Review: Steady and pulsed pedestals, the how and why of post-receptoral pathway separation

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In the mid-1990s, the Pokorny and Smith research group began a series of psychophysical experiments with the aim of separately measuring magnocellular (MC)- and parvocellular (PC)-pathway mediated achromatic contrast discrimination. Three paradigms provide complementary information: The pulsed-pedestal paradigm reveals PC contrast gain, the steady-pedestal paradigm reveals steady-state MC-pathway sensitivity, and the pedestal-$\Delta$-pedestal paradigm reveals MC contrast gain. Further studies investigated the temporal and spatial summation properties of the underlying mechanisms and extended the work to include measures of spatial resolution, chromatic contrast discrimination, the detection and identification of stimulus polarity, and the inferred retinal mechanisms mediating illusory distortions. Other laboratories have also applied the methods to the study of normal and clinically impaired vision. This review describes the pedestal methodologies, how they relate to physiology, and how they have been and should be employed.

Keywords: contrast gain, ganglion cells, magnocellular/parvocellular, retina, spatial vision, temporal vision


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Introduction

Psychophysical studies of the visual system using detection and discrimination tasks are considered to access early retinal pathways as opposed to more complex studies of appearance, which certainly must involve processing beyond the retina. While psychophysics is not a method for measuring neural function directly, convergent evidence from primate neurophysiology and the current understanding of the human visual system suggests that the contrast gain functions estimated by the three pedestal paradigms described here are likely attributable to the magnocellular (MC) and parvocellular (PC) pathways. The text, in discussing psychophysical results, refers loosely to MC and PC mediation, as these neural-pathway specific functions are inferred from psychophysics. The methodologies are described in general terms (for details, refer to the original publications).
About 15 years ago, we began a series of psychophysical experiments with the aim of separately measuring MC- and PC-pathway contrast discrimination (Pokorny & Smith, 1997). In a series of publications, the temporal and spatial summation properties of psychophysically defined MC- and PC-pathway mechanisms were explored, and subsequently included measures of spatial resolution and detection and identification of stimulus polarity. A series of clinical studies, as collaborative efforts, was also carried out using the methodology. In addition, other researchers used the methodology to study visual function in interesting ways in both normal vision and in a variety of vision disorders and systemic diseases.

Here, I begin by describing the psychophysical paradigms, then retinal physiological responses and the theory of how the features of the psychophysical results relate to the physiology. Finally, I will discuss applications of the techniques to the understanding of normal visual function and to alterations in visual function caused by disease.

The basic paradigms

The pedestal paradigms are unique in that they are designed to differentiate the MC and PC pathways by their contrast responsivity. In this framework, the slopes of the psychophysical contrast discrimination thresholds are compared with typical values from physiology to determine whether they follow the contrast gain signatures of the MC or the PC pathway.

The spatial display is a simple, 4-square stimulus array (the pedestal) in a larger constant luminance surround (Figure 1). An important feature is that the test stimulus is identical for the pulsed- and steady-pedestal conditions; only the pre- and post-adaptation displays differ.

Pulsed-pedestal paradigm

The pulsed-pedestal paradigm begins with adaptation to a steady, spatially homogeneous background. The 4-square stimulus array appears only during the trial period. A trial consists of a brief presentation of a 4-square array at a fixed supra-threshold contrast increment or decrement replacing the background. The 4-square stimulus array appears only during the trial period, with the single test square at a higher or a lower retinal illuminance than the other three (Figure 1, upper panel). The observer’s task is to discriminate which member of the 4-square array differs from the other three. Test square retinal illuminance is adjusted on successive trials by a staircase procedure to determine the contrast discrimination threshold. Data from this paradigm are interpreted as revealing PC contrast gain.

Steady-pedestal paradigm

The steady-pedestal paradigm presents the 4-square stimulus array continuously during an adaptation period as a fixed luminance increment or decrement in the larger constant luminance surround. In this paradigm, only the retinal illuminance of the single test square changes during the trial period (Figure 1, middle panel). The stimulus presentation is identical for both paradigms; all that differs is the intertrial array and adaptation. Data from this paradigm are interpreted as revealing Steady-state MC-pathway sensitivity.
Pedestal-Δ-pedestal paradigm

For the pedestal-Δ-pedestal paradigm (Figure 1, bottom panel), the protocol is identical to the steady-pedestal condition in all respects except that during the trial, the retinal illuminance of all 4 squares is incremented or decremented (a pedestal-Δ-pedestal), with the single test square incremented or decremented by a different amount from the other three squares. Data from this paradigm are interpreted as revealing MC contrast gain.

Rationale and theory

The contrast-response function: Where does it originate?

The contrast-response function refers to the dependence of response amplitude on stimulus contrast. Characteristically, the response grows linearly with small increases in contrast from an adapting field, shows decreases in gain with further increases in contrast, and eventually saturates at high contrasts. Contrast gain originates in the retina, likely at the bipolar cell layer. I am not aware of primate physiological studies addressing the origin, but recordings from tiger salamander (Burkhardt, 2010) and guinea pig retina (Beaudoin, Borghuis, & Demb, 2007) support the bipolar cell as the major contributor. In the tiger salamander, bipolar cell responses are nonlinear, showing high gain for small contrasts, some 10–15 times greater than that of cones, but then approach saturation for higher contrasts. The contrast gain of amacrine and ganglion cells is somewhat higher than for bipolar cells, but the differences are not large.

Primate physiology: Characteristics of magnocellular and parvocellular contrast responses

There has been rapid growth of information concerning the early processing of visual signals in the primate retina and lateral geniculate nucleus (LGN). Two major processing streams that can be differentiated both by anatomy and physiology have been identified. These are the magnocellular (MC) and parvocellular (PC) pathways. The retinal ganglion cell appears to act as a contrast detector over a wide range of luminance. The MC pathway is classically considered to have an important role in contrast detection and in providing input to higher order pattern and motion processing (Shapley & Enroth-Cugell, 1984). The PC pathway is classically considered to have its role in providing input to higher order chromatic processing and is usually considered to mediate high spatial frequency resolution and serve an input to higher order pattern processing (Lennie, 1993).

Retinal and lateral geniculate recordings (Kaplan & Shapley, 1986; Lee, Pokorny, Smith, Martin, & Valberg, 1990) have shown that the changes in spike frequency accompanying changes in stimulus contrast are much larger for recordings from single cells in the MC pathway than for cells in the PC pathway. With adaptation to a steady stimulus field, cells in both pathways each achieve a constant resting level, on the order of 5–20 spikes/s (Greschner et al., 2011; Troy & Lee, 1994). This steady state firing rate does not vary greatly with photopic luminance level (Kaplan, Purpura, & Shapley, 1987). With an increase in stimulus contrast, the amplitude response of the MC pathway initially shows rapid growth, followed by decreases in responsivity with increasing contrast. In comparison, the PC-pathway amplitude response shows a steady growth rate with the increasing size of the contrast signal (Figure 2A).

A Michaelis–Menten saturation function can describe data for either cell class:

$$ R = R_0 + R_{\text{max}} C/(C_{\text{sat}} + C), $$ (1)

where $R$ represents the response amplitude in impulses per second (ips), $R_0$ represents the resting response level, $R_{\text{max}}$ represents the maximal response amplitude, $C$ represents the Michelson contrast, and $C_{\text{sat}}$ represents the semisaturation constant (the contrast at which response amplitude is half of $R_{\text{max}}$). In electrophysiological studies, such curves are characterized by their percent contrast gain, $(R_{\text{max}} / C_{\text{sat}}) / 100$, or by the initial linear rise from zero contrast.

