ROD AND CONE CONTRIBUTIONS TO MESOPIC VISION

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ABSTRACT

Mesopic light levels span approximately 3-4 log units in the natural viewing environment, including many indoor lighting settings, and most twilight or nighttime outdoor and traffic lighting environments. Traditional studies of the contribution of the different photoreceptor types to mesopic vision have been hampered by an inability to modulate the rod or cone systems independently. Our approach differs from the traditional studies in employing a four-primary method that allows independent control of the stimulation of the four receptor types in a stimulus field. We developed a general method for adjusting the radiances of four lights to silence up to three photoreceptor classes and change the excitation of the nonsilenced classes in a specified manner. Here, we include an overview of rod anatomy and physiology and a description of the logic and implementation of the four-primary methodology. Data and analysis are given for two functional areas that may impact lighting solutions; dark-adapted rods suppress cone vision, and how rod and cone reaction times vary at scotopic, mesopic and photopic adaptation levels.

Keywords: rods, cones, mesopic vision, four-primary method, rod pathways

1. INTRODUCTION

There is a literature on the effects on visual performance of illuminants differing in spectral composition under photopic, mesopic and scotopic conditions (He et al., 1997; Rea et al., 1997; Adrian, 1998; Lewis, 1999; Walkey et al., 2007). For lights equated for photopic function, performance at mesopic and scotopic levels degrades most for illuminants deficient in short wavelength light. Here, we present two sets of experiments that show the scientific basis for the reported empirical results. The experiments use a four-primary photostimulator we devised, which allows independent control of the stimulation of the four photoreceptor types in the human retina. We developed a general method for adjusting the radiances of the four lights to silence up to three photoreceptor classes and change the excitation of the nonsilenced class in a specified manner. We provide examples from two studies related to mesopic temporal processing. The first investigates the suppression of cone flicker detection by dark adapted rods. The second provides systematic reaction time measurements for stimuli that isolated rod and cone excitation at light levels ranging from scotopic to photopic.

In this article, we review anatomical and physiological studies related to mesopic vision, the theoretical and technical aspects of the four-primary methodology, and some unique findings concerning mesopic temporal processing.

2. RODS AND CONES SHARE NEURAL PATHWAYS FROM EYE TO BRAIN

Modern anatomical and physiological studies have identified three major neural retinogeniculate pathways in the primate visual system that convey retinal information into visual cortex (reviewed by Dacey, 2000). The pathways are named after the layers of lateral geniculate nucleus (LGN) that receive inputs from distinct types of ganglion cells and project to different areas of primary visual cortex. The Magnocellular layer of LGN receives inputs from parasol ganglion cells. This pathway (the so-called Magnocellular, MC-pathway) processes the summed output of the long (L-) and middle (M-) wavelength sensitive cones to signal luminance information. Both cone types contribute to the center and surround of the receptive field of MC-cells (Lee, 1996). The Parvocellular layer of the LGN receives inputs from midget ganglion cells. This pathway (so-called Parvocellular, PC-pathway) mediates spectral opponency of L- and M- wavelength sensitive cones to signal chromatic and luminance information. Both cone types have the classical center-surround receptive field configuration. Four subgroups of PC-cells have been identified: +L/M (“Red-ON”), -L/+M (“Red-OFF”), +M/-L (“Green-ON”) and -M/+L (“Green-OFF”) cells. Each cell type shows the characteristic response of center and surround receptive fields for
cone contrast. The Koniocellular (KC-) layer of LGN receives inputs from small bistratified as well as other ganglion cells (Dacey & Lee, 1994). This pathway (so-called the Koniocellular, KC- pathway) differences short wavelength (S-) cone signals from the sum of the L- and M- cones. The link between the three retinogeniculate pathways to psychophysics is well established. Physiological recordings (Derrington et al., 1984; Lee et al., 1990) indicate that MC-, PC- and KC- cells show preferred response to luminance (L+M), chromatic [L/(L+M)], and S/(L+M) signals, respectively. Therefore, psychophysical experiments can be designed to infer the functions of the MC-, PC-, and KC-pathways by varying (L+M), L/(L+M), and S/(L+M), respectively (Pokorny & Smith, 2004).

