Detection and discrimination of achromatic contrast: A ganglion cell perspective

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The magnocellular (MC) pathway in the primate has much higher achromatic contrast sensitivity than the parvocellular (PC) pathway, and is implicated in luminance contrast detection. But MC pathway responses tend to saturate at lower achromatic contrast than do PC pathway responses. It has been proposed that the PC pathway plays a major role in discriminating suprathreshold achromatic contrast, because the MC pathway is in saturation. This has been termed the pulsed-pedestal protocol. To test this hypothesis, responses of MC and PC pathway ganglion cells have been examined under suprathreshold conditions with stimulus configurations similar to those in psychophysical tests. For MC cells, response saturation was much less for flashed or moving edges than for sinusoidal modulation, and MC cell thresholds predicted for these stimuli were similar to psychophysical discrimination (and detection) data. Results suggest the protocol is not effective in segregating MC and PC function.

Introduction

Visual perception involves both detection of targets against a background, based on their luminance or color, and discrimination between targets, again based on luminance or color as well as shape. There is extensive psychophysical evidence for separate channels mediating detection of luminance and color, each with different temporal and spatial properties. These channels have been associated with different cell systems in the primate afferent visual pathway. The roles for these pathways in suprathreshold psychophysical tasks are less clear. Suprathreshold tasks introduce complexities, such as ganglion cell saturation, due to, for example, contrast gain controls in the retina, as well as cortical mechanisms (Sun, Swanson, Arvidson, & Dul, 2008). An analysis of suprathreshold tasks by Pokorny and Smith (1997), focused on the role of ganglion cell saturation. A "pulsed-pedestal" method was introduced, to identify neural pathways mediating suprathreshold discrimination of luminance changes. This brief note evaluates the physiological assumptions of this method.

There are three major pathways in the afferent visual system of primates that have been closely associated with luminance and chromatic channels. The magnocellular (MC) pathway has been established as the physiological substrate for tasks by which the luminosity function is defined, such as flicker photometry (Lee, Martin, & Valberg, 1988) and the minimally distinct border (Kaiser, Lee, Martin, & Valberg, 1990; Valberg, Lee, Kaiser, & Kremers, 1992). It is likely to support detection of luminance contrast (Lee, Pokorny, Smith, Martin, & Valberg, 1990; Lee, Sun, & Zucchini, 2007). The parvocellular (PC) pathway receives opponent input from the middle- (M) and long-wavelength (L) sensitive cones and provides support for detection of chromatic changes along a |L-M| (red-green) dimension. It is worth noting that the achromatic contrast responsivity of MC cells is matched, in terms of cone contrast, by PC cells' responsivity to the |M-L| signal (Lee et al., 2007). Last, cells with short-wavelength (S) cone input support chromatic detection dependent on the S-cone; this pathway is not discussed here, because the pulsed-pedestal method was developed for assessing contributions of MC and PC pathways to luminance detection and discrimination.

The relative contributions of the MC and PC pathways to suprathreshold vision are less certain (Kaplan, Purpura, & Shapley, 1987; Shooner & Mullen, 2020; Valberg, Seim, Lee, & Tryti, 1986). For

Citation: Lee, B. B., & Swanson, W. H. (2022). Detection and discrimination of achromatic contrast: A ganglion cell perspective. *Journal of Vision*, *22*(8):11, 1–13, https://doi.org/10.1167/jov.22.8.11.

https://doi.org/10.1167/jov.22.8.11 Received February 3, 2022; published July 18, 2022 ISSN 1534-7362

achromatic and chromatic brightness estimation, the PC (and S-cone) pathways are likely to play a major role (Valberg et al., 1986). For discrimination of small differences in luminance between two separated targets, the situation is less clear. As stated above, responses in the MC pathway saturate at high contrast (Kaplan et al., 1987). Achromatic responses of the PC pathway are weak, but show little saturation, so they may contribute to discrimination of suprathreshold contrast differences between such targets (Pokorny & Smith, 1997). The design of the pulsed-pedestal paradigm is based on this assumption. A range of studies applying this paradigm are reviewed in Pokorny (2011), and it continues to be used both in psychophysical (Shooner & Mullen, 2020) and clinical contexts (Creupelandt, Maurage, Lenoble, Lambot, Geus, & D'Hondt, 2021; Power, Conlon, & Zele, 2021).

Most studies of the MC and PC pathways have concentrated on their contrast gain, the initial slope of the contrast-response relation. This is likely to be related to detection performance. Responses at higher contrasts (and response saturation) in MC and PC on and off pathways, and the way response saturation depends on stimuli configuration, have received less attention. We take up these questions. The pulsed-pedestal paradigm was developed based on the responses of ganglion cells to a sinewave grating at 4 Hz (Kaplan & Shapley, 1986), for which the half-saturation constant (the contrast at which the response is half the saturation value) was a low contrast, 0.1, or 10%. However, we reported that MC cells had an average half-saturation constant that was much higher for pulses (Swanson, Sun, Lee, & Cao, 2011). We find that response saturation, especially in the MC pathway, is dependent on the temporal configuration of the stimulus, and whether it increments or decrements relative to a mean luminance level, as well as other factors, such as the possible role of eye movements. This complex pattern of responses is discussed in relation to the psychophysical results in the literature; their relation to the underlying physiology is likely to be more complex than expected.

Methods

Some of the data used were obtained during experiments described elsewhere (Lee et al., 1990; Lee, Pokorny, Smith, & Kremers, 1994; Lee, Rüttiger, & Sun, 2005; Swanson et al., 2011) but were at that time analyzed with other goals. Data acquisition methods described overlap with those in these previous papers. Ganglion cell activity was recorded from the retinas of macaques (*M. fascicularis*). After initial intramuscular injection of ketamine hydrochloride, anesthesia was induced with thiopental (10 mg/kg) 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°C. On completion of recording, the animal was euthanized with an overdose of barbiturate. 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.

Cells were recorded as previously described. Positions of the fovea and the optic disk were ascertained with the aid of a fundus camera. Recordings came from parafoveal retina (5–15 degrees). A gas-permeable contact lens focused at 226 cm from the eye onto the retina. Cell classification was based on the cell's responses to achromatic or chromatic stimuli presented on a CRT screen. MC cells were generally identified by their transient responses and high achromatic contrast responsivity. PC cells were identified by their tonic responses and spectral opponency. Spike activity was recorded with a resolution of 0.1 msec.

In most experiments, visual stimuli were generated through a Visual Stimulus Generator (VSG; Cambridge Research Systems, Cambridge, UK) and presented on a CRT monitor (Sony Trinitron, frame rate 100 Hz), 226 cm from the animal's eye. Gamma correction was achieved using the VSG system and phosphor spectra measured using a Photoresearch Spectroradiometer. This provided a basis for calculation of mean chromaticity. Mean background level was 10 cd/m^2 with a mean chromaticity close to equal energy white. Various stimulus configurations were used, as described in the Results section. In one set of experiments (Figure 1), an LED visual stimulator was used, by which a uniform 4 degree stimulus was centered on the receptive field (see Lee et al., 1990, where further details can be found). Mean retinal luminance in this case was ca. 2000 td.

