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Adaptation to Peripheral Flicker

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With strict fixation, a flickering disk presented in the peripheral retina rapidly appeared to lose contrast and stop flickering, owing to adaptation. Subjects measured this adaptation by continually adjusting the flicker amplitude of a peripherally viewed disk to hold it just at threshold. Results: (1) The contrast threshold for flicker increased logarithmically over time. (2) The slope of the temporal decay function increased with eccentricity (1–16 deg) and with decreasing disk size (8 deg–3.6 min arc). (3) M-scaling the stimulus size could abolish the dependence upon eccentricity for small disks, but not completely for large disks. (4) The temporal decay rate increased with flicker rate (3–15 Hz), as though each cycle of flicker elevated contrast threshold equally. Copyright © 1996 Elsevier Science Ltd.

Adaptation Flicker Cortical magnification factor Peripheral vision

INTRODUCTION

If a novel target pops up in the peripheral visual field, an observer normally makes a saccade to bring the target into the fovea. As a result of this efficient saccadic fixation reflex, we rarely let an object dwell at a fixed location in the peripheral retina. When this is done in the laboratory such an object tends to fade from view rather rapidly. This subjective fading was first noted for stationary objects by Troxler (1804). However, even moving or twinkling objects are apt to fade.

This makes sense ecologically because such novel, attention-getting peripheral targets provoke a fixation reflex that promptly removes them from the periphery to the fovea, so they seldom dwell in the periphery long to need much long-term or sustained processing. We shall briefly review studies of subjective fading of flickering peripheral stimuli and then describe our own experiments.

Peripheral flicker

There have been at least four published investigations of peripherally viewed flicker. Frome *et al.* (1981) showed that threshold measurements of flashed peripheral test spots were affected by continuing presentation. With repeated presentations of a 50 msec flash every 0.5 sec, thresholds rose progressively, sometimes reaching more than ten times their initial values. This loss in sensitivity was not simply due to retinal light adaptation. With 15 min of rapid flash presentation there was an initial sharp recovery in sensitivity after which there remained some loss of sensitivity even after 35 min. Habituation occurred within both rod and cone systems and transferred between them. The effect was specific to the size and spatial frequency but not the orientation of the habituating stimulus.

Schieting and Spillman (1987) studied flicker adaptation in the peripheral retina, as we have done. They noted that with strict fixation, a small flickering spot presented in the peripheral retina rapidly appeared to lose contrast and stop flickering within 35 sec, before fading away completely. The time required for this adaptation to occur decreased with:

1. decreasing depth of modulation (97–9%);
2. decreasing stimulus diameter (2 deg–7 min arc);
3. increasing retinal eccentricity (20–50 deg); and
4. increasing flicker frequency (1–7 Hz).

Adaptation was twice as fast in the temporal as in the nasal retina. When changes in retinal eccentricity were compensated for by taking into account the cortical magnification factor, the time needed for perceived flicker to disappear remained constant at all eccentricities. With dichoptic stimulation interocular transfer was about 35%, suggesting a cortical contribution to flicker adaptation. Harris *et al.* (1990) confirmed that time to disappearance became shorter at higher temporal frequencies, but they enquired whether this was a true frequency dependence or whether it reflected the amount above threshold of the adapting flicker, since threshold contrast varies with frequency. They measured time to disappearance at contrasts which were multiples of the contrast threshold or were matched across frequencies. They found that near threshold all frequencies adapted at

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similar rates. However, at small multiples of threshold higher temporal frequencies had faster adaptation rates, confirming Schieting and Spillman. They concluded that higher temporal frequencies really are more adaptable than low ones. Hammett and Smith (1990) measured adaptation to counterphase flickering gratings instead of to flickering spots. They found that as temporal frequency was raised, adaptation time decreased in conditions of constant physical modulation depth but increased in conditions of constant perceived modulation depth. They concluded that while adaptation time was clearly related to modulation depth, its relation to temporal frequency was ambiguous.

