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Effect of eccentricity on luminance-pedestal flicker thresholds

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Abstract

We investigated the effect that spatially coincident luminance increments (*luminance pedestals*) have on flicker thresholds at several eccentricities and target sizes. Luminance pedestals elevated flicker amplitude-thresholds more when stimuli were presented eccentrically, both at low (4 Hz) and high (20 Hz) temporal frequencies. Altering the size of the eccentric stimulus failed to equate central and eccentric thresholds at all pedestal amplitudes. Comparisons with flicker thresholds at various background luminances suggests that the increase in luminance-pedestal flicker thresholds peripherally is due to increased suppressive rod–cone interactions, increased effectiveness of luminous contrast on edge-sensitive flicker mechanisms, as well as increased gain in the light adaptation response. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The projection of visual space on to the striate cortex is not uniform, with cortical receptive fields representing larger regions of visual space eccentrically than centrally (Hubel & Wiesel, 1974; Van Essen, Newsome, & Maunsell, 1984). Such changes with eccentricity can be described by the cortical magnification factor, M , which relates the area in the cortex to the angle in visual space it represents (Drasdo, 1977). Scaling eccentric stimulus sizes by the cortical magnification factor will equate sensitivity across the visual field for certain visual functions (Rovamo, Virsu, & Näsänen, 1978), but not others (Rovamo & Raninen, 1984). The cortical scaling factor may be predicted from the change in ganglion cell density with eccentricity (Drasdo, 1977).

Flicker sensitivity to a stimulus of constant angular size is known to vary across the visual field, and so investigators have attempted to account for this by scaling stimulus size with eccentricity (Kelly, 1984; Mäkelä, Rovamo, & Whitaker, 1994; Raninen & Rovamo, 1987; Tyler, 1985; Tyler & Hamer, 1990; Tyler & Silverman,

1983). This has had limited success, as different scaling factors have been observed at high and low temporal frequencies (Mäkelä et al., 1994; Raninen & Rovamo, 1987; Tyler & Silverman, 1983). Moreover, it has been suggested that some changes in flicker sensitivity with eccentricity may related to changes in photoreceptor dimensions, rather than changes in ganglion cell density or cortical magnification (Tyler, 1985). The effect that eccentricity has on sensitivity to luminance-pedestal flicker stimuli is not apparent, as these stimuli contain both a luminance increment (*luminance pedestal*) and a flickering component. The component regulating sensitivity change with eccentricity in such stimuli is not known.

We have previously shown that a spatially coincident luminance pedestal can elevate flicker amplitude-thresholds, and that this elevation is greater when the stimulus is presented eccentrically (Anderson & Vingrys, 2000). The method of action of the luminance pedestal has been attributed to three mechanisms (Anderson & Vingrys, 2001b). Firstly, luminance pedestals raise thresholds through increased local (i.e. within the spatial confines of the spot) light adaptation. Secondly, at low temporal frequencies (≤ 7.5 Hz) luminance pedestals raise thresholds by creating a luminous-contrast at the edge of the stimulus that decreases the sensitivity of edge-sensitive flicker mechanisms (Spehar & Zaidi, 1997; Watson, 1986). Thirdly, the relatively dark area surrounding the luminance pedestal allows rod photoreceptors within the

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surround to raise high temporal frequency (≥ 20 Hz) flicker thresholds within the test area (Goldberg, Frumkes, & Nygaard, 1983). Therefore, the increased effectiveness of luminance pedestals in the periphery could be due to changes with eccentricity in some or all of these three factors.

The fixed stimulus size used in our earlier studies (Anderson & Vingrys, 2000, 2001b) would be physiologically smaller in the periphery, due to changes in receptive-field dimensions (Hubel & Wiesel, 1974). It is known that small stimuli can defeat adaptational processes and cause saturating responses (Buss, Hayhoe, & Stromeyer III, 1982; Tyler & Liu, 1996), and so this could explain the increased effectiveness of luminance pedestals in the periphery. However, rod–cone suppressive effects also are known to increase in the periphery (Alexander & Fishman, 1984, 1986; Lange, Denny, & Frumkes, 1997), which would be expected to further elevate luminance-pedestal flicker thresholds at high temporal frequencies. In addition, spatial resolution is known to decrease in the periphery (Green, 1970; Hilz & Cavonius, 1974), but it is unclear what effect this may have on spatial-frequency dependent edge-sensitive flicker mechanisms (Spehar & Zaidi, 1997; Watson, 1986) that are perturbed by luminance-pedestal flicker at low temporal frequencies.