Results

Responses and saturation with sinusoidal stimulation

A basic premise of the pulsed-pedestal paradigm is rapid saturation of MC cell responses. Kaplan and Shapley (1986) reported a half-saturation constant of 0.1 contrast at 4 Hz for MC cells. We confirm this

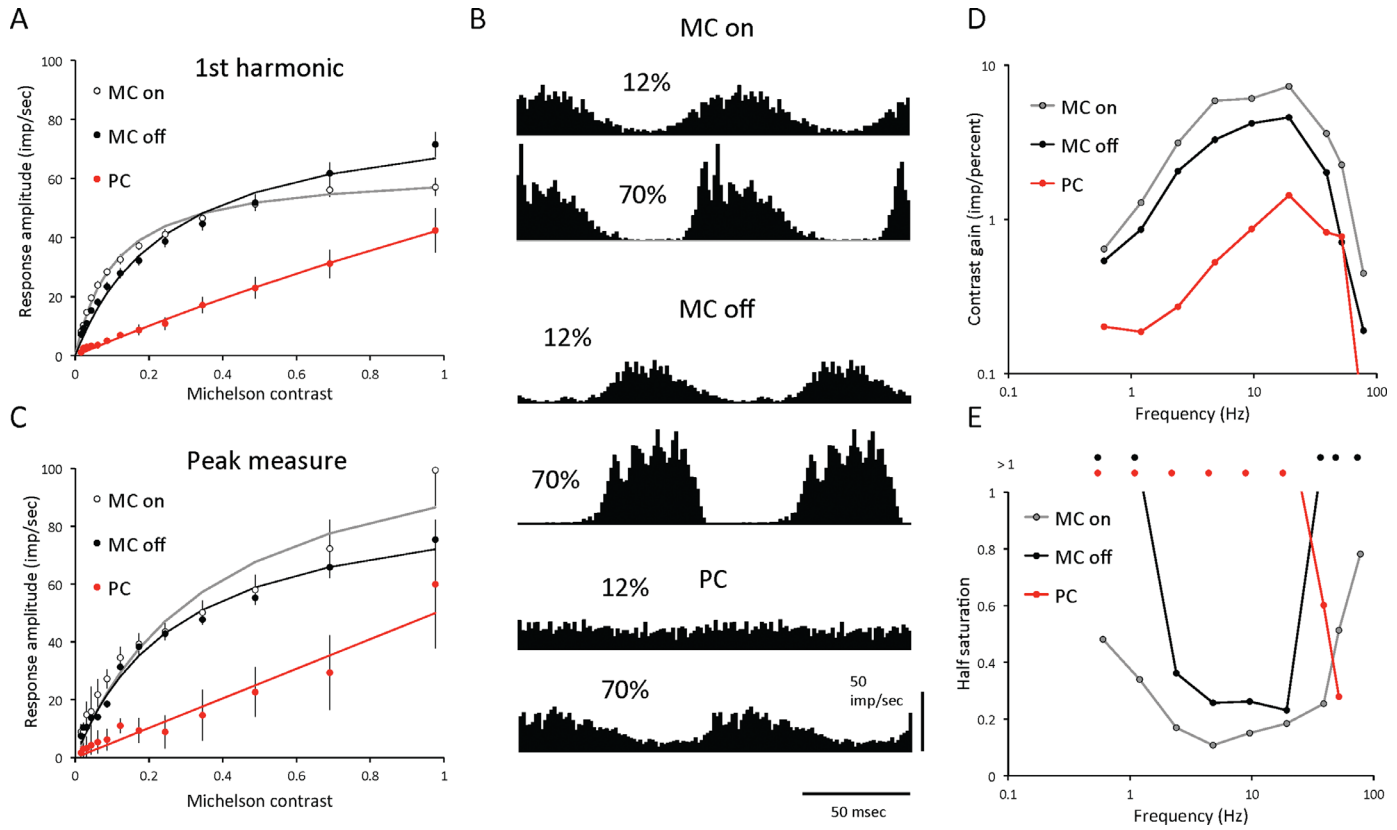

Figure 1. **Response saturation with sinusoidal modulation.** (**A**) Averaged contrast-response curves of ganglion cells; 4 degree uniform field, ca. 2000 td, 4.8 Hz, ca. 6 sec activity. Mean data from 10 cells for each curve. Standard error bars are shown in this and subsequent figures. Data taken from Lee et al. (1990). Amplitudes were first-harmonic amplitudes from Fourier analysis of spike trains. MC cell data have been fitted with saturation functions (Equation 1), PC cells with linear fits. (**B**) Averaged histograms of different cell classes at different contrasts for the same stimuli. Responses of MC on and off cells at 12% contrast are approximately sinusoidal in shape but at 70% contrast response distortions are apparent, different for the MC cell types. PC cell responses are weak and sinusoidal in shape at 70% contrast. (**C**) Peak amplitudes were derived for the different cell classes. These curves show, for MC cells, less saturation than in **A**. This may be attributed to energy in harmonics higher than the first contributing to the peak-to-trough amplitude. (**D**) Data from the cell samples (first harmonic) were fitted with saturation functions over a range of temporal frequencies. Contrast gain as a function of frequency for the cell groups, averaged over the cell samples. MC cell MTFs show a band-pass shape (Lee et al., 1990). PC cell contrast gain is lower. (**E**) MC cell mean half-saturation constants from the fit functions. These are lowest around 4 Hz with a value of 0.1 as a lower bound. Below and above 4 Hz half-saturation constants increase although MC cell contrast gain remains high.

finding for on-center cells but show that response saturation is generally not so rapid at other frequencies or in off-center cells, and response patterns are more complex.

First-harmonic response amplitudes of MC and PC cells as a function of sinusoidal temporal modulation of a uniform field are shown in Figure 1A (4.8 Hz modulation of a 4-degree, uniform field, data averaged over 10 MC on-center, 10 MC off-center, and 10 PC cells. The sample is drawn from a previous study (Lee et al., 1990). First-harmonic response amplitude rises steeply as a function of contrast for the MC cells, but saturates at higher contrast. This is especially marked for the on-center cells, whose responses flatten out above ca. 0.3 to 0.4 contrast. Off-center cells show less marked saturation. PC cell responses are weak and the contrast-response function is close to linear. Responses have been fitted by the saturation function:

$$R = R_{max}C/(\sigma + C) \quad (1)$$

where R is response, R_{max} is the asymptotic maximum response, C is contrast and σ is the half-saturation constant. The initial slope of the contrast-response function gives the contrast gain, in imp/sec per percent contrast (i.e. per 0.01 contrast). Typically, achromatic contrast gain is ca. 10 times greater for MC than PC cells. Contrast gains (R_{max}/σ; fitted for each cell separately and averaged) were 5.76 for MC on-center

cells, 4.28 for MC off-center cells and 0.52 for PC cells. These values are in the usual range. The rapid saturation of on-center cells resembles the published data (Kaplan & Shapley, 1986). The mean half-saturation constants were 0.119 (SD = 0.045) for on-center cells and 0.175 (SD = 0.07) for off-center cells. This difference was not significant (*t*-test, $p = 0.13$).