For the PC pathway, the contrast gain for achromatic stimulation is less than 1; values of 0.15–0.50 are typical. For the MC pathway, the contrast gain for achromatic stimulation is greater than 1; values of 5–8 are typical (Kaplan & Shapley, 1986).

Model for contrast response, contrast detection, and discrimination

A threshold can be measured at the neuron’s resting level and this can be considered a contrast detection threshold. A contrast threshold can also be measured by measuring a criterion difference in two contrast responses, which is considered a contrast discrimination. The equation for such thresholds, $\Delta C$, is derived from Equation 1:

$$ \Delta C = (\delta/R_{\text{max}})(C_{\text{sat}} + C)^2/[C_{\text{sat}} - (\delta/R_{\text{max}})(C_{\text{sat}} + C)], $$ (2)

where $\delta$ is the criterion. The predicted thresholds obtained with a common criterion of 10 ips (e.g., Lee, Martin, &
Valberg, 1989) are shown in Figure 2B. Here, a logarithmic ordinate is used to allow comparison of physiology with psychophysics, but the abscissa is linear, as is typical of physiological data. It is also possible to use the derivative of Equation 1 as an indicator of responsivity (Shapley & Enroth-Cugell, 1984). In this case, contrast detection is reciprocally related to contrast gain.

MC-pathway cells are much more sensitive than are PC-pathway cells at threshold (Kaplan & Shapley, 1986). In Figure 2B, note that, despite the high sensitivity of the MC pathway at detection threshold, discrimination thresholds deteriorate with increasing contrast as the responses approached saturation. In comparison, the PC pathway is relatively insensitive at threshold, but discrimination does not deteriorate appreciably with increased contrast.

Rationale for the psychophysical design

Many visual system cells have been shown to have a center/surround receptive field organization. An ON-center cell gives a brisk response to positive Weber contrast, and an OFF-center cell gives a brisk response to negative Weber contrast. The dynamic range in the preferred stimulus direction (e.g., luminance increment for an ON cell) allows a graded response with contrast changes. The dynamic range in the nonpreferred direction is small and cells cease firing when confronted with a small change in the nonpreferred contrast direction (Schiller, 1992). Thus, when the 4 squares are incremented in luminance, the ON pathway mediates responses, and when the 4 squares are decremented in luminance, the OFF pathway mediates responses. When the 4-square array is pulsed for a brief period of time, the spike rate for the cells attuned to the preferred polarity will increase. With variation in pulse luminance, the discrimination threshold (i.e., luminance difference) between the three reference squares and the test square required for threshold will vary according to the position on the contrast-response function, i.e., as the function becomes shallower at higher contrast levels (Figure 2A), the excursion in test luminance required to reach a criterion will increase.

In our studies, we restricted the pedestal Weber contrast levels to be between 0.5 and 2.0, which are comparable to the Michelson contrasts used in the physiological experiments that characterized MC- and PC-pathway contrast gains. If the responses of ON and OFF cells are plotted on a common axis, the two limbs of the function form a V shape. Figure 3 shows predictions based on the average primate cell response characteristics (Kaplan & Shapley, 1986) shown in Figure 2. The data are plotted as a function of the pulse retinal illuminance rather than Weber contrast, and with a logarithmic abscissa, since this is a familiar form for psychophysical data. The V-shaped functions are centered on the retinal illuminance, 2.07 log Trolands. Predictions for MC- and PC-pathway cells have been normalized to a threshold of 1 Troland (Td) to allow comparisons of the slopes. The solid curves give the prediction based on the derivative a vanishingly small criterion; predictions for 5- and 10-ips criteria are shown for comparison. Criteria of 5 and 10 ips are commonly used for measurement of responsivity (e.g., Lee et al., 1990). The effects of a real criterion on the normalized thresholds include (a) a variation in the contrast at which saturation becomes evident and (b) a minor variation in the initial slope of the contrast gain function. The slope of the discrimination function at low contrasts, however, is primarily determined by the percent contrast gain, \( (R_{\text{max}} / C_{\text{sat}}) / 100 \).
Within this framework, the slopes of the psychophysical contrast discrimination threshold functions can be compared with typical values from physiology to see whether they follow the contrast gain signatures of the MC or the PC pathway. Although ON- and OFF-center cells of either pathway in the macaque retina have different anatomical (Dacey & Petersen, 1992) and biochemical bases (Wässle, Grünert, Martin, & Boycott, 1994), there is no obvious difference in their response to achromatic contrast. From psychophysical measurements, some human observers show a greater sensitivity to decrements than to increments (Bowen, Pokorny, & Smith, 1989; Whittle, 1986). These differences are relatively small, and in developing the models to account for the data obtained in the pedestal paradigms, we created templates with equal incremental and decremental sensitivities.

### Psychophysical measurement of contrast gain

In single-cell electrophysiological measurements, the three parameters $\delta$, $R_{\text{max}}$, and $C_{\text{sat}}$ uniquely establish contrast discrimination. In psychophysics however, the threshold involves higher order processes that combine inputs from arrays of retinal cells. Therefore, to compare contrast discrimination in humans to single-cell data, only the shapes of the contrast discrimination functions are relevant, not the absolute levels. Further, to make clear the need to differentiate ON- and OFF-response behavior, we considered pulse data and plotted the inferred OFF-cell responses to decrements and ON-cell responses to increments from the background.

Figure 3, plotted in a threshold versus illuminance (TVI) format with logarithmic axes, shows predictions for contrast discrimination behavior that can be compared with psychophysical data. The TVI format is a variant of that proposed by Stiles (1978) for chromatic adaptation. Data plotted in this format obey the Stiles’ displacement laws: The position of the data on the abscissa reflects the adapting properties of the background. The position of the data on the ordinate reflects the sensitivity of the observer to the spatiotemporal properties of the test pulse. The predictions shown in Figure 3 are taken from Figure 2B, with an arbitrary normalization for both axes. The abscissa shows contrast multiplied by retinal illuminance normalized to the background. The ordinate is normalized to an absolute contrast threshold of 1 Td. It is clear that PC- and MC-pathway behavior can be differentiated by the characteristic slopes of their contrast discrimination functions, i.e., shallow or deep V shapes.

If the contrast-response functions of the retinal MC and MC pathways are related to the form of the threshold vs. pulsed contrast functions of human observers by the model in Equation 2, then the form of these psychophysical functions will resemble the form of the model threshold versus contrast functions (Figure 2B). Experiments done with the pulsed-pedestal and pedestal-$\Delta$-pedestal paradigms test this implication. As we will see, in fact the psychophysical functions do not resemble either model function, but they resemble the MC function at low contrasts and the PC function at high contrasts. Thus, the two model functions can account for the results in this paradigm, if we add the additional assumption that the threshold at any pedestal contrast is determined by the response that is most sensitive at this contrast.

Our approach, therefore, was to measure contrast discrimination for a succession of luminance excursions from a steady adapting field. Sample data (Figure 4) show the characteristic response profiles, i.e., characteristic slopes in the V-shaped functions for the three pedestal paradigms and the presumed mechanisms mediating sensitivity for each of the paradigms.

