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Dark-adapted rod suppression of cone flicker detection: Evaluation of receptoral and postreceptoral interactions

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Abstract

Dark-adapted rods in the area surrounding a luminance-modulated field can suppress flicker detection. However, the characteristics of the interaction between rods and each of the cone types are unclear. To address this issue, the effect that dark-adapted rods have on specific classes of receptoral and postreceptoral signals was determined by measuring the critical fusion frequencies (CFF) for receptoral L-, M-, and S-cone and postreceptoral luminance ([L+M+S] and [L+M+S+Rod]) and chromatic ([L/(L+M)]) signals in the presence of different levels of surrounding rod activity. Stimuli were generated with a two-channel photostimulator that has four primaries for a central field and four primaries for the surround, allowing independent control of rod and cone excitation. Measurements were made either with adaptation to the stimulus field after dark adaptation or during a brief period following light adaptation. The results show that dark-adapted rods maximally suppressed the CFF by ~6 Hz for L-cone, M-cone, and luminance modulation. Dark-adapted rods, however, did not significantly alter the S-cone CFF. The [L/(L+M)] postreceptoral CFF was slightly suppressed at higher surround illuminances, that is, higher than surround luminances resulting in suppression for L-cone, M-cone, or luminance modulation. We conclude that rod-cone interactions in flicker detection occurred strongly in the magnocellular pathway.

Keywords: Rod cone interaction, Flicker detection

Introduction

Rods and cones share neural pathways in the retina (Daw et al., 1990; Sharpe & Stockman, 1999). Anatomical studies have identified two primary rod pathways. In one pathway, rods synapse with rod ON-bipolar cells and then transmit information to cone ON- and OFF-bipolar cells via AII amacrine cells. In the other pathway, rods couple to neighboring cones via gap junctions and convey graded signals via cone ON- and OFF-bipolar cell circuitry (Kolb, 1977; Nelson, 1977; Smith et al., 1986; Schneeweis & Schnapf, 1995). It has been previously suggested that the rod ON-bipolar and AII amacrine pathway transmit high-gain rod signals at low scotopic light levels, while the rod-cone gap-junction pathway transmits low-gain rod signals at high scotopic and mesopic light levels (Sharpe & Stockman, 1999). These joint neural substrates provide the basis for the many examples of interactions between rod and cone signals (for a review, see Buck, 2004). In particular, dark-adapted rods suppress cone-mediated flicker at high temporal frequencies when the target is detected by rods and cones (local interaction, MacLeod, 1972) or when rods are dark-adapted in the region surrounding a cone-detected target (lateral interaction, Lythgoe & Tansley, 1929; Goldberg et al., 1983; Alexander & Fishman, 1984; Coletta & Adams, 1984). The focus of the current investigation is on lateral interactions.

In mammals, the physiological mechanisms controlling lateral rod-cone interactions in flicker detection are unknown. Based on intracellular recordings at a distal locus in the amphibian retina, Frumkes and Eysteinsson (1987, 1988) proposed that lateral rod-cone interaction is mediated by horizontal cells, by an inhibitory feedback mechanism from horizontal cells to cones. In the primate retina, there are two types of horizontal cells, distinguished by the classes of cone input. H1 cells are innervated by the long-wavelength-sensitive (L-) and middle-wavelength-sensitive (M-) cone pedicles but have very few short-wavelength-sensitive (S-) cone contacts; H2 cells have extensive S-cone contacts and fewer L- or M-cone contacts (Dacey et al., 1996). The role of horizontal cells in the suppressive rod-cone interaction in flicker detection in primates is uncertain.

Modern anatomical and physiological studies have identified three major neural retinogeniculate pathways in the primate visual system: the parvocellular (PC-), magnocellular (MC-), and koniocellular (KC-) pathways (Dacey, 2000). The PC-pathway mediates spectral opponency of L- and M-cones to signal chromatic information. The MC-pathway processes the summed output of the L- and M-cones to signal luminance information. The KC-pathway differences S-cone signals from the sum of the L- and M-cones.