However, response amplitude based on the first harmonic does not fully capture suprathreshold responses. This is illustrated in Figure 1B. Averaged responses of three cell samples are shown to give an overview of response patterns. At low contrast (0.12), response histograms are roughly sinusoidal, indicating that first-harmonic amplitude captures the response. However, at high contrast (0.7), for MC cells, this is no longer the case, and significant response distortion is apparent. Higher harmonic components became prominent in the Fourier spectra of responses; these were greater for on-center than off-center cells (data not shown). The shape of the response distortion differs for on- and off-center cells; possible physiological substrates are later discussed.

To assess the possible effect of this response distortion on the amplitude of the response, we estimated peak response amplitude from the histograms using a 30 msec window, comparable to the critical duration for achromatic stimuli. A similar analysis has been used for luminance and chromatic perturbations and perimetric stimuli, to assess the relation between the physiological signal and psychophysical thresholds (Lee et al., 2007; Swanson et al., 2011). Briefly, the peak response, averaged over the window, was located and coherently averaged for the different cells. These peak measures for all 10 cells per group are plotted in Figure 1C. For MC cells, these curves show a steep increase at low contrast, as with the first harmonic, but then saturation effects are less apparent, at least for on-center cells; response amplitude continues to increase up to 1.0 contrast. Data have been fitted with the saturation function. The fit is less satisfactory than in Figure 1A, but the data show less indication of saturation. Mean half-saturation constants over the cell sample increased significantly, to 0.438 and 0.294 for on-center and off-center cells, respectively (paired *t*-test, $p = 0.0021$ for on-center cells and $p = 0.023$ for off-center cells).

As an alternative to the peak measure, we calculated the coherently averaged sum of the second to fifth harmonics. This sum increased monotonically with contrast, with more distortion for the on-center MC cells. Adding the first and higher harmonics yielded amplitudes very similar to the peak-to-trough measure, with data closely resembling the curves in Figure 1C.

The analysis in Figures 1A, 1B, and 1C is at just one frequency (4.8 Hz). We estimated half-saturation constants over a broad temporal frequency range using the same cell sample. Figure 1D shows contrast gain as a function of temporal frequency; the data resemble those from the earlier study (Lee et al., 1990). MC cells are more contrast sensitive than PC cells over the whole frequency range, with a band-pass temporal response. It is of note that even at the lowest temporal frequency (0.61 Hz), contrast gain is much higher for MC than PC cells. Figure 1E shows half-saturation constants for the cell sample. There is a broad minimum in the mid-frequency range, but generally half-saturation constants distribute around 0.2 (20% contrast) or higher. At lower and higher temporal frequencies, half-saturation constants increase, whereas contrast gain remains high. A similar pattern was observed with the peak measure, but with higher half saturation constants (data not shown).

The aim of this detailed preliminary analysis is to show that even with sinewaves a half-saturation constant of 0.1 (10% contrast) for MC cells is seldom achieved; 0.1 is a lower bound of a broad range of values up to four times greater. We stress this because predictions of the pulsed-pedestal analysis are critically dependent on this value, as analyzed in the Discussion section. We now turn to stimulus configurations closer to the pulsed-pedestal paradigm itself.

Responses and saturation with flashed targets

In the psychophysical paradigm (Pokorny & Smith, 1997; Sun et al., 2008; Swanson et al., 2011), four separate, square targets are set in a surround. The targets may be below, the same as, or of higher luminance than the surround; they are termed pedestals. In the "steady-pedestal" condition, the pedestals are steady and one target is briefly incremented or decremented in luminance. The observer must detect which target is modulated. In the "pulsed-pedestal" condition, all squares are pulsed from the background level, but one, which the observer must discriminate, has a higher (or lower) luminance than the others. It is argued that in the steady-pedestal condition, MC cells may mediate detection, but in the pulsed-pedestal condition, the MC pathway is in saturation at higher pedestal contrasts, and the PC pathway supports discrimination.

We measured responses of ganglion cells to briefly flashed stimuli (50 msec, 2 degree targets, with a background luminance 10 cd/m^2) under different conditions designed to simulate those used psychophysically. We first consider MC and PC responses as a function of stimulus contrast and estimate the degree of response saturation; similar data have been reported previously (Swanson et al., 2011). The Weber rather than the Michelson contrast is used, although these measures are comparable. Figure 2A shows averaged histograms (ca. 10 cells of each class) to indicate the pattern of responses. We show actual