Anatomical and single-unit electrophysiological studies have shown that rods and cones share neural pathways and have joint inputs to retinal ganglion cells (reviewed by Daw et al., 1990; Sharpe & Stockman, 1999). Rod signals are conveyed to ganglion cells by two primary pathways whose contributions are dependent on the illumination level. One pathway is via ON rod bipolars, All amacrine cells, and ON and OFF cone bipolars. This is a slow but high gain pathway and is hypothesized to mediate rod vision at low light levels. The second pathway transmits rod information via rod–cone gap junctions and ON and OFF cone bipolars. This is a fast pathway and is hypothesized to mediate rod vision at high scotopic and mesopic light levels (Figure 1). A third insensitive rod pathway between rods and OFF cone bipolars has been identified, but so far has been evident only in rodents.

Several physiological studies have assessed rod input to the three major retinogeniculate pathways. A consistent finding is that there is strong rod input to the MC- pathway, either at the ganglion cell

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**Figure 1.** Rod pathways in the primate retina. Slow pathway: Rods->Rod Bipolars->All Amacrine Cells->Cone Bipolars (red ellipse); Fast pathway: Rods->Cones->Cone Bipolars (blue ellipse).

Circuitry of Primate Retina

Receptor Terminals

Outer Plexiform Layer

Inner Nuclear Layer

Outer sub-layer

Inner Plexiform Layer

Inner sub-layer

Ganglion Cell Layer

On-off bipolar cells

Off-diffuse bipolar cells

On-off bipolar cells

On-midget bipolar cells

Off-midget bipolar cells

Parasol Cells

Midget Cells

Small Bistratified Cell

Small bodied Inner Cell

Rod Bipolar

Midget Ganglion Cell

On-Off ganglion cell

On ganglion cell

Off ganglion cell

Courtesy of Barry Lee
level (Gouras & Link, 1966; Virsu & Lee, 1983; Virsu et al., 1987; Lee et al., 1997) or the LGN level (Purpura et al., 1988). The demonstration of rod input to the PC- and KC-pathways is less clear. Some studies have shown weak rod input to the PC-pathway (Wiesel & Hubel, 1966; Virsu et al., 1987; Lee et al., 1997) and at least one study did not find any measurable rod input (Purpura et al., 1988). Lee et al. (1997) found no rod input to parafoveal +S/(L+M) ganglion cells, but two recent studies have demonstrated strong rod input in the retinal periphery (Crook et al., 2009; Field et al., 2009).

3. LIMITATIONS OF CONVENTIONAL METHODOLOGIES FOR STUDYING MESOPIC VISION

Traditional studies of the contribution of the different photoreceptor types to mesopic vision have been limited by an inability to modulate one or the other of the receptor systems independently. There are three traditional strategies in observers with normal vision and each has shortcomings. The first takes advantage of the fact that rods and cones recover sensitivity in the dark at different rates following the termination of a desensitizing light. The increase in visual sensitivity in the dark has two phases. During the first phase, cones mediate thresholds, and visual sensitivity increases rapidly before stabilizing within 10 minutes. The time period in which cone-mediated sensitivity remains stable is called the cone plateau. During the second phase, rods mediate thresholds and sensitivity increases gradually, stabilization occurs following 20-30 minutes. Measurements obtained under dark-adapted and cone-plateau conditions have been compared to characterize potential rod contributions (e.g. Stabell & Stabell, 1999). This approach has the limitation that the two measurements are made under differing adaptation conditions, and visual function depends on adaptation. A second traditional strategy is to compare measurements obtained from foveal and parafoveal presentations (e.g. Thomas & Buck, 2006). The rationale is that the density of rods is high in the peripheral retina but there are few or no rods in the fovea. Evidence has shown, however, that the temporal properties of rod vision and the chromatic properties of cone vision vary with retinal location, which may make comparisons between data collected in the fovea and parafovea ambiguous. A third strategy is to use one chromaticity to favor rod isolation and another chromaticity to favor cone isolation (e.g. Conner, 1982; Frumkes et al., 1986). This strategy has a drawback; measurements are limited to light levels where rods are more sensitive than cones. This strategy cannot completely isolate rod activity because, in the dark adapted eye, rods and cones have roughly the same sensitivity at long wavelengths (Crawford & Palmer, 1985) and S- and M-cones do not completely adapt to a long wavelength light. Further, there is a chromatic component to the cone stimulus that may alter measured function.