In this paper, we extend our early observations to consider the eccentricity-related effects in light adaptation, rod–cone interactions and edge-sensitive flicker mechanisms on luminance-pedestal flicker thresholds. We find that the eccentricity related changes to thresholds cannot be abolished by manipulating stimulus size, indicating that different scaling factors exist for the various factors involved in determining luminance-pedestal flicker thresholds.

2. General methods

2.1. Subjects

Six subjects (20–30 years) participated in the experiments. Extensive investigations were performed on a single observer who had a history of migraine (McKendrick, Badcock, Heywood, & Vingrys, 1998) but had normal flicker sensitivity during the period of data collection. To ensure validity and general applicability of our findings (Anderson & Vingrys, 2001a), the results of this subject were compared to those from a group of five normal (non-migrainous) subjects tested over a limited parameter set.

Subjects viewed all stimuli monocularly with their preferred eye. In Experiments 1 and 2, subjects viewed stimuli using their habitual spectacle correction and natural pupils. In Experiment 3, the pupil was dilated

with 0.5% tropicamide and a correction for the viewing distance (1 m) included. An artificial pupil was not used, due to the difficulty in obtaining adequate alignment with eccentrically presented stimuli. With mydriasis, the subject's pupil was 8 mm in diameter, and so a 0.6 neutral density filter was used to approximate retinal illuminances to the 4 mm diameter artificial pupils used previously (Anderson & Vingrys, 2001a,b). Of the three mechanisms involved in luminance-pedestal flicker sensitivity (see Section 1), it is likely that rod–cone interactions are most critically dependent upon the absolute retinal illuminance. As such, a correction for the Stiles–Crawford effect was not made, as rods show little Stiles–Crawford effect (Alpern, Ching, & Kitahara, 1983). Eccentric stimuli were presented 15° nasally, with eccentricity being measured from the centre of the spot target.

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

2.2. Apparatus and procedure

Spot stimuli were generated on a calibrated video monitor (VSG 2/3 graphics card (Cambridge Research Systems Ltd., Kent, UK) and Hitachi™ HM-47231-D monitor (frame rate 120 Hz)). A two-interval forced choice paradigm and a ZEST procedure (King-Smith, Grigsby, Vingrys, Benes, & Supowit, 1994) were used to estimate threshold, with subjects required to choose the interval containing the flicker. Both intervals contained a spatially coincident luminance pedestal. Stimuli were presented for 750 ms, with 17 ms inter-stimulus delay. Stimulus size was specified as a diameter. All other stimulus parameters have been described in detail elsewhere (Anderson & Vingrys, 2000, 2001b).

2.3. Analysis

A paired *t*-test was used to compare paired data, whereas comparisons between more than two conditions used a one-way repeated measures ANOVA (RM ANOVA) and a Tukey all-pairwise multiple comparison procedure. The criterion for significance was $p < 0.05$.

3. Experiment 1: Effect of size on flicker and increment thresholds

3.1. Aims and methods

Previous studies have shown that different scaling factors exist at low and high temporal frequencies that

account for flicker threshold changes with eccentricity (Mäkelä et al., 1994; Raninen & Rovamo, 1987; Tyler & Silverman, 1983). We wanted to confirm these earlier observations for our stimulus configuration, and compare the effect of stimulus size on both flicker and luminance increment thresholds.

Mean-modulated (i.e. no pedestal) flicker thresholds and luminance increment thresholds were measured centrally for a 0.5° spot target, and at 15° for a range of target sizes (0.5 – 8°). The local background and surround luminance for both stimulus classes was 4 cd/m^2 .