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Physiological investigations suggest that rod input is strong in the MC-pathway with evidence of weak or absent input to the PC- and KC-pathways (Lee et al., 1997).

Several psychophysical investigations have suggested that rod interaction is either specific to L-cones or greater for L-cones than M-cones, both in trichromats and dichromats. In trichromatic observers, the suppression of luminance flicker sensitivity has been primarily observed with long-wavelength test lights (Coletta & Adams, 1984). In dichromats, an elevation of flicker detection threshold during the rod component of dark adaptation has been reported as evident in deuteranopes, but not in protanopes (Coletta & Adams, 1985; Frumkes et al., 1988; Frumkes, 1990). It is unclear from anatomy and physiology why this might be the case.

In this study, the critical fusion frequencies (CFF) for receptoral L-cone, M-cone, or S-cone excitations and postreceptoral luminance ([L+M+S] and [L+M+S+Rod]) and chromatic ([L/(L+M)]) modulations were measured in the presence of different surround light levels, to alter the level of rod activity. We should mention the rationale of the choice of luminance stimuli. From psychophysics (Smith & Pokorny, 1975) and retinal physiology (Lee et al., 1989), it is now broadly understood that the $V(\lambda)$ function represents a weighted sum of the L- and M-cone photopigment spectra expressed at the corneal level (L+M). If luminance is changed, say by a neutral density filter, then the actual change in photoreceptor excitation is [L+M+S+Rod]. With our photostimulator we have the freedom to either allow rod excitation to vary along with L- and M-cone excitation as for naturally occurring changes in luminance, or we can fix rod excitation and only vary cone luminance [L+M+S]. Since S and Rod do not contribute to $V(\lambda)$, these changes do not alter luminance, only chromaticity and rod excitation.

No psychophysical study has considered the possible interaction between rods and S-cones, or between rods and L/(L+M) postreceptoral signals in flicker detection. We generated two types of luminance modulation, one with cone modulation but steady rod excitation [L+M+S], and the second with both cones and rods modulated [L+M+S+Rod], as would occur with a conventional light stimulus. The time-averaged chromaticity, rod excitation, and luminance were the same for all conditions. Measurements were made either following 30-min dark adaptation or during the cone component of dark adaptation following light adaptation to a 10,000 Td broadband light with a correlated color temperature of 5100°K. The experimental design affords the ability to identify the retinogeniculate pathway(s) mediating rod suppression of cone flicker detection.

Materials and methods

Apparatus

A two-channel Maxwellian view photostimulator, with four primaries for a central field and four primaries for a surround, was used to control excitation of the rods and three cone types independently (Shapiro et al., 1996). A complete description of the design of the photostimulator is given by Pokorny et al. (2004), and an example of its implementation is detailed in Cao et al. (2005). The primaries were derived from light-emmitting diode (LED)-interference filter combinations yielding dominant wavelengths of 459 nm (blue), 561 nm (greenish-yellow), 516 nm (green), and 658 nm (red). The radiances of the primaries were controlled by amplitude modulation of a 20-kHz carrier feeding into an eight-channel analog output Dolby sound card (M-Audio-Revolution 7.1 PCI) with a 24-bit digital-to-analog converter (DAC) operating at a sampling rate of 192 kHz. The output of the DAC was demodulated (Puts et al., 2005) and sent to voltage-to-frequency converters that provided 1-μs pulses at frequencies up to 250 kHz to control the LEDs (Swanson et al., 1987). The sound card with demodulator has a precision of greater than 16 bits (Puts et al., 2005). All stimuli were generated using custom engineered software driven by a Macintosh G5 PowerPC computer.

Calibration procedures

The photostimulator was calibrated using a two-step procedure. The first step pertained to the measurement of the spectral distribution and the linearization of physical light for each LED. The second involved observer calibrations to compensate for individual differences in prereceptoral filtering and receptoral spectral sensitivities. Details of the calibration procedures have been described (Sun et al., 2001; Pokorny et al., 2004; Cao et al., 2005).