Each of the paradigms produces a characteristic function when contrast discrimination thresholds are plotted against the incremental and decremental pedestal luminances. The pulsed-pedestal paradigm yields shallow V-shaped curves in which discrimination depends on the contrast between pedestal and background. The pedestal-$\Delta$-pedestal paradigm yields steep V-shaped functions. The steady-pedestal paradigm shows monotonic variation of contrast threshold with pedestal luminance, independent of the fixed surround luminance.

Psychophysical data do not have independent access to $R_{\text{max}}$, $C_{\text{sat}}$, and $\delta$ of Equation 2. With psychophysics, we can abstract two pieces of information from data: the slope of the V shape and the sensitivity at the minimum.
While Equation 2 can be used to fit psychophysical data, there is an alternate form that includes the parameters of $C_{\text{sat}}$, criterion, and overall scaling (Smith, Sun, & Pokorny, 2001; Snippe, 1998):

$$ \log \Delta I = \log[(C_{\text{sat}} + |C|)^2/(C_{\text{sat}} - (K_C)(C_{\text{sat}} + |C|)] + \log(K_P I_S), $$

where $|C|$ represents the absolute value of the pulsed Weber contrast $(\Delta I/I_S)$, $C_{\text{sat}}$ represents the saturating contrast, $K_C$ represents the criterion increment firing rate (comparable to $\delta/R_{\text{max}}$ of a single cell), and $K_P$ represents the overall scaling constant. The overall scaling constant, $K_P$, incorporates threshold sensitivity for the presumed pathway mediating thresholds that may depend on stimulus parameters such as the test square area.

For the steady-pedestal paradigm, a line of unit slope with a vertical scaling factor describes the data:

$$ \log \Delta I = \log(I) + \log(K_M I_S), $$

where $K_M$ represents the vertical scaling parameter for the presumed MC-pathway mediated thresholds. For the steady-pedestal paradigm, the single parameter fit describes the data. The data for large decremental contrasts deviate to higher thresholds, particularly for small array sizes (subsequently shown in Figure 8). The probable cause of these deviations is spread light (Pokorny & Smith, 1997). The effect of spread light is expected to be greatest for the smaller arrays (Smith et al., 2001).

The pedestal-$\Delta$-pedestal paradigm:

Methodological details

Because of the high gain of the MC pathway, accessing contrast gain discrimination parameters requires very small contrast steps. If measurements are taken at the surround retinal illuminance, even for a short duration presentation time, there is at most a 0.7 log range between the thresholds for the pulsed-pedestal and steady-pedestal paradigms. The operating range can be extended if measurements are taken at a pedestal retinal illuminance away from the surround retinal illuminance, where the separation between the steady-pedestal and pulsed-pedestal thresholds is larger. In the pedestal-$\Delta$-pedestal paradigm, the 4-square array was present continuously as a steady pedestal relative to the surround. During a trial, three squares were presented at the pedestal-$\Delta$-pedestal retinal illuminance; the fourth was at the variable test retinal illuminance (Figure 1, bottom panel).

The pedestal-$\Delta$-pedestal thresholds (Figure 4) show rapid threshold increases with the size of the $\Delta$-pedestal, producing a steep V shape. When the model described in Equation 2 is fit to pedestal-$\Delta$-pedestal data, the computed contrast gains are in the range measured from primate MC-pathway cells (Kaplan & Shapley, 1986). With this paradigm, an extremely small $\Delta$-pedestal results in a remarkable loss of sensitivity. For instance, a $\Delta$-pedestal of 0.02 log unit results in a sensitivity loss of about 0.65 log unit.

The steep V-shaped function is observed for $\Delta$-pedestal values that result in thresholds that lie between the steady- and pulsed-pedestal functions. When the $\Delta$-pedestal was extended to lower $\Delta$-pedestal values, the slope of the measured thresholds abruptly became shallower. The dashed line represents the PC-pathway contrast gain slope renormalized to the predicted pulsed-pedestal threshold at the pedestal retinal illuminance. This calculation has no free parameters and the line captures the data well.

Effects of stimulus parameters:

Temporal summation

Temporal and spatial summation can be assessed for the pulsed- and steady-pedestal paradigms by varying the spatiotemporal parameters of the test. According to the Stiles’ displacement laws, these manipulations should displace the psychophysical functions vertically on the threshold axis without changing their shape. To evaluate temporal summation, measurements were taken at a series of pulse durations from 16.67 ms to 133.33 ms (Pokorny & Smith, 1997). As can be seen in Figure 5, with brief durations, doubling the stimulus presentation time roughly halved the incremental luminance required for threshold. This was true for both the pulsed- and steady-pedestal data. This behavior extended to longer durations for the
pulsed- than for the steady-pedestal condition. With successive duration doublings, at some point, the separations became smaller and then negligible, indicating partial rather than full summation.

The data of Figure 5 allow us to evaluate temporal summation functions for each of the two paradigms. For the pulsed-pedestal condition, the arms of the V-shaped function were discontinuous, with the minimum threshold at the surround retinal illuminance. The stimulus condition at the surround retinal illuminance was identical for the two paradigms and threshold was mediated by the more sensitive mechanism, in this case the MC pathway.

Figure 6 shows the temporal summation functions for the two paradigms. Thresholds are plotted as a function of stimulus duration, with both axes expressed in logarithmic units. The steady-pedestal thresholds were taken from the linear data fits as the values at the surround retinal illuminance. For the pulsed-pedestal paradigm, thresholds were estimated from the sensitivity predicted at the intersection of the two limbs of the V-shaped function. Both temporal summation functions include a linear portion for brief test pulse durations where the luminance required for threshold decreases proportionally with increases in stimulus duration. At longer durations, threshold luminance becomes independent of stimulus duration. The curves fitted to the data points are from a model of pulse detection derived from sinusoidal temporal contrast sensitivity functions measured to pure luminance and pure chromatic modulation (Swanson, Ueno, Smith, & Pokorny, 1987).

The results are indicative of the temporal summation functions for the mechanisms mediating contrast detection and discrimination for the steady-pedestal paradigm compared with contrast discrimination for the pulsed-pedestal paradigm. Note that two different temporal signatures emerge: a short integration signature derived from steady-pedestal thresholds integrating luminance contrast over 40–50 ms and a long integration signature for pulsed-pedestal thresholds integrating luminance contrast to durations greater than 200 ms.

It can be seen that the luminance template sums over 40–50 ms and provides good agreement with steady-pedestal paradigm data. This function follows the same time course as the classical critical duration data for the detection...
Effects of spatial parameters

**Pulsed-pedestal: Sensitivity is controlled by the edges between test and surround fields**

Smith et al. (2001) reduced the surround sizes in the pedestal paradigms to investigate the feature of the surround that controlled adaptation. Figure 7 shows data for the pulsed-pedestal paradigm using the 2.07° four-square array and surround sizes of 2.21° and 2.07°; data with an 8° surround are plotted for comparison. The 2.21° surround provided a 4.2' border around the test targets and a 4.2' crosshair separating the four squares. The 2.07° surround provided only a 4.2' crosshair separating the squares. The data show that the arms of the V-shaped functions for both surround sizes are indistinguishable in shape from the 8° surround data. Thresholds were determined by the spatiotemporal contrast step generated with respect to the surround. Discrimination remained controlled by the surround even under the limiting condition that the display provided only a narrow 4.2' crosshair separating the squares. This result suggested that, as for chromaticity discrimination for stimuli varying in L- and M-cone excitation (Smith, Pokorny, & Sun, 2000; Zele, Smith, & Pokorny, 2006) or S-cone excitation (Cao, Zele, Smith, & Pokorny, 2008), the visual system can use the information generated along the extensive borders of the discrimination targets. Perhaps the most striking experimental results were that "the edge is all that matters" and a crosshair as narrow as 4.2' can control discriminative performance.