3.2. Results

Thresholds decreased as stimulus size was increased (Fig. 1, unfilled symbols). The initial size effect conformed to Piper's law for spatial summation (Fig. 1, dotted line), although departures from this law occurred at low temporal frequencies (unfilled circles and squares) for larger stimulus sizes (Mäkelä et al., 1994). Comparable increment and 4 Hz flicker thresholds were found for a 0.5° central spot (filled symbols) and a 2° stimulus at 15° eccentricity (0 Hz: -0.87 ± 0.01 vs -0.87 ± 0.04 , $p = 0.93$; 4 Hz: -1.05 ± 0.02 vs -1.07 ± 0.03 , $p = 0.74$). The same result was found with the normal group for increment thresholds (diamonds; -0.64 ± 0.04 vs -0.61 ± 0.02 , $p = 0.74$). However, the 20 Hz stimulus showed a different spatial scale. A 1° diameter eccentric target provided the best match to

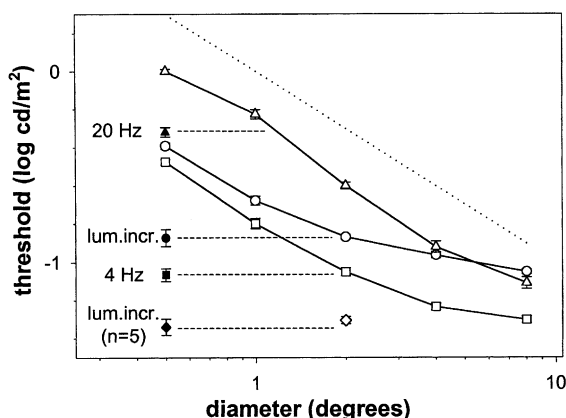


Fig. 1. Effect of stimulus diameter on mean-modulated (no pedestal) flicker and increment thresholds. Individual filled datum points were measured with central fixation, whereas unfilled points (and lines) were collected at 15° . Circles, luminance increment; squares, 4 Hz; triangles, 20 Hz. Datum points give the average of 10 observations for a single observer \pm SEM. The diamonds show the average of 5 observers (\pm SEM) for a luminance increment stimulus, where the data have been translated -0.7 log units, for clarity. The dotted line has a gradient of -1 , indicating Piper's law.

central thresholds, although a significant difference still remained with this size (-0.32 ± 0.03 vs 0.23 ± 0.02 , $p = 0.003$). This difference in spatial scaling for low and high temporal frequencies has been found previously (Mäkelä et al., 1994; Tyler & Silverman, 1983). We will demonstrate later that the group results for flickering targets were also similar to those of the individual observer.

Our results show that it is possible to equate central and eccentric thresholds for luminance increment and 4 Hz mean-modulated flicker thresholds using a common scaling factor based on target size (0.5° vs 2°). However, this same scaling does not apply to the 20 Hz stimulus, where a 2° target produced significantly reduced thresholds. The next experiment will consider whether these scaling factors apply to luminance-pedestal flicker.

4. Experiment 2: Effect of size on luminance-pedestal flicker

4.1. Aims and methods

We wanted to determine whether the spatial scaling found in Experiment 1 could be applied to luminance-pedestal flicker thresholds at various pedestal amplitudes. Since the spatial scaling for luminance increments and high temporal frequency (20 Hz) stimuli differ, we considered those conditions where luminance pedestals or flicker thresholds were appropriately scaled when testing with high temporal frequency luminance-pedestal flicker.

Flicker thresholds were determined for a number of pedestal amplitudes, thereby generating threshold-vs-amplitude (TvA) functions (Anderson & Vingrys, 2000). Functions were determined centrally for a 0.5° target (4 and 20 Hz) and eccentrically for several target sizes (4 Hz, 0.5° and 2° ; 20 Hz, 0.5° , 1° and 2°). Low pedestal magnitudes were not investigated, as it has been shown previously that the TvA functions at such pedestals are flat (Anderson & Vingrys, 2000). Surround and local background luminances were 4 cd/m^2 .

