

Multiple processes mediate flicker sensitivity

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Abstract

By systematically manipulating the luminance of a flickering spot and the area immediately surrounding it, we investigated why thresholds from flickering stimuli that cause a change in average luminance are elevated relative to those from stimuli with no luminance change. Threshold elevation resulted from local light adaptation and from temporal-frequency-specific interactions between the spot and its surround: at low frequencies, the contrast between the spot and the surround elevated thresholds, whereas at high frequencies, dark adaptation within the surround elevated thresholds. Our findings suggest that two common ways of determining temporal sensitivity may give markedly different outcomes. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Historically, the temporal sensitivity of the visual system has been investigated using two types of flickering stimuli. Mean-modulated flickering stimuli (Fig. 1, upper schematic) modulate luminance about a background level, and so effect no change in the time-averaged luminance (for example, DeLange 1958 and Roufs 1972). However, luminance-pedestal flicker (Fig. 1, lower schematic) is achieved by modulating a luminance increment, resulting in both a flickering component and an increase in time-averaged luminance (a luminance pedestal) above the background level (for example Alexander & Fishman, 1984; Eisner, 1994).

Do both stimuli provide the same information about the visual system? Previous work has shown that the luminance pedestal in luminance-pedestal flicker acts to increase flicker thresholds (Anderson & Vingrys, 2000). However, the mechanisms by which this elevation occurs are not clear. Several investigations give some clues as to how luminance pedestals may affect flicker thresholds. Local (that is, within the spatial extent of the flickering stimulus) light adaptation is known to

increase flicker thresholds, especially at low flicker rates (DeLange, 1958; Kelly, 1961; Roufs, 1972). In luminance-pedestal flicker, the average luminance of the stimulus is higher, so thresholds may be raised by this local mechanism.

However, regions surrounding the stimulus may also be important. It is known that the complete absence of a surrounding field of light (Kelly, 1959, 1969; Keeseey, 1970; Roufs, 1972) or the presence of a surround whose luminance is unmatched to the stimulus (Spehar & Zaidi, 1997) can elevate thresholds at low flicker rates. This is thought to arise from the contrast created at the edge of the flickering field, which saturates edge sensitive flicker mechanisms (Watson, 1986). In luminance-pedestal flicker, the luminance pedestal creates a contrast at the edge of the field that may elevate thresholds. However, this is not the only surround effect. If the surround luminance does not saturate rod photoreceptors, rod–cone interactions can occur that suppress flicker sensitivity within the stimulus area (Goldberg, Frumkes, & Nygaard, 1983; Alexander & Fishman, 1984; Coletta & Adams, 1984), especially at high flicker rates. Although the local luminance increases in luminance-pedestal flicker, the surround luminance does not and so suppressive rod–cone interactions may develop. In addition, cone–cone interactions may also manifest under certain conditions (Coletta & Adams, 1986; Eisner, 1994).

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Therefore, luminance-pedestal flicker may perturb retinal mechanisms that remain unaffected by mean-modulated flicker, which may explain the unusual adaptational characteristics (Eisner, 1994, 1995; Eisner, Shapiro, & Middleton, 1998; Vingrys & Demirel, 1998) and unexpected losses in early disease states (Eisner & Samples, 1991; McKendrick, Badcock, Heywood, & Vingrys, 1998; McKendrick, Vingrys, Badcock, & Heywood, 2000; Phipps, Guymer, & Vingrys, 1999; Vingrys & Pesudovs, 1999) demonstrated with luminance-pedestal flicker stimuli. We sought to determine to what extent local light adaptation, the loss of surround matching, and the light adaptation of surrounding photoreceptors can explain luminance-pedestal flicker thresholds.