4. FOUR-PRIMARY COLORIMETRY: METHOD FOR INDEPENDENTLY STIMULATING RODS AND CONES AT A COMMON ADAPTATION LEVEL

4.1. Theoretical basis

There are four types of photoreceptors in human retina, including short-wavelength sensitive cones (S-cones), middle-wavelength sensitive cones (M-cones), long-wavelength sensitive cones (L-cones) and rods. The theoretical basis for achieving independent control of the activities of four types of photoreceptors (S-cones, M-cones, L-cones and rods) in the human retina is silent substitution (Estévez & Spekreijse, 1982) and the details are provided by Shapiro et al (1996). In short, the rod spectral sensitivity, \( r(\lambda) \), is characterized by the CIE scotopic luminosity function, \( V'(\lambda) \), and the S, M and L cone spectral sensitivities, \( s(\lambda) \), \( m(\lambda) \), and \( l(\lambda) \), by the Smith-Pokorny cone fundamentals (Smith & Pokorny, 1975) applied to the CIE 1964 10° color matching functions (Shapiro et al., 1996). The relative spectral sensitivity functions of the S-, M-, L-cones and the rods are shown in Figure 2.

![Figure 2. The spectral sensitivity functions of the S-, M-, L- cones and rods.](image)
For any light source with the spectral distribution of $\tilde{Q}(\lambda)$, the S, M, L cone excitations and rod excitations (R) are computed as:

$$S = C_p, \tilde{K}_m \sum_{\lambda} \tilde{Q}(\lambda) S(\lambda)$$  \hspace{1cm} (1)

$$M = C_p, \tilde{K}_m \sum_{\lambda} \tilde{Q}(\lambda) M(\lambda)$$  \hspace{1cm} (2)

$$L = C_p, \tilde{K}_m \sum_{\lambda} \tilde{Q}(\lambda) L(\lambda)$$  \hspace{1cm} (3)

$$R = C_p, \tilde{K}_m \sum_{\lambda} \tilde{Q}(\lambda) R(\lambda)$$  \hspace{1cm} (4)

where $C_p, K_m$ is a factor equal to the pupil size times $K_m$, a constant that relates lumens to watts. For a four-primary photostimulator, suppose that the spectral distributions of the four LEDs at their maximal outputs are $\tilde{P}_1, \lambda$, $\tilde{P}_2, \lambda$, $\tilde{P}_3, \lambda$, $\tilde{P}_4, \lambda$. With $\alpha \equiv [p_1 \ p_2 \ p_3 \ p_4]$ representing the proportion of its maximum for each LED, the photoreceptor excitations $\beta \equiv [S \ M \ L \ R]$ can be computed using linear algebra $\beta = \alpha A$, where $A$ is a matrix with each row representing photoreceptor excitations at the maximum output of each LED (see Equation 5).

$$A = C_p A$$

$$\begin{bmatrix}
\sum P_{1,\lambda(1)} & \sum P_{2,\lambda(1)} & \sum P_{3,\lambda(1)} & \sum P_{4,\lambda(1)} \\
\sum P_{1,\lambda(2)} & \sum P_{2,\lambda(2)} & \sum P_{3,\lambda(2)} & \sum P_{4,\lambda(2)} \\
\sum P_{1,\lambda(3)} & \sum P_{2,\lambda(3)} & \sum P_{3,\lambda(3)} & \sum P_{4,\lambda(3)} \\
\sum P_{1,\lambda(4)} & \sum P_{2,\lambda(4)} & \sum P_{3,\lambda(4)} & \sum P_{4,\lambda(4)}
\end{bmatrix}$$  \hspace{1cm} (5)