It is often forgotten that all visual patterns ultimately fade when the retinal image is stabilized (Sharpe, 1972). The involuntary eye movements prevent this stabilization effect, but their range (and other parameters) are optimized for central vision and for seeing fine detail. People whose acuity is degraded in later life by macular degeneration develop different eye movements to prevent an equivalent of the "Troxler effect". Thus they fixate nonfoveally, and the spatial precision of their eye movements is scaled to the eccentricity of their preferred fixation area (White & Bedell, 1990). So in practice, it is easy to show that the "peripheral events" fade rapidly, but when the secondary effects caused by "fading" are prevented by suitable experimental controls, the rules of pattern and movement detection are similar; Murray *et al.* (1983) found that the spatial resolution for detecting a pattern (P) was twice as fine as for its motion (M), as one would expect from the Reichardt (1961) model of movement detection in which two adjacent outputs are required to signal movement. This P:M ratio was consistently 2 in central vision and for a wide range of eccentricities.

Cortical magnification factor

It is not obvious whether peripheral disks rapidly became invisible because flicker sensitivity is worse in the periphery, or whether because the cortical representation for a disk of fixed size falls off rapidly with eccentricity. This might make a more eccentric disk effectively smaller so far as the visual system was concerned, since there would be fewer cortical neurons available to analyze its properties. Many forms of visual sensitivity functions decrease monotonically with increasing eccentricity when measured with the same stimuli at different retinal positions. But these tasks become independent of visual field location when the decrease in the density of retinal ganglion cells and the increase in their receptive-field size toward the retinal periphery are compensated for by increasing stimulus area in inverse proportion to the human cortical magnification factor squared (M-scaling). When the stimuli are normalized in size in this way so that their calculated cortical representations become equivalent at different eccentricities, the visual sensitivity functions become similar at all eccentricities (Pointer, 1986; Watson, 1987). This normalization has proved effective for tasks that include:

- acuity for letters (Anstis, 1974);
- vernier acuity (Levi, Klein & Aitsebaomo, 1985);
- judgments of visual numerosity (Parth & Rentschler, 1984);
- wavelength discrimination (Van Esch *et al.*, 1984);
- binocular rivalry (Blake *et al.*, 1992)
- motion and displacement thresholds for oscillating gratings (Johnston & Wright, 1985; Wright & Johnston, 1985); and various kinds of temporal modulation from 0 to 25 Hz (movement, counterphase flicker, and on–off flicker) and different threshold tasks (detection, orientation discrimination, and discrimination of movement direction), independently of the subjective appearances of the gratings at threshold (Virsu *et al.*, 1982). The stimulus gratings were also normalized in area, spatial frequency, and translation velocity;
- photopic critical flicker frequency (CFF) (Rovamo & Raninen, 1984: Raninen & Rovamo, 1986). It was also necessary to reduce stimulus luminance in inverse proportion to Ricco's area (F-scaling).

It is true that some deviations from perfect M-scaling have been reported for thresholds for grating motion thresholds (Wesemann & Norcia, 1992), letter identification (Strasburger *et al.*, 1991) and visibility of gaussian blurred circular disks (Bijl *et al.*, 1992), in some acuity tasks (Virsu *et al.*, 1987), and in phase discrimination for f + 3f compound gratings (Stephenson *et al.*, 1991). Overall, however, the evidence shows that central and peripheral vision are qualitatively similar in spatiotemporal visual performance. The quantitative differences observed without normalization were caused by the spatial sampling properties of retinal ganglion cells that are directly related to the values of M used in the normalization.

In this paper, we measured adaptation to a disk that flickered at low amplitude in square-wave at 5 Hz in the retinal periphery. To anticipate, we found that such a disk would rapidly fade from view if left alone, and to keep it visible the observer had to increase the amplitude of its flicker logarithmically over time. We also found that smaller or more peripheral spots faded most rapidly, so we examined the relationship between size and eccentricity as affected by the cortical magnification factor.