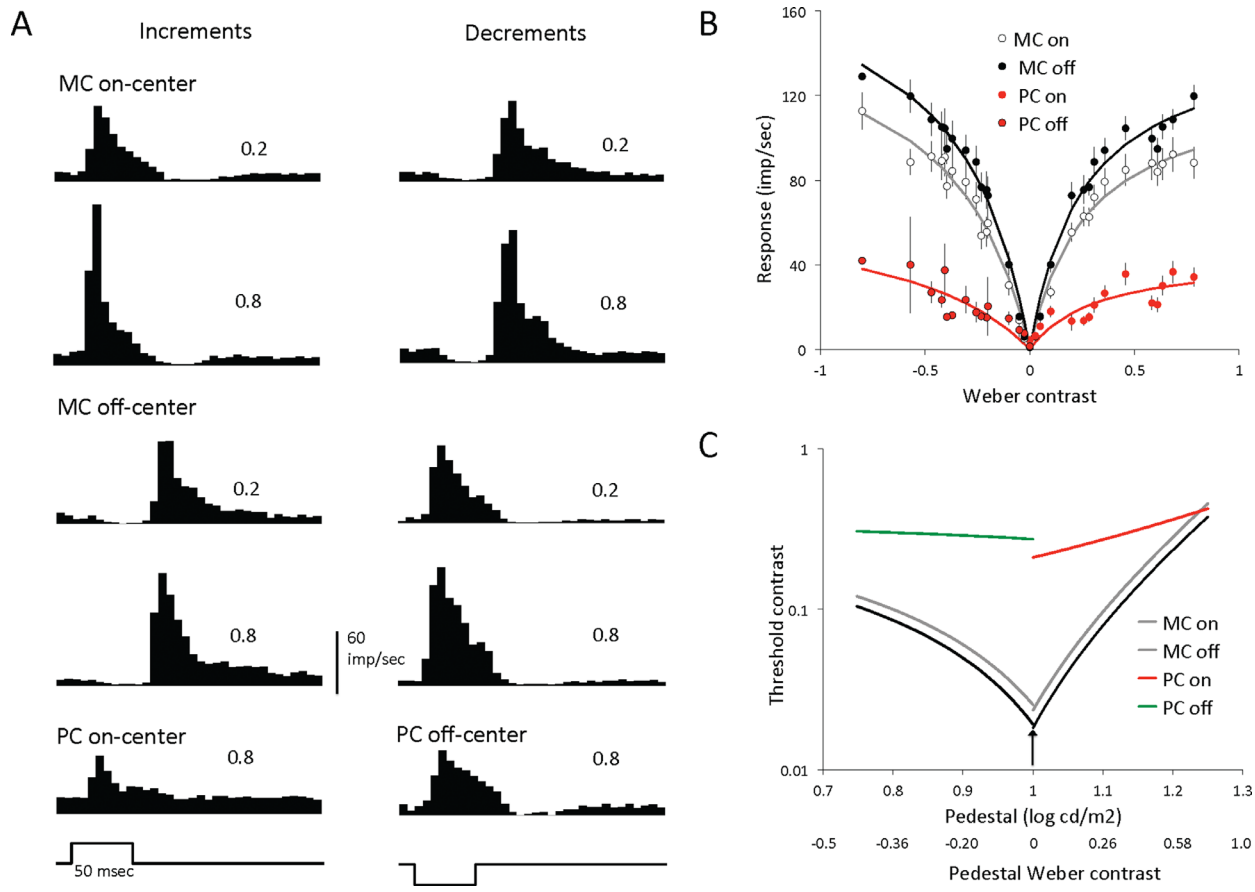

Figure 2. **Response saturation with flash stimuli.** (**A**) Positive and negative flash (50 msec) responses at two contrasts for on, off MC and PC cells, averaged over 20 responses (2 degree field, 10 cd/m^2 background). On- and off-center MC cells give responses to both positive and negative flashes. Responses are more transient at high contrast. PC cell responses are only apparent at high contrast. (**B**) Response amplitude (50 msec window, maintained activity subtracted) as a function of contrast for different cell groups (average of 8–10 cells for each class/condition). Curves show fits of Equation 1. (**C**) The fit parameters from **B** are used to predict detection/discrimination thresholds for a detector with a 10 imp/sec threshold criterion. The x axis is transformed relative to the pedestal luminance. Using Equation 2, detection (arrowed) and discrimination thresholds are predicted; further details are in the text.

responses because they illustrate several features that may be significant for detection and discrimination.

For MC on- and off-center cells, responses to 0.2 and 0.8 contrast increments and decrements are shown. Vigorous responses are present to both increments and decrements for both cell classes (with appropriate changes in timing). The dual, on-off response is expected from MC cells' transient responses and highly biphasic impulse response. The possibility that either on- or off-center cells might support detection of a luminance increment (or decrement) is consistent with earlier reports (Krauskopf, 1980; Rashbass, 1970). This is taken up in the Discussion section. At high contrast, the MC response peak is of shorter duration, especially for on-center cells, as noted previously (Lee et al., 1994). Averaged responses for PC cells are shown at only 0.8 contrast, because 0.2 contrast responses were indistinguishable from noise. PC cell responses are sustained and reverse-polarity responses were not found.

Response amplitudes (averaged over a 50 msec window, relative to maintained activity) were averaged over the cell samples and are plotted in Figure 2B for the various conditions, as a function of positive (incremental) or negative (decremental) Weber contrast. First, the responses of MC cells are more vigorous than those of PC cells, as expected. Second, MC cells show some degree of response saturation. This was assessed by fitting the averaged curves with Equation 1. Half-saturation constants are again a measure of the rapidity with which responses plateau, and for MC on cells these were 0.27 and 0.40 for incremental and decremental responses, and for MC off cells 0.26 and 0.35. These values are greater than for sinusoidal modulation. In the Discussion section, we consider reasons for this difference, which may primarily be

due to the finite time course of contrast gain control mechanisms.

Other features of MC cell responses are of note. Response amplitudes appear larger for decremental than incremental responses, and larger for off-center cells than on-center cells. To assess this more closely, data for each cell were fitted with Equation 1 and fit values compared using ANOVA. First, contrast gain was calculated for all four conditions. These values showed no significant difference. Second, half-saturation constants also showed no significant difference. However, the R_{max} parameter was larger for decremental than incremental pulses (on-center cells = 136 inc, 193 dec and off-center cells = 125 inc, 224 dec; $p < 0.001$); a difference for on and off cells had a significance level of $p = 0.08$. There were no significant interactions of these parameters between on- and off-center cells. These effects are not large but may relate to recent reports of larger contributions of off responses in a perceptual framework (Kremkow, Jin, Komban, Wang, Lashgari, Li, Jansen, Zaidi, & Alonso, 2014). Other possible physiological mechanisms influencing responses are taken up in the Discussion section.

To predict how curves such as those in Figure 2B might support detection and discrimination, one can base a calculation on a criterion change in spike rate, as in Pokorny and Smith (1997). Neurometric studies of luminance and chromatic detection have indicated that a change of 5 to 10 imp/sec in a single cell approximates detection threshold (Lee et al., 2007) or a smaller change in several cells (Swanson et al., 2011). Equation 1 can be used to predict the change in contrast (ΔC) required to produce a change in firing rate of δR. Equation 2 gives the response ($R + \delta R$) to the combined contrasts ($C + \Delta C$).

$$R + \delta R = R_{max}\,(C + \Delta C)\,/\,(\sigma + C + \Delta C) \quad (2)$$

Subtracting Equation 1 from 2 and re-arranging yields

$$\Delta C = \frac{\frac{\delta R}{R_{max}}(\sigma + C)^2}{\sigma - \frac{\delta R}{R_{max}}(\sigma + C)} \quad (3)$$

For detection, the change ΔC represents detection contrast on a steady background. For discrimination in the pulsed pedestal condition, it is assumed that the observer must detect differences in firing rate; this will depend on where the pulsed pedestal stimulus sits on the contrast response curve. Using the curves of Figure 2B, the predicted contrasts required for discrimination can be calculated.

It is possible to rescale the x axis of Figure 2B in terms of log luminance, as in Pokorny and Smith (1997) and in Figure 2C. The arrow indicates the 10 cd/m^2 surround/background. Flash luminances (decremental and incremental) are plotted along the x-axis. The Weber contrasts have been noted for comparison; due to the log axis, these are asymmetric around the arrowed point. Figure 2C shows the predictions for the different cell classes, with a 10 imp/sec criterion. The y-axis is in terms of log Weber contrast.

All the MC cell curves converge to a minimum near 10 cd/m^2, the steady background detection threshold (arrowed). Threshold contrast is predicted to be ca. 0.02, which is close to the detection threshold with a 33 or 66 msec pulse (Pokorny & Smith, 1997). The predicted discrimination thresholds rise steeply on either side of the background level. However, the predicted discrimination thresholds based on MC cells do not exceed those from PC cells. We explain these curves further in the Discussion section, and a detailed description is also given in Pokorny and Smith (1997). A comparison with their psychophysical data is also provided in a later section.

