sensitivity for a 25 ms pulse was at least 0.5 log unit below asymptotic sensitivity for long pulses. Therefore we considered that luminance responses made no significant contribution to detection of the chromatic pulses.

2.1.3. Procedure

A temporal two-interval forced-choice adaptive staircase method was used to measure contrast sensitivity as a function of pulse duration at the fovea, at 9.5° eccentricity (nasal retina −9°, −3°) and at 21° eccentricity (−15°, −15°), using a movable fixation point so that the stimulus was always presented on the same part of the monitor. Each staircase began at maximum contrast, and used a 2-down-1-up rule with step sizes of 0.3 log unit until the second reversal and 0.15 unit thereafter. Staircases terminated at eight reversals, and the mean of the last six reversals was used as the threshold estimate. Every six trials a stimulus was presented that was 0.5 log unit higher than the staircase value; these trials did not drive the staircase and were used in maximum likelihood analysis of the staircases (Swanson & Birch, 1992). Thresholds were considered non-measurable and were excluded from data analysis if the difference between the subjects' threshold and the available maximum contrast was less than 0.15 log unit. Data were considered unreliable and were excluded from data analysis if the difference between the sensitivities estimated with the maximum-likelihood technique and with the mean of reversals was greater than 0.15 log unit (Swanson & Birch, 1992).

For each pulse duration, color direction and observer, contrast sensitivity was measured on two different days. If means of reversals for the two days differed by less than 0.2 log unit then the average was taken, otherwise additional staircases were gathered and the median was taken.

2.1.4. Data analysis

Data were fit with a peak detector template, using two free parameters: sensitivity and critical duration. More complex detector models incorporating temporal probability summation have been developed for detection of luminance pulses (Gorea & Tyler, 1986; Watson, 1979), but a simple peak detector template has been found to be sufficient for good fits to chromatic pulse-detection data (Smith, Bowen, & Pokorny, 1984). For each stimulus pulse duration, the response of the detector at time t from the onset of the response (in seconds) was determined using the two-parameter impulse response $R(t)$, defined as

$$R(t) = S[t^{n-1}\mathrm{e}^{-1000\pi t/D}]/(n-1)! \quad (1)$$

The sensitivity parameter, S, scales the template vertically while the critical duration parameter, D, scales the template horizontally. The value for n was fixed at 5 to reduce free parameters; this value has previously been used successfully to fit chromatic pulse detection data (Smith et al., 1984). The sensitivity parameter, S, is the contrast sensitivity for a 1 ms pulse. The critical duration parameter, D, is the duration (in ms) at which sensitivity becomes 0.05 log unit lower than predicted by linear summation (Bloch's law), and is 0.25 log unit below the asymptotic sensitivity at long durations. For a given sensitivity S and critical duration D, the time-varying response of the peak detector was computed by convolving the pulse with the impulse response. Sensitivity of the peak detector was computed as the reciprocal of the maximum value reached by the convolution.

Data analysis was performed using the software Igor Pro 6.02 (Wavemetrics, Inc., Lake Oswego, Oregon). Contrast sensitivity versus pulse duration was plotted as the pulse integration function and the peak detector template was fit using a Levenberg-Marquardt algorithm (an iterative, non-linear least-squares method which terminates based on the rate of decline in κ^2). Goodness-of fit was determined from the κ^2 values and the standard errors of the parameters.

2.2. Physiology

Ganglion cell activity was recorded from the retinas of juvenile macaques (*Macaca fascicularis*). After initial intramuscular injection of ketamine, anesthesia was induced with thiopental and maintained with isoflurane in a 70%:30% N_2O_2 mixture (1–2% during surgery and 0.2–1% during recording). Local anesthetic was applied to points of surgical intervention. The electroencephalogram and the electrocardiogram were continuously monitored as a control for anesthetic depth. Muscular relaxation was maintained by intravenous infusion of gallamine triethiodide (5 mg/kg/h) together with approximately 6 mL/h/kg of dextrose Ringer. End-tidal PCO2 was kept near 4% by adjusting the rate and depth of ventilation, and body temperature was maintained near 37.5 °Cs. All procedures were approved by an on-campus Institutional Animal Care and Use Committee and conformed to the ARVO Statement for the Use of Animals in Ophthalmic and Vision Research.

A contact lens with the internal radius matched to the corneal curvature was used to focus the eye on a back projection tangent screen that was 228 cm from the animal's tested eye. The screen was used for mapping receptive fields and for projecting stimuli for cell classification. Positions of the fovea and the optic disk were ascertained with the aid of a fundus camera. Clarity of the optic media was checked frequently, and, if the smaller retinal vessels could no longer be recognized, recording from that eye was terminated and the second eye prepared. On completion of recording the animal was sacrificed with an overdose of barbiturate.

Details of the recording technique and the cell classification are given elsewhere (Lee, Martin, & Valberg, 1989). Briefly, after extracellular activity of a ganglion cell was isolated, the cell type was determined by using flashed spots. Cell responses to stimuli of different, equiluminous colors were then recorded as an aid to cell classification. We recorded ganglion cells from the parafoveal retina, typically at eccentricities of between 3 and 10 deg.

2.2.1. Apparatus and stimuli

Responses were measured using a three-channel Maxwellian view system, as described elsewhere (Lee et al., 1990). Briefly, three light-emitting diodes (LEDs) with dominant wavelengths at 638 ("red"), 554 ("green"), and 470 nm ("blue") provided a 4.7 deg stimulus field, which was centered on the receptive field of the cell. Measurements were made using only the red and green LEDs, each of which pro-