METHODS

The stimulus was a small flickering disk on a monitor screen, with the flicker amplitude under the subject's control. The disk, which appeared on a computer-controlled monitor on a white background, was positioned vertically above the fixation spot (to avoid the blind spot) at an eccentricity of 1, 2, 4, 8, or 16 deg. The spot initially alternated between the white of the surround and a light grey which was 2% darker. The flickering spot was always either the same as or darker than the surround (a spatial decrement). During binocular viewing with

TABLE 1. Disk diameters in three experiments

Retinal eccentricity	1°	2°	4°	8°	16°
1. Constant-size disks	0.5°	0.5°	0.5°	0.5°	0.5°
2. Large M-scaled disks	0.5°	1°	2°	4°	8°
3. Small M-scaled disks	—	0.06°	0.12°	0.25°	0.5°

strict fixation, subjects reported that at first they could see the flicker but this faded out after a few seconds and the disk became invisible. They were provided with two computer keys which increased or decreased the flicker amplitude, and they adjusted these over time to keep the flicker just visible. This process continued for 80 sec. Data were recorded and analyzed off-line later. Three runs were taken in random order at each of the five eccentricities. Results were collected from four undergraduate subjects who were naive to the purpose of the experiment.

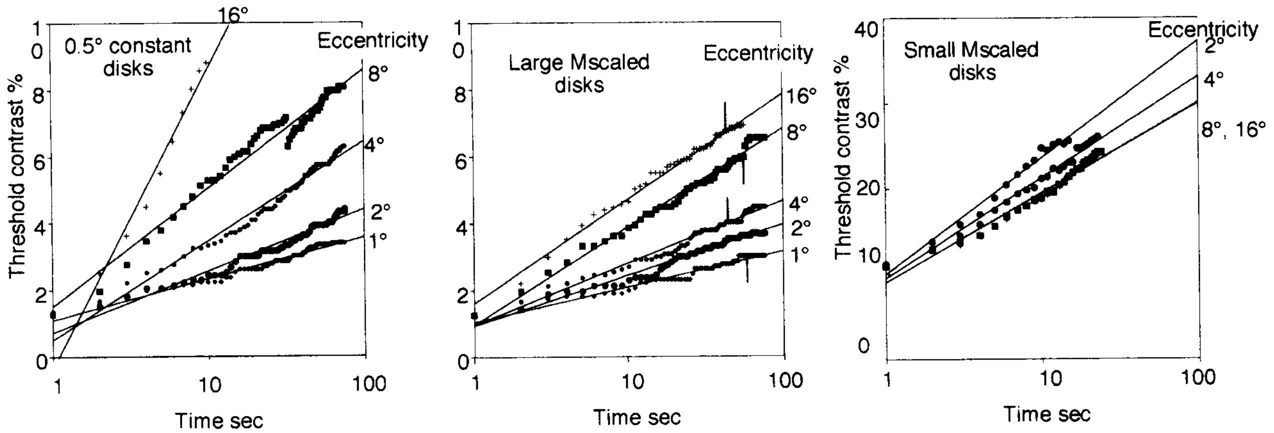
The disk size was varied in three conditions, as shown in Table 1.

- In Condition 1 (Constant-size disks) the disk diameter was 0.5 deg at all eccentricities.
- In Condition 2 (Large M-scaled diameter) the disk diameter was 0.5 deg at an eccentricity of 1 deg, as in condition 1, but it was expanded with increasing eccentricity to counteract the cortical magnification factor, reaching a diameter of 8 deg at an eccentricity of 16 deg. So the disk areas increased according to M-scaling squared.
- In Condition 3 (Small M-scaled diameter) the disk diameter was 0.5 deg at an eccentricity of 16 deg, as in condition 1, but it was reduced with decreasing eccentricity to counteract the cortical magnification factor, reaching a diameter of 0.06 deg (3.6 min arc) at an eccentricity of 2 deg. This was the same ratio of disk diameter to eccentricity as Schieting and Spillman (1987) used. (Apparatus limitations precluded our taking measurements at an eccentricity of 1 deg in this condition.)
- Note that the relative M-scaling ratios were the same in conditions 2 and 3, as the disk diameter doubled when the eccentricity doubled. However, the diameters of the disks were 16 times larger in condition 2 than in condition 3.