For light adaptation, collimated light from a 24-V, 150-W tungsten halogen lamp illuminated a rear-projection screen (Da-Lite DA180, Warsaw, IN). This in combination with a color-correcting filter (Lee 80A, Hampshire, UK) produced a light with a correlated color temperature of 5100°K. The observer fixated a point on the diffuser screen during light adaptation. The luminance in cd/m^2 of the broadband light was measured at multiple locations of the diffuser. The resultant values were averaged and then converted into retinal illuminance in trolands.

Stimuli

We measured flicker-fusion thresholds for six types of stimuli, each designed to modulate a single receptoral or postreceptoral mechanism. Receptoral L-cone, M-cone, and S-cone excitations, postreceptoral luminance ([L+M+S], [L+M+S+Rod]), and chromatic ([L/(L+M)]) stimuli were temporally modulated in a 2-deg circular field positioned at 7.5 deg temporal eccentricity and set within a steady 13-deg surround. The spatial configuration of the stimuli is shown in the upper panel of Fig. 1.

For all conditions in this study, the time-averaged chromaticity of the light in the center and surround fields was metameric to the equal-energy-spectrum (EES; L/(L+M) = 0.667, S/(L+M) = 1.0). The center field was sinusoidally modulated around a mean illuminance of 80 photopic Tds. To minimize flicker adaptation, the modulated field was presented in a 1-s raised cosine envelope that alternated with a 1-s steady field (Fig. 1, lower panel). The L-cone, M-cone, [L+M+S] or [L+M+S+Rod] signals were modulated at 15% Michelson contrast, the S-cone was modulated at 30%, and the [L/(L+M)] signal was modulated at 5%. For each condition, the Michelson contrast was set to a level near the gamut limit of the photostimulator. The surround was set to a steady retinal illuminance of 0, 0.05, 0.5, 5, 20, or 80 photopic Tds.

Procedure

Prior to the start of each session, the observer dark adapted for 30 min (dark adaptation; DA) or light adapted to a 10,000 photopic Td broadband light for 2 min (light adaptation; LA). This light adaptation regimen produced about a 12.5% rod bleach and would be expected to lead to a cone plateau duration of 4–5 min (Wolf & Zigler, 1954; Pugh, 1975). The time needed to complete a single condition was between 2 and 5 min. For each trial of each