Detection and steady pedestal luminance

In the psychophysical paradigm with brief flashes, detection thresholds were measured on different steady pedestals relative to the background. Amplitude sensitivity decreased with an increasing pedestal level following Weber's law (i.e. contrast sensitivity was constant; Figure 6 in Pokorny & Smith, 1997). We measured amplitude-response functions with different steady pedestal intensities, to test cell behavior under these conditions. Incremental pulses were used for on cells, and decremental pulses for off cells (ca. 10 cells of each class). We show averaged response amplitudes as a function of flash amplitude in candela (not contrast), to indicate the effect of pedestal level in Figure 3A. Two of the five steady levels tested are shown. For MC cells, responses to a given candela increment (or decrement) are smaller at the higher pedestal level (lines show fits of Equation 1; solid lines are for 3.15 cd/m^2 pedestal, dashed for 7.92 cd/m^2 pedestal), consistent with lower responsivity at the higher adaptation level (i.e. light adaptation to the steady pedestal). Data for PC cells show less difference in responsivity. To assess the degree of light adaptation, amplitude thresholds for detection (10 imp/sec firing increment) were calculated using Equation 3. These are plotted in Figure 3B; five pedestal levels were tested. For MC cells, thresholds increase with pedestal luminance; the straight lines show the linear fit (correlation coefficient 0.980 for on cells and 0.981 for off cells). Slopes were 0.82 for MC on-center cells and 1.01 for MC off-center cells, close to Weber behavior (1.0). However, for PC cells, there was

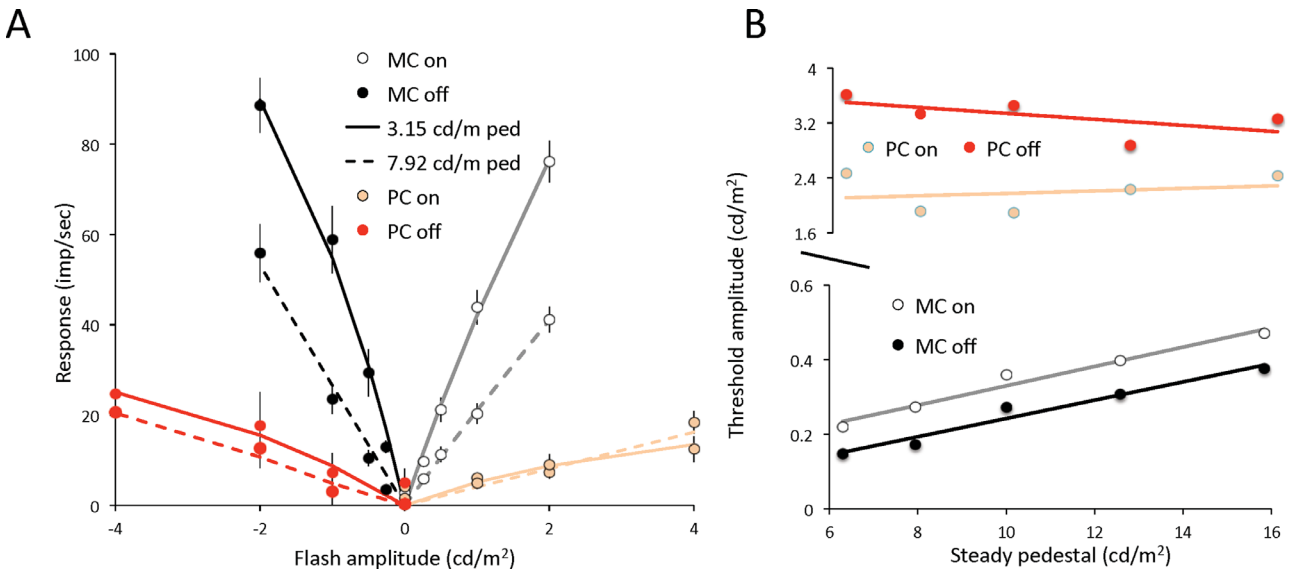

Figure 3. **Effect of steady pedestal on cellular contrast sensitivity.** (**A**) Response amplitudes of MC and PC cells (mean of 8–10 cells) when flashes are presented on different steady pedestal backgrounds. Data for two of five pedestals are shown (3.15, 7.92 cd/m^2). The x axis represents absolute flash amplitude. For MC cells, the high pedestal level generates smaller responses than the lower pedestal level. This effect is not obvious in PC cells. (**B**) Contrast sensitivity (threshold amplitude; 10 imp/sec criterion) for MC and PC cells as a function of steady pedestal luminance. The y axis is interrupted because PC cells are much less responsive. For MC cells a close to Weber relationship is apparent, as discussed in the text.

little indication of light adaptation over the restricted range of pedestal illuminances tested. It has been previously been demonstrated that PC cell responsivity falls short of Weber's law (Lee et al., 1990), as discussed further in Smith, Pokorny, Lee, and Dacey (2008).

In conclusion, MC cell contrast sensitivity matches closely the psychophysical data for detection with different pedestal luminances, with thresholds following Weber's law. This is as suggested by Pokorny and Smith (1997).