4.2. Results

The results for the single observer can be seen in Fig. 2. The general form of the TvA functions were similar to those reported previously (Anderson & Vingrys, 2000), except that the central TvA at 4 Hz (upper panel, filled circles) showed a significant facilitatory effect for the low pedestal amplitude (log amplitude = 0, $p = 0.001$). It is important to note that this facilitation was not seen in the group data (Fig. 3, filled circles). Consistent with our previous conclusions, we do not believe that luminance

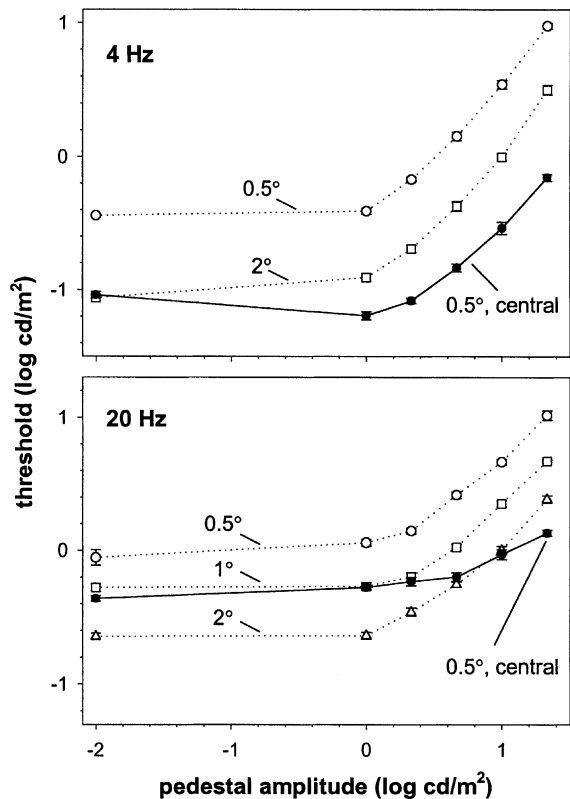


Fig. 2. Effect of stimulus size on luminance pedestal vs flicker threshold (TvA) functions for different eccentricities and sizes of target. Upper panel: 4 Hz; filled circles, 0.5° (central fixation); open circles, 0.5° (eccentric fixation); open squares, 2° (eccentric fixation). Lower panel: 20 Hz; filled circles, 0.5° (central fixation); unfilled circles, 0.5° (eccentric fixation); unfilled squares, 1° (eccentric fixation); unfilled triangles, 2° (eccentric fixation). Each datum point gives the average of 10 observations from one subject \pm SEM. The no-pedestal condition is plotted at -2 on the abscissa.

pedestals facilitate flicker thresholds (Anderson & Vingrys, 2000).¹

Fig. 2 confirmed that the use of a 2° stimulus equated 4 Hz flicker thresholds when no pedestal (plotted at log

¹ It is unlikely that averaging has masked a facilitory effect in the group data, as it would be expected that increased variability would result at the 0 log pedestal point (in contrast, it is the least variable point on the TvA function). It is possible that the facilitation reflects the high level of training in the single observer, as training can alter the form of discrimination functions at low masking contrasts (Kontsevich & Tyler, 1999). Alternatively, this subject reported retinal rivalry under the zero pedestal condition when using central fixation, and this may have raised the mean-modulated flicker threshold. Similar effects have been reported for static targets (Wildsoet, Wood, Maag, & Sabdia, 1998). Although both rapid flicker (18 Hz) and stimulus transients (as present in low frequency square wave flicker) have been found to disrupt binocular rivalry in centrally fixated grating patches (Lee & Blake, 1999), the affect that these have with luminance-pedestal flicker is not clear. If rivalry effects are specific for low temporal frequencies, then this could explain why the high temporal frequency data (Fig. 2, lower panel) do not show a similar effect.