2. Methods

2.1. Subjects

Six subjects (20–36 years) participated in the experiments. Retinal illumination was controlled with a 4 mm diameter artificial pupil and mydriasis (0.5% tropicamide), except in the experiment using continuous pedestals. Subjects were optically corrected for the viewing distance (1 m) in experiments using mydriasis. All stimuli were presented at 5° nasal eccentricity in the

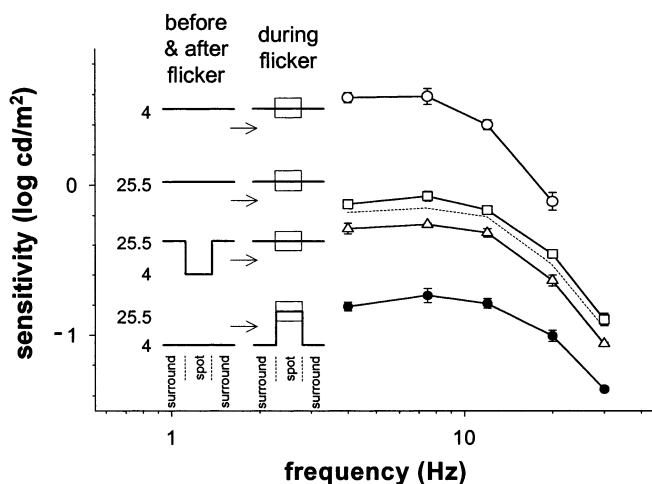


Fig. 1. Flicker thresholds for various stimulus and background conditions. Mean-modulated flicker at 4 cd/m² (unfilled circles) and 25.5 cd/m² (unfilled squares) backgrounds. Luminance-pedestal flicker for a 21.5 cd/m² pedestal on a 4 cd/m² background (filled circles), and with the surround raised to 25.5 cd/m² (unfilled triangles). Each datum shows the mean (\pm S.E.M.) of five observations for a single subject. The dashed curve represents the unfilled triangle data translated upwards by 0.115 log units (see text for details). Schematics give the luminance profiles of the spot and surrounds (thick lines) before and after (left) and during (right) stimulus presentation, with the thin lines showing the up/down modulation of the flickering stimulus; luminous extents are shown on the left of the schematics.

preferred eye. The study complied with the tenets of the Declaration of Helsinki and was approved by our institutional human experimentation committee, with all subjects giving informed consent prior to participation.

Thorough investigations were performed on a single observer, whose results were compared to a group of five subjects, established over a limited parameter set.

2.2. Apparatus and procedure

Stimuli were presented on a calibrated television monitor system [VSG 2/3 graphics card (Cambridge Research Systems Ltd., Kent, UK) and Hitachi™ HM-47231-D monitor (frame rate 120 Hz)]. The monitor subtended 19.3° × 13.7° (W × H) and was surrounded by a square white background (4 cd/m², 53° × 53°).

Stimuli were 0.5° diameter white (1931 CIE, $x = 0.283$, $y = 0.319$) spots. Square wave flicker was used, with thresholds taken as mean-to-peak amplitudes. Stimuli were presented with their positive going phase at onset and were 750 ms in duration (4, 12 and 20 Hz), except for the 7.5 Hz (800 ms) and 30 Hz (767 ms) stimuli. Except in the experiment with continuous pedestals, luminance pedestals were of the same duration and were presented at the same time as the flickering stimulus. An inter-stimulus interval of 17 ms (two frames) was used (Anderson & Vingrys, 2000).

Thresholds were measured using a two-interval forced-choice paradigm and a ZEST procedure (King-Smith, Grigsby, Vingrys, Benes, & Supowit, 1994) of 30 trials. For most subjects, thresholds were determined from the geometric mean of two estimates. For the single observer, thresholds were the geometric means of either five or 10 measurements (see figure legends). Significant differences ($P < 0.05$) between thresholds were determined using a one-way repeated-measures ANOVA and a Tukey all pairwise multiple comparison procedure.

Subjects were pre-adapted to the surround luminance for at least 2 min prior to experimentation and did not commence a new trial until any afterimage from the previous trial had faded, which typically took less than a minute.