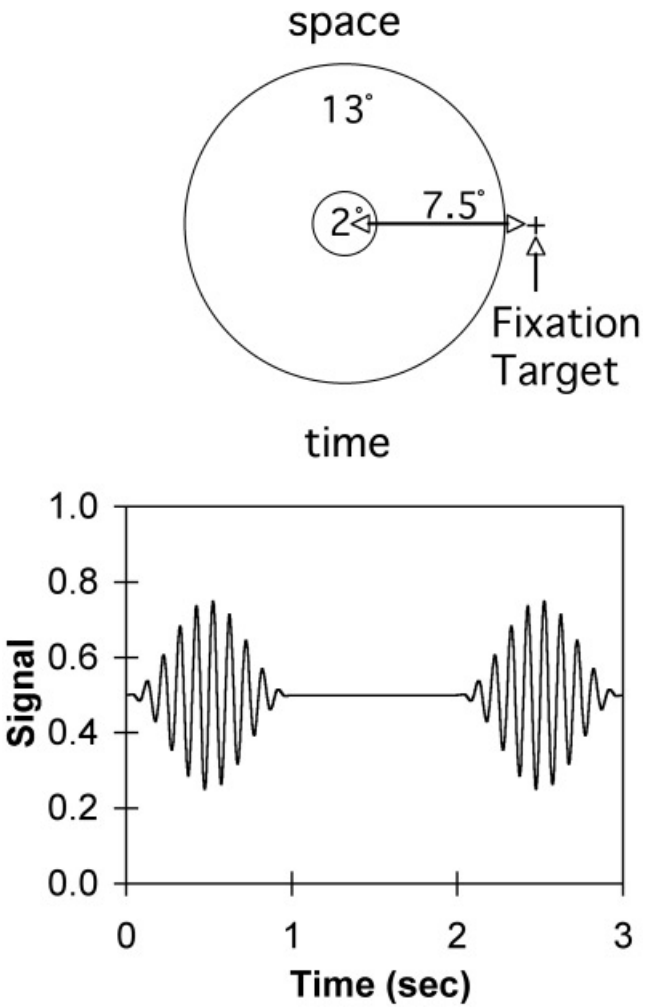

Fig. 1. The spatial configuration and the temporal profile of stimuli used for the CFF measurements. The upper schematic shows the 2-deg central field set within a 13-deg surround at 7.5-deg temporal eccentricity. The center and surround were metameric to an equal-energy spectrum. The lower schematic gives an example of a 10-Hz signal that was modulated sinusoidally in the center field within a 1-s raised cosine envelope that was alternated with a 1-s steady center field.

condition, the computer randomly set an initial temporal frequency between 5 and 30 Hz. The observer altered the temporal frequency using a method of adjustment to determine the CFF by pressing buttons on a game pad sensed by the computer. Two buttons allowed increases or decreases in temporal frequency in 1-Hz step sizes while another two buttons altered the frequency in larger, 5-Hz steps. Once the CFF was determined, the observer pressed a button to record the setting, and the next trial was initiated.

There were six trials in each condition. The observer completed 10–15 conditions following the period of dark adaptation but only a single condition after light adaptation. There was no evidence in the light adaptation data to suggest rod intrusion during the 2–5-min adjustment period, since the measured CFF for each trial was similar within the same condition. Each condition was repeated three times on different days. The mean CFF and standard error for each combination of modulation type and surround illuminance are reported. To compare the effect of adaptation condition (dark or light adaptation) on the measured CFF for each observer, analysis of variance (ANOVA) was conducted with the adaptation condition and surround illuminance as the main effects for each modulation type.

As a control, we measured CFF of the [L+M+S+Rod] signal modulated at 5% contrast with 0- and 0.05-Td surround illuminances under dark and light adaptation conditions.

Observers

Two experienced psychophysical observers, the authors D.C. and A.J.Z., participated. Both observers have normal color vision (assessed by the Neitz OT anomaloscope and Farnsworth-Munsell 100-Hue test). A refractive correction lens was placed on the instrument side of the 2-mm artificial pupil for D.C. The Institutional Review Board at the University of Chicago approved all experimental procedures.

Results

Dark-adapted measurements

The CFF (Hz) as a function of surround illuminance (expressed in photopic Td) after dark adaptation is shown for each modulation type in the left panel of Fig. 2 (D.C., upper panel; A.J.Z., lower panel). The characteristics of the data sets were similar for both observers, with few exceptions. The CFF for all receptoral and postreceptoral signals measured after dark adaptation had two components. At surround illuminances ≤0.5 Td, CFF was approximately constant. Above 0.5 photopic Td, CFF increased monotonically with increasing light level. In all cases the CFF for [L+M+S] and [L+M+S+Rod] modulations were higher than the CFF for the L-, M-, S-, and [L/(L+M)] modulations. The CFF for L-cone modulation was always higher than that for M-cone modulation. For observer D.C., the upper segment had a mean slope of 4.4 (range 3.6–5.0) Hz/log(Td) for the L-cone, M-cone, [L+M+S], and [L+M+S+Rod] modulations, 1.9 Hz/log(Td) for the [L/(L+M)] modulation, and 1.6 Hz/log(Td) for the S-modulation. For A.J.Z., the mean slope of the upper, monotonic segment was 3.6 (range 3.1–4.5) Hz/log(Td) for all modulation types except the S-cone, which was approximately constant for the range of surround illuminances tested.