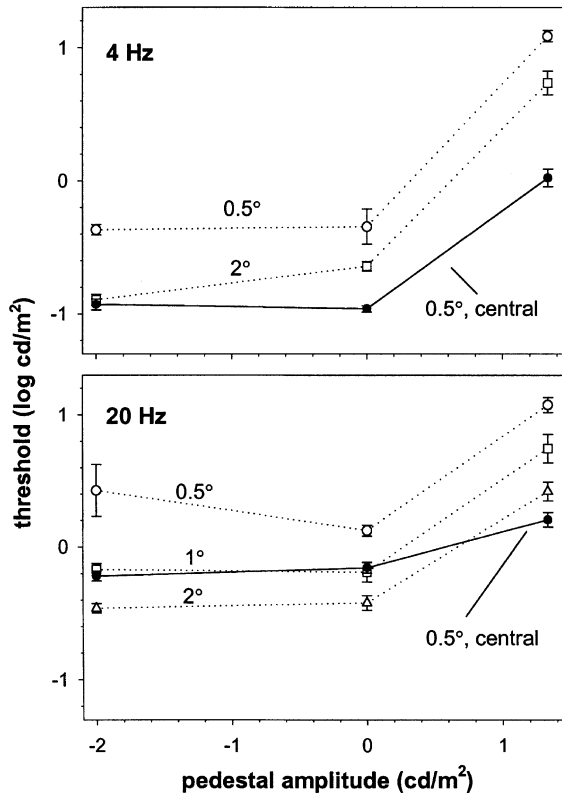


Fig. 3. Effect of stimulus size on luminance pedestal vs flicker threshold (TvA) functions for different eccentricities and sizes of target. Each datum point gives the average data from 5 subjects \pm SEM. Other details as in Fig. 2.

value -2) was present, as found in Experiment 1. Despite this, however, thresholds did not remain equal in the presence of a luminance pedestal. Moreover, the same magnitude luminance pedestal raised thresholds more effectively when presented eccentrically. Comparison of the amount of threshold elevation caused by the 21.5 cd/m^2 luminance pedestal (RM ANOVA) showed that the two different sized eccentric stimuli (unfilled symbols) were equally effective at raising thresholds, and that the central stimulus (filled symbols) produced significantly less threshold elevation. Analysis of the data from the group of normal observers (Fig. 3, upper panel) revealed identical findings.

The 20 Hz TvAs (Fig. 2, lower panel) were similar to the 4 Hz condition, although the ascending slopes of the functions were reduced (Anderson & Vingrys, 2000). The eccentric 1° stimulus (unfilled squares) gave mean-modulated flicker thresholds equivalent to the central 0.5° stimulus (-0.36 ± 0.02 vs -0.28 ± 0.03 , $p = 0.08$), but flicker thresholds diverged for these sizes at high pedestal amplitudes. It is possible that this divergence arose because the luminance pedestal dictated flicker threshold scaling. When an eccentric 2° stimulus (unfilled triangles) was used to equate pedestal detection, the slope of the ascending portion of the TvA was still

different to the central condition, however. Indeed, the amount of threshold elevation caused by the maximum (21.5 cd/m²) luminance pedestal showed that all three eccentric stimuli raised flicker thresholds to the same degree (RM ANOVA), whereas the central stimulus raised thresholds significantly less, consistent with the findings for the 4 Hz stimulus. Analysis of the threshold elevations at 20 Hz for the normal group revealed identical findings (Fig. 3, lower panel), although the amount of threshold elevation for the 0.5° stimulus was taken as the difference between 21.5 and 1 cd/m² pedestals, owing to the highly variable result obtained for the mean-modulated condition.

The effect of reducing stimulus size appeared to be an upwards translation of the TvA function (Figs. 2 and 3). To confirm this effect, we translated the TvAs of Fig. 2 vertically, using a Chi square minimisation technique, to see if the eccentric curves gave a common template. The shape of the eccentric TvA functions (Fig. 4, unfilled symbols) was common for different stimulus sizes, but differed from the centrally determined data (filled symbols). This means that no scaling factor exists that can equate all peripheral luminance-pedestal flicker thresholds to central thresholds.