3. Results

3.1. Local light-adaptation effects

An experiment was designed to determine the role of local light adaptation in luminance-pedestal flicker. Mean-modulated flicker thresholds were determined for 0.5° spot targets at a background of 4 cd/m² (Fig. 1, upper schematic). Luminance-pedestal flicker thresholds were also determined from the same 4 cd/m² background, using a 21.5 cd/m² luminance pedestal

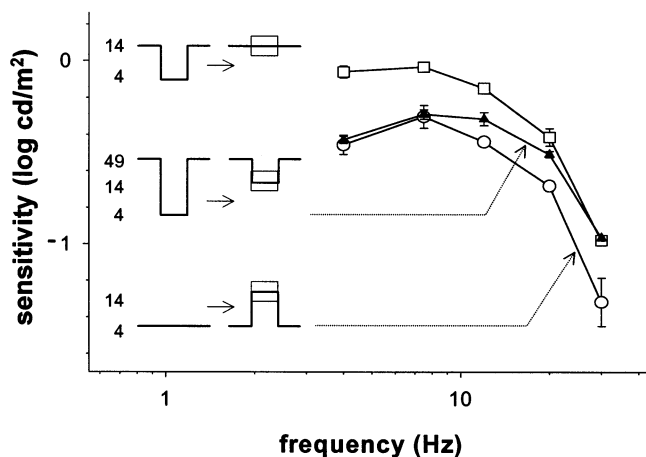


Fig. 2. Effect of surround luminance on luminance-pedestal flicker thresholds. The average luminance of the luminance-pedestal flicker stimulus is fixed at 14 cd/m², for three surround levels: dim (4 cd/m², unfilled circles); matched (14 cd/m², unfilled squares); and bright (49 cd/m², filled triangles). Each datum represents the mean (\pm S.E.M.) of five observations from a single observer. The schematics are as defined in Fig. 1.

(Fig. 1, lower schematic), thereby giving the flickering stimulus an average luminance of 25.5 cd/m².

The results for a single observer are shown in Fig. 1, and are similar to those obtained from a group of five observers. The mean-modulated data (unfilled circles) show a typical low-pass function, although sensitivity to the 30 Hz stimulus could not be measured reliably. Luminance-pedestal flicker sensitivity at the same background (filled circles) is approximately 1 log unit poorer. Therefore, the presence of a luminance pedestal acts to decrease flicker sensitivity, consistent with previous work (Anderson & Vingrys, 2000).

If the luminance pedestal is altering sensitivity purely by a process of local light adaptation, then luminance-pedestal flicker sensitivity (Fig. 1, filled circles) should be equivalent to that of a mean-modulated stimulus having the same local luminance (25.5 cd/m², unfilled squares). This is not so; at all frequencies, there is a decrease in luminance-pedestal flicker sensitivity above that predicted by a change in local light adaptation. What is the cause of this additional sensitivity loss? The introduction of a surround that matches the average luminance of the flickering stimulus (unfilled triangles) increases luminance-pedestal flicker sensitivity to close to that obtained from the mean-modulated stimulus with the same local luminance (unfilled squares). This shows that the surround is also important in determining luminance-pedestal flicker thresholds, and this surround effect is investigated further in the following section.

The presence of a matched surround in luminance-pedestal flicker does not make sensitivity identical to the mean-modulated condition (Fig. 1, unfilled triangles

versus unfilled squares, respectively). This suggests that the short duration of the pedestal also affects sensitivity. We tested this possibility at 4 and 20 Hz using a 21.5 cd/m² luminance-pedestal that was present either continuously or only during the presentation of the flickering stimulus (750 ms). For both temporal frequencies, the average thresholds were lower with continuous pedestals [0.53 ± 0.05 versus 0.64 ± 0.06 log cd/m² at 4 Hz, 0.77 ± 0.06 versus 0.89 ± 0.06 log cd/m² at 20 Hz (mean \pm S.E.M.)], although these differences were only significant for the 20 Hz data ($P = 0.01$; 4 Hz, $P = 0.29$). These results show that the short duration of the stimulus affects luminance-pedestal flicker sensitivity. Adjusting for the average difference (0.115) makes the two curves in Fig. 1 (unfilled squares and dashed line) differ by less than 0.1 log units.