**Spatial summation**

In an experiment evaluating the effect of altering the array size on the pedestal contrast discrimination functions, the height and width of the 4-square array were varied between 0.32° and 7.87°, with the length of one side of a single test square subtending between 0.125° and 3.9° (Smith et al., 2001). Figure 8 presents results in the same
format as Figure 5. The upper panel shows data for the pulsed-pedestal paradigm and the lower panel shows data for the steady-pedestal paradigm. The different array sizes are identified by different symbols. For the pulsed-pedestal paradigm data, the arms of the V-shaped function did not vary in slope with stimulus size. In the steady-pedestal paradigm, threshold rose monotonically as a function of pedestal luminance. The data sets for the different array sizes were displaced but are parallel. For both paradigms, the thresholds decreased as stimulus array size increased. The change in sensitivity was more pronounced for the steady-pedestal paradigm than the pulsed-pedestal paradigm.

Area-illuminance functions were derived by plotting the thresholds as a function of the area of a single square in the 4-square array (Figure 9). Again, threshold sensitivity for the pulsed-pedestal condition was predicted at the intersection of the two limbs of the V-shaped function. Data for the pulsed-pedestal paradigm show a shallow linear decrease in log threshold with log area. Data for the steady-pedestal paradigm show a steeper decrease in threshold with log area for small array sizes with an asymptote above one square degree.

The pulsed- and steady-pedestal paradigms were designed to compare psychophysically accessed contrast gain with single-cell contrast gain data in the retina or lateral geniculate nucleus (LGN). This comparison required the inclusion of a free vertical scaling factor in Equation 2 to recognize that the psychophysical sensitivity includes additional contributions such as averaging or summation at higher cortical levels. A similar point can be made in considering the spatial summation data. The sizes of retinal receptive fields in the fovea and parafovea are much smaller than the psychophysical stimuli employed. PC-pathway cells show a center size of 3' in the central 10° of the retina, while MC-pathway cell center sizes are approximately twice that size (Croner & Kaplan, 1995). Obviously, the area-illuminance summation observed psychophysically cannot be related to the spatial dimensions of single-cell receptive fields. The spatial summation data (Figure 9), thus, indicate a difference between the averaging or summation properties of MC and PC pathways at higher cortical levels.

MC-pathway spatial summation: A modern investigation of area summation at the fovea (Davila & Geisler, 1991) established that Ricco’s law (threshold is inversely proportional to the area stimulated) could reflect spatial summation due to the optical point spread function of the eye, while Piper’s law (threshold is inversely proportional to the square root of the area stimulated) is consistent with probability summation. The steady-pedestal spatial summation data coincide in shape with data in the literature obtained under dark adaptation (reviewed in Baumgardt, 1972; Graham, 1965). Asymptotic sensitivity is approached when the length of a test square side is between 1.0° and 1.5°.

PC-pathway spatial summation: The pulsed-pedestal data exhibited a gradual linear decrease on the log–log axes, with continual improvement in sensitivity over the entire range of stimulus size evaluated. Spatial summation, to large angular degrees, is consistent with data on the precision of color matches, where improvement in precision is seen when the diameter of the colorimetric field is increased from 2° to 8° or larger (Brown, 1952; Yebra, Garcia, & Romero, 1994).

A hypothesis consistent with the data is that area-illuminance summation for the PC pathway involves probability summation along the borders where the test and surround fields juxtapose. In a study of chromatic contrast discrimination, Smith et al. (2000) suggested that border elements adapted to the surround determined threshold in the chromatic steady-pedestal paradigm. A similar interpretation can be applied to the achromatic pulsed-pedestal paradigm data. The spatial summation function may, thus, represent probability summation along border elements.

Detection and identification of achromatic stimuli

When equiluminant chromatic stimuli are used, observers can identify the color direction of the pulsed test at detection threshold. We have noted no difference in detection and identification for chromatic contrast discrimination (Smith et al., 2000). If an observer makes the discrimination, he or she also correctly identifies the polarity of the test relative to the pedestal chromaticity.
Conversely for achromatic contrast detection, as previously shown, the polarity of the contrast (“brighter” or “darker”) cannot be identified reliably at detection threshold (Tolhurst & Dealy, 1975); a slightly greater luminance (about 0.10 log unit) was needed for polarity identification.

A natural question arises on the nature of polarity identification for achromatic stimuli using the pulsed- and steady-pedestal paradigms. This question was addressed by running four interleaved staircases, interleaving a detection criterion and a polarity criterion for both the increment and decrement staircases (Kachinsky, Smith, & Pokorny, 2003). On each trial, the observer identified the test square and responded whether the test square was brighter or darker than the three other pedestal squares. For the pulsed-pedestal condition, the pulse polarity was correctly identified at the detection threshold. These data suggest that when the PC pathway is involved in achromatic detection, it also signals the stimulus polarity. For the steady-pedestal paradigm, at detection threshold, the probability of correct pulse polarity identification was at chance. Polarity identification required approximately 0.15 log unit more contrast than detection of the correct square. The data for the steady-pedestal paradigm concur with Tolhurst and Dealy (1975). In the steady-pedestal paradigm, both ON and OFF channels are at their adaptation point and it appears that a steady-pedestal stimulus may be detected via either channel.

**Genesis of PC-pathway contrast gain**

Is there a relationship between chromatic content in natural environments and the evolution of color vision mechanisms? Some have suggested that both the spectral locations of the L- and M-cone photopigments (Osorio & Vorobyev, 1996; Sumner & Mollon, 2000) and PC-pathway chromatic contrast gain (von der Twer & MacLeod, 2001) evolved to match the chromatic content of the natural environment, expressly to avoid response saturation that may occur with large shifts in chromaticity.

The PC pathway conveys both chromatic and achromatic information, with PC-pathway neurons being more responsive to chromatic (L–M) than to achromatic (L + M) stimuli. PC-pathway contrast-response functions span a range appropriately matched to the environmental distribution of natural colors (von der Twer & MacLeod, 2001). One hypothesis is that PC-pathway cell codes for color may have been selected to avoid saturation, thus minimizing error in the perceptual estimation of stimulus parameters for natural colors.

Observers with X-linked red–green color vision deficiencies have altered or reduced forms of color vision (Pokorny, Smith, Verriest, & Pinckers, 1979). Anomalous trichromats, with reduced separation of their L- and M-cone spectral sensitivities, have diminished chromatic input to PC-pathway cells. Dichromats, with absent L or M cones, should have no chromatic input to PC-pathway cells. Therefore, the PC-pathway contrast gain of color defectives might be released from any constraint imposed by the chromatic environment.