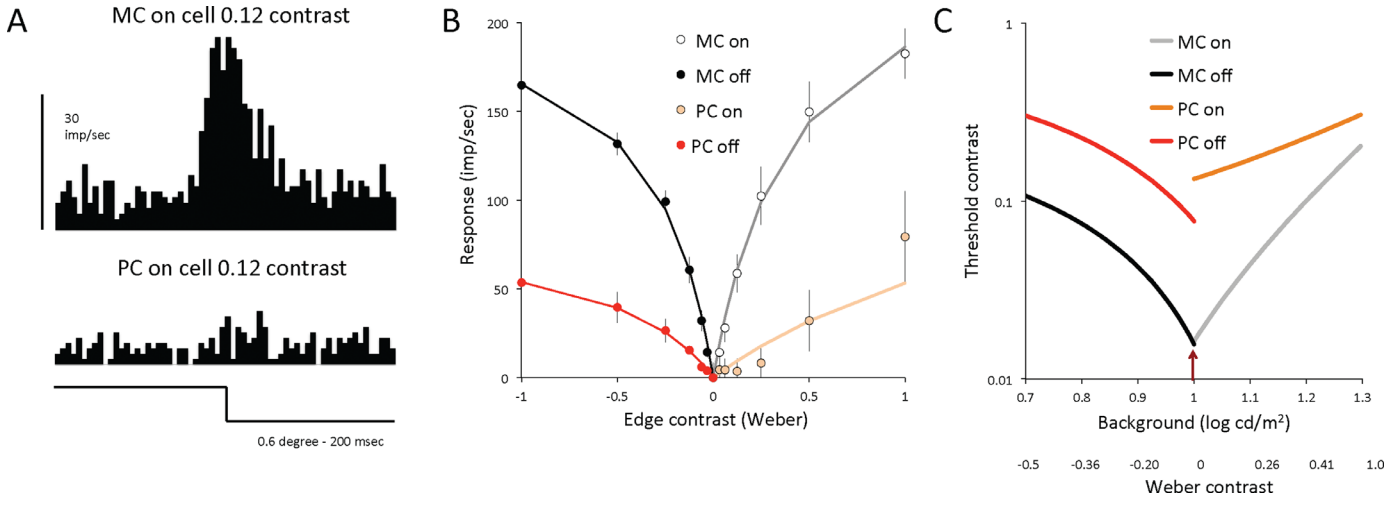

Figure 4. **Contrast-response relationships with moving stimuli.** (**A**) Cell response histograms from moving edge responses (4 deg/sec, 0.12 Weber contrast) for MC and PC cells. MC cell response is vigorous. (**B**) Mean response amplitude as a function of contrast for different cell classes (3–8 cells per class). Amplitude measured from a 50 msec window and maintained activity subtracted. Solid lines show fits of Equation 1. (**C**) Fit parameters are used to predict detection/discrimination thresholds for a detector with a 10 imp/sec threshold criterion, as in Figure 2C.

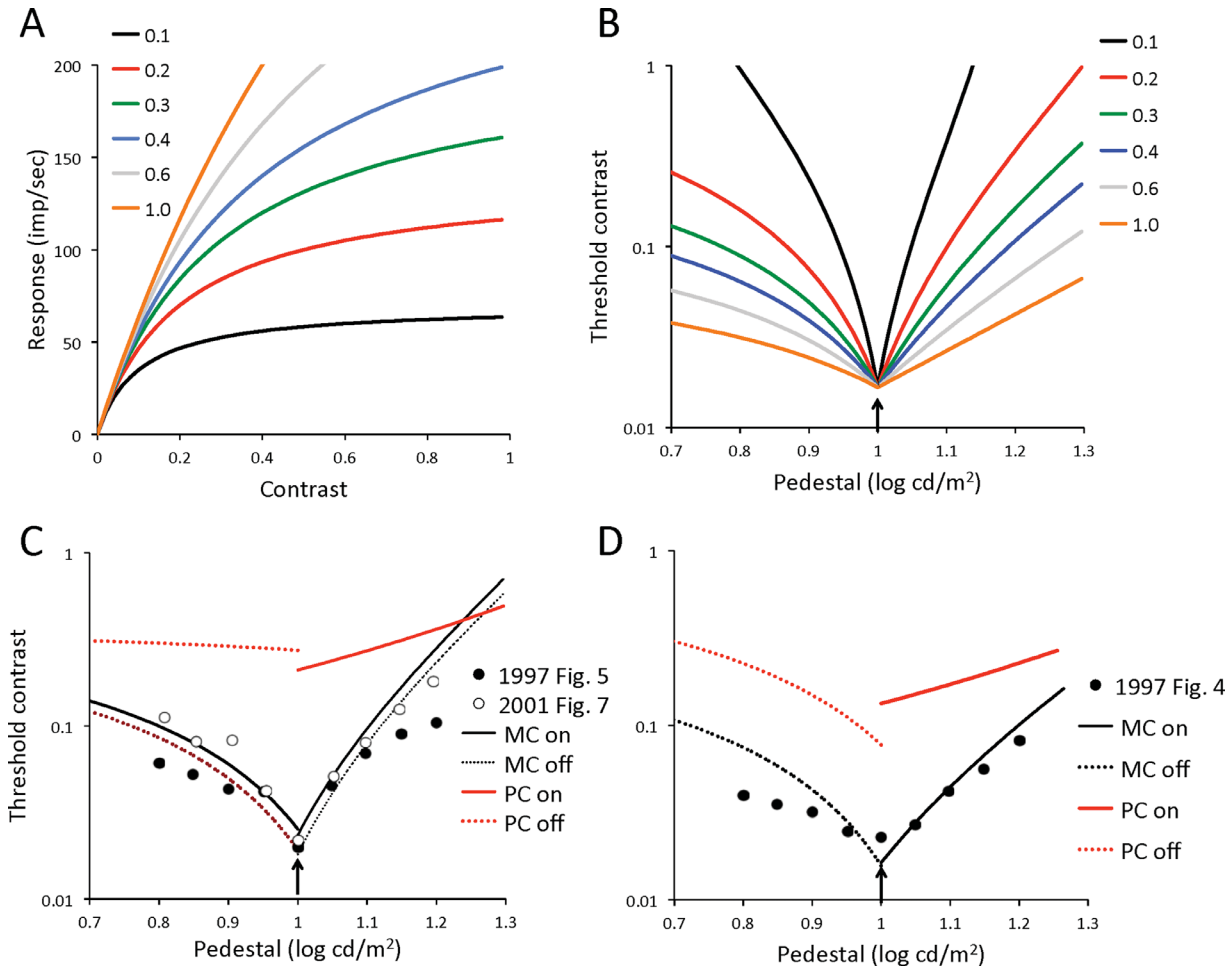

Figure 5. **Model and cell responses compared to psychophysical data.** (**A**) Set of contrast response curves with different half-saturation constants using Equation 1. R_{max} has been adjusted for each curve so as to give the same initial slope (contrast gain of 7 imp/% contrast for all curves). (**B**) Detection (arrowed) and discrimination curves for the half-saturation constants using Equation 2. A 10 imp/sec criterion was used. Curve shape is strongly dependent on half-saturation constant. (C) Flash response detection/discrimination for psychophysical data compared with MC and PC cell curves. The data points have been replotted from Pokorny and Smith (1997) and Smith et al. (2001). The cell curves have been replotted from Figure 2C. Both psychophysical and physiological data were acquired at mid-photopic levels, and the psychophysical data have been scaled appropriately. Psychophysical and MC cell data differ in detail, but the MC pathway has the ability to support both detection and discrimination. (**D**) Moving stimulus response detection/discrimination curves for psychophysical data compared with MC and PC cell curves. Psychophysical data have been replotted from Pokorny and Smith (1997). Physiological curves are from Figure 4, with scaling as in **C**. Again, the MC pathway has the ability to support both detection and discrimination.

Raised cosine stimuli

The pulsed-pedestal paradigm was also used (Pokorny & Smith, 1997) with a slow raised-cosine pulse (duration 1.5 sec, equivalent to 0.66 Hz), rather than a brief stimulus flash. Data are shown in their Figure 4, where it can be seen that discrimination thresholds rise as the pedestal level moves away from the surround, as with the flashed presentation. From the troland values for detection relative to background trolands, detection thresholds can be calculated as ca. 0.02 contrast, similar to flashed stimuli.