3.2. Surround effects

The improved luminance-pedestal flicker sensitivity with a matched surround (Fig. 1, triangles) could have resulted from increased light adaptation due to the surround or from the removal of the contrast at the edge of the flickering field. The following experiment considers both of these possibilities by systematically manipulating the luminance of the surround.

All stimuli used a 10 cd/m² luminance pedestal presented on a 4 cd/m² background, giving the flickering stimulus an average luminance of 14 cd/m². Three conditions were investigated that differed only by the luminance of the surround, being 4, 14 or 49 cd/m². The highest and lowest surround luminances were selected to give the same Michelson contrast (56%) between the average luminance of the flickering stimulus and the surround, but of opposite polarity (Spehar & Zaidi, 1997). The middle luminance was selected to provide a zero-contrast condition.

The results for a single observer can be seen in Fig. 2. The presence of a surround matched to the average luminance of the stimulus (squares) improves sensitivity at both high and low temporal frequencies when compared to luminance-pedestal flicker thresholds obtained with a dim surround (circles), consistent with Fig. 1.

However, the curve for the bright surround (triangles) has a different shape compared with the other two curves. This surround gives sensitivities that are similar to the dim surround at low temporal frequencies, but similar to the matched surround at high temporal frequencies. In between these two extremes, there is a smooth transition. The results for low temporal frequencies (≤ 7.5 Hz) are consistent with sensitivity changes arising from the contrast between the pedestal and the surround, as both positive and negative contrasts produced comparable sensitivities (triangles and circles, respectively). However, the results at high tem-

poral frequencies (≥ 20 Hz) indicate that it is the low absolute luminance of the surround (circles) that decreases flicker sensitivity. Given that the matched (squares) and bright (triangles) surrounds give comparable sensitivities at high temporal frequencies, the effect of light adaptation in the surround must asymptote by 14 cd/m^2 ($2.2 \log \text{ Td}$). The group data (Fig. 3) have been plotted to highlight these low and high temporal frequency differences. Dimmer and brighter surrounds create an edge contrast that elevates thresholds at low temporal frequencies (4 Hz, filled circles), whereas only dim surrounds elevate thresholds at high temporal frequencies (30 Hz, unfilled circles).

3.3. Spatial extent of surround effects

The previous experiment demonstrated that spot/surround interactions depend upon edge contrast at low temporal frequencies, but upon absolute surround luminance at high temporal frequencies. Given these differences, we wished to determine whether the spatial extents of these surround effects also differed. We did this by progressively expanding the outer dimension of an annular surround to determine the critical diameter for these two effects, as shown by the schematics in Fig. 4.

A luminance-pedestal flicker stimulus with an average luminance of 25.5 cd/m^2 (4 cd/m^2 background, 21.5 cd/m^2 pedestal, Fig. 4 schematics, small circle) was

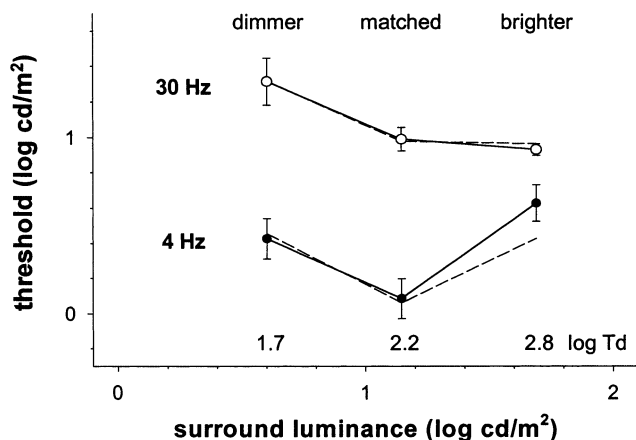


Fig. 3. Influence of surround luminance, expressed as a luminance and retinal illuminance ($\log \text{ Td}$), on luminance-pedestal flicker thresholds. The contrasts of the highest and lowest luminances are the same, but of opposite polarity. Unfilled circles, 30 Hz; filled circles, 4 Hz. Each datum gives the mean (\pm S.E.M.) threshold from five observers. For the 4 Hz data, thresholds from the dimmer and brighter surround condition were not significantly different, but were significantly elevated relative to those from the matched surround condition (RM-ANOVA: see text for details). For the 20 Hz data, thresholds from the matched and brighter surround conditions were not significantly different, but were significantly lower than the dimmer surround condition. The dotted lines are replotted from Fig. 2 (single observer) for the two flicker rates.