RESULTS

Results for Conditions 1–3 are shown in Fig. 1(a)–(c) (means of four subjects × three readings). Figure 1 shows that on every run in every condition, as time went on the subject became progressively less sensitive to the peripheral flicker and his or her amplitude threshold rose logarithmically with time (contrast threshold = $m \log t + c$). The correlation coefficient r^2 between the data and the fitted logarithmic curves was 0.96 or better in all cases. The steeper the time decay curves in Fig. 1, the more rapid the threshold elevation and the worse the flicker sensitivity.

In Condition 1, when the disks had a fixed diameter of 0.5 deg regardless of eccentricity, sensitivity decreased much more rapidly for the more eccentric disks. Note that the logarithmic time decay curves at eccentricities of 1 or 2 deg had shallow slopes, but as eccentricity increased



a b c

FIGURE 1. Subjects viewed a peripheral flickering disk and adjusted the flicker amplitude to hold it at threshold. Thresholds increased logarithmically over time as sensitivity decreased, giving straight lines on this log-time plot. Steeper time decay curves indicate more rapid adaptation (mean of four observers × three readings). Vertical bars show 1 SE. (a) For a fixed disk diameter of 0.5 deg, eccentric disks disappeared most rapidly. Disks at eccentricities of 1 or 2 deg needed only slight amplitude increases to remain visible but disk at 16 deg disappeared from view within 15 sec. (b) M-scaling of large disks partly compensated for eccentricity. Curves are more closely bunched than in (a). Full compensation would have superimposed all the curves. (c) M-scaling of small disks overcompensated for eccentricity. Curves are now reversed in order, being lower (better sensitivity) at 8 and 16 deg than at 2 deg. Small disks were overall much harder to see, however: note that y scale is different from (a) and (b).

the slopes became steeper, until a disk at 16 deg eccentricity disappeared from view within 10–15 sec.

Results for the large M-scaled disks (Condition 2) are shown in Fig. 1(b). Once again contrast thresholds rose logarithmically with time. Notice that if the M-scaling had compensated for retinal variations, all the data for different eccentricities would be superimposed in a single curve, but this was clearly not the case. Performance still fell off with increasing retinal eccentricity; the 1 deg curve was lowest (best), the 16 deg curve was highest, and other eccentricities lay in between. It is true that the performance gap between different eccentricities has been narrowed, because the curves are more tightly bunched, but they are nowhere near being superimposed. So M-scaling compensated only partially for the effects of eccentricity. We thought it possible that these large disks might exceed the limits of spatial summation, in which case sensitivity might fail to benefit from enlarging the more peripheral disks. So we repeated the M-scaled experiment using a set of much smaller disks, ranging in diameter from 3.6 min arc (0.06 deg) at 2 deg eccentricity to 27 min arc (0.46 deg) at 16 deg eccentricity. These sizes were chosen to match the ratio of size to eccentricity used by Schieting and Spillman (1987).

Results for the small M-scaled disks (Condition 3) are shown in Fig. 1(c). Overall the slopes were much higher than for the larger disks, showing that flicker was far harder to see in small than in large disks. Notice that the y scale in Fig. 1(c) is different from Fig. 1(a) and (b). For the constant size or large M-scaled disks in Fig. 1(a) and (b) it took in the order of 80 sec for the contrast threshold to approach 10%, but for the small M-scaled disks in Fig. 1(c) it took only about 20 sec for the contrast threshold to approach 30%. In addition, M-scaling actually overcompensated for eccentricity with these small disks. The curves are not merely bunched together but actually reversed in order, with the curve for 16 deg eccentricity below the 1 deg curve instead of above as it was in Fig. 1(a) and (b).