To display a light for a specific photoreceptor excitation, the unique scaling coefficient for each LED can be found; i.e. $\alpha = [A]^{-1}$. With this principle, to modulate rod excitations in a square-wave, for instance, with a contrast of $C$ and steady cone excitation, background photoreceptor excitations are $\beta_0 = [S \ M \ L \ R_0]$ and the peak photoreceptor excitation is $\beta_1 = [S \ M \ L \ R_1]$, where $(R_1 - R_0) / R_0 = C$. First, calculate $\alpha_0 = \beta_0 A^{-1}$, and $\alpha_1 = \beta_1 A^{-1}$, then present $\alpha_0$ and $\alpha_1$ in a temporal order defined by a square-wave form. In doing so, rod excitations can be modulated while keeping the S-, M-, and L- cone excitations constant. Similarly, the stimulation of one cone type (S, M or L cones) can be modulated while keeping the excitations of the remaining photoreceptor types constant. One can also modulate the excitations of two or three photoreceptor types, such as modulating L cone and rod excitations while keeping M and S cone excitations constant. For cone stimuli, stimulation of one type of cone, or the combination of cone types [such as luminance at a constant chromaticity, (L+M)], can be achieved. Figure 3 describes how changes in rod excitation can be accomplished while maintaining constant cone excitations.

Figure 3. Achieving rod isolation with four primaries. The chromaticities of the four primaries (460, 516, 558 and 660 nm) are shown in the CIE $10^\circ$ chromaticity diagram. The gray dot represents the chromaticity for a light metameric to an equal-energy-spectrum light (EES). In color matching, the EES chromaticity can be matched by a combination of three primaries (460, 516 and 660 nm). The same chromaticity can be matched by another set of primaries (460, 558 and 660 nm). When the two sets of primaries match the same chromaticity, they produce the same cone excitations. Note the two sets of primaries differ in one primary, with the rods being more sensitive to the 516 nm light than to the 558 nm light. Varying the proportion of the two matches over time produces rod modulation while maintaining a constant cone chromaticity.

4.2. Design of the four-primary photostimulator

For the two-channel four-primary photostimulator (Pokorny et al., 2004), one channel is used to produce a central field and the second channel illuminates a surround. The center and surround are created with the combination of four primary channels, with light from four light emitting diodes (LEDs) combined by the use of a fiber optic assembly. Four fiber optic bundles are merged into a single bundle with the output...
fed into an integrating bar spatial homogenizer terminated by a diffuser. Spectral composition is controlled by the LED spectra and interference filters sandwiched between each LED and the fiber optic bundle. The primary wavelengths for both center and surround are 460 nm, 516 nm, 558 nm and 660 nm, all with half-bandwidths of about 10 nm. Two camera lenses collimate light from the diffusers, one for the center and one for the surround. A photometric cube with a mirrored ellipse on the hypotenuse forms the center-surround field configuration. A field lens places images of the diffusers in the plane of an artificial pupil for Maxwellian view. Figure 4 shows the optical setup (left panel) and a picture (right panel) of the four-primary photostimulator.

The radiances of the primaries are controlled by an eight-channel analog output Dolby soundcard (M-Audio-Revolution 7.1 PCI). The desired output waveform is programmed as an amplitude modulation of a 20 kHz carrier. The soundcard has a 24-bit digital-to-analog converter (DAC) operating at a sampling rate of 192 kHz. The output of the DAC is demodulated (Puts et al., 2005) and sent to voltage-to-frequency converters that provide 1 μs pulses at frequencies up to 250 kHz to control the LEDs (Swanson et al., 1987). In addition to precise control of the photoreceptor excitations, the four-primary photostimulator has precise temporal stimulus control.

Figure 4. The optical setup and a picture of the four primary photostimulator.