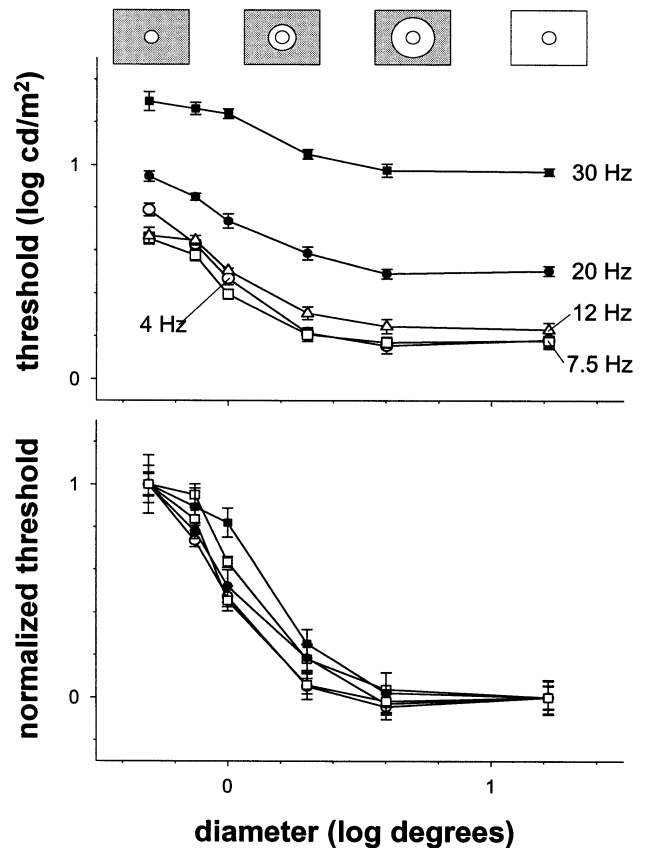


Fig. 4. Effect of surround size on luminance-pedestal flicker thresholds (local luminance 25.5 cd/m^2). The abscissa gives the outer diameter of an annular (25.5 cd/m^2) surround, with $\log 1.22$ representing the full field condition and $\log -0.30$ the no surround condition. Upper panel: threshold data for the frequencies indicated on the figure. Lower panel: normalised data from the upper panel (see text for details). Each datum gives the average (\pm S.E.M.) of 10 observations from a single subject. Schematics of the stimulus/surround configuration are given at the top of the figure with the flickering stimulus shown as the small central circle.

presented with a continuous 25.5 cd/m^2 annular surround of various dimensions. The surround inner diameter was always 0.5° , but the outer diameter ranged from 0.75° to 4° . In addition, no surround and full field surround conditions were included. Beyond the outer limit of the annular surround (including the no surround or full field surround), luminance was maintained at 4 cd/m^2 .

The effect of surround diameter for a single observer can be seen in Fig. 4 (upper panel), and is representative of the group of five observers. As the surround expands, thresholds progressively fall until a critical diameter is reached, after which thresholds remain constant. Comparison of the critical diameter at different temporal frequencies is hindered by the differing magnitudes of the surround effects. As a consequence, thresholds were normalised to 1 under the no surround condition and zero for the full field condition (Fig. 4, lower panel). The normalisation shows that there is

little difference between the spatial extents of surround effects at low or high temporal frequencies, with the critical diameter being between 2° and 4° (0.3 and 0.6 log).