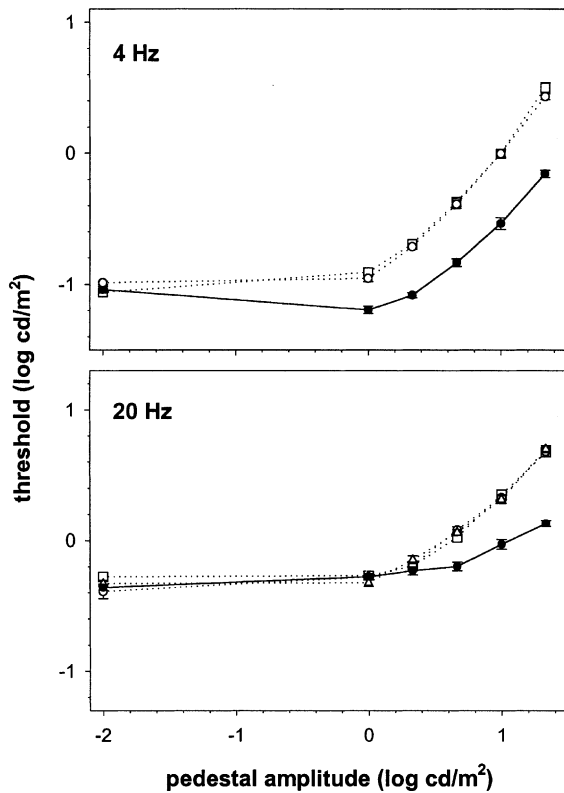


Fig. 4. Effect of vertical translation on eccentric TvAs. Upper panel: data as given in Fig. 2, except that the open circles (0.5° spot, eccentric fixation) have been vertically translated by -0.54 log units. Lower panel: data as given in Fig. 2, except that the open circles (0.5° spot, eccentric fixation) and open triangles (2° spot, eccentric fixation) have been vertically translated by -0.34 and 0.31 log units, respectively.

5. Experiment 3: Surround vs local effects

5.1. Aims and methods

It has been suggested that luminance pedestals can raise flicker thresholds via three mechanisms (Anderson & Vingrys, 2001b), as described in Section 1. In the following experiment, we determined whether the increased effectiveness of luminance pedestals in the periphery was due to a change in all or only some of these mechanisms.

Luminance-pedestal flicker thresholds were determined at 4 and 20 Hz, using a 21.5 cd/m² luminance pedestal presented on a 4 cd/m² local background and surround, giving the flickering stimulus an average luminance of 25.5 cd/m². Mean-modulated flicker thresholds were also determined for the same temporal frequencies on 4 and 25.5 cd/m² backgrounds, with matched surrounds. The spatial profiles of these stimuli are schematically represented on the left of Fig. 5. The

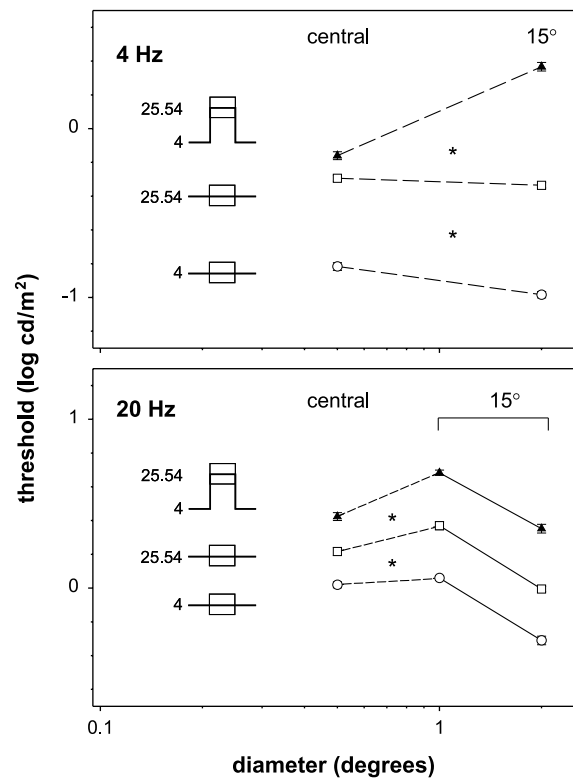


Fig. 5. Effect of stimulus size on mean-modulated and luminance-pedestal flicker thresholds. Unfilled circles, 4 cd/m² background mean-modulated flicker; unfilled squares, 25.5 cd/m² background mean-modulated flicker; filled triangles, luminance-pedestal flicker (21.5 cd/m² luminance pedestal on a 4 cd/m² background). Data for the 0.5° diameter stimulus were obtained with central fixation, and those for 1° or 2° stimuli were obtained at 15° eccentricity. Asterisks are positioned between pairs of line segments that significantly diverge or converge (see text for details). Schematics give the luminance profiles of the spot and surrounds (thick lines), along with the up/down modulation of the flickering stimulus (thin lines); luminous extents are shown on the left of the schematics.