4.3. Advantages of the four-primary photostimulator

Compared with traditional methodologies, the four-primary photostimulator offers several advantages. First is its capability of modulating one type of photoreceptor while keeping the excitation of the other three constant. Therefore, the four-primary photostimulator allows changes in rod or cone stimulation while maintaining the same adaptational cone chromaticity and luminance level, a critical requirement for the study of mesopic vision. Second, it can simultaneously control rod and postreceptoral signals, allowing assessment of the contributions of rods to postreceptoral luminance or chromatic processing. Third, it allows direct measurements of rod and cone functions instead of inferred from the comparison of measurements during the cone-plateau and 30-min in the dark, or inferred from the comparison of measurements between fovea and parafovea. Finally, calibration procedures have been defined that allow compensation for observer prereceptoral filtering and the small receptoral spectral sensitivity differences encountered among color-normal observers. These observer calibrations are designed to ensure that good receptor isolation can be achieved for each observer despite observer differences.

5. FOUR-PRIMARY COLORIMETRY: METHOD FOR INDEPENDENTLY STIMULATING RODS AND CONES AT A COMMON ADAPTATION LEVEL

Over the past 15 years, we have investigated mesopic vision using the four-primary photostimulator, covering color perception (Sun et al., 2001a; Cao et al., 2005; Cao et al., 2008a), chromatic discrimination (Cao et al., 2008b), and temporal processing (Sun et al., 2001b; Cao
et al., 2006, 2007; Zele et al., 2007, 2008; Cao & Pokorny, 2010). Here we provide two examples related to mesopic temporal processing, the first is rod suppression of cone flicker detection and the second is mesopic rod and cone reaction time. These examples use the impulse response function of the rod and cone system as a tool to help in analyzing mesopic temporal processing.

5.1. Rod-cone interactions in temporal vision

Figure 5 shows a comparison of dark adaptation function for single pulses of light (Bartlett, 1965) and light modulated at 20 Hz (Goldberg et al., 1983). As rods dark-adapt, cone thresholds for pulsed lights asymptote (red line, Fig. 5), but modulated light thresholds at 20 Hz increase (green line, Fig. 5). We have performed two sets of experiments to investigate this phenomenon. The first looks at which receptoral and postreceptoral mechanisms exhibit the suppression of cone sensitivity. The second set of experiments asks whether the suppression is idiosyncratic to temporally modulated light or whether it is a general loss of temporal resolution.

We measured critical fusion frequencies (CFF) for receptive L-, M-, S- cone and postreceptoral luminance ([L+M], and [L+M+Rod]) and chromatic, [L/(L+M)] stimuli in the presence of different levels of surrounding rod activity (Cao et al., 2006). The stimulus field was 2° in diameter, positioned within a 13° surround, and centered at 7.5° in the temporal retina. The receptive or postreceptoral excitation was modulated sinusoidally around a mean retinal illuminance of 80 Td. The surround was set to a steady retinal illuminance of 0, 0.05, 0.5, 5, 20 or 80 Td. Measurements were made either with adaptation to the stimulus field after dark adaptation (DA), or during a brief period following light adaptation (LA). Figure 6 shows the measured CFF for various receptive and postreceptoral stimuli under dark adaptation condition (DA, Fig. 6A) or light adaptation condition (LA, Fig. 6B) from one observer, with the lateral suppressive rod-cone interaction occurring at low surround illuminances ≤0.5 Td. The results show that dark-adapted rods maximally suppressed the CFF by ~6 Hz for L-cone, M-cone, and luminance modulations (Fig. 6C). Dark-adapted rods however, showed no statistically significant suppression of S-cone CFF and only a small suppression of [L-M] CFF (not shown). Thus the largest suppression was found for stimuli that included a luminance component, and we infer that the lateral suppressive rod-cone interaction in cone-mediated flicker detection is strong in the MC-pathway.