4. Discussion

The effects of luminance-pedestal and mean-modulated flicker on visual sensitivity differ through three factors. Locally, luminance-pedestal flicker thresholds are elevated by increased light adaptation, as the luminance pedestal increases average luminance. At low flicker rates, thresholds are further elevated by the edge contrast produced between the luminance pedestal and the surrounding field. At high flicker rates, thresholds are further raised by interactions from the dim surround present in luminance-pedestal flicker. We will consider the nature of these surround effects below.

Light adaptation to the surround improved sensitivity at high flicker rates, and this effect was found to asymptote at or before $2.2 \log \text{Td}$ ($2.7 \log \text{scotopic Td}$) (Fig. 3, unfilled circles). This finding is consistent with a decrease in rod–cone suppression, as previously reported both centrally (Vingrys & Demirel, 1998) and at 20° eccentrically (Alexander & Fishman, 1984) for white backgrounds, and is also consistent with the commencement of rod saturation for backgrounds above $2 \log \text{scotopic Td}$ (Aguilar & Stiles, 1954). The critical surround diameter for our effect was found to be between 2° and 4° (0.3–0.6 log, Fig. 4), which agrees with previous work on rod–cone interactions measured at the same eccentricity (Alexander & Fishman, 1984; Coletta & Adams, 1986), but is larger than the spatial extent ($\sim 1^\circ$) reported for cone–cone interactions at this eccentricity (Coletta & Adams, 1986). Therefore, our results are consistent with rod–cone interactions causing flicker suppression at high flicker rates with dim surrounds, although more direct evidence, such as spectral sensitivity measurements, would be required to directly implicate rods. The data of Conner and MacLeod (1977), however, suggest that rods may be weakly sensitive to 30 Hz flicker at the average retinal illuminance of the luminance-pedestal flicker stimulus ($2.7 \log \text{scotopic Td}$), although their data were obtained using a stimulus of 9° diameter. Assuming that Piper's law holds at high temporal frequencies (Mäkelä, Rovamo, & Whitaker, 1994), the 0.5° stimulus used in the experiments above would return thresholds that are over a log unit higher than those found by Conner and MacLeod, and would be unmeasurable. In addition, special techniques are required to demonstrate rod responses at such high illuminances (Aguilar & Stiles, 1954); the stimulus used in the above experiment gives equal modulation contrasts to both photoreceptor classes, and so does not preferentially stimulate rods.

As such, detection by rod photoreceptors can be excluded, and it may be assumed that flicker detection is via the cone photoreceptors.

Our luminance-pedestal flicker results are consistent with previous studies that have shown suppressive rod–cone interactions, as all these studies have used luminance-pedestal flicker (Goldberg et al., 1983; Alexander & Fishman, 1984, 1986; Coletta & Adams, 1984, 1986; Frumkes & Eysteinson, 1988; Peachey, Alexander, & Derlacki, 1990; Lange & Frumkes, 1992; Vingrys & Demirel, 1998). Interestingly, rod–cone interactions do not appear to be present under mean-modulated flicker conditions, where increasing luminance decreased flicker sensitivity (Fig. 1). Mean-modulated flicker data at comparable retinal illuminances show that light adaptation serves to decrease flicker sensitivity [see Watson's (1986) replotting of DeLange's (1958) mean-modulated data], consistent with our mean-modulated results. We therefore conclude that the presence of a luminance pedestal is important in uncovering suppressive rod–cone interactions. An adaptation model similar to that proposed by Eisner (Eisner, 1995; Eisner et al., 1998) may account for the pedestal's actions.