Developmental variations can produce neural plasticity (Pinaud, Tremere, & De Weerdt, 2005). An example of neural plasticity in color vision is demonstrated by the congruence of unique yellow settings across observers despite the substantial variation in L- to M-cone ratios found in the population (Brainard et al., 2000; Pokorny, Smith, & Wesner, 1991). From birth, people live in environments that are, for the most part, similar, and it is likely that this homogeneity of red–green color vision is created via an adaptation to the long-term average environmental illuminant (Mollon, 1982; Pokorny & Smith, 1977). It appears that the visual system can use information from experience to compensate for individual differences in cone ratios. Deficiencies in a sensory system can, by means of neural plasticity, result in enhancement of other aspects of the deficient sensory system. With this consideration, we can ask whether enhanced achromatic visual perception exists as a result of the reduction in color perception in males with X-linked red–green color vision deficiencies. Lutze, Pokorny, and Smith (2006) reported no quantitative differences between normal and color defective observers in psychophysically determined achromatic processing in the PC pathway (Figure 10). The average C_sat and K values for color-normal observers, anomalous trichromats, and dichromats were similar, and there were no statistically significant differences in inferred PC-pathway contrast gain. There was no evidence of enhancement of achromatic processing as compensation for reduced chromatic processing in the PC system in color defectives. This implies that parvocellular contrast gain is not plastic but fixed by some unspecified genetic process.

Studies of the PC-pathway system in nonhuman primates have also shown that contrast gain functions with achromatic stimuli are similar in dichromacy and trichromacy. Female marmosets, which are New World primates, can either be trichromats or dichromats, while all male marmosets are dichromats. PC-pathway contrast gain is similar in marmosets with either type of color vision (Blessing, Solomon, Hashemi-Nezhad, Morris, & Martin, 2004; Yeh, Lee, Kremers, Cowing et al., 1995). Further, the marmoset data reveal similar PC-pathway contrast gain to that reported for the trichromatic macaque Old World monkey.

The developmental genetics and environmental cues that contribute to the development of the PC-pathway derived achromatic processing aspect of the color vision system, whether in trichromats or dichromats, seem to be the same. Given the absence of variation in PC-pathway achromatic contrast gain within Old and New World primates and humans, PC-pathway contrast gain appears to have been established in a common ancestor of both Old and New World monkeys.
Figure 10. *Pulsed-pedestal* (circles) and *steady-pedestal* (squares) data for: (A) normal trichromats, (B) anomalous trichromats, and (C) dichromats. The average $C_{sat}$ and $K$ values for color normals, dichromats, and anomalous trichromats were similar; there were no statistically significant differences in inferred PC contrast gain. (Lutze et al., 2006)
Variants of pulsed- and steady-pedestal paradigms

Spatial contrast sensitivity

The MC and PC pathways are distinguished by differing spatial, temporal, and contrast gain properties. A number of psychophysical studies (Legge, 1978; Wilson, 1980) have used the temporal waveform of the stimulus to distinguish the roles of both MC and PC pathways in spatial frequency processing. These results suggested that the MC pathway is more sensitive at low spatial frequencies and PC pathway is more sensitive at high spatial frequencies. While these studies established contributions of both pathways to the psychophysical spatial contrast sensitivity function, the method of mechanism separation via manipulation of temporal parameters mitigates against precise analysis of the relative contributions.

The pulsed- and steady-pedestal paradigms were adapted to look at spatial frequency processing in the PC and MC pathways (Leonova, Pokorny, & Smith, 2003). Narrowband, spatially localized test patterns of various spatial frequencies were superimposed on a large uniform pedestal. The spatial profile of the pattern was the sixth derivative of a Gaussian (D6; Swanson & Wilson, 1985). This pattern has a 1-octave spatial frequency bandwidth and has a local appearance in space, similar to an even symmetric Gabor function (Figure 11, top). Stimuli were presented as a 26.7-ms pulse.

Figure 12 shows two spatial contrast sensitivity functions derived from the pulsed-pedestal (closed symbols) and steady-pedestal (open symbols) paradigms. The pulsed-pedestal function assumed a band-pass in shape with peak sensitivity near 2 cpd. The steady-pedestal paradigm function showed a predominantly low-pass shape, with sensitivity declining abruptly beyond 4 cpd. The functions are consistent with the existence of two mechanisms with differing low-frequency behavior, with the pulsed-pedestal paradigm function being mediated by the PC pathway and the steady-pedestal paradigm function being mediated.

Figure 11. Spatial contrast sensitivity stimulus display. (A) Appearance of spatially localized stimuli of varying peak spatial frequency. (B) Stimulus sequence for the steady-pedestal paradigm. During the test interval, a D6 pattern of positive contrast was presented briefly (45 ms). (C) Stimulus sequence for the pulsed-pedestal paradigm. During the test interval, a D6 pattern of positive contrast was presented in the center of a pedestal square that had a decremental luminance, with both stimuli presented simultaneously for 45 ms. For both paradigms, the D6 was presented with either a vertical or horizontal orientation, chosen randomly. An adapting field was presented continuously for both paradigms (Zele et al., 2007).
by the MC pathway, at least at low frequencies. This hypothesis can be examined more closely in a plot of threshold retinal illuminance as a function of pedestal retinal illuminance (Figure 13), comparing the pulsed-pedestal (closed symbols) and steady-pedestal paradigms (open symbols). The upper panel presents results at the four lower spatial frequencies (0.25, 0.5, 1.0, and 2.0 cpd) and the lower panel shows results for the three higher spatial frequencies (4.0, 8.0, and 16.0 cpd).

For the pulsed-pedestal paradigm, the thresholds increased as the pedestal retinal illuminance diverged from the surround illuminance, resulting in contrast-dependent V-shaped curves. For the four low spatial frequencies, thresholds showed a similar, shallow dependence on pedestal contrast (upper panel). At high spatial frequencies, the V shapes were shallower (lower panel). The thresholds decreased as spatial frequency of the test increased from 0.25 to 2.0 cpd and then increased for spatial frequencies above 2.0 cpd. For the steady-pedestal paradigm, thresholds increased monotonically with pedestal retinal illuminance. Thresholds were similar between 0.25 and 2.0 cpd (upper panel) and increased with spatial frequency above 2 cpd (lower panel). At low spatial frequencies, the thresholds for the pulsed-pedestal paradigm were higher than for the steady-pedestal paradigm, but above 4 cpd, there was little difference in the thresholds.

The dependence of the data on the paradigm at low spatial frequencies was parallel to that observed with the 4-square array. For the pulsed-pedestal paradigm, the V-shaped functions could be fitted with the same models as developed for the 4-square data. The four lower spatial frequencies showed similar slopes and were fitted simultaneously with a shared value of $C_{sat}$. The values of $C_{sat}$ were within the range for $C_{sat}$ noted for the 4-square data. At higher spatial frequencies, the slopes declined (i.e., higher values for $C_{sat}$). This is to be expected since the operating range at the higher spatial frequencies was between the high contrast required for threshold and $R_{max}$. With the increase in the parameter $C_{sat}$, the data approached linearity at high spatial frequencies. For the steady-pedestal paradigm, thresholds increased monotonically with pedestal retinal illuminance.