Light-adapted measurements

The right panels of Fig. 2 show the critical fusion frequency (Hz) for each modulation type as a function of the surround illuminance (photopic Td) measured during the cone component of dark adaptation, following light adaptation. The CFF is approximately constant for surround illuminances ≤0.5 Td and increases monotonically at higher light levels. The data show a similar two-component relationship with light level when compared to the results for dark adaptation (left panels), with one essential exception. The CFF values at surround light levels ≤0.5 Td for the L-cone, M-cone, [L+M+S], and [L+M+S+Rod] modulations were higher than those measured during dark adaptation (compare corresponding left and right panels for each observer in Fig. 2). The following section considers the magnitude of these differences.

Magnitude and specificity of the lateral suppressive rod-cone interaction

To determine the magnitude of the rod suppression on the cone CFF, Fig. 3 plots the difference between the light-adapted (LA)

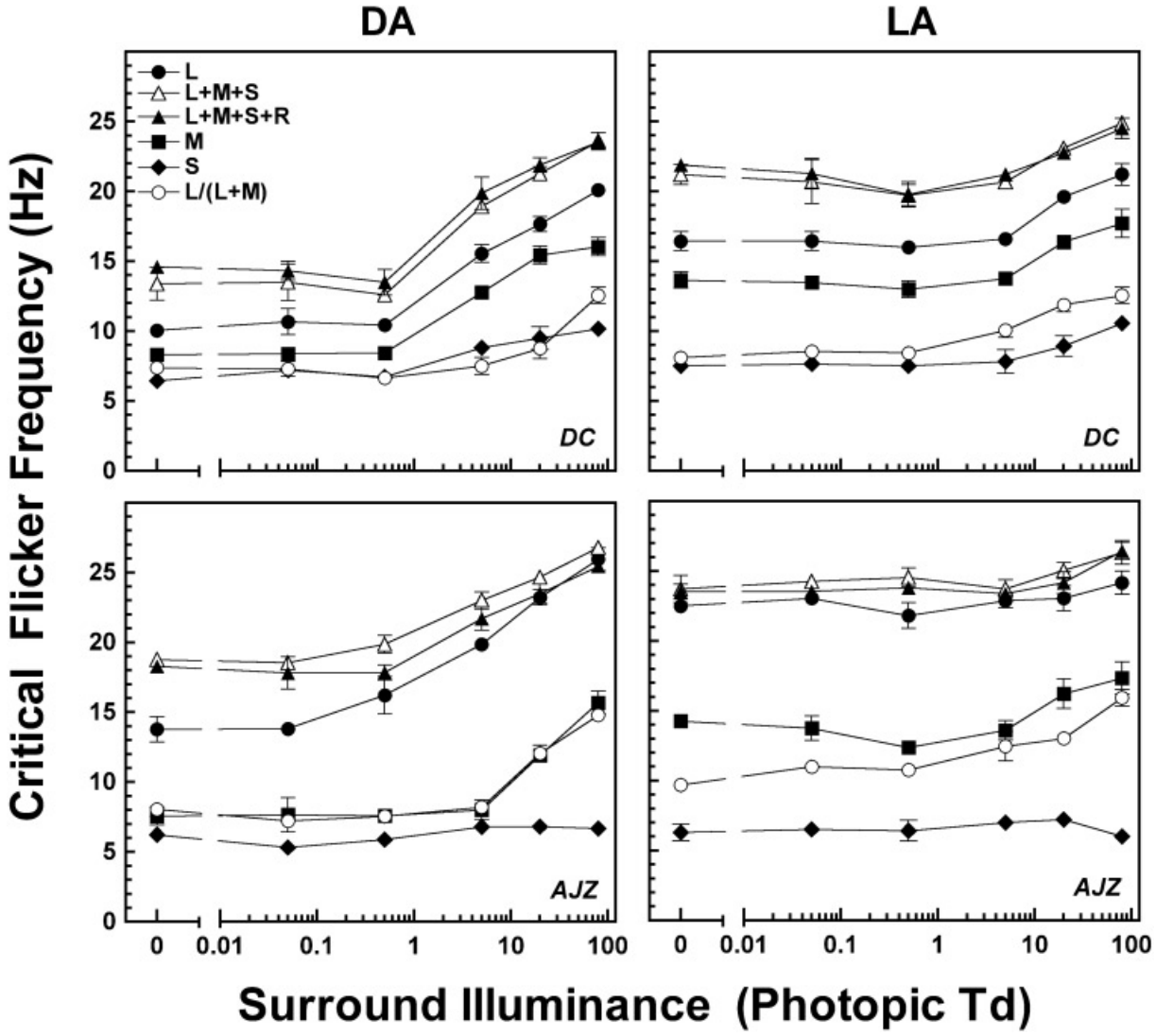

Fig. 2. CFF measurements following the dark and light adaptation. The left panel shows the CFF for the dark-adapted (DA) condition as a function of surround illuminance (photopic Td). The right panel shows the CFF measured following the light adaptation (LA). The upper row gives the data for observer D.C., the lower row shows the corresponding data for observer A.J.Z.

and dark-adapted (DA) conditions. The upper row of Fig. 3 shows the difference for the L-cone, M-cone, [L+M+S], [L+M+S+Rod] modulations, and the lower row shows the S-cone and [L/(L+M)] data. The data for observer D.C. are shown in the left panels and for observer A.J.Z. in the right panels. ANOVA indicated