difference between the two mean-modulated conditions determines the amount of change in flicker thresholds that can be attributed to light adaptation alone. Any luminance-pedestal flicker threshold elevation above the mean-modulated 25.5 cd/m² condition can be attributed to either edge-contrast effects at low (4 Hz) temporal frequencies, or rod–cone interactions at high temporal frequencies (20 Hz) (Anderson & Vingrys, 2001b).

5.2. Results

At 4 Hz (Fig. 5, upper panel), comparison of the 4 cd/m² and 25.5 cd/m² mean-modulated flicker thresholds (unfilled circles and unfilled squares, respectively) showed larger differences between mean-modulated thresholds eccentrically (0.52 ± 0.03 vs 0.65 ± 0.03 , $p = 0.02$), indicating an increased effect of light adaptation with eccentricity. In addition, the difference between the 25.5 cd/m² mean-modulated flicker thresholds (unfilled squares) and the luminance-pedestal flicker thresholds (filled triangles) increased in the periphery (0.13 ± 0.09 vs 0.70 ± 0.09 , $p < 0.001$), suggesting that the effects of edge-contrast increased in the periphery.

At 20 Hz (Fig. 5, lower panel), comparing the 4 and 25.5 cd/m² mean-modulated flicker thresholds (unfilled circles and unfilled squares, respectively) suggested that the effect of light adaptation increased significantly with eccentricity, but was not altered by the size of the eccentric stimulus (RM ANOVA). Similarly, the difference between luminance-pedestal flicker thresholds (filled triangles) and 25.5 cd/m² mean-modulated flicker thresholds (unfilled squares) increased in the periphery, but did not change with eccentric stimulus size (RM ANOVA), suggesting that the effects of rod–cone interactions increased in the periphery.

6. Discussion

The experiments described in this paper demonstrate that differences between central and eccentric luminance-pedestal flicker thresholds cannot be abolished by manipulating stimulus size. It has been found previously that changes in stimulus size do not alter the shape of the temporal contrast sensitivity function, but merely effect a vertical shift in overall sensitivity (Kelly, 1969). The results of Mäkelä et al. (1994) suggest that this behaviour is also true for peripherally presented targets, as Piper's law was found to hold (for small test sizes) for all temporal frequencies to 30 Hz and eccentricities to 20°. Similarly, Tyler and Hamer (1990) found no change in the temporal response characteristic at high temporal frequencies at 35° for a 1000-fold change in stimulus area. Our results suggest that this idea can be extended to luminance-pedestal flicker, as stimulus size simply shifts the TvA template vertically (Figs. 2 and 4) over

the 1.2 log unit change in area investigated. As eccentrically determined luminance-pedestal TvAs have different slopes to those obtained centrally, vertical translation of the TvA is insufficient to make the central and eccentric TvAs overlap (see Fig. 4). Given these qualitative differences with eccentricity, it is important to examine their possible causes.

In Experiment 3, luminance-pedestal flicker thresholds at high temporal frequencies (Fig. 5, lower panel, filled symbols) were higher than mean-modulated flicker thresholds of the same average luminance (Fig. 5, lower panel, unfilled squares). We have previously attributed this extra threshold elevation to suppressive effects on cone photoreceptors from unsaturated rod photoreceptors in the area surrounding the stimulus (Anderson & Vingrys, 2001b). This extra threshold elevation was found to increase in the periphery, suggesting that rod–cone interactions between the surround and the test spot increase for a peripherally presented target (Fig. 5, lower panel), and this is consistent with previous findings (Alexander & Fishman, 1984). There is evidence that the increase in rod–cone interactions in the periphery is due to an increased capacity of the lateral channels mediating this effect (Alexander & Fishman, 1986). The work of Alexander and Fishman (1986) showed that the magnitude of the rod–cone suppressive effect was independent of test size in their eccentrically presented target, suggesting it was not due to spatial scaling phenomena (Drasdo, 1977; Hubel & Wiesel, 1974). We found a similar result for our stimuli (20 Hz, Fig. 5). This finding also suggests that local light adaptation from the luminance pedestal is ineffective in reducing rod–cone suppressive effects, consistent with previous work (Alexander & Fishman, 1984; Coletta & Adams, 1986; Goldberg et al., 1983). It should be noted, however, that rod–cone flicker interactions are absent when very large targets (50°) are used (Arden & Hogg, 1985).