These results are replotted in Fig. 2. Here the log slope of each time decay curve (m, where $y = m \log t + c$, and y is threshold contrast and t is time) is plotted as a function of eccentricity, so that each curve in Fig. 1 is reduced to a single point in Fig. 2. For the constant-sized disks in Condition 1, the function relating log-slope to eccentricity in Fig. 2 sloped steeply up to the right, showing that flicker perception got worse in the periphery, and it was positively accelerated, showing that the loss was greatest as the eccentricity increased from 8 to 16 deg. The values of the constant c (not illustrated) were always small (< 1.7) and were not systematically related to difficulty of seeing flicker.

The effects of M-scaling depended upon the sizes of the disks. A horizontal function in Fig. 2 would mean that M-scaling compensated perfectly for eccentricity. In fact, the function obtained sloped slightly upwards for large disks and slightly downwards for small disks in Fig. 2, showing that M-scaling undercompensated for the large

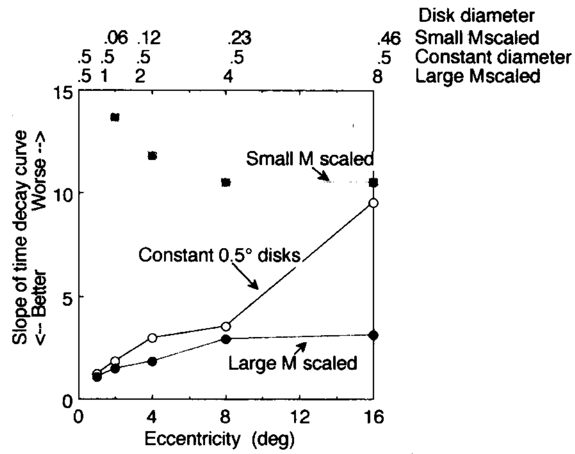


FIGURE 2. Slope of each curve in Fig. 1 is replotted here as a single point. For constant sized disks, slope rose steeply (disks disappeared sooner) with increasing eccentricity. For large M-scaled disks, they rose only slowly with eccentricity, showing undercompensation. For small M-scaled disks, they actually fell with eccentricity, showing overcompensation; however, the whole function is high up, showing that small flickering disks were hard to see.

disks and overcompensated for the small disks. We shall return to this point in the Discussion.

For the constant disks the log-slope m at 16 deg was 7.8 times larger (worse) than at 1 deg eccentricity, showing a very pronounced loss of flicker sensitivity with eccentricity. It was only 3.0 times higher for the large M-scaled disks, showing a much smaller loss of flicker sensitivity with eccentricity. Thus, M-scaling mitigated the fall-off in performance with eccentricity, but it certainly did not fully compensate for it. For the small M-scaled disks the log-slope m was actually 1.3 times larger (worse) at 2 deg than at 16 deg, showing that M-scaling overcompensated for eccentricity, since flicker sensitivity actually improved as one went further out from the fovea.

Presumably at some intermediate disk size the M-scaling would exactly compensate for eccentricity.

As one would expect, the curve for the constant 0.5 deg diameter disks in Fig. 2 intersected with the curve for the large M-scaled disk at 1 deg eccentricity, where both disks were 0.5 deg, and it sloped upwards to intersect with the curve for the small M-scaled disk at 16 deg eccentricity, where both disks were also 0.5 deg. Thus results were consistent across conditions.