that the effect of adaptation condition (dark or light adaptation) was significant at the 0.05 level for all the modulation types except S-cone modulation for both observers (S-cone modulation: $F(1,29) = 0.41$, $P = 0.53$ for D.C.; $F(1,29) = 1.02$, $P = 0.32$ for A.J.Z.), suggesting a significant rod suppression of all of the modulations except S-cones.

The L-cone, M-cone, [L+M+S], and [L+M+S+Rod] modulation exhibited similar patterns of change in CFF; the mean difference (dashed line) across the four types of modulations at each surround illuminance is plotted in the upper row of Fig. 3. The difference between the light- and dark-adapted CFF at low surround illuminances (≤0.5 Td) was ~6 Hz (range 5–9 Hz) for both observers. At higher surround illuminances (≥5 Td), the difference in CFF was ~1.5 Hz for D.C. For A.J.Z., at higher surround illuminances, the difference in CFF was small except for the M-cone modulation.

The differences in dark- and light-adapted CFFs for the S-cone (filled diamonds) and [L/(L+M)] (unfilled circles) modulations are plotted in the lower row of Fig. 3. For both observers, there was no statistical evidence indicating any difference in CFF with the dark- and light-adapted conditions for the S-cone modulation. The differences for the [L/(L+M)] modulation increased with surround illuminance, reaching a maximum at 2–20 Td and a minimum at center-surround equiluminance (80 Td). The magnitude of the difference at the maximum was less than 3–4 Hz.

For the control experiment, CFF was unmeasurable for the [L+M+S+Rod] signal modulated at 5% contrast with 0- and 0.05-Td surround illuminances under dark adaptation: both observers did not see flicker at any temporal frequency. Following light adaptation, the CFF was 11–13 Hz.