It is important to consider why the rod–cone suppressive effects suggested by this study are not reported in studies that considered flicker sensitivity under conditions of no surround and matched surrounds (Kelly, 1959; Keesey, 1970; Roufs, 1972). In all of these studies, the test spots were 1° or greater in diameter and had retinal illuminances exceeding 1000 Td. These larger and brighter spot sizes would be expected to increase light adaptation to the pool of photoreceptors determining rod–cone interactions (Frumkes & Eysteinson, 1988) especially as it has been shown that surround adaptation effects are decreased at large stimulus sizes (Eisner, 1992). The use of central fixation in these studies also would assist adaptation, as the spatial extent of rod–cone interactions is smaller centrally (Coletta & Adams, 1986). However, contrary to these proposals is evidence that local light adaptation is ineffective in reducing suppressive rod–cone interaction (Goldberg et al., 1983; Alexander & Fishman, 1984; Coletta & Adams, 1986). Nevertheless, the use of high test illuminances would mean that photoreceptors surrounding the stimulus are light-adapted by scattered light and the intermittent exposures associated with fixational instability (Demirel & Vingrys, 1994).

We found that the low temporal frequency surround effect is proportional to the contrast between the stimulus and its surround (Fig. 2). This result agrees with that of Spehar and Zaidi (1997) and suggests that this effect is mediated by edge detecting contrast sensitive mechanisms (Watson, 1986). Kelly (1975) has modelled the temporal frequency response of such mechanisms, and his results are consistent with our findings (flat response with a minimum beyond 10 Hz). The critical

surround diameter of between 2° and 4° (Fig. 4) indicates involvement of low spatial frequency edge sensitive mechanisms. Other studies have variously found edge sensitivity can be mediated by relatively low (Kelly, 1969; McKendrick, Badcock, & Vingrys, 2000) or high (Levinson, 1964; Keeseey, 1970) spatial frequencies. As there is evidence that edge-detecting mechanisms are sensitive to a range of spatial frequencies (Kulikowski & King-Smith, 1973; Shapley & Tolhurst, 1973), all these data may reflect the operation of a common mechanism.

We found that the low and high flicker rate surround effects had similar spatial extents (Fig. 4). There is neurophysiological evidence that horizontal cells are involved in the lateral transmission of rod–cone suppressive flicker interactions and that the spatial dimension of this effect relates to the size of the horizontal cell neurosyncytium (Frumkes & Eysteinson, 1988; Nelson, Pflug, & Baer, 1990; Pflug, Nelson, & Ahnelt, 1990). Therefore, it is possible that horizontal cells also mediate edge contrast sensitivity for flickering stimuli. The temporal frequency response of these contrast-sensitive lateral elements is reduced above 10 Hz (Kelly, 1975). Although this may appear at odds with the high temporal frequency nature of rod–cone interactions, it is not inconsistent with the fact that rod–cone flicker suppression reflects a tonic effect from dark-adapted rods (Goldberg et al., 1983). Therefore, it is possible that horizontal cells are important substrates for both low and high temporal frequency surround effects.

The presence of rod–cone interactions in luminance-pedestal flicker has potential clinical applications. The low background luminance (3.2 cd/m²) of the bowl perimeter used by a number of investigators who report flicker thresholds (McKendrick et al., 1998; McKendrick, Vingrys, Badcock & Heywood, 2000a; Phipps et al., 1999; Vingrys & Pesudovs, 1999) would most likely expose the rod–cone interactions described in this paper. This may allow luminance-pedestal flicker perimetry to be used to detect early rod dysfunction, as proposed by Vingrys and Demirel (1998). Arden and Hogg (1985a,b) have reported exaggerated rod–cone suppressive flicker interactions in otherwise normal observers who complain of difficulty seeing at night, and it has been suggested that these individuals may constitute more than 1% of the normal adult population (Lange & Frumkes, 1992). It would be expected that such individuals would return abnormally elevated luminance-pedestal flicker thresholds at high temporal frequencies, despite normal increment thresholds. Therefore, perimetric luminance-pedestal flicker thresholds may be able to provide diagnostic information similar to specialized flicker-dark-adaptometry techniques (Arden & Hogg, 1985b), but with the advantage of spatially localizing any area of sensitivity loss.

In summary, luminance-pedestal flicker sensitivity results from a balance between a number of retinal mechanisms whose operations can be substantially different under mean-modulated flicker conditions. As such, flicker sensitivity determined with luminance-pedestal flicker stimuli may differ from mean-modulated flicker sensitivity.

Acknowledgements

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