Effects of flicker rate

We measured the adaptation to different flicker rates, namely 3, 5, 8, 12, and 15 Hz, all for a 2 deg disk at an eccentricity of 4 deg. (The 5 Hz condition was the same as the 4 deg eccentricity condition in Condition 2.) Results are shown in Fig. 3(a). Figure 3(a) shows that flicker thresholds rose logarithmically with time, as before. The correlation coefficient r^2 between data and fitted logarithmic curves was 0.94 or better in all cases. Performance fell off monotonically with flicker frequency. The threshold contrast for seeing 3 Hz flicker

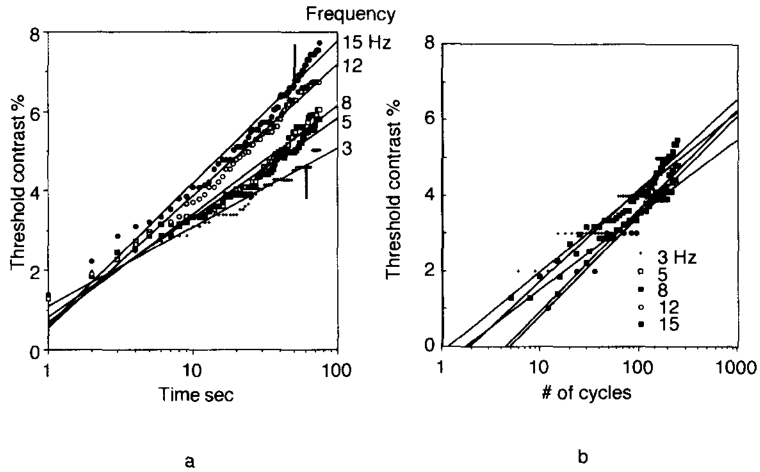


FIGURE 3. (a) Threshold contrasts were higher, and time decay curves steeper, with increasing flicker frequency (mean of four observers × three readings). Vertical bars show 1 SE. (b) Same curves are replotted as a function of total number of flicker cycles. This tends to superimpose all the curves, showing that total number of elapsed cycles determines the time course of flicker sensitivity.

never went above 5%, but it rose to above 7% for 15 Hz flicker after 60 sec exposure.

Since sensitivity fell off more rapidly for higher temporal frequencies, we wondered whether it fell by a fixed amount for each cycle of flicker, so we replotted the same data in Fig. 3(b) as a function of the number of elapsed cycles. For this plot the x axis is changed from seconds to numbers of cycles and the 3 Hz curve is effectively stretched horizontally threefold, the 15 Hz curve 15-fold, and so on. If the hypothesis were true and the number of cycles were the relevant variable, then all the datum points for different frequencies would now lie along, the same time decay curve. Although this is not entirely true, it is clear that the curves are much more tightly bunched in Fig. 3(b) than in Fig. 3(a). This is further brought out in Fig. 4, in which each curve in Fig. 3(a) and (b) is reduced to a single point. The open circles in Fig. 4 show the log slope for each time decay curve, taken from Fig. 3(a) (m, where $y = m \log t + c$), as a function of its frequency, and the filled circles show the log slope for each time decay curve taken from Fig. 3(b) as a function of the number of elapsed cycles. In Fig. 4 the frequency data (open circles) show a monotonic increase of log slope with frequency, and the log slope was three times greater (worse) for 15 Hz than for 3 Hz. The number-of-cycles data (filled circles), on the other hand, lay more nearly on a horizontal line, with the log slope being only 1.27 times greater (worse) for 15 Hz than for 3 Hz. We conclude that to a first approximation, each doubling of the number of elapsed flicker cycles, rather than the temporal frequency *per se*, elevates the contrast threshold by a fixed amount. This disagrees with Schieting and Spillmann's finding that time-to-disappearance of a flickering spot became shorter as the frequency increased, but became longer when these frequencies were converted into the number of elapsed cycles.