The V-shaped functions obtained with the pulsed-pedestal paradigm are consistent with mediation by the PC pathway. The situation for the steady-pedestal paradigm is that observed with the 4-square array. The V-shaped functions could be fitted with the same models as developed for the 4-square data.
paradigm is more complex. Since a monotonic function was obtained, there is no characteristic signature of either pathway. Further, since adaptation was to a large pedestal without any contrast information, either pathway could mediate thresholds. A second experiment that incorporated a temporal stimulus profile that contained no abrupt transients, a 1-s raised cosine, yielded near identical V-shaped functions for both pulsed- and steady-pedestal paradigms. This stimulus is poorly detected by MC-pathway cells and allows examination of the PC pathway. The contrast sensitivity functions for both the pulsed- and steady-pedestal paradigms were band-pass and it may be inferred that these were both PC pathway mediated. Thus, the low-pass steady-pedestal data obtained with brief stimulus presentations were consistent with MC mediation. The 4-square data showed the MC pathway to be much more sensitive than the PC pathway to brief, pulsed stimuli. The same result is true for the low spatial frequencies: The pulsed-pedestal data lie above the steady-pedestal data (upper panel of Figure 13). However, at 4 cpd, there is little difference in threshold between the two paradigms. From the data obtained with the stimulus that contained no abrupt temporal transients, we infer that the spatial contrast sensitivity at spatial frequencies above 4 cpd is determined predominantly by the PC pathway for both pulsed- and steady-pedestal paradigms.

For both paradigms, the spatial contrast sensitivity functions are consistent with other psychophysical studies (Kulikowski & Tolhurst, 1973; Legge, 1978; Wilson, 1980). The human psychophysical data represent an upper envelope of a population of receptive fields varying in size and sensitivity. They do not resemble single-cell data of macaque retinal ganglion cells; single-cell data show band-pass characteristics (Croner & Kaplan, 1995; Derrington & Lennie, 1984; Lee, Kremers, & Yeh, 1998). The center Gaussian radii estimated near the fovea are 2–4 min of arc, which is much smaller than the values fitted to the data of Figure 12. Thus, although the psychophysical data are consistent with activation of a given inferred retinal pathway, there is considerable reorganization of the retinal outputs before the determination of psychophysical sensitivity.

For the spatial summation study described above, the pulsed-pedestal paradigm yielded data that showed partial spatial summation for test squares up to 4°. The steady-pedestal paradigm yielded data consistent with spatial summation studies in the classical literature. The discrepancy between the extensive PC-pathway spatial summation and superior high spatial frequency sensitivity gives clues to the nature of higher order cortical processing. As outlined earlier, for simple spatial stimuli, it is the contrast signal generated at the edges of the stimulus that controls discrimination, i.e., the summation is along contrast edges. The prolonged temporal summation shown by the PC pathway is post-retinal (Lee et al., 1990; Yeh, Lee, & Kremers, 1995). It appears that one property of cortical processing in the PC pathway is the sacrifice of temporal resolution to achieve higher order mechanisms tuned to both spatial frequency and orientation and capable of high spatial frequency processing.

A modification of the pedestal-Δ-pedestal paradigm

When the pedestal-Δ-pedestal paradigm was first developed, the task seemed difficult, but it proved possible to obtain systematic data from well-practiced observers. However, it did not seem feasible to attempt the paradigm in a clinical environment where there is usually only a brief period of testing time available. Sun, Swanson, Arvidson, and Dul (2008) developed a clever variant of the pedestal-Δ-pedestal that provided an easier task. The stimulus was modified so that during each trial the luminance of three of the squares was increased by a fixed Δ-pedestal for a period of 227 ms. The test square, which was randomly chosen, contained an additional luminance increment for the first 27 ms, and then returned to the same luminance level as the other squares for the remaining 200 ms. Observers found this task much easier to perform. In the clinical protocol, Sun et al. measured thresholds for pedestal increments using the modified pedestal-Δ-pedestal paradigm. The data assumed a two-lobe function, which could be fit by vertical scaling of the Pokorny and Smith (1997) MC and PC contrast discrimination templates. It was possible to derive MC and PC sensitivities and contrast gain estimates from measurements in a single direction (pedestal increments), requiring fewer than 10 data points to make reliable parameter estimates. Control experiments showed this procedure to yield contrast gain parameters equivalent to those from the pulsed-pedestal and pedestal-Δ-pedestal paradigms.

Clinical applications

Studies of normal and clinically impaired vision

Since the original publication of the pedestal paradigm methodology in 1997, it has been adapted to a variety of contexts. The pedestal paradigms have been used to explore a number of aspects of normal vision (Table 1).

In the clinical domain (Table 2), many diseases yield concurrent losses of sensitivity for both the inferred PC- and MC-pathway function. Of particular interest are conditions in which function is altered for one but not the other pathway. Perhaps the most striking examples come from studies of the neuropsychological disorders of autism and schizophrenia.

Autism is a disorder of neural development, characterized by impaired social interaction and communication and by restricted and repetitive behavior. Autism typically appears during the first three years of life. Pulsed- and
<table>
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<th>Author(s)</th>
<th>Description</th>
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<tr>
<td>Aging</td>
<td>McKendrick, Sampson, Walland, and Badcock (2007)</td>
<td>Lower spatial contrast sensitivity functions (CSFs) for both steady and pulsed pedestals</td>
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<td></td>
<td>Elliott and Werner (2010)</td>
<td>Age-related changes for both the pulsed-pedestal and pedestal-Δ-pedestal conditions; greater for pulsed</td>
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<td>Spatial resolution</td>
<td>Leonova et al. (2003)</td>
<td>Pulsed-pedestal presentation of localized, spatially narrowband patterns produced band-pass CSFs; steady-pedestal data yielded low-pass CSFs</td>
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<td></td>
<td>McAnany and Alexander (2006)</td>
<td>Conventional letter optotypes yielded low-pass CSFs both for steady- and pulsed-pedestal conditions; spatially band-pass filtered letters yield band-pass pulsed-pedestal CSFs</td>
</tr>
<tr>
<td>L–M chromatic contrast discrimination</td>
<td>Smith et al. (2000)</td>
<td>Steady- and pulsed-pedestal measurements yielded identical V-shaped functions, interpreted as mediation exclusively by the PC pathway</td>
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<td></td>
<td>Zele et al. (2006)</td>
<td>L–M chromatic contrast discrimination is determined by either the spatial or temporal contrast difference between the test field and the surrounding area</td>
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<td>S-cone chromatic contrast discrimination</td>
<td>Cao et al. (2008)</td>
<td>S-cone mediated discrimination between a pedestal and adapting surround is equivalent for stimuli containing spatial, temporal, or spatial and temporal chromatic contrast between the test field and the surround</td>
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<tr>
<td>Temporal dynamics/early light adaptation</td>
<td>Pokorny, Sun, and Smith (2003)</td>
<td>Measured pedestal-Δ-pedestal contrast discrimination time course of sensitivity changes to small luminance increments and decrements</td>
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<td>Retinal locus</td>
<td>Alexander, Barnes, and Fishman (2005)</td>
<td>Relative to foveal data, 6.3° eccentricity CSFs shifted leftward on a log spatial frequency axis</td>
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<td></td>
<td>McAnany and Levine (2007)</td>
<td>Higher contrast sensitivity in the lower visual field for pulsed-pedestal condition; no visual field anisotropy for the steady pedestal</td>
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<td></td>
<td>McKendrick et al. (2007)</td>
<td>At mid-peripheral locations, lower CSFs for steady- and pulsed-pedestal conditions</td>
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<td>Detection and identification of stimulus polarity</td>
<td>Kachinsky et al. (2003)</td>
<td>For pedestal-Δ-pedestal stimuli near threshold, identification required less of a luminance change than polarity identification; no difference for pulsed-pedestal stimuli</td>
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<td>Geometric illusion</td>
<td>Puts, Pokorny, and Smith (2004)</td>
<td>Pulsed- and steady-pedestal data for the Zöllner illusion are consistent with the PC mediation</td>
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<td>Audio–visual interactions</td>
<td>Jaekl and Soto-Faraco (2010)</td>
<td>Steady-pedestal CSFs obtained in the presence of acoustic white noise bursts showed greater low spatial frequency sensitivity than CSFs without noise; no sensitivity difference in pulsed-pedestal data</td>
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Table 1. Studies of normal vision.
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### Other ophthalmic and systemic disease