However, at frequencies below 1 Hz, it can be seen (see Figure 1D) that both MC and PC cells have very low contrast gain. This would imply low psychophysical contrast sensitivity at low temporal frequencies, as occurs when modulated targets are set in a dark surround (Swanson, Ueno, Smith, & Pokorny, 1987). Why are detection (and discrimination) thresholds so low with the raised cosine stimulus? One possibility is a role of eye movements translating target edges across the retina (Ennis, Cao, Lee, & Zaidi, 2014) although Pokorny and Smith (1997) suggest an alternative explanation. A detailed psychophysical and

physiological context for these possibilities is provided in the Discussion section. We consider here the signal delivered by edges moving across the retina.

We had previously measured responses of MC and PC to moving edges, and interpreted the results in a vernier context (Rüttiger, Lee, & Sun, 2002). We use these data here to provide contrast-response curves. Figure 4A shows responses of an MC cell and a PC cell to a drifting edge (4 deg/sec, 0.12 contrast). The MC cell shows a vigorous transient response, but the PC cell's response is barely discernible. Peak firing rates were measured in a 60 msec window. Mean data for MC and PC cells are shown in Figure 4B (5–10 cells for each class), as a function of Weber contrast across the edge. Incremental and decremental edges were used for on-center and off-center cells. The response amplitudes show a similar pattern to those in Figure 2. MC cells deliver a vigorous response with some saturation, whereas PC cells deliver weak responses. Data are fitted by Equation 1. Contrast gain values were much higher for MC cells (6.3 and 6.9 for MC on-center and off-center cells) compared to PC cells (0.57 and 1.47 for on-center and off-center cells). The movement speed of 4 deg/sec is close to the median speed associated with naturally occurring eye movements (Rucci & Poletti, 2015). One can then use Equation 2 to predict thresholds, as done in Figure 2C. The resulting curves are shown in Figure 4C. Around the background level (arrowed), predicted thresholds are ca. 0.015 contrast for MC cells, and discrimination thresholds increase on either side of this minimum. PC cell threshold curves are much higher. These data will be compared with psychophysical results in Figure 5. In any event, with moving stimuli, as may occur with eye movements, low contrast thresholds can be generated.

Discussion

We first consider these results in a physiological context and then take up psychophysical considerations.

Response saturation and other nonlinearities

At low contrast, linear models can often describe ganglion cell activity satisfactorily. For example, the responses of MC and PC cells to sinewaves and pulses are linearly related (Enroth-Cugell & Robson, 1966; Lee et al., 1994). With increasing contrast, some distortion of response waveform occurs, resulting in increased energy in harmonics beyond the first. One factor is response rectification, due to the impossibility of negative firing rates. This is less apparent in PC cells, because their responses to luminance contrast are weak, but becomes apparent with these cells if chromatic modulation is used and responses are vigorous. MC cell responses show additional nonlinearities. One is response compression due to contrast gain controls. This is mediated by a rapid nonlinear feedback mechanism in the inner retina (Shapley & Victor, 1978; Shapley & Victor, 1981). However, as indicated in Figure 1, response distortion differs in on-center and off-center cells, which would not be expected if contrast gain controls acted on on- and off-center cells in the same way. Light adaptation gain controls might also sculpt responses. Light adaptation in cones and inner retina appears to be rapid but not instantaneous (Lee, Dacey, Smith, & Pokorny, 1999; Shapley & Enroth-Cugell, 1984; Smith et al., 2008; Yeh, Lee, & Kremers, 1996). Such a light adaptation effect might distort the waveforms in Figure 1B. We have recently proposed a model, including light adaptation and contrast gain modules, to account for macaque ganglion cell responses to natural scenes (Schottdorf & Lee, 2021); this model reproduces the phase distortions seen in Figure 1B (data not shown). In any event, first harmonic measurements do not fully capture underlying processes at high contrast.

With flashed stimuli, contrast gain and light adaptation mechanisms would also sculpt responses. As in a previous analysis with a larger range of contrasts (Lee et al., 1994), with increasing contrast the responses become more transient. This may be due to contrast gain controls with a finite time course; early response components get through before the gain control cuts in. A similar effect is seen in the responses of MC cells to high-frequency flicker. The response saturation seen at low temporal frequencies is much less apparent, causing a characteristic change in temporal tuning (Smith et al., 2008).

In the current experiments, stimuli were centered on the receptive field. In a study of physiological responses to perimetric stimuli (Swanson et al., 2011), we had measured responses as a function of receptive field locus relative to the stimulus; the effects were minor.

With moving edges, the edge stimulus also evokes responses that may be less affected by contrast gain controls. Response of MC cells to edge stimuli are dominated by response components in a high spatiotemporal frequency band (Cooper, Lee, & Cao, 2016). High temporal frequencies are less affected by contrast gain controls. In addition, such mechanisms appear to sum over a spatial area larger than the receptive field center (Shapley & Victor, 1979). With a moving edge, compared to a coarse grating, such spatial summation might be less effective.

These physiological considerations indicate that response saturation of MC cells can be dependent on stimulus configuration in a complex manner, and half-saturation constants are seldom as low as 0.1 contrast.

Psychophysical considerations

The possibility that either on- or off-center cells might support detection of a luminance increment (or decrement) is consistent with early reports suggesting that incremental and decremental flashes are difficult to distinguish at detection threshold (Krauskopf, 1980; Rashbass, 1970). The physiological data in Figure 2 provide a substrate for this finding. With increasing pulse duration and small stimuli in a surround, discrimination becomes easier (Cohn & Lasley, 1985), presumably as on- and off-center cell responses become separate in time and space. If either on or off mechanisms might support detection with brief flashes, the thresholds may be lower than for an individual on or off system, due to probability summation, or other factors.

Use of the pulsed-pedestal protocol to separate contributions of the MC and PC pathways critically depends on rapid saturation of the MC pathways; a half-saturation constant of 0.11 was used for MC cells in the original modeling (Pokorny & Smith, 1997). Figures 5A and 5B illustrate the role of half-saturation constant on results of the model. Figure 5A shows contrast-response curves from Equation 1, for half-saturation constants from 0.1 to 1.0 (10% to 100% contrast) as indicated in the legend. R_{max} has been adjusted to give the same contrast gain in all cases (7.0, similar to the mean for MC cells). Figure 5B shows the equivalent detection/discrimination threshold predictions from Equation 2. The arrow shows detection threshold without a pedestal (i.e. one of the four targets is presented just on the background). It is identical in all cases because contrast gain is the same in all cases. With incremental or decremental pulsed pedestals, the V-shape curve defining discrimination threshold broadens rapidly as half-saturation constant increases. The slopes of contrast-response curves relate to contrast discriminability, providing a context to examine the psychophysical data in the light of the physiological results.