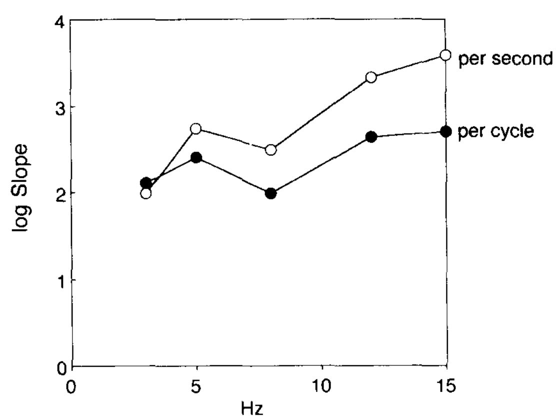


FIGURE 4. Slope of each curve in Fig. 3 is replotted here as a single point. ○, Slope of time decay curves rises, showing more rapid adaptation, as flicker frequency increases. ●, Horizontal function shows that adaptation is a constant as a function of total elapsed flicker cycles.

DISCUSSION

Our results confirm those of Schieting and Spillman (1987), Harris *et al.* (1990), and Hammett and Smith (1990). We confirmed that smaller, more eccentric disks flickering at higher frequencies are most apt to disappear. We differ from Schieting and Spillmann in a few minor respects; they found that M-scaling compensated for eccentricity for small disks, whereas we found that it it undercompensated for large disks and overcompensated for small disks. They found that neither frequency nor total number of cycles fitted their results for the effect of flicker rate on disappearance rate, whereas we found that total number of cycles gave a good fit.

A more important difference lay in our method. Whereas they measured the time at which a given flickering disk disappeared, giving a single number as a measure of flicker lability, we adjusted the flicker continuously to measure the logarithmic decay of its visibility, giving a continuous curve over time. We plotted the full biography of flicker sensitivity instead of just the date of its death, so to speak. Notice that our time decay curves do not portray the pure time constants of a neural integrator. Instead they delineate its activity within a negative feedback loop, namely its response to being continuously adapted by a threshold-level stimulus.

Our results do not show perfect M-scaling. Whitaker *et al.* (1992) measured the rate of decline with increasing eccentricity of several position and movement acuities. For each task, the decline of acuity with eccentricity could be quantified by the parameter E_2 which represents the eccentricity at which stimulus size must double in order to match foveal performance. All tasks were found to obey the concept of spatial scaling in that performances at any two eccentricities could be matched simply by a change of scale. However, the rate at which performance deteriorated with eccentricity varied over an enormous range (100:1) depending upon the task itself. Acuity fell off much more rapidly for static tasks (spatial-interval or spatial-bisection judgments) than for dynamic tasks (apparent motion with or without a landmark). The advantage of such diverse peripheral gradients is clear, since it is more advantageous for survival to preserve movement detection than precise spatial judgements in the periphery, but the mechanisms are still unknown.

Our own results for flicker in Fig. 2 do not fit this spatial scaling model. Perfect M-scaling would give horizontal straight lines in Fig. 2. In fact, the lines for large and small M-scaled disks slope slightly upwards and downwards with increasing eccentricity. That is, although flicker was overall much harder to see in the small than the large M-scaled disks, performance actually improved with eccentricity for the small disks and the M-scaling overcompensated for the reduced flicker sensitivity at greater eccentricities. This might be an effect of Ricco's area, which is known to vary with eccentricity (Rovamo & Raninen, 1984; Raninen & Rovamo, 1986). We speculate that F-scaling the stimuli, that is reducing their stimulus luminance in inverse proportion to Ricco's area, might bring the flicker data closer to perfect M-scaling. It would be interesting to collect data for a dark-adapted eye, which has larger spatial summation areas.

It is hoped that these studies of peripheral sensitivity to flicker in normal subjects may provide a baseline against which to evaluate early visual losses in glaucoma, a disease which starts by attacking peripheral vision and sensitivity to flicker (Glovinsky *et al.*, 1992; Katz *et al.*, 1993). Such testing might help to provide the early diagnosis and prompt treatment which are the keys to successful management of this disease (Kaufman & Mittag, 1994).

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