The second series of studies was designed to test whether lateral suppressive rod–cone interactions are stimulus specific, that is, only occur with the use of temporally periodic stimuli, or if the suppression is a more general visual phenomenon that can also alter cone sensitivity to double pulsed stimuli. To test this proposal, cone pathway contrast sensitivity was measured using periodic and double pulsed stimuli under viewing conditions that altered the level of rod activity in the area surrounding the stimulus (Zele et al., 2008). The stimuli (2° center/13° surround, 80 Td) were similar to CFF measurements except only the cone luminance modulation ([L+M]) was used. Cone temporal contrast sensitivity functions were measured for frequencies between 3-26 Hz, using a double yes-no random staircase procedure. Two-pulse discrimination (Ikeda, 1986; Burr & Morrone, 1993) was measured with a pair of 4 ms rectangular pulses displayed successively at
stimulus onset asynchronies (SOA, the time delay between two pulses) varying between 14 to 270 ms. Measurement conditions included two incremental pulses or an incremental and a decremental pulse. Cone pathway impulse response functions were derived from the periodic and pulsed data using two independent techniques. For the temporal contrast sensitivity data, the IRFs were derived using a Kramers-Kröning relation to reconstruct the temporal phase spectrum with a minimum phase assumption (Stork & Falk, 1987). Scaling and extrapolations at the low and high frequencies were conducted according to procedures described by Swanson et al., (1987). For the two-pulse summation data, we estimated the IRF using the exponentially damped, frequency modulated sinusoid model without assuming a minimum phase (Burr & Morrone, 1993). The results showed that after dark adaptation, temporal contrast sensitivity was attenuated at frequencies greater than 6–8 Hz, two-pulse contrast sensitivity decreased and the timing was altered. The mathematically derived IRFs demonstrate that after dark adaptation, the cone pathway IRF amplitude decreased and the time-to-peak was delayed. Thus dark-adapted rods altered the amplitude and timing of cone pathway temporal impulse response functions (Figure 7 for Observer DC).

5.2. Rod and cone reaction times
We measured simple reaction times for rod or cone incremental and decremental stimuli at retinal illuminance levels varying from scotopic to photopic (Cao et al., 2007). The mean reaction times decreased with higher contrast and retinal illuminance level for isolated rod (Figure 8) and isolated cone (Figure 9) stimuli. At mesopic light levels (2 and 20 Td), rod and cone reaction times were comparable at 2 Td but cone reaction times were shorter than rod reaction times (Figure 10).

**Figure 7.** The derived IRFs from TCSF (top) and two-pulse summation function (bottom) under light adapted (dark lines) or dark adapted (green lines) condition (Zele, Cao & Pokorny, 2008).

**Figure 8.** Reaction times to isolated rod stimuli (open circles: rod increment; solid circles: rod decrement). Data from Cao, Zele & Pokorny 2007.
We fitted the data with a model incorporating rod and cone impulse response functions and an accumulation process that triggers a motor response (Cao et al., 2007). The sensory processing model used prototypical rod and cone temporal impulse response functions for the different light levels (Figure 11). These functions were derived from published psychophysical temporal contrast sensitivity functions and two-pulse summation data and thus included post-retinal temporal filtering. The rod or cone stimulus at each contrast and light level was convolved with the corresponding temporal impulse response function.

The model assumed the motor response was initiated when the integrated response reached a criterion value. This model fitted the data well (solid lines in Figs. 8-10) and found that an irreducible minimum reaction time for the rod stimuli were ~20ms longer than that for the cone stimuli, consistent with physiological measurements. This model provided a computational framework to describe the variation in reaction time with light level, stimulus contrast, stimulus polarity, and receptor class modulated.

6. DISCUSSION

A point we emphasize is that in mesopic vision, rod and cone signals are largely interchangeable in terms of postreceptoral visual processing. Evidence from physiology and psychophysics indicates that in photopic vision the MC-pathway is predominant in the mediation of thresholds for flicker (Schiller et al., 1990), motion (Merigan et al., 1991; Chapman et al., 2004), object localization (Laycock et al., 2007) and detection of changes in contrast (Pokorny & Smith, 1997). We may infer that these functions would be largely MC-pathway mediated at mesopic light levels.