Figure 5C compares psychophysical data for the flashed-pulse paradigm with physiological prediction curves from Figure 2. The psychophysical data were drawn from Figure 5 in Pokorny and Smith (1997), and Figure 7 in Smith, Sun, and Pokorny (2001). Each of these figures contained data from different sets of observers that have been averaged. The x axis in those papers was centered around a background illumination, with no pedestal, of ca. 200 td. The 10 cd/m^2 background in the physiological experiments would be similar. The psychophysical data have been shifted along the x axis to center around 10 cd/m^2 (1 log(cd/m^2), to permit comparison with the physiology. The physiological curves in Figure 5C are as in Figure 2. The two sets of psychophysical data are broadly similar. Both roughly conform to the physiological prediction for MC cells. Half-saturation constants for the physiological data, MC on- and off-center cells, cluster around 0.3. Other psychophysical data also show a similar pattern consistent with the MC cell prediction (Sun et al., 2008).

It should be noted that, from a physiological perspective, detection and discrimination differ. If a target must be detected (the arrow point), this involves detection at a single visual field location among the four. This might be a less complex task than discrimination, when signals across different loci (the four stimuli) must be compared at a central, cortical site. This might affect exact shapes of the psychophysical curves. In any event, the comparison in Figure 5C indicates that the flashed pulsed-pedestal does not require dual mechanisms. The MC pathway provides an adequate substrate.

For the slow, raised-cosine pedestal experiments, the mode of detection becomes critical. Psychophysical detection experiments show that modulated targets set in a surround are much better detected at lower temporal frequencies when the surround is equiluminant rather than dark (Kelly, 1969; Kelly, 1971). Possible explanations for this effect have now focused on the role of eye movements, which move the edge of the target across the retina, providing a transient signal (Casile, Victor, & Rucci, 2019; Ennis et al., 2014). In an equiluminant surround, this provides an immediate signal for detection (or discrimination) as the retinal image moves across the low-contrast edge at certain temporal phases of the modulation. With a dark surround, edge contrast is always very high so that low-contrast target modulation is undetectable. This approach is in line with recent studies that have stressed the role of eye movements in many aspects of spatial perception (Rucci & Poletti, 2015). In addition, eye movements provide a ready explanation to many contrast-based visual illusions (Shapiro, Charles, & Shear-Hyman, 2005). It thus seemed worthwhile to test whether the achromatic contrast responses of MC and PC cells to moving edges match in any way the raised cosine pedestal results.

Figure 5D shows a comparison of psychophysical data with our physiological results as in Figure 5C. The psychophysical data are from Figure 4 from Pokorny and Smith (1997), again averaged over observers and x-axis shifted. The physiological curves are from Figure 4. There is reasonable correspondence between the psychophysical data and the MC cell prediction, except that the psychophysical slopes are somewhat shallower than the MC cell slopes for off edges. However, it should be noted that only 4 deg/sec physiological data were available. We suggest that another speed, or range of speeds, might provide a better fit to the psychophysical data.

Noise and numerosity

In previous papers, we have considered detectability of spike train signals in relation to noise (Lee et al., 2007; Sun, Ruttiger, & Lee, 2004; Swanson et al., 2011). With a detector having a critical duration comparable to that of a luminance mechanism, a spike rate increment of 5 to 10 imp/sec combined with central pooling over a few cells could support psychophysical sensitivity, for example, in perimetry (Swanson et al., 2011). This would also be the case for the Pokorny/Smith flashed stimuli protocol, for detection or discrimination.

On the other hand, for the raised cosine protocol, the sinewave frequency is low, and the contrast gain of both MC and PC cells is low. To achieve high psychophysical contrast sensitivity when retinal input cells have low contrast gain, some form of cortical pooling has been suggested. Pokorny (2011) states "threshold involves higher order processes that combine inputs from arrays of retinal cells," so that absolute levels of physiological response are made irrelevant by some cortical deus ex machina. However, in one early model (Watson, 1992), it was concluded that summation over many thousands of cells would be required to achieve an increase of detectability of a log unit. There is no evidence for such cortical mechanisms, and they would seem inconsistent with some of the fine spatial effects noted in the pulsed-pedestal raised-cosine protocol (Smith et al., 2001). We find an alternative explanation in terms of eye movement is more parsimonious.

An additional consideration is how spike train signal-to-noise changes as contrast and response amplitude increase. This might influence suprathreshold discrimination. With drifting gratings, response variability (i.e. noise) changes little with increasing contrast (Croner, Purpura, & Kaplan, 1993), although increasing temporal frequency has a major effect (Sun et al., 2004). These effects could be modeled on the basis of a spike generating mechanism and impulse statistics (Sun et al., 2004). This would suggest contrast-related changes in spike train signal-to-noise are unlikely to have a major effect on our analysis. Another factor is cell numerosity. Midget ganglion cells are more numerous than parasol cells in central retina by a factor of 6 to 7. As suggested by Shapley and Perry (1986), summation of ganglion cell signals increases signal-to-noise with the square root of cells summed (Lee et al., 2007). This could improve PC cell sensitivity by a factor of 2 to 3, without changing the shape of the curve. This factor is unlikely to materially affect our conclusions.

Concluding remarks

Eye movements are likely to play a role in other pedestal experiments where the raised cosine stimulus has been used. For example, in more complex spatial contexts, such as the use of Gabor-like spatial frequency configurations (Leonova, Pokorny, & Smith, 2003), the role of eye movements remains a major uncontrolled variable, which makes those data interesting but inconclusive. Generally, the importance of edge effects in the raised cosine protocol may be related to the role of eye movements.

An additional uncertainty with the PC pathway in detection and discrimination is the possible low-pass central filtering of its signals. PC cells respond to chromatic modulation upto 30 to 40 Hz (Lee et al., 1990), yet chromatic modulation is not perceived beyond ca. 10 Hz (Swanson et al., 1987). This suggests some kind of central low-pass temporal filtering. It is difficult to demultiplex luminance and chromatic components of the PC-pathway signal (Cooper, Sun, & Lee, 2012; Valberg et al., 1992), so it is likely that such low-pass filtering would attenuate both achromatic and chromatic response components. The effect of such filtering on processing of brief flashes is unclear.

However, suprathreshold discrimination may critically depend on the task; for spatial tasks, eye movements may provide a transient, perceptually relevant spatial signal for sharp edges, but for brightness and chromatic discrimination related to surface quality, eye movements may be less relevant. Although discrimination of suprathreshold achromatic and chromatic differences in the natural environment might depend on a combination of MC and PC pathway activities, the pulsed-pedestal protocol would not seem to adequately separate the functions of these two pathways.

Keywords: ganglion cells, contrast, parvocellular, magnocellular

Acknowledgments

The authors thank Ding Cao, Paul Martin, Joel Pokorny, Lukas Rüttiger, Vivianne Smith, and Hao Sun for help with experiments and for permission to use resulting data. We also thank Joel Pokorny for discussion and comments on the manuscript.

Supported in part by the National Eye Institute of the National Institutes of Health under Award Numbers R01EY013112 (B.B.L.) and R01EY024542 (W.H.S.). The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health.

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