| Condition                                      | Reduced                 | Reduced                  | Reduced                                                | Reduced                 | Reduced               | Reduced              | Reduced                                | Reduced                                | Reduced                              | Reduced                | Reduced                       | Reduced                    | Normal          | Never-medicated |
| Glaucoma                                       | Reduced                 | Reduced                  | Reduced                                                | Reduced                 | Reduced               | Reduced              | Reduced                                | Reduced                                | Reduced                              | Reduced                | Reduced                       | Reduced                    | Normal          | enhanced |
| Diabetes                                       | Reduced                 | Reduced                  | Reduced                                                | Reduced                 | Reduced               | Reduced              | Reduced                                | Reduced                                | Reduced                              | Reduced                | Reduced                       | Reduced                    | Normal          | normal |

### Conditions involving cortical function

| Condition                                      | Reduced                 | Reduced                  | Reduced                                                | Reduced                 | Reduced               | Reduced              | Reduced                                | Reduced                                | Reduced                              | Reduced                | Reduced                       | Reduced                    | Normal          | Never-medicated |
| Amblyopia                                      | Reduced                 | Reduced                  | Reduced                                                | Reduced                 | Reduced               | Reduced              | Reduced                                | Reduced                                | Reduced                              | Reduced                | Reduced                       | Reduced                    | Normal          | enhanced |
| Migraine                                       | Reduced                 | Reduced                  | Reduced                                                | Reduced                 | Reduced               | Reduced              | Reduced                                | Reduced                                | Reduced                              | Reduced                | Reduced                       | Reduced                    | Normal          | normal |

Table 2. Studies of clinically impaired vision.
steady-pedestal contrast discrimination measurements on children with “autism spectrum conditions” (Plaisted Grant & Davis, 2009) revealed a significant ($p = 0.001$) decrease in steady-pedestal threshold sensitivity when compared from data from the age-matched “neurotypical children,” while there was no significant difference in pulsed-pedestal sensitivity ($p = 0.281$).

Schizophrenia is a mental disorder characterized by a disintegration of the process of thinking and of emotional responsiveness. It most commonly manifests as auditory hallucinations, paranoid or bizarre delusions, or disorganized speech and thinking, and it is accompanied by significant social or occupational dysfunction. Schizophrenia is most commonly diagnosed between the late teen years and early 30s. Schizophrenic patients are typically unable to filter sensory stimuli and may have enhanced perceptions of sounds, colors, and other features of their environment. Pulsed- and steady-pedestal spatial contrast sensitivity measurements on never-medicated, first episode patients with schizophrenia (Kiss, Fabian, Benedek, & Keri, 2010) exhibited significantly enhanced contrast sensitivity in the steady-pedestal conditions ($p < 0.001$), whereas the patients did not differ from control participants in pulsed-pedestal sensitivity ($p > 0.10$).

Patients with autism and schizophrenia both have pulsed-pedestal sensitivity that did not differ from age-matched controls, suggesting that PC-pathway function is normal in patients with both conditions. Under the steady-pedestal condition, patients with autism exhibited lower sensitivity, whereas patients with schizophrenia showed greater than normal sensitivity. The implication is that MC-pathway function is altered in different ways by the two diseases, while the PC pathway retains normal function.

Optimizing parameters for clinical evaluation

It is usually the case that in a clinical setting, patients can be scheduled for only a limited time period for psychophysical testing. Therefore, test design has to be time efficient, with tasks performable by naive observers who may have undergone other tests earlier in the day and may be fatigued. Realistically, test time should be no longer than 30–60 min. The task has to be one that is easy for the observer to comprehend and perform.

How much data is needed?

While it would be nice to obtain comprehensive parametric data for a function being evaluated, realistically, with efficient forced-choice procedures, it is only possible to run 10–15 four-square or spatial contrast sensitivity conditions in a 45-min period. The majority of clinical studies cited below have been able to attain meaningful data within these constraints. Estimates of pulsed-pedestal sensitivity and contrast gain can be made with as few as 2 or 3 measurements on each arm of the V-shaped function. Estimating steady-pedestal sensitivity can be made with a single measurement at the adapting retinal illuminance, but to establish confidence in the sensitivity estimate, it is prudent to measure thresholds for incremental and decremental retinal illuminances as well.

Why seek a large separation between pulsed- and steady-pedestal functions?

Steady-pedestal thresholds are determined by the most sensitive mechanism. Under stimulus conditions that produce little or no separation between steady- and pulsed-pedestal thresholds, it may be difficult to infer the mechanism mediating steady-pedestal thresholds. Thus, the strategy is to choose stimulus parameters that produce a large separation. This is important if a clinical condition causes selective loss in MC- or PC-pathway mediated function. From the temporal and spatial summation data (Figures 6 and 9), a good choice is a briefly presented stimulus, <50 ms, where each of the 4 squares subtends about 1° visual angle.

Which paradigm to use?

The contrast discrimination and spatial contrast sensitivity pedestal paradigms reveal different aspects of visual function. The contrast discrimination paradigms provide knowledge of contrast gain and asymptotic sensitivity. An example of contrast discrimination measurements providing valuable information can be found in a study of age-related functional differences in PC- and MC-pathway contrast gain (Elliott & Werner, 2010). The study included a comparison of pulsed-pedestal and pedestal-$\Delta$-pedestal data from younger (mean age 25.5 years) and older (mean age 73.4 years) age groups. Results indicate that both MC and PC pathways undergo age-related changes, but functional losses appeared greater for the PC pathway for the conditions tested. Since the methodology was designed to minimize the effects of pre-receptoral filtering and ocular aberrations, the observed differences were likely of neural origin.

The contrast discrimination and spatial contrast sensitivity pedestal paradigms may, at times, lead to differing interpretations of visual loss accompanying disease. This can be seen in studies of patients with retinitis pigmentosa (RP). In a study of contrast discrimination, some patients with RP showed no threshold elevation for the pulsed-pedestal paradigm despite steady-pedestal paradigm discrimination thresholds that were elevated by as much as 0.5 log unit above the upper limit of normal observers (Alexander, Pokorny, Smith, Fishman, & Barnes, 2001). A second study evaluated spatial contrast sensitivity (Alexander, Barnes, Fishman, Pokorny, & Smith, 2004a). The patients showed losses of spatial contrast sensitivity for both the steady- and pulsed-pedestal paradigms, indicating that both the MC- and PC-pathway contrast-processing streams can be affected in RP. Further, the
patients’ deficits in spatial contrast sensitivity were equivalent for the two paradigms.