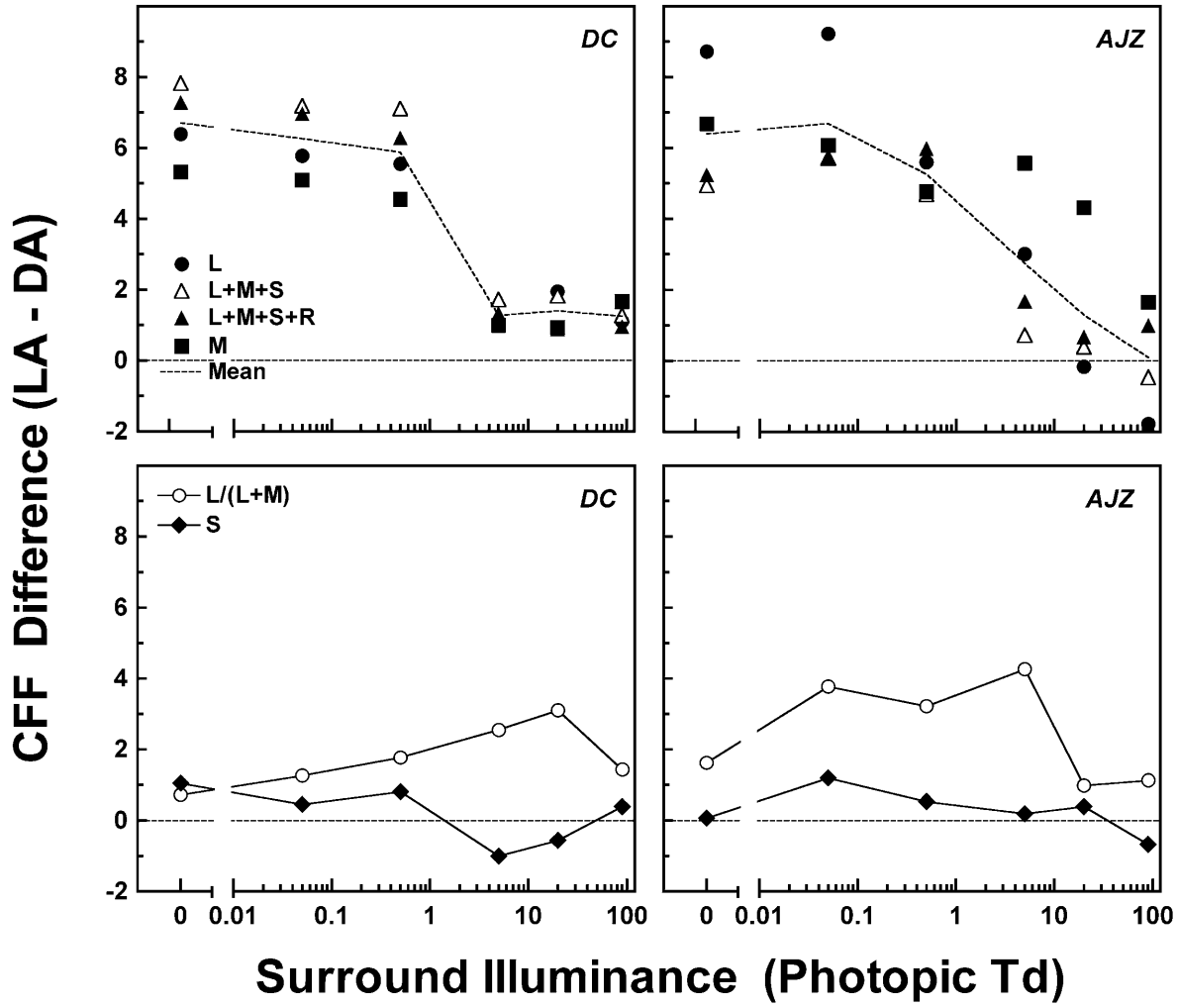

Fig. 3. The difference in CFF between the dark and light adaptation conditions. The upper row shows the data for the L-cone, M-cone, [L+M+S], and [L+M+S+Rod] modulations. The dashed line indicates the mean of the four modulation types. The lower row gives the difference between the S-cone and [L/(L+M)] chromatic modulation. The left panels show the data for D.C., the right panels for A.J.Z.

Discussion

To examine the rod influence on cone flicker detection, the CFF for receptoral and postreceptoral stimuli were measured in the presence of surround illuminances ranging from 0 to 80 photopic Tds. There were four key findings in this study. First, the lateral suppressive rod-cone interaction occurring at low surround illuminances (≤0.5 Td) is specific to certain receptoral and postreceptoral modulations: the L-cone, M-cone, [L+M+S], and [L+M+S+Rod] modulations. All of these modulations contained luminance variation, and for all, the difference in CFF between light and dark adaptation was ~6 Hz. From physiological studies, it is known that MC-pathway units respond vigorously to all of these modulation patterns (Yeh et al., 1995) and rod inputs to the retinogeniculate pathways are predominantly in MC-cells (Lee et al., 1997). From our results, we infer that the lateral suppressive rod-cone interaction in cone-mediated flicker detection is strong in the MC-pathway.