From anatomy and physiology we know that rods and cones share common pathways. The principal rod pathway at mesopic light levels is via gap junctions between rod and cone photoreceptors. Gap junctions allow for electrical communication between cells. Physiological recordings of rod and cone photoreceptor impulse response functions are similar, showing a difference in the time to peak response on the order of 12–20 ms (Schneeweis & Schnapf, 1999; Verweij et al., 1999). Primate rod and cone photovoltage responses measured directly in cones show comparable high frequency sensitivity (Hornstein et al., 2005). There is some high-
pass filtering of rod signals measured in cones. For responses to stimulus change, cone signals and rod signals conveyed by gap junctions can be similar.

Decision processing for detection or action is cortically mediated, and a reasonable assumption is that decision processing uses the same rules no matter what type of photoreceptors initiate early visual processing (Cao & Pokorny, 2010). Once information leaves the retina, rod and cone initiated events should be processed in the same manner in the central nervous system. Thus at mesopic light levels near threshold temporal and spatial function should be comparable, whether vision begins with rod or cone activation. The temporal properties are similar, as described in the experiments reported here; for spatial vision, the dimensions of the cone driven receptive fields should determine common spatial properties for cone or rod input. This analysis does not take into account rod-cone interactions that may occur in the distal retina. The experiments we describe on dark-adapted rod suppression of cone temporal function were done relatively close to the fovea, at an eccentricity of 7.5°. Under these conditions, our results show that dark-adapted rods suppress cone temporal vision by 50%. The same degree of suppression occurs for directly viewed foveal stimuli (Coletta & Adams, 1984). The suppression in the peripheral retina is much greater, on the order of 90% (Alexander & Fishman, 1986). Thus using illuminants that effectively stimulate rods can dramatically improve cone function.

The reaction time data show that at mesopic levels, responses to rod and cone excitation can be similar. Again, these data were obtained at a retinal location near the fovea. At greater eccentricities, where rod density is higher and cone density lower, impulse response amplitude would be higher and reaction times for rods would be expected to be faster that for cones.

What insights may be gained from the analysis of impulse response functions? Different tasks can use input information in different ways. For example, our modelling of the reaction time data is based upon the idea that the initial rising portion of the impulse response function is a principal determinant of reaction time. However temporal order judgments, another measure of perceptual latency, yield a different dependence on field luminance. With reduction in luminance, reaction time shows a considerable change in latency whereas temporal order judgments exhibit far less dependency (Roufs, 1974; Jaskowski, 1992). This is not likely due to a change in the motor component of reaction time (Miller & Low, 2001). It is plausible to assume that reaction time is dependent on the initial portion of the internal stimulus representation whereas temporal order is dependent on the peak (Sternberg & Knoll, 1973) or temporal centroid (Williams & Lit, 1983) of the representation. Another example of performance tasks using different aspects of cortical input information can be seen in discrepancies between reaction times and the exposure durations required for detection of sinusoidal gratings with variation in grating contrast (Ejima & Ohtani, 1987). Aside from stimulus detection, stimulus strength affects the accumulation of sensory evidence until a criterion decision threshold is reached. At near-threshold stimulus contrasts, speeded responses are slower and accuracy is lower (e.g. Luce, 1986). What governs detection threshold sensitivity? One would expect the visual system to integrate over the internal stimulus representation, using all available information to decide if a stimulus is present or not.

How can we reconcile the improvement in sensitivity with dark adaptation in the case of single pulses of light with the loss of sensitivity for temporally modulated light? With dark adaptation, the amplitude of the impulse response function decreases, but this is accompanied by a longer integration time. The integrated area of the impulse response function does not change in a dramatic way. For the temporally modulated stimuli, analysis involves convolving the impulse response function with the temporal waveform of the modulated light. Detection of the modulation would occur when the modulation of the convoluted function reaches some criterion amplitude. Thus with rod dark-adaptation having the effect of lowering the amplitude and increasing the integration time, the modulated stimulus would have to be either increased in contrast or decreased in temporal frequency to reach the criterion.

The message here is: From a basic science perspective, to optimize visual function at mesopic light levels, get rods involved!
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