It is likely that the disparity between these findings is related to key differences in the physiological processes that determine threshold under the two stimulus configurations. The contrast discrimination paradigm required observers to identify the location of a pedestal square that differed in contrast from three other pedestal squares, all of which were relatively large (1° in width). As reviewed earlier, pulsed-pedestal contrast discrimination is based on the luminance contrast at the edges of the targets, and edge information is a major determinant of threshold sensitivity.

A hypothesis considered by Alexander et al. (2004a) was that the retinal degeneration associated with RP may result in a substantial loss of receptive fields within the PC pathway. This loss may not have been revealed in the contrast discrimination measurements because of the availability of abundant edge information in the pedestal squares. By comparison, spatial contrast sensitivity measurements showed an equivalent reduction in sensitivity for both the steady- and pulsed-pedestal paradigms, indicating that both the MC- and PC-pathway contrast-processing streams can be affected in RP. The spatial patterns used in the spatial contrast sensitivity measurements were spatially localized, circular in shape, and limited in spatial frequency bandwidth. The stimuli contained little edge information that could contribute to detection. Thus, in the studies of patients with RP, the spatial contrast sensitivity paradigm, employing spatial stimuli of limited extent, appears to have provided a more sensitive measure of PC pathway dysfunction than does the contrast discrimination paradigm with large pedestal squares.

**Effects of disease locus on contrast gain and contrast sensitivity: A conceptual framework**

Visual processing may be altered by disturbance of function at a sequence of sites within the visual pathway. Figure 14 presents a schematized framework for viewing potential sources of alteration of contrast gain and sensitivity.

**Figure 14.** A framework for viewing potential sources of alteration of contrast gain and sensitivity. The contrast gain V-shaped function and sensitivity are established in the retina and may be modified by alterations prior to the site, within the contrast gain generating mechanism, or at post-generation sites. A number of diseases associated with damage to receptors, retinal mechanisms, optic nerve, and the brain that have been evaluated with pedestal protocols are included in the figure.
sensitivity. The contrast gain V-shaped function and sensitivity are established in the retina and may be modified by alterations prior to the site, within the contrast gain generating mechanism, or at post-generation sites. A number of diseases associated with damage to receptors, retinal mechanisms, optic nerve, and brain are included in the figure. It may be noted that a disease that causes dysfunction at a specific locus may alter function at other sites in the visual pathway as well. For example, a loss of gain at the photoreceptor level may change post-receptoral adaptation parameters, which, if moderate, could result in a masking of the photoreceptor deficit. If the photoreceptor gain change is more severe, it could produce an alteration in temporal contrast sensitivity. In this case, the functional loss is not directly related to the site of insult.

Some photoreceptor diseases would be expected to have a greater effect on sensitivity than on contrast gain. Diseases that cause mechanical disruption of the receptor layer, thus resulting in the majority of light rays striking the photoreceptors off axis, lead to a reduction in quantal absorption (e.g., central serous choroidopathy, acute multifocal placoid pigment epitheliopathy; Pokorny, Smith, & Ernest, 1980). On the pedestal tasks, this would lead principally to a change in sensitivity. A reduction in photopic light level reduces cone contrast gain only modestly for both the psychophysically estimated PC (Sun, 1998) and MC (Cao & Pokorny, 2010) systems. Even a tenfold decrease in quantum catch would not substantially change contrast gain parameters. Degenerative diseases are more complex. While sensitivity changes accompanying retinitis pigmentosa are well documented (Seiple, Hologpigan, Greenstein, & Hood, 1993), there is evidence that post-receptoral sites are affected as well. Retinitis pigmentosa results in both a change in the sensitivity of the cone transduction process and a delay in the responses of the inner retina (Hood & Birch, 1996). It is uncertain whether contrast gain assessed by either the pulsed- or pedestal-Δ-pedestal paradigm would be abnormal.

The brain responds rapidly and reliably to spatial and temporal details of the visual input. This occurs in the presence of noise from both the sensory input and neural pathways. Information in a spike train is limited by variability in the spike timing. This variability is caused by noise from several sources, which may be broadly categorized as photoreceptor noise, noise originating in the inner retina, including synapses and membrane channels (van Rossum, O’Brien, & Smith, 2003), and post-ganglion cell noise (Gutkin, Ermentrout, & Rudolph, 2003), following the establishment of the retinal contrast gain function. Spontaneous cone photopigment isomerization appears not to be a major source (Fu, Kefalov, Luo, Xue, & Yau, 2008); photoreceptor noise likely originates in the downstream phototransduction steps. Retinal ganglion cells integrate noisy synaptic inputs and transform them into spike trains that include noise. Noise arising in the optic nerve or brain can change the parameters of contrast gain in a specific way. One way of characterizing the precision of information carried in a spike train is by the signal-to-noise ratio. Recordings from cat X and Y (Passaglia & Troy, 2004) and primate PC and MC ganglion cells (Croner, Purpura, & Kaplan, 1993) show noise to be relatively independent of contrast. Since spike rate increases with contrast, the signal-to-noise ratio increases with contrast. Assume that 4-square contrast discrimination can be degraded by the presence of sufficient noise. Then, noise arising at a locus subsequent to the generation of retinal contrast gain will alter the psychophysically measured contrast gain function in a specific way. The signal-to-noise ratios for a discrimination near the adapting retinal illuminance will be lower than the signal-to-noise ratio for a discrimination that involves a large step from the adapting retinal illuminance. Thus, the arms of the V will assume shallower slopes. There are two significant implications of this analysis. First, the congruence of contrast gain parameters from primate retina and from young human observers suggests that post-ganglion cell noise is not of sufficient magnitude to alter sensitivity. Second, post-ganglion cell noise may play a role in contrast discrimination of older observers. For both the pulsed-pedestal and pedestal-Δ-pedestal paradigms, Elliott and Werner (2010) reported that older observers required more contrast to discriminate contrast changes at low pedestal contrasts compared to higher pedestal contrasts, indicative of a specific type of shallowing of the contrast gain slope.

Response compression or a disruption of the fidelity of information at higher spike frequencies has the potential to produce a different alteration in the contrast gain function. With a large contrast step from the adapting retinal illuminance, a higher than normal contrast would be required to make a discrimination. Thus, discrimination near the adapting retinal illuminance could be normal or near normal, whereas discrimination for a large contrast stimulus from the adapting retinal illuminance could be impaired. This is the pattern seen in many patients with optic neuritis (Cao et al., submitted for publication).

Here, I have developed a framework to aid in understanding the underlying bases of different response patterns. For either paradigm, sensitivity can vary independently of contrast gain due to alteration of early and late events in the visual process; both a decrease in photoreceptor quantum efficiency and a change in the cortical decision process can alter sensitivity without a substantive change in contrast gain. I outlined how two different processes arising in the optic nerve or brain can change the parameters of contrast gain. In principle, both noise and response compression subsequent to the generation of retinal contrast gain can alter measured contrast gain, but the sensitivity profiles would be different. Noise lowers sensitivity near the adapting retinal illuminance while leaving discrimination for large contrast steps...
unimpaired, whereas response compression may leave sensitivity near the adapting retinal illuminance unimpaired while decreasing threshold sensitivity for large contrast steps.

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