Second, by independently controlling the modulation of different receptor classes, we found that for both observers, dark-adapted rods suppressed L- and M-cone flicker detection at low surround illuminances, illuminances that were near or below cone threshold. One observer (A.J.Z.) showed strong rod suppression of M-cone flicker detection at higher surround illuminances. This contrasts with past findings that rods primarily interacted with L-cones when flicker sensitivity was measured with a fixed 25-Hz temporal modulation of different wavelength lights on a 500-nm background (Coletta & Adams, 1984). In the Coletta and Adams evaluation of rod interactions with L- and M-cones, rod excitation varied with the wavelength of the test light. Our experimental design controlled the adaptation level of the rods and cones, and all modulations were evaluated at the same time-average chromaticity and rod excitation level. The measured L- and M-cone CFFs were consistent with CFF differences between protanopes and deuteranopes (Pokorny & Smith, 1972; Lutze et al., 1989).

Third, the suppressive rod-cone interaction was not statistically significant for the S-cone modulations. It is known from physiological studies that KC-pathway units respond vigorously to S-cone and luminance-containing modulations (Yeh et al., 1995) and that there is no physiologically measurable rod input to KC-ganglion

units (Lee et al., 1997). In accord with the physiological data, our results fail to show KC-pathway involvement in the suppressive rod-cone interaction in flicker detection.

Fourth, rod suppression with the chromatic [L/(L+M)] flicker detection had a different pattern of suppression and was reduced relative to that found for luminance-containing modulations. The rod suppression peaked at a surround illuminance of ~5 Td. Physiological recordings in the ganglion cells have indicated that the PC-units have weak inputs from rods (Lee et al., 1997), consistent with our finding of weak suppression of chromatic [L/(L+M)] signals. In the main experiment we used 5% chromatic [L/(L+M)] modulation and 15% luminance-containing modulations. We conducted a control experiment using a 5% [L+M+S+Rod] modulation to assess whether stimulus contrast was an important parameter. CFF was measurable during light adaptation but not under dark adaptation, indicating a strong rod suppression of cone flicker detection. Therefore the difference in the magnitudes of rod suppression on the [L/(L+M)] modulation and luminance-containing modulations cannot be attributed to the different contrast levels.

In this study we investigated receptoral and postreceptoral signals that may be involved in rod suppression of cone flicker detection. The neural mechanisms mediating this suppression are unclear. Yang and Wu (1989) showed in amphibians a faster horizontal cell response following the onset of background illumination due to changes in rod activity. These results implied a possible role of horizontal cells, as suggested by Frumkes and Eysteinsson (1987, 1988). However across species, the same cell type may not perform the same function. For example, chromatically opponent horizontal cells are seen in almost every retina of cold-blooded species that contains at least two different spectral types of cone (Twig et al., 2003), whereas primate horizontal cells exhibit only additivity of cone inputs (Dacey et al., 1996). Verweij et al. (1999) measured primate H1 cells' receptive fields for rod- and cone-mediated responses and found them spatially coextensive, consistent with the H1 rod signal arising from rod-cone gap junctions. H1 cell sensitivity was 1 log unit poorer for rods than for cones, and H1 cells were insensitive in the low scotopic range, which was opposite to our finding that suppression occurred only at low surround illuminances. Taken together, the results from physiological recording in primates and our psychophysical results suggest that the primate H1 cell is not securely established as the locus of rod suppression of cone flicker detection. We found that the rod suppression occurs predominantly for stimuli inferred to be mediated by the MC-pathway, suggesting mediation at a level higher than the horizontal cells.

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