Luminance-pedestal flicker thresholds at low temporal frequencies (Fig. 5, upper panel, filled symbols) were higher than mean-modulated flicker thresholds of the same average luminance (Fig. 5, upper panel, unfilled squares). We have previously attributed this extra threshold elevation to the luminous-contrast created by the luminance pedestal, which depresses the sensitivity of edge-sensitive flicker mechanisms (Anderson & Vingrys, 2001b). We found this edge effect also increased in the periphery (Fig. 5, upper panel). Previously, we have suggested that there may be some commonality between the lateral elements mediating this edge effect and those mediating rod–cone interactions (Anderson & Vingrys, 2001b). If the increase in eccentric rod–cone interactions seen in Experiment 3 resulted from an increased capacity of the lateral pathway mediating these effects (Alexander & Fishman, 1986), it is not surprising that the low temporal frequency edge effects also increased eccentrically (as found in Experiment 3).

However, it is known that spatial resolution decreases in the periphery (Green, 1970; Hilz & Cavonius, 1974; Rovamo et al., 1978) and so it may also have been expected that the effect of edges are reduced with peripherally presented targets. As this is not supported by our findings, it implies that the dependence of edge effects on higher spatial frequencies, as reported for centrally fixated targets (Kelly, 1969), is reduced when targets are presented peripherally.

Experiment 3 demonstrated that the effect of light adaptation on flicker thresholds increased in the periphery, both at low and high temporal frequencies (Fig. 5, difference between unfilled squares and unfilled circles). Although we found that the effect of light adaptation was greater at low temporal frequencies, as expected (DeLange, 1958; Kelly, 1961; Roufs, 1972), the change with eccentricity is not significantly different for the two temporal frequencies (diff = 0.02 log units, $p = 0.72$). It is known that small target sizes can defeat adaptational processes and cause saturating responses (Buss et al., 1982; Tyler & Liu, 1996), and so it may be expected that this is the cause of this increased light adaptation effect with eccentricity for luminance-pedestal flicker stimuli (see Section 1). The 20 Hz data given in Fig. 5, however, showed that stimulus size had little bearing upon this light adaptation effect, and so size dependent saturation effects are not the cause for these peripheral differences. As such, our data suggest light adaptation has a higher gain in the periphery, at both high and low temporal frequencies.

6.1. Spatial scaling factors

Experiment 1 showed how mean-modulated flicker thresholds altered with stimulus size (Fig. 1). From this result, it is possible to determine the spatial scaling value, E_2 , which gives the eccentricity where stimulus size must be doubled to maintain equal sensitivity with the fovea (Mäkelä et al., 1994). Assuming that the increase in scaling factor with eccentricity is linear (Kelly, 1984; Mäkelä et al., 1994), we find that E_2 is equivalent to 5° for our 4 Hz stimulus, as a 4 times larger stimulus at 15° gave identical thresholds to the foveal condition. However, a perfect match between foveal and eccentric stimuli was not obtained for the 20 Hz stimulus. Assuming Piper's law holds for the high temporal frequency stimulus, then a linear regression (slope = -0.97 , $R^2 = 0.99$) through the 20 Hz data of Fig. 1 suggests that a 1.1° stimulus at 15° eccentricity would match foveal thresholds, returning an E_2 of 12.5° . Given our moderately low retinal illuminance of approximately 50 td in Experiment 1 (assuming a 4 mm diameter pupil), these values are consistent with those reported by Mäkelä et al. (1994) for high (980 td) and low (1.4 td) retinal illuminances.

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